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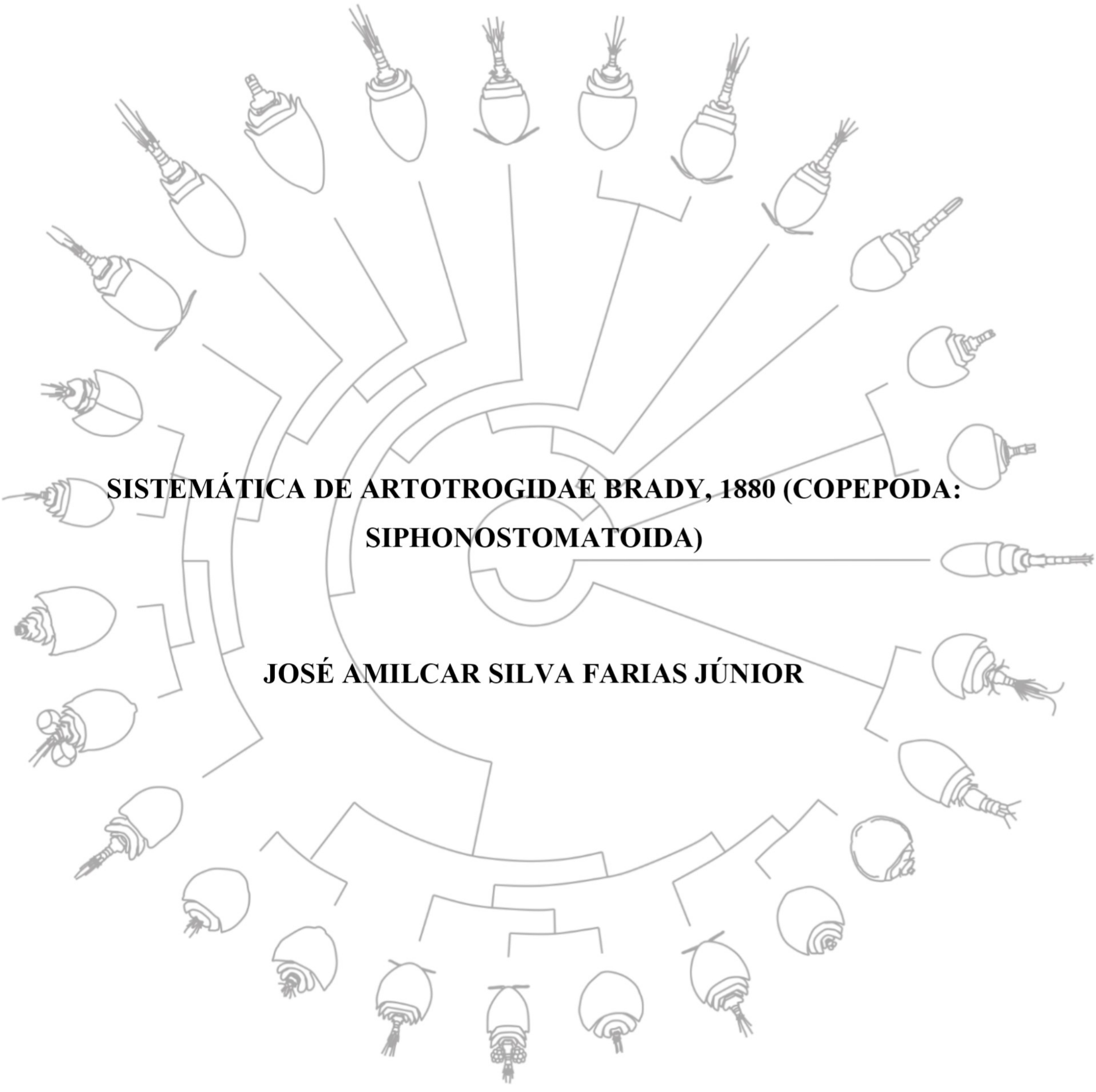

SISTEMÁTICA DE ARTOTROGIDAE BRADY, 1880 (COPEPODA: SIPHONOSTOMATOIDA)

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Salvador

2024

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Título:

SISTEMÁTICA DE ARTOTROGIDAE BRADY, 1880 (COPEPODA: SIPHONOSTOMATOIDA)

Tese apresentada ao Instituto de Biologia da Universidade Federal da Bahia para obtenção do Título de Doutor em Zoologia pelo Programa de Pós-Graduação em Biodiversidade & Evolução

Orientador: Dr. Rodrigo Johnsson Tavares da Silva

SALVADOR
2024

Dados internacionais de catalogação-na-publicação
(SIBI/UFBA/Biblioteca Universitária Reitor Macedo Costa)

Farias Júnior, José Amilcar Silva.
Sistemática de Artotrogidae Brady (Copepoda: Siphonostomatoida) / José Amilcar Silva Farias Júnior. - 2024.
166 f.: il.

Orientador: Prof. Dr. Rodrigo Johnsson Tavares da Silva.
Tese (doutorado) - Universidade Federal da Bahia, Instituto de Biologia, Salvador, 2024.

1. Zoologia. 2. Invertebrados. 3. Copépode - Classificação. 4. Copépode - Filogenia. 5. Crustáceos. I. Silva, Rodrigo Johnsson Tavares da. II. Universidade Federal da Bahia. Instituto de Biologia. III. Título.

CDD - 595.3
CDU - 595.3

Comissão Examinadora

Título

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Orientador: Rodrigo Johnsson Tavares da Silva

Tese de Doutorado submetida ao Programa de Pós-Graduação em Biodiversidade e Evolução da Universidade Federal da Bahia como parte dos requisitos necessários à obtenção do título de Doutor na área de Zoologia.

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Dedicatória

Dedico esta Tese de Doutorado à Dona Ivana, minha mãe. Minha mainha, à quem devo todo êxito que por ventura venha a alcançar, sempre.

Epígrafe

"*Podemos sorrir, nada mais nos impede*

Não dá pra fugir dessa coisa de pele"

Acyr Marques e Jorge Aragão, 1986.

Agradecimentos

À minha família, minha mãe Dona Ivana Marinho, meu pai Seu José Amilcar Silva, e a minha avó Dona Maria José Pereira por serem a base de tudo, por terem me ensinado os valores que construíram o meu caráter e me guiarão sempre. À minha companheira Iaslane Bonfim por todo amor, carinho e companheirismo, estando ao meu lado durante essa árdua jornada, nos momentos dos desafios e nos momentos de vitória e alegria. Agradeço também à minha irmã Alana, meu irmão João Ícaro e meus sobrinhos Laura e Miguel por serem motivo de alegria para minha vida.

Ao meu orientador Prof. Dr. Rodrigo Johnsson pelo convite para fazer parte do LABIMAR há 11 anos atrás, e por me mostrar a beleza que estes pequenos animais possuem. E que, junto a Profa. Dra. Elizabeth Neves, agradeço pelas inúmeras oportunidades de conhecer pessoas, lugares, e de desenvolver habilidades que foram, são e serão importantíssimas no desenvolvimento da minha vida profissional.

À Dra. Jéssika Alves pelo imprescindível apoio, discussões, sugestões e auxílio com os caminhos, macetes, e resolução de bugs relacionados aos softwares referentes a filogenia.

Aos colegas e amigos membros da equipe do LABIMAR – Alana Moura, Ana Caetano, André Divino, Beatriz Gomes, Bruna Bahiana, Dalton Santos, Fernanda Dourado, Lucas Silva, Marcelo Andrade, Mariane Amorim, Pamella Santos, Paula Barreto, Raissa Yannick, Rebeca Macedo, Riane Maurício, Rosa Mácola, Sabrina Neves, Saulo Freitas, Thalia Nepomuceno e Vanessa Sanderli – por todo apoio durante os dias de trabalho, e por tornarem o ambiente de pesquisa muito mais leve e divertido, sem vocês este trabalho não seria possível.

Aos meus amigos Ana Beatriz, Alisson Santana, e Aurea Silva, por estarem sempre “logo ali”, não só nos melhores momentos e risadas, mas também quando necessário ser o dedo que aponta, os ouvidos que apoiam e o ombro amigo que conforta.

Às instituições e pesquisadores – Naturalis Biodiversity Center, nas pessoas do Dr. Bram van der Bijl e a Dra. Wendy van Bohemen; ao Natural History Museum (University of Oslo), nas pessoas do Dr. Lutz Bachmann e a Dra. Åse Wilhelmsen; ao Great North Museum: Hancock, na pessoa do Dr. Dan Gordon; ao The Field Museum Chicago, na pessoa do Dr. Jochen Gerber; ao Central Marine Fisheries Research Institute, na pessoa do Dr. M. Rajkumar; e ao Smithsonian National Museum of Natural History, nas pessoas do Dr. Adam Stergis, Dr. Chad Walter, Dr. Karen Osborn and Dr. William Moser – por todas as informações fornecidas para o levantamento dos espécimes depositados em coleções zoológicas e empréstimos de material analisado.

À Dra. Adriane Pereira Wandeness, ao Dr. Paulo Henrique Costa Corgosinho, ao Dr. Riccardo Mugnai, e ao Dr. William Ricardo Amâncio Santana, como titulares, ao Dr. Felipe Bezerra Ribeiro, ao Dr. Gilmar Perbiche Neves, ao Dr. Luis Ernesto Arruda Bezerra, e ao Dr. Wagner Ferreira Magalhães, como suplentes, pela disponibilidade de aceitar fazer parte da banca, e pelas contribuições que serão feitas durante a arguição durante o Exame de Defesa do Doutorado, que certamente serão de suma importância para a conclusão deste trabalho.

Ao Prof. Dr. Wagner Ferreira Magalhães, ao Prof. Dr. Paulo Henrique Costa Corgosinho e à Profa. Dra. Adriane Pereira Wandeness por aceitarem o convite para participar da banca e contribuírem com o processo de Exame de Qualificação do Doutorado.

À Petrobrás, através do projeto "Avaliação e pesquisa do coral sol na Baía de Todos-os-Santos", à CAPES e à FAPESB, pelo auxílio financeiro no período do doutoramento, sem o qual não seria possível o desenvolvimento deste trabalho.

E por fim, ao Programa de Pós Graduação em Biodiversidade e Evolução e à coordenação do mesmo, nas pessoas da Profa. Dra. Alessandra Selbach Schnadelbach e da Profa. Dra. Vanessa R. Paixão-Côrtes, que sempre foram muito prestativas e gentis com as demandas que lhes foram solicitadas.

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Resumo

Copépodes são pequenos crustáceos com uma imensa abundância e diversidade, que colonizaram com sucesso os mais variados ambientes aquáticos e que atuam como um componente imprescindível na cadeia alimentar. Os copépodes da ordem Siphonostomatoida vivem associados a quase todos os filos de metazoários conhecidos. A família Artotrogidae, em especial, teve sua classificação extensivamente discutida ao longo do último século. Entretanto, parte significativa dos seus gêneros foi descrita há mais de 100 anos e possui lacunas, que até o presente momento não foram reanalisados a luz das técnicas taxonômicas mais recentes e nem foram submetidos a estudos filogenéticos. Assim, este trabalho tem como objetivo realizar o estudo taxonômico da família Artotrogidae, e analisar filogeneticamente a família a fim de propor hipóteses de relacionamentos filogenéticos dos seus gêneros e obter melhor entendimento dos potenciais padrões evolutivos da família. Como resultados, no capítulo 1 descrevemos um novo gênero para a família Artotrogidae, e que se diferencia dos demais sobretudo pela morfologia única da sua primeira perna. No capítulo 2, descrevemos uma nova espécie para o gênero *Bradypontius,* redescrevemos *Artotrogus sarsi* Kim I.H., 1996 e *Dyspontius striatus* Thorell, 1859, e revisamos a diagnose de 11 gêneros da família, além de discutir a distribuição e a associação destes animais com variados invertebrados marinhos. E, por fim, no capítulo 3 propomos uma hipótese de relacionamento filogenético para os gêneros de Artotrogidae baseada em 103 caracteres morfológicos onde apresentamos a subdivisão da família em duas novas subfamílias, Subfamília nov.1 e Subfamília nov. 2; o gênero *Discopontius* passa a ser classificado como Artotrogidae; e os principais padrões evolutivos observados no formato do corpo e na morfologia dos apêndices são apresentados e discutidos.

Abstract

Copepods are little crustaceans with an immense abundance and diversity, that colonized successfully the most of the aquatic habitats, and stablished as an essential part of the food chain. About half of the known species live associated with almost all metazoans phyla. Those of the order Siphonostomatoida exhibit a mouth structure specialized on drawn food from its host's body. Artotrogidae, specially, had its classification extensively discussed on the last century. Although, but a significant part of its genera was described more than a century ago, with gaps, and most of it was not reanalyzed with most recent taxonomical tools or were object of a phylogenetic analysis. Thus, this work aims to conduct the taxonomic study of Artotrogidae, and perform a phylogenetic analysis to stablish phylogenetic relationship hypothesis and a better understanding of potential evolutionary trends. As results, on chapter 1 we describe a new Artotrogid genus that differs from others mostly for its unique first leg morphology. On chapter 2, we described a new species of Bradypontius, redescribed Artotrogus sarsi Kim I.H., 1996 e Dyspontius striatus Thorell, 1859, revised the diagnosis of 11 family genera, and discussed the distribution and the association of those animals with a wide range of marine invertebrates. And on chapter 3, we proposed a phylogenetic relationship hypothesis based on 103 morphological characters where we present the subdivision of the family on two new subfamilies, Subfamily nov. 1 and Subfamily nov. 2; the genus Discopontius is stablished as belonging to the family Artotrogidae, and the major evolutionary trends observed on the body shape and on appendages morphology are presented and discussed.

Introdução Geral

Devido à presença marcante na cultura alimentar humana alguns crustáceos, como camarões, caranguejos e lagostas, estão entre os animais marinhos mais populares (Rupert *et al*., 2005). Os copépodes, por outro lado, são pequenos crustáceos que devido ao seu tamanho diminuto estão entre os menos conhecidos no grupo (Rupert *et al*., 2005). O nome do táxon é oriundo da junção dos termos gregos "*kope*" e "*podos*" que significam, respectivamente, remo e pés, em alusão às suas pernas natatórias achatadas – que são unidas por uma estrutura chamada placa intercoxal, que é a responsável pelo movimento sincronizado dos ramos, assemelhando-se aos remos de uma embarcação (Huys & Boxshall, 1991). Apesar de não serem tão populares como seus parentes próximos, estes animais estão entre os mais abundantes dentre todos os metazoários e estão presentes nos mais diferentes tipos de ambientes, como por exemplo: águas marinhas e continentais, lagos hipersalinos, lagos de água doce, em grandes altitudes e em ambientes crípticos como musgo e serapilheira (Huys & Boxshall, 1991; Kihara & Rocha, 2007; Matsumura-Tundisi & Tundisi, 2011; Vad *et al*. 2012; Anufriieva, 2015; Corgosinho *et al*., 2017). Além disso, estes animais são responsáveis por representar um papel vital na cadeia alimentar marinha sendo a ligação entre o fitoplâncton (produtores primários) e animais consumidores de zooplâncton (Huys & Boxshall, 1991; Schnetzer & Caron, 2005).

Os copépodes possuem cerca de 14.900 espécies válidas e estão organizados em nove ordens: Cyclopoida Burmeister, 1834; Siphonostomatoida Burmeister, 1835; Monstrilloida Sars G.O., 1901; Calanoida Sars G.O., 1903; Harparcticoida Sars G.O., 1903; Misophrioida Gurney, 1933; Mormonilloida Boxshall, 1979; Platycopioida Fosshagen, in Fosshagen & Iliffe, 1985 e Gelyelloida Huys, 1988. Tamanha diversidade também é refletida nas formas de vida, que podem ser de vida-livre, simbióticos, associados e parasitas (Walter & Boxshall, 2024).

Siphonostomatoida Burmeister, 1835

A ordem Siphonostomatoida possui cerca de 2900 espécies válidas, divididas em 40 famílias (WoRMS, 2024). As espécies conhecidas dos animais desta ordem vivem associados a outros organismos, construindo relações com quase todos os filos de metazoários conhecidos (Huys & Boxshall, 1991). Assim, os sifonostomatóides, são, em sua maioria, parasitas de vertebrados, vivendo associados tanto à parte externa ou interna dos seus hospedeiros, prendendo-se às partes mais vulneráveis como por exemplo brânquias, globo ocular e trato digestivo (Huys & Boxshall, 1991). Esse modo de vida é baseado em um aparelho bucal adaptado composto por: um sifão, formado pela fusão do labro e do lábio, associado a uma maxila bilobada, e a uma mandíbula alongada em forma de estilete que, junto à grande diversidade morfológica do grupo, provavelmente lhes conferiu um sucesso na exploração dos hospedeiros (Kabata, 1979; Huys & Boxshall, 1991). Tais estruturas foram recentemente encontradas também em *Siphonis* Mercado-Salas, Khodami & Martínez Arbizu, 2019, um gênero de Aegisthidae (ordem Harpacticoida), apresentando-se como evidências morfológicas de convergência evolutiva entre as ordens (Mercado-Salas *et al*., 2019).

Além do sifão é comum membros desta ordem apresentarem perda ou redução de estruturas, sobretudo de locomoção, como indícios de especialização ao parasitismo (Huys & Boxshall, 1991). Entretanto, outra parcela da ordem vive em estreita relação aos mais diversos táxons de invertebrados, não se caracterizando, na maior parte das vezes, como parasitas e sendo denominados como associados, apresentando menos modificações nos seus apêndices de locomoção, embora todos apresentem o sifão (Huys & Boxshall, 1991).

Caracterização de Artotrogidae Brady, 1880

Os copépodes da família Artotrogidae são caracterizados por possuir um prossomo achatado; um urossomo reduzido; primeiro segmento pedígero fusionado a cabeça formando o cefalossomo; segundo e terceiro segmentos pedígeros livres posteriormente bem desenvolvidos; o quarto segmento pedígero tipicamente reduzido; urossomo com cinco segmentos; segmento genital duplo em fêmeas; três segmentos abdominais livres e ramo caudal com 6 cerdas (Boxshall & Halsey, 2004). Além de outras características como rostro bem desenvolvido; antênula com 8 a 14 artículos na fêmea com esteto no artículo terminal (oriundo da fusão dos artículos ancestrais XXI–XXVIII), e de 9 a 17 artículos no macho com estetos presentes em diversos artículos além do presente no último segmento assim como na fêmea; antena com coxa e base separadas, endópodo com dois artículos, exópodo com um artículo reduzido ou ausente; mandíbula reduzida a um estilete mas com palpo ausente; maxílula bilobada: maxila com dois artículos, sincoxa (oriunda da fusão entre a pré-coxa e a coxa) e garra (representando a base); maxilípede com 5 artículos, endópodo com 3 artículos e garra distal; pernas tipicamente birremes, perna 4 ausente ou com endópodo reduzido ou ausente, perna 5 reduzida ou ausente, perna 6 representada por 1 ou 2 cerdas próxima ao opérculo genital (Boxshall & Halsey, 2004).

Os Artotrogidae possuem diversos caracteres compartilhados com o ancestral hipotético para Siphonostomatoida, proposto por Huys & Boxshall (1991), em relação às demais famílias da ordem. Podemos citar por exemplo a presença de um grande número de estetos na antênula do macho, chegando a 14 em alguns casos ou a cerdação maior nas pernas. Por outro lado, características como a ausência do palpo mandibular e fusão dos segmentos distais da antênula destoam do ancestral hipotético (Huys & Boxshall, 1991). Pouco se sabe acerca da biologia destes animais. Além disso, são sempre encontrados em pequeno número, fato que, somado a presença de um trato digestivo bem desenvolvido, levaram Boxshall & Halsey (2004) a sugerirem que possivelmente estes passem parte de sua vida longe dos hospedeiros. Já foram encontrados associados a esponjas (Stock, 1965; Neves & Johnsson, 2008), corais (Snelgrove & Lewis, 1989; Johnsson & Neves, 2005), zoantídeos (Johnsson, 2001), briozoários (Kim I.H., 1996, 1998; Johnsson & Rocha, 2002), algas (Kim I.H., 1996; Lee J. & Kim I.H., 2023), ascídias (Kim I.H., 1996) além de outros hospedeiros não identificados.

A família está organizada em 23 gêneros e 131 espécies. Três destes gêneros (*Cryptopontius* Giesbrecht, 1899, *Bradypontius* Giesbrecht, 1895 e *Artotrogus* Boeck, 1859) englobam mais da metade das espécies descritas para a família e apresentam uma distribuição cosmopolita (Conradi, 2014). Dez gêneros (*Abyssopontius* Stock, 1985; *Antarctopontius* Eiselt, 1965; *Artogordion* Ivanenko, Bandera & Conradi, 2018; *Cribopontius* Giesbrecht, 1899; *Glannapontius* Holmes, 1998; *Glyptotrogus* McKinnon, 1988; *Pulicitrogus* Kim I.H., 1998; *Chejupontius* Lee & Kim I.H., 2023; *Tardotrogus* Eiselt, 1961 e *Thoostoma* Wilson, 1924) apresentam apenas uma espécie descrita, alguns destes descritos há décadas, ou até há um século, e desde então não mais registrados (Boxshall & Halsey, 2004).

Se considerarmos o ano da criação dos gêneros da família, observamos que 11 dos mesmos foram descritos no período entre o final do século XIX e meados do século XX, embora algumas descrições possuam ótimas ilustrações, outras foram pobres em detalhes e incompletas, sem dar a devida atenção à caracteres que ganhariam relevância com o avanço dos estudos no grupo (Boeck, 1859; Thorell, 1859; Scott T., 1898; Giesbrecht, 1895; 1899; Sars G.O., 1918; Hansen, 1923); *Arctopontius* Sars G.O., 1915 (5 espécies);

Artotrogus Boeck, 1859 (13 espécies); *Bradypontius* Giesbrecht, 1895 (23 espécies); *Cryptopontius* Giesbrecht, 1899 (27 espécies); *Dyspontius* Thorell, 1859 (7 espécies); *Myzopontius* Giesbrecht, 1895 (4 espécies); *Neopontius* Scott, 1898 (4 espécies); *Pteropontius* Giesbrecht, 1895 (5 espécies) e *Sestropontius* Giesbrecht, 1899 (2 espécies) são exemplos de gêneros descritos neste período e com algumas novas espécies descritas recentemente (Boxshall & Halsey, 2004; WoRMS, 2024)

Histórico Taxonômico de Artotrogidae Brady, 1880

As primeiras espécies hoje atribuídas a Artotrogidae foram descritas no final da década de 1850: *Artotrogus orbiculares* Boeck, 1859 e *Dyspontius striatus* Thorell, 1859 (Boeck, 1859; Thorell, 1859). Após um interstício de 15 anos, tivemos uma década onde os trabalhos de Brady & Robertson (1876), Brady (1880), Thomson (1883) e Scott T. (1888) trouxeram grandes contribuições para o conhecimento da família. Neste período, o número de espécies chegou a 10, e apenas um novo gênero foi descrito: *Conostoma* Thomsom, 1883 - hoje *Thoostoma*, sinonímia por nome já atribuído a uma espécie de ave - (Wilson, 1924). Ao final do século 19 os trabalhos de Wilhelm Giesbrecht trouxeram grandes avanços para o grupo, com 16 novas espécies e 6 novos gêneros descritos (Giesbrecht, 1895; 1899).

A primeira década do século XX foi marcada pelo trabalho de Brady (1910), onde 10 novas espécies foram descritas, embora 8 delas tenham sido posteriormente sinonimizadas ou redescritas e designadas a outros gêneros. Cinco anos depois, Sars G.O. (1918) descreve apenas 1 novo gênero e 4 novas espécies, entretanto, redescreve e fornece descrições e ilustrações riquíssimas, em detalhes, que se destacam até os dias de hoje. Criam-se diagnoses detalhadas, distintas para gêneros e espécies, o que até então era uma grande lacuna (Sars G.O., 1918). Estes trabalhos marcaram o período entre o final do século XIX e o início do século XX, que é conhecido hoje como a “Era de Ouro da Copepodologia” (Damkaer, 2002).

Os trabalhos de Giesbrecht (1895, 1899) e Sars G.O. (1918), propuseram as primeiras diagnoses distintas e detalhadas para famílias, gêneros e espécies; pondo fim à uma tendência presente neste período que tornavam os gêneros *Artotrogus* e *Dyspontius* “depósitos” de espécies. Mais da metade das espécies descritas neste período foram designadas a estes gêneros, o que só viria a ser modificado algumas décadas depois com as redescrições feitas por Nicholls (1944), Eiselt (1961,1965) e Kim (1996).

Após a primeira guerra mundial (1914-1918), e uma notável pausa nos avanços sobre copépodes artrotrogídeos, novas espécies só voltaram a ser descritas nos trabalhos de Hansen (1923) e Wilson (1923, 1932), para os gêneros *Artotrogus*, *Bradypontius*, *Cryptopontius*, além do novo gênero *Metapontius* Hansen, 1923. Uma única exceção foi o trabalho publicado por Sars G.O. (1918). Outro período de pausa é notado entre a segunda metade da década de 1930 até a metade da década de 1940. Esta pausa é interrompida brevemente pelos trabalhos de A. G. Nicholls (1944) e Sewell (1949), que descrevem, 10 espécies para os gêneros *Artotrogus* Boeck, 1859, *Bradypontius* Giesbrecht, 1895, *Cryptopontius* Giesbrecht, 1899, *Myzopontius* Giesbrecht, 1895 e *Pteropontius* Giesbrecht, 1895. Ao longo de toda a década de 50 não houveram novas publicações.

Um grande número de estudos volta a surgir durante a década de 1960: Eiselt (1961) descreve 2 novos gêneros e 6 novas espécies. Junto a isso, os trabalhos de Wiborg (1964), Eiselt (1965), Ummerkutty (1966), Stock (1966) e Murnane (1969) marcam a década de 60 com a descrição de 16 novas espécies e 4 novos gêneros: *Neobradypontius* Eiselt, 1961, *Tardotrogus* Eiselt, 1961, *Antarctopontius* Eiselt, 1965 e *Sewellopontius* Ummerkutty, 1966. Após isso, novamente seguiu-se uma década inteira (1970) sem novas publicações para Artotrogidae.

Na década de 1980, foram publicados os trabalhos de Ho (1984), Stock (1985), Eiselt (1986) e McKinnon (1988) e foram descritos o novo gênero *Glyptotrogus* McKinnon, 1988, e 3 novas espécies. Já na década de 1990, houve um grande aumento dos números de espécies descritas nos trabalhos de Malt (1991), Kim (1996 e 1998) e Holmes (1998) que descreveram três novos gêneros – *Ascidipontius* Kim I.H, 1996, *Glannapontius* Holmes, 1998 e *Pulicitrogus* Kim I.H, 1998 – e 19 novas espécies.

Após o início do século XXI, os novos gêneros, *Artogordion* Ivanenko, Bandera & Conradi, 2018, *Chejupontius* Lee & Kim I.H., 2023 e 21 novas espécies foram descritos para ciência através dos trabalhos de Kim (2009; 2016), Johnsson (2001), Johnsson & Rocha (2002), Johnsson, Rocha & Boyko (2002), Johnsson & Neves (2005), Neves & Johnsson (2008), Varela (2012), Ivanenko *et al*. (2016), Farias *et al*. (2020) e Lee & Kim (2023)., totalizando 24 gêneros e 121 espécies na família Artotrogidae, ocorrendo neste período as primeiras descrições de Artotrogidae para o Atlantico Sul (Neves & Johnsson, 2008; Farias *et al*., 2020).

Classificação e Relações Filogenéticas em Artotrogidae

Ao descrever *Artotrogus*, Boeck (1859) discutiu a então classificação dos crustáceos proposta de Milne-Edwards, que separava em diferentes táxons os copépodes e suas formas parasitas através da morfologia do seu aparato bucal. Junto a *Artotrogus* Boeck (1859) também descreveu o gênero *Asterocheres* (hoje atribuído à Asterocheridae), e não os designou diretamente a um táxon superior. Entretanto, já propôs que as novas espécies representavam formas intermediárias entre os parasitas e os de vida livre (Boeck, 1859).

Já Thorell (1859), propôs uma nova subdivisão de Copepoda, semelhante a Milne-Edwards, baseada na morfologia do aparato bucal: Gnasthostoma, copépodes equipados com abertura bucal ampla e mandíbulas bem desenvolvidas, sem sifão; Poecilostoma, copépodes com a estrutura bucal semelhante ao anterior, porém sem as mandíbulas; e Siphonostoma, copépodes com cone oral e mandíbulas em forma de estilete. Os gêneros ali descritos, *Dyspontius* e *Ascomyzon,* foram incluídos na nova família Ascomyzontidae (subdivisão Siphonostoma), juntamente com os gêneros descritos por Boeck *Asterocheres* e *Artotrogus*, por compartilharem entre outras características, estas que destaco: corpo largo e achatado; antênula apresentando de 9 a 20 segmentos; antena curta, com 3 a 4 segmentos, e armada com garra; sifão longo, com palpos; três pares de maxilas, o primeiro par birreme; pernas achatadas, birremes, exceto o quinto par que era incompleto ou ausente.

A classificação de Copepoda e o posicionamento dos copépodes parasitas foram extensivamente discutidos em diversos estudos nas décadas seguintes, e o estabelecimento de Siphonostomatoida como uma ordem coesa, incluindo os parasitas de peixes, se deu no final da década de 1970 (Kabata, 1979). Embora, a autoridade de Siphonostomatoida seja atribuída a Burmeister (1835), por ter sido o primeiro autor a utilizar o clado como um nível superior a família, ainda que com uma grafia anterior – *Siphonostoma* (Ivanenko *et al*. 2001).

A família Artotrogidae foi erguida por Brady (1880), ainda em meio a discussões sobre a classificação dos copépodes parasitas, mas já incluía os gêneros *Artotrogus* e *Dyspontius* juntamente com *Cyclopicera* e *Acontiophorus,* gêneros hoje atribuídos a Asterocheridae. Dentre as características diagnósticas da família destacam-se: corpo largo e achatado, arredondado ou suboval; antênula apresentando de 9 a 20 segmentos; antena curta, apresentando de 3 a 4 segmentos, as vezes apresentando exópodo; boca desenvolvida como um sifão composto pelo alongamento do labro e do lábio; mandíbulas em forma de estilete, simples ou provida de um palpo filiforme; maxílula birreme e armada com cerdas; primeiro e segundo par de "perna-mandíbulas" (maxila e maxilípede) preênseis; primeiros quatro pares de pernas birremes (exceto o quarto par em *Dyspontius*), ramos com 3 segmentos; quinto par pequeno, composto por 1 segmento, ou ausente.

Giesbrecht (1899) sinonimizou Ascomyzontidae Thorell, 1859 e Artotrogidae Brady, 1880 a Asterocheridae, e incluiu na subfamília Dyspontiinae os gêneros *Myzopontius*, *Neopontius*, *Cribropontius*, *Sestropontius*, *Bradypontius*, *Cryptopontius*, *Dyspontius*, *Pteropontius*, *Dystrogus* e *Artotrogus*. Estes foram agrupados por compartilharem, entre outras características: segmentos pedígeros com epímeros projetados; antênula da fêmea apresentando de 8 a 12 segmentos, com esteto no segmento terminal; antênula do macho apresentando de 9 a 12 segmentos, geniculada, e com esteto no último ou penúltimo segmento, podendo apresentar estetos nos segmentos proximais; exópodo antenal pequeno; sifão com cone oral curto ou longo; mandíbulas sem palpo; quarto par de pernas semelhante aos anteriores, podendo apresentar ramo interno reduzido ou ausente; ou ausência de ambos os ramos da perna.

Giesbrecht apontou que os gêneros *Myzopontius*, *Neopontius*, *Cribropontius* e *Sestropontius* eram provavelmente os mais próximos a Asterocherinae, por apresentarem o quarto par de pernas birreme. Entretanto, características como a forma menos achatada do corpo, a forma menos alargada do segmento genital e a estrutura mais rica da antena os diferenciavam da subfamília. O autor também já destacava a variação observada no padrão de desenvolvimento do quarto par de pernas nos demais gêneros. Segundo o autor, *Bradypontius* apresentava o primeiro estágio no padrão de redução do ramo interno da perna, pois o apresentava com uma forma mais estreita e cilíndrica, com a cerdação bastante reduzida. Enquanto que *Pteropontius*, *Dyspontius* e *Cryptopontius* apresentava o ramo interno ausente, estabelecendo um padrão intermediário; e *Artotrogus* e *Dystrogus* não apresentavam um quarto par de pernas. Giesbrecht (1899) também abordou a classificação de *Thoostoma* – então *Conostoma* – que poderia ser incluído em Dyspontiinae, entretanto, a descrição original possuía muitas lacunas e a ausência de tais informações tornava a classificação do gênero dentro da família Asterocheridae impossível.

Em 1918, Sars G.O. apresenta uma nova classificação para os gêneros organizados por Giesbrecht (1899). De acordo com o autor, a família Asterocheridae *sensu* Giesbrecht, compreendia uma variação demasiadamente grande de caracteres e, portanto, não poderia ser mantida como uma única família. Assim, os gêneros anteriormente incluídos em Dyspontiinae foram separados em três diferentes famílias:

A primeira família é Myzopontiidae, compreendendo os gêneros *Myzopontius* e *Neopontius*. Dentre as características que definem a família destacam-se: corpo estreito, com projeções póstero-laterais sutis; antênula afilada, com esteto no segmento terminal; mandíbulas sem palpo; pernas natatórias como em Ascomyzontidae (birremes); último par de pernas com protópodo não articulado e exópodo com tamanho reduzido.

A segunda família é Dyspontiidae, que incluía os gêneros *Dyspontius*, *Cryptopontius*, *Arctopontius*, *Bradypontius* e *Cribropontius*. Dentre as características diagnósticas destacam-se: corpo bastante alargado e achatado, projeções póstero-laterais bem desenvolvidas; quarto segmento pedígero geralmente menor; mandíbulas sem palpo; pernas natatórias com ramos mais estreitos, ramo interno do quarto par mais ou menos reduzido, ou ausente; ultimo par extremamente pequeno e rudimentar.

A terceira família é Artotrogidae, que apesar de compartilhar o nome, não era equivalente a família proposta por Brady (1880), e incluía apenas o gênero *Artotrogus*. Dentre as características diagnósticas elencadas destacam-se: corpo bastante alargado, mais ou menos ciclopiforme, segmentos pedígeros posteriores imperfeitamente desenvolvidos; urossomo curto; três pares de pernas natatórias como em Dyspontiidae, quarto par de pernas ausente; ultimo par não articulado do segmento pedígero.

Enquanto que Hansen (1923) optou por não seguir a divisão de Asterocheridae em diversas famílias menores, Wilson (1932) manteve a classificação proposta por Sars. Já nos trabalhos de Nicholls (1944) e Sewell (1949) uma abordagem mista foi adotada; ambos os autores mantiveram as famílias oriundas da subfamília Dyspontiinae feita por Sars, e também mantiveram a família Asterocheridae *sensu* Giesbrecht como um sinônimo da subfamília Asterocherinae, não adotando a família Ascomyzontidae *sensu* Sars.

Em 1960, Eiselt publica uma revisão extensiva dessas espécies, e neste estudo descreve dois novos gêneros *Pseudotrogus* e *Neobradypontius*, que de acordo com o autor, estabeleciam a ponte entre Dyspontiidae e Artotrogidae. De maneira semelhante, o gênero *Metapontius*, descrito décadas antes por Hansen (1923), atuava como um elo entre Myzopontiidae e Dyspontidae. Assim, portanto, ambas as famílias deveriam ser sinonimizadas sob o nome de Artotrogidae, nome criado por Brady (1880), agora *sensu* Eiselt (1961).

Artotrogidae ficou definido como copépodes que apresentavam: abdômen com 5 segmentos em machos, e com 4 segmentos em fêmeas; corpo apresentando formato alongado a circular, com comprimento entre 0,8 a 5,5 mm; antênula apresentando de 9 a 17 segmentos em machos, e de 8 a 14 segmentos em fêmeas, com esteto no segmento terminal e podendo apresentar estetos adicionais em outros segmentos em machos; antena não convertida em apêndices preênseis, apresentando de 3 a 4 segmentos, penúltimo segmento mais curto do que o último, e consideravelmente mais longo do que o ramo externo; mandíbula sem palpo; ramo interno da maxílula normalmente mais estreito e mais longo que o ramo externo da maxílula; pares de pernas 1 a 4 normalmente desenvolvidos ou apresentando reduções em vários graus, podendo estar completamente ausente na perna 4, quinto par de pernas rudimentar, com um segmento, com 3 ou menos cerdas, ou representada apenas por cerdas.

Por esta definição Eiselt descartou a inclusão de *Cletopontius* Thompson I.C. & Scott A., 1903 e *Discopontius* Nicholls, 1944 por apresentarem um abdômen com 3 segmentos. O autor indicou que *Cletopontius* deveria ser incluído em Asterocheridae, enquanto que o posicionamento de *Discopontius* ficou incerto devido a não apresentar palpo mandibular. Já *Thoosotma* (então *Conostoma*), não seria incluído, por apresentar os quatro pares de pernas com 2 artículos.

A reclassificação de Artotrogidae realizada por Eiselt foi amplamente adotada pelos estudos seguintes (Ummerkutty, 1961; Stock, 1965; 1966; 1985; Kim I.H., 1996; Holmes, 1998). Exceto por McKinnon (1988), que a citou, mas em seguida afirmou que o estudo apresentava apenas espécies que se enquadravam em Artotrogidae sensu Sars, apresentando três pares de pernas. Ho (1984), que ao descrever uma nova espécie de *Pteropontius*, a incluiu na família Dyspontidae, com grafia incorreta e autoridade erroneamente atribuída a Giesbrecht, ao invés de Sars. E Malt (1991), que incluiu uma nova espécie de *Cryptopontius* a família Dyspontiidae, com autoridade erroneamente atribuída a Thorell, ao invés de Sars.

Holmes (1998) apresentou o primeiro estudo a tentar relacionar estes copépodes, entretanto, através da "*Average Linkage Cluster Analysis*", método analítico delineado por Sokal & Sneath (1963) pelos princípios da escola fenética, que determina o relacionamento das espécies analisadas através da média das distâncias das similaridades das características morfológicas. Como resultado, *Glannapontius* Holmes, 1998, novo gênero proposto no estudo foi relacionado como pertencente à família Artotrogidae. A análise indicou que o novo gênero possuía *Myzopontius* como gênero mais próximo, e ambos seriam mais próximos do agrupamento formado pelos gêneros *Bradypontius* e *Dyspontius* (Holmes, 1998). O agrupamento formado pelos quatro gêneros formou-se separadamente do agrupamento composto por sete espécies da família Asterocheridae.

Em sua tese, Johnsson (2003) avaliou o relacionamento filogenético das famílias de Siphonostomatoida associadas a invertebrados marinhos, com ênfase em Asterocheridae. Neste estudo foram incluídas 19 famílias associadas a invertebrados, 4 famílias associadas a peixes, 2 gêneros *incerta sedis*. E neste contexto abrangente, foram incluídos 20 gêneros de Artotrogidae, com exceção de *Metapontius* (Johnsson, 2003). Artotrogidae foi considerada uma família monofilética mediante a inclusão de 3 outros gêneros: *Australomyzon* Nicholls, 1944 (Asterocheridae), *Bythocheres* Humes, 1988 (*incerta sedis*) e *Hyalopontius* (Megapontiidae), sobretudo por compartilharem fusões nos segmentos III e IV, XV e XVI, XVII e XVIII, XIX e XX da antênula da fêmea (com exceção a *Australomyzon*), a ausência do palpo mandibular (com exceção a *Australomyzon*), e a presença de cerdação máxima no terceiro exópodo das pernas 2, 3 e 4 (Johnsson, 2003).

Com uma classificação historicamente debatida, ainda não há estudos filogenéticos que investiguem a relação entre os gêneros da família Artotrogidae através de uma abordagem restrita. Assim, se faz necessário e são objetivos do presente estudo: (1) Investigar taxonomicamente a diversidade de Artotrogidae e realizar a revisão taxonômica das espécies tipo dos gêneros da família através de empréstimos de material depositados em coleções zoológicas; (2) Propor hipótese(s) de relacionamento filogenético para os gêneros de Artotrogidae, através de dados morfológicos, a fim de contribuir com a elucidação de potenciais padrões evolutivos na família.

Capítulo 1 – A new genus of Artotrogidae (Copepoda: Siphonostomatoida) with an uncommon leg morphology

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Artigo submetido para publicação no periódico Zoologischer Anzeiger

A new genus of Artotrogidae (Copepoda: Siphonostomatoida) with an uncommon leg morphology

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Abstract: Artotrogidae Brady, 1880 is a cosmopolitan family with 23 valid genera and 131 known species. However, a considerable number of these species were subject of reexaminations and redescriptions recently. And, with the crescent number of new species discovered, it is becoming possible to better understand their limits. This study presents a new genus and species of Artotrogidae, recovered from unidentified hosts in debris of benthonic samples from Todos-os-Santos Bay, northeastern coast of Brazil. The new organism exhibits a unique morphological characteristic for first leg that differentiates it from all other genera of the family.

Key words: symbiotic copepods, invertebrate associate, uncommon first leg,

1. Introduction

Artotrogidae Brady, 1880 is a cosmopolitan family with species found associated with a wide variety of hosts, ranging from sponges to urochordates. Even so, many species of the family were recovered from mixed benthonic samples (Boxshall and Halsey 2004; Ivanenko *et al*. 2018; Lee, J. and Kim I.H., 2023). Nowadays the family includes 23 valid genera and 119 known species (WoRMS, 2024).

A significant part of the family species was described between the second half of the nineteenth and the early decades of the twentieth century (Boeck, 1859; Thorell, 1859;

Brady and Roberston, 1876; Brady, 1880; 1899; 1910; Thomson, 1883; Scott T, 1888; 1898; 1905; 1912; Giesbrecht, 1895; 1899; Sars, 1915; Hansen, 1923; Wilson, 1923; 1924;), period known as the "golden age of the copepodology" (Damkaer, 2002). However, since de 1960s, the genera and species described during this period have been the target of extensive reexaminations and redescriptions that, allied with new species recently discovered, have expanded the understanding about their limits (Eiselt, 1961; 1965; Stock, 1965; 1966; McKinnon, 1988; Kim I.H., 1996; Johnsson and Rocha, 2002; Johnsson and Neves, 2005; Lee, J and Kim I.H., 2023). Nonetheless, a significant number of genera of the family is still monospecific (WoRMS, 2024).

Despite the great number of known species, only five artotrogid species belonging to two genera are recorded from the South Atlantic Ocean: *Bradypontius ancistronus* Neves and Johnsson, 2008; *Cryptopontius aesthetascus* Neves and Johnsson, 2008; *Cryptopontius expletus* Neves and Johnsson, 2008; *Cryptopontius pentadikos* Farias, Neves and Johnsson, 2020 e *Cryptopontius phyllogorgius* Farias, Neves and Johnsson, 2020 (Neves and Johnsson, 2008; Farias *et al*. 2020). Aiming this knowledge gap this study investigations bring to light the description of a unique new artotrogid genus and species.

2. Material and Methods

The copepods were found at seven different locations on Todos-os-Santos Bay (Figure 1). Samples were collected on the submersed surface of pier decks incrusted with a diverse benthonic community, such as sponges, barnacles, molluscs, hydroids, bryozoans, ascidians, and corals. The material was fixed in 10% formalin for 48 hours and posteriorly preserved in 70% ethanol.

The copepods were sorted out under a stereo microscope. Specimens were analyzed immersed in glycerin and mounted on temporary slides with adhesive plastic rings to avoid crushing (Kihara and Rocha, 2009). Examination, photos, measurements, and drawings of the body aspect were made with the aid of a Zeiss Axio Lab.A1 microscope equipped with a digital camera AxioCam ERc 5S connected to an iPad (7th generation) with Zeiss Labscope Software (version 4.0.2). The holotype and allotype were dissected directly on a permanent slide with CMC-9 mounting media for the appendages analysis (Kihara and Rocha, 2009). The Illustrations were vectorized with CorelDRAW 2021 software (version 23.1.0.389).

For the legs armature formula, Roman numerals represent spines and Arabic numerals represent setae (Huys and Boxshall, 1991). For antennule armature, Roman numerals represent ancestral segments (Huys and Boxshall, 1991).

The type material and additional material analyzed were deposited in the Crustacea zoological collection of the Museu de História Natural da Bahia of the Universidade Federal da Bahia, Brazil.

For Confocal Laser Scanning Microscopy, a paratype was stained with a 1:1 solution of Congo Red and Acid Fuchsin overnight, following the procedure described by Corgosinho *et al*. (2017). The specimens were examined using an Axio Observer.Z1 equipped with LSM900; images were obtained through an experiment of extended depth of focus on ZEN 3.0 (blue edition) and the final images were post-processed using the maximum projection method, detailed acquisition information on Table 1.

3. Results

Order Siphonostomatoida Burmeister, 1835
Family Artotrogidae Brady, 1880
Genus Artotrogidae gen. nov.
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3.1. Diagnosis

Artotrogidae. Body cyclopiform, dorso-ventrally flattened. Carapace ornamented with scale-like structures showing integumental organs. Prominent dorsal crest and rostrum. Radial bands on the lateral margins of the cephalosome. Epimera of the cephalosome, second, and third pedigerous somites projected posteriorly. Medio-posterior margin of the second and third pedigerous somite with posteriorly elevated projections medially aligned. Urosome 5-segmented on female, genital double-somite with two pairs of produced posteriorly projected epimera. Male urosome 6-segmented, genital somite and first post-genital somite with a pair of projected epimera produced posteriorly. Female antennule 8-segmented. Male antennule 9-segmented, with additional aesthetascs on segments 2, 3, 5, 6, 7, and 8, showing an incomplete segmentation on the terminal segment; and significantly large spine on segment 7. Antennal exopod represented by seta, and 2-segmented endopod. Maxillule bilobed. Maxilliped 5-segmented. Leg 1 uncommonly reduced, with single-segmented ramus. Leg 1, 3, and 4 with coxa and basis fused. Leg 2 and 3 biramous and 3-segmented. Leg 4 lacking endopod.

3.2. Remarks

When redefining Artotrogidae, Eiselt (1961) described, among other characteristics, the legs 1 to 4 as being: "*normal ausgebildet oder in verschiedenem Ausbaße reduziert, P4 bis zu seinem völligen Fehlen*", (leg 1 to leg 4 normally developed or reduced to various degrees, leg 4 to its complete absence). In fact, the different levels of reduction patterns of leg 4 on Artotrogidae performed an important role in the differentiation of the genera, splitting the family in a few groups: (1) Leg 4 biramous with 3-segmented exopod and endopod (*Abyssopontius* Stock, 1985, *Antarctopontius* Eiselt, 1965, *Artogordion* Ivanenko, Bandera and Conradi, 2018, *Bradypontius* Giesbrecht, 1895, *Cribropontius* Giesbrecht, 1899, *Glannapontius* Holmes, 1998, *Myzopontius* Giesbrecht, 1895, *Neobradypontius* Eiselt, 1961, *Neopontius* Scott T., 1898, and, *Sestropontius* Giesbrecht, 1899); (2) Leg 4 biramous with 3-segmented exopod and 2-segmented endopod (*Arctopontius* Sars G.O., 1915 e *Metapontius* Hansen, 1923); (3) Leg 4 with 3-segmented exopod, without endopod (*Ascidipontius* Kim I.H., 1996; *Chejupontius* Lee, J. and Kim I.H., 2023, *Cryptopontius* Giesbrecht, 1899, *Dyspontius* Thorell, 1859, *Pteropontius* Giesbrecht, 1895, *Pulicitrogus* Kim I.H., 1998, and, *Sewellopontius* Ummerkutty, 1966); (4) Leg 4 reduced to a protopod (*Pseudotrogus* Eiselt, 1961); and (5) Leg 4 absent (*Glyptotrogus* McKinnon, 1988, *Artotrogus* Boeck, 1859 and *Tardotrogus* Eiselt, 1961).

Artotrogidae gen. nov. shares the uniramous leg 4 with a 3-segmented exopod with the 7 genera included in the third group, but these taxa can be easily differentiated by the level of reduction patterns found on their leg 1: *Ascidipontius*, *Chejupontius*, *Cryptopontius*, *Dyspontius*, and *Pulicitrogus* exhibit a biramous 3-segmented leg 1, with the exopod formula: (I-0, 0-0; II, 3), (I-0; 0-1; II, I, 2 or II, I, 1), (I-1; I-1; III, 4 or III, 5), (I-1; I-1 or 0-1; II, 5 or II,4), (I-0; 0-1; II, 3), respectively, characterizing minor modifications in the pattern, showing only a few elemental reductions (Thorell, 1859;

Giesbrecht, 1899; Sars, 1915; Kim I.H., 1996; 1998; 2016; Johnsson, 2001; Farias *et al.*, 2021; Lee, J. and Kim I.H., 2023). This is completely different from Artotrogidae **gen. nov.** which shows only one-segmented ramus on leg 1.

Sewellopontius species can exhibit a moderate reduction pattern, with leg 1 exopod 2- or 3-segmented, with the formula (I-0 or 0-0; 0-1; II,3) or (I-0; II, 3 or II, 4) (Lee, J. and Kim, 2023; Kim I.H., 1996; Ummerkutty, 1966). Therefore, also differing from the one-segmented ramus of leg 1 in the new genus.

The species included in the genus *Pteropontius* exhibited the most reduced pattern of leg 1, with both exopod and endopod 2-segmented, with the formula (0-1 or I-0; II, 3 or II, 4). This pattern has been confirmed with the recent redescription of the type species by Lee J. and Kim I.H. (2023) and differentiates it from the new genus.

3.3. Regarding leg 1 reduction patterns

In addition to the redescription of *Pteropontius cristatus* Giesbrecht, 1895, Lee J. and Kim I.H. (2023) also described two new species for the genus *Sewellopontius*: *S. pterophorus* Lee J. and Kim, I.H., 2023 and *S. macrochelatus* Lee J. and Kim, I.H., 2023. The limits of these two genera were discussed, resulting in the comb. nov. for *Pteropontius trimerus* Kim I.H., 1996 as *Sewellopontius trimerus* (Kim I.H., 1996).

Sewellopontius trimerus represented an exception to the reduction pattern previously discussed: While all the other species of *Pteropontius* exhibit 2-segmented rami, *S. trimerus* exhibits a 2-segmented exopod and a 3-segmented endopod on leg 1. This species also exhibit a 9-segmented antennule, a 2-segmented antennal endopod, and one postero-lateral projection on genital segment. Instead of an 8-segmented antennule, 1-segmented antennal endopod and two postero-lateral projections, respectively, as the other *Pteropontius* species.

Another exception to the pattern is *Pteropontius pediculus* Stock, 1966. This species was described based on a single male specimen found associated with the coral *Echinopora lamellosa* (Esper, 1791) on Mauritius (Stock, 1966). Stock (1966) classified the specimen as “somewhat aberrant”, alluding to the uncommon morphology of the reduced first leg, which shows a fused protopod. Considering the erection of the new genus, it’s possible to observe the differences between *P. pediculus* from all other four

Pteropontius species, such as the 2-segmented antennal endopod (instead of 1-segmented); leg 1 with single segmented ramus (instead of biramous and 2-segmented); leg 1 and leg 3 with coxa and base fused (instead of articulated). Thus, since these characteristics previously mentioned are diagnostic of the new genus, *P. pediculus* should be moved to Artotrogidae gen. nov., with a new combination as Artotrogidae gen. nov. *pediculus* (Stock, 1966) comb. nov.

3.4. Etymology

3.5. Type species by original designation

Artotrogidae gen. *et* sp. nov.

Other species:
Artotrogidae *gen* nov. *pediculus* (Stock, 1966) comb. nov.

Artotrogidae *gen. et* sp. nov.
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(Figs. 2-5)

3.6. Material examined

Holotype female (UFBA4130), dissected on permanent slide; allotype male (UFBA4133), dissected on permanent slide; paratype male (UFBA4131) preserved in ethanol and, paratype female (UFBA4132) preserved in ethanol; collected at Barra do Paraguaçu pier (Salinas da Margarida city – 12°50'25.0"S 38°47'40.9"W), found in mixed benthonic samples.

3.7. Additional material

Female (UFBA4092) and female (UFBA4093) preserved in ethanol, from mixed benthonic samples from Marina de Itaparica pier (Itaparica Island – 12°53'21.2"S 38°41'04.2"W). Female (UFBA4112), preserved in ethanol, from mixed benthonic sample from Bom Jesus pier (Bom Jesus dos Passos Island – 12°45'42.4"S 38°38'09.5"W). Male (UFBA4098), female (UFBA4099), male (UFBA4100), female (UFBA4101), female (UFBA4102), female (UFBA4103) preserved in ethanol, two females (UFBA4134), from mixed benthonic samples from Estação de Medidas

Magnéticas de Itaparica pier (Itaparica Island – 12°52'47.9"S 38°41'10.1"W). Male (UFBA4137) and male (UFBA4138), preserved in ethanol, from mixed benthonic samples from Bimbarras pier (Bimbarras Island – 12°43'36.1"S 38°38'02.7"W). Three females (UFBA4316), male (UFBA4317), two females and a male (UFBA4139), and two females (UFBA4187), preserved in ethanol, from mixed benthonic samples from Madre de Deus pier (Madre de Deus city – 12°43'58.8"S 38°37'22.8"W). Female (UFBA4777), female (4778), and a juvenile (UFBA4779), preserved in ethanol, from Terminal dos Passos pier (Bom Jesus dos Passos Island – 12°45'20.7"S 38°38'21.5"W).

3.8. Female description

Body cyclopiform (Fig. 5a), dorso-ventrally flattened, 888 µm long. Carapace adorned with scale-like structures showing sensilla on each integumental organs (Fig. 5a; b), and radial bands along the margins (Fig. 2b); body length: width ratio 1.6:1. Cephalosome slightly wider than long (539 × 553 µm); with robust dorsal crest, ranging from posterior medial margin to prominent rostrum; also bearing radial bands along the margins and ending in projected epimera. Second and third pedigerous somites with serrulated margins, and showing medial posterior margins with dorsal elevated projections aligned with dorsal crest. The second pedigerous somite significantly wider than long (88 × 327 µm), with produced projected epimera. Third pedigerous somite wider than long (100 × 287 µm), with the elevated structure on the posterior medial margin projecting over the double-genital somite. The fourth pedigerous somite is twice as wide as long (31 × 62 µm), and strongly reduced. Prosome longer than wide (703 x 553 µm), prosome: urosome length ratio 1.2:1.

Urosome 5-segmented, longer than wide (245 × 212 µm) (Fig. 2c). Fifth pedigerous somite wider than the fourth (30 × 96 µm). Genital double-somite nearly twice as wide as long (110 × 214 µm) exhibiting two pairs of projected epimera. First and second post-genital somites wider than long (28 × 78 µm, and 19 × 56 µm). First one partially covered by genital somite. Robust anal somite, wider than long (42 × 77 µm), showing row of five parallel perforations. Caudal rami longer than wide (49 × 28 µm), armed with two smooth and small dorsal setae, and distally armed with 4 setae. Caudal rami length: width ratio 1.7:1.

Antennule (Fig. 2d) 8-segmented, total length measuring 249 μm long. Length measurements made along the medial margins = 51, 63, 25, 18, 20, 12, 19, and, 41 μm long, respectively. Segmental homologies and armature as follow: I – 1; II-VIII – 6; IX-XII – 4; XIII-XIV – 1+s; XV-XVI – 1; XVII-XVIII – 1; XIX-XX – 1; XXI-XXVIII – 10+ae. All setae naked, two distal long setae almost as long as the aesthetasc, which is 93 μm long.

Antenna 4-segmented (Fig. 2e), total length measuring 100 μm long (without distal setae), Coxa and basis unarmed, 10 and 35 μm long, respectively. Exopod reduced to seta, 22 μm long, almost as long as the first endopodal segment. Endopod 2-segmented, first segment 25 μm long and unarmed, second segment 30 μm long, 1.2 times longer than the first one, armed medially armed with plumose seta, and distally with 3 setae: a small slender seta, 2 stout ones, unequally sized, and an elongated plumose seta.

Oral cone (Fig. 2a) 260 μm long, reaching basis of the maxilliped. Mandible with long stylet inserted in the oral cone, showing 4 teeth-like projections at the tip, palp absent (Fig. 2f).

Maxillule bilobed (Fig. 2g), inner lobe longer than outer one, 109 μm long (broken, as long as the oral cone on paratypes), exhibiting a tapering shape and naked margins, with long plumose seta; the outer lobe 55 μm long, with row of setules on the outer margin, and two strong distal setae; the longer seta has a plumose inner margin and spinules along the outer margin, the shorter one shows spinules on the inner margin and naked outer margin.

Maxilla stout (Fig. 3a), syncoxa naked, measuring 202 μm long, with proeminent bump on the outer margin; (detached) strong basis (claw), 230 μm long, remarkably recurved, and armed with small stout seta on medio-distal margin. Maxilliped 5-segmented (Fig. 3b), total length 291 μm long (not including distal claw); coxa 36 μm long, armed with single seta on inner margin, and row of setules on outer margin; basis unarmed, 136 μm long. Endopod 3-segmented, first segment unarmed, 28 μm long; second segment 38 μm long, armed with distal inner seta; third segment 53 μm long, armed with robust seta and terminal claw. Terminal curved claw measuring 82 μm long.

Leg 1 (Fig. 3c) showing no segmentation between coxa and basis, forming protopod, and exhibiting long seta on the distal outer margin. The first leg has a single-segmented ramus, armed with 3 distal unequal-sized setae (Fig. 5c).

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

Outer margins of exopodal segments of legs 2 to 4 (Figs. 3d – f) armed with spinules. Endopodal segments of leg 2 (Fig. 3d) showing setules along the outer margin. Third endopodal segment of leg 3 (Fig. 3e) exhibiting strong distal spine. The distal spine of the third exopodal segment of legs 3 and 4 (Figs. 3e – f) slightly bending on the proximal region.

Both protopod and exopod of fifth leg are extremely reduced, represented by 1 and 2 setae, respectively.

3.9. Male description

Body cyclopiform (Fig. 4a), longer than wide, smaller but comparatively slightly slender than female (530 × 292 µm), body length: width ratio 1.8:1. Cephalosome longer than wide (319 × 292 µm), cephalosome length: width ratio: 1.1:1. Prosome longer than wide (402 × 292µm), prosome: urosome length ratio 2.5:1. Urosome 6-segmented, longer than wide (158 ×110 µm). Genital somite (Fig. 4b) wider than long (63 × 148 µm), with only a pair of epimera posteriorly projected. The first post-genital somite almost as wide as the genital somite (35 × 123 µm), also showing epimera posteriorly projected. The second post-genital somite almost entirely covered by the first one, and followed by the third somite, both wider than long (17 × 63 µm and 13 × 48 µm), respectively. Anal somite robust, almost twice wider than long (36 × 63 µm). Caudal rami longer than wide (31 × 22 µm), bearing two dorsal small naked setae and four terminal setae, caudal rami length: width ratio 1.4:1.

Male antennule (Fig. 4c) 9-segmented, total length along the medial margin measuring 312 µm long. Segments measurements: 31, 60, 12, 15, 35, 23, 49, 27, and, 60 µm long, respectively. Segmental homologies as follows: I (0); II-VI (3+5ae); VII (1+ae); VIII (0); IX-XII (2+s+3ae); XIII-XIV (1+ae); XV-XVIII (3+s+ae); XIX-XX (1+ae); XXI-XXVIII (9+ae). All setae naked. Large spine on the segment XV-XVIII measuring 46 µm long, almost reaching proximal margin of the last segment. Terminal aesthetasc measuring 147 µm long.

Maxilla (Fig. 4d) with unarmed syncoxa, 179 µm long, narrower than the female; and strong basis (grasping claw) 208 µm long, armed with small stout seta on medio-distal margin.

First leg of the male (Fig. 4e) shares the uncommon reduced morphology of the female. Although the protopod segment is bulkier (65µm long × 49 µm wide), and exhibits a small seta on the distal inner margin in addition to the long seta on the distal outer margin. And finally, the third leg (Fig. 4f) shows small distal seta on the third exopodal segment.

All other features as seen on female.

3.10. Etymology

3.11. Remarks

The only congener of the new species, Artotrogidae gen nov. *pediculus* (Stock, 1966), was described based on a male, and some sexual dimorphic features can only be compared with the male of the new species.

The male body from both species is similar, but Artotrogidae gen nov. *pediculus* differs from Artotrogidae gen et sp nov. in features such as the elongated cephalosome with radial bands, instead of circular-shaped; medio-posterior projection of the third pedigerous somite not reaching the genital somite, instead of not only covering the fifth but also covering the proximal part of the genital somite; and finally, the second post-genital somite exhibiting posteriorly projected epimera, while on the new species it has no projection and is almost entirely covered by the first one (Stock, 1966).

The male antennule of Artotrogidae gen nov. *pediculus* shows an aesthetasc on segment 4, two on segment 5, two on segment 7; and the terminal aesthetasc is 4 times thicker than the others (Stock, 1966). While the new species male antennule exhibits no aesthetasc on segment 4, three on segment 5, none on segment 7; and the terminal aesthetasc is only twice thicker than the others. The male antenna of Artotrogidae gen nov. *pediculus* shows features not seen in the new species, such as the plumose exopodal seta, the row of setules on the first endopodal segment, and the crest-like structures on the inner margin of the first and second endopodal segments (Stock, 1966). Artotrogidae gen et sp nov. exhibits a naked exopodal seta, and unadorned endopodal margins.

The maxillule of *K. pediculus* shows a row of setules on the proximal inner margin, and a minute lateral seta on the distal margin of the inner lobe (Stock, 1966). Both features are not observed in the new species. The maxilla basis (grasping claw) of *K. pediculus* shows 3 spine-like projections and a row of denticles (Stock, 1966), while the new species exhibits only one stout seta.

On the maxilliped Artotrogidae gen nov. *pediculus* shows a plumose basal inner seta on the first segment; two rows of long setules, and a medial serrated spine on the second segment; and endopodal armature formula (2, 1, 1) (Stock, 1966). While the new species shows a naked seta on the first segment, a smooth second segment, and endopodal armature formula (0, 1, 1).

Despite sharing the uncommon morphology of the legs, such as the reduction of the first, and the fusion of the coxa and basis on the third and fourth legs; *K. pediculus* exhibits a few more differences to point out from the new species: on the first leg, the single-segmented ramus shows a row of setules (instead of smooth margins); the armature formula of the third endopodal segment of leg 3 is (1, 2, 3) (instead of (1, 1+I, 3)); and the fifth leg exopod is represented by 3 (instead of 2) terminal setae (Stock, 1966).

4. Discussion

The variation in the armature formula of the legs is a crucial systematic tool to understand the diversity of the associated copepods, from species to ordinal level. Moreover, fusions or loss of ramal segments can be observed in most copepod orders, when one, both rami, or the entire leg is absent (Huys and Boxshall, 1991). According to Huys and Boxshall (1991), many harpacticoid species exhibit a reduced first leg adapted to function as a raptorial limb.

Ferrari (1998) studied the third thoracopod developmental patterns of *Dioithona oculate* (Farran, 1913). Five developmental stages corresponding to copepodid I to V were described. In the first stage, the leg exhibited a bilobed bud with 3 and 2 setae, presumably indicating the initial formation of the exopod and endopod respectively. In the second stage, the segment bearing the setae is transformed on a biramous limb. And posteriorly, in the next stages, new segments are added proximally on the distal segment forming the 3-segmented biramous leg (Ferrari, 1998). The leg 1 of Artotrogidae gen. et sp. nov. morphology suggests that the development of the limb stopped in the first stage, not undergoing the transformation expected to appear on copepodid II.

On a study about copepods from hydrothermal ecosystems, Heptner and Ivanenko (2002) made a functional analysis on the morphology of locomotory limbs; characterizing swimming, crawling, and swimming-crawling types of copepods. Features used on the characterization of crawling copepods are the fused coxa and basis [1] (legs 1, 3, and 4) forming a wide protopod [2] (legs 3 and 4), the way leg branches are positioned folded up [3] to the flattened body [4]. These characteristics are observed on Artotrogidae gen. et sp. nov.. While the presence of intercoxal plates [1] (legs 1, 2, and 3), the articulated and similar-sized coxa and basis (leg 2) [2], and the swimming seta on all legs [3] are features described as found on the swimming type copepods. By exhibiting traits of both types, Artotrogidae gen. et sp. nov. features suggest the intermediate characteristics of the swimming-crawling type of copepods.

Among the siphonostomatoid species, there are some highly modified families in which one or many legs are absent; but only Nanaspididae Humes and Cressey, 1959 (holothurians parasites), Pseudocycnidae Wilson, 1922 (fish parasites), and Stellicomitidae Humes and Cressey, 1958 (starfish parasites) species are recorded to have a reduced biramous and 1-segmented leg 1 (Boxshall and Halsey, 2004). Thus, leg 1 with a single-segmented ramus of Artotrogidae gen. et sp. nov. is so far a unique feature on Siphonostomatoida.

Acknowledgements

AF thanks the LABIMAR members for the logistical support, and for the efforts during sampling and sorting. The authors are grateful to the Chico Mendes Institute for Biodiversity Conservation (ICMbio) for collecting permission (Sisbio No 15161-1).

Funding

This study is part of the project ‘Assessment and research of sun coral in Todos-os-Santos Bay’, a cooperation agreement between UFBA and CENPES/PETROBRAS.

This work was supported by the CENPES/PETROBRAS [under grant number 5850.0107361.18.9].

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Figure Legends

Figure 1. Collection sites: A) Bahia state highlighted on the South America map; B) Pier sites: 1) Barra do Paraguaçu pier, 2) Marina de Itaparica pier, 3) Bom Jesus pier, 4) Estação de Medidas Magnéticas de Itaparica pier, 5) Madre de Deus pier, 6) Bimbarras pier, 7) Terminal dos Passos pier. Natural benthic communities highlighted in green.

Figure 2. Artotrogidae gen et sp nov., Holotype female (UFBA4130): a) Body, dorsal view; b) radial bands and detailed ornamentation of the carapace; c) urosome; d) antennule; e) antenna; f) oral cone and stylet tip; g) maxillule. Scale bars: a – b: 100 µm; c – e: 50 µm; f: 20 µm; g: 50 µm.

Figure 3. Artotrogidae gen et sp nov., Holotype female (UFBA4130): a) maxilla; b) maxilliped; c) leg 1; d) leg 2; e) leg 3; f) leg 4; g) leg 5. Scale bars: a – f: 50 µm; g: 20 µm.

Figure 4. Artotrogidae gen et sp nov., Allotype male (UFBA4133): a) body, dorsal view; b) urosome; c) antennule; d) maxilla; e) leg 1; f) third exopodal segment of leg 3. Scale bars: a: 100 µm; b – e: 50 µm.

Figure 5. Confocal Laser Microscopy. Artotrogidae gen et sp nov., Paratype female (UFBA4132) a) body, dorsal view; b) body, ventral view; c) dissected leg 1 morphology in detail. Scale bars: a – b: 100 µm; c: 50 µm.

Table Legends

Table 1. Detailed confocal laser scanning microscopy (CLSM) acquisition settings.

Figures

Figure 1

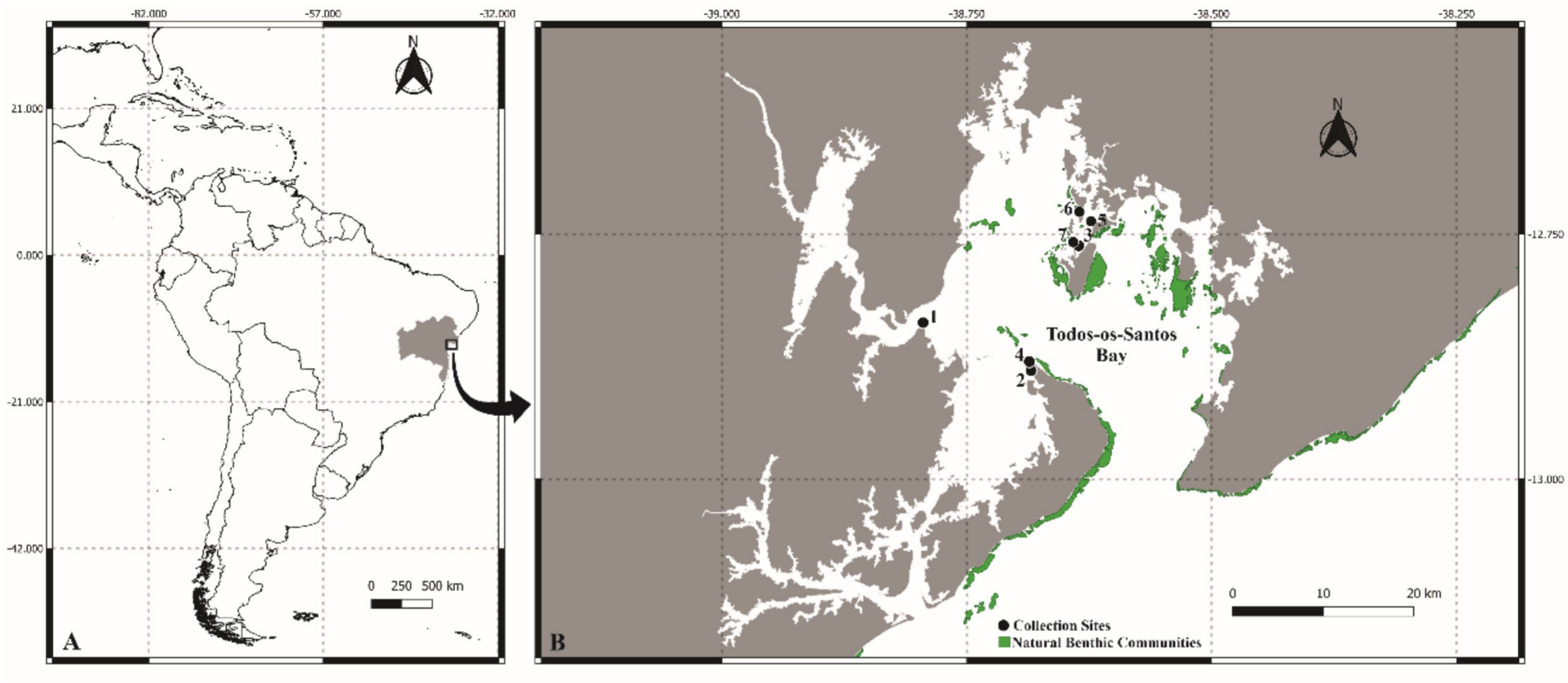


Figure 2.

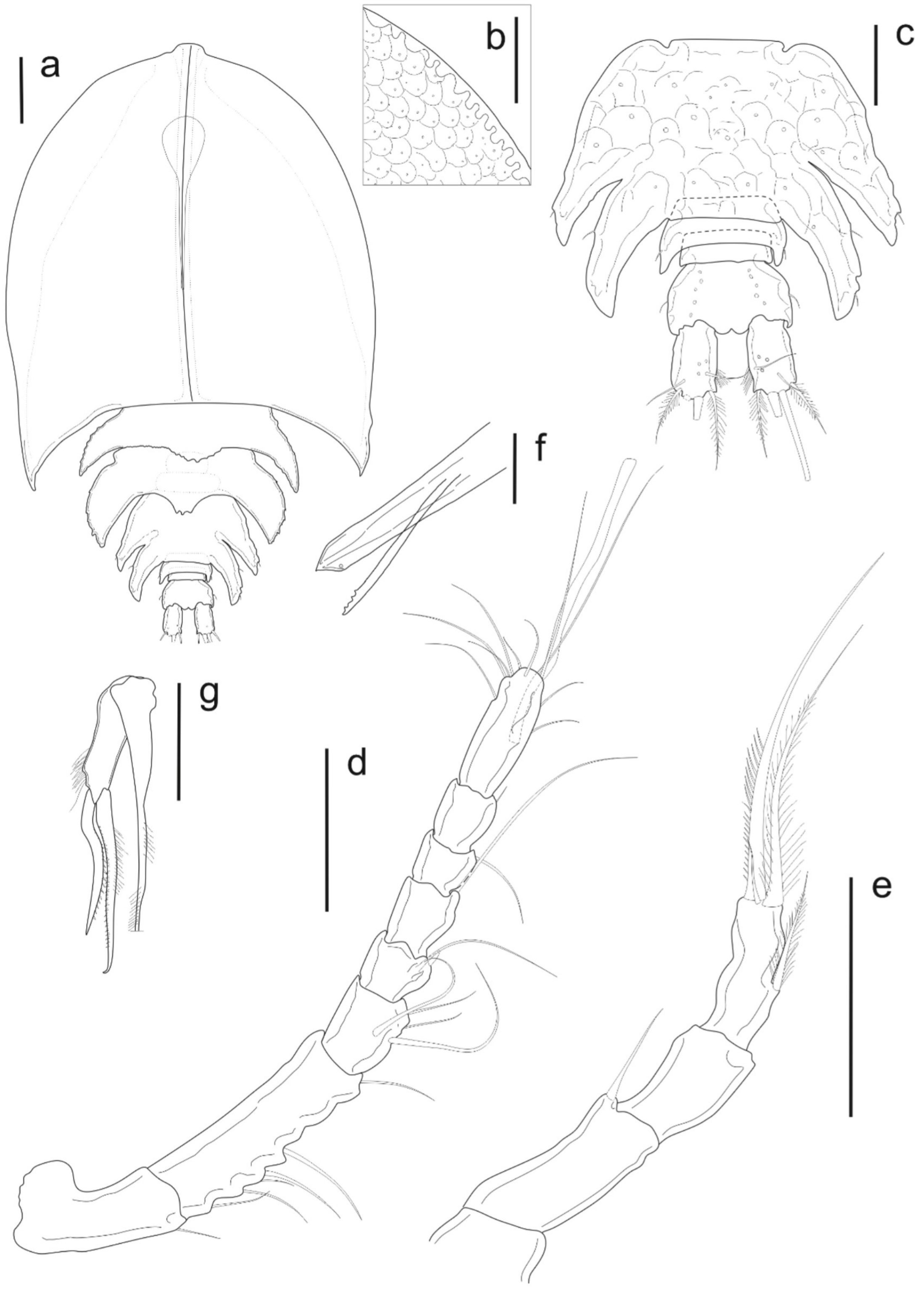


Figure 3

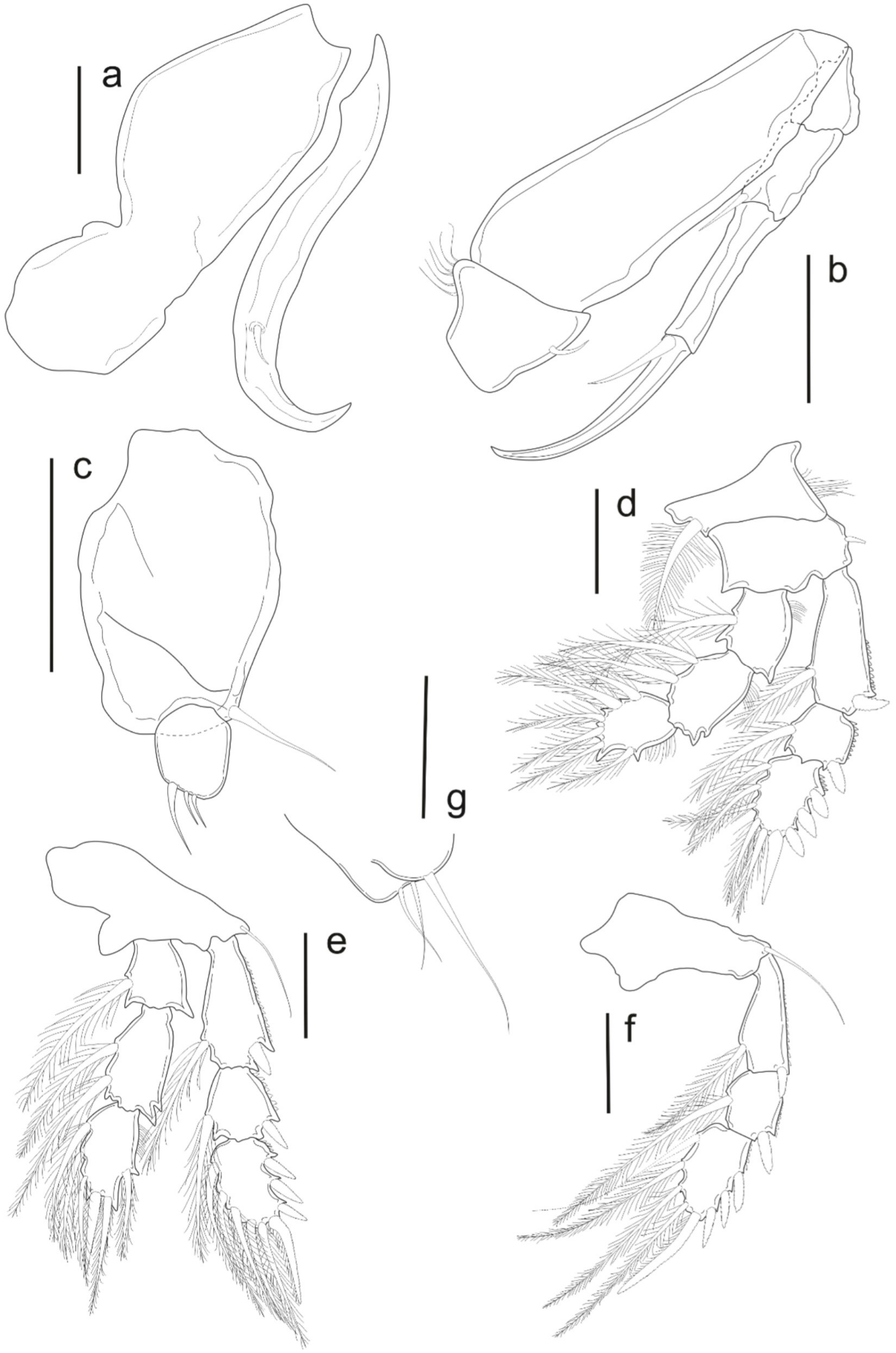


Figure 4

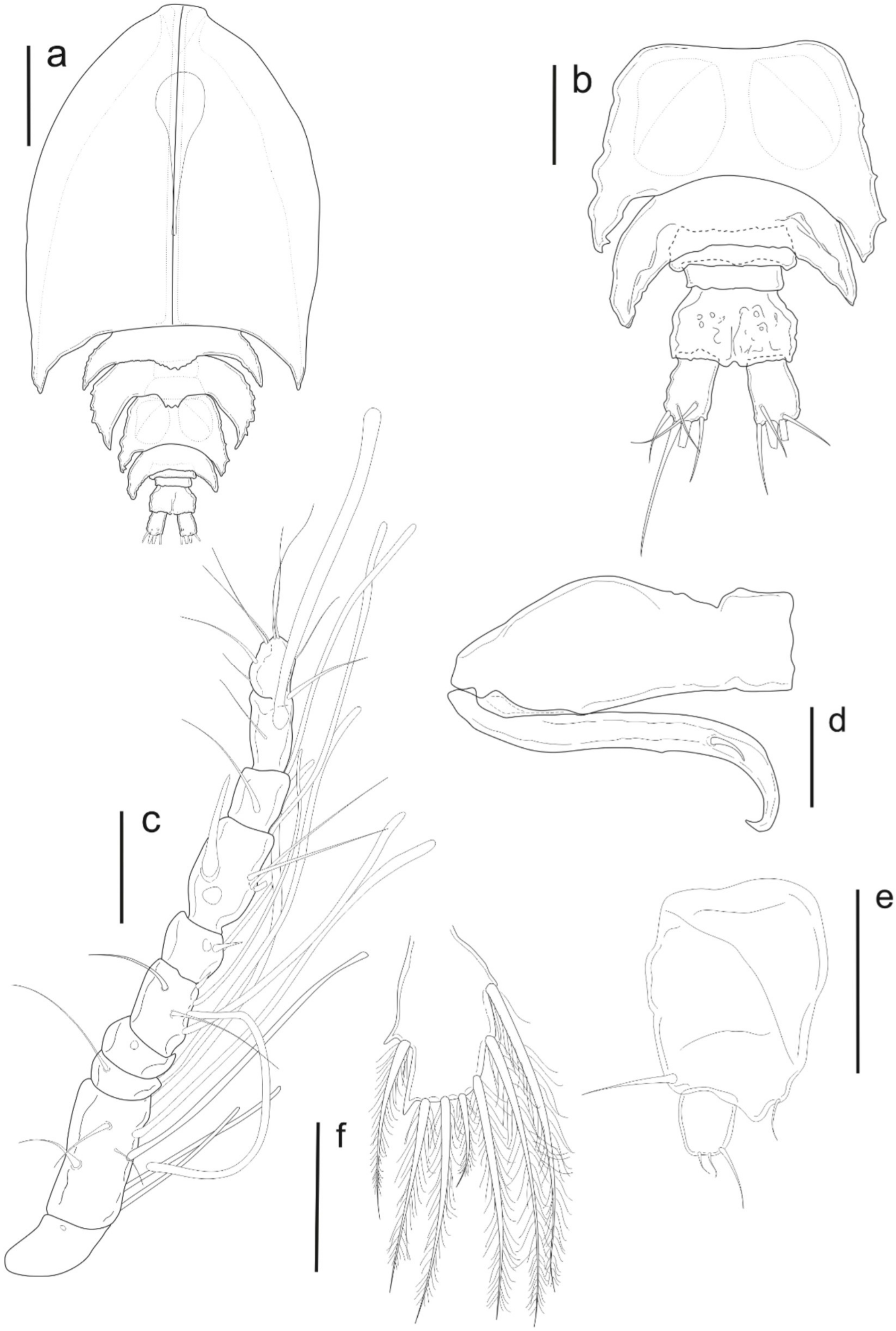
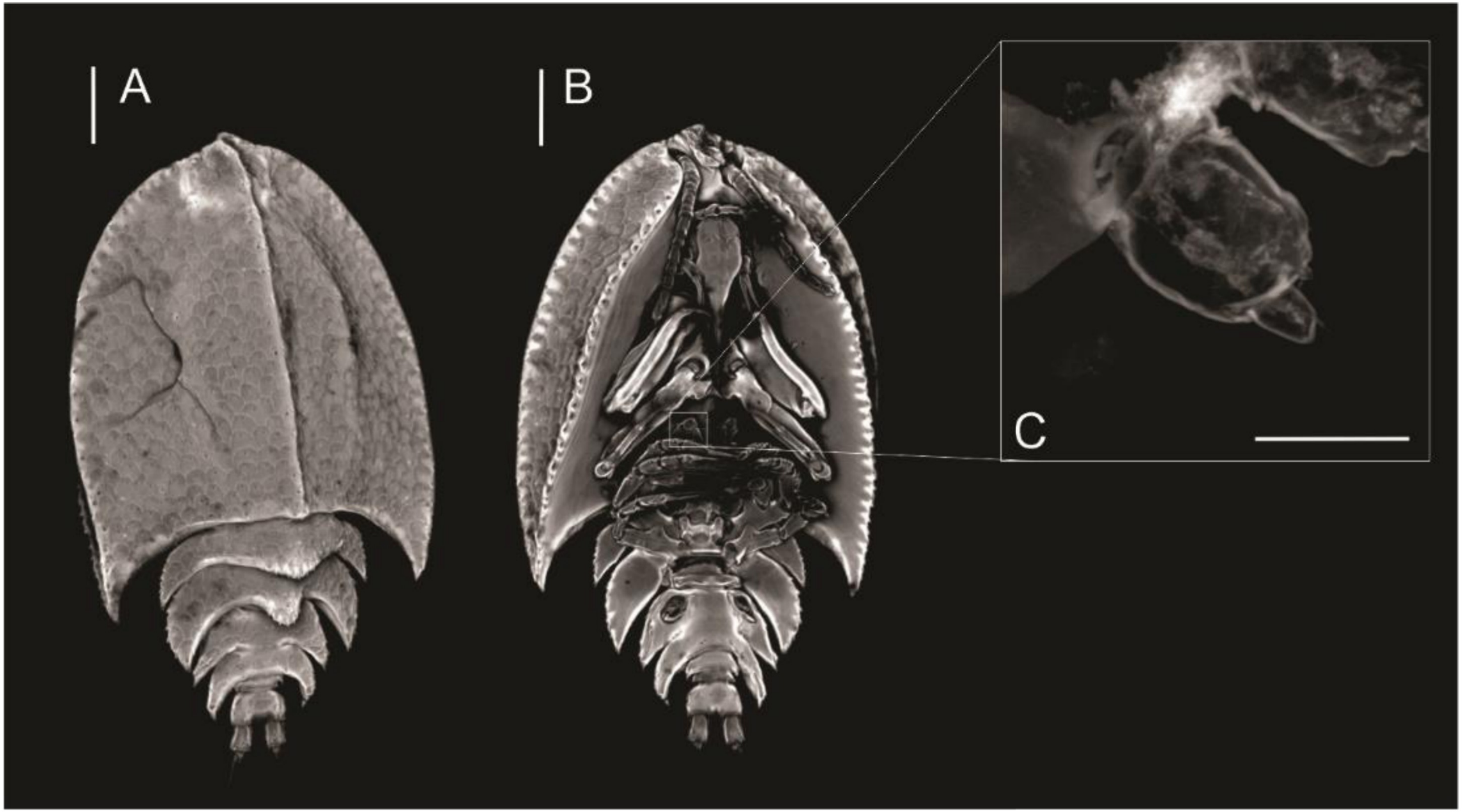


Figure 5



Tables

Figure	Objective	Pinhole	Laser Wavelength	Detection Wavelength	Detector Gain
Figure 5A	Plan-Apochromat 10x/0.45 M27	1.00 AU / 25 µm	561 nm / 1.00 %	568 - 621 nm	600 V
Figure 5B	Plan-Apochromat 10x/0.45 M27	1.00 AU / 25 µm	561 nm / 1.80 %	568 - 621 nm	605 V
Figure 5C	LD Plan-Neofluar 40x/0.6 Korr M27	1.00 AU / 74 µm	561 nm / 55 %	568 - 621 nm	750 V

Capítulo 2 – A new species of *Bradypontius* Giesbrecht, 1895 (Copepoda: Siphonostomatoida) with redescriptions and revised diagnosis of eleven centenary Artotrogidae genera

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Artigo a ser submetido para publicação no periódico Zootaxa

A new species of *Bradypontius* Giesbrecht, 1895 (Copepoda: Siphonostomatoida) with redescriptions and revised diagnosis of eleven centenary Artotrogidae genera

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RUNNING HEAD: New species, redescriptions, and revised diagnosis of Artotrogidae genera

Abstract

This study aims to describe a new species of *Bradypontius* found in a rhodolite bank in Fernando de Noronha Archipelago, to redescribe two species, and review the diagnostic characters from 11 centenary genera. Therefore, enabling a better understanding of the genera limits and establishing a comprehensive diagnosis. The new species differs from its congeners by a unique set of characteristics on antennule segmentation, maxillule, maxilliped, legs 4, 5, and 6 armature formula. A significant part of Artotrogidae valid genera was discovered about a century ago with poorly detailed comparative descriptions. Based on the review of the historical knowledge plus the additional information brought with recently described species, *Artotrogus sarsi* and *Dyspontius striatus* are redescribed and the diagnoses of *Arctopontius*, *Artotrogus*, *Bradypontius*, *Cribropontius*, *Cryptopontius*, *Dyspontius*, *Myzopontius*, *Neopontius*, *Pteropontius*, *Sestropontius* and *Metapontius* are revised.

Key words: symbiotic copepods, marine invertebrate associates, taxonomy

Introduction

Artotrogidae is a diverse family of siphonostomatoid copepods with a cosmopolitan distribution (Boxshall & Halsey, 2004; Johnsson & Neves, 2005; Kim I.H., 2007; Neves & Johnsson, 2008; Varela, 2012; Conradi, 2014; Kim I.H., 2016; Ivanenko *et al*., 2018; Farias *et al*., 2020; Lee & Kim I.H., 2023). They are commonly registered on washings of mixed invertebrate samples, and some are found in association with a wide variety of marine invertebrates such as sponges, cnidarians, bryozoan and ascidian hosts (Boxshall & Halsey, 2004; Farias *et al*., 2020; Lee & Kim I.H., 2023). The family has 24 genera with 122 valid species, with *Artotrogus* Boeck, 1859, *Bradypontius* Giesbrecht, 1895 and *Cryptopontius* Giesbrecht, 1899 as the most specious genera, with 65 species, more than 50% of the species of the family (WoRMS, 2024).

About half of the known family genera were described between the half of the nineteenth and the beginning of the twentieth century (WoRMS, 2024), a period described by Damkaer (2002) as the "*golden age of copepodology*". The earliest discovered species of the family had poorly detailed descriptions, limited by their time, not exhibiting distinct diagnoses to respective genus and species levels (Thorell, 1859; Boeck, 1859, Brady & Roberston, 1876; Brady, 1880; Scott, T., 1898). Giesbrecht (1895; 1899) and Sars G.O. (1918) published pioneer studies with distinct characterization for both levels, but they also presented many appendages poorly described comparatively with previously mentioned taxa. With the knowledge provided by the recently discovered and redescribed species, this study proposes the revised diagnosis of eleven century-old Artotrogidae genera to better establish their limits. It also brings the description of a new species of *Bradypontius*, and the redescription of two of these earliest species.

Material and Methods

The holotype and paratypes of the new species were dissected directly CMC-9 mounting media, for the appendages analysis (Kihara & Rocha, 2009). The Illustrations were vectorized with CorelDRAW 2021 software (version 23.1.0.389). Specimens were analyzed on temporary slides, immersed in glycerin and mounted with adhesive plastic rings to avoid crushing (Kihara & Rocha, 2009). Specimens examination, measurements, drawings and photos were made on Zeiss Axio Lab.A1 microscope equipped with a digital camera AxioCam ERc 5S connected to an iPad (7^{th} generation) with Zeiss Labscope Software (version 4.0.2). Specimens of the redescribed species *Artotrogus sarsi* and *Dyspontius striatus* were lent by the Natural History Museum (University of Oslo). Species which the type series were not found, declared lost or not loaned were examined with an extensive throughout analysis of the bibliography. The distribution is discussed based on the marine bioregionalization of the world proposed by Spalding *et al*. (2007).

For legs armature formula, Arabic numerals represent setae and Roman numerals represent spines (Huys & Boxshall, 1991). For antennule armature formula, Roman numerals represent hypothetical ancestral segments (Huys & Boxshall, 1991).

Results

Bradypontius Giesbrecht, 1895

Amended diagnosis of *Bradypontius* Giesbrecht, 1895: Artotrogidae. Body cyclopiform. Cephalosome expanded. Cephalosome and pedigerous somites with significantly projected epimera. Genital somite widened. Antennule 8 to 13-segmented on females, 9 to 12-segmented on males. Antenna 4-segmented, 2-segmented endopod, and 1-segmented exopod. Oral cone long, tapered distally. Maxilliped 4 or 5-segmented plus claw. Maxilla robust, with recurved claw. Maxillule lobes unequal sized. Legs 1 to 4 biramous and 3-segmented. Leg 4 with endopod slender and reduced setation. Leg 5 reduced to a small exopod.

Type species: *Bradypontius magniceps* Giesbrecht, 1895
Not *Artotrogus orbicularis* Brady & Robertson, 1876 p.197
Not *Artotrogus magniceps* Brady, 1880. Vol.3. p.61 – 63. P. XCIII. Fig. 1 – 9.
Bradypontius magniceps Giesbrecht, 1895. p.182 – 183.
Bradypontius magniceps Giesbrecht, 1899. P.27 – 29, 41 – 44,107 – 108, 213. Taefel 6. Figs. 41 – 44.
Bradypontius magniceps Scott, 1901. p.473
Bradypontius magniceps Sars G.O., 1918. p.124 – 126. Pl. LXXIII
Bradypontius magniceps Wilson, 1936. p.374.
Bradypontius magniceps Shih *et al*, 1971. p.214.
Bradypontius magniceps Gotto, 1993. p.175. Fig. 43 A – D.

Other species:

Bradypontius ancistronus Neves & Johnsson, 2008
Bradypontius caudatus Sars G.O., 1915
Bradypontius crassisetus Kim I.H., 1996
Bradypontius cubensis Varela, 2012
Bradypontius culicis Lee & Kim I.H., 2023
Bradypontius dentatus Hansen, 1923

Bradypontius groenlandicus Hansen, 1923

Bradypontius halocynthiae Kim I.H., 1996

Bradypontius heteroporus Kim I.H., 1996

Bradypontius inermis Nicholls, 1944

Bradypontius macginitei Eiselt, 1986

Bradypontius major Sars G.O., 1915

Bradypontius ovatus Nicholls, 1944

Bradypontius papillatus (Scott T., 1888)

Bradypontius pichoni Stock, 1966

Bradypontius poorei Johnsson, 2002

Bradypontius serratipes Nicholls, 1944

Bradypontius serrulatus Brady, 1910

Bradypontius siphonatus Giesbrecht, 1895

Bradypontius tenuipes Hansen, 1923

Bradypontius typicus (Brady, 1910)

Bradypontius unidens Hansen, 1923

Remarks: The first species of the genus was initially identified by Brady & Robertson (1876) as *Artotrogus orbicularis* Boeck, 1859 and was collected at "*Robin Hood's Bay*", eastern coast of the United Kingdom. It was posteriorly described as *Artotrogus magniceps*, a new species by Brady (1880). Later, Giesbrecht (1895) erected the genus *Bradypontius* to accommodate this species as *Bradypontius magniceps* (Brady, 1880). There was no type series deposit information in any of the previously cited studies. However, the are some specimens at the Natural History Museum (UK) identified as *Artotrogus magniceps*, former name of the species, collected at *"Yorkshire; 1.1/2 miles off Scarborough"* about 22 km from where it was originally found.

As in *Artotrogus*, this genus also was the target of many discussions, and its latest diagnosis was made by Sars G.O. (1918). Sars poorly described some characteristics of the genus, once many statements were made in comparison with previously described species with statements such as: "*somewhat more produced tail*"; "*antennule more or less slender*"; "*antenna of the usual structure*"; and "*maxilliped comparatively slender*" (Sars G.O., 1918, p. 124). Those features are now understood as stated in the amended diagnosis (Sars G.O., 1918, Pl. LXXIII).

Most of *Bradypontius'* records are concentrated in the Temperate Northern Atlantic Realm (Brady, 1880; Scott T., 1888; Giesbrecht, 1895; 1899; Sars G.O., 1918; Hansen, 1923); but the records on the Arctic (Hansen, 1923; Eiselt, 1986), Southern Ocean (Brady, 1910; Johnsson & Rocha, 2002), Tropical Atlantic (Neves & Johnsson, 2008; Varela, 2012), Western Indo-Pacific (Stock, 1966), Temperate Australasia (Nicholls, 1944), and Temperate Northern Pacific (Kim I.H., 1996; Lee & Kim I.H., 2023) contribute to the understanding of its cosmopolitan distribution (Fig. 1I). Bryozoans (10%) are the most common hosts registered for *Bradypontius* species, followed by algae (4%), ascidians (4%), cnidarians (3%) and, sponges (3%). Although, more than three-quarters of the species had no identified invertebrate hosts (76%). (Fig. 1I).

Description of *Bradypontius* sp nov. 1

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(Figs. 2 – 5)

Material examined. Holotype female (UFBA2201), preserved in ethanol. Paratype female (UFBA2202) dissected and mounted on permanent slide; paratype female (UFBA4135) dyed in Congo Red and Acid Fuchsin (1:1 solution), preserved in ethanol; paratype female (UFBA4136) dissected and mounted on permanent slide. All specimens were found associated with rhodoliths collected at Ressureta diving point, located in the channel between the islands Ilha do Meio and Ilha Rata, at Fernando de Noronha archipelago (3º49'51''S, 32º23'34''W) on October 22th, 2014 at 12-13m (Fig. 2).

Female. Body dorso-ventrally flattened (Fig. 4A). Total body length 1064 µm long (excluding caudal rami setae); major body width 677 µm wide. Prosome laterally expanded on posterior margins, exhibiting numerous perforations (Fig. 3A–B). First pedigerous somite fused to the cephalosome. Cephalosome with slightly projected round epimera. Second pedigerous somite 438 µm wide, with considerably projected pointed epimera; length of the projection exceeding length of the somite measured along midline. Third pedigerous somite 362 µm wide, slightly narrower than the second, with substantially wide projected epimera; tip of the projected epimera reaching beyond midlength of the genital double-somite. Fourth pedigerous somite 182 µm wide, almost half the width of the third pedigerous somite, substantially shorter than the others, with considerably projected epimera, reaching beyond the posterior margin of the fifth pedigerous somite. Body length:width ratio = 1.6:1. Prosome length:width ratio = 1.2:1.

Urosome (Fig. 4B) slightly longer than wide (242 × 206 µm), length:width ratio = 1.2:1. Fifth pedigerous somite wider than long (41 × 153 µm), with sightly laterally projected epimera. Genital double-somite wider than long (91 × 206 µm), length:width ratio = 0.4:1. Lateral medial margins moderately projected, with long seta near genital aperture. First post-genital somite wider than long (25 × 113 µm), with pointed epimera. Second post-genital somite wider than long (30 × 96 µm) with sightly pointed epimera. Anal somite wider than long (53 ×90 µm), length:width ratio = 0.6:1. Caudal rami almost as long as wide (41 × 39 µm).

Antennule (Fig. 4C) 10-segmented, total length measuring 273 µm long. Length of the segments measured along posterior margin = 31, 18, 534, 15, 31, 17, 31, 26, and 50 µm long, respectively. Segmental homologies and armature as follow: I - 1, II - 2, III–VII - 10, VIII - 2, IX–XII - 6, XIII–XIV - 1 +spine, XV–XVI – 3, XVII – XVIII - 2, XIX–XX – 2, XXI–XVIII – 11+ae. All setae unadorned, a distal long seta almost as long as the aesthetasc on the terminal segment. Aesthetasc on last segment, measuring 134 µm long.

Antenna (Fig. 4D) 145 µm long (not including distal setae). Coxa and basis unarmed, 25 and 41 µm long, respectively. Exopod 1.7x longer than wide, armed with 2 distal setae, inner one 3.8x longer than outer one. Endopod 2-segmented, first segment unarmed; second segment 1,2x times longer than the first one, armed medially with plumose seta, and distally with 3 setae. The first seta short, the second one stout, plumose with half the length of the third seta, which is stout and significantly long.

Oral cone (Fig. 4A) 992 µm long, reaching anal somite. Mandible (Fig. 5A) with long stylet showing 8 projected teeth-like structures at the tip, palp absent. Maxillule (Fig. 4E) bilobed. Inner lobe shows long setules along the inner margin, armed with long delicate seta. Outer lobe shows long setules along the outer margin, and armed with 2 distal setae, a long one, and the other seta with half the length of the former one, both sightly ornamented with small setules. Inner lobe twice longer than outer lobe.

Maxilla (Fig. 5B) with thin basis (claw) 1.6x longer than syncoxa, 407 and 260 µm, respectively. Claw showing two small teeth-like setae on the medio-distal margin. Maxilliped (Fig. 5C) 5-segmented plus terminal claw (67, 248, 64, 24, 61 and 156 µm long, respectively). Syncoxa armed with small strong seta on the inner margin, ornamented with long setules on the outer margin. Long basis with an inner medial unarmed strong seta. Endopod 3-segmented, first segment unarmed, second and third segment armed with distal seta. Long terminal claw recurved distally.

Legs 1 to 4 (Figs. 5D – G) biramous, 3-segmented. Armature formula as follows:

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

The endopodal rami of legs 1 to 4 are longer than the exopodal rami. The third spine of the third exopodal segments of legs 1 and 4 are more robust than the others. Legs 1 to 3 showing two plumose distal spines on distal margin of the third endopodal segment, outer spine exhibiting about half the size of the inner one. Legs 2 to 4 showing a strong distal spine on third exopodal segment, displaying serrated outer margin and plumose inner margin.

Leg 1 to 3 with second exopodal, first, and second endopodal segments showing projected teeth-like structures on both inner and outer distal margins. Coxa, basis, and all segments of both rami of leg 1 exhibiting smooth margins. All leg 1 setae are thinner than the setae from the other legs. Leg 2 exhibiting long and robust inner seta on inner margin of the coxa. Inner coxal seta of leg 3 plumose. First and second endopodal segments of leg 4 unarmed, third segment exhibiting two small distal setae.

Leg 5 (Fig 5H) with protopod fused to the fifth pedigerous somite, represented by a seta. Free segment of the fifth leg wider than long (101 x 14 µm) and showing 2 strong setae. Leg 6 (Fig. 4B) represented by long lateral seta next to the genital apertures.

Male. Unknown.

Etymology:

Remarks. The genus *Bradypontius* has 22 valid species (WoRMS, 2024), and these species exhibit different fusions patterns on the antennular segmentation proximal to ancestral segments (IX-XII). *Bradypontius* sp nov. 1 exhibits the (III-VII) pattern, and it is shared with four other congeners: *Bradypontius siphonatus* Giesbrecht, 1897;

Bradypontius groelandicus Hansen, 1923; *Bradypontius macginitiei* Eiselt, 1986 and *Bradypontius halocynthiae* Kim I.H., 1996 (Table 2) (Giesbrecht, 1897; Hansen, 1923; Eiselt, 1986; Kim I.H., 1996).

Bradypontius sp nov. 1 differs from *Bradypontius groelandicus*, *Bradypontius halocynthiae*, and *Bradypontius macginitiei*, among other characteristics, by exhibiting the first two endopodal segments of leg 4 unarmed; maxillary claw armed with 3 distal setae; and oral cone reaching the anal somite.

Bradypontius siphonatus can be distinguished from *Bradypontius* sp. nov. 1 by showing the oral cone reaching leg 2, maxillule inner lobe with 2 setae, maxilliped formula (1, 0, 2, 1, 1+claw), leg 5 armed with 3 setae, and leg 6 represented by 3 setae (Giesbrecht, 1897).; rather than oral cone reaching the anal somite, maxillule inner lobe with 1 seta, maxilliped formula (1, 1, 0, 1, 1+claw), leg 5 armed with 2 setae, and leg 6 represented by 1 seta as seen in the new species

***Artotrogus* Boeck, 1859**

Amended diagnosis of *Artotrogus* Boeck, 1859: Artotrogidae. Body greatly expanded, round shield-form, cephalosome, and pedigerous somites showing projected epimera imbricated. The last two pedigerous somites almost completely hidden, not showing projections. Urosome short. Female genital somite showing lamellar projections expanded posteriorly. Caudal rami short. Antennule 8 to 11-segmented, with aesthetasc on the terminal segment. Antenna 4-segmented, 1-segmented exopod, 2-segmented endopod armed with well-developed distal seta. Oral cone well developed, with a robust proximal margin, and distal margin tapered. Maxillule with unequal-sized lobes. Maxilla short, strongly built. Maxilliped short strongly built and 4-segmented. Legs 1 to 3 biramous and 3-segmented. Leg 4 absent. Leg 5 without free segment, represented by seta.

Type species: *Artotrogus orbicularis* Boeck, 1859
Artotrogus orbicularis Boeck, 1859. p. 171 – 184. Pl. I.
Not *Artotrogus orbicularis* Brady & Robertson, 1875. p.197
Artotrogus orbicularis Giesbrecht, 1895. p. 181.

Artotrogus orbicularis Giesbrecht, 1899. p. 93, 111. Tafel 10. Fig. 33 – 35. ok
Artotrogus orbicularis Acloque, 1899. p. 198
Artotrogus orbicularis Scott, T., 1898, p. 272 – 273; Pl. XIV; Figs. 12 – 21.
Artotrogus orbicularis Thompson & Scott, 1903. p. 292
Not *Artotrogus orbicularis* Sars, 1918. p. 133. Pl.78
Artotrogus orbicularis Wilson, 1936 p.374
Artotrogus orbicularis Shih *et al*., 1971. P.213.
? *Artotrogus orbicularis* Eiselt, 1986 p.295 – 300. Abb. 1 – 2
Artotrogus orbicularis McKinnon, 1988 p. 973
Artotrogus orbicularis Gotto, 1993 p.175 Fig. 431I-J ok
Artotrogus orbicularis Kim I.H., 1996 p.399,405,413

Other species:

Artotrogus acutus Kim I.H., 1996
Artotrogus gladiator (Giesbrecht, 1899)
Artotrogus gordoni Kim I.H., 2009
Artotrogus haikungae McKinnon, 1988
Artotrogus halocynthiae Kim I.H., 1996
Artotrogus incidentus Kim I.H., 1996
Artotrogus latifurcatus Nicholls, 1944
Artotrogus muricatus Lee & Kim I.H., 2023
Artotrogus parmatus Lee & Kim I.H., 2023
Artotrogus rotundus Kim I.H., 1996
Artotrogus sardae McKinnon, 1988
Artotrogus sarsi Kim I.H., 1996

Remarks: This genus was erected by Boeck (1859), based on the description of *Artotrogus orbicularis* Boeck, 1859. It was the first Artotrogidae species described (Boeck, 1859). In 1899, Giesbrecht stated that the *Artotrogus* diagnosis was problematic, because Boeck's original description had some very important data missing, and the additional information provided by Brady (1876), Hansen (1886), and Thompson (1893), which described other specimens, were not enough (Boeck, 1859; Brady, 1876; Hansen, 1886; Thompson, 1893; Giesbrecht, 1899). Thus, Giesbrecht chose to restrict *Artotrogus* to *A.*

orbicularis and created the genus *Bradypontius* to the other species. It was only in 1918, that Sars G.O. redescribed in detail *A. orbicularis* providing a distinct diagnosis to the genus and species (Giesbrecht, 1899). In 1944, Nicholls (1944) provided a discussion about *Artotrogus* and concluded that only *A. orbicularis* and *A. latifurcatus* were valid species. Eiselt (1986) also redescribed *A. orbicularis* based on specimens from Alaska. A decade later, Il-Hoi Kim (1996), made a new discussion about the genus and proposed: *A. orbicularis* sensu Boeck, 1859 and sensu Giesbrecht, 1899; *A. latifurcatus* Nicholls, 1944; *A. haikungae* McKinnon, 1988 and *A. sardae* McKinnon, 1988 were valid species and also proposed "*nomen novum*" to *A. orbicularis* sensu Sars G.O., 1918 as *A. sarsi* Kim I.H., 1996. It was not possible to find information about the deposit of the original *A. orbicularis* sensu Boeck, 1859 specimen.

The century-old diagnosis of Sars, stated when only one species was known to the genus, remains as the latest formally published. Sars diagnosis doesn't properly describe antennule and antenna morphology, simply stated as comparatively smaller than previously described taxa; which also happens to the description of the maxilla and maxilliped, stated only as powerfully developed. The genus, now, has 11 valid species, and with the knowledge provided by this new species, it is possible to determine: Antennule varying from 8 to 11 segments, most of the species have 8 or 9 segments, while the only species showing 11-segmented antennule is *Artotrogus latifurcatus* Nicholls, 1944. The antenna is 4-segmented; exhibiting a 1-segmented exopod, and 2-segmented endopod armed with well-developed distal seta; the maxilla is short, strongly built, just like the maxillipeds which also exhibits 4 segments plus claw (Giesbrecht, 1899; Sars G.O., 1918; Nicholls, 1944; Eiselt, 1986; McKinnon, 1988; Kim I.H., 1996).

Artotrogus' distribution (Fig. 1II) is mostly recorded for the Temperate Northern Pacific (Kim I.H., 1996; Lee & Kim I.H., 2023), but there are records from the Arctic (Eiselt, 1986); Temperate Northern Atlantic (Boeck, 1859; Giesbrecht, 1899; Sars G.O, 1918) and, Temperate Australasia Realms (Nicholls, 1944; McKinnon, 1988; Kim I.H., 2009).

As *Bradypontius*, bryozoans are the most common registered hosts (20%) (Kim I.H., 1996; Kim I.H., 2009), but there are records of association with algae (14%) (Lee & Kim I.H., 2023), ascidians (13%) (Kim I.H., 1996) and, mollusks (13%) (Boeck, 1859; Sars G.O, 1918). Almost half of the recorded species had no invertebrate identified hosts (Giesbrecht, 1899; Nicholls, 1944; Eiselt, 1986; McKinnon, 1988) (Fig. 1II).

Redescription of *Artotrogus sarsi* Kim I.H., 1996

(Figs. 6–8)

Material examined: 1 female (F21596), collected by G.O. Sars on the Norwegian coast; 1 female (F21597) collected by M. Sars in Manger (Norwegian west coast); both without sampling dates, lent by Natural History Museum (University of Oslo).

Female. Body (Fig. 6A) flattened disk form. Total body length 3139 µm (excluding caudal setae); major body width 2972 µm. Prosome with laterally and posteriorly expanded pedigerous somites. First, pedigerous somite fused to the cephalosome. The second and third pedigerous somites are similar in length, with rounded epimera. Third pedigerous somite covers the fourth and fifth pedigerous somites, partially covering the genital somite. Length:width ratio = 1.1:1. Prosome length:width ratio = 0.1:1. Prosome: Urosome length ratio 5.7:1.

Double genital somite (Fig. 6B) 1.6x wider than long, anterolaterally rounded, with posterior margin projected, reaching the second post-genital somite; mid-ventral region showing sensilla. Post-genital somites 3.2, 4.8, and 1.4x wider than long, respectively. First post-genital anal somites with 2 ventral sensilla each. Anal plate absent. Caudal rami 1.2x longer than wide; setae I absent, setae II to VII with the following proportion 1.0, 1.1, 5.7, 8.3, 1.1, 1.2. All plumose.

Antennule (Fig. 6C) measuring 975 µm long, not including setae, 9-segmented. Basal portion with 4 segments, relatively wide; distal portion with 5 segments slightly narrower than proximal region. Measures of segments along the posterior margin: 8.2, 2.1, 5.7, 2.0, 1.1, 2.6, 1.0, 1.5, and 3.3 respectively. Segmental homologies and armature formula as follows: I-1; II-2; III-VIII-12; IX-XIII-7; XIV-1+spine; XV-XVI-2; XVII-XVIII-2; XIX-XX-2; XXI-XXVIII-9+ae. Aesthetasc on the terminal segment measuring 264 µm.

Antenna (Fig. 6D) with 567 µm (including claw). Coxa and basis without setae. Exopod twice longer than wide, with distal seta. Endopod 2-segmented, 1.0 and 1.6 µm, first segment without seta but with distal margin covered with setules; second segment with medial plumose seta and two distal setae, the longer one unadorned and not modified as a claw.

Oral cone (Fig. 6A) measuring 917 µm long, 0.3x the length of the body, wedge-shaped, reaching the insertion between maxilla and maxilliped. Mandible (Fig. 6E) comprising only stylet with distal margin serrated, palp absent. Maxillule (Fig. 7A) bilobed, both lobes with two distal setae. Inner lobe 1.7x longer than the outer lobe, possessing plumose seta, and inner margin ornamented with long setules along the distal margin; outer lobe with both plumose setae.

Maxilla (Fig. 7B) with claw 1.2x longer than the syncoxa and recurved on the distal margin. Maxilliped (Fig. 7C) 4-segmented and distal claw. Length of segments and claw 2.0, 4.5, 1.0, 1.3, and 3.0 µm long respectively. Syncoxa with small seta; basis with minute seta on medial inner margin. Endopod 2-segmented, both segments showing seta on distal inner margin. The terminal claw distally recurved with row of setules on the medial margin.

Legs 1 to 3 (Fig. 7D and 8A–B) biramous, 3-segmented. Leg 4 absent. Armature formula of legs 1 to 3 is as follows:

	Coxa	**Base**	**Exopod**	**Endopod**
Leg 1	0-1	1-1	I-1; I-1; III, 2, 3	0-1; 0-2;1, 2, 3
Leg 2	0-1	1-0	I-1; I-1; III, I, 5	0-1; 0-2;1, 1, 3
Leg 3	0-1	1-0	I-1; I-1; III, I, 5	0-1; 0-2;1, 1+I, 3
Leg 4	absent			

Leg 5 (Fig. 8C) reduced to free segment with 2 distal setae.

Male. Unknown

Remarks: In his redescription, Sars G.O. (1918) mentioned the presence of small distal seta on the terminal endopodal segment of the antenna; two small setae on the maxilla, one in the syncoxa and the other in the medial margin of the claw. Those setae were not observed in the material examined. In the medial margin of the basis of the maxilliped was observed a seta not described by Sars.

Such combination of characteristics is not observed in any other *Artotrogus* species (Boeck, 1859; Giesbrecht, 1899; Sars G.O., 1918; Nicholls, 1944; McKinnon, 1988; Kim I.H., 1996; 2009; Lee & Kim I.H., 2023), and should not invalidate *A. sarsi*. The absence of seta on the syncoxa and medial margin of the maxillary claw is also observed on *A. orbicularis*, but it differs from the redescribed species by showing three distal setae on the terminal segment of the antenna (Boeck, 1859; Giesbrecht, 1899). Two long distal setae on the terminal segment of the antenna observed on this redescription of *A. sarsi* is a unique feature between *Artotrogus* species (Boeck, 1859; Giesbrecht, 1899; Sars G.O., 1918; Nicholls, 1944; McKinnon, 1988; Kim I.H., 1996; 2009; Lee & Kim I.H., 2023). *Artotrogus sarsi* also differs from *A. orbicularis* by the morphology of the genital somite, a feature widely used to differentiate *Artotrogus* species (Kim, 1996; Lee & Kim I.H., 2023). Both species are also distinguishable by the shape of maxilla and maxilliped base, which are slender and stouter, respectively (Boeck, 1859; Giesbrecht, 1899).

***Dyspontius* Thorell, 1859**

Amended diagnosis of *Dyspontius* Thorell, 1859: Artotrogidae. Body cyclopiform. Cephalosome elongated. Second, third, and fourth pedigerous somites with projected epimera. Genital somite considerably expanded. Antenna 9-segmented. Antenna 4-segmented, exopod 1-segmented, endopod 2-segmented. Oral cone is robust, with the basal part slightly dilated. Maxillule unequal sized. Maxilla elongated, with distal claw recurved, as long as the syncoxa. Maxilliped 5-segmented. Leg 1 to 3 biramous and 3-segmented. Third exopodal segment of leg 1 with only 2 outer spines and 4 setae. Leg 4 endopod absent. Leg 5 with a small free segment.

Type species: *Dyspontius striatus* Thorell, 1859
Dyspontius striatus Thorell, 1859; p. 80 – 82; Pl. 14; Fig. 22.
Dyspontius striatus Hesse, 1866; p. 69 – 73.
Dyspontius striatus Brady, 1880; vol. 3; p. 66 – 68; Pl. 92; Figs. 1 – 13.
Dyspontius striatus Giesbrecht, 1895; p. 184.
Dyspontius striatus Giesbrecht, 1899; p. 33 – 36, 109 – 110; Tafel 1, Fig. 10, Tafel 7, Figs. 1 – 11.
Dyspontius striatus Scott, 1906; p.360.
Dyspontius striatus Norman & Brady, 1909 p.150.
Dyspontius striatus Sars G.O., 1918; p. 118 – 120; Pl. LXX.
Dyspontius striatus Wilson, 1936; p. 375.

Dyspontius striatus Shih *et al*., 1971; p. 214.
Dyspontius striatus Gotto, 1993; p. 172.

Other species:

Dyspontius alatus Kim I.H., 2016
Dyspontius curticaudatus Scott T., 1905
Dyspontius fringilla (Giesbrecht, 1895)
Dyspontius gerardius Johnsson, 2001
Dyspontius passer (Giesbrecht, 1897)
Dyspontius tristanensis Wiborg, 1964

Remarks: This genus was erected by Thorell (1859) based on the description of *Dyspontius striatus* Thorell, 1859, it was originally placed under the family Ascomyzontidae. The specimen was found among debris of sessile invertebrates scraped from the surface of a boat. When Sars G.O. (1918) organized the family Dyspontiidae, *D. striatus* was made its type species. It is now considered an Artotrogidae species since the merge of Myzopontiidae and Dyspontiidae made by Eiselt (1961). The type specimens were collected at Christineberg, western coast of Sweden. There was no register of deposits of the type series. The material analyzed by Sars, from Manger, northwest coast of Norway, was borrowed from Natural History Museum (University of Oslo), analyzed, and redescribed.

The latest and more detailed diagnosis of *Dyspontius* was published by Sars G.O. (1918). Besides having some poorly described appendages, it also has a species-level characteristics stated as a generic diagnostic. The maxillule lobes setae number was stated as "*inner one carrying a single apical seta, the outer one 2 such seta*" (Sars G.O., 1918, p. 118); but since the genus now has 7 valid species, it is possible now to understand that such character is variable among species (Giesbrecht, 1895; Giesbrecht, 1897; Scott, 1905, Johnsson, 2001; Kim I.H., 2016).

Dyspontius' distribution (Fig. 1III) is mostly restricted to the Temperate Northern Atlantic (Thorell, 1859; Giesbrecht, 1895; 1897; Scott T., 1905; Sars G.O., 1918; Johnsson, 2001), but there is a record to the Temperate Northern Pacific realm (Kim I.H., 2016). More than half of the invertebrate hosts recorded for *Dyspontius* species (56%) were not identified (Thorell, 1859; Giesbrecht, 1899; Scott T., 1905; Sars G.O., 1918).

Even though, there are records for algae (11%) (Sars G.O., 1918), ascidians (11%) (Sars G.O., 1918), cnidarians (11%) (Johnsson, 2001), and sponge (11%) hosts (Kim I.H., 2016) (Fig. 1III).

Redescription of *Dyspontius striatus* Thorell, 1859

(Figs. 9 – 11)

Material examined: 1 female and 1 male (F20442), collected by M. Sars, at Manger (Northwest Norway coast), no date information, lent by Natural History Museum (University of Oslo).

Female. Body (Fig. 9A) cyclopiform, elongated. Total body length 1522 um (excluding caudal setae); major body width 881um. First pedigerous somite fused to the cephalosome. The second and third somites similar in length, with rounded epimera. The fourth pedigerous somite partially narrower and slightly covered by the previous. Length:width ratio 1.7:1; prosome length:width ratio 1.2:1; prosome: urosome ratio 2.5:1.

Genital double-somite (Fig. 9B) 1.5x wider than long, anterior half expanded, with two setae in the genital area; posteroventral region showing sensilla. First post-genital somite 2.1x wider than long, with two ventral sensilla. The second post-genital somite is 2.1x wider than long. Anal somite 1.6x wider than long, also showing 2 ventral sensilla. Anal plate absent. Caudal rami 1.5x longer than wide, seta I absent, setae II to VII measuring 1.1; 1.5;3.8;4.4;1.7;1. Setae II and VII unadorned, other setae plumose.

Antennule (Fig. 9C) measuring 350 μm long, not including terminal setae, 9-segmented. Segments measured along the outer margin: 4.8; 5.9; 1; 1.8; 1.2; 1.7; 1.4; 2; 4.1, respectively. Segmental homologies and armature as follow: I- 1; II-VII- 9; VIII- 1; IX-XIII-6+spine; XIV- 1+spine; XV-XVI- 2; XVII-XVIII- 2; XIX-XX- 2; XXI-XXVIII-11+ae. Terminal aesthetasc 60 μm long.

Antenna (Fig. 9D) 194 μm long (including claw). Coxa and basis unadorned; exopod 2.5x longer than wide, armed with 2 distal unadorned setae. Endopod 2-segmented, 1 and 1.1 μm long, respectively. First segment unadorned, second one armed with proximal unadorned seta, subdistal short seta, and two spine-like setae close to the claw, claw seta-like, straight, 83 μm long.

Oral cone (Fig. 9A) 679 μm long, about 40% the length of the body, pear-shaped, with posterior tubular projection, reaching intercoxal plate of the leg 1. Mandible (Fig. 9E) comprising stylet 195 μm long, with distal margin extended and serrated; palp absent. Maxillule (Fig. 10A) bilobed, inner lobe 1.1x longer than the outer, possessing 2 long and plumose setae, 1 small and short setae, ornamented by long setules along the inner margin; outer lobe armed with 2 plumose setae. Maxilla (Fig. 10B) with claw 1.9x longer than syncoxa, distal margin recurved and tapered. Maxilliped (Fig. 10C) 6-segmented; 3, 7.5, 1, 2, 1.8, 4,6 μm long, respectively. Syncoxa armed with seta, unadorned basis, endopod 3-segmented, each segment armed with single seta; terminal claw recurved, with inner margin ornamented with setules.

Legs 1 to 3 (Figs. 10D – F) biramous, 3-segmented. Leg 4 (Fig. 11A) uniramous. Armature formula as follows:

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

Leg 5 (Fig. 11B) with protopod fused to fifth pedigerous somite and an outer seta. The free segment with reduced size, as long as wide, with 2 distal unadorned setae.

Male. Body (Figure 11C) cyclopiform and elongated, 1537 μm long (excluding caudal setae); major body width 850 μm long. First pedigerous somite fused to the cephalosome. The second and third pedigerous somites are similar in length, with posteriorly projected epimera. Fourth pedigerous somite narrower than the previous, also with posteriorly projected epimera. Body length:width ratio 1.8:1; prosome length:width ratio 1.3:1. Prosome: urosome ratio: 2.3:1.

Genital somite (Figure 11D) 1.7x wider than long, rounded, with 3 setae (leg 6) on the posterior margin. Four post-genital somites, 3.2, 2.7, 2.5, and 1.4 μm long, respectively, wider than long, with posterior angle slightly narrow and posteriorly projected. Showing sensilla along the ventral margin of the anal somite. Caudal rami 1.3x longer than wide; setae I absent, setae II to VII 1, 1.6, 4.5, 13.8, 2, 1.2 μm long, respectively. Setae II and VII unadorned; other setae plumose.

Antennule (Figure 11E) 368 μm long (excluding setae), 11-segmented. Segmental length measured along the posterior margin: 7, 5, 1, 1, 1, 1, 1, 5, 2, 4, 1. Segmental homologies and armature as follow: I- 2; II-V- 7+4 ae; VI- 2+ae; VII- 1+ae; VIII-2+ae; IX-XIII- 5+2ae; XIV- 1+ae+spine; XV-XVII- 5+3ae; XVIII- 2; XIX-XX- 2; XXI-XXVIII- 7+ae. Aesthetasc on last segment measuring 68 μm long.

Other appendages as observed on the female.

Remarks: The differences found in this redescription show that the maxillule outer and inner lobes exhibit 3 and 2 setae, respectively; instead of 2 and 3, as described initially by Sars (1918, Pl. LXX). In addition, it's possible to observe 4, instead of 3 setae, on the distal margin of the antennal endopod. Besides the number, Sars G.O. (1918) described the endopodal terminal seta as slender, but they were observed as very stout, except for the minute subdistal seta. The setae mentioned by Sars near the articulated claw of the maxilla basis, and on the maxilliped basis were not observed. Finally, the ornamentation of the third exopodal segment of leg 4 has the formula II, I, 5 instead of III, I, 5 as described by Sars.

The distal armature formula of the antennal endopod exhibited a unique setation for the genus, all other *Dyspontius* species show 3 distal setae. Similarly, the observed ornamentation of the third exopodal segment of leg 4 is also not observed in any other *Dyspontius* species. On the other hand, the main characteristics in the diagnosis of the species, like the armature of the third exopodal segment of leg 1 and the absence of the endopod of leg 4, were confirmed. Thus, the validity of the species is not questioned.

Arctopontius **Sars G.O., 1915**

Amended diagnosis of *Arctopontius* Sars G.O., 1915: Artotrogidae. Body cyclopiform, cephalosome, second and third pedigerous somite with projected epimera. Genital somite wide, laterally projected. Antennule 8- or 9-segmented, with aesthetasc on the terminal segment. Antenna 4-segmented, with 1-segmented exopod and 2-segmented endopod. Oral cone long. Maxillule inner lobe longer than outer. Maxilla with a strong syncoxa and recurved claw. Maxilliped 5-segmented. Legs 1 to 3 biramous, 3-segmented. Leg 4 biramous, exopod 3-segmented, endopod 2-segmented. Leg 5 with a small free segment.

Type species: *Arctopontius expansus* Sars G.O., 1915.
Arctopontius expansus Sars G.O., 1918. P. 122 – 123 Pl. LXXII

Other species:
Arctopontius adelphus Kim I.H., 2016
Arctopontius expansus Sars G.O., 1915
Arctopontius hanseni Eiselt, 1986
Arctopontius minutus Kim I.H., 2016
Arctopontius novenarius Johnsson, 2002

Remarks: Genus erected by Georg Ossian Sars (1918) on the description of *Arctopontius expansus* Sars G.O., 1915. Two females were collected at Hammerfest, Norway's northern coast, at the depth of 36 meters. The host was not identified (Sars G.O., 1918). There is no evidence of deposit of the type series. But the webpage of the Natural History Museum (University of Oslo) provided information about deposits of some of the Sars species. According to the collection management, despite containing all data from the other species from the same publication of Sars, the type material of *A. expansus* was not among them. So, it may be considered lost.

The original description of the genus does not describe the antenna, maxilla, maxilliped, and leg 5 properly; they are simply treated as small, normal, or rudimentary, respectively, in comparison to previously described species in the paper. It also describes the third exopod of leg 1 armed with 2 outer spines (Sars G.O., 1918). Posteriorly, 4 new species were described for the genus, providing new evidence to better understand its limits: *Arctopontius hanseni* Eiselt, 1986 was the first species to show a third exopodal segment of leg 1 armed with 3 outer spines (Eiselt, 1986, Abb. 6), a feature later confirmed by *Arctopontius novenarius* Johnsson, 2002, *Arctopontius adelphus* Kim I.H., 2016 and, *Arctopontius minutus* Kim I.H., 2016 (Johnsson & Rocha, 2002; Kim I.H., 2016). Whilst, *A. novenarius* was the only species showing a 9-segmented antennule, instead of 8 (Johnsson & Rocha, 2002, Fig. 7 C); and 5 setae on the second endopodal segment of leg 4, instead of 1; both characteristics are exhibited by the other *Arctopontius* species (Johnsson & Rocha, 2002, Fig. 8 E).

Arctopontius is recorded in the Arctic (Eiselt, 1986), Temperate Northern Atlantic (Sars G.O., 1918), Southern Ocean (Johnsson & Rocha, 2002), Eastern Indo-Pacific (Johnsson & Neves, 2005), and Temperate Northern Pacific (Kim I.H., 2016). Most of its species were recorded as associated with bryozoan hosts (29%) (Johnsson & Rocha, 2002; Kim I.H., 2016), but there are records of cnidarian (14%) (Johnsson & Neves, 2005) and, sponge (14%) hosts (Kim I.H., 2016). Almost half (43%) of its species has no identified invertebrate hosts (Sars G.O., 1918; Eiselt, 1986) (Fig. 12I).

***Cribropontius* Giesbrecht, 1899**

Amended diagnosis of *Cribropontius* Giesbrecht, 1899: Artotrogidae. Body cyclopiform. Cephalosome with bifid projected epimera. Pedigerous somites with very prominent projected epimera, third pedigerous somite epimera projected slightly further than the second. Female genital somite slightly wider than long. Caudal rami long, with short setae. Antennule 9-segmented, robust. Antenna 4-segmented, exopod 1-segmented, endopod 2-segmented. Oral cone rather strong and short. Maxillule lobes unequally sized. Maxilla short and sturdy. Maxilliped 5-segmented, all segments and setae strongly built. Legs 1 to 4 biramous and 3-segmented. Leg 4 inner margin of the third endopodal segment with reduced setation. Leg 5 exopod small, longer than wide.

Type species: *Cribropontius normani* (Brady & Robertson, 1876)
Not Dyspontius normani Brady & Roberston, 1876. p. 197
Not Artotrogus normani Brady, 1880. vol.3. p. 63. Pl. 91. Figs. 12 – 15. Pl. 92. Fig. 14. Pl. 93. Fig. 10.
Not Bradypontius normani Giesbrecht, 1895. p. 183.
Cribropontius normani Giesbrecht, 1899. p. 86 – 88, 107. Tafel 7. Fig. 40 – 47.
Cribropontius normani Sars G.O., 1918. P. 130 – 132. Pl. LXXVII
Cribropontius normani Gotto, 1993. p. 174. Fig. 42 P – S.

Remarks: This species was initially described as *Dyspontius normani* by Brady & Robertson (1876). Posteriorly, according to Sars G.O. (1918), the species was erroneously cited by Brady (1880) as *Artotrogus normani*, despite having a biramous fourth leg. Giesbrecht (1895) erected the genus *Bradypontius*, naming it as *Bradypontius normani*. Soon after, Giesbrecht (1899) erected a new genus, *Cribropontius*, with *Cribropontius normani* (Brady & Robertson, 1875) as type species. Sixteen years later, Sars G.O. (1918), provided a formal distinct diagnosis for the genus and species, redescribing *C. normani*, using specimens that T. Scott sent to him. There was no type series deposit information available from the previously cited studies. The website of the Natural History Museum (UK) indicates the existence of a few specimens identified as *Artotrogus normani, the* former name of the species*,* however, this material was not available for examination. On the opposite, the National Museum of Natural History (USA) lent 256 specimens of *Cribropontius* sp., collected on the Arctic Ocean, and a thorough analysis of these specimens proved it to be *Bradypontius macginitei* Eiselt, 1986 specimens.

The latest and more detailed diagnosis of *Cribropontius* Giesbrecht, 1899 published by Sars G.O. (1918) lacks much information since it was described comparatively to *Bradypontius* Giesbrecht, 1899 and other Dyspontiidae sensu Sars. Its antennule is stated as "*comparatively stout*", its antenna as with "*the terminal joint comparatively short*", and its maxilla and maxilliped as "*very powerfully developed*". The amended diagnosis included the detailed morphology of all previously cited appendages. The diagnosis of Sars also described the legs 1 to 4 of *Cribropontius* "*as described in Bradypontius*" (Sars G.O., 1918, p. 130), now it is understood as having only an inner third endopodal margin with reduced setation, instead of a total setation reduction as seen in *Bradypontius* (Sars G.O., 1918, Pl. LXXVII). *Cribropontius* distribution (Fig. 13C) is restricted to the Temperate Northern Atlantic realm, and no invertebrate hosts were identified on these records (Brady & Robertson, 1876; Sars G.O., 1918).

Cryptopontius Giesbrecht, 1899

Amended diagnosis of *Cryptopontius* Giesbrecht, 1899: Artotrogidae. Body cyclopiform. Cephalosome with slightly projected epimera. Pedigerous somites 2 and 3 with projected epimera slightly recurved backward, almost concealing the somite 4. Urosome short, with long caudal rami seta. Antennule with 8 to 10 segments in females, with aesthetasc on terminal segment; 8 to 12 segments in males with additional aesthetascs. Antenna 4-segmented, exopod 1-segmented, sometimes rudimentary, endopod 2-segmented. Oral cone well developed; basal region robust, distal region very slender. Maxillule with slender lobes unequally sized. Maxilla with narrow and long claw. Maxilliped with 4 or 5 segments, and recurved claw. Legs 1 to 3 biramous and 3-segmented. Leg 1 with 3 spines, 4 or 5 setae on the third exopodal segment. Leg 4 with endopodal ramus absent, or reduced to a knob. Leg 5 represented by a free segment, sometimes rudimentary.

Type species: *Cryptopontius thorelli* (Giesbrecht, 1899)
Dyspontius thorelli Giesbrecht, 1895; p. 185
Cryptopontius thorelli Giesbrecht, 1899; p. 30 – 33, 108 – 109, Tafel 8; Figs. 13 – 26.
Cryptopontius thorelli Stock, 1965; p.315.
Cryptopontius thorelli Gotto, 1993; p. 173; Fig. 42 A – F.

Other species:

Cryptopontius acutus Kim I.H., 2007
Cryptopontius aesthetascus Neves & Johnsson, 2008
Cryptopontius ascidius Kim I.H., 1996
Cryptopontius bilobatus Lee & Kim I.H., 2023
Cryptopontius brevicaudatus (Brady, 1899)
Cryptopontius brevifurcatus (Giesbrecht, 1895)
Cryptopontius capitalis (Giesbrecht, 1895)
Cryptopontius digitatus Kim I.H., 1996
Cryptopontius donghaensis Kim I.H., 1996
Cryptopontius expletus Neves & Johnsson, 2008
Cryptopontius gracilis Wilson C.B., 1932
Cryptopontius graciloides Ummerkutty, 1962
Cryptopontius ignotus (Brady, 1910)
Cryptopontius longipes Nicholls, 1944
Cryptopontius madeirensis Johnsson, 2001
Cryptopontius minor Stock, 1965
Cryptopontius orientalis Ummerkutty, 1962

Cryptopontius paracapitalis Nicholls in Eiselt, 1962

Cryptopontius pentadikos Farias, Neves & Johnsson, 2020

Cryptopontius phyllogorgius Farias, Neves & Johnsson, 2020

Cryptopontius proximus Nicholls, 1944

Cryptopontius quinquesetus Kim I.H., 1996

Cryptopontius ricinius Malt, 1991

Cryptopontius similis Nicholls, 1944

Cryptopontius tanacredii Johnsson, Rocha & Boyko, 2002

Cryptopontius tenuis (Giesbrecht, 1895)

Remarks: The species was initially described in 1895 by Giesbrecht as *Dyspontius thorellii*. Posteriorly in 1899, Giesbrecht reanalyzed and provided detailed male and female redescription, erecting a new genus *Cryptopontius.* However, he did not create a distinct diagnosis for the genus and species (Giesbrecht, 1895; Giesbrecht, 1899). A separate diagnosis for the genus was proposed only in 1918 by G.O. Sars (1918). There are no deposit information of type series. However, specimens of *C. thorelli* were found deposited at Naturalis Biodiversity Center (Netherlands), under the number ZMA.CRUS.F.100932. Those specimens were collected at Poiret, Banyuls (France), Mediterranean region relatively near Naples (Italy), the type locality.

As many others Artotrogidae species the latest and most detailed diagnosis of *Cryptopontius* was published by Sars G.O. (1918). But it lacks many characteristics which were poorly described at that time. Both antennule and antenna described together as "*as in Dyspontius*", maxillipeds described as "*normal*" and, leg 5 as "*similar to that in Dyspontius*" (Sars G.O., 1918, p. 120). *Cryptopontius* now has 26 valid species, and the understanding of its variation is much clearer. The amended diagnosis now presents the detailed morphology of the antennule, antenna, and maxilliped for the genus. It also includes the variation of the free segment of the leg 5 which can be represented by a segmented exopod in some species, but can also be exhibited as a knob armed with setae (Giesbrecht, 1895; Brady, 1910; Wilson, 1932; Nicholls, 1944; Ummerkutty, 1961; Stock, 1965; Malt, 1991; Kim I.H., 1996; Johnsson, 2001; Johnsson, Rocha & Boyko, 2002; Kim I.H., 2007; Neves & Johnsson, 2008; Farias *et al*., 2020).

Cryptopontius has a cosmopolitan distribution (Fig. 12II), but most of its species were recorded in the Temperate Northern Atlantic (Giesbrecht, 1899; Wilson C.B., 1932; Stock, 1965; Johnsson, 2001), Temperate Northern Pacific (Kim I.H., 1996; Lee J. & Kim I.H., 2023) and Temperate Australasia (Brady, 1899; Nicholls, 1944; Eiselt, 1962). While some punctual records were provided for the Eastern Indo-Pacific (Johnsson, Rocha & Boyko, 2002) Tropical Atlantic (Neves & Johnson, 2008; Farias et al. 2020), Western Indo-Pacific (Ummerkutty, 1961); Southern Ocean (Brady, 1910); and Central Indo-Pacific realms (Malt, 1991; Kim I.H., 2007). Half of the recorded species had no identified invertebrate host, but sponges (17%) (Ummerkutty, 1961; Stock, 1965; Malt, 1991; Neves & Johnsson, 2008; Farias *et al*., 2020) and algae (17%) (Ummerkutty, 1961; Lee J. & Kim I.H., 2023; Johnsson, 2001; Neves & Johnsson, 2008) are the most commonly recorded. There are also records for bryozoans (8%) (Johnsson, Rocha & Boyko, 2002; Kim I.H., 2007; Farias *et al*., 2020), ascidians (4%) (Kim I.H., 1996) and, cnidarians (4%) hosts (Kim I.H., 1996).

***Metapontius* Hansen, 1923**

Amended diagnosis of *Metapontius* Hansen, 1923: Artotrogidae. Cephalosome greatly expanded on female, notably narrower on male, with postero-lateral corners nearly rectangular and not produced. Second, third, and fourth pedigerous somites short, and with postero-lateral projections. Anal somite and caudal rami longer than wide. Female antennule 14-segmented, and 17-segmented on males. Antennal endopod 2-segmented with thick distal spines, exopod not discovered (possibly rudimentary or absent). Maxilla strongly built, with a strongly recurved claw. Maxilliped endopod 2-segmented, with thick distal spines and short-recurved terminal claw. Oral cone pear-shaped, short, reaching the basis of the maxilliped. Both rami of maxillule short, inner lobe longer than outer one. Legs 1 to 3 biramous and 3-segmented. Leg 4 with 3-segmented exopod, and 2-segmented endopod exhibiting reduced armature formula. Leg 5 free small exopod bearing 2 setae.

Type species: *Metapontius latispinis* Hansen, 1923

Metapontius latispinis Hansen, 1923. P. 12 Pl. I. Fig. 8a – i.

Remarks: The genus was erected by Hansen (1923) based on the type species *Metapontius latispinis* Hansen, 1923, with specimens collected on the northwestern coast of the Faroes Islands, at 861 m deep. According to the author, all specimens from this study were deposited in the collection of the "*Copenhagen Museum*" (Hansen, 1923, p. 1). Syntypes of the species were found on the webpage of the Natural History Museum of Denmark (University of Copenhagen) under the numbers CRU-007052 and CRU-007053. However, this material was not available for examination.

The original diagnosis of *Metapontius* is richly detailed for some features of the genus, but it lacks a proper description of the antenna, maxilla, and maxilliped; described as "*4-jointed as usual*", "*unusually robust*" and, "*robust*", respectively (Hansen, 1923, p. 11 – 12). It also does not refer to the segmentation of legs 2 to 3, and the reduced armature formula of the leg 4 endopod.

The genus was monospecific for almost a hundred years until the description of *Metapontius walteri* Johnsson & Neves (2005). This new species was placed within *Metapontius* largely based on the 2-segmented leg 4 endopod, character shared with *Arctopontius,* and the length of the maxillule lobes. However, the species should not be placed in the genus since it exhibits other important diagnostic features from *Arctopontius*: (1) the cephalosome, second, and third pedigerous somites present well developed postero-lateral projections, while in *Metapontius* it shows a rectangular shape and does not exhibit such projections at all; (2) the 8-segmented female antennule of *M. walteri* exhibits the II–VIII ancestral segments fusion pattern, while the 14-segmented female antennule of *Metapontius* exhibits ancestral segments from I to IX articulated; (3) the maxillule inner lobe is slightly longer than outer, but in *Metapontius* is the opposite, with the outer lobe being described as longer than the inner; (4) the 3-segmented maxilliped endopod differs from the 2-segmented exhibited by *Metapontius*, which is poorly described on the original description, but it is clear on the illustration; and finally (5), both anal somite and caudal rami are wider than long, differing from the anal somite longer than wide and the caudal rami twice longer than wide exhibited by *Metapontius*. Thus, *M. walteri* should be moved to *Arctopontius*, with a new combination as *Arctopontius walteri* (Johnsson & Neves, 2005). With the removal of *A. walteri*, *Metapontius* occurrence is restricted to the Temperate Northern Atlantic realm (Fig. 13C) (Hansen, 1923). The invertebrate host of *Metapontius latispinis* was not identified.

***Myzopontius* Giesbrecht, 1895**

Amended diagnosis of *Myzopontius* Giesbrecht, 1895: Artotrogidae. Cephalosome moderately widened. Prosome somite with slightly projected epimera. Fourth pedigerous somite with postero-lateral margin projected and reaching the fifth somite. Genital somite and caudal rami much longer than wide. Female antennule 9- to 12-segmented, 12- to 13-segmented on males, with additional aesthetascs. Antennal endopod 2-segmented, second segment elongated; exopod 1-segmented. Oral cone well-developed reaching between legs 2 and 4. Maxillule with outer lobe longer than inner. Maxilla with slender distal claw tapering distally. Maxilliped endopod 3-segmented. Legs 1 to 4 biramous and 3-segmented. Leg 5 with free exopod.

Type species: *Myzopontius pungens* Giesbrecht, 1895
Myzopontius pungens Giesbrecht, 1895, p. 182.
Myzopontius pungens Scott, 1899; p. 114 – 115; Pl. 9; Fig. 1 – 10;
Myzopontius pungens Giesbrecht, 1899, p. 106, pl. 1, fig. 6, pl. 6, figs. 1–14.
Myzopontius pungens Sars G.O., 1917, p. 113, pl. 68.
Myzopontius pungens Wilson, 1936. p. 375.
Myzopontius pungens Shih *et al*., 1971. p. 214.
Myzopontius pungens Kim I.H., 1998, p. 449 – 452, fig. 29 – 30.

Other species:

Myzopontius australis Nicholls, 1944
Myzopontius innominatus (Brady, 1910)
Myzopontius venustus Kim I.H., 1996

Remarks: This genus was erected by Giesbrecht (1895) based on the description of *Myzopontius pungens* Giesbrecht, 1895, to the golf of Naples, the species had a brief genus diagnosis, with a proper species description. Only in 1899, Giesbrecht provided a species description for males and females of *Myzopontius* (Giesbrecht, 1895; 1899). In 1915, Sars created Myzopontiidae, including *Myzopontius* and *Neopontius*, once included by Giesbrecht in Dyspontiinae (Sars G.O., 1918), also providing a diagnosis for the genus.

Besides the type species, the genera also have three other species: *M. innominatus* (Brady, 1910), *M. australis* Nicholls, 1944 and *M. venustus* Kim I.H. 1996 (Nicholls, 1944; Eiselt, 1961; Kim I.H., 1996). As well as other species described by Giesbrecht, there was no information about type series deposit. However, the search for specimens found syntypes deposited at the Natural History Musem of Denmark (University of Copenhagen), under the number "CRU 007901". However, this material was not available for examination.

The latest *Myzopontius* diagnosis published by Sars G.O. (1918) lacks many key features important to differentiate the genus, such as the antennule and antenna segmentation, which ranges from 9- to 12-segments on females, exhibiting minor variations (Sars G.O., 1918; Nicholls, 1944; Kim I.H., 1996). It also misses the morphology of oral appendages, being comparatively described or stated generically as "*slender", "very small"* and "*very narrow*" (Sars G.O., 1918, p. 113), now its armature formula and segmentation are included considering the newly described species (Sars G.O., 1918; Nicholls, 1944; Kim I.H., 1996).

Myzopontius distribution (Fig. 12III) is recorded to the Temperate Northern Atlantic (Sars G.O., 1918; Giesbrecht, 1899), Temperate Northern Pacific (Kim I.H., 1996), Southern Ocean (Brady, 1910), Western Indo-Pacific (Stock, 1966) and, Temperate Australasia (Nicholls, 1944). The host of the majority of the species of the genus was invertebrates not identified (66%) (Sars G.O., 1918; Giesbrecht, 1899; Brady, 1910; Nicholls, 1944), but there are records for algae (25%) (Stock, 1966; Kim I.H., 1996) and, ascidians (13%) hosts (Kim I.H., 1996).

Neopontius **Scott T., 1898**

Amended diagnosis of *Neopontius* Scott, 1898: Artotrogidae. Cephalosome slightly widened, tapering anteriorly. Produced rostrum. Third and fourth pedigerous somites with slightly produced epimera. Urosome longer than wide. Genital somite and caudal rami much longer than wide. Female antennule 12-segmented, 14-segmented on males, with no additional aesthetascs. Antennal endopod 1 or 2-segmented, exopod 1-segmented. Oral cone short. Maxillule inner lobe longer and wider than outer lobe. Maxilla with long-recurved claw, armed with strong spine medially. Maxilliped syncoxa and basis fused (on *M. rectus* Lee & Kim I.H., 2023), endopod 3-segmented, armed with strong spines distally on the second and third segments. Legs 1 to 4 biramous and 3-segmented. Leg 5 free exopod well developed, oar-shaped.

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Type species: *Neopontius angularis* Scott, 1898

Scott, 1898; p. 271; Pl. XIV; Fig. 1 – 11.

Sars G.O., 1918; p. 115; Pl. LXIX

Gotto, 1993; p. 174; Fig. 42 G – K.

Other species:

Neopontius dilatatus Sars G.O., 1916

Neopontius rectus Lee & Kim I.H., 2023

Neopontius sivertseni Wiborg, 1964

Remarks: Genus erected by Thomas Scott (1898) based on the description of *Neopontius angularis* Scott T., 1898. It was collected at Otter spit, Loch Fyne, northwestern coast of the United Kingdom. There was no information about type series deposit. Posteriorly, Giesbrecht (1899) proposed the first diagnosis for the genus, and then Sars G.O. (1918) provided a complete redescription of the type species with detailed diagnosis of the genus and a new species, *N. dilatatus* Sars G.O., 1916 (T. Scott, 1898; Giesbrecht, 1899; Sars G.O., 1918). The genus now has 4 valid species, including *N. sivertseni* Wiborg, 1964 and *N. rectus* Lee & Kim I.H., 2023 (WoRMS, 2024).

The diagnosis made by Sars provide a detailed description of the body aspect and a few appendages of the genus; but it lacks a proper description of the antennule, and antenna, including the segmentation and armature. It also lacks a proper description of oral appendages and legs 1 to 4, which were described comparatively with *Myzopontius*. With the knowledge provided by the new described species it is possible to better understand the limits of the genus, especially regarding the single-segmented antennal endopod and fused maxilliped syncoxa and basis from *N. rectus*, two important features included on the diagnosis.

Neopontius reported occurrence (Fig.13A) is mostly concentrated in the Temperate Northern Atlantic realm (Scott T., 1898; Sars G.O., 1918); but there is a record of the Temperate Northern Pacific (Lee & Kim I.H., 2023). No invertebrate host was identified as associated with the genus (Scott T., 1898; Sars G.O., 1918; Lee & Kim I.H., 2023).

***Pteropontius* Giesbrecht, 1895**

Amended diagnosis of *Pteropontius* Giesbrecht, 1895: Artotrogidae. Body cyclopiform. Dorso-ventrally flattened. Cephalosome expanded, with acute projected epimera. Well-developed rostrum. Second, third, and fourth pedigerous somites with projected epimera. Genital somite with two pairs of wing-like projections, except *P. quartus*. Female antennule 9-segmented, 10-segmented in males. Antennal endopod 1-segmented. Oral cone short. Maxilla robust with recurved claw. Maxilliped endopod 3-segmented. Leg 1 with 2-segmented endopod and exopod. Legs 2 and 3 biramous and 3-segmented on both rami. Leg 4 uniramous, with coxa and basis fused. Leg 5 rudimentary, with 1-segmented small exopod (Giesbrecht, 1895; Nicholls, 1944; Sewell, 1949; Ho, 1984, Lee & Kim I.H., 2023).

Type species: *Pteropontius cristatus* Giesbrecht, 1895
Pteropontius cristatus Giesbrecht, 1895; p. 184.
Pteropontius cristatus Giesbrecht, 1899; p. 36 – 38, 110; Tafel 7, Fig. 24 – 39.
Pteropontius cristatus Stock, 1965; p. 312 – 313; Fig. 10 A – B.

Other species:
Pteropontius barbatus Nicholls, 1944
Pteropontius cristatus Giesbrecht, 1895
Pteropontius decorus Ho, 1984
Pteropontius quartus Sewell, 1949

Remarks: Genus erected by Giesbrecht (1895), based on the description of *Pteropontius cristatus* Giesbrecht, 1895. As in *Myzopontius*, Giesbrecht provided a brief genus diagnosis and did not make a species description. Only in 1899, Giesbrecht published a proper description of the new genus and species based on males and females (Giesbrecht, 1895; 1899). In 1918, Sars created the family Dyspontiidae, in which he included seven genera, including *Pteropontius*. However, unlike *Myzopontius,* the author did not provide a diagnosis for the genus (Sars G.O., 1918). Just like others Giesbrecht species described in the gulf of Naples, there was no type series deposit register. More recently, Lee & Kim (2023) published a redescription of *Pteropontius cristatus* found on washings of different invertebrates from Ulleung Island, South Korea (Japan Sea), but the authors did not provide a diagnosis to the genus. The authors stated that no significant difference was found between the specimen found in Korean waters from the specimen found in the Mediterranean. Lee & Kim (2023) also stated that the specimen studied by Stock (1965) was probably a different species since it showed a 3-segmented endopod on leg 1, however, there was no sufficient data to confirm its taxonomic identity. The genus now has four valid species, and with the knowledge provided by these it is possible to better understand its limits (Giesbrecht, 1895; 1899; Sars G.O., 1918; Stock, 1965; Lee & Kim I.H., 2023; Farias *et al*., in prep).

The distribution (Fig. 13B) of *Pteropontius* is recorded to the Temperate Northern Atlantic (Giesbrecht, 1899), Western Indo-Pacific (Sewell, 1949); Temperate Northern Pacific (Ho, 1984; Kim I.H., 1996; Lee J. & Kim I.H., 2023) and, Temperate Australasia (Nicholls, 1944). More than half of the species (67%) had no identified invertebrate hosts, but some species were found associated with ascidians (17%) (Kim I.H., 1996), sponges (16%) (Ho, 1984).

***Sestropontius* Giesbrecht, 1899**

Amended diagnosis of *Sestropontius* Giesbrecht, 1899: Artotrogidae. Body cyclopiform. Cephalosome and first pedigerous somite with acute projected epimera. Pedigerous somites 3 and 4 with rounded projected epimera. Antennule 8 to 13-segmented in females, 10-segmented in males with additional aesthetascs. Antenna 4-segmented, with 1-segmented exopod and 2-segmented endopod. Oral cone long and tapered distally. Maxillule unequal sized. Maxilla robust, long, and delegate claw. Maxilliped endopod 3-segmented. Legs 1 to 4 biramous and 3-segmented. Leg 5 elongated.

Type species: *Sestropontius bullifer* Giesbrecht, 1899
Sestropontius bullifer Giesbrecht, 1899. p.88, 107, 215. Pl. 9. Fig. 1 – 13.
Sestropontius bulliger Giesbrecht, 1899. p.26 – 27. (misspelling)
Sestropontius bullifer Stock, 1965. p.310 – 312. Fig. 7.

Other species:

Sestropontius mckinnoni Johnsson, 2002

Remarks: Genus erected by Giesbrecht (1899), based on the description of *Sestropontius bullifer* Giesbrecht, 1899. It was described on three male specimens from the Gulf of Naples. The female was only described six decades later by Stock (1965). It was found associated with the sponge *Hymeniacidon* Bowerbank, 1858, in a shallow rocky region near to the Arago Laboratory, Banyuls, southern coast of France (Stock, 1965). There was no type series deposit register. But specimens of *S. bullifer* were found at the Naturalis Biodiversity Center (Netherlands). Those specimens were collected by Stock at "*Poiret, Banyuls"*, southern coast of France, a relatively close location to the Giesbrecht's specimens (Giesbrecht, 1899; Stock, 1965). The genus remained monospecific for more than 100 years until the description of *S. mckinnoni* Johnsson (2002) (Johnsson & Rocha, 2002).

Giesbrecht (1899) made a diagnosis for *Sestropontius* based on the male, comparing the genus with *Cribropontius*, and citing differences such as antenna "*differently structured, despite also being 10-segmented*" *[Greifantennen abweichend gegliedert (wenn auch ebenfalls 10gliedrig)];* oral cone "*reaches to the leg 2*" *[Sipho bis zum 2. Fusse reichend]*; maxilla and maxilliped "*not particularly thick*" *[Maxille und Maxilliped nicht besonders dick]* (Giesbrecht, 1899, p. 107). A century later, with the knowledge of the sexually dimorphic features of the female and a new species for the genus, it was possible to better understand the limits of the genus. The amended diagnosis now brings features of the general aspect of the body; antenna, maxilla, and maxilliped segmentation; and legs 1 to 3 armature formula (Stock, 1965, Fig. 7 a – e). It is now also possible to better understand the antennule segmentation, for example, before known as 10-segmented, then 8-, now includes the possibility of 13 segments (Johnsson & Rocha, 2002, Fig. 1 c).

Sestropontius was originally recorded for the Temperate Northern Atlantic realm (Giesbrecht, 1899; Stock, 1965), and two other species were posteriorly recorded for the Southern Ocean (Fig. 13C) (Johnsson & Rocha, 2002; Conradi, 2014). Half of the records had no identified invertebrate hosts (Giesbrecht, 1899; Conradi, 2014), but there is a record for sponges (Stock, 1966) and for bryozoans hosts (Johnsson & Rocha, 2002).

Conclusion

The rich diversity of Artotrogidae species has been studied since the nineteenth century. Some of the first discovered genera and species descriptions were limited by their time; despite the extensive and splendid efforts made by G. S. Brady (1880; 1910); W. Giesbrecht (1895; 1899) and G. O. Sars (1918), a few features were not observed or they were simply comparatively described. With this study, some genera had their diagnostic characteristics redefined, gathering the current knowledge of the recently described species and modern taxonomical standards. Other genera, despite remaining monospecific, could also be better delimited with the current definition of which characteristics are supposed to be treated as a genus or as a species diagnostic.

Some of the genera treated in this study suggested a cosmopolitan distribution, such as *Bradypontius*, *Artotrogus*, *Arctopontius*, *Cryptopontius*, and, *Myzopontius* although, the majority of the records are closely related to the location of specialists, as in the British Islands, North Sea, Mediterranean Sea, Japan Sea, and South Australian coast. The lack of occurrence in others regions could be attributed to the lack of specialists in those areas, since Artotrogidae family diversity has been proven to be very rich. The only exceptions were two genera that presented a restricted distribution, *Metapontius* (North Sea) and *Cribropontius* (Mediterranean Sea), which may be caused by the existence of a single known-species. Contrarily *Arctopontius* exhibited an occurrence that suggests it may prefer temperate and Artic/Antarctic waters. Regarding hosts, among the genera studied here, bryozoans are the most commonly registered, about 10% of the records, followed by algae, sponges, ascidians, cnidarians, and mollusks. .

Acknowledgements

The authors thank Dr. Lutz Bachmann and Dra. Åse Wilhelmsen (Natural History Museum – University of Oslo); Dr. Adam Stergis, Dr. Chad Walter, Dr. Karen Osborn, and Dr. William Moser (National Museum of Natural History (Smithsonian Institution) for the information provided and support on the loan of the analyzed specimens. And also thank Dr. Bram van der Bijl and Dra. Wendy van Bohemen (Naturalis Biodiversity Center) for the information provided about the type specimens deposited in the zoological collections. The authors are grateful to the Chico Mendes Institute for Biodiversity Conservation (ICMbio) for collecting permission (Sisbio No 15161-1). This study is part of the project 'Assessment and research of sun coral in Todos-os-Santos Bay', a cooperation agreement between UFBA and CENPES/PETROBRAS. This work was supported by the CENPES/PETROBRAS [under grant number 5850.0107361.18.9].

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Figure Legends

Figure 1. Infographic showing world distribution, biogeographic realms of Spalding *et al*., (2007) and hosts. A) *Bradypontius* Giesbrecht, 1895; B) *Artotrogus* Boeck, 1859; C) *Dyspontius* Thorell, 1859. Details on Table 1.

Figure 2. Collection site of *Bradypontius* sp nov. A) Archipelago location highlighted on South America; B) Fernando de Noronha Archipelago; C) Collection site on Ressureta diving point, channel between Ilha Rata and Ilha do Meio.

Figure 3. Confocal Laser Scanning Microscopy of *Bradypontius* sp nov., paratype female (UFBA4135). A) dorsal view; B) ventral view. Scale bar: 200µm.

Figure 4. *Bradypontius* sp nov., holotype female (UFBA2202). A) body, dorsal view; B) urosome, ventral view; C) antennule; D) antenna; E) maxillule. Scale bars: A = 250µm; B = 50 µm; C – E = 40µm.

Figure 5. *Bradypontius* sp nov., holotype female (UFBA2202). A) tip of the mandible stylet; B) maxilla; C) maxilliped; D) leg 1; E) leg 2; F) leg 3; G) leg 4; H) leg 5. Scale bars: A = 10µm; B = 200µm; C – G = 50µm and H = 20µm.

Figure 6. *Artotrogus sarsi* Kim I.H., 1996. Female: A) body, dorsal view, oral cone is drawn dashed line; B) urosome, without the fifth pedigerous somite, dorsal view; C) antennule; D) antenna; E) mandible stylet tip. Scale bars: A = 1000 µm; B = 200 µm; C – E = 100 µm.

Figure 7. *Artotrogus sarsi* Kim I.H., 1996. Female: A) maxillule; B) maxilla; C) maxilliped; D) P1. Scale bars: A – B = 200 µm; C = 50 µm.

Figure 8. *Artotrogus sarsi* Kim I.H., 1996. Female: A) P2; B) P3 and C) P5. Scale bars: A – C = 100 µm.

Figure 9. *Dyspontius striatus* Thorell, 1859. Female: A) body, dorsal view; B) urosome, without fifth pedigerous somite, dorsal view; C) antennule; D) antenna; E) mandible stylet tip. Scale bars: A = 200 µm; B - D = 50 µm; E = 100 µm.

Figure 10. *Dyspontius striatus* Thorell, 1859. Female: A) maxillule; B) maxilla; C) maxilliped; D) P1; E) P2; F) P3. Scale bars: A - F = 50 µm.

Figure 11. *Dyspontius striatus* Thorell, 1859. Female: A) P4; B) P5. Male: C) body, dorsal view; D) urosome, ventral view; E) antennule. Scale bars: A - B, D - E = 50 µm; c = 200 µm.

Figure 12. Infographic showing world distribution, biogeographic realms of Spalding *et al*., (2007) and hosts. A) *Arctopontius* Sars G.O., 1915; B) *Cryptopontius* Giesbrecht, 1899; C) *Myzopontius* Giesbrecht, 1895. Details on Table 3.

Figure 13. Infographic showing world distribution, biogeographic realms of Spalding *et al*., (2007) and hosts. A) *Neopontius* Scott T., 1898; B) *Pteropontius* Giesbrecht, 1895; C) *Sestropontius* Giesbrecht, 1899*, Metapontius* Hansen, 1923 *and, Cribropontius* Giesbrecht, 1899. Details on Table 4.

Table Legends

Table 1. Figure 1 table, area records numbers, species, hosts, biogeographic realm (Spalding *et al*., 2007), and, data sources for *Bradypontius* Giesbrecht, 1895; *Artotrogus* Boeck, 1859; *Dyspontius* Thorell, 1859. NHM – Natural History Museum (UK).

Table 2. Diagnostic differences between the discussed *Bradypontius* species.

Table 3. Figure 12 table, area records numbers, species, hosts, biogeographic realm (Spalding *et al*., 2007), and, data sources for *Arctopontius* Sars G.O., 1915; *Cryptopontius* Giesbrecht, 1899; *Myzopontius* Giesbrecht, 1895. NHM – Natural History Museum (UK).

Table 4. Figure 13 table, area records numbers, species, hosts, biogeographic realm (Spalding *et al*., 2007), and, data sources for *Neopontius* Scott T., 1898; *Pteropontius* Giesbrecht, 1895; *Sestropontius* Giesbrecht, 1899*, Metapontius* Hansen, 1923 *and, Cribropontius* Giesbrecht, 1899. NHM – Natural History Museum (UK).

Tables

Table 1

***Bradypontius* Giesbrecht, 1895 – Fig. 1I**				
Number	**Species**	**Host**	**Biogeographic Realm**	**Data source**
a	*Bradypontius macginitei* Eiselt, 1986	n. id.	Arctic	Eiselt, 1986
b	*Bradypontius cubensis* Varela, 2012	Algae	Tropical Atlantic	Varela, 2012
c	*Bradypontius groenlandicus* Hansen, 1923	n. id.	Arctic	Hansen, 1923
	Bradypontius tenuipes Hansen, 1923	n. id.	Arctic	Hansen, 1923
	Bradypontius unidens Hansen, 1923	n. id.	Arctic	Hansen, 1923
d	*Bradypontius ancistronus* Neves & Johnsson, 2008	Porifera	Tropical Atlantic	Neves & Johnsson, 2008
e	*Bradypontius dentatus* Hansen, 1923	n. id.	Temperate Northern Atlantic	Hansen, 1923
f	*Bradypontius magniceps* (Brady, 1880)	n. id.	Temperate Northern Atlantic	Brady, 1880
	Bradypontius papillatus (Scott T., 1888)	n. id.	Temperate Northern Atlantic	Scott T., 1888
g	*Bradypontius magniceps* (Brady, 1880)	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
	Bradypontius major Sars G.O., 1915	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
	Bradypontius papillatus (Scott T., 1888)	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
h	*Bradypontius siphonatus* Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
i	*Bradypontius pichoni* Stock, 1966	Cnidaria	Western Indo-Pacific	Stock, 1966
j	*Bradypontius poorei* Johnsson, 2002	Bryozoa	Southern Ocean	Johnsson & Rocha, 2002
k	*Bradypontius serrulatus* Brady, 1910	n. id.	Southern Ocean	Brady, 1910
	Bradypontius typicus (Brady, 1910)	n. id.	Southern Ocean	Brady, 1910
l	*Bradypontius crassisetus* Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Bradypontius heteroporus Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Bradypontius halocynthiae Kim I.H., 1996	Ascidiacea	Temperate Northern Pacific	Kim I.H., 1996
	Bradypontius culicis Lee & Kim I.H., 2023	n. id.	Temperate Northern Pacific	Lee & Kim I.H., 2023
m	*Bradypontius inermis* Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944

	Bradypontius ovatus Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	Bradypontius serratipes Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	***Artotrogus* Boeck, 1859 – Fig. 1II**			
a	*Artotrogus orbicularis* Boeck, 1859	n. id.	Arctic	Eiselt, 1986
b	*Artotrogus orbicularis* Boeck, 1859	Mollusca	Temperate Northern Atlantic	Boeck, 1859
	Artotrogus orbicularis Boeck, 1859	n. id.	Temperate Northern Atlantic	NHM Database
	Artotrogus sarsi Kim I.H., 1996	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
c	*Artotrogus gladiator* (Giesbrecht, 1899)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
d	*Artotrogus acutus* Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Artotrogus halocynthiae Kim I.H., 1996	Ascidiacea	Temperate Northern Pacific	Kim I.H., 1996
	Artotrogus incidentus Kim I.H., 1996	Ascidiacea	Temperate Northern Pacific	Kim I.H., 1996
	Artotrogus rotundus Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Artotrogus muricatus Lee & Kim I.H., 2023	Algae	Temperate Northern Pacific	Lee & Kim I.H., 2023
	Artotrogus parmatus Lee & Kim I.H., 2023	Algae	Temperate Northern Pacific	Lee & Kim I.H., 2023
e	*Artotrogus latifurcatus* Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	Artotrogus sardae McKinnon, 1988	n. id.	Temperate Australasia	McKinnon, 1988
	Artotrogus haikungae McKinnon, 1988	n. id.	Temperate Australasia	McKinnon, 1988
f	*Artotrogus gordoni* Kim I.H., 2009	Bryozoa	Temperate Australasia	Kim, I.H., 2009
	***Dyspontius* Thorell, 1859 – Fig. 1III**			
a	*Dyspontius gerardius* Johnsson, 2001	Cnidaria	Temperate Northern Atlantic	Johnsson, 2001
b	*Dyspontius curticaudatus* Scott T., 1905	n. id.	Temperate Northern Atlantic	Scott T., 1905
c	*Dyspontius striatus* Thorell, 1859	n. id.	Temperate Northern Atlantic	Thorell, 1859
	Dyspontius striatus Thorell, 1859	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
	Dyspontius striatus Thorell, 1859	Algae	Temperate Northern Atlantic	Sars G.O., 1918
	Dyspontius striatus Thorell, 1859	Ascidiacea	Temperate Northern Atlantic	Sars G.O., 1918
d	*Dyspontius fringilla* (Giesbrecht, 1895)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Dyspontius passer (Giesbrecht, 1897)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
e	*Dyspontius alatus* Kim I.H., 2016	Porifera	Temperate Northern Pacific	Kim I.H., 2016

Table 2

		***Bradypontius* sp nov. 1**	***Bradypontius groelandicus* Hansen, 1923**	***Bradypontius halocynthiae* Kim I.H., 1996**	***Bradypontius macginitiei* Eiselt, 1986**	***Bradypontius siphonatus* Giesbrecht, 1897**
Antennule	segments nº	10	11	10	10	10
	fusion pattern	I, II, III-VII, VIII				
Oral cone	reach	Anal segment	Leg 3	Leg 2	Leg 1	Leg 2
Maxillule	inner seta	1	1	3	2	2
	outer seta	2	2	3	2	2
Maxilla	distal claw seta	3	2	2	1	3
Maxilliped	formula	1,1,0,1,1 +claw	1,1,0,1,1 +claw	1,1,2,1,1 +claw	1,1,1,1,1 +claw	1,0,2,1,1 +claw
Leg 4	endopod formula	0; 0; 2	0-1; 0-2; 1,1,2	0-1; 0-2; 1,1+I, 2	0-1; 0-2; 1,2,2	0; 0; 2
Leg 5	seta nº	2	2	3	3	3
Leg 6	seta nº	1	2	2	1	3

Table 3

Number	Species	Host	Biogeographic Realm	Data source
	***Arctopontius* Sars G.O., 1915 – Fig. 12I**			
a	*Arctopontius hanseni* Eiselt, 1986	n. id.	Arctic	Eiselt, 1986
b	*Arctopontius expansus* Sars G.O., 1915	n. id.	Temperate Northern Atlantic	NMNH Database
c	*Arctopontius expansus* Sars G.O., 1915	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
d	*Arctopontius novenarius* Johnsson, 2002	Bryozoa	Southern Ocean	Johnsson & Rocha, 2002
e	*Arctopontius minutus* Kim I.H., 2016	Porifera	Temperate Northern Pacific	Kim I.H., 2016
	Arctopontius adelphus Kim I.H., 2016	Bryozoa	Temperate Northern Pacific	Kim I.H., 2016
f	*Arctopontius walteri* (Johnsson & Neves, 2005)	Cnidaria	Eastern Indo-Pacific	Johnsson & Neves, 2005
	***Cryptopontius* Giesbrecht, 1895 – Fig. 12II**			
a	*Cryptopontius tanacredii* Johnsson, Rocha & Boyko, 2002	Cnidaria	Eastern Indo-Pacific	Johnsson, Rocha & Boyko, 2002
b	*Cryptopontius gracilis* Wilson C.B., 1932	n. id.	Temperate Northern Atlantic	Wilson C.B., 1932
c	*Cryptopontius aesthetascus* Neves & Johnsson, 2008	Porifera	Tropical Atlantic	Neves & Johnsson, 2008
	Cryptopontius expletus Neves & Johnsson, 2008	Algae	Tropical Atlantic	Neves & Johnsson, 2008
	Cryptopontius pentadikos Farias, Neves & Johnsson, 2020	Porifera	Tropical Atlantic	Farias, Neves & Johnsson, 2020
	Cryptopontius phyllogorgius Farias, Neves & Johnsson, 2020	Cnidaria	Tropical Atlantic	Farias, Neves & Johnsson, 2020
d	*Cryptopontius madeirensis* Johnsson, 2001	Algae	Temperate Northern Atlantic	Johnsson, 2001
e	*Cryptopontius brevifurcatus* (Giesbrecht, 1895)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Cryptopontius capitalis (Giesbrecht, 1895)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Cryptopontius thorelli (Giesbrecht, 1895)	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Cryptopontius minor Stock, 1965	Porifera	Temperate Northern Atlantic	Stock, 1965
	Cryptopontius thorelli (Giesbrecht, 1895)	Porifera	Temperate Northern Atlantic	Stock, 1965
f	*Cryptopontius graciloides* Ummerkutty, 1962	Algae	Western Indo-Pacific	Ummerkutty, 1961
	Cryptopontius orientalis Ummerkutty, 1962	Porifera	Western Indo-Pacific	Ummerkutty, 1961

g	*Cryptopontius ignotus* (Brady, 1910)	n. id.	Southern Ocean	Brady, 1910
h	*Cryptopontius ricinius* Malt, 1991	Porifera	Central Indo-Pacific	Malt, 1991
i	*Cryptopontius acutus* Kim I.H., 2007	Cnidaria	Central Indo-Pacific	Kim I.H., 2007
j	*Cryptopontius ascidius* Kim I.H., 1996	Ascidiacea	Temperate Northern Pacific	Kim I.H., 1996
	Cryptopontius digitatus Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Cryptopontius donghaensis Kim I.H., 1996	n. id.	Temperate Northern Pacific	Kim I.H., 1996
	Cryptopontius quinquesetus Kim I.H., 1996	Bryozoa	Temperate Northern Pacific	Kim I.H., 1996
	Cryptopontius bilobatus Lee & Kim I.H., 2023	Algae	Temperate Northern Pacific	Lee & Kim I.H., 2023
k	*Cryptopontius longipes* Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	Cryptopontius proximus Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	Cryptopontius similis Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	Cryptopontius paracapitalis Nicholls in Eiselt, 1962	n. id.	Temperate Australasia	Eiselt, 1962
l	*Cryptopontius brevicaudatus* (Brady, 1899)	n. id.	Temperate Australasia	Brady, 1899
	Myzopontius **Giesbrecht, 1895 – Fig. 12III**			
a	*Myzopontius pungens* Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
b	*Myzopontius pungens* Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Myzopontius pungens Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	NHM Database
	Myzopontius pungens Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
c	*Myzopontius australis* Nicholls, 1944	Algae	Western Indo-Pacific	Stock, 1966
d	*Myzopontius innominatus* (Brady, 1910)	n. id.	Southern Ocean	Brady, 1910
e	*Myzopontius venustus* Kim I.H., 1996	Algae	Temperate Northern Pacific	Kim I.H., 1996
	Myzopontius pungens Giesbrecht, 1899	Ascidiacea	Temperate Northern Pacific	Kim I.H., 1996
f	*Myzopontius australis* Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944

Table 4

Record	Species	Host	Biogeographic Realm	Data source
	***Neopontius* Scott T., – 1898 Fig. 13/I**			
a	*Neopontius angularis* Scott T., 1898	n. id.	Temperate Northern Atlantic	Scott T., 1898
b	*Neopontius angularis* Scott T., 1898	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
	Neopontius dilatatus Sars G.O., 1916	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
c	*Neopontius rectus* Lee & Kim I.H., 2023	n. id.	Temperate Northern Pacific	Lee & Kim I.H., 2023
	***Pteropontius* Giesbrecht, 1895 – Fig. 13/II**			
a	*Pteropontius cristatus* Giesbrecht, 1895	n. id.	Temperate Northern Atlantic	Giesbrecht, 1895
b	*Pteropontius quartus* Sewell, 1949	n. id.	Western Indo-Pacific	Sewell, 1949
c	*Pteropontius decorus* Ho, 1984	Porifera	Temperate Northern Pacific	Ho, 1984
	Pteropontius decorus Ho, 1984	Ascidia	Temperate Northern Pacific	Kim, 1996
	Pteropontius cristatus Giesbrecht, 1895	n. id.	Temperate Northern Pacific	Lee & Kim I.H., 2023
d	*Pteropontius barbatus* Nicholls, 1944	n. id.	Temperate Australasia	Nicholls, 1944
	***Metapontius* Hansen, 1923; *Cribropontius* Giesbrecht, 1899 and *Sestropontius* Giesbrecht, 1899 – Fig. 13/III**			
a	*Metapontius latispinis* Hansen, 1923	n. id.	Temperate Northern Atlantic	Hansen, 1923
b	*Cribropontius normani* (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	Brady & Robertson, 1876
	Cribropontius normani (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	Sars G.O., 1918
	Cribropontius normani (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	NHM Database
	Cribropontius normani (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	NHM Database
	Cribropontius normani (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	NHM Database
	Cribropontius normani (Brady & Robertson, 1876)	n. id.	Temperate Northern Atlantic	NHM Database
c	*Sestropontius bullifer* Giesbrecht, 1899	n. id.	Temperate Northern Atlantic	Giesbrecht, 1899
	Sestropontius bullifer Giesbrecht, 1899	Porifera	Temperate Northern Atlantic	Stock, 1965
d	*Sestropontius mckinnoni* Johnsson, 2002	Bryozoa	Southern Ocean	*Johnsson & Rocha, 2002*
e	*Sestropontius italicae* Conradi, 2014	n. id.	Southern Ocean	Conradi, 2014

Figures

Figure 1

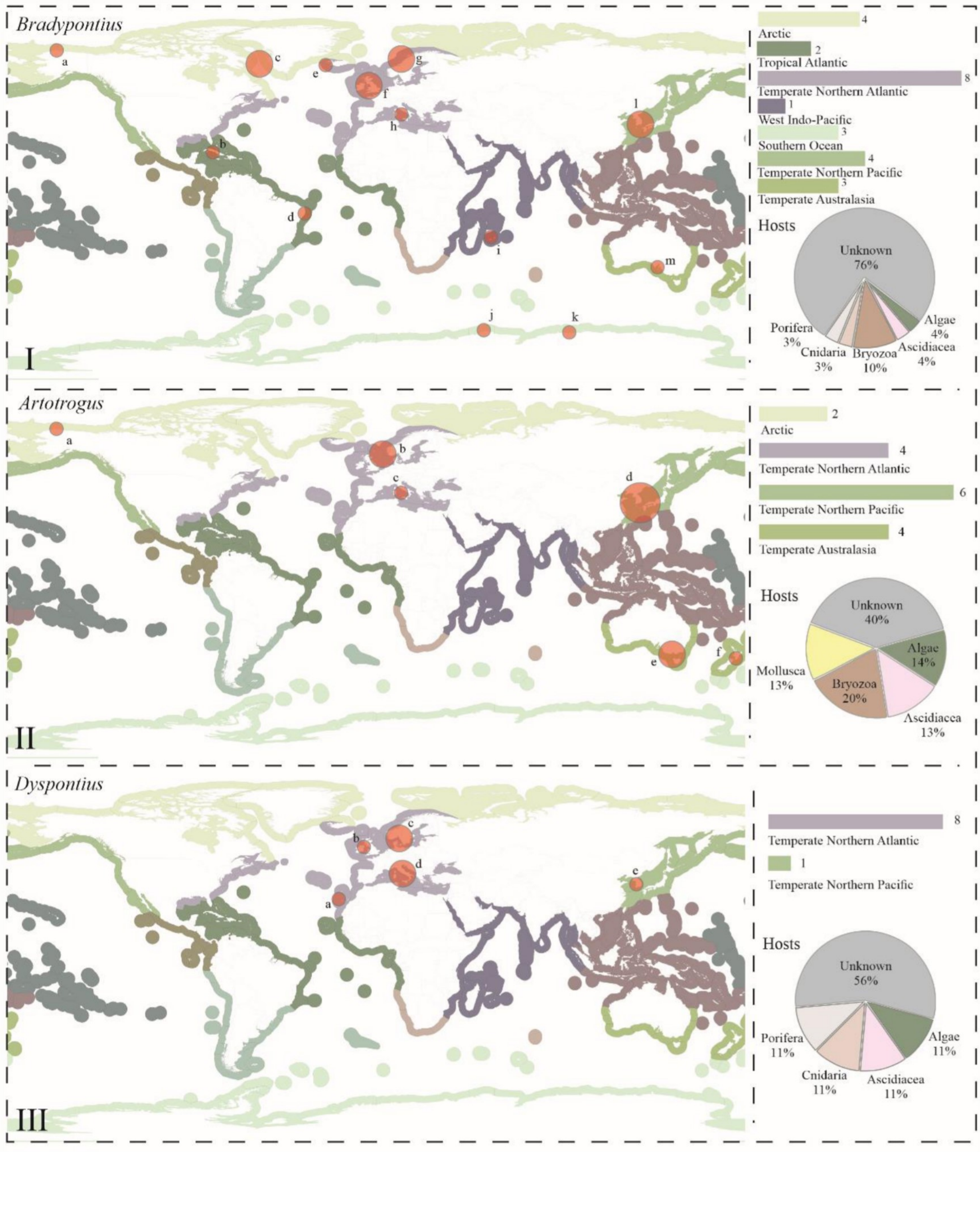


Figure 2

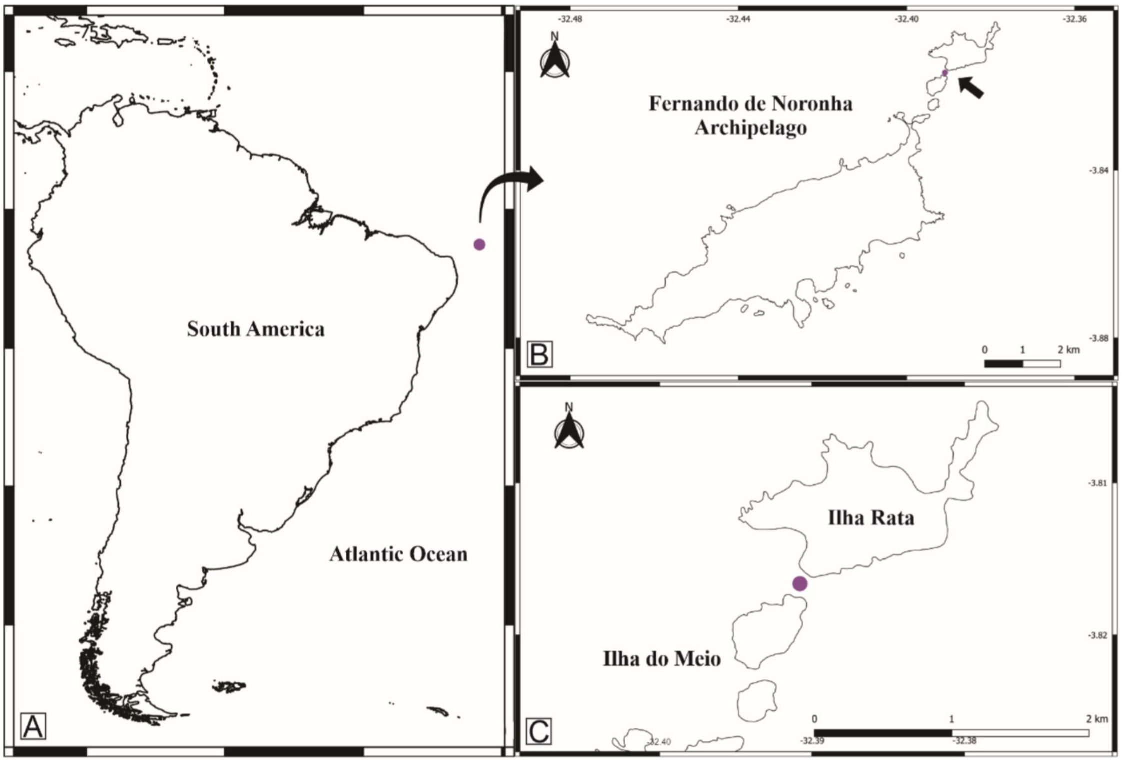

South America
Atlantic Ocean
A
Fernando de Noronha
Archipelago
B
Ilha Rata
Ilha do Meio
C

Figure 3

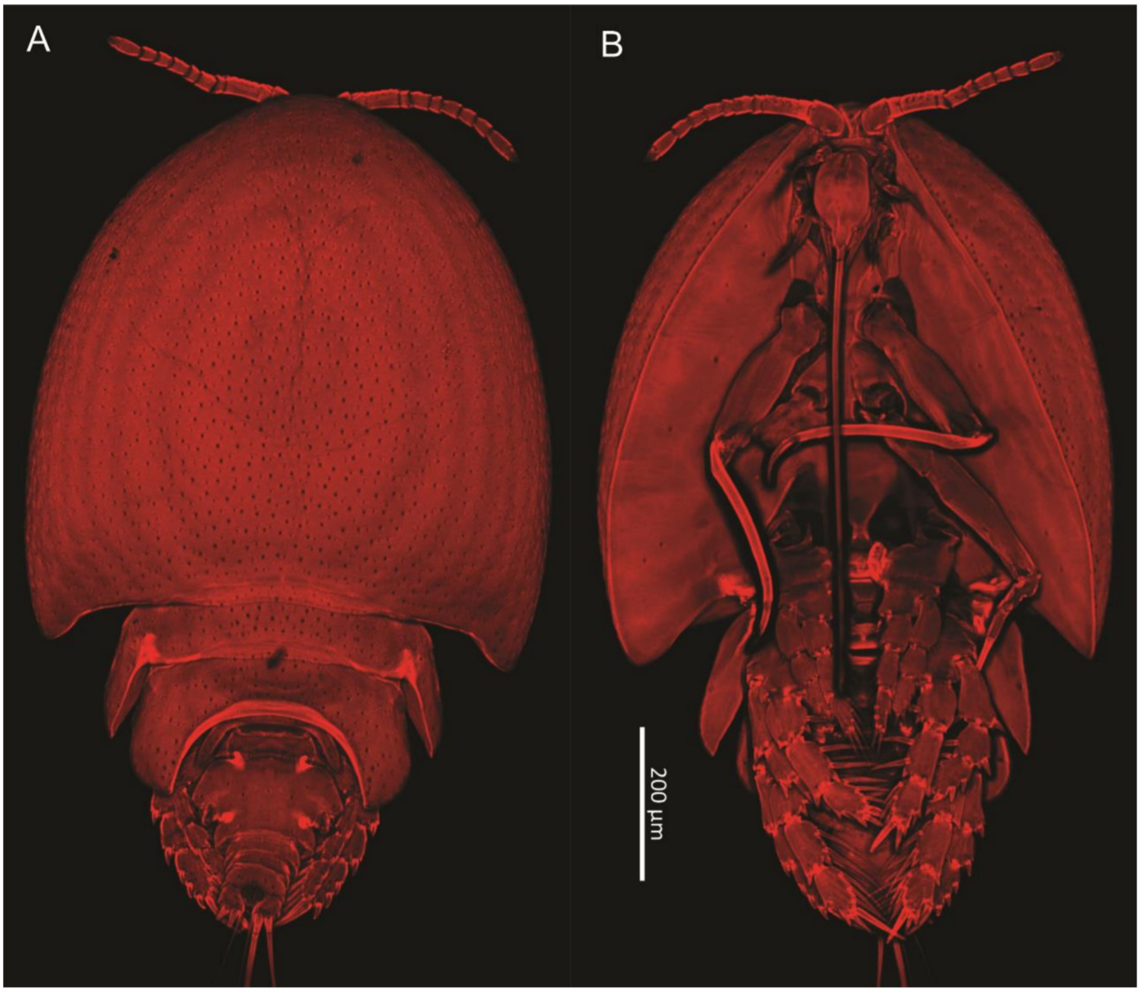
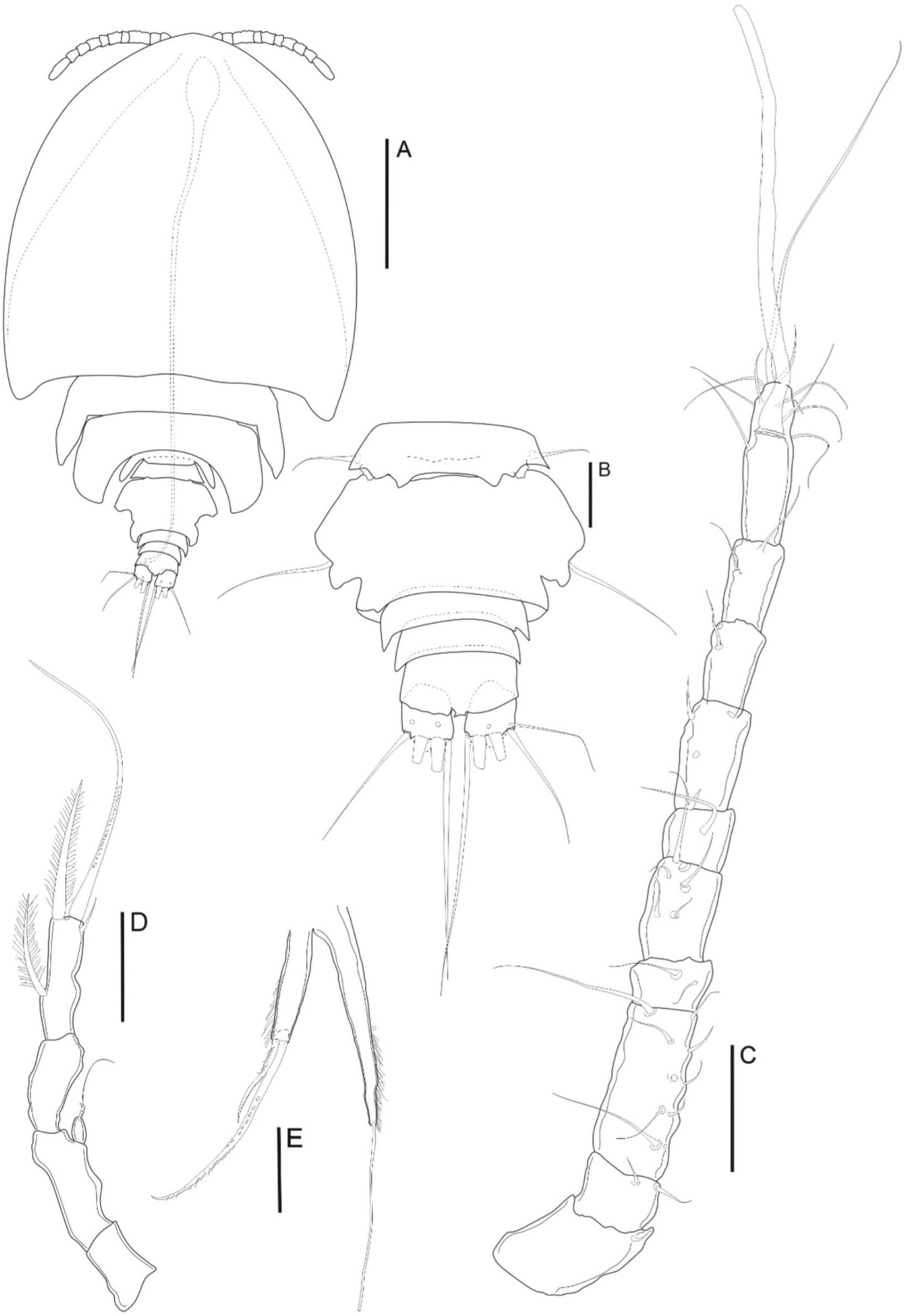


Figure 4



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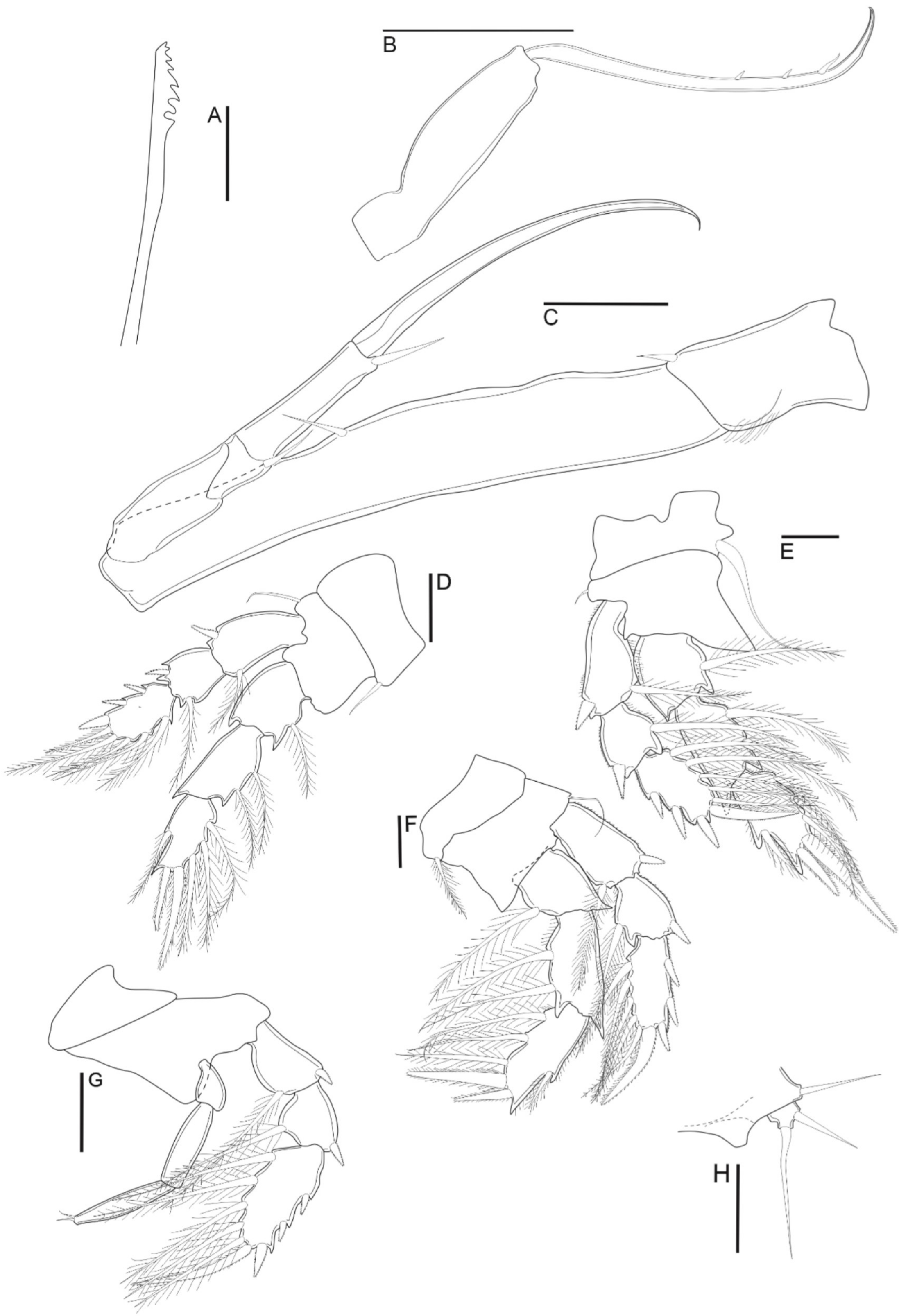

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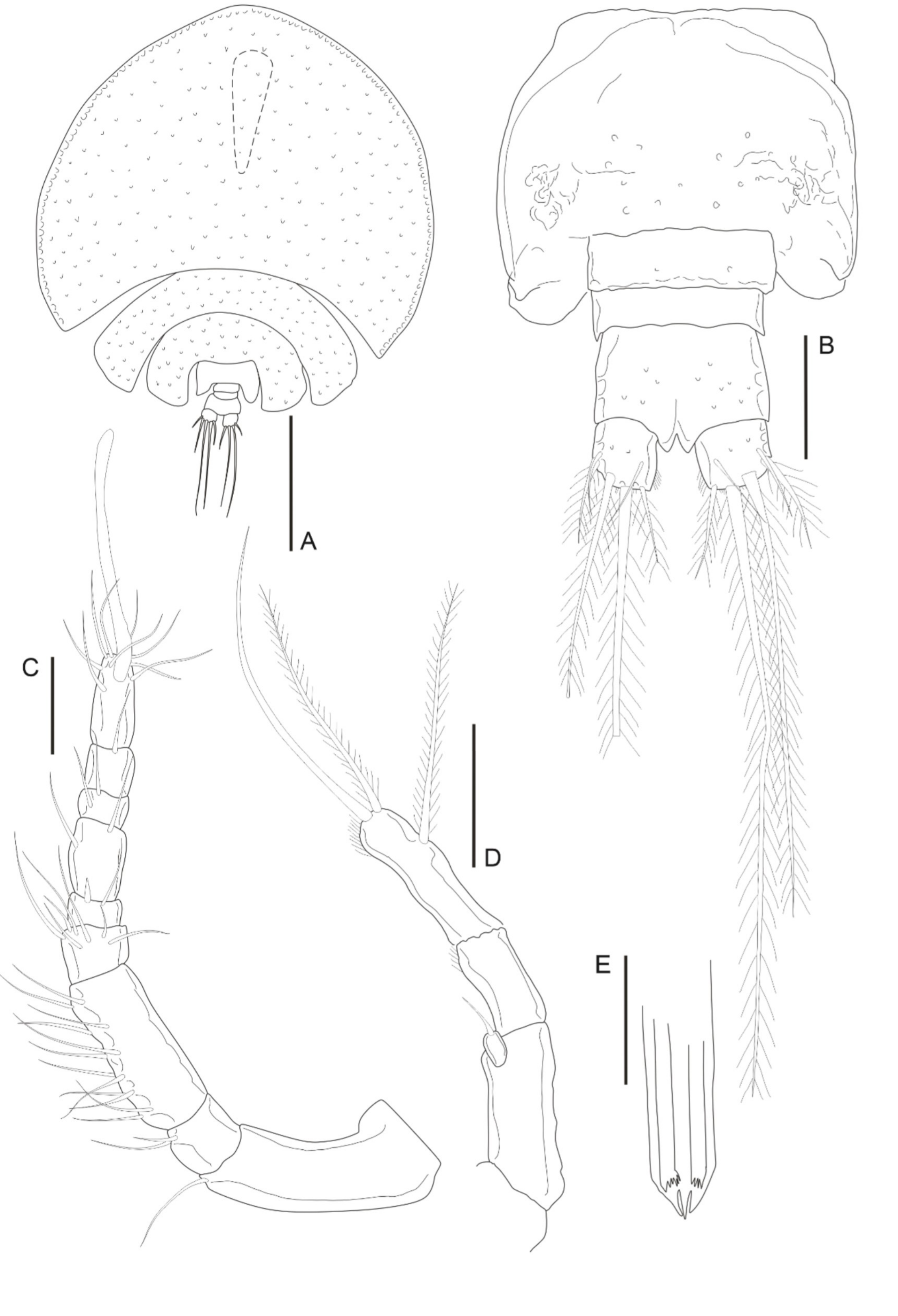

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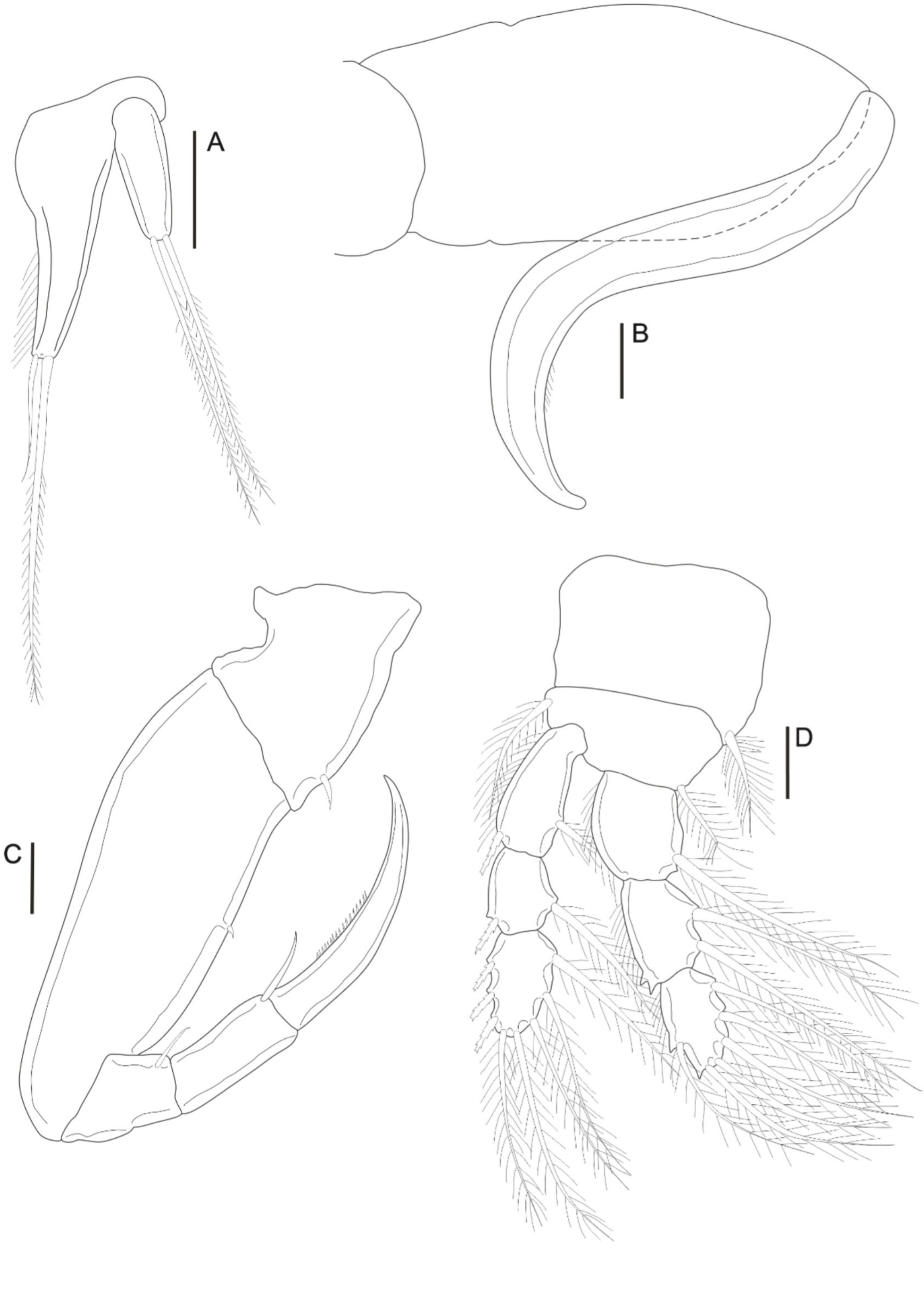

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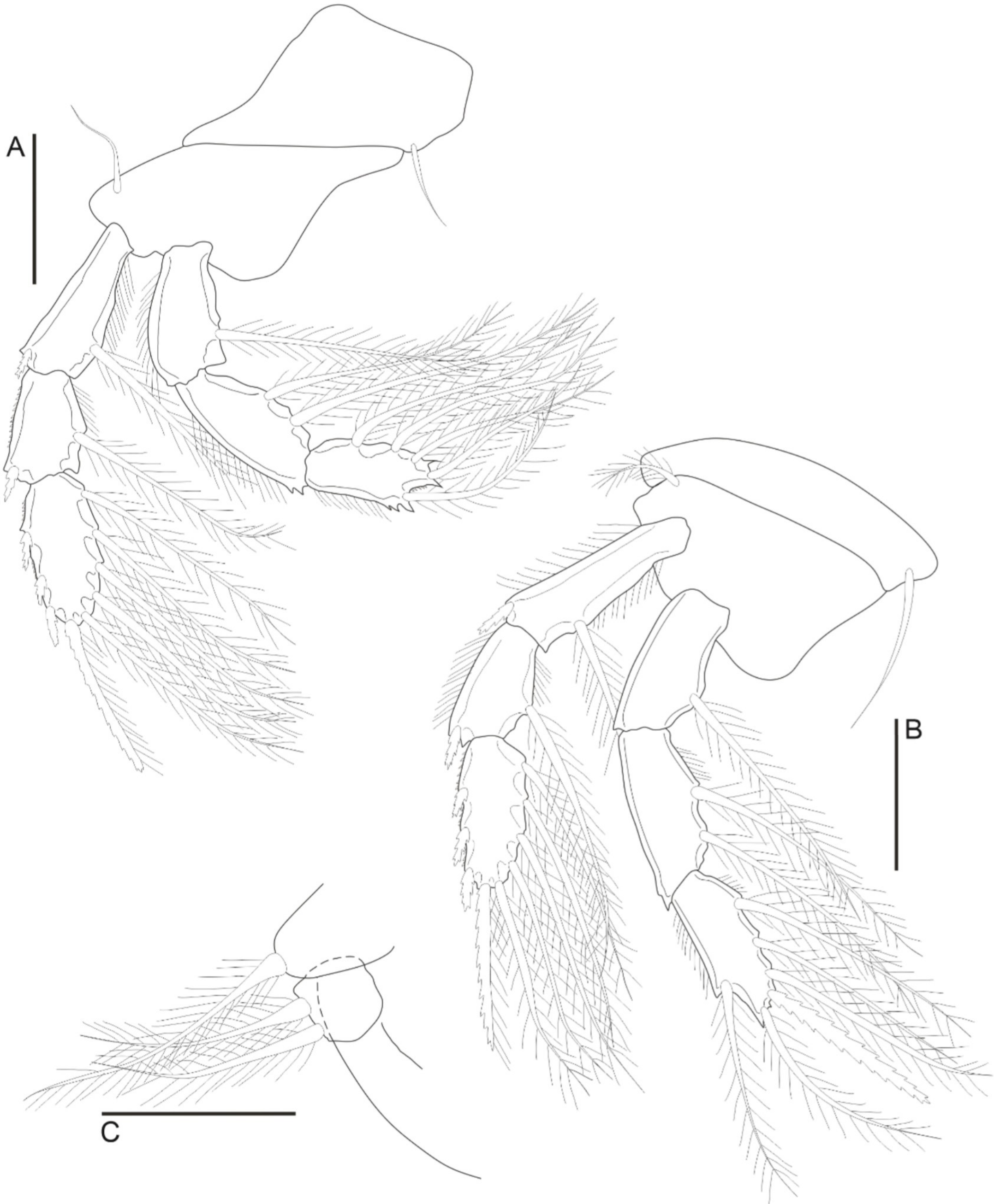

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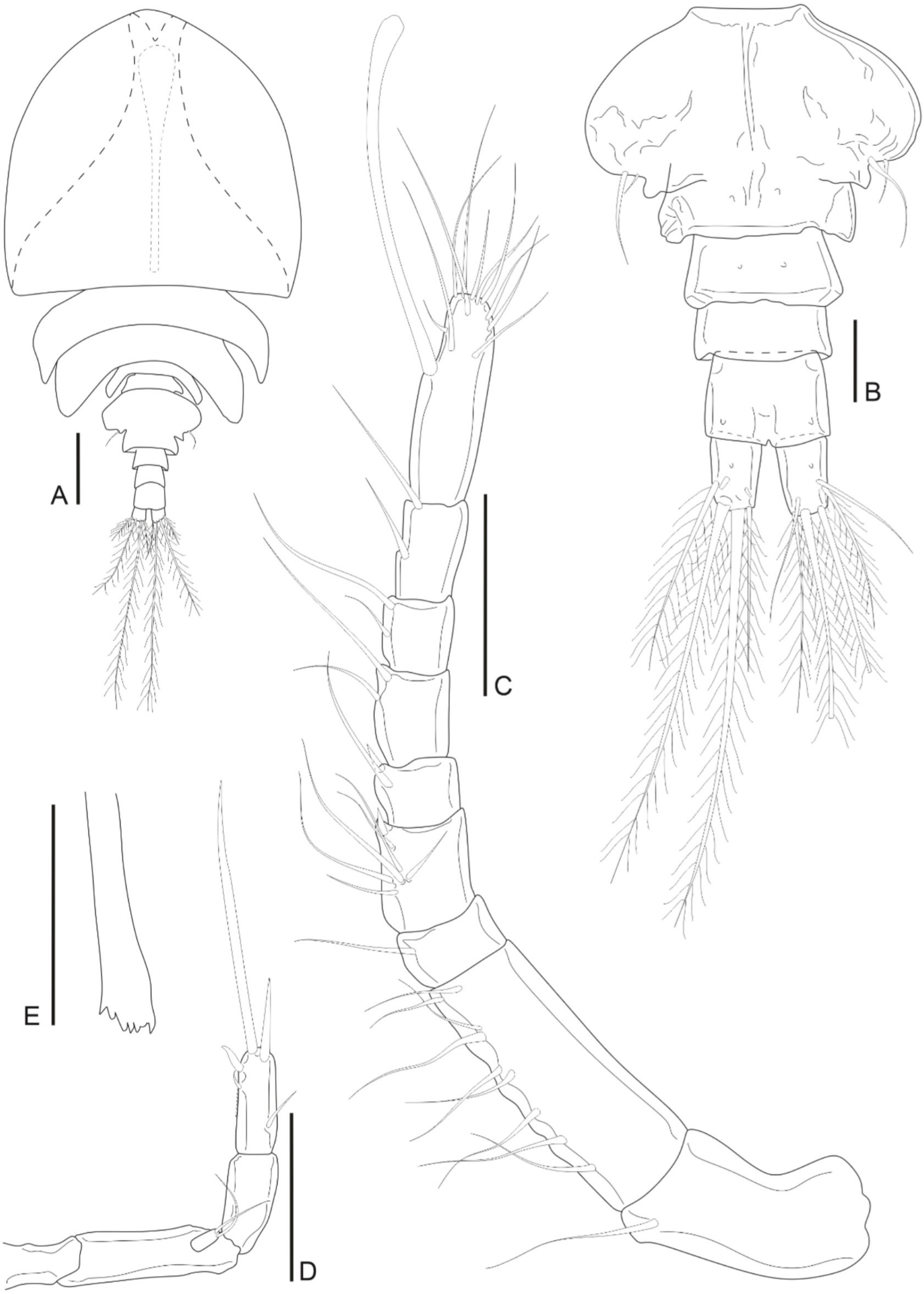

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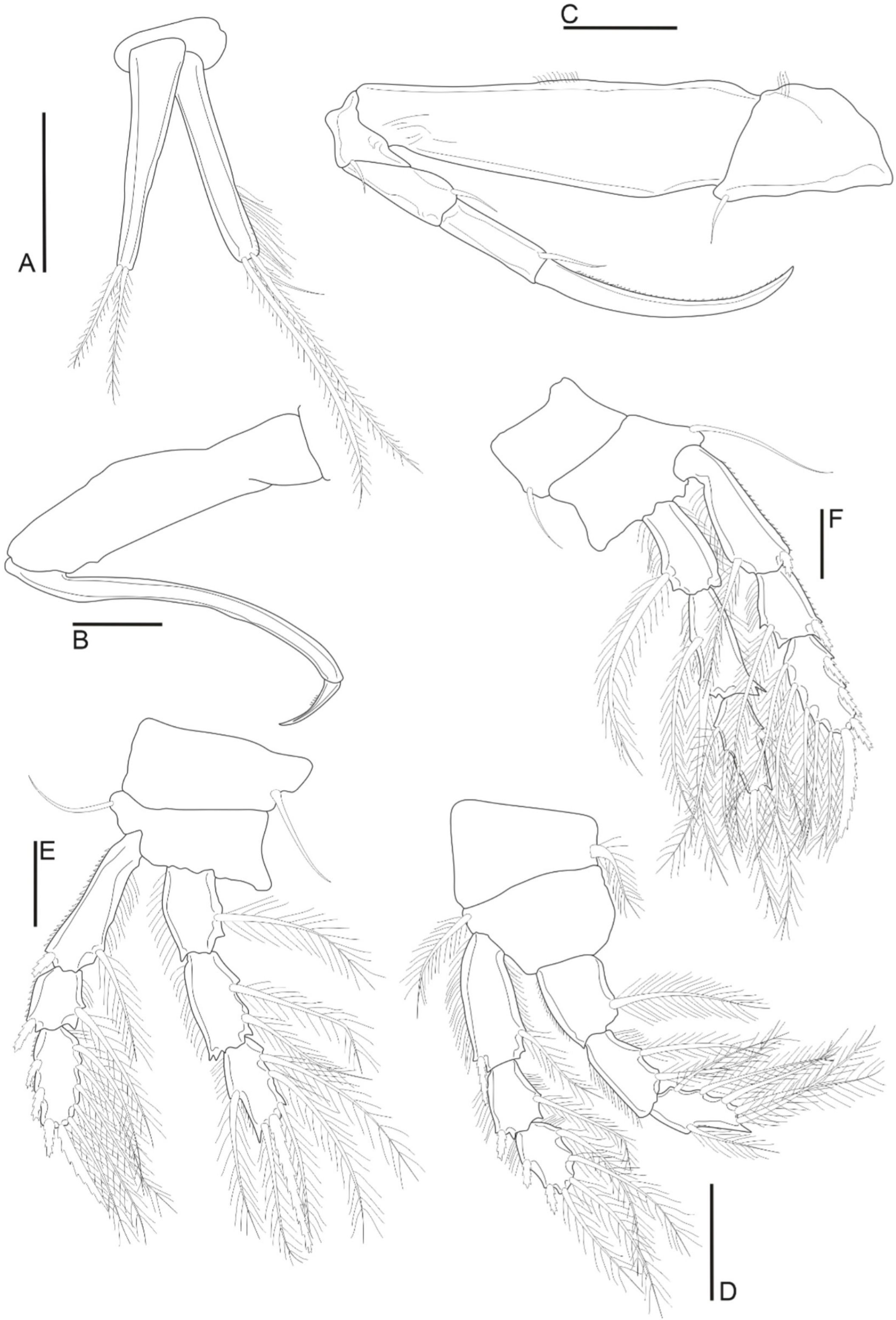


Figure 11

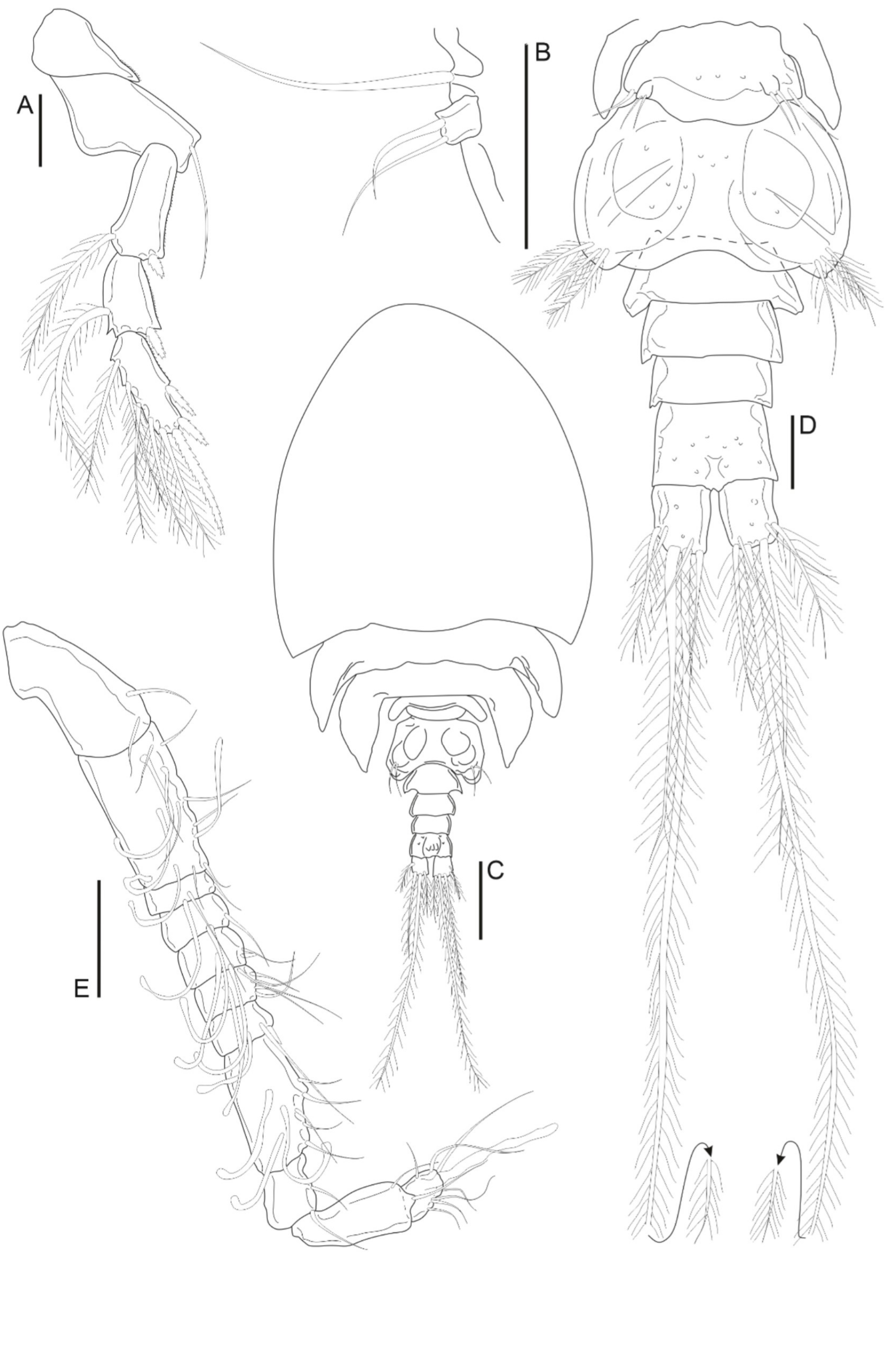
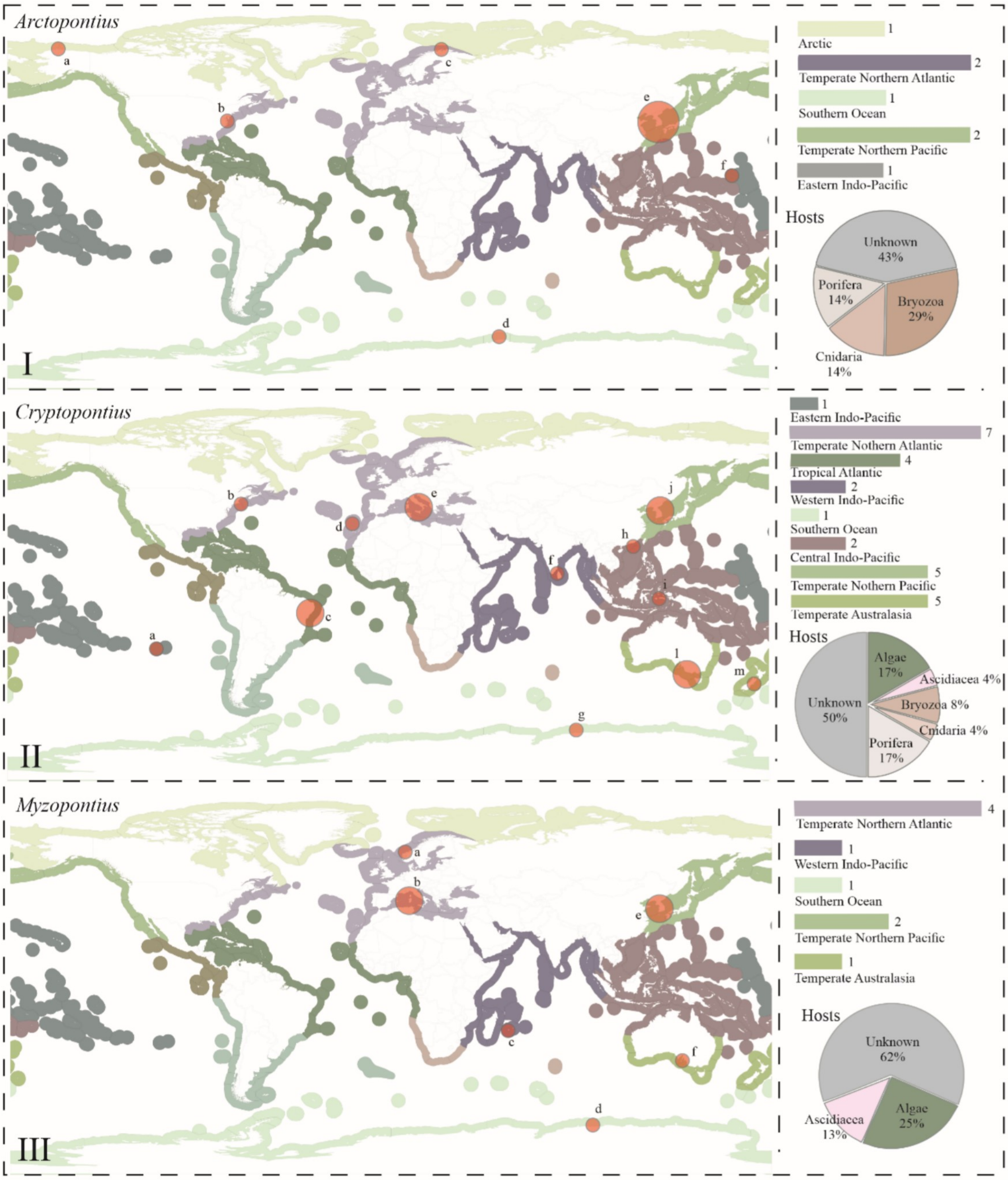
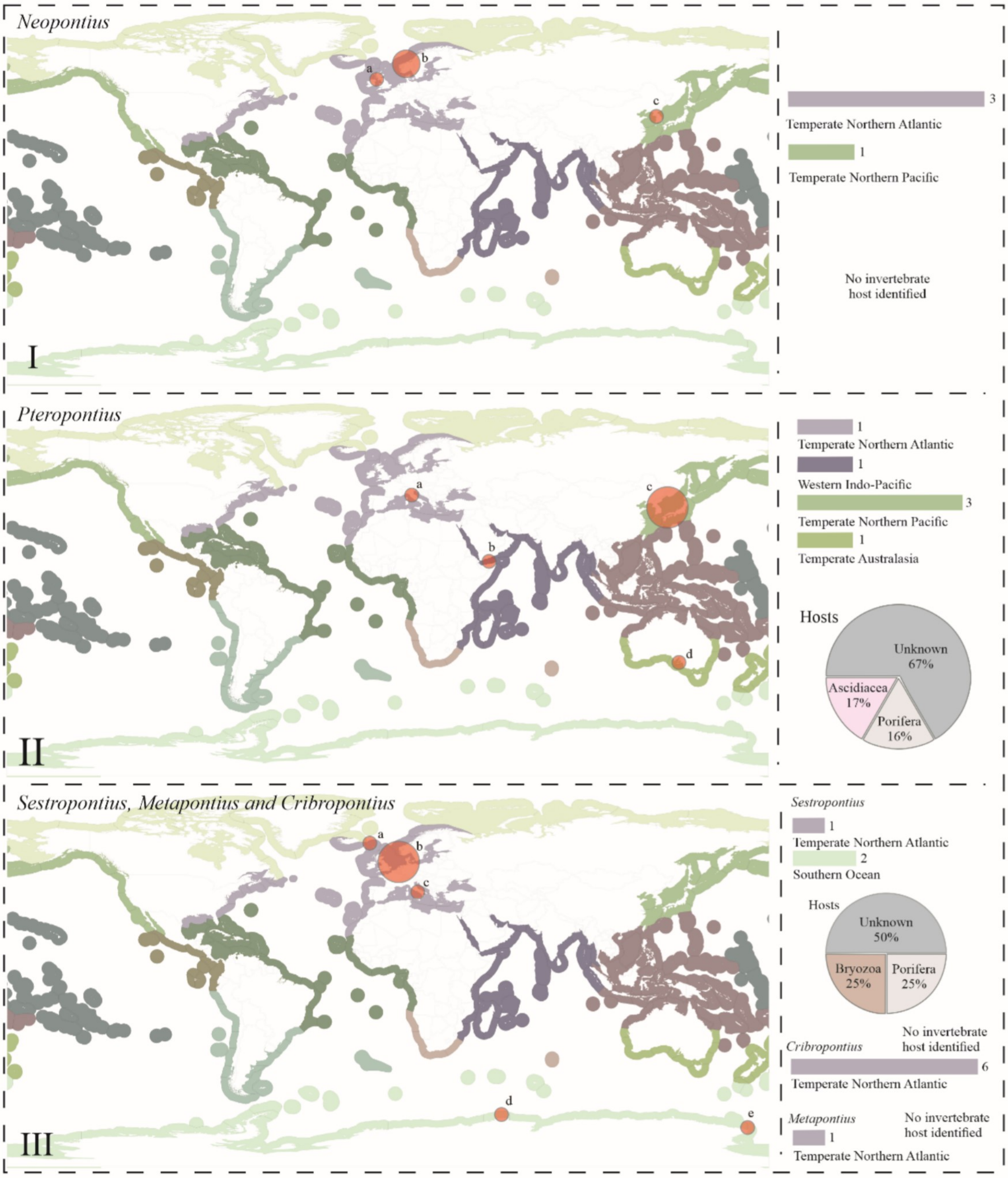


Figure 12



Arctopontius
I
Arctic 1
Temperate Northern Atlantic 2
Southern Ocean 1
Temperate Northern Pacific 2
Eastern Indo-Pacific 1
Hosts
Unknown 43%
Porifera 14%
Bryozoa 29%
Cnidaria 14%
Cryptopontius
II
Eastern Indo-Pacific 1
Temperate Nothern Atlantic 7
Tropical Atlantic 4
Western Indo-Pacific 2
Southern Ocean 1
Central Indo-Pacific 2
Temperate Nothern Pacific 5
Temperate Australasia 5
Hosts
Algae 17%
Ascidiacea 4%
Bryozoa 8%
Cnidaria 4%
Porifera 17%
Unknown 50%
Myzopontius
III
Temperate Northern Atlantic 4
Western Indo-Pacific 1
Southern Ocean 1
Temperate Northern Pacific 2
Temperate Australasia 1
Hosts
Unknown 62%
Ascidiacea 13%
Algae 25%

Figure 13



Neopontius
a
b
c
I
3
Temperate Northern Atlantic
1
Temperate Northern Pacific
No invertebrate host identified
Pteropontius
a
b
c
d
II
1
Temperate Northern Atlantic
1
Western Indo-Pacific
3
Temperate Northern Pacific
1
Temperate Australasia
Hosts
Unknown 67%
Ascidiacea 17%
Porifera 16%
Sestropontius, Metapontius and Cribropontius
a
b
c
d
e
III
Sestropontius
1
Temperate Northern Atlantic
2
Southern Ocean
Hosts
Unknown 50%
Bryozoa 25%
Porifera 25%
Cribropontius
No invertebrate host identified
6
Temperate Northern Atlantic
Metapontius
No invertebrate host identified
1
Temperate Northern Atlantic

Capítulo 3 – Phylogenetic relationships of the Artotrogidae Brady, 1880 (Copepoda, Siphonostomatoida) genera

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Artigo a ser submetido para publicação no periódico Zoologischer Anzeiger

Phylogenetic relationships of the Artotrogidae Brady, 1880 (Copepoda, Siphonostomatoida) genera

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Abstract

Artotrogidae is a diverse siphonostomatoid family with a cosmopolite distribution. Despite its historically discussed classification, there is no phylogenetic analysis focusing on its genera relationships. A phylogenetic analysis based on 103 female morphological characters and 27 species of the family was made under equal and implied weighting. Based on the results obtained it is proposed to subdivide the family into two subfamilies: Artotrogidae subfamily nov. 1 and Artotrogidae subfamily nov 2. *Discopontius* is recovered as an Artotrogidae genus closely related to *Pseudotrogus* and *Arctopontius*. Morphological evolutionary trends are observed for the antennule segmentation, for the body shape, and for the legs segmentation and armature formula.

1. Introduction

Artotrogidae systematics has already been extensively discussed in the last century (Brady, 1880; Giesbrecht, 1899; Sars G.O., 1918; Eiselt, 1961). Since its origin, the first described genera were intrinsically related to the Asterocheridae family (Boeck, 1859; Thorell, 1859). On the classifications proposed by Thorell (1859), Brady (1880), and Giesbrecht (1899), both lineages of siphonostomatoid associated with invertebrates shared the same family. While G.O. Sars (1918) was the first to separate them, drawing a clear distinction on a family level. However, Sars split the known Artotrogidae genera into three different families: Myzopontiidae, Dyspontiidae, and Artotrogidae sensu Sars, based on the body shape, and mostly by different patterns of reduction on leg 4 (Sars G.O., 1918).

Only a few decades later, on the extensive revision of J. Eiselt (1961), the author stated that two of his newly described genera *Pseudotrogus* Eiselt, 1961 and *Neobradypontius* Eiselt, 1961, exhibited features that placed them as the link between Dyspontiidae and Artotrogidae *sensu* Sars; and similarly, the genus *Metapontius* Hansen, 1923 showed features suggesting it as the link between Myzopontiidae and Dyspontiidae. Thus, the author concluded that the three families should be one, following the principle of priority, under the name of Artotrogidae, but with a different diagnosis (Eiselt, 1961). The classification proposed by Eiselt for Artotrogidae was initially well accepted (Ummerkutty, 1961; Stock, 1965; 1966; 1985; Kim I.H., 1996; Holmes, 1998); with a few exceptions (Ho, 1984; McKinnon, 1988a; Malt, 1991).

Holmes (1998) studied the relationships between his newly described genus and species, *Glannapontius maculatus* Holmes, 1998, and three other Artotrogidae genera: (*Myzopontius*, *Bradypontius,* and *Dyspontius*) through a fenetic methodology. In this study, *Glannapontius* appeared as related to *Myzopontius*, and these genera showed a close relation to *Bradypontius,* and *Dyspontius*, clearly separated from the Asterocheridae genera used in the analysis (Holmes, 1998).

In his thesis, Johnsson (2003) studied the phylogenetic relationships of the siphonostomatoid families, focusing on Asterocheridae. In the analysis, 19 families associated with invertebrates, 4 families associated with fishes, and 2 *incerta sedis* genera were analyzed. In this comprehensive context, 20 artotrogid genera were included, except *Metapontius* Hansen, 1923, *Sewellopontius* Ummerkutty, 1966 and the recently described *Artogordion* Ivanenko *et al*., 2018, *Chejupontius* Lee J., and Kim I.H., 2023, Artotrogidae Gen. *et* sp nov Farias *et al*., in prep. The family was found to be monophyletic by including 3 other genera: *Australomyzon* (Asterocheridae), *Bythocheres* (*incerta sedis*) e *Hyalopontius* (Megapontiidae), overall, by sharing fused segments (III–IV, XV–XVI, XVII–XVIII, XIX–XX) on female antennule (except *Australomyzon*), the absence of the mandibular palp (except *Australomyzon*), and the maximum armature formula on the third exopodal segment of legs 2, 3 and, 4.

With this complex historically discussed classification, no phylogenetic study focusing on the relationships within the family has been proposed since. Therefore, this study aims to propose the first phylogenetic hypothesis of relationships among Artotrogidae genera, and describe possible evolutionary patterns occurring in the family.

2. Material and methods

2.1. Taxonomical analysis

The examined specimens were provided by zoological crustacea collections from Museu de História Natural da Universidade Federal da Bahia, Naturhistorisk Museum, Natural Museum of Natural History, and South Australian Museum. The species and genera whose loan could not be granted were analyzed based on the original descriptions, or posterior redescriptions of the species. All examined material and literature are detailed in (Table 1).

The specimens were observed on temporary slides, mounted in immersed glycerin, with adhesive plastic rings to avoid crushing the organism (Kihara and Rocha, 2009). Measurements were made along the midline with the aid of ZEISS Axio Lab.A1 microscope, equipped with an iPad (7th generation) and digital camera lucida from Zeiss Labscope Software (version 4.0.2). Illustrations were vectorized with the Software CorelDraw 2021 (version 23.1.0.389). On the antennule segments, Roman numerals represent ancestral segments, and the Arabic numerals are the number of setae. On the armature formula of the legs 1 to 4, Roman numerals represent spines and Arabic numerals represent setae (Huys and Boxshall, 1991).

2.2. Data Matrix

The data matrix (Table 2) was constructed based on 27 terminal taxa: 24 valid species of Artotrogidae, and 3 outgroups. 103 morphological characters statements were selected: 1–11 of aspects of the body; 12–25 of antennule; 26–32 of the antenna; 33–50 of oral appendages; 51–103 of legs morphology. Among these, 88 characters are binary and 15 are multistate. Multistate characters 1, 4, 8, 9, 10, 26, 29, 30, 34, 38 and, 40 were considered ordered. The character statements list (Table 3) was based on specimen analysis and previously published bibliography (Huys and Boxshall, 1991), and the character statements follow the fundamental functional components stated by Sereno (2007).

2.3. Ingroup and outgroup selection

Ingroup – 23 type species of valid genera of Artotrogidae: *Abyssopontius altus* Stock, 1985; *Arctopontius expansus* Sars G.O., 1915; *Artogordion ridgeus* Ivanenko et al., 2018; *Ascidipontius concavus* Kim I.H.,1996; *Bradypontius magniceps* (Giesbrecht, 1895); *Chejupontius variabilis* Lee and Kim I.H., 2023; *Cribropontius normani* (Giesbrecht, 1899); *Cryptopontius thorelli* (Giesbrecht, 1895); *Dyspontius striatus* Thorell, 1859; *Glannapontius maculatus* Holmes, 1998; *Glyptotrogus tangaroae* McKinnon, 1988a; *Metapontius latispinis* Hansen, 1923; *Myzopontius pungens* Giesbrecht, 1895; *Neobradypontius antarcticus* Eiselt, 1961; *Neopontius angularis* Scott, 1898; *Pseudotrogus uncinatus* (Eiselt, 1961); *Pteropontius cristatus* Giesbrecht, 1895; *Pulicitrogus compressus* Kim I.H.,1998; *Sestropontius bullifer* Giesbrecht, 1899; *Sewellopontius rectiangulus* Ummerkutty, 1966; *Tardotrogus challengeri* Eiselt, 1961 and Artotrogidae Gen. *et* sp. nov. (Farias *et al*., in. prep.). *Artotrogus orbicularis* Boeck, 1859 and *Antarctopontius spinipes* Eiselt, 1965 original descriptions lack much essential information. Thus, *A. orbicularis* was replaced with *Artotrogus sarsi* Kim I.H., 1996,. The species remains the most similar to the type species of *Artotrogus*. Regarding *An. spinipes,* the species is still monospecific, and it was described based on a male specimen, and most of its body morphological features were missing. The female is still unknown, and it was not possible to replace the species, thus, it was removed from the analysis.

Outgroups – Asterocheridae is the most closely related family to Artotrogidae (Boxshall and Halsey, 2004). So, the type species of the family seemed to be a good outgroup to be included, since it would be the most similar non-Artotrogid taxon, providing the base to test the monophyly of the family. As the type specimen of *Asterocheres lilljeborgi* Boeck, 1859 could not be found, *Asterocheres reginae* Boxshall and Huys, 1994 was selected as a substitute, and its data were based on the literature. As stated by the authors, the species displays many of the plesiomorphic character states of Siphonostomatoida, such as 21-segmented antennule, 3-segmented antenna endopod, and 1-segmented exopod, 2-segmented mandibular palp, and 3-segmented maxilliped endopod; so, despite not being the type species of the genus, it could easily represent the family. Furthermore, we also added another Asterocheridae species: *Discopontius discoides* Nicholls, 1944, which was first described as a Dyspontiidae (*sensu* Sars). This family was synonymized to Artotrogidae; however, *D. discoides* despite sharing the absence of the mandibular palpus, it was not placed within the family, mainly due to the fusion of the pedigerous somites 3 and 4, resulting in 3 free pedigerous somites, one less than in Artotrogidae (Eiselt, 1961). It also has two antennule segments after the aesthetasc, which is an asterocherid feature (Nicholls, 1944). Additionally, *Cyclopicina longifurcata* (Scott T., 1901) was selected as a Cyclopoida representant. This species displays many of the most plesiomorphic characters among others from its order; such as 26 antennular segments, only one less than the maximum known for any other copepod, and the setation formula of the legs shows the maximum number of elements than any other cyclopoid species (Huys and Boxshall, 1990), thus, it may be a good species to represent the hypothetical ancestral order.

2.4. Phylogenetic analysis

The character matrix was built using WINCLADA (Nixon, 2002). Data were analyzed using "traditional search", heuristic search based on parsimony in TNT 1.6 (Goloboff and Morales, 2023). Two analyses were performed: 1) EW (equal weighting) and 2) IW (implied weighting), both with 9999 replications, saving 10 trees per replication. The script selected concavity constant value (*k*=5.078125), which was set by the script setk.run (S. Arias, unpublished data), which evaluates the best value matches the data (*setk.run*) and how strongly homoplasy is downweighed (Goloboff et al., 2008). The swapping algorithm used was TBR (tree bisection reconnection). The support values for each branch were calculated using Symmetric resampling (not distorted by weights/costs), with 5000 replicates, (P=33) (Goloboff *et al*. 2003); and using Bremmer support (Bremmer, 1994) up to 1 step longer through traditional search, values given as relative numbers, both evaluated with TNT 1.6 (Goloboff and Morales, 2023).

3. Results

The EW analysis retrieves a single most parsimonious tree with the best score (TBR): 317 (0,366 consistency index, 0,482 retention index) (Fig. 2 left). The IW analysis under concavity constant (*k*) value 5.078125 (*setk.run* script selected) retrieved two most parsimonious trees with the best score (TBR): 23.23400 (0.359 consistency index, 0.466 retention index), a strict consensus tree (Nelsen) was calculated (Fig. 1).

Although this was not the main purpose of this study, both analyses have successfully retrieved the monophyly of the Artotrogidae, with the genera *Asterocheres* and *Australomyzon*, recognized as belonging to Asterocheridae, and placed as sister-group of Artotrogidae. *Cyclopicina*, as expected once it is from another order, is located basally in relation to Asterocheridae and Artotrogidae clade.

Relevant results observed in both phylogenetic analyses are indicated below followed by the incongruences between them, which are pointed out, but they are going to be thoroughly discussed posteriorly.

1) *Discopontius* is recorded as part of the Artotrogidae clade. However, its position within the family is not exact;

2) 3 genera (*Metapontius, Abyssopontius* and *Artogordion*) are placed in a basal position regarding the Artotrogidae, the first two genera are retrieved as sister-groups but the position of *Artogordion* is variable;

3) subsequently the following genera are retrieved: *Myzopontius, Neopontius* and *Glannapontius*. The last genus, *Glannapontius*, is always observed as sister-group of a clade containing the majority of the Artotrogidae genera;

4) within this main Artotrogidae clade we observe two subclades in both analyses and the composition between them differs due to the following aggrupation (*Arctopontius* (*Pseudotrogus* + *Discopontius*) which changes between both subclades;

5) the first subclade has the following genera: *Sestropontius*, *Cribropontius*, *Neobradypontius*, *Glyptotrogus* and *Artotrogus*;

6) the second subclade aggregates ((*Sewellopontius* + *Tardotrogus*) + (*Pteropontius* + Artotrogidae gen. *et* sp. nov,)) in both analyses, it also includes *Pulicitrogus*, *Chejupontius*, *Ascidipontius*, *Cryptopontius*, *Dyspontius* and *Bradypontius* – all of them with different phylogenetic relationships, except *Bradypontius* which is always retried basally in the clade.

Based on the better establishment of the internal relationships of Artotrogidae genera, evidenced by the higher support values obtained, we decided to follow the results yielded by the IW analysis under concavity constant (*k*) value 5.078125 (Figure 1). Bold character transformations indicate unambiguous synapomorphies. Nodes synapomorphies on Table 4, terminal taxa synapomorphies on Table 5.

3.1. Systematics, clades and characters transformations

The results obtained by the IW analyses shows that the morphology of the antennule is an extremely important aspect of defining the Artotrogidae family (Clade 37). Six unambiguous synapomorphies, all of them located on the first three cephalic appendages, antennule, antenna, and mandible. Three of them are located on the medial portion of the segmentation of the antennule, which means between the characteristic fusion of ancestral segments IX-XII and the XXI segment with the aesthetask. Therefore the absence of the articulations between the ancestral segments XV–XVI, XVII–XVIII, XIX–XX (**Char. 22: 0→1; Char. 23: 0→1; Char. 24: 0→1**) indicates a pattern that the six original ancestral segments are united two by two. On the distal portion of the antennule – posteriorly to the ancestral segment XXI (**Char. 25: 0→1**) occurs the fusion of this segment with all the posterior ancestral segments, XXII to XXVIII. One additional synapomorphy is located on the antennal endopod, which shows the presence of three distal setae (**Char. 31: 0→1**). The last synapomorphy is the absence of the mandibular palp (**Char. 36: 0→1**).

Artogordion, Metapontius, and *Abyssopontius* compose the first Artotrogidae sub-clade that is recovered, being the sister group of all other genera (Fig. 3). The clade is characterized by the unarmed third endopodal segment of the maxilliped (**Char. 48: 0→1**) as an unambiguous synapomorphy. *Metapontius* and *Abyssopontius* (clade 38) appear as a new clade inside clade 39 by showing four homoplastic synapomorphies: the absence of the articulation between the ancestral antennular segments XIII–XIV (Char. 21: 0→1), being an additional medial pair of segments on the antennule that has lost its articulation; the absence of the seta e2 on leg 1 (Char. 68:0→1); the reversion of the seta f4 on leg 4 to a plumose shape (Char. 96: 1→0) and the absence of the protopod seta on leg 5 (Char. 100: 0→1).

As in clade 37, which represents the Artotrogidae, and in clade 39, articulation of the ancestral segments of the antennule has an important role in understanding the relationships of within the family. So far, all loss of segmentations are restricted to the medial and distal portion of the appendage, and the basal portion has remained without any lost articulation. However, clades 36, 35, and 34 have, subsequently, as synapomorphic modifications on the articulations on the basal region of the antennule.

Clade 36 shows the loss of articulation of antennule segments II-III (**Char. 14: 0→1**). plus, this clade also shows the concave shape of the posterior medio-dorsal margin of the cephalosome (Char. 3: 1→0). Based on those two diagnostic characteristics we proposed the Subfamily nov. 2. *Myzopontius* is the only genus of the clade that is restricted to these modifications.

On clade 35 occurs the loss of the articulation between antennule segments III-IV (**Char. 15:0→1**) and also a new modification on the medial region of the antennule on segments XIII-XIV (Char. 21:0→1). *Neopontius* shares this modification with the remaining genera of clade 34 but *Neopontius* does not show further alterations.

Finally, clade 34 has additionally lost articulations of segments IV–V, V–VI, VI–VII, and VII–VIII (**Char. 16:0→1, 17:0→1, 18:0→1**, 19:0→1), respectively, as observed in *Glannapontius* and the genera from clade 33. The clade 34 also exhibits the syncoxa relative size as long as the basis (Char. 40: 0→1) on one of the most parsimonious trees as a homoplastic autapomorphy.

The remaining Artotrogidae species placed on clade 33 splits into two lineages (clade 42 and clade 32). From the clade 33 on, the modifications are not centered on the antennule anymore but on the general shape. Both lineages share transformations on the body aspect as synapomorphies. First, the posterolateral projections of the third pedigerous somite distal margin reaching the genital somite (**Char. 4: 0→1**); and, the width of the anal somites exceeding the length (**Char. 10: 1→2**), plus, they also share the **plumose** shape of the seta f4 as a reverted transformation on leg 4 (Char. 98: 1→0).

On the first lineage (clade 42) *Sestropontius*, *Cribropontius,* and Clade 41 are in an unsolved polytomy (Fig. 4) by showing a single seta on the distal margin of the antennal exopod (**Char. 29: 2→3**) as a synapomorphy.

Clade 41 places *Neobradypontius* as a sister group of clade 40 sharing three homoplastic synapomorphies, which are the cephalosome showing more than three-quarters of the body size (Char. 1: 1→2), the third pedigerous somite posterolateral projections reaching beyond the genital somite (Char. 4: 1→2), and the caudal rami length as long as width (Char. 11: 0→1).

Ultimately, within clade 40, *Glyptotrogus,* and *Artotrogus* share the absence of leg 4 also as a homoplastic synapomorphy (Char. 85: 0→1).

The second lineage (clade 32) presents two clades (31 and 47), both of them sharing the absence of a seta on the basis of the maxilliped (Char. 45: 1→0). This character is a reversion to a plesiomorphic state.

The clade 31 exhibits *Arctopontius expansus* as sister group of clade 30 (Fig. 5) by sharing characters that indicates a trend towards reductions on leg 4 endopod, Firstly the absence of three setae f1, f3 – as homoplastic transformations – and f6 – as a synapomorphy (Char. 94: 1; 95: 1; **98: 1)**, secondly the absence of the second endopodal articulation (Char. 91: 1). The clade 31 also shows the urosome length as long as the width (Char. 8: 0→1), as another homoplastic transformation. Finally, *Pseudotrogus* and *Discopontius* compose clade 30 by sharing prosome relative size above three-quarters of the body (Char. 1: 1→2), the absence of the articulation of the ancestral antennular segments XII–XIII (Char. 20: 0→1) and the absence of the seta c9 on leg 2 (Char. 76: 0→1) as three homoplastic synapomorphies; plus, the presence of the articulation of the ancestral antennular segments XIII-XIV (Char. 21: 1→0) and the seta f4 of the leg 2 plumose (Char. 78: 1→0).

The second clade of lineage 2 (clade 47) has *Bradypontius* as the sister group of the remaining species (clade 46) united by the oral cone reaching between the first and the fifth intercoxal sclerite (Char. 34: 0→1), and the maxillary syncoxa shorter than the basis, as a reversion to a plesiomorphic condition (Char. 40: 1→0) on one of the most parsimonious trees.

In clade 46, *Dyspontius* and its sister group, clade 45, exhibit two synapomorphies on leg 4, (1) the absence of the coxal inner seta (**Char. 87: 0→1**) and (2) the absence of the endopod (**Char. 90: 0→1**). they also share the reverted state of the articulation between the ancestral antennular segments VII–VIII (Char. 19: 1-0); a reduction on the leg 1 armature represented by the absence of seta c8 (Char. 63: 0-1).

Clade 45 presents *Cryptopontius* as sister of the remaining Artotrogidae species (clade 44) by sharing the absence of the seta e2 on leg 1.

Clade 44 (Fig. 6) splits into two clades (43 and 49), both of which share some armature formula reductions on leg 1: the absence of seta a3, seta b1 and seta f1 (Char. 57: 0→1, **Char. 58: 0→1, Char. 69: 0→1**), the latter two being unambiguous synapomorphies. It also exhibits the reversion of the fifth pedigerous somite length size, which is as long as the length of the fourth, as a synapomorphy for the clade **(Char. 7: 1→0)**.

Clade 43 is composed of *Ascidipontius*, *Chejupontius* and *Pulicitrogus*. *Ascidipontius* is placed as a sister group of clade 50 by sharing the absence of the seta f3 as a homoplastic synapomorphy (Char. 62: 0→1); and seta c7 on the first leg (**Char. 70: 0→1**) as an unambiguous synapomorphy. *Chejupontius* and *Pulicitrogus* (Clade 50) share the spiniform-shaped c4 seta (**Char. 61: 0→1**) and the presence of the coxal inner seta (**Char. 87: 1→0**), both on leg 4, as a plesiomorphic condition, as synapomorphies. It also shares the absence of the seta c9 on leg 4 (Char. 89: 0→1) as a homoplastic synapomorphy.

The last clade (49) also splits into two other clades (48 and 51), both clades share three different homoplastic transformations of three different appendages: the fourth pedigerous somite width sizes up to half of the width size of the third (Char. 5: 1→2); the antennal exopod represented by seta (Char. 26: 1→2); and the absence of the leg 5 exopod (Char. 101: 0→1).

Artotrogidae gen. *et*. sp. nov. and *Pteropontius* (clade 48) exhibit the absence of the second exopodal articular division on leg 1 (**Char. 55: 0→1)** as an unambiguous synapomorphy. It also shows the genital segment with two posterolateral projections (Char. 9: 0→1), and the absence of articulation between the ancestral antennular segments VII–VIII (Char. 19: 0→1) as homoplastic synapomorphies.

Tardotrogus and *Sewellopontius* (clade 51) have three homoplastic synapomorphies uniting these two genera: the urosome and caudal rami length as long as the width (Char. 8: 0→1, Char. 11: 0→1); and the absence of the articulation between second and third endopodal segments of the maxilliped (Char. 49: 0→1). The only unambiguous synapomorphy of the clade is the absence of the seta a2 on leg 1 **(Char. 56: 0→1)**.

4. Discussion

Based on the phylogenetic hypothesis proposed in this study, the antennule segmentation, the body shape, the armature formula, and the leg segmentation play a major role in the unraveling of the Artotrogidae family relationships. Characteristics of the other cephalic appendages have minor or no influence on the family-level relationships. Therefore, those evolutionary trends were discussed on the following topics.

4.1. Antennule

The development of copepod antennules from larva to adult has been extensively studied in recent decades, and with the works of Dahms (1989), Boxshall and Huys (1998), and Schutze (2000) it is possible to understand that the total number of antennular segments are resulting of articulation additions, and the called – fused segments – are usually resulting of the failure of the expression of those articulations (Boxshall and Huys, 1998).

The 28-segmented ancestral hypothetic copepod antennule proposed by Huys and Boxshall (1991), showing no fused segments, has been widely accepted since it was proposed (Huys and Boxshall, 1991, Figure 1.5.1, p. 21). Based on this scheme, the plesiomorphic state of the antennule on siphonostomatoid copepods is 21-segmented, 7 less than the hypothetical model. This pattern is a result of the formation of the fused segments IX–XII, XXII–XXIII, XXIV–XXV, and XXVI–XXVIII (Figure 3). In this study, it is possible to understand that the artotrogid antennule is shaped by a high number of transformations towards the reduction of the total number of segments to a maximum of 17 and a minimum of 8 segments.

The family Artotrogidae exhibits as autapomorphies the fusion of the ancestral segments XV–XVI, XVII–XVIII, XIX–XX, and XXI–XXVIII, thus, leading to a maximum of 17 segments on the female antennule observed on the three genera included on the clade 39 (Subfamily nov. 1). When compared with the 21-segmented siphonostomatoid female antennule, artotrogids show the number of segments on medial region of the antennule (i.e., between segments IX–XII and XXI) reduced from 8 to 4;

and the number of segments on distal region (i.e., segment XXI to the end) reduced from 4 to 1 (Figure 3). These fusions were observed to be stable, but two genera, *Discopontius* and *Glannapontius,* show specific exceptions to this pattern. Therefore, these are considered reversions to the articulated ancestral state. Based on the proposed pattern of development of Siphonostomatoid antennules on Boxshall and Huys (1998), all those articulations usually appear in late copepodid stages, between the molt from copepodite 4 to 5, or from copepodite 5 to the adult female (Boxshall and Huys, 1998, Figure 8, p. 774).

While the transformations on the medial and distal portion of the antennule are diagnostic characters to the family, a set of sequential fusions on the proximal portion (i.e., before the IX–XII) are the main diagnostic characters of specific artotrogid clades 36, 35 and 34, and unlike the previously discussed segments, those articulations failed to appear on earlier copepodid stages (Boxshall and Huys 1998).

The articulations II–III (clade 36), failed to appear on the molt to the copepodid 4. The articulations III–IV (clade 35), failed to appear on the molt to the copepodid 3. Finally the articulations on clade 34 failed to appear on different copepodid stages, V–VI on the molt to the copepodid 1; IV–V and VI–VII on the molt to the copepodid 4; and, VII–VIII on the molt to the copepodid 5 (Boxshall and Huys, 1998, Figure 8, p. 774).

The formation of fused segments is more commonly observed in males of all orders, and they appear secondarily on the molt from copepodite 5 to male adult (Huys and Boxshall, 1991; Boxshall and Huys, 1998). Boxshall and Huys (1998) suggested that, besides geniculation and mating behavior, it may be related to an enhancement of sensorial ability. Regarding geniculation, artotrogids present the siphonostomatoid type, with a proximal geniculation between segments XIII and XIV, and a distal geniculation between segments XX and XXI (Huys and Boxshall, 1991).

Despite being focused on female specimens, it is possible to observe that in Artotrogidae the articulation between the segments XX and XXI, where the distal geniculation occurs, was not only preserved throughout the analyzed specimens but it a preserved articulation on all copepod orders (Boxshall and Huys, 1998).

However, the articulation of the proximal geniculation (XIII and XIV) is not preserved in the female antennule of some clades, being lost in clades 38 and 35, although a reversion is observed in a small group of terminal taxa (*Artotrogus*, *Discopontius*, *Pseudotrogus*, *Dyspontius*, *Ascidipontius*, Artotrogidae gen. *et* sp nov.). Once the male representatives show these two geniculations as part of the reproductive behavior (Huys and Boxshall, 1991, p. 331–337) a thorough analysis among the species that shows the segments XIII and XIV united should indicate a possible sexual dimorphism or if it also happens on the male specimens. This second possibility may have impact on the copulatory process once it appears that the mating behavior of certain artotrogid genera would lay only on the grasping ability of the distal geniculation.

4.2. Body shape

Unlikely on the antennule development, there is a lack of studies that analyze the formation of produced epimera, a characteristic feature of Artotrogidae species. In this investigation, those characters appeared to be occurring correlated to the proportional reduction of the length of the urosomites (clades 33 and 41), shortening the posterior portion of the body and consequently differentiating the body shape from the cyclopoid typically observed on asterocherids (Boxshall and Huys, 1994) and free-living cyclopoids (Huys and Boxshall, 1990) towards a more specific and characteristic shape of the Artotrogidae.

On clade 33, the projected epimera of the third pedigerous somite reaching the genital somite appears as an apomorphy, clearly distinguishing these with an artotrogid body shape from those with a cyclopoid body shape. A proposed next step is observed on the genera *Neobradypontius*, *Artotrogus*, *Glyptotrogus* (clade 41), and *Pseudotrogus* (clade 30), where the third pedigerous somite exhibits quite projected epimera, reaching beyond the genital somite. This next level of modification develops within the artotrogid species with a circular body shape appearing on two different clades, suggesting two independent events.

The circular body shape observed on artotrogid species is similar from the shield-like observed on Entomolepididae species (Borges *et al*. 2021). This body morphology may provide a lower hydrodynamic resistance, which could be, in addition to the dorso-ventrally flattened body plan, another beneficial adaptative trait to copepods that live associated on the surface of their hosts.

The body of an Entomolepididae can exhibit a reduced number of free pedigerous somites, a result of the absent articulation between the third and fourth pedigerous somites (Boxshall and Halsey, 2004). In addition, they do not exhibit the epimera lateral margins posteriorly projected, instead, their fourth pedigerous somite is generally well developed and the medial posterior margin is widened, concealing the whole urosome, as seen in *Spongiopsyllus* Johnsson, 2000 and *Entomopsyllus* Mckinnon, 1988 (McKinnon, 1988b; Johnsson, 2000), but except for *Parmulella* Stock, 1992 and *Neoparmulella* Farias, Neves and Johnsson, 2020, which have most of their urosome exposed (Stock, 1992; Farias *et al*. 2021).

4.3. Legs

Despite being defined by homoplastic characters; it is clear that the leg morphology and armature formula played a crucial role in the evolution of the two lineages (clades 32 and 42). The segmentation and armature formula of copepods' legs are considered crucial systematic tools to study the diversity from species to ordinal level. In addition, a wide roll of modifications can be observed in most copepod orders, in which a segment, a ramus, or both rami can be absent; and sometimes the entire leg can be lost (Huys and Boxshall, 1991).

The artotrogid family is known for presenting such variations the different levels of reduction observed in some genera were already used by G.O. Sars (1918) to separate them into three different families. That classification was replaced with Eiselt's (1961) with the discovery of new genera that, according to the author, appeared to be the link between these three taxa.

Eiselt's (1961) classification brought back the historically discussed idea, first proposed by Giesbrecht (1899), that the different reduction patterns of leg 4 constituted a gradient, and so, it was expected to see a clade with *Bradypontius*, which exhibits a narrow endopod with reduced armature formula, as the first step towards the loss of leg 4. Followed by *Metapontius,* which was suggested by Eiselt (1961) to be like among the initial levels, by exhibiting a 2-segmented endopod. The genera without endopod would be the third step towards reduction. *Pseudotrogus*, with the reduced leg 4, would be the link between them and those with a completely absent leg, the last step (Giesbrecht, 1899; Sars G.O., 1918; Eiselt, 1961).

However, the phylogenetic hypothesis proposed by this study suggests that those different levels of reduction observed on leg 4 occur independently in different clades within a specific group of Artotrogidae genera, the clade 33:

a) The first lineage of this group (clade 42), *Cribropontius*, *Sestropontius,* and *Neobradypontius* share a biramous leg 4 with 3-segmented rami; and the absence of leg 4 on *Artotrogus* and *Glyptotrogus* (clade 40) occurred within this clade in parallelism with *Tardotrogus* on clade 48 (Figure 4).
b) On the second lineage (clade 32), a biramous leg 4 with 3-segmented exopod and 2-segmented endopod occurs in clade 31 and is shared by *Arctopontius* and *Discopontius*. A step forward on this reduction trend of a 2-segmented endopod, is exhibited by *Pseudotrogus*, which shows an unsegmented ramus armed with 2 setae. A further reduction also happens on the coxa and basis of leg 4 of this genus, which forms a protopod thus differing from the plesiomorphic condition of the remaining genera of clade 31. The absence of the second segmental articulation on the endopodal ramus also occurred in parallelism with *Metapontius* (clade 38) (Figure 4).
c) The only level of reduction to establish a monophyletic clade was the uniramous leg 4 exhibited by the genera in clade 46, with *Bradypontius*, which has a biramous and 3-segmented leg 4, as its sister clade (Figure 5).

Therefore, different from Giesbrecht's (1899) and Eiselt's (1961) hypothesis of *Bradypontius* representing the first step of the levels of reductions on leg 4 as a unique chain of events, those observations establish evidence that the different levels of reduction on artotrogid species are not a result of a single evolutionary trend, instead, they arose three times on three different clades with a biramous 3-segmented leg 4.

Among those genera with an absent endopod on leg 4 (clade 46), a different pattern of reductions takes place and draws the line between within the lineages, initially at a minor level with the cumulative serial loss of setal elements on leg 1, which ends in a major reduction of segments on clade 51 (Figure 5).

First a seta (e2) is lost on the second endopodal segment on clade 45. This is followed by the loss of a spine (b1) on the third exopodal segment, and a seta (f1) on the third endopodal segment on clade 44. This clade splits into two groups, the first unites the three artotrogid genera known for Korean coast, *Ascidipontius*, *Pulicitrogus,* and, *Chejupontius* (clade 43), sharing the loss of a seta (f3) on the third endopodal segment. In addition, *Pulicitrogus* and *Chejupontius* (clade 50) are grouped by the loss of the coxal inner seta, the loss of the seta (c9), and the change to a spiniform shape of the distal seta (c4). The second group (clade 49) is initially assembled by a different set of characters, such as the antennal exopod represented by seta, and the absence of the exopodal segment on leg 5; but its internal clades, 48 and 51, are also defined by the losses on leg 1. The genera inside clade 48 share the loss of a spine (a2) on the first exopodal segment; and the genera inside clade 51 are the only artotrogid genera to exhibit segmental reductions on leg 1.

The modifications exhibited by *Pteropontius* and Artotrogidae gen. et sp nov. constitute a major step and change the perspective observed on the setal reduction of clade 46. On the study of the development of thoracopods of a cyclopoid species Ferrari (1998) described the developmental phases corresponding to the five copepodid stages in which a synchronized chain of segmentation occurred through a pleiotropic regulatory process. Following this model, new segments are added proximally on the most distal segment, thus, the 2-segmented rami showed by *Pteropontius* indicates that the second exopodal and endopodal segment observed in this genus are homologous to the third on other genera, and this morphology is a result of a failure on the process on the formation of the second exopodal and endopodal segment, considering a 3-segmented ramus. The unsegmented ramus exhibited by Artotrogidae gen. *et* sp nov. seems to have stopped on the first proposed stage of the development of the leg. In addition, the great variation in the armature formula and segmentation exhibited by the artotrogid legs, appears to be affected by a second set of 8 regulatory processes, also proposed by the same study, which determines the morphology of each ramus (Ferrari, 1998).

4.4. Appendages related to feeding behavior

Characters related to the antennal exopod setation (clades 42 and 49); oral cone relative size (clade 47); maxilla setation, and syncoxa size (clade 32, 34 and 47); and, maxilliped endopod segmentation (clade 48) were considered homoplastic on the analysis. Except for the distal setation of the antennal endopod and the absence of the mandibular palpus, unambiguous synapomorphies of the family; and the setation of the endopod of the maxilliped, an unambiguous synapomorphy of the subfamily nov. 1 (clade 48).

The antenna of siphonostomatoid copepods is frequently subchelate, forming a grasping appendage with the development of a distal claw-like seta, used for the attachment of the copepod body in its host (Huys and Boxshall, 1991). This condition is exhibited, as an apomorphic character state, in two terminal taxa: *Glannapontius* and

Discopontius. The majority of the genera exhibited a well-developed but delegate distal setae, not showing signs of grasping ability, as a plesiomorphic character state. While the exopod, of which the function is not clear, showed a known pattern of reduction for siphonostomatoid copepods (Huys and Boxshall, 1991). The ramus is usually 1-segmented in the order, as seen in most of the analyzed taxa, but could also be found represented by seta as in *Glannapontius*, *Tardotrogus,* and clade 51 or vestigial as seen in *Abyssopontius*.

When describing the feeding behavior of *Asterocheres* associated with sponges, Mariane and Uriz (2001) suggested that the mandibular palpus could act as a sensory appendage. Although the absence of the mandibular palpus is synapomorphic on Artotrogidae, it is not clear what are the effects of its absence. Similarly, with small variations between the clades, it was not possible to determine if the changes in the armature formula or segmentation of the grasping maxilla and maxilliped affected its function.

Considering that artotrogids are found associated with a wide variety of registered invertebrate hosts, such as sponges (Ummerkutty, 1961; Stock, 1965; Ho, 1984; Malt, 1991; Neves and Johnsson, 2008; Kim I.H., 2016), cnidarians (Stock, 1966; Johnsson, 2001; Johnsson and Neves, 2005; Kim I.H., 2007; Farias *et al*., 2020), bryozoans (Kim I.H., 1996; Johnsson and Rocha, 2002; Lee and Kim I.H., 2023), mollusks (Boeck, 1859), ascidians (Kim I.H., 1996) and algae (Ummerkutty, 1961; Eiselt, 1966; Neves and Johnsson, 2008, Farias *et al*., 2020; Lee and Kim I.H., 2023); this may be a evidence that the artotrogids are generalists with regard to preferred hosts or associated organism. In addition, most of artotrogid species are found in low numbers, with a few exceptions, such as: *Glannapontius maculatus* Holmes, 1998 (27 specimens) (Holmes, 1998); *Bradypontius macginitiei* Eiselt, 1986 (157 specimens) and *Arctopontius hanseni* Eiselt, 1986 (43 specimens) (Eiselt, 1986), that were obtained with different collect methods and no host specificity care.

Additionally, the presence of well-developed lateral gut caeca on *Artotrogus*, similar to the one observed in *Hyalopontius* Sars G.O., 1909, led Boxshall and Halsey (2004) to suggest that those species may have an intermittent feeding behavior, spending most of their time away of possible hosts. According to the author, true parasites such as Lernaeopodidae have a narrow tubular midgut lacking lateral caeca, as those species live permanently attached to their hosts, there is no need to store food (Boxshall, 1986). The well-developed gut morphology pointed to *Artotrogus* can also be observed on *Myzopontius*, *Cryptopontius*, *Dyspontius,* and *Bradypontius* on Giesbrecht's illustrations (1899, Tf. 1, Fig. 6–10, 12; Tf. 6, Fig. 30, 38; Tf. 2, Fig. 28; Tf. 8, Fig. 31; Tf. 10, Fig. 34), and therefore, may be attributed to the family.

Thus, once artotrogid species seem to exhibit pieces of evidence of a great capacity to explore different sources of food, the morphology of the appendages related to the feeding behavior may be highly variable among the genera, and therefore having a smaller or no role on the unraveling of the family relationships.

5. Conclusion

A heuristic search based on parsimony brought new evidence that elucidates Artotrogidae genera relationships. Two new subfamilies are proposed and the genus *Discopontius* is recorded as part of the family, closely related to *Pseudotrogus* and *Arctopontius*. Results unraveled three major evolutionary trends on the antennule segmentation, body shape, and, leg armature formula and segmentation.

Acknowledgements

The authors thank to Dr. Lutz Bachmann and Dra. Åse Wilhelmsen (Natural History Museum – University of Oslo); and to Dr. Adam Stergis, Dr. Chad Walter, Dr. Karen Osborn, and Dr. William Moser (National Museum of Natural History - Smithsonian Institution) for the support on the loan of the analyzed specimens. The authors are also grateful to the Chico Mendes Institute for Biodiversity Conservation (ICMbio) for collecting permission (Sisbio No 15161-1).

Funding

This study is part of the project 'Assessment and research of sun coral in Todos-os-Santos Bay', a cooperation agreement between UFBA and CENPES/PETROBRAS.

This work was supported by the CENPES/PETROBRAS [under grant number 5850.0107361.18.9].

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Figure Legends

Figure 1. Strict consensus of the two most parsimonious trees on Implied Weights (*k*=5.078125). Each branch showing character number (above) and character state (under), black dots indicate non-homoplastic apomorphies; empty dots indicate homoplastic apomorphies. Node Number (above), Bremer (left) and CG (symmetric resampling) (right) values inside the boxes on the side of each node.

Figure 2. Comparison between Strict consensus of the two most parsimonious trees on Implied weights (*k*=5.078125) (left) and Equal weights tree (right). Node Number (above), Bremer (left) and CG (symmetric resampling) (right) values on each branch.

Figure 3. Evolutionary trends on Artotrogidae antennules. Colored asterisks represent articulation losses resulting in compound antennule segments, each color indicates an equivalent clade on the cladogram on left. Antennule illustration of *Asterocheres reginae* Boxshall and Huys, 1994 adapted from Boxshall and Huys (1994). Roman algorism representation of ancestral segments based on Huys and Boxshall (1991).

Figure 4. Evolutionary trends on Artotrogidae legs 2 and 4 in clade 33. Colored markers represent different changes: asterisks represent setal losses; star represents change of setal shape; square represents loss of articulation; triangle represents absence of leg. Each color indicates an equivalent clade on the cladogram on left. Ancestral copepod leg illustration adapted from Huys and Boxshall (1991); armature formula coding adapted from Johnsson (2003).

Figure 5. Evolutionary trends on Artotrogidae legs 1 and 4 in clade 46. Colored markers represent specific changes: filled asterisks represent setal losses; empty asterisk represents loss reversion; star represents change of setal shape; squares represent loss of segmental articulation. Each color indicates an equivalent clade on the cladogram on left. Ancestral copepod leg illustration adapted from Huys and Boxshall (1991); armature formula coding adapted from Johnsson (2003).

Table Legends

Table 1. Terminal taxa on the phylogenetic analysis

Table 2. Data matrix

Table 3. Character statements following the fundamental functional components stated by Sereno (2007).

Table 4 – Nodes synapomorphies on Implied Weight analysis (*k*=5.078125). Bold indicate reversed synapomorphies. Asterisk indicate synapomorphies found in one of the two most parsimonious trees.

Table 5 – Terminal taxa synapomorphies on Implied Weight analysis (*k*=5.078125). Bold indicate reversed synapomorphies. Asterisk indicate synapomorphies found in one of the two most parsimonious trees.

Figures

Figure 1.

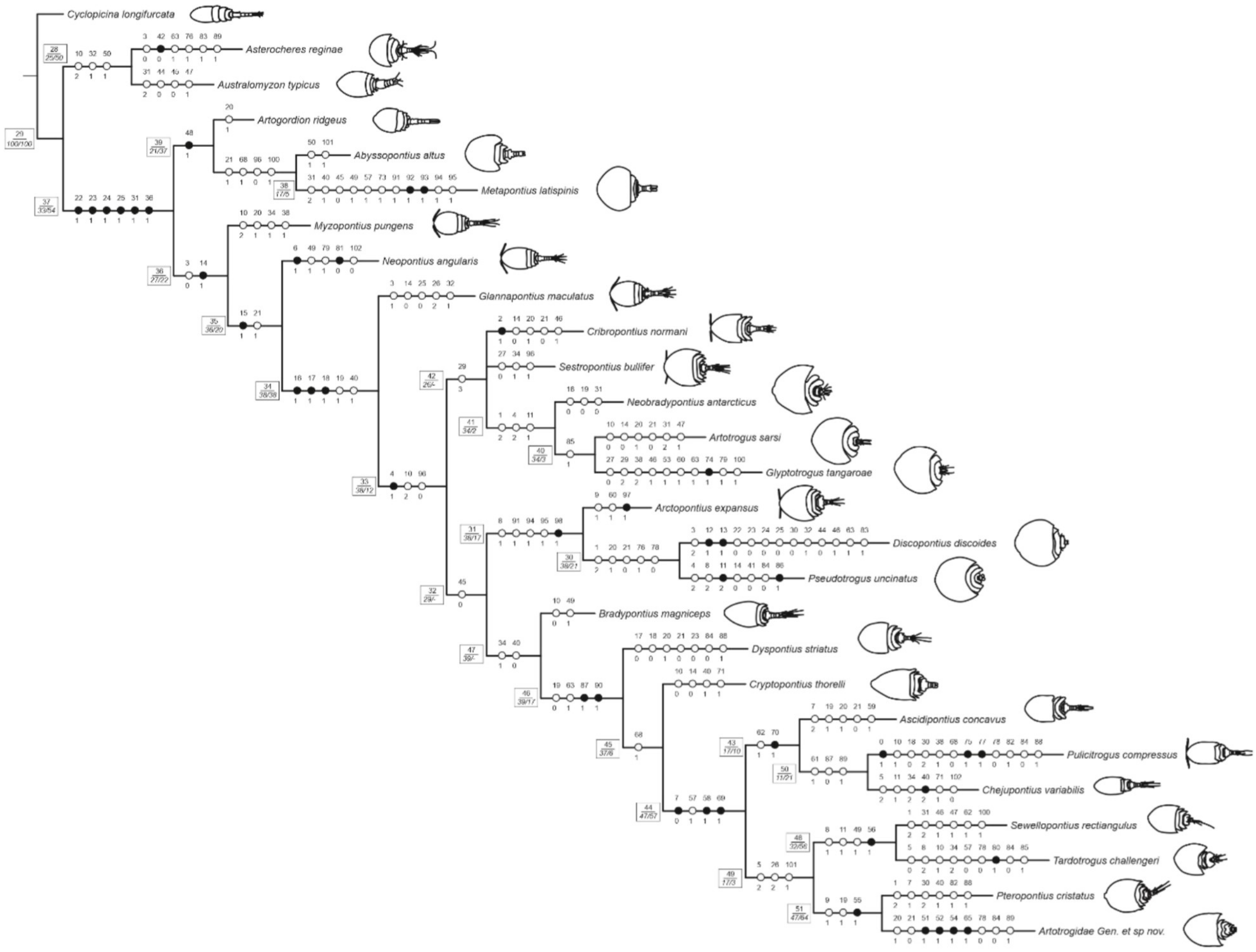
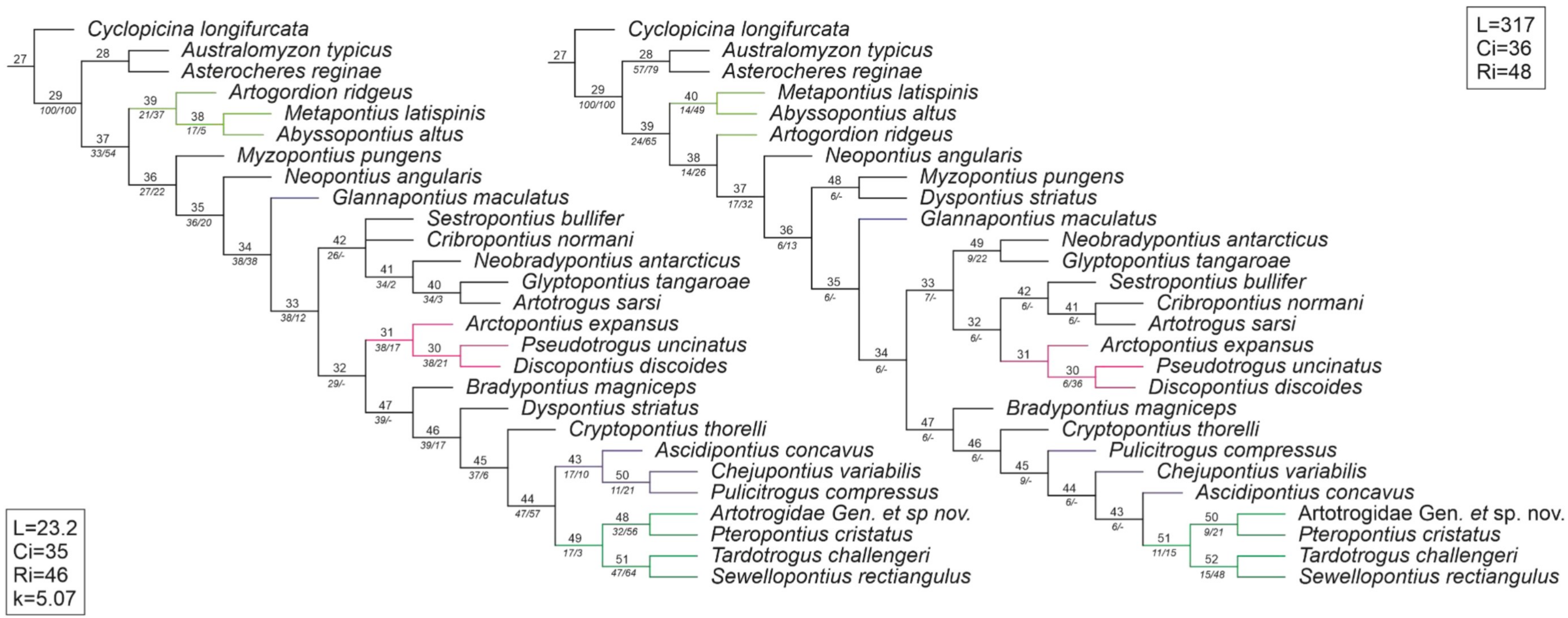
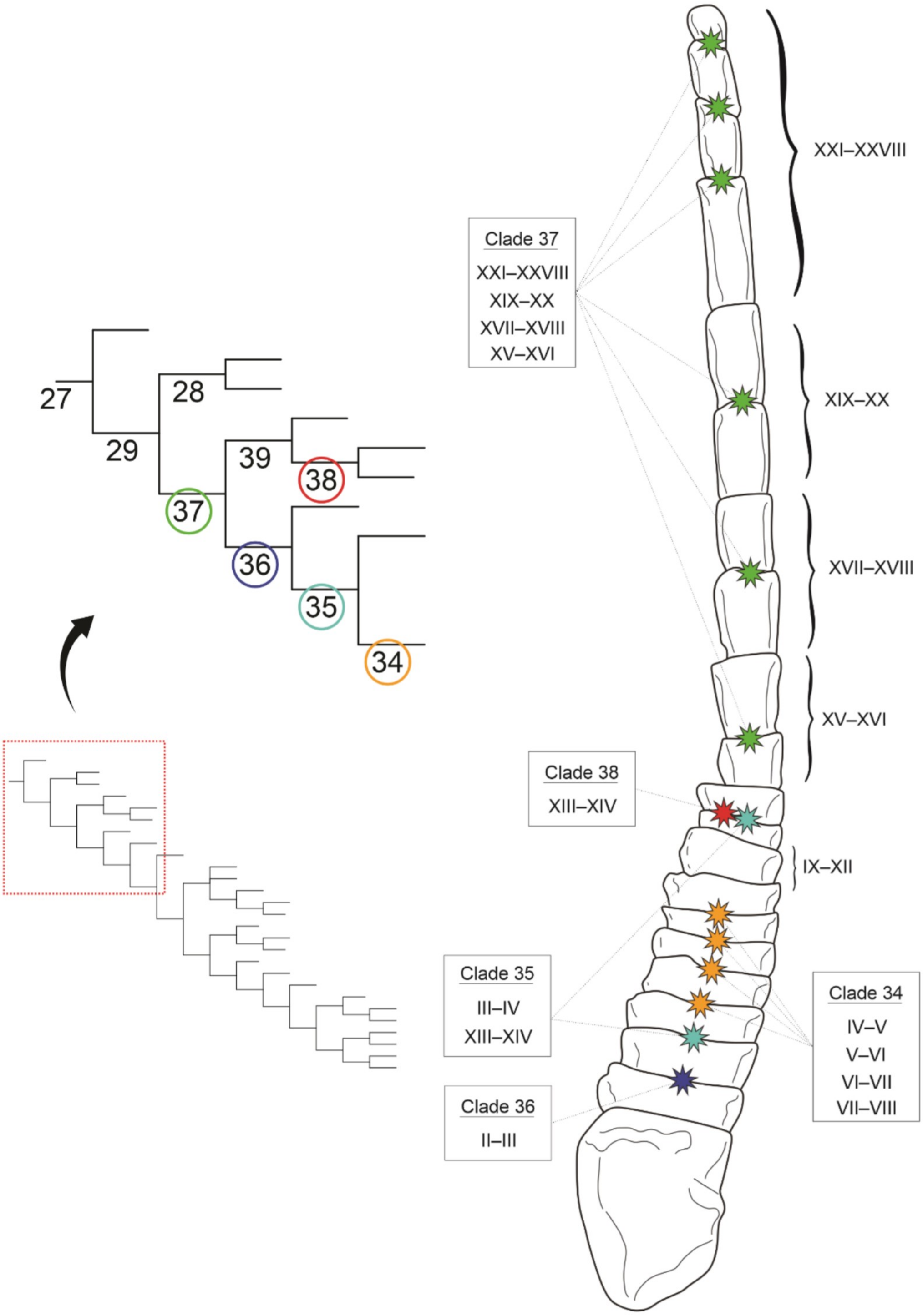


Figure 2.



Cyclopicina longifurcata
Australomyzon typicus
Asterocheres reginae
Artogordion ridgeus
Metapontius latispinis
Abyssopontius altus
Myzopontius pungens
Neopontius angularis
Glannapontius maculatus
Sestropontius bullifer
Cribropontius normani
Neobradypontius antarcticus
Glyptopontius tangaroae
Artotrogus sarsi
Arctopontius expansus
Pseudotrogus uncinatus
Discopontius discoides
Bradypontius magniceps
Dyspontius striatus
Cryptopontius thorelli
Ascidipontius concavus
Chejupontius variabilis
Pulicitrogus compressus
Artotrogidae Gen. et sp nov.
Pteropontius cristatus
Tardotrogus challengeri
Sewellopontius rectiangulus
L=23.2
Ci=35
Ri=46
k=5.07
Cyclopicina longifurcata
Australomyzon typicus
Asterocheres reginae
Metapontius latispinis
Abyssopontius altus
Artogordion ridgeus
Neopontius angularis
Myzopontius pungens
Dyspontius striatus
Glannapontius maculatus
Neobradypontius antarcticus
Glyptopontius tangaroae
Sestropontius bullifer
Cribropontius normani
Artotrogus sarsi
Arctopontius expansus
Pseudotrogus uncinatus
Discopontius discoides
Bradypontius magniceps
Cryptopontius thorelli
Pulicitrogus compressus
Chejupontius variabilis
Ascidipontius concavus
Artotrogidae Gen. et sp. nov.
Pteropontius cristatus
Tardotrogus challengeri
Sewellopontius rectiangulus
L=317
Ci=36
Ri=48

Figure 3



27
28
29
39
38
37
36
35
34
Clade 37
XXI–XXVIII
XIX–XX
XVII–XVIII
XV–XVI
Clade 38
XIII–XIV
Clade 35
III–IV
XIII–XIV
Clade 36
II–III
Clade 34
IV–V
V–VI
VI–VII
VII–VIII
XXI–XXVIII
XIX–XX
XVII–XVIII
XV–XVI
IX–XII

4

Figure 4

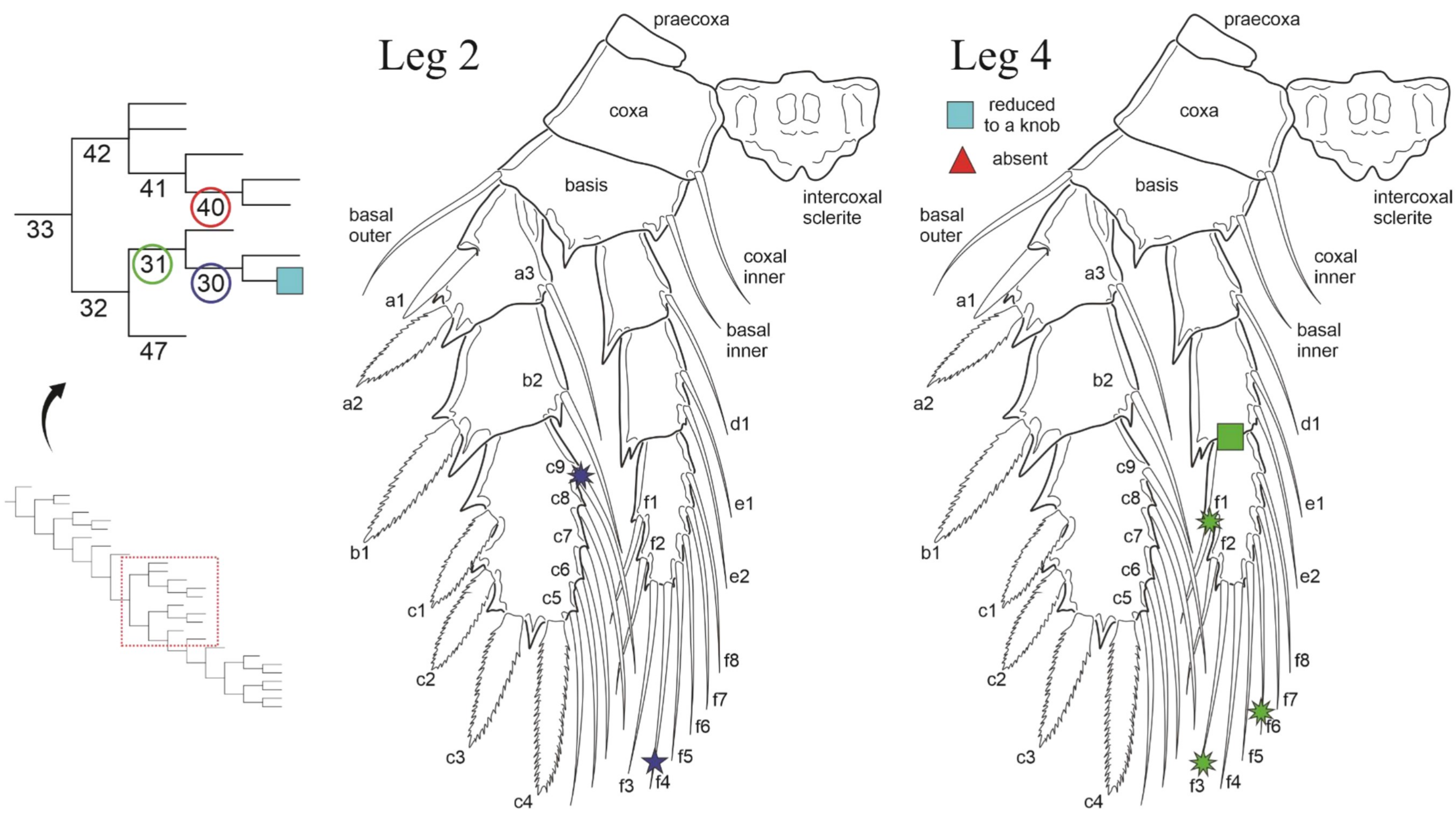
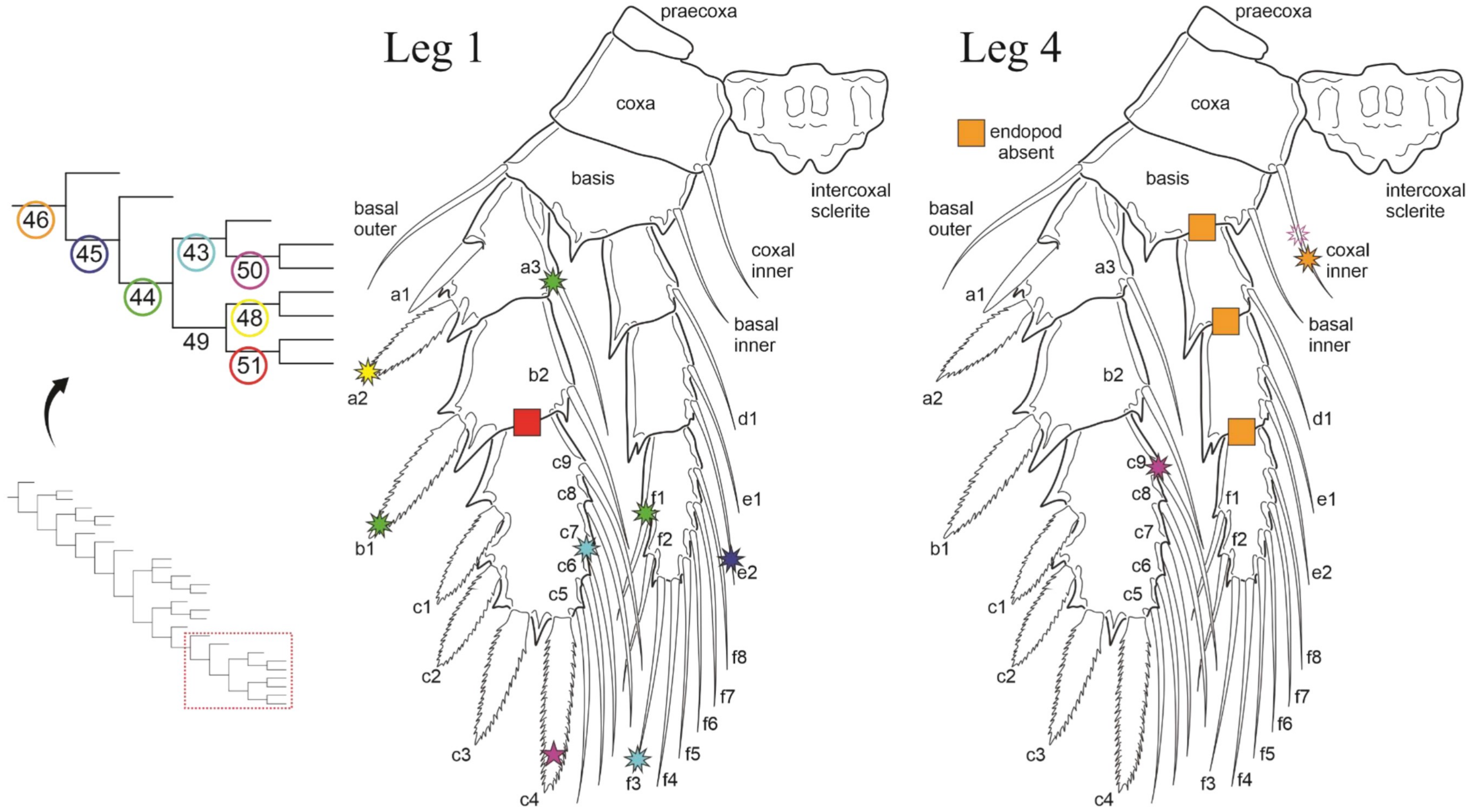

33
42
41
40
31
30
32
47
Leg 2
praecoxa
coxa
basis
intercoxal sclerite
basal outer
coxal inner
basal inner
a1
a2
a3
b1
b2
c1
c2
c3
c4
c5
c6
c7
c8
c9
d1
e1
e2
f1
f2
f3
f4
f5
f6
f7
f8
Leg 4
reduced to a knob
absent

Figure 5


46
45
44
43
50
48
49
51
Leg 1
praecoxa
coxa
basis
intercoxal sclerite
basal outer
coxal inner
basal inner
a1
a2
a3
b1
b2
c1
c2
c3
c4
c5
c6
c7
c8
c9
d1
e1
e2
f1
f2
f3
f4
f5
f6
f7
f8
Leg 4
endopod absent
praecoxa
coxa
basis
intercoxal sclerite
basal outer
coxal inner
basal inner
a1
a2
a3
b1
b2
c1
c2
c3
c4
c5
c6
c7
c8
c9
d1
e1
e2
f1
f2
f3
f4
f5
f6
f7
f8

Tables

Table 1.

Taxon	**Data source**
***Abyssopontius altus* Stock, 1985**	(Stock, 1985)
***Antarctopontius spinipes* Eiselt, 1965**	removed
***Arctopontius expansus* Sars G.O., 1915**	(Sars G.O., 1918)
***Artogordion ridgeus* Ivanenko *et al*., 2018**	(Ivanenko *et al*., 2018)
***Artotrogus sarsi* Kim I.H., 1996**	**F21597**
***Ascidipontius concavus* Kim I.H., 1996**	**USNM 285404**
***Bradypontius magniceps* (Giesbrecht, 1895)**	redescription (Sars G.O., 1918)
***Chejupontius variabilis* Lee J. & Kim I.H., 2023**	(Lee J and Kim I.H., 2023)
***Cribropontius normani* (Giesbrecht, 1899)**	redescription (Sars G.O., 1918)
***Cryptopontius thorelli* (Giesbrecht, 1895)**	(Giesbrecht, 1899)
***Dyspontius striatus* Thorell, 1859**	**F 20442**
***Glannapontius maculatus* Holmes, 1998**	**USNM 282718**
***Glyptotrogus tangaroae* McKinnon, 1988**	(McKinnon, 1988a)
***Metapontius latispinis* Hansen, 1923**	(Hansen, 1923)
***Myzopontius pungens* Giesbrecht, 1895**	redescription (Kim I.H., 1996)
***Neobradypontius antarcticus* Eiselt, 1961**	(Eiselt, 1961)
***Neopontius angularis* Scott, 1898**	redescription (Sars G.O., 1918)
***Pseudotrogus uncinatus* (Eiselt, 1961)**	redescription (Johnsson and Rocha, 2002)
***Pteropontius cristatus* Giesbrecht, 1895**	(Lee J. and Kim I.H., 2023)
***Pulicitrogus compressus* Kim I.H., 1996**	**USNM 285411**
***Sestropontius bullifer* Giesbrecht, 1899**	(Giesbrecht, 1899)
***Sewellopontius rectiangulus* Ummerkutty, 1966**	(Ummerkutty, 1966)
***Tardotrogus challengeri* Eiselt, 1961**	(Eiselt, 1961)
***Asterocheres reginae* Boxshall & Huys, 1994**	(Boxshall and Huys, 1994)

***Australomyzon typicus* Nicholls, 1944**	**SAM C3986**
***Discopontius discoides* Nicholls, 1944**	**SAM C3975**
***Cyclopicina longifurcata* (Scott T., 1901).**	redescription (Huys and Boxshall, 1991)

Table 2.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Cyclopicina longifurcata	0	0	0	1	0	0	0	2	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0
Asterocheres reginae	0	1	0	0	0	2	0	1	0	-	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0
Australomyzon typicus	0	?	0	1	0	?	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	2
Discopontius discoides	0	2	0	2	1	?	0	?	1	0	2	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	2	0	1
Abyssopontius altus	0	1	0	1	0	2	0	1	0	-	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	3	-	-	-	1	1
Arctopontius expansus	0	1	0	0	1	1	0	2	1	1	2	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	2	1	1
Artogordion ridgeus	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	3	1	1
Artotrogus sarsi	0	2	0	0	2	?	0	?	0	0	0	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	3	1	2
Ascidipontius concavus	0	1	0	1	1	1	0	2	0	-	2	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	2	1	1
Bradypontius magniceps	0	1	0	0	1	1	0	1	0	-	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	2	1	1
Chejupontius variabilis	0	1	0	2	1	2	0	0	0	0	2	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	2	1	1
Cribropontius normani	0	1	1	0	1	1	0	2	0	-	2	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	3	1	1
Cryptopontius thorelli	0	1	0	2	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	2	1	1
Dyspontius striatus	0	1	0	1	1	1	0	1	0	0	2	0	0	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	0	2	1	1
Glannapontius maculatus	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	1	1	1	1	1	0	1	1	1	1	0	2	1	0	2	1	1
Glyptopontius tangaroae	0	2	0	0	2	?	0	?	0	-	2	1	?	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	2	1	1
Metapontius latispinis	0	1	0	1	0	?	0	?	0	-	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	?	?	1	2
Myzopontius pungens	0	1	0	0	0	1	0	1	0	-	2	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0	2	1	1
Neobradypontius antarcticus	0	2	0	0	2	2	0	1	0	1	2	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	3	1	0
Neopontius angularis	0	0	0	0	0	1	1	2	0	-	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	0	2	1	1
Pseudotrogus uncinatus	0	2	0	0	2	2	0	2	2	0	2	2	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	2	1	1
Pteropontius cristatus	0	2	0	0	1	2	0	1	0	1	2	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	2	1	0	2	2	1
Pulicitrogus compressus	1	1	0	2	1	1	0	0	0	-	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	2	2	1
Sestropontius bullifer	0	1	0	0	1	1	0	2	0	1	2	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	3	1	1
Sewellopontius rectiangulus	0	2	0	0	1	2	0	0	1	0	2	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	?	?	?	?	1	2
Tardotrogus challengeri	0	1	0	0	1	0	0	0	2	0	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	2	1	0	3	1	1
Artotrogidae Gen. *et* sp nov	0	1	0	0	1	2	0	0	0	1	2	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	2	1	0	3	1	1

Table 2. (cont.)

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	60	61	62	63	64	65	66	67	68
0	0	-	0	0	0	-	0	-	-	-	0	-	-	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
1	1	0	1	0	1	0	1	0	0	0	1	1	1	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
1	1	?	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
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0	1	-	1	1	1	2	1	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
0	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	1	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	1
0	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	1	2	1	1	1	0	1	2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	0	1
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0	1	1	1	1	1	0	1	1	0	1	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
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1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	1	0	1	1	1	2	1	0	1	1	1	1	1	1	0	0	0	-	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
0	1	0	1	1	?	?	1	1	0	1	1	?	0	0	0	?	1	0	0	?	?	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1
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0	1	0	1	1	1	0	1	0	1	?	1	?	?	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	1	0	1	1	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
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0	1	0	1	1	1	0	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	-	-	-	-	-	-	-	-	-	1	-	-	-

Table 2. (cont.)

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	94	95	96	97	98	99	100	101	102
0	0	0	0	0	0	0	0	0	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
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0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
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0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	-	-	1	1	0	1	1	1	0	0	1
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0	0	1	0	0	0	0	0	0	1	?	?	?	?	?	?	0	0	?	?	?	1	-	-	-	-	-	-	-	-	?	?	0	1
0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	-	-	-	-	-	-	-	-	1	0	0	1
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0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1
0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1
0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
0	0	0	0	0	?	0	0	0	0	?	?	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-
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1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	-

Table 3.

Character
0. **Body, flattening plan:** dorso-ventrally (0), laterally (1), flattened.
1. **Prosome relative length:** up to half (0), up to three-quarters (1), above three-quarters (2), of the body.
2. **Cephalosome, posterolateral margin, shape:** entire (0), bifid (1).
3. **Cephalosome, posterior mediodorsal margin, shape:** concave (0), straight (1), convex (2).
4. **Third pedigerous somite, posterolateral projection, relative reach:** doesn't reach (0), does reach (1), goes beyond (2), the genital segment.
5. **Fourth pedigerous somite, relative size:** almost as long as (0), up to three-quarters of (1), up to half of (2), up to a quarter of (3), the third.
6. **Fifth pedigerous somite, length:width ratio:** wider than long [≥1:1,1] (0), longer than wide [≤1:0,9] (1).
7. **Fifth pedigerous somite, relative size:** almost as long as (0), up to 3/4 of (1), up to 1/2 of (2), up to a 1/4 of (3), the fourth.
8. **Urosome, length:width ratio:** wider than long [≥1:1,1] (0), as long as wide [1:1], longer than wide [≤1:0,9] (1).
9. **Genital somite, posterolateral projections, number:** one (0), two (1).
10. **Anal somite, length:width ratio:** wider than long [≥1:1,1] (0), as long as wide [1:1] (1), longer than wide [≤1:0,9] (2)
11. **Caudal rami, length:width ratio:** wider than long [≥1:1,1] (0), as long as wide [1:1] (1), longer than wide [≤1:0,9] (2).
12. **Third and fourth pedigerous somites, articulation:** present (0), absent (1)
13. **Fifth pedigerous and genital somite, articulation:** present (0), absent (1).
14. **II and III antennule segments, articulation:** present (0), absent (1).
15. **III and IV antennule segments, articulation:** present (0), absent (1).
16. **IV and V antennule segments, articulation:** present (0), absent (1).
17. **V and VI antennule segments, articulation:** present (0), absent (1).
18. **VI and VII antennule segments, articulation:** present (0), absent (1).
19. **VII and VIII antennule segments, articulation:** present (0), absent (1).
20. **XII and XIII antennule segments, articulation:** present (0), absent (1).
21. **XIII and XIV antennule segments, articulation:** present (0), absent (1).
22. **XV and XVI antennule segments, articulation:** present (0), absent (1).
23. **XVII and XVIII antennule segments, articulation:** present (0), absent (1).
24. **XIX and XX antennule segments, articulation:** present (0), absent (1).
25. **XXI antennule segment, posterior articulation:** present (0); absent (1).
26. **Antennal exopod, development:** 2-segmented or more (0); 1-segmented (1); represented by seta (2); unarmed (3)
27. **Antennal exopod, lateral seta:** present (0), absent (1).
28. **Antennal exopod, distal setae:** present (0), absent (1).
29. **Antennal exopod, distal setae, number:** more than 3 (0), 3 (1), 2 (2), 1 (3), seta.
30. **Antennal endopod, segments, number:** 3 segments (0), 2 segments (1), 1 segment (2)
31. **Antennal endopod, distal setae, number:** more than 3 (0), 3 (1), 2 (2), 1 (3).
32. **Antennal endopod, seta IV, shape:** setiform (0), modified as a claw (1).
33. **Oral cone:** absent (0), present (1).

34. **Oral cone, relative length:** doesn’t reach the first (1), reaches between first and fifth (2), reaches beyond the (3), intercoxal sclerite (s).

35. **Gnathobasis, shape:** robust (0), stylet-like (1).

36. **Mandibular palp:** present (0), absent (1).

37. **Maxillule, shape:** well-developed (0), reduced to 2 lobes (1).

38. **Maxillule, inner lobe, relative size:** longer than (0), as long as (1), shorter than (3), the outer.

39. **Maxilla, development:** well-developed (0), reduced to syncoxa and base (1).

40. **Maxilla, syncoxa, relative size:** shorter than (0); as long as (1); longer than (2), the base

41. **Maxilla, base, shape:** claw-like (0), sigmoid (1)

42**. Maxilla, pre-coxa aesthetasc:** present (0), absent (1)

43. **Maxilliped:** well-developed (0), reduced (1).

44. **Maxilliped, syncoxa seta:** absent (0), present (1).

45**. Maxilliped, base seta:** absent (0), present (1).

46. **Maxilliped, first endopodal segment seta:** absent (0), present (1).

47. **Maxilliped, second endopodal segment seta:** absent (0), present (1).

48. **Maxilliped, third endopodal segment seta:** absent (0), present (1).

49.**Maxilliped, first and second endopodal segments, articulation:** present (0), absent (1).

50. **Maxilliped, second, and third endopodal segments, articulation:** present (0), absent (1).

51. **Leg 1, development:** well-developed (0), reduced (1).

52. **Leg 1, coxal inner margin seta:** present (0), absent (1).

53. **Leg 1, basal outer margin seta:** present (0), absent (1).

54. **Leg 1, first exopodal articular division:** present (0), absent (1).

55. **Leg 1, second exopodal articular division:** present (0), absent (1).

56. **Leg 1, seta a2:** present (0), absent (1).

57. **Leg 1, seta a3:** present (0), absent (1).

58. **Leg 1, seta b1:** present (0), absent (1).

59. **Leg 1, seta b2:** present (0), absent (1).

60. **Leg 1, seta c1:** present (0), absent (1).

61. **Leg 1, seta c4, shape:** plumose (0), spiniform (1).

62. **Leg 1, seta c7:** present (0), absent (1).

63. **Leg 1, seta c8:** present (0), absent (1).

64. **Leg 1, seta c9:** present (0), absent (1).

65. **Leg 1, endopod:** present (0), absent (1).

66. **Leg 1, second endopodal articular division:** present (0), absent (1).

67. **Leg 1, seta e1:** present (0), absent (1)

68. **Leg 1, seta e2:** present (0), absent (1)

69. **Leg 1, seta f1:** present (0), absent (1)

70. **Leg 1, seta f3:** present (0), absent (1)

71. **Leg 1, seta f4, shape:** plumose (0), spiniform (1).

72. **Leg 1, seta f6:** present (0), absent (1)

73. **Leg 1, seta f7:** present (0), absent (1)

74. **Leg 2, basal outer margin, seta:** present (0), absent (1).

75. **Leg 2, seta c1:** present (0), absent (1).

76. **Leg 2, seta c9:** present (0), absent (1).

77. **Leg 2, seta f3:** present (0), absent (1).

78. **Leg 2, seta f4, shape:** plumose (0), espiniform (1).
79. **Leg 3, coxal inner margin seta:** present (0), absent (1).
80. **Leg 3, basal outer margin seta:** present (0), absent (1).
81. **Leg 3, basal inner margin seta:** present (0), absent (1).
82. **Leg 3, seta c1:** present (0), absent (1).
83. **Leg 3, seta c9:** present (0), absent (1).
84. **Leg 3, seta f4, shape:** plumose (0), espiniform (1).
85. **Leg 4:** present (0), absent (1).
86. **Leg 4, development:** well developed (0), reduced (1).
87. **Leg 4, coxal inner margin seta:** present (0), absent (1).
88. **Leg 4, seta c1:** present (0), absent (1)
89. **Leg 4, seta c9:** present (0), absent (1)
90. **Leg 4, endopod:** present (0), absent (1)
91. **Leg 4, second endopodal articular division:** present (0), absent (1).
92. **Leg 4, seta e1:** present (0), absent (1)
93. **Leg 4, seta e2:** present (0), absent (1)
94. **Leg 4, seta f1:** present (0), absent (1)
95. **Leg 4, seta f3:** present (0), absent (1)
96. **Leg 4, seta f4, shape:** plumose (0), espiniform (1).
97. **Leg 4, seta f5:** present (0), absent (1)
98. **Leg 4, seta f6:** present (0), absent (1)
99. **Leg 5, protopod:** present (0); absent (1)
100. **Leg 5, protopod, seta:** present (0); absent (1)
101. **Leg 5, exopod:** present (0); absent (1)
102. **Leg 5, exopo, shape:** well developed (0), reduced (1).

Table 4.

Clade	Exclusive synapomorphies	Homoplastic synapomorphies
28		10(2); 32(1); 50(1)
29		
30		1(2); 20(1); **21(0)**; 76(1); **78(0)**
31	98(1)	8(1); 91(1); 94(1); 95(1); 7(2)*
32		45(1)
33	4(1); 10(2)	**96(0)**
34	16(1); 17(1); 18(1)	19(1); 40(1)*
35	15(1)	21(1)
36	14(1)	**3(0)**
37	22(1); 23(1); 24(1); 25(1); 31(1); 36(1)	
38		21(1); 68(1); **96(0)**; 100(1)
39	48(1)	
40		85(1)
41		1(2); 4(2); 11(1)
42	29(3)	
43	70(1)	62(1)
44	**7(0)**; 58(1); 69(1)	57(1)
45		68(1)
46	87(1); 90(1)	**19(0);** 63(1)
47	**40(0)**	34(1)
48	55(1)	9(1); 19(1)
49		5(2); 26(2); 101(1)
50	61(1); **87(0)**	89(1)
51	56(1)	8(1); 11(1); 49(1)

Table 5.

Clade	Exclusive synapomorphies	Homoplastic synapomorphies
Cyclopicina longifurcata	-	-
Asterocheres reginae	**42(0)**	**3(0)**; 63(1); 76(1); 83(1); 89(1)
Australomyzon typicus	31(2);	**44(0); 45(0);** 47(1)
Artogordion ridgeus		20(1); 7(2)*
Metapontius latispinis	73(1); 92(1); 93(1)	31(2); 40(1); **45(0)**; 49(1); 57(1); 91(1); 94(1); 95(1)
Abyssopontius altus		50(1); 101(1)
Myzopontius pungens		10(2); 20(1); 34(1); 38(1)
Neopontius angularis	6(1); **81(0)**	49(1); 79(1); **102(0)**; 7(2)*
Glannapontius maculatus	3(1)	**14(0)**; **25(0)**; 26(2); 32(1)
Sestropontius bullifer	96(1)	**27(0)**; 34(1)
Cribropontius normani	2(1)	**14(0)**; 20(1); **21(0)**; 46(1)
Neobradypontius antarcticus	**31(0)**	**18(0); 19(0)**
Glyptopontius tangaroae	**29(2)**; 38(2); 53(1); 74(1)	**27(0)**; 46(1); 60(1); 63(1); 79(1); 100(1)
Artotrogus sarsi		**10(0)**; **14(0)**; 20(1); **21(0)**; 31(2); 47(1)
Arctopontius expansus	97(1)	9(1); 60(1)
Pseudotrogus uncinatus	11(2); **41(0)**; 86(1)	4(2); 8(2); **14(0)**; **84(0)**
Discopontius discoides	3(2); 12(1); 13(1); **22(0)**; **24(0)**; **30(0)**	**23(0)**; **25(0)**; 32(1); **44(0)**; 46(1); 63(1); 83(1)
Bradypontius magniceps		**10(0)**; 49(1)
Dyspontius striatus	**17(0)**	**18(0)**; 20(1); **21(0)**; **23(0)**; **84(0)**; 88(1)
Cryptopontius thorelli		**10(0)**; **14(0)**; 40(1); 71(1)
Ascidipontius concavus	7(2); 59(1)	19(1); 20(1); **21(0)**
Chejupontius variabilis	34(2); 40(2)	5(2); 11(1); 71(1); **102(0)**
Pulicitrogus compressus	0(1); **68(0)**; 75(1);77(1)	**10(1)**; **18(0)**; 30(2); 38(1); **78(0)**; 82(1); **84(0)**; 88(1)
Artotrogidae Gen. *et* sp. nov.	51(1); 52(1); 54(1); 65(1)	20(1); **21(0)**; **78(0)**; **84(0)**; 89(1)
Pteropontius cristatus	7(1)	1(2); 30(2); 40(1); 82(1); 88(1)
Tardotrogus challengeri	**5(0)**; 34(2); **57(0)**; 80(1)	8(2); **10(1)**; **78(0)**; **84(0)**; 85(1)

Sewellopontius rectiangulus	1(2); 31(2); 46(1); 47(1); 62(1); 100(1)

Conclusões Gerais

1. Artotrogidae gen. *et* sp nov. é descrito como um novo gênero para a família Artotrogidae. A primeira perna com um único ramo uni-articulado do novo gênero não é observada em nenhum outro artotrogídeo, sendo o maior grau de redução da perna 1 encontrado na família.

2. *Bradypontius* sp nov. é descrita como uma nova espécie para a família Artotrogidae. A nova espécie diferencia-se das demais pelo conjunto combinado de diferenças no padrão de articulação da antênula, e na fórmula da armadura da maxílula, maxila e pernas 4, 5 e 6. Além disso, o cone oral alongado apresentado por *Bradypontius* sp nov, cujo comprimento ultrapassa o ramo caudal, é uma característica exclusiva no gênero.

3. A espécie *Artrogus sarsi* Kim I.H., 1996 é redescrita, e os aspectos relacionados a morfologia e fórmula da armadura do endópodo da antena, endópodo da maxila e dos artículos do endópodo do maxilípede são observados diferentemente do originalmente descrito por G.O. Sars (1918). Entretanto, a combinação destes caracteres não é observada em nenhuma outra espécies do gênero *Artotrogus* Boeck, 1859, e, portanto, não geram dúvidas sobre a validade da espécie.

4. *Dyspontius striatus* Thorell, 1859 é redescrita, e os aspectos relacionados a fórmula da armadura dos lobos da maxílula, do endópodo da antena, e do terceiro artículo do exópodo da perna 4 destoaram do originalmente redescrito por G.O. Sars (1918). A fórmula da armadura da porção distal do endópodo da antena e do terceiro artículo do exópodo da perna 5 são únicas dentre as espécies do gênero *Dyspontius* Thorell, 1859. Além disso, as principais características diagnósticas da espécie foram confirmadas, e assim, a validade da espécie deve ser mantida.

5. A espécie *Metapontius walteri* Johnsson & Neves, 2005 foi movida para o gênero *Arctopontius* Sars, 1915 como *Arctopontius walteri* (Johnsson & Neves, 2005).

6. As diagnoses de onze gêneros da família Artotrogidae são revisadas à luz do atual conhecimento da diversidade do grupo, e, de acordo com os novos padrões taxonômicos de descrição de espécies.

7. A distribuição da família Artotrogidae é cosmopolita, mas a notável distribuição destes animais deve-se principalmente aos gêneros mais ricos *Bradypontius* Giesbrecht, 1895 e *Cryptopontius* Giesbrecht, 1899.

8. Regiões específicas do mundo, como as Ilhas Britânicas, costa da Noruega, Golfo de Nápoles, costa da Coréia do Sul e costa sul da Australia, apresentam-se como grandes centros de diversidade, e essa grande concentração de registros é relacionada ao baixo número de taxonomistas e a realização de estudos localizados nestas regiões especificas.

9. Copépodes artotrogídeos são considerados generalistas, sendo registrados associados a uma grande variedade de hospedeiros. Dentre os onze gêneros revisados, cerca de 60% das espécies não tiveram seus hospedeiros invertebrados identificados. Entretanto, dentre aqueles cujos hospedeiros invertebrados foram identificados, a maioria (10%) foram encontrados associados a briozoários, seguidos de algas (9%), esponjas (8%), ascídias (6%), cnidários (3%) e moluscos (2%).

10. Apesar deste não ser o objetivo principal do estudo, a análise filogenética baseada em 103 caracteres morfológicos fortaleceu as evidências da reconhecida monofilia da família Artotrogidae. Os gêneros *Asterocheres* Boeck, 1859 e *Australomyzon* Nicholls, 1944, reconhecidos como Asterocheridae, formaram um grupo monofilético irmão da família alvo desta investigação.

11. As seguintes sinapomorfias caracterizam a família Artotrogidae: Antênula da fêmea com ausência de articulação entre os artículos ancestrais XV-XVI (22:1); XVII-XVIII (23:1); XIX-XX (24:1); XXI-XXVIII (25:1); margem distal do endópodo da antena armado com 3 cerdas (31:1); e palpo mandibular ausente (36:1).

12. A família Artotrogidae teve seus gêneros divididos em dois clados monofiléticos principais, clado 36 e 39, e estes foram propostos como Subfamília nov. 1 e Subfamília nov. 2.

13. A Subfamília nov. 1 detém os gêneros *Artogordion*, *Abyssopontius* e *Metapontius*, e é caracterizada pela ausência de cerda no terceiro segmento do endópodo do maxilípede (48: 1).

14. A Subfamília nov. 2 detém os gêneros *Myzopontius*, *Neopontius*, *Glannapontius*, *Cribropontius*, *Sestropontius*, *Neobradypontius*, *Artotrogus*, *Glyptotrogus*, *Arctopontius*, *Discopontius*, *Pseudotrogus*, *Bradypontius*, *Dyspontius*, *Cryptopontius*, *Ascidipontius*, *Pulicitrogus*, *Chejupontius*, *Sewellopontius*, *Tardotrogus*, *Pteropontius* e Artotrogus gen. *et* sp nov., e é caracterizada por apresentar a antênula da fêmea com ausência de articulação entre os artículos ancestrais II-III (14: 1), e por apresentar a margem posterior médio-dorsal com forma côncava (3: 0).

15. O gênero *Discopontius*, como resultado deste estudo, é incluído na família Artotrogidae, num clado interno da Subfamília nov. 2, tendo *Pseudotrogus* como táxon irmão no clado 30, e ambos relacionados a *Arctopontius* no clado 31, sobretudo por compartilhar reduções no número de artículos no endópodo e da cerdação da perna 4 (91: 1, 94: 1, 95:1, 98:1).

16. A família Myzopontiidae Sars G.O., 1918, que originalmente incluía os gêneros *Myzopontius* e *Neopontius*; a família Dyspontiidae (Sars G.O., 1918), que originalmente incluía *Dyspontius*, *Cryptopontius*, *Arctopontius*, *Bradypontius*, *Cribropontius*, *Pteropontius* e *Sestropontius*; e a família Artotrogidae *sensu* Sars, que originalmente incluía os gêneros *Artotrogus* e o gênero inválido *Dystrogus* (Sars G.O., 1918) não foram recuperados como grupos monofiléticos neste estudo, corroborando com a classificação proposta por Eiselt (1961), e assim permanecem como inválidas.

17. A ausência de articulações na antênula da fêmea em artotrogídeos é um caráter chave na compreensão da evolução das linhagens da família. As linhagens da família são

definidas por uma sequência de reduções na porção proximal da antênula (i.e., anterior ao artículo fusionado IX–XII), que pode chegar a formar um único artículo resultante da fusão II–VIII.

18. De maneira semelhante, a cerdação e a segmentação das pernas tem um papel muito relevante para elucidação dos clados mais internos da família. Diferentemente do proposto por estudos anteriores, os diferentes níveis de redução de cerdação e do número artículos da perna 4 não constituem uma única tendência evolutiva. Além disso, a hipótese de relacionamento filogenético proposta por este estudo propõe que os diferentes níveis de reduções observados em Artotrogidae ocorreram em três diferentes clados da família, a partir de grupos com a perna 4 birreme e 3-segmentada.

19. Apenas os artotrogídeos que não possuem os três artículos do endópodo na perna 4 formaram um clado (46) monofilético. E entre estes, uma sequência de perdas de cerdas na perna 1 forma uma segunda tendência de perdas. Esta segunda tendência de perdas atingem um maior grau no clado que contém os gêneros *Pteropontius* e Artotrogidae gen. *et* sp nov., onde pode ocasionar a ausência de um ou mais artículos em ambos os ramos.

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