GIOVANNA MONTICELLI CARDOSO

REVISÃO TAXONÔMICA E ANÁLISE FILOGENÉTICA EM BATHYTROPIDAE VANDEL, 1952 (CRUSTACEA: ISOPODA: ONISCIDEA)

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biologia Comparada

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Dra. Bianca Laís Zimmermann

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Dra. Maríndia Deprá

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Dr. Filipe Michels Bianchi

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“*Somewhere, something incredible is waiting to be known.*”

Carl Sagan

SUMÁRIO

PREFÁCIO

Os isópodos terrestres são popularmente conhecidos como “tatuzinhos de jardim”. São amplamente distribuídos pelos ambientes terrestres, podendo ser encontrados desde a zona litorânea até áreas desérticas. Várias adaptações foram necessárias para o domínio do ambiente terrestre, e foram reflexo de diferentes processos evolutivos que são responsáveis pela grande diversidade encontrada atualmente. Conhecer e compreender um pouco sobre a diversidade e a evolução deste grupo é um dos grandes objetivos desta tese. Ao longo deste trabalho foi possível estudar diversos grupos taxonômicos que auxiliaram na compreensão do grupo em destaque, e permitiram o desenvolvimento das análises morfológicas e filogenética.

A tese inicia com uma introdução geral, onde são abordadas algumas questões não inclusas nos artigos científicos, visando contextualizar o leitor acerca do tema abordado pelos capítulos subseqüentes. Em seguida, cinco capítulos são apresentados na forma de artigos científicos. Os primeiros três capítulos são apresentados na íntegra conforme as normas dos periódicos onde foram publicados. Os últimos dois capítulos são apresentados conforme as normas dos periódicos aos quais serão submetidos.

O primeiro capítulo foi publicado no periódico *Zootaxa*, no ano de 2015, descreve um novo gênero pertencente à Trachelipodidae. Este gênero, *Levantoniscus* Cardoso, Taiti & Sfenthourakis, 2015, é composto duas novas espécies e uma nova combinação para a espécie *Bathytropa wahrmani* Strouhal, 1968, que devido à presença de pulmões pleopodais diferia das demais espécies de *Bathytropa*. O segundo capítulo foi publicado no periódico *Tropical Zoology*, no ano de 2016; neste artigo, as espécies de *Dubioniscus* Vandel, 1963 são revisadas, inclusive *Dubioniscus negrae* Vandel, 1973 que corresponde ao sinônimo sênior de *Cubanoscia romanorum* Vandel, 1981. O terceiro capítulo foi submetido ao periódico *Studies on Neotropical Fauna and Environment* e descreve duas novas espécies de *Neotroponiscus* Arcangeli, 1936. O quarto capítulo aborda a revisão do gênero *Neotroponiscus* e será submetido ao *Journal of Natural History*. O último capítulo será submetido ao *Zoologica Scripta*, tem por finalidade testar a monofilia de *Neotroponiscus* e investigar as relações do grupo dentro de Bathytropidae. Por fim, conclusões e perspectivas são abordadas nos Considerações Finais.

RESUMO

A ordem Isopoda é um dos o grupo mais diverso dentre os crustáceos, sendo composta por dez subordens. Os representantes da subordem Oniscidea, conhecidos como "tatuzinhos de jardim", obtiveram grande sucesso no domínio do ambiente terrestre. Para isso, foram necessárias várias adaptações morfológicas, fisiológicas e comportamentais, tais como comportamento gregário para diminuição da perda de água, presença de marsúpio fechado para reprodução e a presença de pulmões pleopodais. Apesar do grupo apresentar ampla uma distribuição geográfica, as espécies apresentam limitada capacidade de dispersão. Essa baixa dispersão resulta em isolamento de populações e alta diversidade genética. Dessa forma, o número de espécies dos isópodos é subestimado, sendo necessários mais esforços taxonômicos a fim de ampliar o conhecimento para o grupo. Frequentemente, revisões taxonômicas resultam em ampliação do número de espécies, reforçando a importância destes estudos para o grupo. Identificações usualmente se baseiam em pequenas variações morfológicas, o que muitas vezes dificulta a distinção entre espécies, sendo dados moleculares representam uma importante ferramenta para a delimitação das relações de parentesco entre espécies. O gênero *Neotroponiscus* ocorre na America do Sul e possui uma grande diversidade de espécies distribuídas ao longo da Mata Atlântica Brasileira. Oito espécies são conhecidas na literatura e foram revisadas para o levantamento de caracteres, necessários para os estudos filogenéticos. Além disso, neste trabalho, cinco novas espécies novas foram identificadas. Com base em dados morfológicos e moleculares a monofilia do gênero foi testada, e o grupo foi recuperado como monofilético. As relações de parentesco entre *Neotroponiscus* e os integrantes da família Bathytropidae foi testada e a família foi recuperada como um grupo parafilético, corroborando para hipóteses anteriores. Estudos futuros com uma abordagem biogeográfica serão importantes para elucidar os padrões de distribuição das espécies de *Neotroponiscus.*

Palavras-chave: isópodos terrestres, tatuzinhos, diversidade, Mata Atlântica.

ABSTRACT

The order Isopoda is one of the most diverse groups among crustaceans. Species from the suborder Oniscidea, commonly known as woodlice, were very successful in conquering the terrestrial environment. For that, many morphological, physiological and behavioral adaptations were necessary, such as, closed marsupium for reproduction, presence of pleopodal lungs, and gregarious behavior to diminish water losses. Although the group has large geographical distribution, species have limited dispersion capacity. This low dispersion results in population isolation and high genetic diversity. Therefore, the number of species of terrestrial isopods is greatly underestimated and more taxonomical studies are necessary in order to broaden the knowledge on the group. Taxonomical revisions on terrestrial isopods frequently result in higher number of species reinforcing the importance of these studies for the fore the mentioned group. Identification is usually based on subtle morphological differences, so molecular data is an important tool to elucidate the relationship within the group. The genus *Neotroponiscus* occurs in South America and has high species diversity throughout the Atlantic Forest. A total of eight species are known from the literature and were reviewed to identify characters that are necessary for phylogenetic studies. In this study, five new species were identified and described. Based on morphological and molecular data, the monophyly of the group was tested and the group was confirmed as monophyletic. The relationship between *Neotroponiscus* and the other species from the family Bathytropidae were also tested, showing that the family represents a paraphyletic group, which corroborates previous suggestions. Future studies with biogeographic approuch will be important to elucidate the distribution pattern of the genus *Neotroponiscus*.

Key-words: terrestrial isopods, woodlice, diversity, Atlantic Forest.

INTRODUÇÃO GERAL

1.1. Aspectos gerais

A ordem Isopoda é um dos o grupo mais diverso dentre os crustáceos (SCHMALFUSS, 2003), com mais de 10.000 espécies descritas. Ela é dividida em dez Subordens: Anthuroidea, Asellota, Calabozoidea, Cymothoidea, Flabellifera, Gnathiidea, Limmnoriidea, Microcerberidea, Oniscidea, Phoratopidea, Phreatoicidea, Sphaeromatidea, Tainisopidea e Valvifera (TAITI, 2016).

Diferente dos demais crustáceos, os isópodos possuem o corpo segmentado, sem carapaça, é achatado dorso ventralmente e divide-se em cabeça, pereon e pleon (VANDEL, 1960, SUTTON, 1980) (Figura 1). A cabeça (ou cefalotórax) é formada por cinco segmentos fusionados e um apêndice do tórax, o maxilípodo, além de dois pares de antenas e um par de olhos (JACKSON, 1926, 1928).

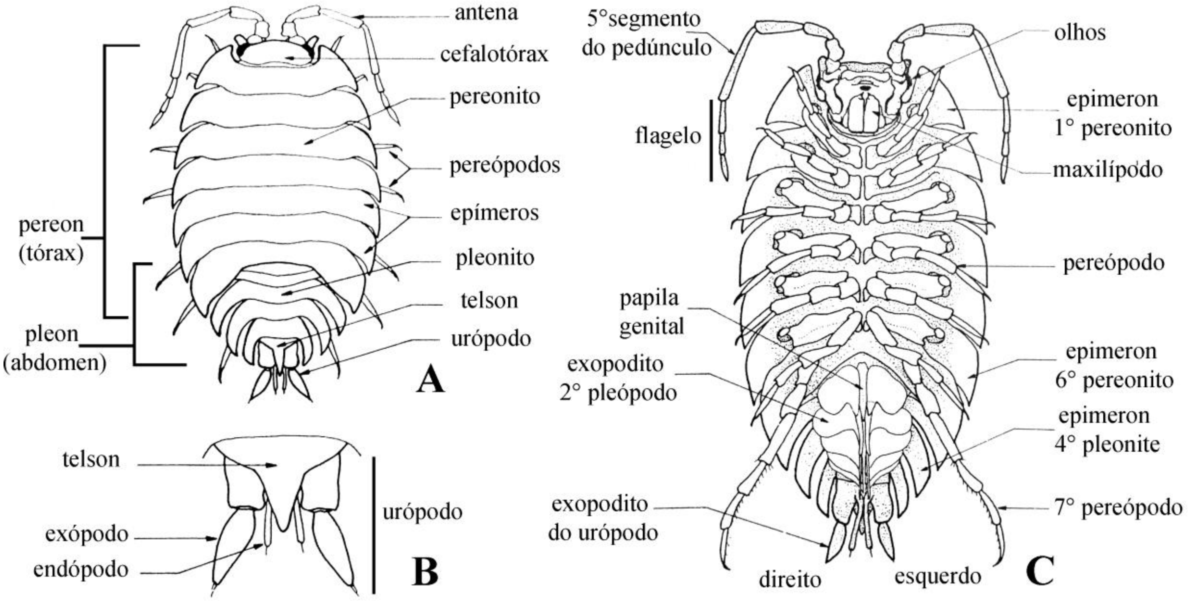

Figura 1. Morfologia geral de um isópodo terrestre, A. visão dorsal do *habitus*; B, visão dorsal do telson e urópodos; C, visão ventral do *habitus*. Fonte: SUTTON (1980), modificado.

Algumas características morfológicas da cabeça são utilizadas para definições de gêneros e espécies, como a linha supra-antenal, que se situa entre as inserções das antenas, dividindo a porção frontal em frons (abaixo da linha) e profrons (acima da linha); e a linha frontal que está entre as margens anteriores dos olhos, acima da linha supra-antenal, e pode formar lobos laterais (em frente aos olhos) e um lobo mediano (no meio desta linha) (JACKSON, 1926; 1928) (Figura 2). O pereon ou tórax possui sete pares de apêndices locomotores, os pereópodos (SUTTON, 1980). O pleon ou abdômen é composto por cinco segmentos não fusionados e seus apêndices, os pleópodos; e o pleotelson que consiste na fusão de um ou mais pleonitos com o telson (SUTTON, 1980; ROMAN & DALENS 1999). Os pleópodos são birremes, e possuem um ramo externo (exópodo), onde podem estar presentes os pulmões pleopodais; e interno (endópodo). Os dois primeiros pares de pleópodos são modificados nos machos como genitália externa para transferência de esperma (SUTTON, 1980; ARAUJO, 1999).

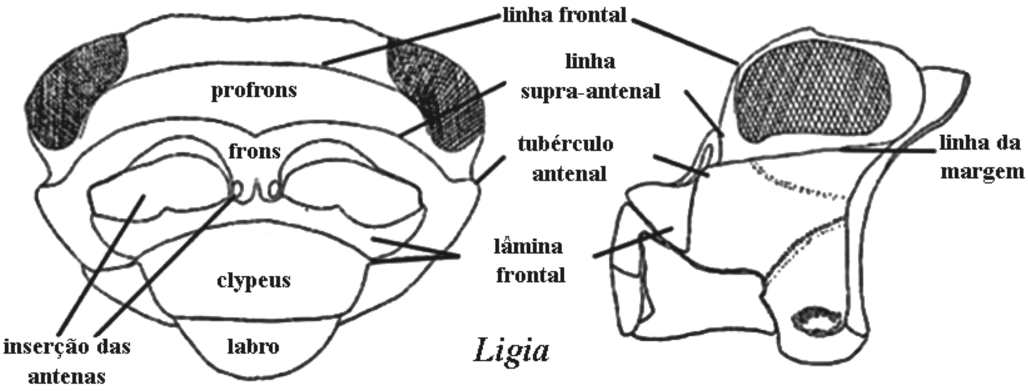

Figura 2. Morfologia geral da cabeça de um isópodo terrestre, A. visão frontal; B, visão lateral. Fonte: JACKSON (1928), modificado.

Os representantes terrestres pertencem à subordem Oniscidea e são popularmente conhecidos como “tatuzinhos de jardim”. Suas espécies ocorrem desde a zona litorânea até as regiões de altitude, incluindo ambientes desérticos e subterrâneos (SCHMIDT, 2002). O grande sucesso no domínio do ambiente terrestre está associado a algumas adaptações morfológicas, fisiológicas e comportamentais (ARAUJO, 1994; SCHMALFUSS, 1998). Entre algumas dessas estratégias comportamentais encontra-se a proteção contra predadores e a perda d’água, a capacidade volvacional e o hábito de agregação (WARBURG, 1987; HORNUNG, 2011). Entre as mudanças morfológicas e fisiológicas encontra-se a redução do tamanho corporal; a cutícula resistente a perde de água; o aumento de estruturas na superfície dorsal; o desenvolvimento de pulmões pleopodais; o sistema condutor de água;e o marsúpio fechado (HORNUNG, 2011).

A agregação é um comportamento adaptativo que proteger os animais contra a dessecação, além disso, a agregação promove a criação de abrigos que representam microclimas e micro-habitats tamponados, promove o crescimento da população ao estimular a reprodução das fêmeas e protege contra predação devido à saturação do predador e a somatória de secreções repulsivas (BROLY et al., 2013).

A umidade é um fator que afeta tanto a distribuição quanto a abundância dos isópodos (WARBURG & LINSENMAIR, 1984). Importantes setas sensoriais estão presentes nas antenas e antênulas, os estetascos (RISLER, 1977; 1978). Seu tamanho e posição foram importantes adaptações à sobrevivência em ambientes terrestres, uma vez que possuem importantes receptores de umidade (HAUG & ALTNER, 1984; SCHMALFUSS, 1998). A primeira antena é diminuta e seu tamanho é uma estratégia adaptativa, pois se mantém protegida de possíveis ataques de predadores, enquanto a segunda antena é usualmente perdida (SCHMALFUSS, 1998).

O exoesqueleto é a principal barreira entre os isópodos e o ambiente, sendo composto por quatro camadas: epicutícula, exocutícula, endocutícula e a camada membranosa, cuja espessura varia conforme a espécie (HILD et al., 2008). A calcita se concentra na porção da exocutícula e sua densidade pode contribuir para a redução de perda de água (HILD et al., 2008). Para seu crescimento, os isópodos realizam a muda, que ocorre em duas fases, a primeira ocorre na porção posterior, seguida pela metade anterior do exoesqueleto (HEELEY, 1941). O carbonato de cálcio é reabsorvido e mobilizado entre as cutículas e os tecidos internos, isto é, o cálcio é transportado da porção anterior para a mineralização da nova cutícula posterior durante a primeira fase da muda, seguido pela mobilização da porção posterior para a mineralização anterior durante a segunda fase da muda (GREENAWAY, 1985; STEEL, 1993; ZIEGLER et al., 2007). A epicutícula forma uma série de estruturas superficiais e estão presentes em todos os isópodos terrestres (SCHMALFUSS, 1978).

Uma grande variedade de ornamentos estão presentes na superfície dorsal, tais como papilas, setas, tricornes, microescalas, cavidades, placas, tubérculos e poros (HOLDICH & LINCOLN, 1974). Alguns ornamentos possuem inervações cuticulares e mediam informações sensoriais (JANS & ROSS, 1963). Estas setas sensoriais podem ser mecanorreceptoras e estimulam respostas tigmocinéticas, estimulando o movimento, ou não, em resposta ao contato (HOLDICH & LINCOLN, 1974). A seta tricorne é constituída por um eixo principal que surge de uma concavidade na superfície da cutícula, com uma aba livre suportada por duas abas laterais (SUTTON, 1972; HOLDICH & LINCOLN, 1974). A aba livre pode apresentar variação dependendo da sua localização (HOLDICH & LINCOLN 1974), ou dependendo da espécie (Figura 3), geralmente possui a forma de concha ou leque, onde a bainha é distalmente alargada com uma margem serrilhada (VANDEL, 1960). Outro tipo de seta sensorial é chamado de "*nodulus lateralis*" (VERHOEFF, 1907), e diferente da seta tricorne, tem uma longa porção livre que ultrapassa a bainha (SCHMIDT, 2002). Sua posição relativa foi definida por VANDEL (1960) e é frequentemente utilizada como um caráter diagnóstico para algumas espécies.

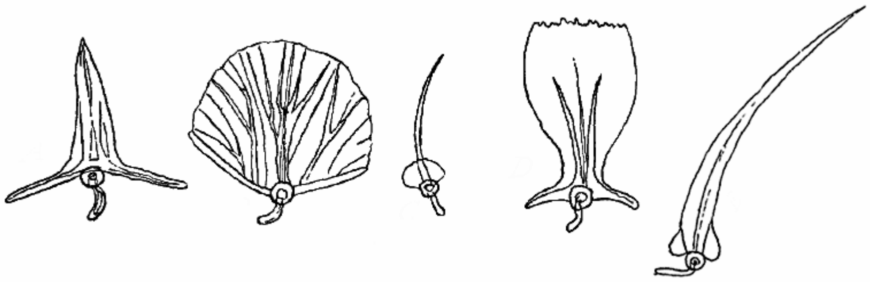

Figura 3. Diferentes tipos de setas. Fonte: VANDEL (1960), modificado.

Os tubérculos podem ser encontrados em diferentes famílias, e presume-se que evoluíram convergentemente devido a condições ecológicas semelhantes (SCHMALFUSS, 1977). O conjunto destas estruturas possui uma função anti-adesiva contra partículas e a tensão superficial da água, impedindo partículas de se aderirem a cutícula (Figura 4) (SCHMALFUSS, 1977; 1978; HOLDICH, 1984).

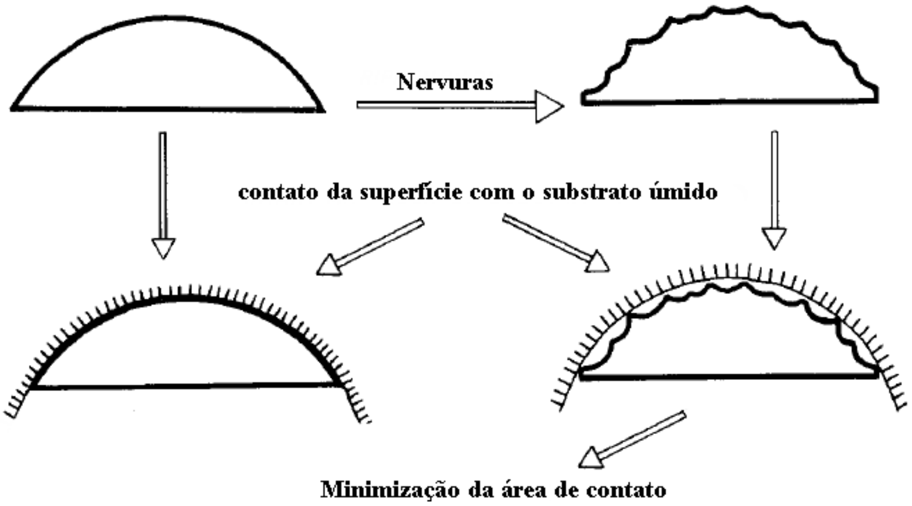

Figura 4. Tergitos em seções transversais. Representação da superfície dorsal e o contato com o substrato. Fonte: SCHMALFUSS (1977).

Em espécies marinhas, as trocas gasosas ocorrem na superfície dorsal dos pleópodos. A mudança para a posição ventral foi importante para o domínio terrestre, como pode ser vista em representantes de *Ligia* Fabricius, 1798, gênero que habita a região litorânea, é considerado ancestral entre Oniscidea (SCHMIDT & WAGELE 2001). O aumento da complexidade dos pulmões foi essencial para a colonização de habitats mais secos e evoluiu independentemente na Subordem Oniscidea (SCHMIDT & WAGELE, 2001). Os órgãos respiratórios apresentam uma variação, podendo ser observado desde uma simples área respiratória com a cutícula delgada a pulmões fechados com a presença de espiráculos (LEISTIKOW & ARAUJO, 2001; PAOLI et al., 2002).

O marsúpio é um caráter diagnóstico da superordem Peracarida (POORE, 2005). Esta estrutura é formada pelo conjunto de oostegitos, apêndices reprodutivos temporários que se desenvolvem na superfície ventral dos apêndices, entre o segundo e quinto segmento torácico, formando uma bolsa incubadora onde oxigênio e água são fornecidos para o desenvolvimento dos ovos e embriões (HOESE, 1983). Os embriões apresentam desenvolvimento direto, independente de uma fonte externa de água, eclodindo dentro do marsúpio no estágio de manca, que pode ser diferenciado do juvenil pela ausência do sétimo pereópodo (HOESE, 1983; ARAUJO et al., 2004; POORE, 2005; APPEL et al., 2011).

SCHMALFUSS (1984) classificou os isópodos em grupos ecomorfológicos. Nessa classificação, a constituição corporal está diretamente correlacionada às estratégias adaptativas e comportamentais que reduzem a pressão de predação, sendo elas: (1) “runners” ou corredores – com pereópodos relativamente longos e fortes, tergitos planos; (2) “clingers” ou aderentes – com corpo achatado, tergitos expandidos lateralmente e pereópodos curtos que aderem ao substrato; (3) “rollers” ou volvacionais – com tergitos convexos e capacidade de enrolar-se em bola; (4) “spineforms” ou espiniformes – com espinhos proeminentes no tegumento, com capacidade volvacional; (5) “creepers” ou rastejadores – com tergitos providos de costelas longitudinais, pereópodos curtos e fracos, geralmente de habitats endógenos; e (6) não conformistas – é composto pelo restante das espécies que não se encaixam dentro das cinco categorias anteriores Figura 5.

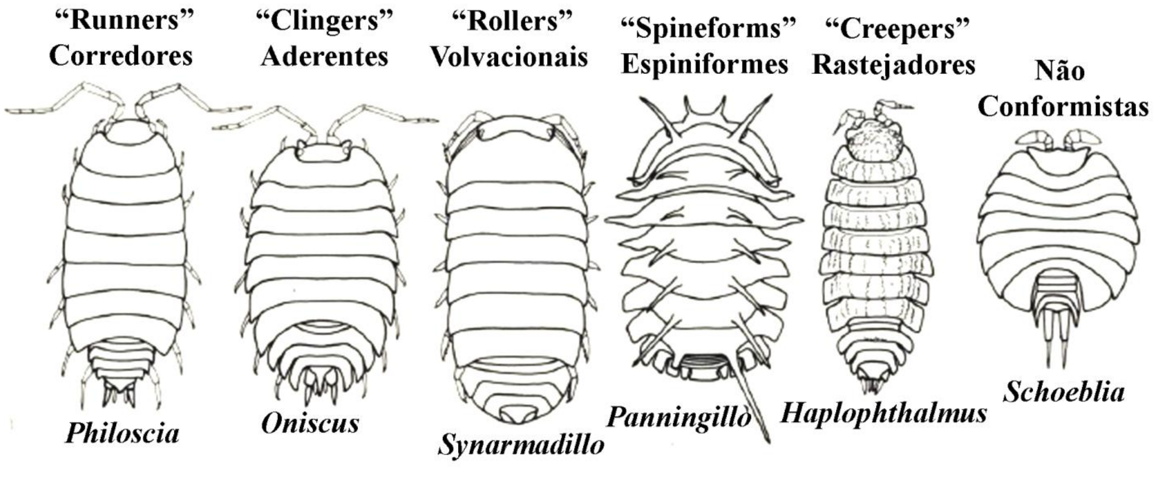

Figura 5. Grupos ecomorfológicos de isópodos terrestres. Fonte: SCHMALFUSS (1984), modificado.

A fauna de isópodos desempenha funções importantes nos ecossistemas terrestres, pois atua na ciclagem de nutrientes e na formação do solo (LAVELLE et al., 2006). Esses organismos são primariamente detritívoros, agindo na quebra mecânica e na fragmentação de folhas, matéria orgânica em decomposição, madeira, fungos e bactérias (ZIMMER, 2003). Além disso, atuam na degradação da celulose devido à presença de bactérias endossimbiontes no seu intestino e hepatopâncreas (ZIMMER et al., 2001). Esses crustáceos também servem de alimento para outros artrópodos como aranhas, escorpiões e insetos, além de vertebrados como anfíbios, répteis e mamíferos (ARAUJO, 1999; PAOLETTI & HASSAL 1999; REZÁC et al., 2008).

1.2. Filogenia de Oniscidea

As relações filogenéticas em Oniscidea, e sua respectiva posição na Ordem Isopoda, foram analisadas por SCHMALFUSS (1989). As cinco linhagens, Ligiidae, Tylidae, Mesoniscus, Crinocheta e Synocheta foram consideradas como um grupo monofilético, com as seguintes sinapomorfias: (1) redução da primeira antena e da maxílula; (2) alteração no tamanho do maxilípodo; e (3) presença de um complexo sistema condutor de água. Ligiidae é o grupo irmão das demais linhagens, que por sua vez possuem uma retração do endópodo do urópodo, redução da antena 1 e alteração nas peças bucais; a próxima divisão separa Mesoniscidea de Synocheta e Crinocheta e considera esses dois últimos como grupos irmãos por partilharem o estado do caráter com a papila genital fusionada (Figura 6).

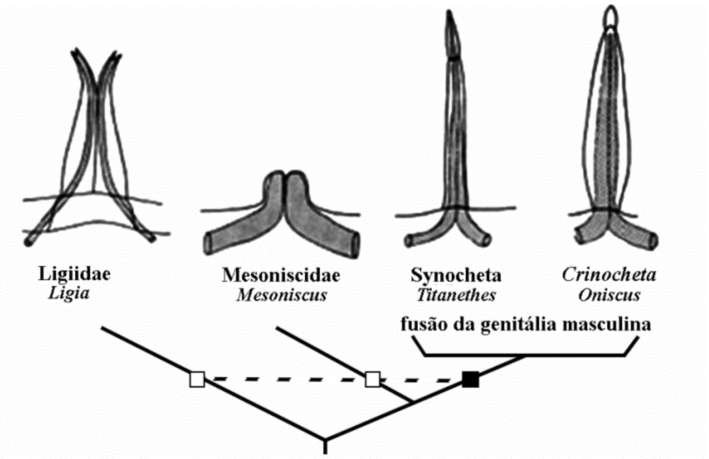

Figura 6. Cladograma apresentado por SCHMALFUSS (1989) para as relações em Oniscidea.

Outra análise morfológica envolvendo Oniscidea infere que Calabozoidea é um grupo irmão de Oniscidea, e Calabozoidea e Oniscidea são grupo irmão dos demais isópodos (BRUSCA & WILSON, 1991). ERHARD (1995, 1998) utilizando características morfológicas e anatômicas do exoesqueleto e da musculatura do pleon suportam a monofilia do táxon. O autor estabeleceu o clado Holoverticata (composto por: Tylidae, Mesoniscidae, Synocheta e Crinocheta) sendo grupo irmão de Ligiidae; o clado Orthogonopoda incluindo Mesoniscidae, Synocheta e Crinocheta; e o clado Euoniscoida incluindo Synocheta e Crinocheta, corroborando com a configuração previamente obtida por SCHMALFUSS (1989) (Figura 7).

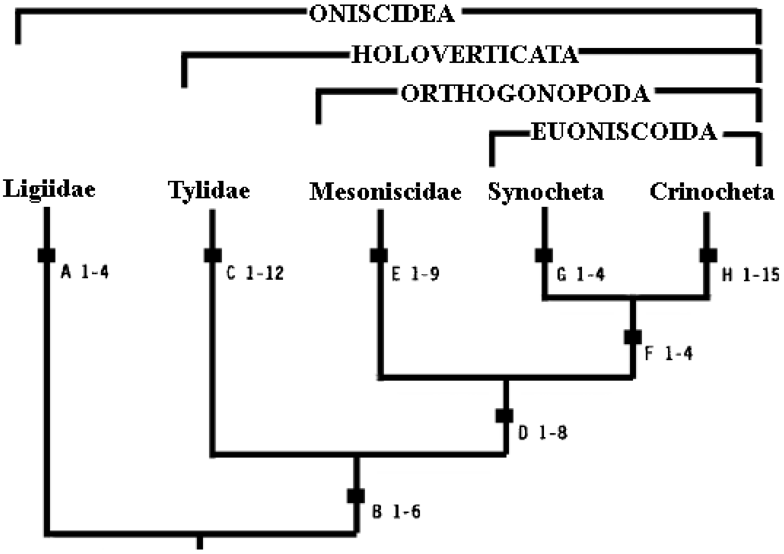

Figura 7. Cladograma apresentado por ERHARD (1998) para as relações em Oniscidea.

As primeiras análises realizadas para Oniscidea, onde foram utilizados dados moleculares, englobaram grupos taxonômicos mais elevados. Crinocheta e Synocheta foram recuperados como grupos monofiléticos (MICHEL-SALZAT & BOUCHON, 2000; MATTERN & SCHLEGEL, 2001), assim como Oniscidea (DREYER & WÄGELE, 2002).

As relações filogenéticas de Crinocheta foram avaliadas por SCHMIDT (2002, 2003) com base em dados morfológicos de 24 famílias, onde obteve as seguintes sinapomorfias: (1) mandíbula sem molares; (2) endópodo do pleópodo1 do macho com furo espermático; (3) redução do sistema condutor de água, (4) cotilédones e (5) tendência a formação da área respiratória na parte dorsal dos exópodos dos pleópodos.

Recentemente, o número de estudos utilizando dados moleculares vem aumentando e a maioria destes com o objetivo de elucidar as relações entre gêneros, espécies e populações (KLOSSA-KILIA et al., 2006; PARMAKELIS et al., 2008; POULAKAKIS & SFENTHOURAKIS, 2008; KARASAWA & HONDA, 2012; KAMILARI et al., 2014; LEE et al., 2014; RAUPACH et al., 2014). Uma grande diversidade genética e uma grande frequência de espécies crípticas vem sendo documentada (HELD, 2003; 2005; JUNG et al., 2008; HURTADO et al., 2010) assim como a existência de complexo de espécies (BRÖKELAND & RAUPACH, 2008; LEE et al., 2014).

Alguns problemas taxonômicos se devem a identificações equivocadas de espécies, muitas vezes por falta de conhecimento ou até mesmo por falta de descrições detalhadas. Muitas vezes diferenças entre espécies são restritas a poucos caracteres, frequentemente inerente a morfologia dos machos e muitas destas características podem ser reflexo de variações intraespecífica (POULAKAKIS & SFENTHOURAKIS, 2008). Sendo assim a utilização de dados moleculares pode representar uma importante ferramenta para a determinação de espécies.

1.3. Bathytropidae Vandel, 1952

A família Bathytropidae por não ter sido bem definida sofreu várias alterações desde sua criação. Seu histórico é brevemente discutido abaixo.

O gênero tipo, *Bathytropa,* foi descrito por BUDDE-LUND (1885) para as espécies *B. meinertii* Budde-Lund, 1885 e *B. costata* Budde-Lund, 1885. As espécies com ocorrência na Argélia, norte da África, foram definidas pela forma do corpo convexa, ligeiramente contrátil, com nervuras ou granulação; olhos medianos; antenas expostas; cabeça com lobos; epímeros grandes e sub-retangulares; telson triangular ou trapezoidal e ausência de pulmões pleopodais. Oniscidea, neste trabalho, era composta por quatro famílias e o gênero foi alocado em 'Onisci'.

O gênero *Neotroponiscus* e a espécie *Neotroponiscus carolii* foram estabelecidos por ARCANGELI (1936). A espécie foi registrada em Piraju, São Paulo (Brasil) e caracterizada pelos lobos cefálicos, tubérculos dorsais e ausência pulmões pleopodais. No momento, Oniscidea era composta por 10 famílias (VERHOEF, 1920) e *Neotroponiscus* foi alocado na família Porcellionidae.

GIAMBIAGI DE CALABRESE (1939) descreveu *Porcellio argentinus* de Punta Lara e *P. daguerrii* da Ilha Delta do Paraná, ambos de Buenos Aires, Argentina. O autor observou que, em particular, a forma não triangular do telson e o tamanho reduzido das antenas destas espécies poderiam indicar seu posicionamento incorreto e sugeriu que pertenciam a outro gênero.

Brasilocellio VERHOEFF (1941) foi proposto para acomodar *B. nodulosus*, também na família Porcellionidae, com material provindo de Nova Teutônia, Santa Catarina (Brasil). Este gênero apresentava algumas semelhanças corporais a *Neotroponiscus* como a forma do *habitus*, as antenas e a ausência pulmões pleopodais. No entanto os gêneros eram distintos na forma do lobo frontal e o tipo de tubérculos. Contudo, a ausência de caracteres masculinos para *Neotroponiscus* limitou as comparações entre os táxons.

A subfamília Bathytropinae VANDEL, 1952 foi estabelecida para incluir os gêneros *Bathytropa* Budde-Lund, 1885, *Neotroponiscus* Arcangeli, 1936, *Brasilocellio* Verhoeff, 1941, *Myrmekiocellio* Verhoeff, 1936 [atualmente em Squamiferidae (SCHMOLZER, 1965)] e *Dubioniscus* Vandel, 1963 [atualmente em Dubioniscidae (SCHULTZ, 1995)] (VANDEL, 1963).

Neotroponiscus foi revisado por LEMOS DE CASTRO (1970a), quem sinonimizou *Brasilocellio* com *Neotroponiscus* e forneceu a redescrição de *N. carolii* juntamente com novos caracteres diagnósticos para o gênero. As espécies *N. argentinus* (Giambiagi de Calabrese, 1939), *N. plaumanni* (Andersson, 1960), N. *daguerrii* (Giambiage de Calabrese, 1939) e *N. vedadoensis* (Boone, 1918) [atualmente *Porcellio lamelatus* Budde-Lund, 1885 (SCHULTZ, 1972)] foram incluídas no gênero. Em um estudo consecutivo, Lemos de Castro (1970b) descreveu quatro novas espécies: *N. littoralis* Lemos de Castro, 1970; *N. lobatus* Lemos de Castro, 1970; *N. lenkoi* Lemos de Castro, 1970; *N. perlatus* Lemos de Castro, 1970 (LEMOS DE CASTRO, 1970b).

Algumas espécies foram descritas e transferidas para *Bathytropa*. O gênero atualmente é composto por *B. colasi* Vandel, 1954 da província de Málaga (Sul da Espanha); *B. dollfusi* Strouhal, 1936 da Grécia e Sicília (Itália), *B. graevei* (Verhoeff, 1940) da Ilha de Ischia (Itália); *B. patanei* Caruso, 1973 e *B. ruffoi* Caruso, 1973 da Sicília (Itália); *B. schembrii* Caruso & Lombardo, 1982 de Malta; *B. granulata* Aubert & Dollfus, 1890 de Marseille; *B. meinertii* Budde-Lund, 1885, *B. costata* (Budde-Lund, 1885), *B. tuberculata* Racovitza, 1908 do Norte da Argélia; e *B. rifensis* Taiti & Rossano, 2015 de Rif (Marrocos) (SCHMIDT, 2003; TAITI & ROSSANO, 2015).

STROUHAL (1968) descreveu *Bathytropa wahrmani* com ocorrência em Israel e Turquia. A espécie foi caracterizada pelos espinhos dorsais, pulmões pleopodais esponjosos e telson largo, características diversas das demais espécies do gênero, o que levou a suposição de que seu posicionamento neste gênero estava incorreto ou que havia a probabilidade de uma perda secundária dos pulmões pelos outros integrantes da família (SCHMIDT, 2003). Esta espécie foi examinada e seu posicionamento e características serão discutidos no capítulo 1.

Mauritaniscus Vandel, 1959 era composto pela espécie *Mauritaniscus pierrei* (Vandel, 1950), e *Mauritaniscus littorinus* (Miller, 1936) [atualmente *Niambia capensis* (Dollfus, 1895), pertencente a Platyarthridae]. O gênero foi transferido de Oniscidea para Bathytropidae por SCHULTZ (1982), já que as espécies possuíam antena biarticulada e pleópodos sem área respiratória. Devido ao fato que a família Platyarthridae também é definida pelo flagelo de antena com duas articulações, ausência de pulmões pleopodais e baixa capacidade volvacional, foi levantada a hipótese que ambas as famílias representassem o mesmo táxon (FERRARA & TAITI, 1989).

Em 1973, três novos gêneros foram estabelecidos, entre eles: *Australoniscus* Vandel, 1973 composto por duas espécies *A. alticolus* Vandel, 1973 do Nepal e *A. springetti* Vandel, 1973 da Austrália; *Papuasoniscus* Vandel, 1973 para *Papuasoniscus holthuisi* Vandel, 1973 da Oceania; e *Laninoniscus* Reca, 1973 para *Laninoniscus giambiagiae* Reca, 1973 da Argentina (VANDEL, 1973a, b; RECA, 1973).

Laninoniscus giambiagiae diferencia-se das demais espécies de Bathytropidae por apresentar os lobos cefálicos pouco desenvolvidos, sendo assim pode ser considerado um gênero mais ancestral dentre os integrantes da família (RECA, 1973).

SCHMALFUSS (1983) reexaminou *Australoniscus alticolus* encontrada no Nepal e sinonimizou o gênero a *Nagurus* Holthuis, 1949 devido à presença de uma área respiratória nos exópodos dos pleópodos. No entanto, destacou que *A. springetti* não se insere em *Nagurus* e que certamente pertence a um gênero diferente, enfatizando a necessidade de revisão do gênero.

Papuasoniscus atualmente é composto por três espécies: *Papuasoniscus golovatchi* Dalens, 1988, *Papuasoniscus holthuisi* Vandel, 1973 e *Papuasoniscus lutaoensis* Jeon & Kwon, 1996. O gênero se distribui pela região tropical da Austrália nas Ilhas Salomão, Bismarck, Togian e Nova Guiné, e na região Oriental, em Taiwan, China (JEON & KWON, 1996).

VANDEL (1981) em um trabalho de descrição dos isópodos terrestres de cavernas de Cuba descreveu o gênero *Cubanoscia* com três espécies: *C. primitiva* Vandel, 1981, *C. romanorum* Vandel, 1981 e *C. próxima* Vandel, 1981. Como na descrição do gênero e das espécies o material tipo não foi designado, o nome é considerado um nome não válido ou não disponível pelo Código Internacional de Nomenclatura Zoológica (ICZN, Art. 13.3). As espécies de *Cubanoscia* presentes na coleção de Vandel no Museu Nacional de História Natural (França) foram examinadas e são discutidas no capítulo 2.

A hipótese de sinonímia de Bathytropidae e Platyarthridae é mencionada por FERRARA & TAITI (1989) e TAITI et al. (1992). No entanto, LEWIS (1998) argumenta contra a sugestão de ambos os trabalhos, pois as famílias apresentam morfologia distinta. Ainda neste trabalho, descreveu *Monitus*, gênero monotípico para a espécie *Monitus testudinatus* Lewis, 1998, encontrado na Austrália, que apresenta uma grande semelhança morfológica com os exemplares de *Neotroponiscus*. Entretanto possui três artículos no flagelo da antena.

Dumetoniscus foi o gênero mais recente descrito para Bathytropidae, ocorrendo em Socotra, Iêmen. *Dumetoniscus graniticus* Taiti & Checcucci, 2009 são isópodos do tipo “runner”, sem capacidade volvacional, cujo tegumento possui tubérculos superficiais e lobos cefálicos bem desenvolvidos, com o lobo frontal triangular (TAITI & CHECCUCCI, 2009).

A posição taxonômica da família Bathytropidae foi analisada por SCHMIDT (2003) que recuperou as famílias Bathytropidae e Platyarthridae independentemente, discordando com a hipótese anterior de sinonímia de FERRARA & TAITI (1989) e TAITI et al. (1992). No entanto, sugeriu que Bathytropidae forma um agrupamento artificial, e que necessita de uma revisão taxonômica e uma análise filogenética mais detalhada para elucidar as relações entre seus membros.

1.4. *Neotroponiscus* Arcangeli, 1936

O gênero possui oito espécies descritas. Algumas espécies foram re-descritas, entre elas, *N. carolii* por LEMOS DE CASTRO (1970a), *N. daguerrii* por RECA (1973) com material da localidade tipo, da Argentina e por ARAUJO et al. (1996), com o primeiro registro para o Rio Grande do Sul, Brasil. Além disso, a disposição do marsúpio das fêmeas de *N. daguerrii* e *N. carolii* foi descrita por APPEL et al. (2011).

O conhecimento da distribuição de algumas espécies foi ampliado, entre elas, *N. daguerrii* e *N. argentinus*, ambas originalmente descritas da Argentina e atualmente possuem registros de distribuição para a região Sul do Brasil (ARAUJO et al.,1996; ALMERÃO et al., 2006; BOOS et al., 2012); *N. lenkoi*, anteriormente conhecida apenas no estado de São Paulo, foi registrada no estado do Rio de Janeiro no Parque Nacional da Tijuca (MUGNAI et al., 2013).

O gênero ocorre nas regiões de Mata Atlântica ao longo da América do Sul (LEMOS DE CASTRO, 1970a). No Brasil, as espécies podem ser encontradas em áreas de mata primária ou secundária, em áreas de encosta ou na região costeira (LOPES et al., 2005), geralmente associadas a bromélias (ARAUJO et al., 1996), em ninhos de formigas (LENKO, 1971) ou cupins (LISBOA et al., 2013). As espécies apresentam baixa capacidade volvacional e tegumento pigmentado; a superfície dorsal geralmente é coberta por espinhos ou tubérculos; a cabeça possui lobos medianos e laterais bem desenvolvidos; e o telson possui as laterais convergentes geralmente com carena na linha mediana (LEMOS DE CASTRO, 1970a).

OBJETIVOS

OBJETIVO GERAL

Revisar a taxonomia e investigar as relações filogenéticas das espécies de *Neotroponiscus*, e esclarecer seu posicionamento em Oniscidea.

OBJETIVOS ESPECÍFICOS

- Analisar o material proveniente de coleções científicas e de coletas, para a identificação das espécies.
- Redescrever e/ou descrever espécies, para o levantamento dos caracteres morfológicos.
- Confirmar e ampliar o conhecimento sobre a distribuição das espécies de *Neotroponiscus* e dos demais gêneros de Bathytropidae, quando possível solucionar os problemas taxonômicos da família.
- Testar a monofilia da família e do gênero, estabelecendo relações de parentesco entre seus integrantes, com base em dados morfológicos e moleculares.

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Capítulo I

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A new genus of Trachelipodidae Strouhal, 1953 (Crustacea, Isopoda, Oniscidea) from the eastern Mediterranean

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Abstract

Levantoniscus n. gen. is erected for two new species from Cyprus: *Levantoniscus bicostulatus* n. sp. and *Levantoniscus makrisi* n. sp. *Levantoniscus wahrmani* (Strouhal, 1968) n. comb. from Israel and southern Turkey is transferred from the genus *Bathytropa* Budde-Lund, 1885 and family Bathytropidae. The new genus is included in the family Trachelipodidae and is characterized by distinct dorsal ornamentation, interlocking pleopods and uncovered pleopodal lungs which are lo-cated in invaginations on pleopod 3–5 exopodites.

Key words: Oniscidea, *Levantoniscus*, new species, Cyprus, Near East

Capítulo II

Artigo publicado na revista Tropical Zoology

CARDOSO ET AL. (2015) Tropical Zoology, 29(3), 111–133.

The genus *Dubioniscus* Vandel, 1963 (Oniscidea, Dubioniscidae) with descriptions of two new species from Brazil

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Abstract

Before the present study, the genus *Dubioniscus* included four species occurring in Central and South Americas. The examination of *Dubioniscus delamarei*, *D. marmoratus* and *D. negreae* allowed us to revise the genus and to move *D. goeldii* to *Calycuoniscus*. Moreover, two new species are described, *D. depressus* **n. sp.** from the state of São Paulo, and *D. elongatus* **n. sp.** from the state of Rio de Janeiro, Brazil.

Keywords: terrestrial isopods; neotropical; Amazon rainforest; Atlantic forest

Capítulo III

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Two new species of *Neotroponiscus* Arcangeli, 1936 (Crustacea, Isopoda, Oniscidea) from Brazilian caves

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Abstract

Neotroponiscus comprises eight species. In this study, two new species of this genus of terrestrial isopods are described. *Neotroponiscus iporangaensis* sp. nov. was collected in limestone caves located in Parque Estadual Turístico do Alto Ribeira (PETAR). *Neotroponiscus tuberculatus* sp. nov. occurs in iron ore caves of the Iron Quadrangle (local name Quadrilátero Ferrífero) and represents the first species of the genus recorded in iron caves. As tourism and mining are common activities in PETAR and in the caves of the Iron Quadrangle, respectively, both species' occurrence is threatened.

Keywords: Terrestrial isopods; woodlice; neotropics.

Capítulo IV

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Taxonomic revision of *Neotroponiscus* Arcangeli, 1936 (Isopoda: Bathytropidae)

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Abstract

The terrestrial isopods from the genus *Neotroponiscus* occur in the Brazilian Atlantic forest. Eight out of the species are re-described: *N. carolii, N. argentinus, N. daguerrii, N. plaumanni*, *N. littoralis*, *N. lobatus*, *N. lenkoi*, *N. perlatus*. New characters to better define the species and new distribution record are provided.

Keywords: Terrestrial isopods, woodlice, neotropics.

Taxonomic revision of *Neotroponiscus* Arcangeli, 1936 (Isopoda: Bathytropidae)

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Abstract

The terrestrial isopods from the genus *Neotroponiscus* occur in the Brazilian Atlantic forest. Eight species are re-described: *N. carolii, N. argentinus, N. daguerrii, N. plaumanni, N. littoralis, N. lobatus, N. lenkoi*, *N. perlatus*. New characters to better define the species and new distribution record are provided.

Keywords: Terrestrial isopods, woodlice, neotropics.

Introduction

Bathytropidae includes 24 species distributed in the genera *Australoniscus* Vandel, 1973, *Bathytropa* Budde-Lund, 1885, *Cubanoscia* Vandel, 1981, *Dumetoniscus* Taiti and Checcucci, 2009, *Laninoniscus* Reca, 1973, *Monitus* Lewis, 1998, and *Neotroponiscus* Arcangeli, 1936 (Taiti and Schotte 2016). The genus *Neotroponiscus* comprises ten species distributed in Argentina, Brazil and Uruguay (Schmalfuss 2003, Taiti and Schotte 2016). In Brazil, the genus is recorded along the Brazilian Atlantic forest and is mainly characterized by the shape and distribution of dorsal tubercles, the cephalic lobes and the pereonite epimera well-development (Lemos de Castro 1970a, 1970b, Mugnai et al. 2013, Lisboa et al. 2014).

Neotroponiscus was proposed to the monotypical *N. carolli* Arcangeli, 1936 from Piraju, state of São Paulo, Brazil. At that moment, the genus was placed in the family Porcellionidae Brandt, 1831 based on the cephalic lobes, dorsal tuberculation and pleopod exopods without pleopodal lungs.

Giambiagi de Calabrese (1939) described *Porcellio argentinus* Giambiagi de Calabrese, 1939 from Punta Lara, and *P. daguerrii* Giambiagi de Calabrese, 1939 from the Delta del Paraná Island, both from Buenos Aires, Argentina. Based on the non-triangular shape of telson with lateral sides straight and small size of antennae, the author suggested that both species could belong to a different genus. Verhoeff (1941) created *Brasilocellio* to allocate *B. nodulosus* Verhoeff, 1941 from Nova Teutônia, state of Santa Catarina, Brazil. According to the author, this genus shows similarities to *Neotroponiscus*, such as the habitus, the number of articles in the antennal flagellum and the absence of pleopodal lungs on pleopod exopods, but bears distinguishable characters as the shape of the frontal lobe and the type of tubercles. However, the absence of male specimens of *Neotroponiscus* limited the comparisons to *Brasilocellio*.

Bathytropinae was established by Vandel (1952) to include the genera *Myrmekiocello* Verhoeff, 1936 [currently considered as *incertae sedis*, according to Taiti and Schotte, 2016], *Bathytropa*, *Neotroponiscus*, *Brasilocellio*, and *Dubioniscus* Vandel, 1963 [currently in Dubioniscidae, according to Schultz, 1995] (Vandel 1963). The author characterized the subfamily by having: body length of 3-5 mm; dorsum pigmented, granulated, with round plaques and triangular scale-setae; large or medium eyes; neopleura 3-5 well-developed, with outline continuous with that of pereonite 7; telson triangular or trapezoidal; and pleopod exopod without pleopodal lungs.

Andersson (1960) described *Brasilocellio plaumanni* Andersson, 1960 from Nova Teutônia, state of Santa Catarina, Brazil. Lemos de Castro (1970a) revised the genus *Neotroponiscus* providing new diagnostic features. In this study *N. carolii*, was re-described, *P. argentinus*, *P. daguerrii*, *B. plaumanni*, and *Leptotrichus vedadoensis* Boone, 1918 [actually accepted as *Porcellio lamellatus* Budde-Lund, 1885] were transferred to *Neotroponiscus* and four species were described: *N. littoralis* Lemos de Castro, 1970 from Cabo Frio, state of Rio de Janeiro, *N. lobatus* Lemos de Castro, 1970 from Sooretama, state of

Espírito Santo, *N. lenkoi* Lemos de Castro, 1970 from Ilha da Vitória, state of São Paulo and *N. perlatus* Lemos de Castro, 1970 from Santa Tereza, state of Espírito Santo (Lemos de Castro 1970b). Recently, Cardoso et al. (2017) described two new species: *N. iporangaensis* Cardoso and Araujo, 2017 in limestone caves from Parque Estadual Turístico do Alto Ribeira (PETAR), state of São Paulo, and *N. tuberculatus* Cardoso and Araujo, 2017 in iron ore caves from Quadrilátero Ferrífero, state of Minas Gerais.

The aim of this study is to review the taxonomy of *Neotroponiscus*, providing detailed descriptions of the species of the genus required to determine the species limits, essential in phylogenetic studies and to understand the dynamics of symbiotic relationships. In addition, new distribution records are provided, increasing the knowledge of the distribution for some species in Brazil.

Material and methods

Specimens were stored in 70% (museum) and absolute ethanol (recent material). Field surveys were conducted along the Atlantic forest in the Brazilian states from Bahia to Rio Grande do Sul. The identifications were based on morphological characters. The species were illustrated with the aid of a *camera lucida* on Olympus CX31 microscope and pictures were obtained with Nikon AZ100. The cuticular structures were studied in a JSM 6060 scanning electron microscope (SEM) at the Centro de Microscopia Eletrônica of UFRGS. The final illustrations were prepared according to Montesanto (2015, 2016).

The specimens used in this study were deposited in the Museu Nacional do Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade de São Paulo (MZUSP); Coleção de Crustáceos do Departamento de Zoologia (UFRGS), Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina.

Systematic account

Family **Bathytropidae** Vandel, 1952

Genus ***Neotroponiscus*** Arcangeli, 1936

Type species ***Neotroponiscus carolii*** Arcangeli, 1936

Brasilocellio Verhoeff, 1941:122;

Neotroponiscus Arcangeli, 1936: 201; Lemos de Castro 1970:89; Souza-Kury 1998: 654; Leistikow and Wägele 1999: 26; Schmalfuss 2003: 162; Schmidt and Leistikow 2004: 59.

Neotropinoscus: Vandel 1952: 145 [erroneous spelling]

Nesiotroponiscus: Vandel 1963: 78 [erroneous spelling]

Diagnosis

Dorsum tuberculated, surface with circular plaques and covered with fan-shaped scale-setae. Pereon and pleon epimera enlarged; pereonite 1 epimeron directed frontwards and surpassing eyes, pereonites 2-7 epimera progressively directed backwards; neopleurae 3-5 outline continuous with that of pereonite 7, falciform, and directed backwards. Cephalon with frontal line delimiting frontal and lateral lobes on upper portion; suprantennal line absent. Telson with convex margins, not covering uropod protopods. Antennal flagellum of two articles, shorter than fifth segment of peduncle, second article almost three times as long as first article. Mandible with molar penicil dichotomized, left mandible with 2+1 penicils, right mandible with 1+1. Maxillula inner endite bearing two hairy penicils, outer distal margin with lateral tip; outer endite of 4+6 teeth, 5 or 4 teeth cleft at apex. Maxilla outer lobe wider than inner lobe. Maxilliped palp with two setae on proximal article; endite subrectangular, median seta surpassing distal margin, distal outer margin with two hooks. Pleopod exopods without respiratory areas. Uropod endopod inserted proximally.

Remarks

Neotroponiscus is characterized by the frontal and lateral lobes in cephalon, pereonites and pleonites epimera expanded laterally, and distinct dorsal ornamentation. It is distinguishable from *Bathytropa* in the convex shape of telson instead of concave, and maxilla outer lobe wider than inner lobe instead slender; from *Monitus* in the antennal flagellum of two articles; from *Papuasoniscus* in the development of frontal lobes; from *Laninoniscus* in the development of frontal lobes, in the absence of suprantennal line, in the tuberculated dorsum instead of smooth and in the shape of telson with convex lateral margins instead of straight; from *Dumetoniscus* in the development of the medial frontal lobe, in the absence of suprantennal line and in the shape of telson with convex lateral margins instead of straight.

Neotroponiscus carolii Arcangeli, 1936

(Figures 1-3, 18A, 19)

Neotroponiscus carolii Arcangeli, 1936: 201, figs 1-4; Van Name 1940: 115, fig 7; Lemos de Castro 1970a: 90, figs 1-2; Lenko1971: 8; Souza-Kury 1998: 655; Leistikow and

Wägele 1999: 27; Schmalfuss 2003: 162; Appel et al. 2011: table 1; Lisboa et al. 2013: 394, fig 1.

Material examined

Brazil, Bahia: Candeias: 3 ♂♂, 2 ♀♀ (UFRGS 6457) RPPN Grande Moinho Aratu (-12.7925º, -38.4711º), May 2007, leg. J. Lisboa; 2 ♂♂, 2 ♀♀ (UFRGS 6458) (-12.7925º, -38.4711º), May 2007, leg. J. Lisboa; 2 ♂♂, 1♀ (UFRGS 6459) Baía de Aratu (-12.7925º, -38.47111º), November 2006, leg. J. Lisboa; 1♀ (UFRGS 6460) Região MT, between Candeias and Salvador (-12.7977º, -38.4763º), September 2007, leg. J. Lisboa. Salvador: 6 ♂♂, 9 ♀♀ (UFRGS 6462) Baía de Aratu, December 2007, leg. J. Lisboa; 3 ♂♂, 7♀♀ (UFRGS 4230) Baía de Aratu, November 2006, leg. J. Lisboa; 1 ♀ (UFRGS 4547) Baía de Aratu, leg. J. Lisboa; 1 ♀ (UFRGS 4548) Baía de Aratu, leg. J. Lisboa. Ilheus: 10 ♂♂, 8 ♀♀ (UFRGS 4731) Reserva Experimental da CEPLAC (-14.7990º, -39.1723º), 28 April 2010, leg. J. Lisboa and P.B. Araujo; 1 ♂, 2 ♀♀ (UFRGS 4735) Reserva Experimental da CEPLAC, 12 November 2010, leg. J Lisboa and IS Campos-Filho; 1 ♂ (UFRGS 6456) CEPLAC, Cocoa plantation (-14.7572º, -39.2332º), 2007, leg. J. Lisboa; 2 ♀♀ (UFRGS 6461) CEPLAC, termite nest (-14.7544º, -39.2305º), 2007, leg. J. Lisboa. Una: 1 ♀ (UFRGS 6467) in bromeliads in the canopy of trees, 27 May 2014, leg. W. da Rocha and col. (E 5.5); 3 ♂♂, 4 ♀♀ (UFRGS 6468) same data (E 5.2); 2 ♂♂, 3 ♀♀ (UFRGS 6469) same data (E 5.6); 4 ♂♂, 2 ♀♀ (UFRGS 6471) 23 September 2013 (S 1.2); 2 ♂♂, 6 ♀♀ (UFRGS 6472) same data (S 1.1); 4 ♀♀ (UFRGS 6473) same data, 15 October 2013 (E 2.1). Itajú do Colonia: 1 ♀, 1 ♂ in slide (UFRGS 6453) road BA-120, between Itajú do Colonia and Itapé (-15.0327º, -39.6041º), 17 September 2013, leg. I.S. Campos-Filho and J. Lisboa.

Re-description

Male body length 5 mm. Brown color with unpigmented spots, antenna fifth segment of peduncle and flagellum pigmented; cephalon with lobes strongly pigmented; epimeron l with unpigmented spots; neopleurae 3-5, uropods, and telson strongly pigmented (Figure 18A). Dorsum with spine-shaped tubercles placed as follows: three transversal lines on cephalon and pereonite 1, two transversal lines on pereonites 2–6, two or one transversal line on pereonite 7, four tubercles on pleonite 1 and 2, two tubercles on pleonites 3–5 (Figures 1A, B). Dorsum with fan-shaped scale-setae (Figure 1C); one *nodulus lateralis* per side, on top of outmost tubercle (Figures 1B, F). Pereonite 1 epimeron developed frontwards, surpassing eyes (Figures 1A, B). Cephalon (Figures 1D, E) with rounded lateral lobes, directed outwards; median lobe with quadrangular shape directed upwards; eyes with 14 ommatidia. Telson (Figure 1G) as wide as long, rounded distal apex and medial carena. Antennula (Figure 1H) distal articles with two apical and two subapical aesthetascs. Antenna (Figures 1I, 18A) when extended back, reaches posterior margin of pereonite 2; flagellum with two sets of aesthetascs. Mandible (Figure 2A, B) as in generic diagnosis. Maxillula (Figure 2C) outer endite with 4+6 teeth, inner set with 4 cleft setae. Maxilla (Figure 2D) as in generic diagnosis. Maxilliped as in Figure 2E. Pereopods with sparse setae on sternal margin of merus and carpus; dactylar organ and ungual seta simple. Uropod (Figure 3A) protopod longer than wide; exopod longer than endopod, surpassing distal margin of telson.

Male: Pereopods (Figure 3 B – D) without modifications. Pleopod 1 (Figure 3E) exopod small (one third of endopod length), rectangular; endopod directed outwards with setules on distal inner margin. Pleopod 2 (Figure 3F) exopod triangular, shorter than endopod. Pleopods 3–5 as in Fig. 3G–I.

Remarks

This species is mainly characterized by the shape and distribution of dorsal tubercles. Here we provide the pattern of the *noduli laterales*, which remained undescribed since the Lemos de Castro’s (1970) description of male specimens.

Distribution

Neotroponiscus carolii is recorded in the states of Bahia (Lemos de Castro 1970a, Lisboa et al. 2013, present work), Espírito Santo (Lemos de Castro 1970a) and São Paulo (Arcangeli 1936, Lenko 1971), Brazil (Figure 19).

Neotroponiscus argentinus (Giambiagi de Calabrese, 1939)

(Figures 4-5, 18B, 19)

Porcellio argentinus Giambiagi de Calabrese, 1939: 634, plate I;

Brasilocellio nodulosus Verhoeff, 1941: 122, figs 8-15; Van Name, 1942: 308, fig 11; Andersson, 1960: 560, fig 11.

Neotroponiscus argentinus Lemos de Castro, 1970a: 93, fig 3; Souza-Kury 1998: 654; Leistikow and Wägele 1999: 26; Schmalfuss 2003: 162; Boss et al. 2012: 1035; Mugnai et al. 2013: 855, map 1.

Material examined

Brazil, Santa Catarina: 1 ♀ (UFRGS 6444) Joinville (-26.3219º, -48.8636º), 3 September 2013, leg. G.M. Cardoso; 1 ♂ (UFRGS 5470) Corupá (26°25’23”S, 49°14’46”W), 27 June 2012, leg. P.B. Araujo; 1 ♂, 1 ♂ in slide, 2 ♀♀ (UFRGS 5468) São João Batista (-27.2644º, -48.8533º), 26 June 2012, leg. P.B. Araujo; 1 ♂, 1 ♀, 1 ♂ in slide (UFRGS 6442) Florianópolis, Trilha do Poção (-27.6107º, -48.5057º), 22 September 2013, leg. F.B. Ribeiro and P.B. Araujo; 2 ♂♂, 2 ♀♀ (UFRGS

6443) Florianópolis, Banhado Ressaca (-27.6848º, -48.5382º), 23 September 2013, leg. F.B. Ribeiro and P.B. Araujo; Rio Grande do Sul: 1 ♀ (UFRGS 4866) Alta Igrejinha (29°34'44.23"S, 50°46'47.10"W), undated, leg. not identified; 1 ♀ (UFRGS 6445) Matinhos (-25.8355º, -48.5706º), 1 December 2013, leg. G.M. Cardoso. Argentina, Buenos Aires: 2 ♂♂, 2 ♀♀ (MACN 34334) Punta Lara (-34.8254°, -57.9684°), 08 December 1968, leg. A Reca (Colección Roberto Taberner); 3 ♂♂, 15 ♀♀ (MACN 34339) INTA Delta, 15 July 1968, leg. A.O. Bachmann (Colección Roberto Taberner).

Re-description

Male body length 5 mm. Light brown color; antenna and cephalon pigmented; pereonite 1 epimeron with unpigmented spot on anterior portion; neoplaurae 3-5 with unpigmented spots on anterior portion; uropods and telson strongly pigmented (Figure 18B). Dorsum with rounded tubercles, placed as follows: three transversal lines on cephalon, two transversal lines on pereonite 1, one transversal line on pereonites 2–7, pleon smooth (Figures 4A, B). Dorsum covered with fan-shaped scale-setae (Figure 4C); one *nodulus lateralis* per side, inserted on outmost tubercle, first *nodulus* placed farther away from lateral and distal margins (Figures 4A, B, F). Pereonite 1 epimeron developed frontwards, reaching eyes (Figures 4A, B). Cephalon (Figures 4D, E) with rounded lateral lobes, directed outwards; median lobe rectangular with round distal margin and directed upwards; eyes with 16 ommatidia. Telson (Figure 4G) wider than long; distal portion rounded. Antennula (Figure 4H) with distal article bearing two apical and two subapical aesthetascs. Antenna (Figures 4I, 18B) when extended back reaches posterior margin of pereonite 1; flagellum with two aesthetascs. Pereopods with sparse setae on sternal margin of merus and carpus; dactylar organ simple and ungual seta spatuliform. Uropod (Figure 5A) protopod wider than long; exopod smaller than endopod, surpassing distal margin of telson.

Male: Pereopods 1 and 7 (Figures 5B, D) without modifications. Pereopod 2 (Figure 5C) with brush of setae on sternal margin of merus and carpus. Pleopod 1 (Figure 5E) exopod sub-circular, wider than long; endopod slightly bent outwards, twice as long as exopod bearing setules on distal inner margin. Pleopod 2 (Figure 5F) exopod triangular; endopod longer than exopod. Pleopods 3–5 as in Figs. 5G-I.

Remarks

The type material of Giambiagi de Calabrese (1939) could not be found in the collection of MACN. *Neotroponiscus argentinus* is characterized by the rounded shape of telson and male pereopod 2 merus and carpus with brush of setae on sternal margin. The *noduli laterales* coordinates matches with the description provided by Andersson (1960). This species clearly differs from *N. carolli* in the round-shaped tubercles, pleon without tubercles, and in the shape of telson, uropods and male pleopod 1 exopod.

Distribution

Neotroponiscus argentinus is recorded from Brazil (states of Espírito Santo, Rio de Janeiro, São Paulo, Paraná and Santa Catarina), and Argentina (Buenos Aires province) (Giambiagi de Calabrese 1939, Verhoeff 1941, Van Name 1942, Andersson 1960, Lemos de Castro 1970a, Mugnai et al. 2013) (Figure 19).

Neotroponiscus daguerrii (Giambiagi de Calabrese, 1939)

(Figures 6-8, 18C, 19)

Porcellio daguerrii Giambiagi de Calabrese, 1939: 635, plate 2; Van Name, 1942: 308, fig 12.

Neotroponiscus daguerrii Lemos de Castro, 1970a: 99, fig 5; Reca 1973: 93, plate 1; Araujo et al. 1996: 122, figs 29-38; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162; Lopes et al. 2005: 101 table I; Almerão et al. 2006: 474; Appel et al. 2011: table 1.

Material examined

Brazil, Rio Grande do Sul: 24 ♂♂, 29♀♀ (UFRGS 6448) Eldorado do Sul, Estação Agronômica UFRGS (-30.1003º, -51.6945º), 16 April 2013, leg. G.M. Cardoso; 25 ♂♂, 50 ♀♀ (UFRGS 6447) Porto Alegre, Estrada dos Alpes (-30.0967º, -51.1860º), 06 April 2013, leg. G.M. Cardoso; 1 ♀ (UFRGS 6454) Viamão, Parque do Itapuã (-30.3837º, -51.0205º), 13 Agost 2013, leg. G.M. Cardoso; 53 ♂♂, 64 ♀♀ (UFRGS 1246) Porto Alegre, Ilha da Pintada (-30.0278º, -52.2594º), 06 July 1989, leg. L.A.M. Schmitt; 8 ♂♂, 18 ♀♀ (UFRGS 1515) Rio Grande, Reserva Ecológica do Taim (-32.5844º, -52.5692º), 17 February 1991, leg. P.B. Araujo. Argentina, Buenos Aires: 7 ♂♂, 18 ♀♀ (MACN 34335) Mocoretá, 17.II.1982, leg. R. Taberner (Colección Roberto Taberner); 4 ♂♂ (MACN 34343) Punta Lara (-34.8254°, -57.9684°), 12 November 1966, leg. A.O. Bachmann (Colección Roberto Taberner); 2 ♀♀ (MACN 34344) Delta del Paraná, 12 December 1976, leg. A.O. Bachmann (Colección Roberto Taberner); 1 ♂, 7 ♀♀ (MACN 34347) INTA Delta, 23 September 1978, E. Angrisano (Colección Roberto Taberner); 10 ♂♂, 38 ♀♀ (MACN 34400) Río Carapachay, Tigre, 31 May 1981, leg. R. Taberner (Colección Roberto Taberner).

Re-description

Male body length 6 mm. Brown color and unpigmented spots, antennae and cephalon pigmented; pereonite 1 epimeron with unpigmented spots on anterior portion; epimera with transversal unpigmented line; neopleurae 3-5 with medial unpigmented spots; uropods slightly pigmented, telson strongly pigmented (Figure 18C). Dorsum with rounded and rectangular tubercles, placed as follows: three transversal lines on cephalon, two transversal lines on pereonite 1, one transversal line on pereonites 2–7; pleon smooth (Figures 6A, B, 8A, B). Dorsum covered with fan-shaped scale-setae (Figures 6C, 8C); one *nodulus lateralis* per side, inserted on outmost tubercle, first *nodulus* placed farther away from distal margin (Figures 6B, F). Pereonite 1 epimeron developed frontward eyes (Figures 6A, B, 8A). Cephalon (Figures 6D, E, 8A) with lateral lobes directed outwards, rectangular, distal margin rounded, smaller than median lobe; median lobe directed upwards, rectangular and distal margin triangular; eyes with 20 ommatidia. Telson (Figures 6G, 8B) wider than long, distal margin quadrangular. Antennula (Figure 6H) with distal article bearing two apical and two subapical aesthetascs. Antenna (Figures 6I, 8E, 18C) when extended back reaches posterior margin of pereonite 1; flagellum with one aesthetasc. Pereopods bearing sparse setae on sternal margin of ischium, merus, and carpus; dactylar organ and ungual seta simple. Uropod (Figure 7A) protopod wider than long; exopod smaller than endopod, surpassing distal margin of telson.

Male: Pereopods 1 and 7 (Figures 7B, D) without modifications. Pereopod 2 (Figure 7C) with dense setae on sternal margin of merus and carpus. Pleopod 1 (Figure 7E) exopod sub-circular, wider than long, distal outer margin straight; endopod bent outwards, twice as long as exopod, bearing setules on distal inner margin. Pleopod 2 (Figure 7F) exopod triangular bearing three setae on the outer margin; endopod longer than exopod. Pleopods 3–5 exopods as in Fig. 7G-I.

Remarks

This species was re-described by Reca (1973) and Araujo et al. (1996). Here we provide illustrations with new information about cuticular surface structures.

Neotroponiscus daguerrii is characterized by the shape of the cephalic lobes, the quadrangular shape of telson and male pereopod 2 with brush of setae on sternal margin of merus and carpus. In lacking tubercles on pleon *N. daguerrii* is similar to *N. argentinus* and *N. plaumanni*; in having the male pereopod 2 bearing a brush of setae on sternal margin of the merus and carpus, the species is similar to *N. argentinus*.

Distribution

Neotroponiscus daguerrii is recorded from Buenos Aires province, Argentina (Giambiagi de Calabrese 1939, Lemos de Castro, 1970a, Reca 1973) and from state Rio Grande do Sul, Brazil (Araujo et al. 1996, present work) (Figure 19).

Neotroponiscus plaumanni (Andersson, 1960)

(Figures 9-10, 19)

Brasilocellio plaumanni Andersson, 1960: 563, figs 12.

Neotroponiscus plaumanni Lemos de Castro, 1970b: 93, fig 4; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162; Boss et al. 2012: 1035;

Material examined

Brazil, Santa Catarina: 1 ♂ (UFRGS 6281) Itajaí, Morro do Baú, 12-17 May 1996; 6 ♂♂, 11 ♀♀ (UFRGS 6284) Itajaí, Morro do Baú, 12-17 May 1996.

Re-description

Male body length 5 mm. Specimens unpigmented due to long preservation in ethanol. Dorsum with rounded tubercles, more elongated or rectangular on pereon, placed as follows: three transversal lines on cephalon, two transversal lines on pereonite 1, one transversal line on pereonites 2–7, pleon smooth (Figures 9A, B). Dorsum with one *nodulus lateralis* per side, inserted on outmost tubercle (Figures 9A, B, F). Pereonite 1 epimeron developed frontwards reaching eyes (Figures 9A, B); pleon epimera falciform directed backwards, in continuous line with that of pereon, (Figures 9A). Cephalon (Figures 9C, D) with rectangular lateral lobes and median lobe; eyes with 16 ommatidia. Telson (Figure 9E) wider than long; convex lateral margins with quadrangular distal part. Antennula (Figure 9F) distal article bearing two apical and two subapical aesthetascs. Antenna (Figures 9G) reaching posterior margin of pereonite 1; flagellum shorter than fifth segment of peduncle with two aesthetascs. Pereopods bearing sparse setae on sternal margin of ischium, merus, and carpus; ungual seta and dactylar organ simple. Uropod (Figure 10A) protopod wider than long; exopod smaller than endopod, surpassing distal margin of telson.

Male: Pereopods (Figure 10B – D) without modifications. Pleopod 1 (Figure 10E) exopod wider than long, with rounded distal projection; endopod with setules on distal internal margin, slightly bent outward. Pleopod 2 (Figure 10E) exopod triangular, shorter than endopod. Pleopods 3–5 (Figure 10F–H) trapezoidal.

Remarks

Neotroponiscus plaumanni is easily recognized by the shape of the cephalic lobes, dorsal tubercles, telson and male pleopod 1 exopod (see also Andersson 1960, Lemos de Castro 1970a). In the absence of tubercles on pleon *N. plaumanni* is similar to *N. daguerrii* and *N. argentinus* but it can be distinguished by the male pereopod 2 merus and carpus with sparse number of setae on sternal margin (vs. dense in *N. daguerrii* and *N. argentinus*). Here we provide the pattern of the *noduli laterales* and additional illustrations of pereopods and male appendages.

Distribution

Neotroponiscus plaumanni is recorded from the state of Santa Catarina, Brazil (Andersson 1960, present work) and from Rocha and Florida department, Uruguay (Lemos de Castro 1970a) (Figure 19).

Neotroponiscus littoralis Lemos de Castro, 1970

(Figure 11, 18D, 19)

Neotroponiscus littoralis Lemos de Castro, 1970b: 1, figs 1,2; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162.

Type material examined

Holotype: 1 ♂ (MNRJ 6171) Brazil, Rio de Janeiro, Ilha de Cabo Frio, 16 December 1965, leg. A. Lemos de Castro and A. Coelho, in bromeliads. Alotype: 1 ♀ (MNRJ 6172) same data as holotype. Paratypes: 3 ♂♂, 6 ♀♀ (MNRJ 6489) same data as holotype; 1 ♀ (MNRJ 6173) Rio de Janeiro, Cabo Frio, Praia do Peró, in bromeliads; January 1960, leg. A. Coelho and S. Ypiranga; 1 ♂, 2 ♀ (MNRJ 6488) Rio de Janeiro, Cabo Frio, Praia Jõao Fernandes, in bromeliads, January 1960, leg. A. Coelho and S. Ypiranga.

Re-description

Male body length approximately 4 mm. Specimens unpigmented due to long preservation in ethanol (Figure 18D). Dorsum with rounded tubercles, placed as follows: three transversal lines on cephalon, three transversal lines on pereonite 1, two transversal lines on pereonites 2–7, tubercles can be fused, and less pronounced; two tubercles on pleonites 1-5 (Figures 11A, B); one *nodulus lateralis* per side, inserted on outmost tubercle (Figures 11A, B). Pereonite 1 epimeron developed frontwards surpassing eyes (Figures 11A). Cephalon (Figure 11C) with round lateral lobes directed outwards; triangular median lobe directed upwards; eyes with 20 ommatidia. Telson as wide as long, with medial carena (Figure 11A); distal margin rounded.

Pereopods bearing sparse setae on sternal margin of merus and carpus; ungual and dactylar organ simple.

Male: Pereopods (Figure 11D - F) without modifications. Pleopod 1 (Figure 11G) exopod rounded, wider than long; endopod with setules on distal internal margin. Pleopod 2 (Figure 11H) exopod triangular, shorter than endopod. Pleopods 3and 4 as in Fig. 11I, J.

Remarks

This species is characterized by the shape of cephalic lobes, dorsal tubercles arrangement and shape of telson. *Neotroponiscus littoralis* resembles *N. carolii* in the shape of dorsal tubercles and uropod protopod longer than wide; but it differs by having tubercles on median portion of pleon (vs. paramedian tubercles in *N. carolii*). Here we provide the pattern of the *noduli laterales* and illustrations of pereopods.

Distribution

Neotroponiscus littoralis is recorded only in the state of Rio de Janeiro, Brazil (Lemos de Castro 1970b) (Figure 19).

Neotroponiscus lobatus Lemos de Castro, 1970

(Figures 12-13, 18E, 19)

Neotroponiscus lobatus Lemos de Castro, 1970b: 5, figs 3-4; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162; Mugnai et al. 2013: 857, map 1.

Type material examined

Holotype: 1 ♂ (MNRJ 6174) Brazil, Espírito Santo, Sooretama, 12 October 1957, leg. O Schubart.

Material examined

Brazil: Minas Gerais: 1 ♂, 1 ♀ (UFRGS 5127) Matozinhos, Gruta MOC N8 (-19.5646º, -44.0598º) 4.-15 April 2011, leg. F. Franco and col. Espírito Santo: 1 ♀ (UFRGS 4232) Cariacica, Reserva Biológica Duas Bocas, 09 November 2006, leg. P.B. Araujo and J. Anza.

Redescription

Male body length 5 mm. Specimens unpigmented due to long preservation in ethanol (Figure 18E). Dorsum with round and rectangular tubercles, placed as follows: three lines on cephalon, two lines on pereonite 1, one line on pereonites 2–7, pleon smooth (Figures 12A, B). One *nodulus lateralis* per side, inserted on outmost tubercle (Figures 12A, B). Pereonite 1 epimeron developed frontwards, reaching eyes (Figures 12A, B). Cephalon (Figure 12C) with

rectangular lateral lobes, directed outwards; median lobe directed upwards with rounded distal margin; eyes with 14 ommatidia. Telson (Figure 12D) wider than long; distal margin quadrangular. Antennula (Figure 12E) distal articles with two apical and two subapical aesthetascs. Antenna (Figures 12F) when extended back reaches posterior margin of pereonite 2. Peropods bearing sparse setae on sternal margin of merus and carpus; ungual and dactylar organ simple. Uropod (Figure 13A) protopod wider than long; endopod smaller than exopod.
Male: Pereopods 1 (Figure 13B – C) without modification. Pleopod 1 (Figure 13D) exopod rectangular, wider than long; endopod with setules on distal internal margin. Pleopod 2 (Figure 13E) endopod longer than pleopod 1. Pleopods 4 and 5 as in Fig. 13G, F.

Remarks

Neotroponiscus lobatus was described based on only one male specimen. One additional record of one female specimen was made by Mugnai et al. (2013) after the description. Here we present one more record of two specimens, totaling the third record for the species. New characters not mentioned by Lemos de Castro (1970b) as position of *noduli lateralis*, antennula and illustration for pereopods and antenna were added in the present work. *Neotroponiscus lobatus* is characterized by the shape of the cephalic lobes and dorsal tubercles, and the well-developed pereonite epimera.

Distribution

Neotroponiscus lobatus is recorded in the state of Espírito Santo (Lemos de Castro 1970b, Mugnai et al. 2013) and Minas Gerais (present work), Brazil (Figure 19).

Neotroponiscus lenkoi Lemos de Castro, 1970

(Figures 14-15, 18E)

Neotroponiscus lenkoi Lemos de Castro, 1970b: 8, fig 6; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162; Mugnai et al. 2013: 856, fig 2, map 1.

Type material examined

Holotype: 1 ♂ (MNRJ 6175) Brazil, São Paulo, Ilha da Vitória, Caraguatatuba, 27 March 1964, leg. K. Lenko. Alotype: 1 ♀ (MNRJ 6175) same data as holotype. Paratypes: 3 ♂♂, 7 ♀♀ (MNRJ 6177) same data as holotype.

Material examined

Brazil, São Paulo: 1 ♂ in slide (UFRGS 6474) Maresias (-23.8247º, -45.5285º), 04 December 2013, leg. G.M. Cardoso; 1 ♂ (UFRGS 6450) Iguape (-24.7635º, -47.7859º), 02 December 2013, leg. G.M.

Cardoso; 1 ♂, 2 ♀♀ (MZUSP 24295) Cananéia, Ilha do Cardoso (-25.0966º, -47.9297º), 24-28 November 2002, leg. Paraná: ♂♂, ♀♀ (MZUSP 24300) Morretes, Parque Estadual do Pau Oco (-24.4166º -48.9333º), 6-11 May 2002, leg. R.R. Silva and B.H. Riete.

Redescription

Male body length approximately 2.5 mm. Specimens with dark brown unpigmented areas; cephalon and antenna strongly pigmented; pereonite 1 epimera and neopleura 3 pigmentless, pereonite 4 epimera slightly pigmented; telson pigmented, uropods light brown (Figure 18E). Dorsum with rounded and rectangular tubercles, placed as follows: two transversal lines round tubercles on cephalon and pereonite 1, one transversal line on pereonites 2–7, tuberculation on pereon is progressively weak, being hardly noticed on pereonites 6 and 7; pleon and telson smooth (Figures 14A, B). Dorsum covered with fan-shaped scale-setae (Figure 14C); one *nodulus lateralis* per side (Figures 14A, B, E). Pereonite 1 epimeron developed frontwards surpassing eyes (Figures 14A), pereonites and neopleura with well-developed epimera, distal margin quadrangular (Figures 14A, F). Cephalon (Figure 14D) with rectangular lateral lobes, directed outwards; pentagonal median lobe, distal margin rounded, directed upwards; eyes with 16 ommatidia. Telson (Figure 14F) wider than long; distal margin quadrangular. Antennula (Figure 14G) distal article with three apical aesthetascs. Antenna (Figure 14H) when extended back reaches posterior margin of pereonite 1. Buccal pieces as in the generic diagnosis. Pereopods bearing sparse setae on sternal margin of ischium, merus, and carpus; ungual setae simple and dactylar organ spatuliform. Uropod (Figure 15A) protopod wider than long; endopod longer than exopod.

Male: Pereopods (Figure 15B – D) without modifications. Pleopod 1 (Figure 15E) exopod rectangular, wider than long; endopod with setules on distal internal margin, bent outward. Pleopod 2 (Figure 15F) exopod triangular, shorter than endopod. Pleopods 3–5 as in Fig. 15G-I.

Remarks

Additional characters not mentioned by Lemos de Castro (1970b) are position of *noduli lateralis*, the antennula, the pereopods bearing sparse setae on sternal margin, ungual setae simple and dactylar organ spatuliform.

Neotroponiscus lenkoi is characterized by the wide body size, cephalon with large median lobe, shallow tuberculation and color pattern. In the absence of tubercles on pleon *N. lenkoi* resembles *N. argentinus*, *N. daguerrii* and *N. plaumanni*; but differs in the quadrangular shape of telson; in having the frontal lobe pentagonal-shaped and the distal margin of telson quadrangular is similar to *N. daguerrii*, but differs in the faint development of tubercles.

Distribution

Neotroponiscus lenkoi is recorded in the states of São Paulo (Lemos de Castro 1970b), Rio de Janeiro (Mugnai et al. 2013) and Paraná (present work), Brazil (Figure 19).

Neotroponiscus perlatus Lemos de Castro, 1970

(Figures 16-17, 18G, 19)

Neotroponiscus perlatus Lemos de Castro, 1970b: 11, figs 7-8; Souza-Kury 1998: 655; Leistikow and Wägele 1999: 27; Schmalfuss 2003: 162.

Type material examined

Holotype: 1 ♂ (MNRJ 6180) Brazil, Espírito Santo, Santa Teresa, 2 November 1944, leg. O. Schubart. Paratype: 1 ♂, 3 ♀♀ (MNRJ 6181) Brazil, Espírito Santo, Domingos Martins, 22 September 1953, leg. O. Schubart.

Material examined

Brazil, Espírito Santo: 1 ♂ in slide, 2 ♀♀, Juv (UFRGS 6451) Santa Tereza (-19.9415º, -40.5824º), 12 March 2014, leg. G.M. Cardoso; 1 ♂ (UFRGS 6452) Cariacica (-20.2414º, -40.4172º), 13 March 2014, leg. G.M. Cardoso.

Re-description

Male body length 3.5 mm. Specimens with brown with yellow unpigmented spots; cephalon, fifth segment and flagellum of antenna strongly pigmented; pereonites 1-7 epimera with unpigmented spots; pleonites 1 and 2 yellowish; telson and uropods pigmented (Figure 18G). Dorsum with rounded tubercles, some specimens with spine tubercles, placed as follows: three transversal lines on cephalon, three transversal lines on pereonite 1, two transversal lines on pereonites 2–7; four tubercles on pleonites 1-3, two tubercles on pleonites 4 and 5 (Figures 16A, B). Dorsum covered with circular plaques and fan-shaped scale-setae (Figure 16C, F); one *nodulus lateralis* per side (Figures 16A, B, F). Pereonite 1 epimeron developed frontwards surpassing eyes (Figures 16A, B). Cephalon (Figures 16D, E) with rectangular lateral lobes, directed outwards; rounded median lobe; eyes with 14 ommatidia. Telson wider than long, medial carena; distal margin rounded (Figure 16G). Antennula (Figure 16H) distal article with two apical and two subapical aesthetascs. Antenna (Figures 16I, 18G) when extended back reaches posterior margin of pereonite 2; flagellum with two aesthetascs. Buccal pieces as in the generic diagnosis. Pereopods bearing sparse setae on sternal margin of merus and carpus; ungual and dactylar organ simple. Uropod (Figure 17A) protopod wider than long; endopod not reaching haft length of exopod; exopod longer than endopod, surpassing distal margin of telson.

Male: Pereopods (Figure 17B – D) without modifications. Pleopod 1 (Figure 17E) exopod rectangular, wider than long; endopod with setules on distal internal margin. Pleopod 2 (Figure 17F) exopod triangular, shorter than endopod. Pleopods 3–5 as in Figs. 17G-I.

Remarks

Additional characters not mentioned by Lemos de Castro (1970b) are the position of *noduli laterales,* the antennula, the pereopods bearing sparse setae on sternal margin, ungual and dactylar organ simple, uropod endopod inserted proximally, exopod longer than endopod. *Neotroponiscus perlatus* is characterized by the shape of tubercles and cephalic lobes. This species resembles *N. carolii* and *N. littoralis* in having tubercles on pleon and carena on telson.

Distribution

Neotroponiscus perlatus is recorded in the state of Espírito Santo, southeastern of Brazil (Lemos de Castro 1970b and present work) (Figure 19).

Acknowledgements

We are grateful to Professors Marcos Tavares and Maria José from MZUSP, Cristiana Serejo from MNRJ, Alejandro Tablado from MACN for the assistance with material from their respective collections; to Giuseppe Montesanto from Università di Pisa for all the help with the scientific illustrations; to Ivanklin Soares Campos-Filho, Wesley da Rocha, Jonathas Lisboa and all people who helped during expeditions and donation of material; to CAPES (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior) for the scholarship granted to GMC; to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for funding this research and for the Productivity Research Scholarship to PBA [MCT/CNPq/MEC/CAPES/PROTAX 562202/2010-2 and PQ 305900/2014-5].

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Figure Captions

Figure 1. *Neotroponiscus carolii.* ♂ UFRGS 6453. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

Figure 2. *Neotroponiscus carolii.* ♂ UFRGS 6453. A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped.

Figure 3. *Neotroponiscus carolii.* ♂ UFRGS 6453. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 4. *Neotroponiscus argentinus.* ♀ UFRGS 6445. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonites 4 and 5, telson and uropods, dorsal view; ♂ UFRGS 6442. H, antennule; I, antenna.

Figure 5. *Neotroponiscus argentinus.* ♂ UFRGS 6442. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 6. *Neotroponiscus daguerrii.* ♂ UFRGS 6447. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonite 5, telson and uropods, dorsal view; H, antennule; I, antenna.

Figure 7. *Neotroponiscus daguerrii.* ♂ UFRGS 6447. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 8. *Neotroponiscus daguerrii.* ♂ UFRGS 6447. A, cephalon and pereonite 1, dorsal view; B, pereonite 7, pleon, telson and uropods, dorsal view; C, tubercle on pereonite 7; D, pereonite 7 outmost tubercle; E, flagellum of antenna; F, pereopod 1, setae on carpus; G, pereopod 1, dactylus. Scale bars: A, B 200 μm, C 50 μm, D, G 20 μm, E 100 μm, F 10 μm.

Figure 9. *Neotroponiscus plaumanni.* ♂ UFRGS 6281. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon and pereonite 1, dorsal view; D, cephalon, frontal view; E, pleonites 3-5, telson and uropods, dorsal view; F, antennule; G, antenna.

Figure 10. *Neotroponiscus plaumanni.* ♂ UFRGS 6281. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 11. *Neotroponiscus littoralis.* ♂ MNRJ 6489. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon and pereonite 1, frontal view; D, pereopod 1; E, pereopod 2; F, pereopod 7; G, pleopod 1; H, pleopod 2; I, pleopod 3 exopod; J, pleopod 4 exopod.

Figure 12. *Neotroponiscus lobatus*. ♂ UFRGS 5127. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon, frontal view; D, pleonites 4 and 5, telson and uropods, dorsal view; E, antennule; F, antenna.

Figure 13. *Neotroponiscus lobatus*. ♂ UFRGS 5127. A, uropod; B, pereopod 1; C, pereopod 2; D, pleopod 1; E, pleopod 2; F, pleopod 4 exopod; G, pleopod 5 exopod.

Figure 14. *Neotroponiscus lenkoi*. ♂ MZUSP 24295 A, habitus, dorsal view; B, habitus, lateral view; UFRGS 6474 C, scale-seta; D, cephalon, dorsal view; E, pereonite 7; F, pleonites 3–5, telson and uropods, dorsal view; G, antennule; H, antenna.

Figure 15. *Neotroponiscus lenkoi*. ♂ MZUSP 24295. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 16. *Neotroponiscus perlatus*. ♂ UFRGS 6451. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonites 4 and 5, telson and uropods, dorsal view; H, antennule; I, antenna.

Figure 17. *Neotroponiscus perlatus*. ♂ UFRGS 6451. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 18. Species of *Neotroponiscus* in dorsal view. A, *N. carolii* ♂ (UFRGS 6453); B, *N. argentinus* ♀ (UFRGS 6442); C, *N. daguerrii* ♂ (UFRGS 6447); D, *N. littoralis* ♂ (MNRJ 6489); E, *N. lobatus* ♂ (UFRGS 5127); F, *N. lenkoi* ♂ (UFRGS 6474); G, *N. perlatus* ♂ (UFRGS 6451). Scale-bar: 1mm.

Figure 19. Distribution map of *Neotroponiscus* species. Type localities are numbered, followed by the distributional records. Brazilian Atlantic Forest in green.

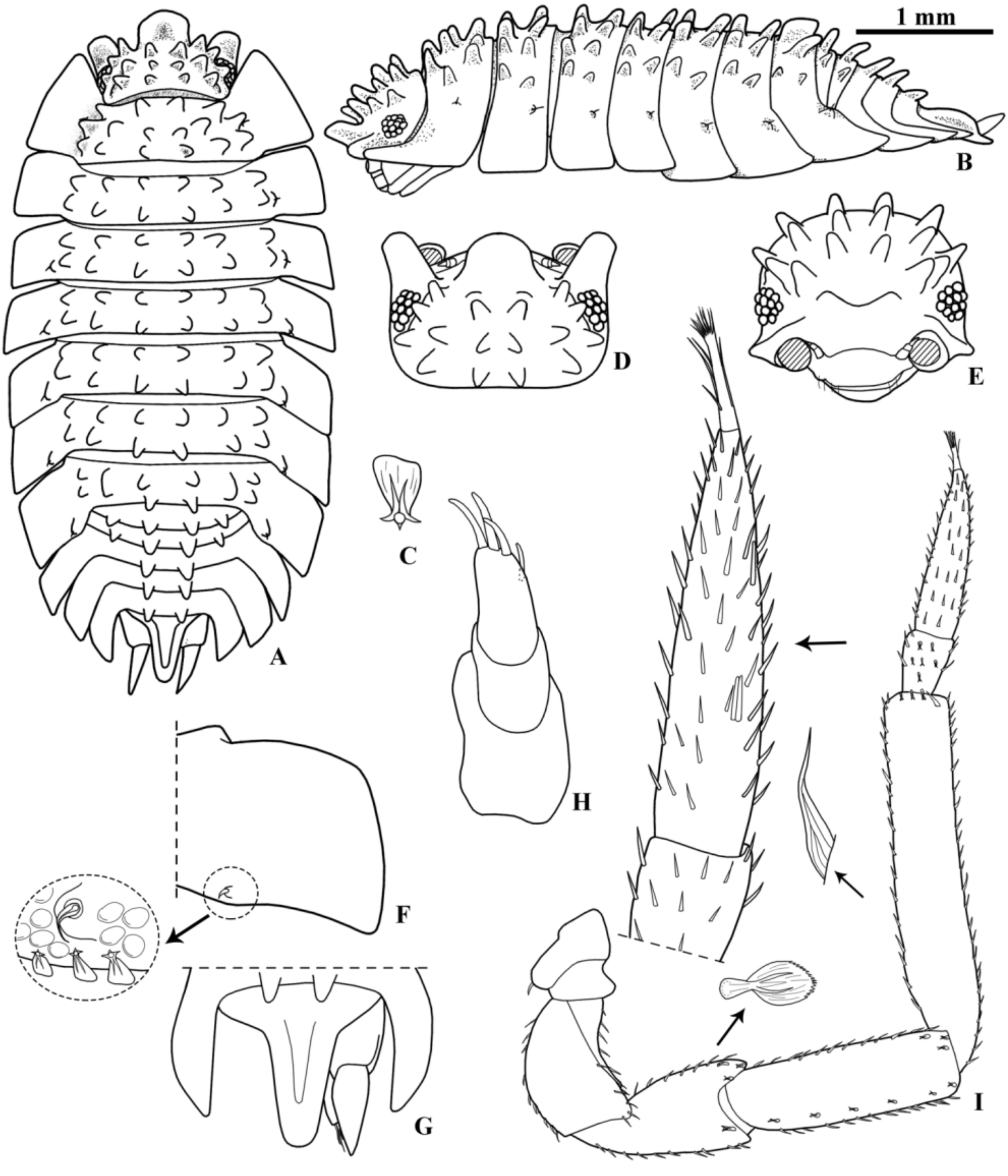

Figure 1. *Neotroponiscus carolii*. ♂ UFRGS 6453. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

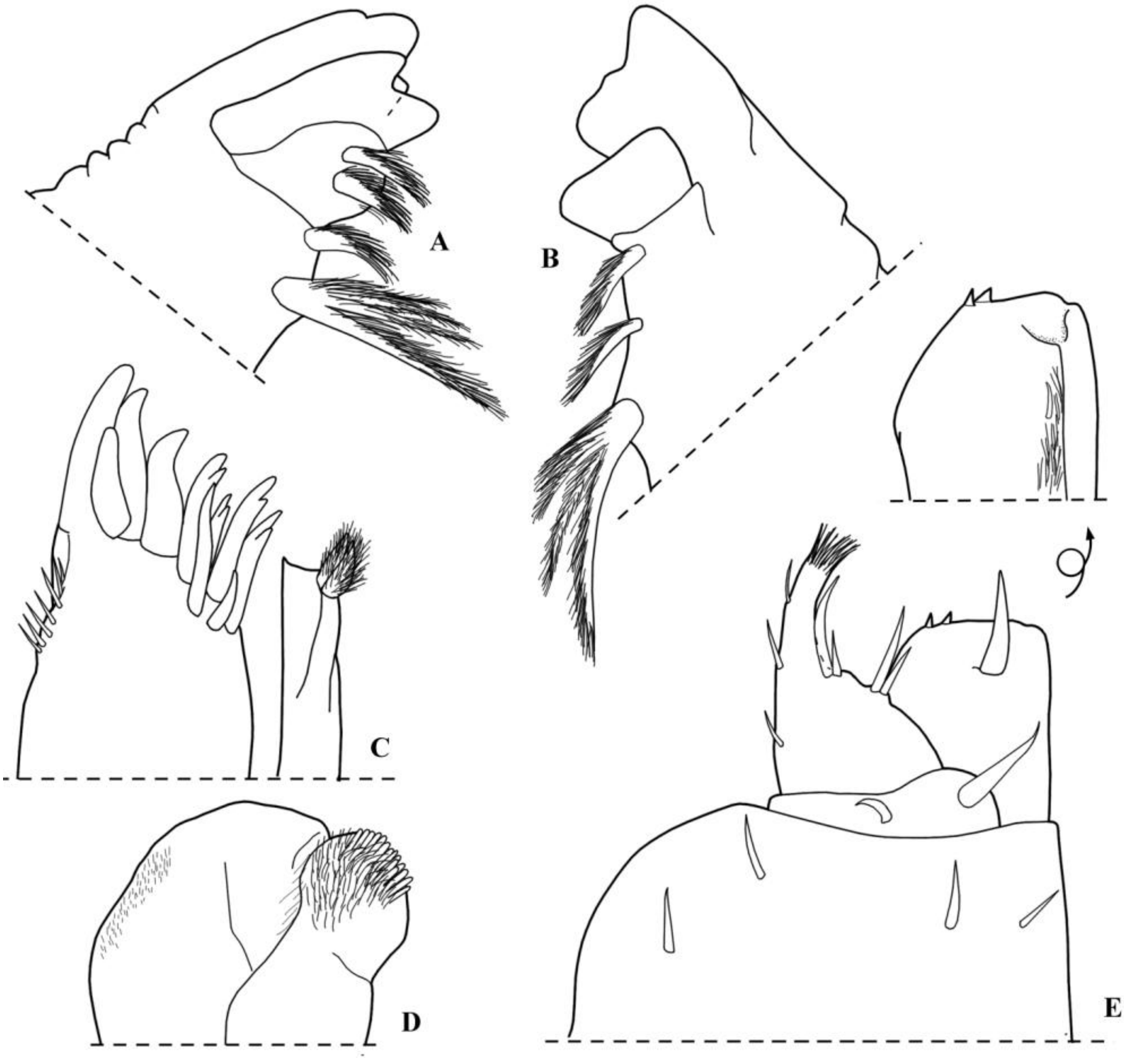

Figure 2. *Neotroponiscus carolii*. ♂ UFRGS 6453. A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped.

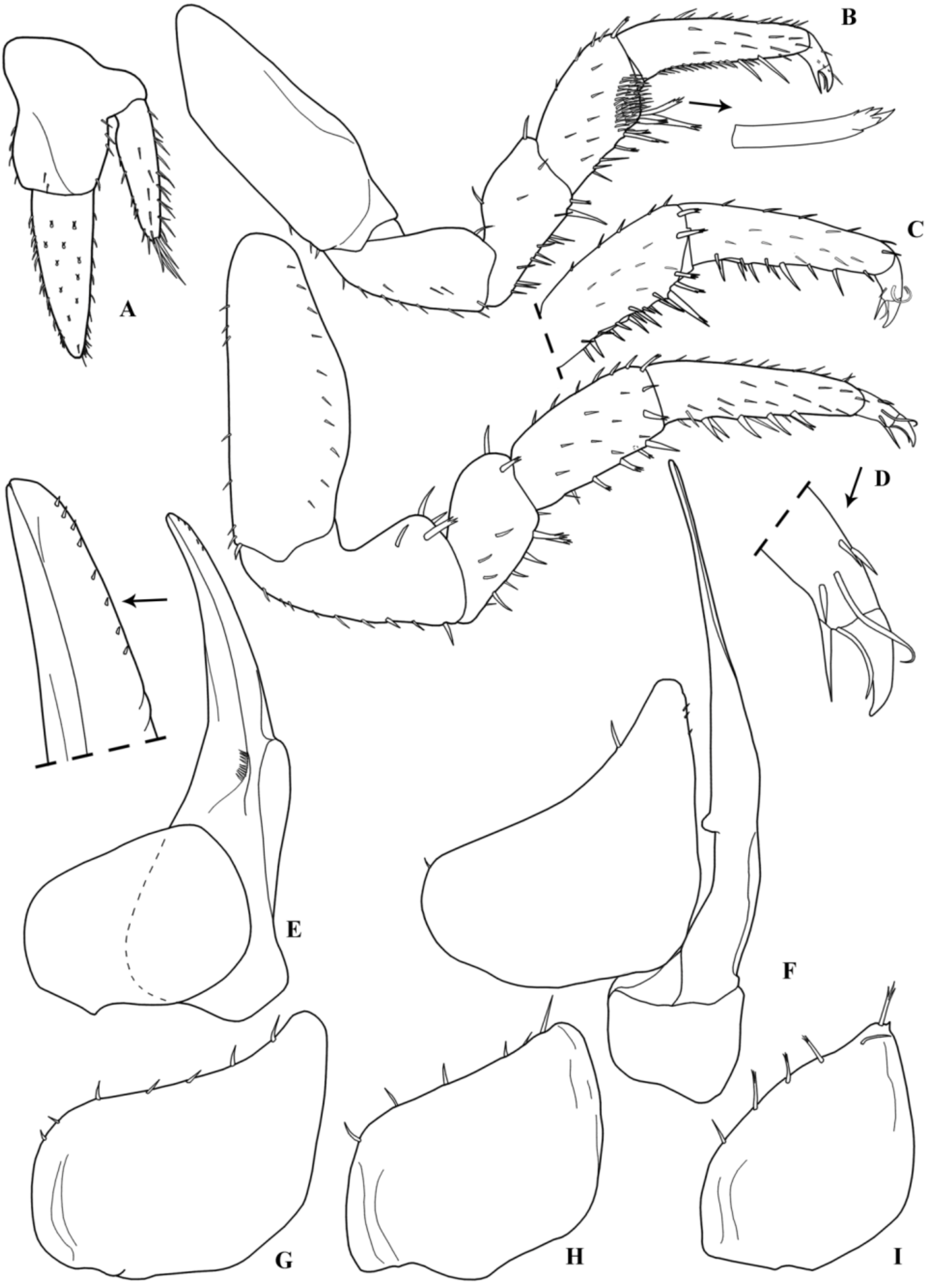

Figure 3. *Neotroponiscus carolii*. ♂ UFRGS 6453. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

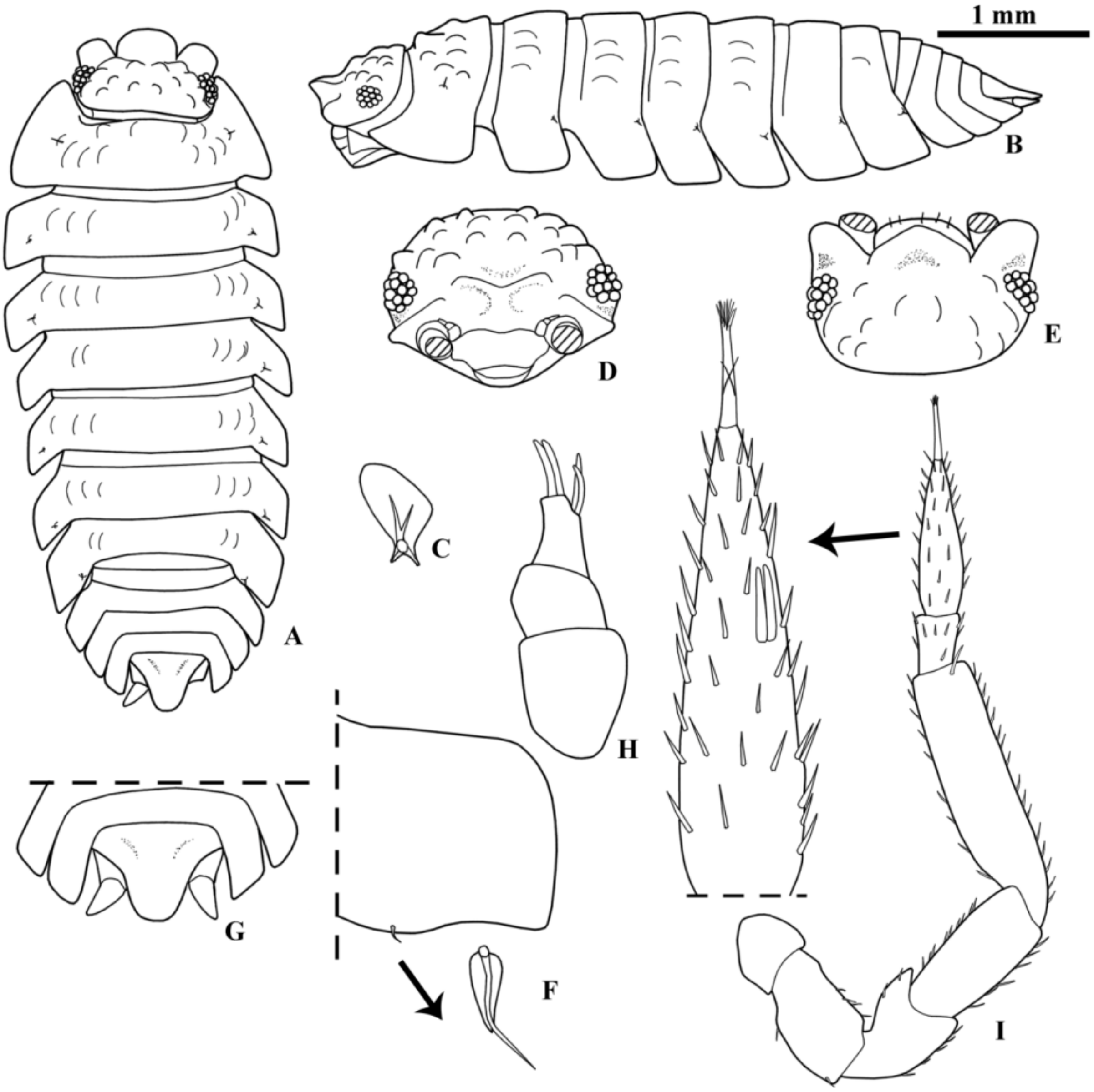

Figure 4. *Neotroponiscus argentinus*. ♀ UFRGS 6445. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonites 4 and 5, telson and uropods, dorsal view; ♂ UFRGS 6442. H, antennule; I, antenna.

Figure 5. *Neotroponiscus argentinus*. ♂ UFRGS 6442. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

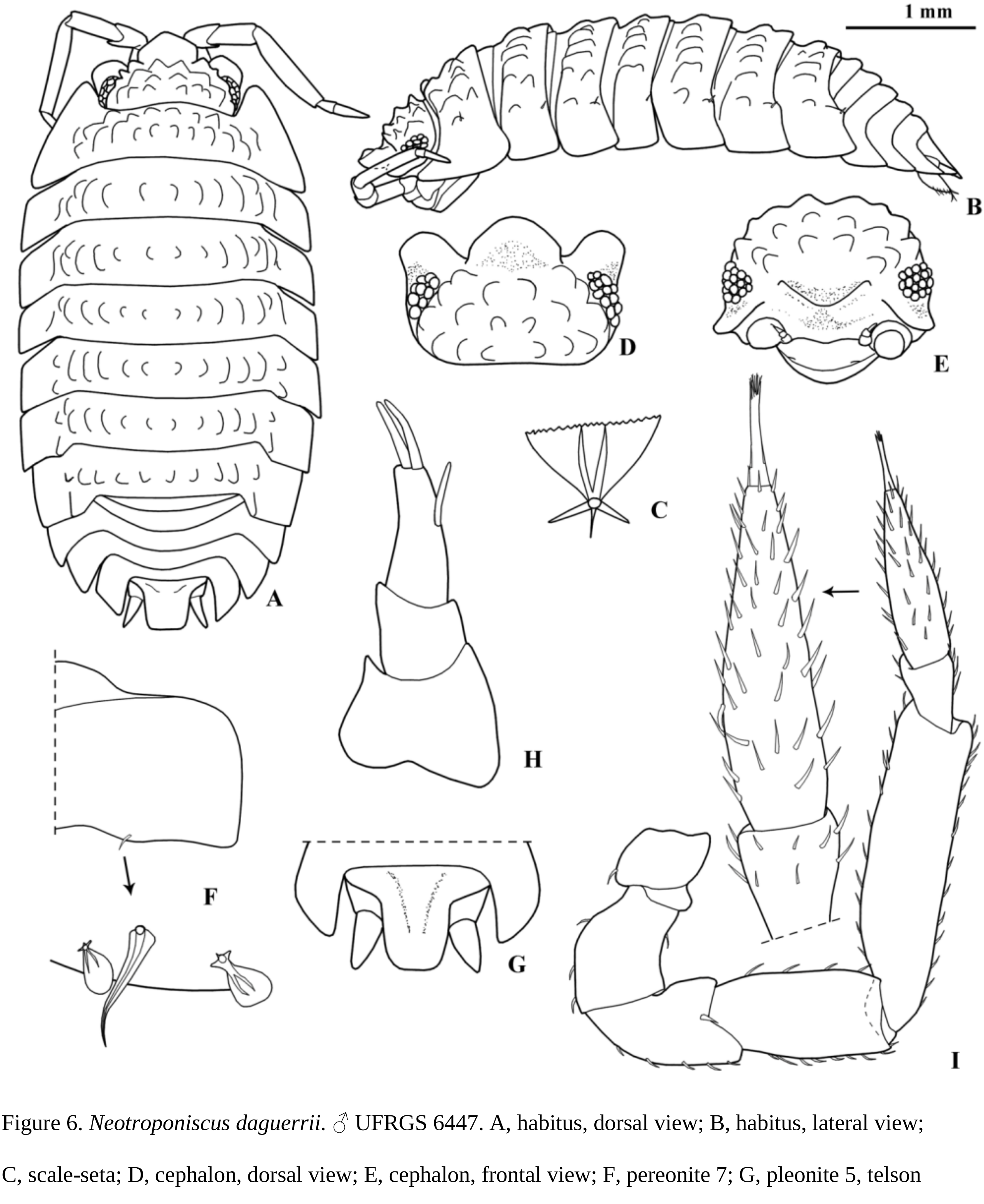

Figure 6. *Neotroponiscus daguerrii*. ♂ UFRGS 6447. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonite 5, telson and uropods, dorsal view; H, antennule; I, antenna.

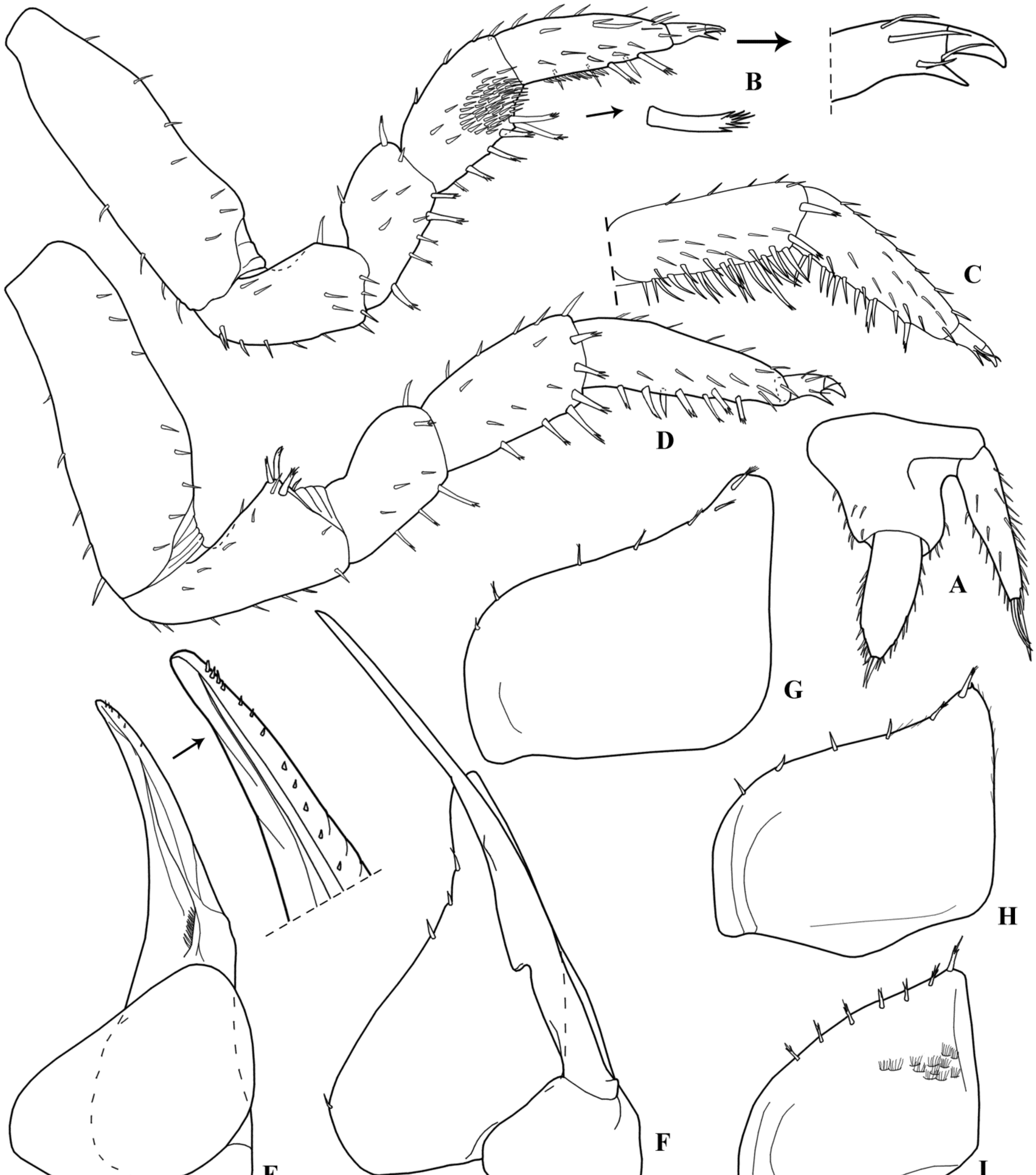

Figure 7. *Neotroponiscus daguerrii*. ♂ UFRGS 6447. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

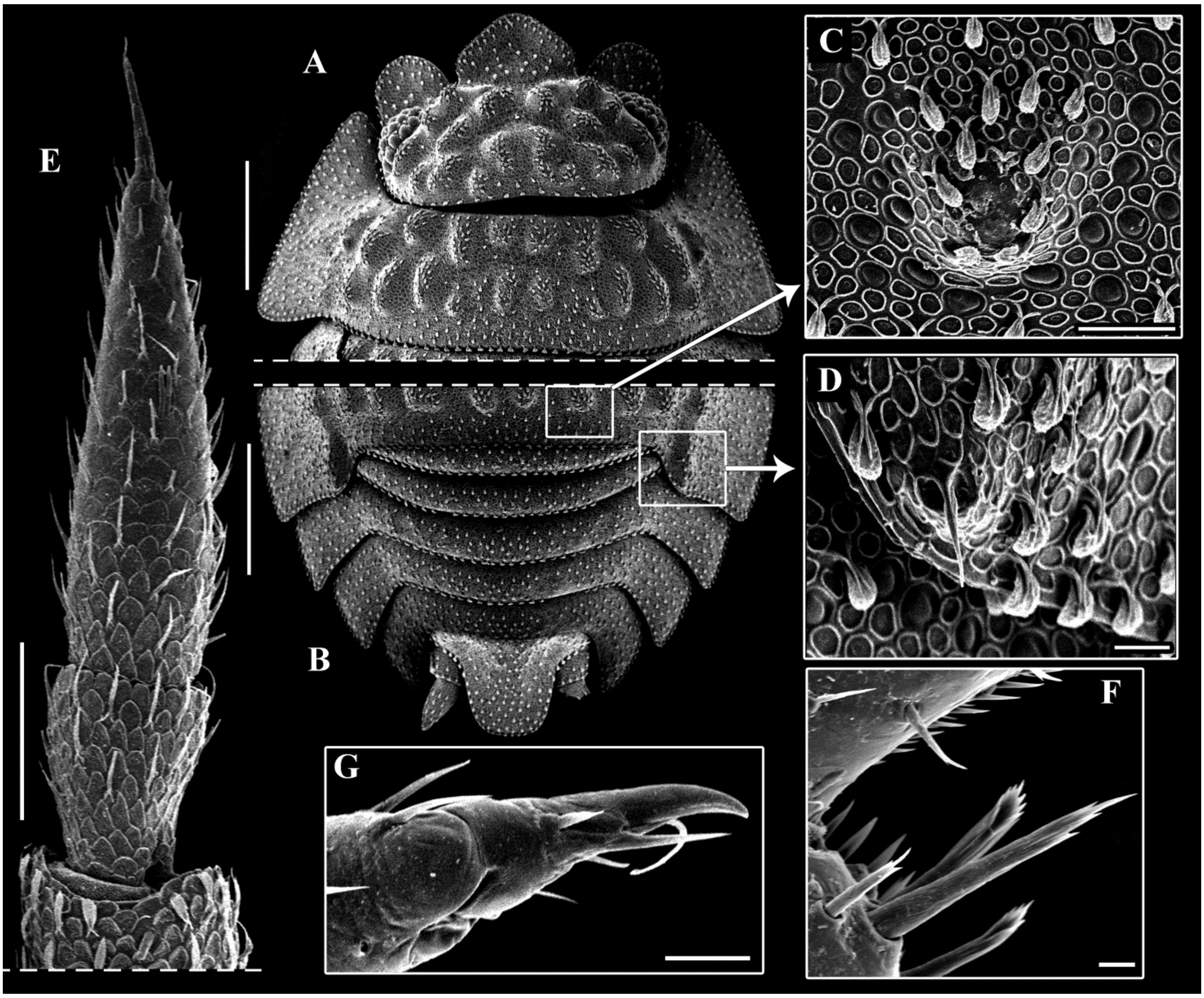

Figure 8. *Neotroponiscus daguerrii*. ♂ UFRGS 6447. A, cephalon and pereonite 1, dorsal view; B, pereonite 7, pleon, telson and uropods, dorsal view; C, tubercle on pereonite 7; D, pereonite 7 outmost tubercle; E, flagellum of antenna; F, pereopod 1, setae on carpus; G, pereopod 1, dactylus. Scale bars: A, B 200 μm, C 50 μm, D, G 20 μm, E 100 μm, F 10 μm.

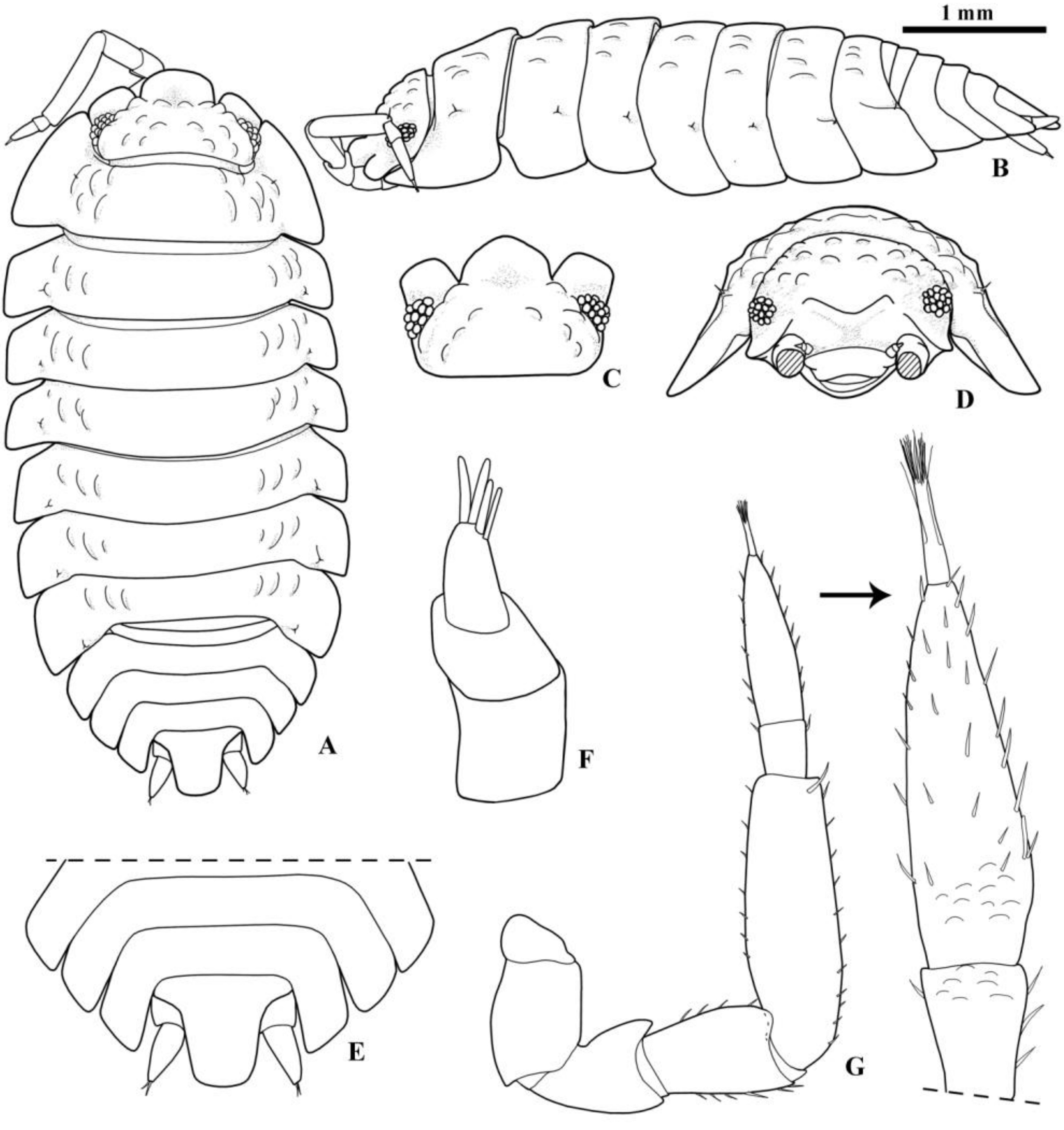

Figure 9. *Neotroponiscus plaumanni*. ♂ UFRGS 6281. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon and pereonite 1, dorsal view; D, cephalon, frontal view; E, pleonites 3-5, telson and uropods, dorsal view; F, antennule; G, antenna.

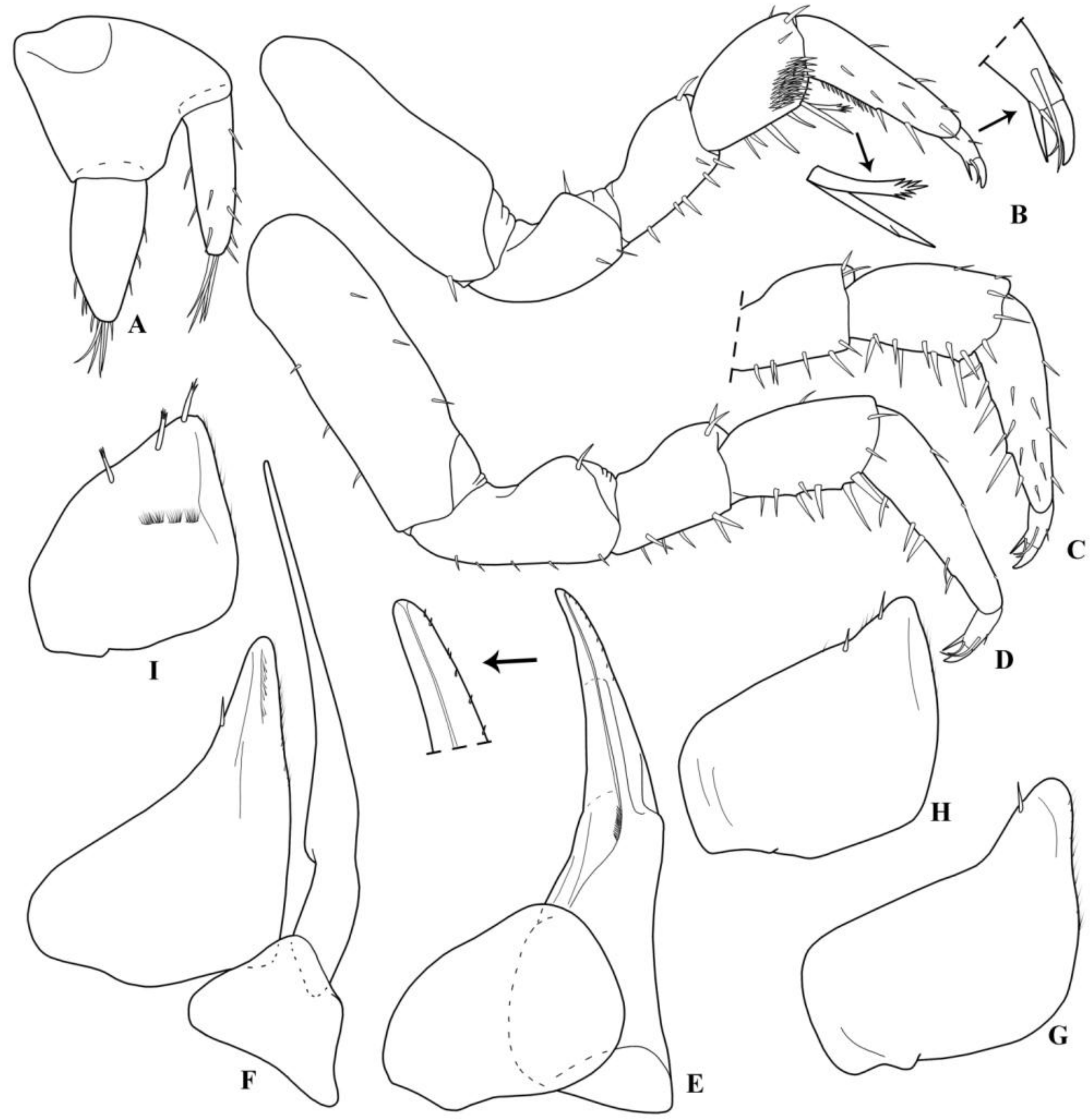

Figure 10. *Neotroponiscus plaumanni*. ♂ UFRGS 6281. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

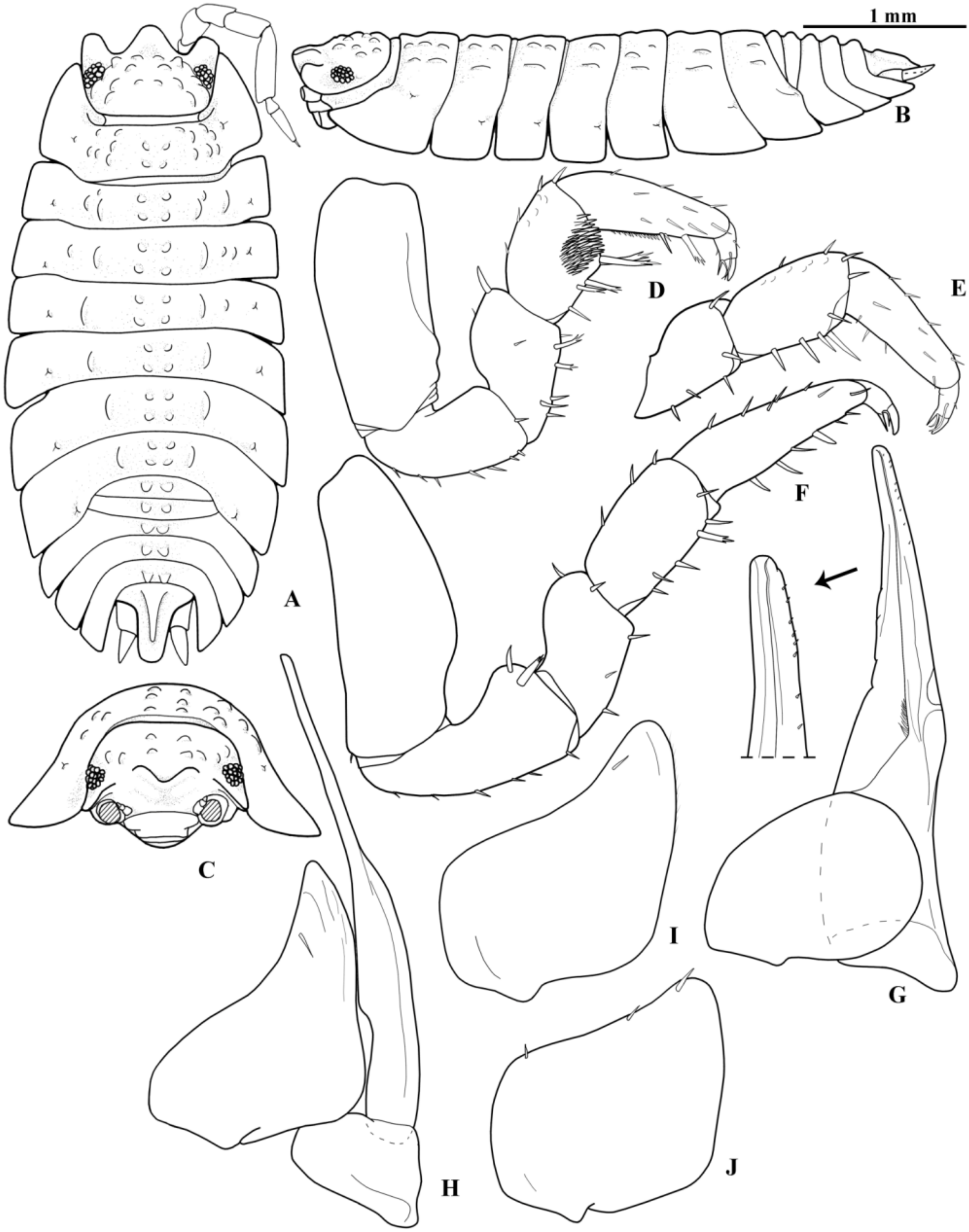

Figure 11. *Neotroponiscus littoralis.* ♂ MNRJ 6489. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon and pereonite 1, frontal view; D, pereopod 1; E, pereopod 2; F, pereopod 7; G, pleopod 1; H, pleopod 2; I, pleopod 3 exopod; J, pleopod 4 exopod.

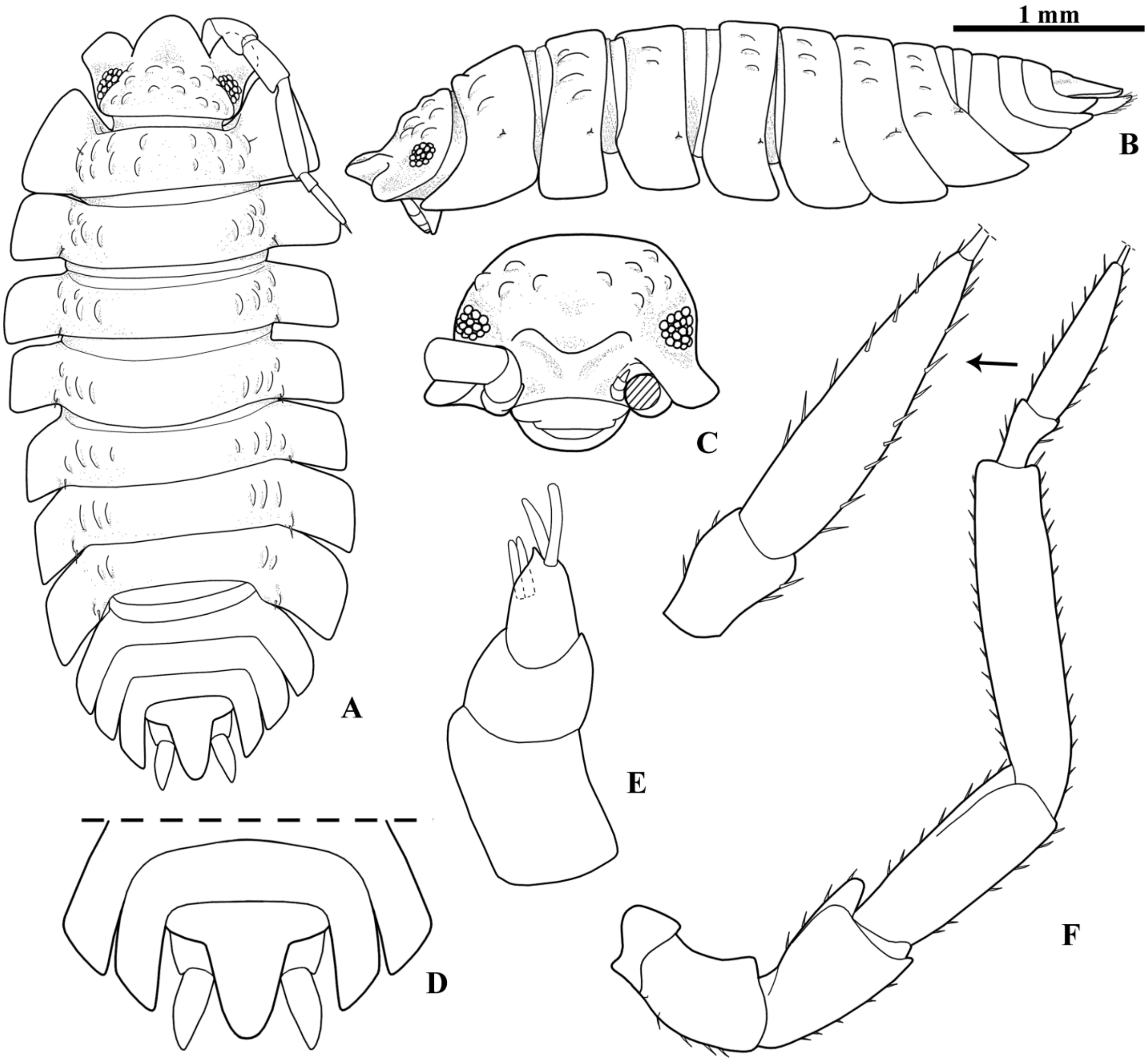

Figure 12. *Neotroponiscus lobatus*. ♂ UFRGS 5127. A, habitus, dorsal view; B, habitus, lateral view; C, cephalon, frontal view; D, pleonites 4 and 5, telson and uropods, dorsal view; E, antennule; F, antenna.

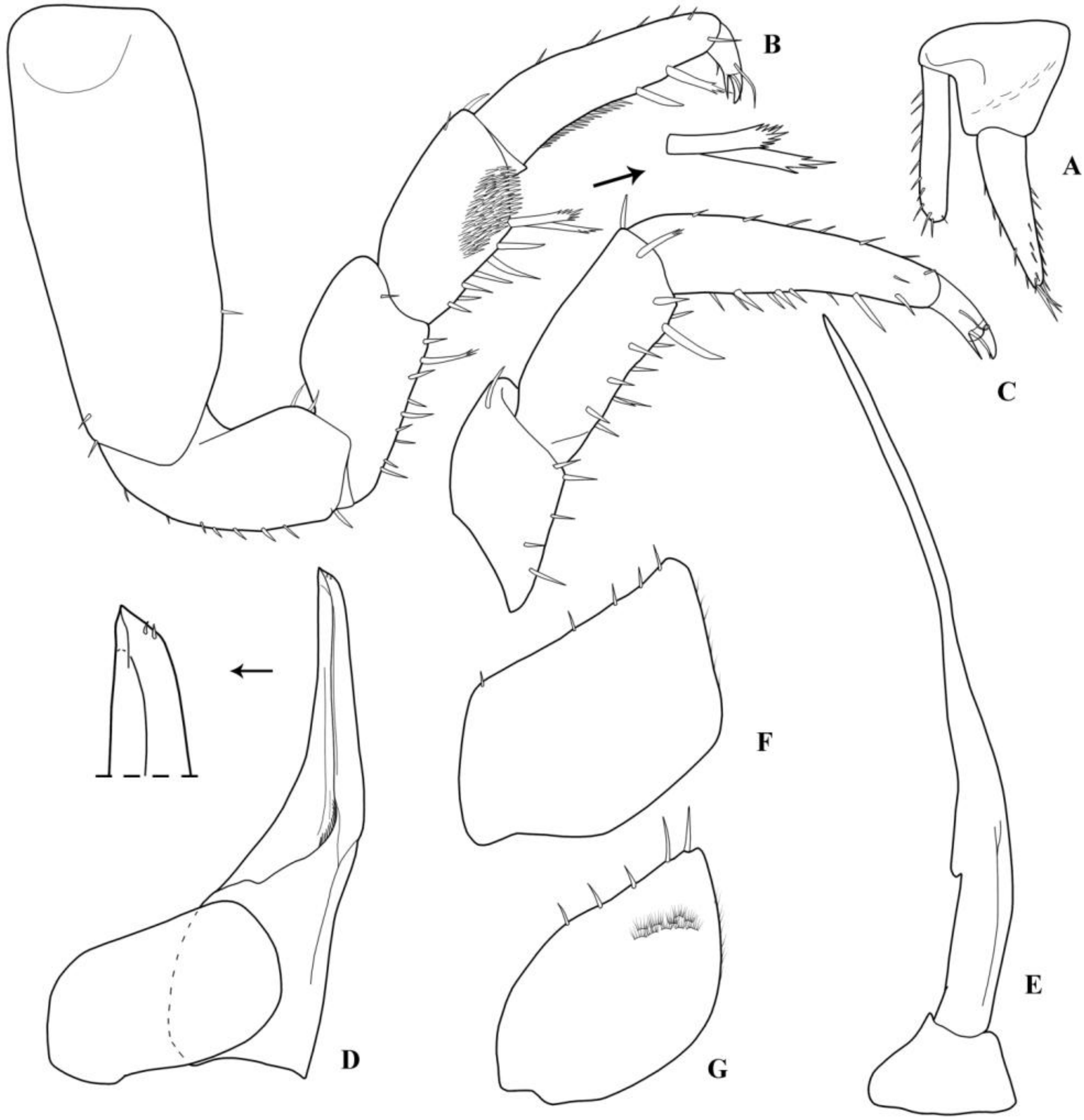

Figure 13. *Neotroponiscus lobatus*. ♂ UFRGS 5127. A, uropod; B, pereopod 1; C, pereopod 2; D, pleopod 1; E, pleopod 2; F, pleopod 4 exopod; G, pleopod 5 exopod.

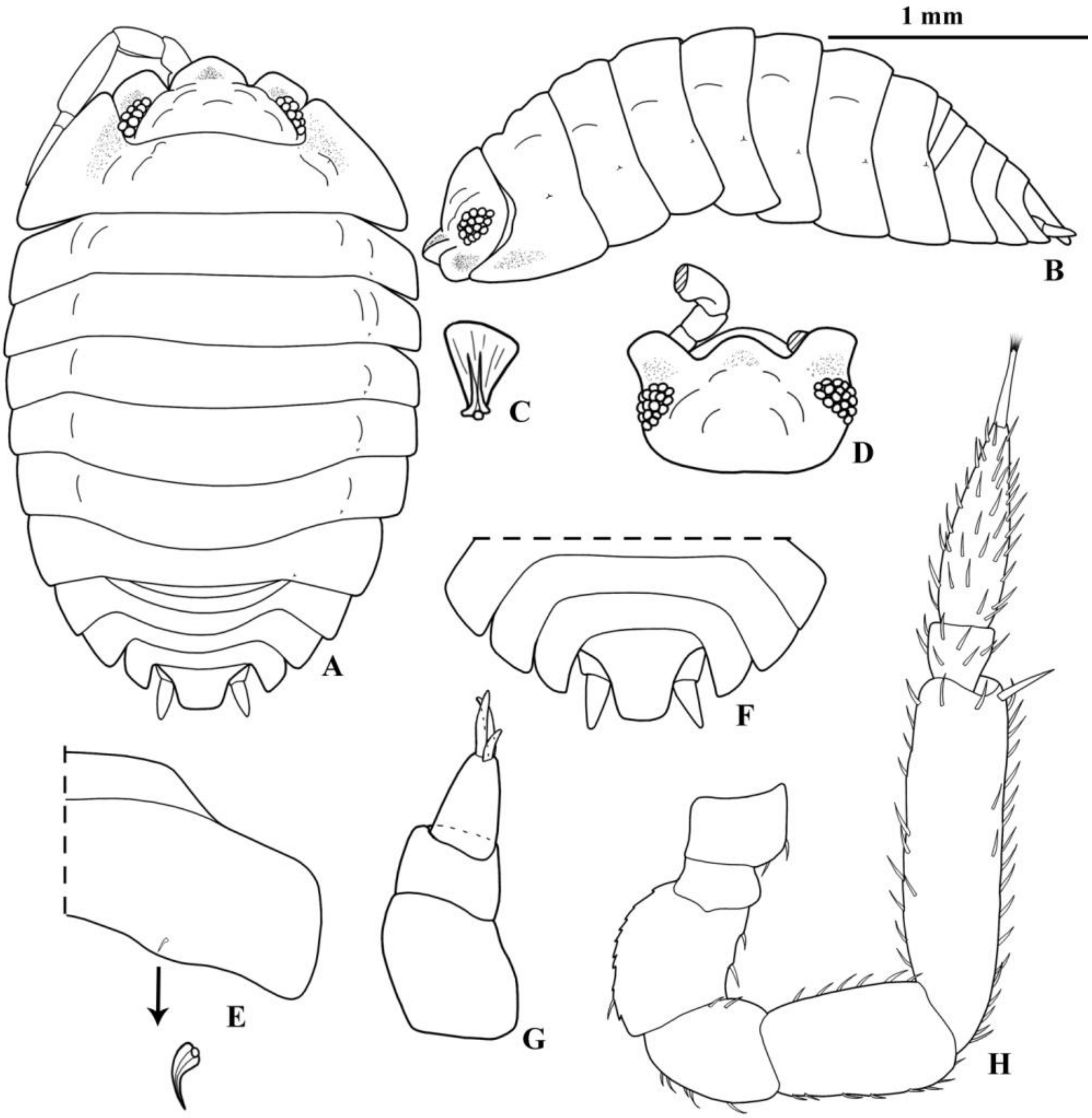

Figure 14. *Neotroponiscus lenkoi*. ♂ MZUSP 24295 A, habitus, dorsal view; B, habitus, lateral view; UFRGS 6474 C, scale-seta; D, cephalon, dorsal view; E, pereonite 7; F, pleonites 3–5, telson and uropods, dorsal view; G, antennule; H, antenna.

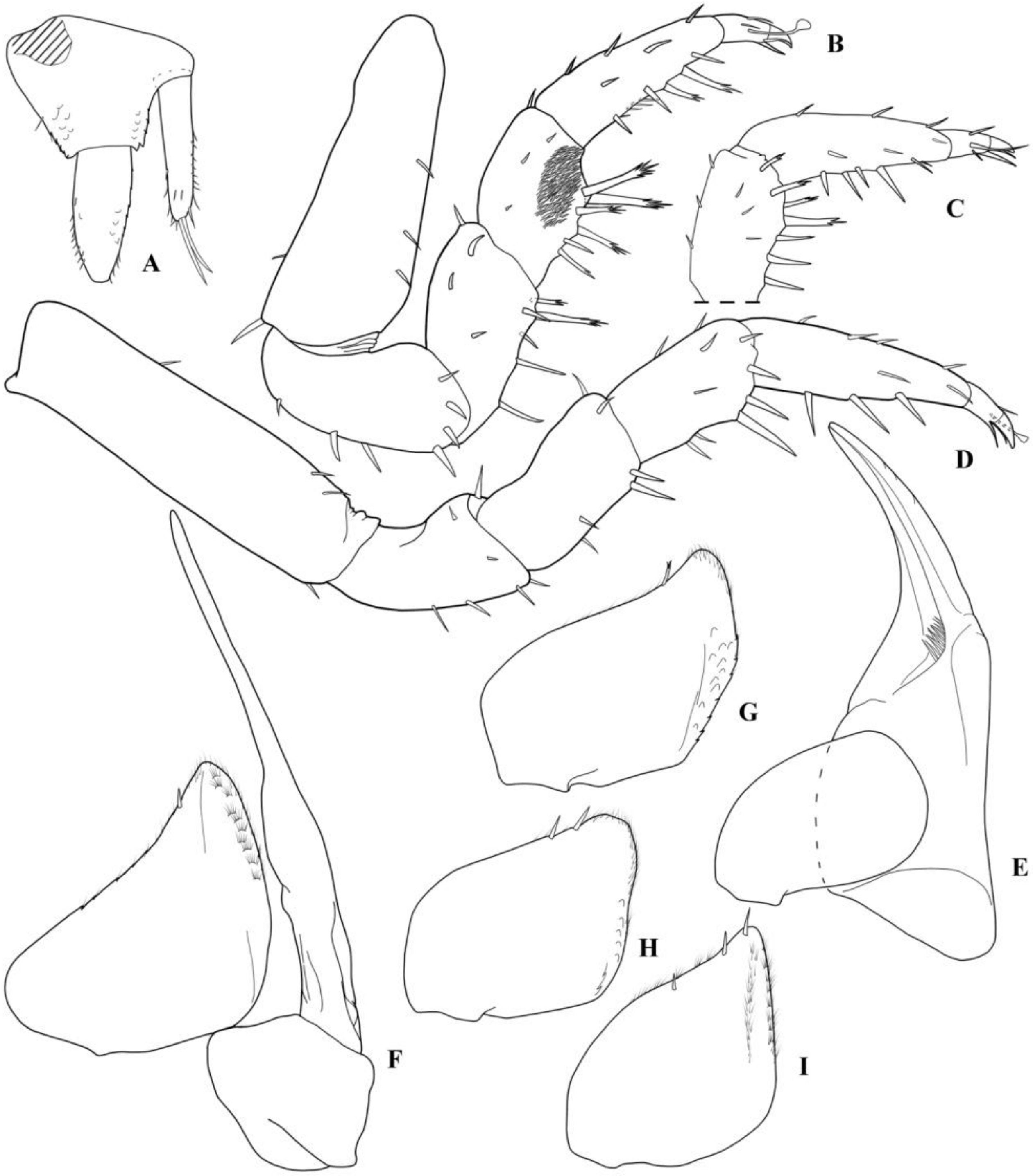

Figure 15. *Neotroponiscus lenkoi*. ♂ MZUSP 24295. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

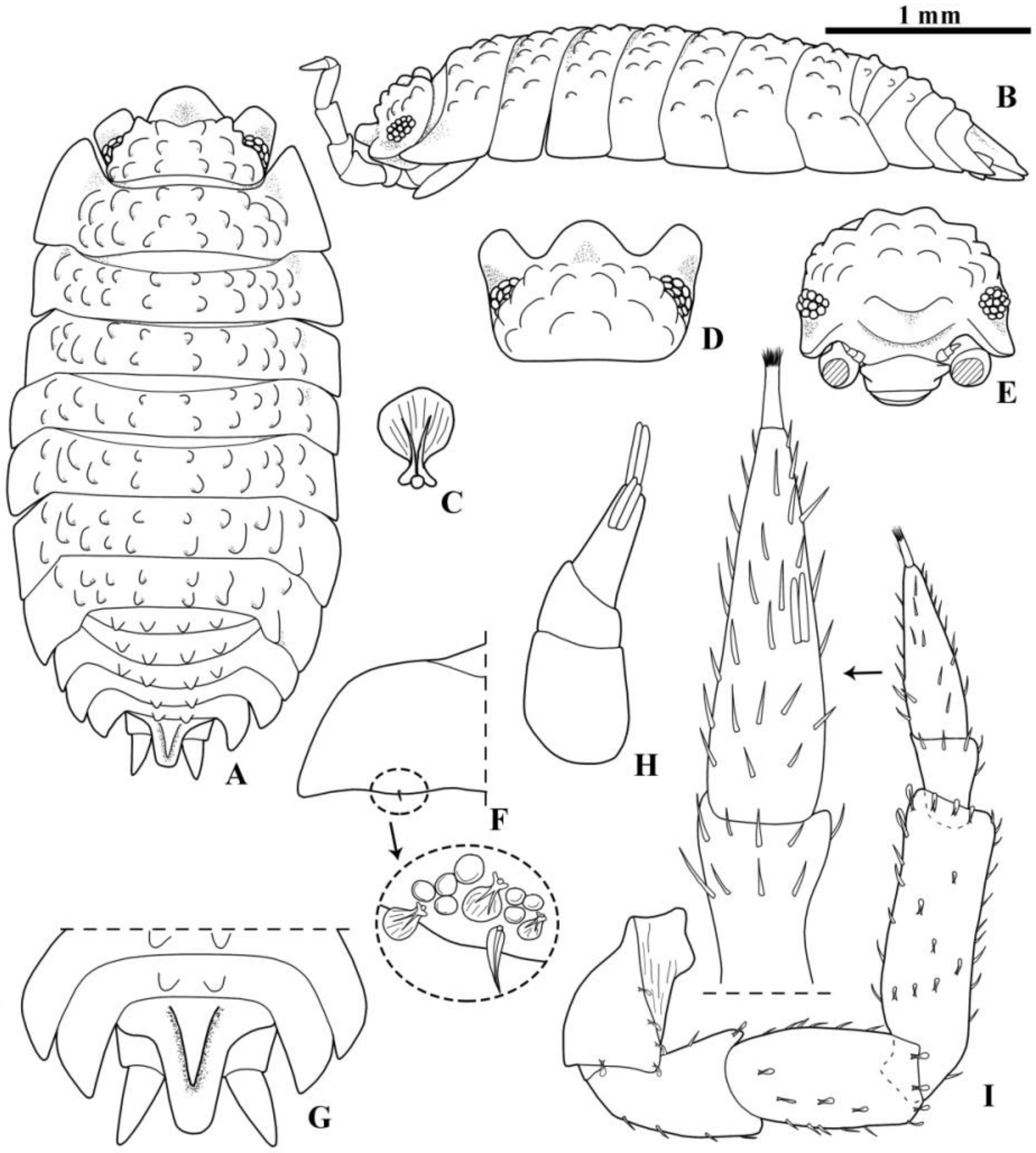

Figure 16. *Neotroponiscus perlatus*. ♂ UFRGS 6451. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, dorsal view; E, cephalon, frontal view; F, pereonite 7; G, pleonites 4 and 5, telson and uropods, dorsal view; H, antennule; I, antenna.

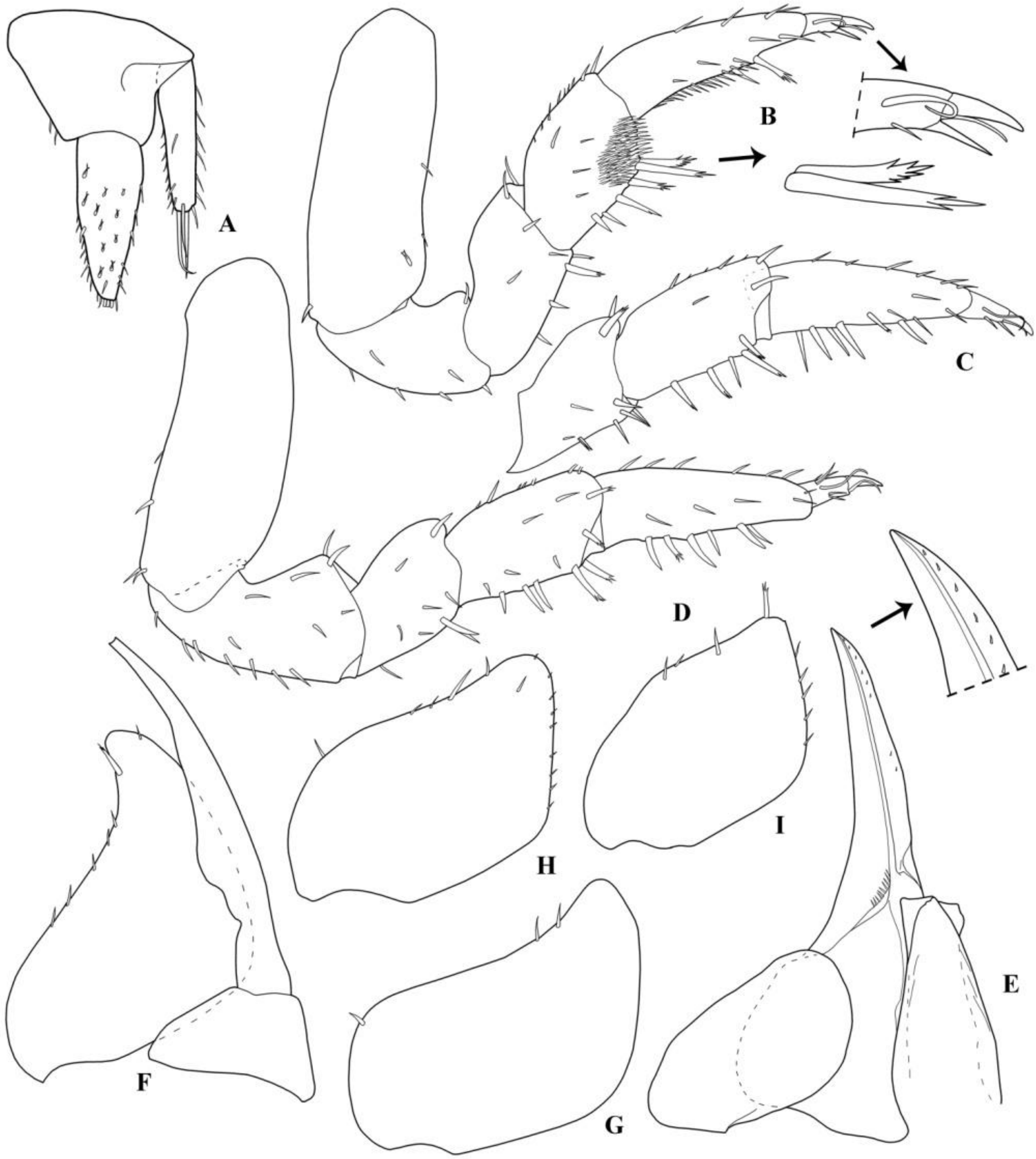

Figure 17. *Neotroponiscus perlatus*. ♂ UFRGS 6451. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

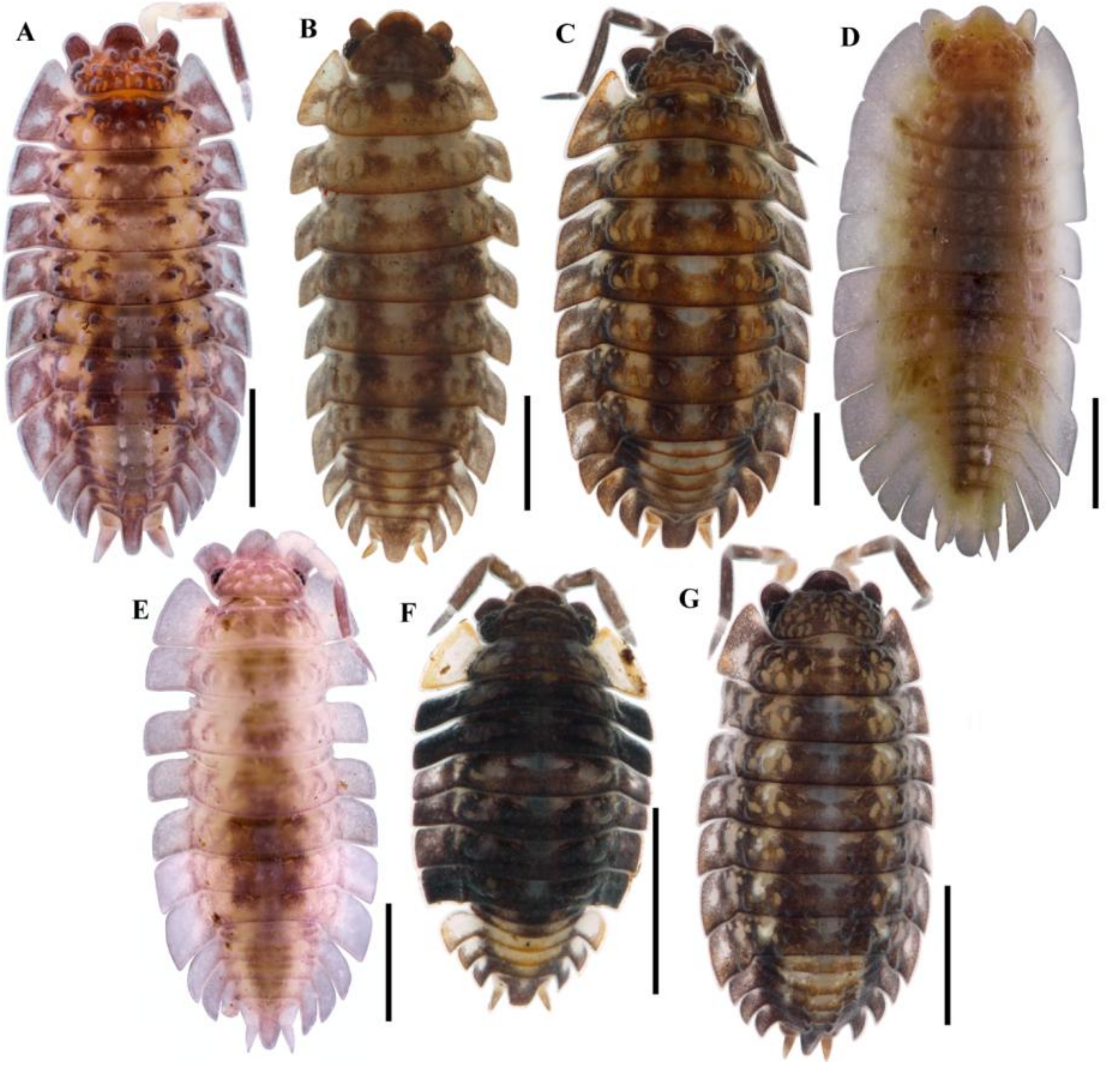

Figure 18. Species of *Neotroponiscus* in dorsal view. A, *N. carolii* ♂ (UFRGS 6453); B, *N. argentinus* ♀ (UFRGS 6442); C, *N. daguerrii* ♂ (UFRGS 6447); D, *N. littoralis* ♂ (MNRJ 6489); E, *N. lobatus* ♂ (UFRGS 5127); F, *N. lenkoi* ♂ (UFRGS 6474); G, *N. perlatus* ♂ (UFRGS 6451). Scale-bar: 1mm.

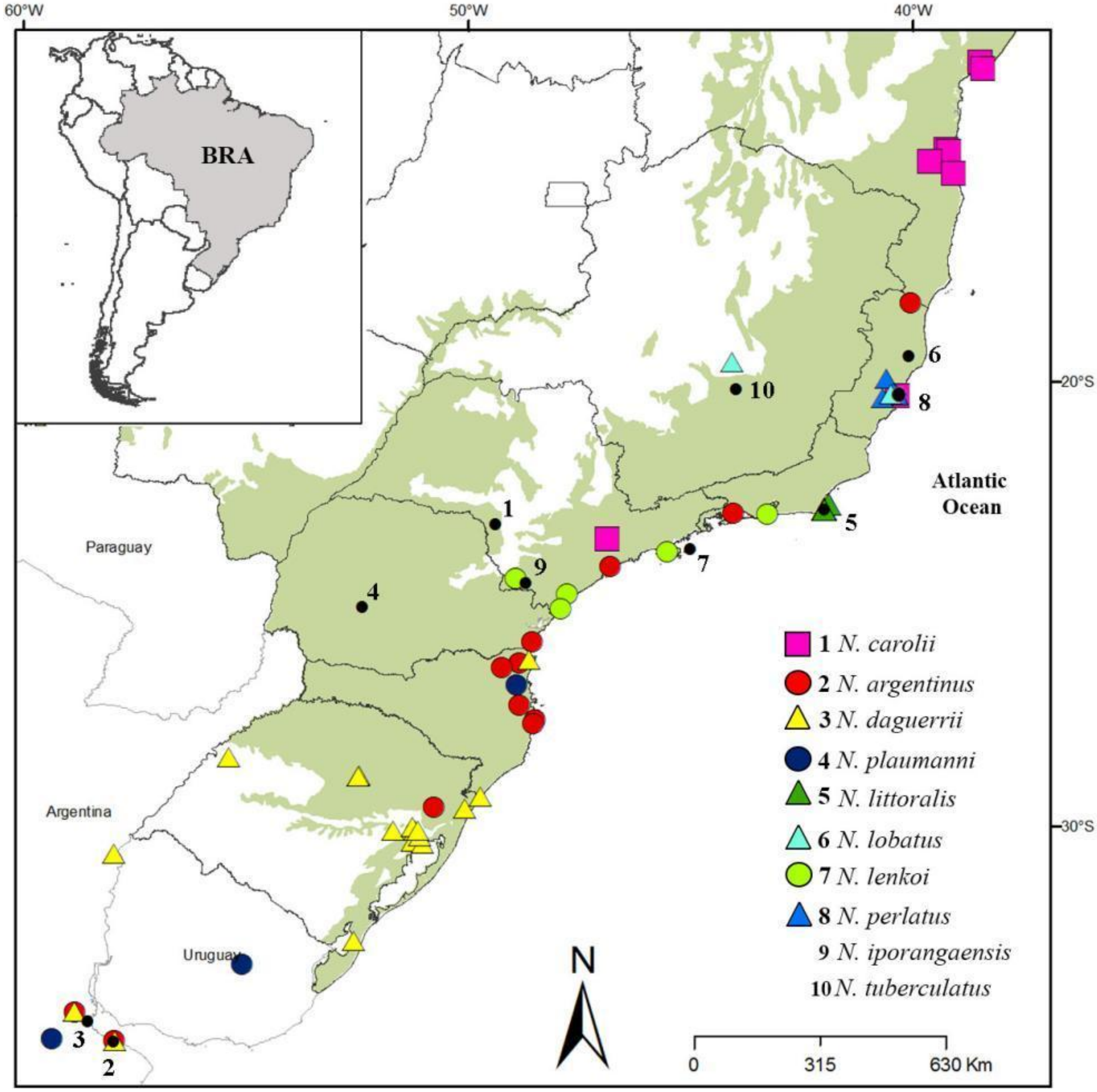

Figure 19. Distribution map of *Neotroponiscus* species. Type localities are numbered, followed by the distributional records. Brazilian Atlantic Forest in green.

Capítulo V

Artigo formatado conforme a revista *Zoologica Scripta*
CARDOSO ET AL. (2017).

Phylogenetic relationships of the terrestrial isopod *Neotroponiscus* Arcangeli, 1936 based on Total evidence analysis (Isopoda, Oniscidea, Bathytropidae), with description of new species

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Abstract

The phylogenetic relationships of the genus *Neotroponiscus* is addressed for the first time with the use of molecular and morphological data. The monophyly of the genus was tested and our results show that *Neotroponiscus* can be considerate monophyletic, and indicate that the family is composed by the genera *Bathytropa* and *Neotroponiscus*. With the aim of this approach three new species of *Neotroponiscus* could be identified. Further analyses with additional data are needed to infer the position of the other taxa placed in this family.

Keywords: Terrestrial isopods, woodlice, neotropics.

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Abstract

The phylogenetic relationships of the genus *Neotroponiscus* is addressed for the first time with the use of molecular and morphological data. The monophyly of the genus was tested and our results show that *Neotroponiscus* can be considerate monophyletic, and indicate that the family is composed by the genera *Bathytropa* and *Neotroponiscus*. With the aim of this approach three new species of *Neotroponiscus* could be identified. Further analyses with additional data are needed to infer the position of the other taxa placed in this family.

Keywords: Terrestrial isopods, woodlice, Neotropics.

Introduction

The genus *Neotroponiscus* Arcangeli, 1936 includes ten species occurring in Brazil, Argentina and Uruguay (Lemos de Castro 1970a,b, Cardoso *et al*. 2017 *in press*, Cardoso & Araujo *in prep*).The genus is mainly recognized by the presence of cephalic lobes, antenna with bi-articulated flagellum, shape and disposal of dorsal tubercles, and well-developed epimera (Lemos de Castro 1970a, b). However, as usual for isopods, the differences between species rely on subtle morphological characteristics, often from male morphology and many of these characteristics may be a reflex of intraspecific variations (Poulakakis & Sfenthourakis 2008).

In the last years, molecular studies in a phylogenetic context within terrestrial isopods have increased in order to elucidate the relationships between genera, species and populations (Klossa-Kilia *et al*. 2006, Parmakelis *et al*. 2008, Poulakakis & Sfenthourakis 2008, Karasawa & Honda 2012, Kamilari *et al*. 2014, Lee *et al*. 2014; Raupach *et al*. 2014, Javidkar *et al*. 2015, Zimmermann *et al*. 2015, Karasawa 2016).

Studies regarding the phylogenetic relationships of terrestrial isopods from the Neotropics addressed mainly the families Philosciidae and Scleropactidae (Leisitkow 1999, 2000, 2001a, 2001b, 2001c, Leistikow & Schmidt 2002, Schmidt 2002, 2003, 2008). The work of Zimmermann *et al*. (2015) used molecular data to reveal the phylogenetic relationships within the genus *Atlantoscia* Ferrara & Taiti, 1981.

This work aims to address for the first time the phylogenetic relationship within the genus *Neotroponiscus* into an integrative view, with the use of molecular and morphological data. Also, it will provide the first approach of the relationships within the family, testing the monophyly of other genera placed in the family until the moment. In addition, *Neotroponiscus* sp. n. from the states of Bahia, Rio de Janeiro and Rio Grande do Sul, resulted from this analysis, are described.

Material and methods

Taxon sampling

The specimens were collected between March 2013 and February 2014, along the Brazilian Atlantic forest from the states of Bahia to Rio Grande do Sul, and stored in 100% ethanol.

The material is deposited at the Coleção de Crustáceos do Departamento de Zoologia (UFRGS). Other material examined in this study are deposited in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina; Muséum

National d’ Histoire Naturelle (MNHN), Paris, France and Museo di Storia Naturale dell’ Università di Firenze, ‘La Specola’(MZUF), Florence, Italy (Table 1).

For the phylogenetic analyses, the ingroup includes all species of *Neotroponiscus*. The outgroups used to polarize the character states and to test the monophyly of *Neotroponiscus* (sensu Nixon & Carpenter 1993), included the other genera of Bathytropidae (*Laninoniscus* Reca, 1973, *Dumetoniscus* Taiti & Checcucci, 2009, *Papuasoniscus* Vandel, 1973, *Monitus* Lewis, 1998, *Bathytropa* Vandel, 1954), and representatives of the families Scleropactidae (1 sp.), Armadillidiidae (2 spp.), Dubioniscidae (2 spp.), Platyarthridae (3 spp.), Pudeoniscidae (5 spp.), Trachelipodidae (3 spp.), Porcellionidae (2 spp.) and Oniscidae (1 sp.) (Table 1).

Some molecular data could not be obtained for four species whose specimens were obtained solely from scientific collections (*N. plaumanni* (Andersson, 1960), *N. littoralis* Lemos de Castro, 1970, *N. lobatus* Lemos de Castro, 1970 and *N. tuberculatus* Cardoso & Araujo, 2017). Also, since it was not possible to obtain DNA sequence of *Bathytropa* nor for the other genera of the family, the taxa are presented only in the complete dataset for the total evidence analyses. The total evidence matrix with complete taxon sampling includes 63 terminals with root at *Circoniscus bezzi* Arcangeli, 1931 (Scleropactidae). A reduced matrix was tested with the species with at least one DNA marker (41 taxa). Some sequences of the outgroup are available in GenBank (NCBI) and were combined hereto build the phylogenetic tree (see Table 1).

Morphological analysis

The specimens were dissected (appendages and pereonites) and mounted on semi-permanent slides in Hoyer medium. The illustrations were made with the aid of a *camera lucida* on Olympus CX31 microscope and pictures were obtained with Nikon AZ100. The cuticular structures were studied in a JSM 6060 scanning electron microscope (SEM) at the Centro de Microscopia Eletrônica at UFRGS. The final illustrations were prepared according to Montesanto (2015, 2016).

The character matrix was built using Mesquite 3.2 (Maddison & Maddison 2017). Characters were coded to include most of the morphological variations. Some characters were adapted from Leistikow (2001a) and Schmidt (2002, 2007) and some new characters are proposed here, most from dorsal cuticular structures, whose definition were based on Holdich & Lincoln (1974) and Vandel (1960). The characters were coded as proposed by Sereno (2007), and treated as unordered (Fitch 1971, Swofford & Maddison 1992). The characters list and states are available in Table 2 (see Appendix S1 for matrix). Missing data were coded as '?' and inapplicable characters as '-'.

The search for the most parsimonious tree was performed on TNT 1.1 (Goloboff *et al.* 2008), and the characters were treated as equally weighted (EW). The EW search was conducted with New Technology Search, with random seed=1 and 100 hits (replications). The parameters were adjusted as follow: Ratch parsimony (Nixon 1999) with 25 up and 5 down-weighting with 20 interactions, trying to explore a wide range of most parsimonious tree in the tree space, increasing accuracy and reducing search time; Tree Drifting (Goloboff 1999) with 20 cycles, and Tree fusing (Goloboff 1999) with 100 interactions, in order to increase the congruence (see also Paladini *et al*. 2014). The Jacknife symmetrical resampling (SR) adopted here as support measure, with the parameters ajusted as follow: 5000 replicates, with 100 additional replicates and 10 trees saved per replicate with SPR+TBR swapping, performed with Traditional Search in TNT (Felsenstein 1985).

DNA extraction, amplification and sequencing

Specimens were dissected before the extraction. DNA was extracted with PureLink®Genomic DNA (Invitrogen/K1820-01) according to the manufacturer's instructions. For the *COI* gene, the primers LCO (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO (5′-TAAACTTCAGGGTGACCAAAAAATCA-3) were used (Folmer *et al.*, 1994); and for *18s*, the primers SSU04 (3'-GCTTGTCTCAAAGATTAAGCC-5') and SSU22 (3'-GCCTGCTGCCTTCCTTGGA-5') were used (Blaxter *et al.* 1998). PCR reactions were performed with a final volume of 25 µl, using 1.0 µl DNA, 0.16 µl Taq Platinum (5U/µl), 2.5 µl 10X buffer, 1.66 µl MgCl2 (50 mM), 0.5 µl of each forward and reverse primer (20 µM), 0.5 µl dNTPs (10 mM) and 18.1 µl ultrapure water. For the amplification of *COI*, the program was used with denaturation step temperature of 95 °C for 5"; annealing with 35 cycles (95 °C for 50', 52 °C for 50' and 72 °C for 50') and extension of 72 °C for 5"; and for *18s* the program was used with denaturation step temperature of 94 °C for 5"; annealing with 35 cycles (94 °C for 30', 52 °C for 50' and 72 °C for 2" 30') and extension of 72 °C for 10". PCR products were purified and sequenced by Macrogen, Inc. (Seoul, South Korea).

The sequences were verified using BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) to confirm their validity with the terrestrial isopods species. The sequences were visually inspected and manually edited using MEGA 6 (Tamura *et al.* 2013). All gene sequences generated in this study will be deposited in the GenBank database (http://www.ncbi.nlm.nih.gov/), accession numbers (XXXXX to XXXXX), shown in Table 1.

Sequence alignment and genetic divergence analysis

Individual gene alignments were performed using the Clustal W algorithm (Thompson *et al*. 1994), implemented in MEGA 6. The pairwise genetic divergences of sequences were calculated using the Kimura two-parameter (K2P) substitution model (Kimura, 1980) in MEGA 6, with 10 000 bootstrap replicates (Hebert *et al*. 2003).

The concatenated alignment were exported as fasta files, then merged with the morphological dataset on Mesquite (Maddison & Maddison 2017), and the final matrix was exported as NEXUS format to conduce the Bayesian analysis.

Phylogenetic analyses

The Bayesian inferences were performed using MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003) on the CIPRES science gateway (Miller *et al*. 2010). The inferences were constructed for each gene, for the concatenated gene dataset, and for total evidence dataset.

The best substitution model was tested on jModelTest 2.1.3 (Darriba *et al*. 2012) under the Akaike Information Criterion (AIC - Akaike 1974) for each gene and GTR+I+G was selected for both data.The morphological data was analyzed under Mk model (Lewis 2001), implemented in MrBayes v3.2.6, based on unordered characters and assuming a gamma-distributed rate generations of the Markov chain Monte Carlo (MCMC). It was used two runs of four million MCMC generations and four chains, sampling every 1,000 generations. The first 25% of the recovered topologies were discarded as burn-in, and the efficiency of the chain was assessed using Tracer v1.6 (Rambaut *et al.* 2015). Final topologies were visualized and edited on Figtree 1.4.0 (Rambaut *et al*. 2014).

Results

Morphological analyses

In the morphological analysis 87 characters were codified, 20 of them proposed here (see Table 2). The missing data had the percentage ratio of 4.9% and the inapplicable characters of 3.3%. The EW parsimony analyses produced 38 equally parsimonious trees, with length of 488 steps (CI = 0.32; RI = 0.60), and the *strictus consensus* resulted in a tree with length 503 steps (CI = 0.31; RI = 0.58), forming a polytomic clade (Appendix S2).

The genus *Neotroponiscus* was recovered with one main clade, including almost all species of the genus, and only *N. lobatus* and *N. lenkoi* were recovered out of this clade. The main clade and these two species of the genus were recovered with unsolved relations with the genus *Bathytropa* and the family Platyarthridae. Sinapomorphic characters for this analysis can be seen in the supplementary material (Appendix S2).

Regarding Bathytropidae, in none of the most parsimonious trees the other genera of the family showed relationships with *Bathytropa* and/or *Neotroponiscus*.

Other important result observed here was the monophyly of the families Pudeoniscidae and Platyarthridae, recovered in the most parsimonious trees.

Molecular phylogenies results

A total of 47 sequences (from *COI* and *18s*) were generated from 29 individuals of *Neotroponiscus* collected in the Brazilian Atlantic forest (Fig 1). All sequences were reduced to the length of the shortest sequence to eliminate spurious values due to unequal sequence length. The final alignment consisted of sequences with 965 bp (being 492 bp for *18s* from 41 species and 472 bp for *COI* from 30 species).

Sequences of the *18s* nucleotide showed 207 variable sites (44.2%), and 155 parsimony informative (33.1%); and of *COI* nucleotide showed 258 variable sites (54.6%), and 225 parsimony informative (47.6%). Within *Neotroponiscus* the sequence divergence of *18s* nucleotide ranged from 0 to 12.4% (average of 6.2%) and *COI* nucleotide from 0 to 24.2% (average of 18.8%) (Appendix S3). Base frequencies for *COI* were composed by A: 25, C: 16.1, G: 21, T 37.9; while *18s* were composed by A: 21.9, C: 23.7, G: 27.9, T 26.6. The average AT content (%AT = 62.9) was higher for *COI* sequences than *18s* (%AT = 48.5). The results for molecular analyses (genes and concatenated dataset) were congruent (Fig 2; Appendix S2) and supported the monophyly of the *Neotroponiscus.*

The Bayesian analyses with the concatenated genes recovered the *Neotroponiscus* clade with *N. lenkoi* as basal taxon and relatively low supported (pp=0.8). *Neotroponiscus lenkoi* showed the highest diversity in relation to the other species, in which the *18s* sequences estimated divergence with *Neotroponiscus* sp. 2 was 12%; in the *COI* sequences the divergence was 24% between *Neotroponiscus* sp. 3 and *Neotroponiscus* sp. 1 (Appendix S3). The clade further divides into two groups, clade A and B, both strongly supported (pp= 0.9 and 1, respectively) (Appendix S2). The Clade A comprises *N. daguerrii*, *N. argentinus* and *Neotroponiscus* sp. 1. The Clade B includes *N. perlatus*, *N. carolii*, *N. iporangaensis*, *Neotroponiscus* sp. 2 and *Neotroponiscus* sp. 3. An unresolved clade was recovered with *N. carolii* and *N. iporangaensis;* however this result might be related with the absence of *COI* sequence for *N. iporangaensis* and the insufficient information from the *18s* marker to resolve the relationship between them, with only 0.3% of divergence (Appendix S3).

Total evidence analyses

The total evidence reconstruction (Fig. 2) recovered *Neotroponiscus* in an unsolved clade with *Bathytropa* (pp=0.72). The main difference between the topology obtained from the reduced matrix and the full matrix is the well-resolved clade of *Neotroponiscus,* which is strongly supported with the reduced data (pp=0.98). *Neotroponiscus lobatus* was recovered with low support (pp=0.61) in an unsolved clade with clades A and B. In the Clade A, *N. plaumanni* was reconstructed as sister group of the clade with *N. daguerrii*, *N. argentinus* and *Neotroponiscus* sp. 1. In the clade B, the species *N. littoralis, N. tuberculatus, N. carolii, N. perlatus* and *N. iporangaensis* were recovered in an unsolved clade.

Regarding Bathytropidae, our results do not support the monophyly of the family with all genera placed in the family until the moment. The results found here indicate that the family is composed by the genera *Bathytropa* and *Neotroponiscus* (see discussion).

Only a few members of Trachelipodidae, Oniscidae, Armadillidae and Porcellionidae were sampled and some inferences can be made here. The family Pudeoniscidae was strongly recovered as a monophyletic unit (pp=0.95). The monophyly of the family Dubioniscidae was also supported here (pp=0.99). Regarding Platyarthridae represented by *Platyarthrus* and *Trichorhina,* the family was not recovered as monophyletic, contradicting the morphological results. Also, the family Trachelipodidae, represented by *Trachelipus* and *Nagurus,* was recovered as paraphyletic.

Systematic account

Genus *Neotroponiscus* Arcangeli, 1936

***Neotroponiscus* sp. 1 (Figs. 3-4)**

Holotype. m, Brazil, Santa Catarina, Blumenau, Parque das Nascentes (-27.0575º, -49.0861º), 27 June 2012, leg. BL Zimmerman & PB Araujo (UFRGS 5587).

Paratypes. Same data as for holotype 4 mm 3 ff (UFRGS 5587). Santa Catarina, Blumenau, Parque das Nascentes (-27.0575º, -49.0861º) 4 mm 3 ff , 27 June 2012, leg. B.L. Zimmerman & P.B. Araujo (UFRGS 6446). Santa Catarina, Blumenau (27°01’44”S 49°05’39”W) 1 m, 27 June 2012, leg. P.B. Araujo (UFRGS 5469). Santa Catarina, Imbituba, Morro Mirim (-28.2444º, -48.6983º), 12-17 May 1996.

Etymology.

Diagnosis. This species is characterized by the shape of dorsal tubercles, the shape of telson, uropod exopod longer than endopod.

Description

Male body length 6.2 mm. Specimens with light brown with unpigmented spots; cephalic lobes and telson pigmented, uropods light brown. Dorsum with rectangular tubercles, placed as follows: three transversal lines on cephalon, two transversal lines on pereonite 1, one transversal line on pereonites 2–7, pleon smooth (Fig 3A, B). Dorsum covered with circular plaques and fan-shaped scale-setae (Fig 3C); one *nodulus lateralis* per side (Fig 3A, B). Pereonite 1 epimeron developed frontwards, surpassing eyes (Fig 3A, B). Cephalon (Fig 3D, E) with rectangular lateral lobes, directed outwards; median lobe pentagonal and directed upwards; eyes with 16 ommatidia. Telson (Fig 3G) wider than long, distal part rounded. Antennula (Fig 3H) distal articles with two apical and two subapical aesthetascs. Antenna (Fig 3I) when extended back, reaching posterior margin of pereonite 1; flagellum of two aesthetascs. Pereopods bearing sparse setae on sternal margin of merus and carpus; carpus with longitudinal antennal brush; ungual seta and dactylar organ simple. Uropod (Fig 4A) protopod wider than long; exopod longer than endopod, surpassing distal margin of telson.

Male: Pereopods 1 and 7 (Fig 4B, D) without modifications. Pereopod 2 (Fig 4C) bearing dense setae on sternal margin of merus and carpus. Pleopod 1 (Fig 4E) exopod small, wider than long and one third of endopod length; endopod slightly bent outwards. Pleopod 2 (Fig 4F) exopod triangular, shorter than endopod. Pleopods 3–5 as in Fig 4G-I.

Remarks. *Neotroponiscus* sp. 1 resembles *N. daguerrii*, *N. argentinus* and *N. plaumanni* by the presence of dense setae on pereopod 2 sternal margin, resembles *N. argentinus* by the distal part of telson rounded, but can be distinguished by the shape of male pleopod 1 exopod and uropod exopod longer than endopod. While from *N. daguerrii* is similar by the shape of male pleopod 1 exopod and distinguished by the distal part of telson rounded (vs. quadrangular in *N. daguerrii*) and uropod exopod longer than endopod.

***Neotroponiscus* sp. 2**

Material examined. Brazil, Bahia, Maraúvis: 2ff (UFRGS), Ba 16 (-14.167º -39.0936º), 18 November 2013, leg. I. Campos-Filho & J. Lisboa.

Observation. This species is characterized by the rounded frontal lobe, dorsal tubercles weakly developed, pleon with two tubercles medially and telson with distal part rounded. The lack of male specimens prevents a detailed the description.

***Neotroponiscus* sp. 3** (Figs 5-7)

Holotype. m, Brazil, Rio de Janeiro, Cabo Frio, Praia do Peró (-22.8670ºS, -41.9850º), 08 March 2014, leg. GM Cardoso (MZUSPXXX).

Paratypes. Same data as for holotype 3 mm 5 ff (MZUSP XXX).

Other material. Búzios, Praia João Fernandes (-22.7394º, -41.8748º) 1 f, 09 March 2014, leg. GM Cardoso (MZUSP XXX).

Etymology.

Diagnosis. This species is characterized by the patterns of coloration, the shape of the cephalic lobes, the development of pereonite epimera and the position of the *noduli laterales*.

Description

Male body length 5.8 mm. Specimens with light brown to yellow color and unpigmented spots; cephalic lobes, fifth segment and flagellum of antenna strongly pigmented; epimera 1, 4 and neopleura 3 less pigmented; telson pigmented, uropods light brown. Dorsum with spine tubercles, placed as follows: three transversal lines on cephalon and pereonite 1, two transversal lines on pereonites 2–7, tubercles can be fused on pereonites 3-7, and less pronounced; two tubercles on pleonites 1-5 (Fig 5A, B). Dorsum covered with circular plaques and fan-shaped scale-setae (Fig 5C, 6B,C); one *nodulus lateralis* per side, first *nodulus* placed farther from lateral and distal margin, *noduli* on pereonites 2-7 near lateral margins (Figs 5A, B, 6A). Pereonite 1 epimeron developed frontwards, surpassing eyes (Fig 5A, B). Cephalon (Fig 5D, E) with rectangular lateral lobes, directed outwards; triangular median lobe, well-developed with round distal margin, directed upwards; eyes with 16 ommatidia. Telson (Fig 5G) wider than long, with medial carena, distal part quadrangular. Antennula (Fig 5H) distal articles with two apical and one subapical aesthetasc. Antenna (Figs 5I) when extended back, reaches posterior margin of pereonite 2; flagellum of two aesthetascs. Pereopods bearing sparse setae on sternal margin of merus and carpus; carpus with longitudinal antennal brush; ungual seta and dactylar organ simple. Uropod (Fig 6A) protopod longer than wide; exopod longer than endopod, surpassing distal margin of telson.

Male: Pereopods 1, 2 and 7 (Fig 6 B – D) without modifications. Pleopod 1 (Fig 6E) exopod small (almost one third of endopod length), wider than long; endopod straight. Pleopod 2 (Fig 6F) exopod triangular, shorter than endopod.Pleopods 3–5 as in Figs 6G-I.

Remarks. *Neotroponiscus* sp. 3 was collected for this study in the same locality as *N. littoralis*, however the shape of the cephalic lobes and the position of the *noduli laterales* are unique characters for this species. In the pattern of coloration the pattern seen in *N. lenkoi* but differs in the well developed tubercles (vs. weakly developed in *N. lenkoi*). In having the carena on telson is similar to *N. carolii, N. littoralis* and *N. perlatus*, but differs in the quadrangular distal margin of telson (vs. round in *N. carolii* and *N. perlatus*) and the oval shape of frontal lobe (vs. round in *N. littoralis* and *N. perlatus*, and quadrangular in *N. carolii*). The oval shape of frontal lobe resembles *N. lobatus*, which differs in the round shape of tubercles (vs. rectangular in *N. lobatus*).

Discussion

Our results show *Neotroponiscus* can be considerate a monophyletic unit. Despite the Parsimony and Bayesian analyses show partial incongruence, the concatenated molecular data strongly supports the monophyly of the genus. These inconsistencies can be attributed to the missing or inapplicable data on both matrixes, and the nature of the segment that evolved differently resulting in some spurious results (see also Wiens 2006).

The genetic divergence values of the mitochondrial sequence (*COI*) were more variable than the nuclear sequence (*18s*), which is caused by the higher metabolic rate of the mitochondria (Brokeland & Rauspach 2008). This pattern is usually observed among crustaceans (Wetzer 2001) and among terrestrial isopods (Lee *et al*. 2014, Zimmermann *et al*. 2015). This high divergence values are usually associated with the restricted dispersal ability of isopods and its dependence to the habitat humidity (Warburg & Linsenmair 1984; Klossa-Kilia *et al*. 2006; Lee *et al*. 2014, Zimmermann *et al*. 2015).

The divergence for *COI* gene previously reported in some studies, ranged from 20 to 32% between *Tylos* species (Hurtado *et al*. 2014), 0 to 18.4% between *Orthometopon* species (Poulakakis & Sfenthourakis 2008), and 14.9% to 30.3% between *Ligia* species (Markow & Pfeiler 2010). In nuclear sequences the divergence was reported with 0.7% between *Spherillo grossus'* populations (Lee *et al*. 2014) and 1.4% to 3.4% divergence between *Haploniscus* species (Brokeland & Rauspach 2008). Nuclear sequences have been used successfully to reconstruct crustacean phylogeny; however our results provided by the 18S phylogeny showed low resolution for *Neotroponiscus* species. Other studies noticed similar results with groups unresolved by *18s* (Lee *et al*. 2014) which suggest that this gene can be used more properly in identifying older processes of divergence (Hillis & Dixon 1991, Spears & Abele 1998, Dreyer & Wägele 2002).

The unresolved relationship between *Neotroponiscus* could be due the limited molecular information and the small divergence rate of the genes used. Differences between *Neotroponiscus* species are small and usually determined by the shape of cephalic lobe and tubercles.Some species such as *N. daguerrii, N. argentinus* and *N. plaumanni*are determined by the shape of telson and density of setae on pereopod 2, the lattercharacter is only seen in males, so the identification is not always possible if no male is sampled. Therefore, an integrative approach combining morphological and molecular information seemsto be necessary to establish the phylogenetic relationships among the species.

Our results strongly support the classification of the family Bathytropidae composed by *Neotroponiscus* and *Bathytropa*. The other Bathytropidae genera, *Laninoniscus*, *Papuasoniscus*, *Monitus* and *Dumetoniscus*, could be analyzed only under morphological aspects, and the topologies constructed here corroborates with the supposition that the family form a paraphyletic taxon sensu Schmidt (2003). Further data, including morphological and molecular, besides more additional taxa are needed to infer the positioning and relationship of this group.

The lack of resolution in the current higher-level classification of Oniscidea is known (Schmalfuss 2003, Schmidt 2003, 2008) and the uncertainty of the composition of the families Platyarthridae and Trachelipodidae were previously addressed by other studies (Schmidt 2003, Javidkar *et al*. 2015). The results presented here are congruent with them, with both families being recovered in paraphyly.

Some phylogenetic hypothesis presented in this study still has low support values in a few clades, showing that a more comprehensive taxon sampling is needed to address these clades. To conclude, our study presented the first hypothesis of internal relationships among *Neotroponiscus* species based on morphological and molecular data simultaneously.

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Supporting Information

Appendix S1 Complete morphological data matrix.

Appendix S2 Phylogenetic reconstruction for each partition separately [*cytochrome oxidase subunit I* (COI), *18S* rRNA (18S)], DNA concatenated, morphological and total evidence reduced datasets.

Appendix S3 Additional tables:

Table 3: Sequence divergence on citocromo c oxidase subunidade I (*COI*) gene between species, including outgroup.

Table 4: Sequence divergence on citocromo c oxidase subunidade I (*COI*) gene between congeneric species of the *Neotroponiscus*

Table 5: Sequence divergence on 18S ribosomal RNA (*18S*) gene between species, including outgroup.

Table 6: Sequence divergence on 18S ribosomal RNA (*18S*) gene between congeneric species of the *Neotroponiscus*.

Figure captions.

Figure 1. Sample species of *Neotroponiscus* along the Brazilian Atlantic Forest (in green). Brazil: BA, Bahia; ES, Espírito Santo; RJ, Rio de Janeiro; MG, Minas Gerais; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

Figure 2. Bayesian inference consensus tree based on molecular markers and morphological characters for the complete taxon analyses with 63 terminals. Numbers close to nodes are Bayesian posterior probabilities (PP).

Figure 3. *Neotroponiscus* sp. 1. ♂ UFRGS 5587. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, frontal view; E, cephalon, dorsal view; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

Figure 4. *Neotroponiscus* sp. 1. ♂ UFRGS 5587. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 5. *Neotroponiscus* sp. 3. ♂ (MZUSP XXX). A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, frontal view; E, cephalon, dorsal view; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

Figure 6. *Neotroponiscus* sp. 3 ♂ (MZUSP XXX). A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

Figure 7. *Neotroponiscus* sp. 3 ♂ (MZUSP XXX). A, habitus, dorsal view; B, cephalon, dorsal view; C, dorsal surface on pereonite 7; D, pleon, telson and uropods, dorsal view. Scale bars: A 1mm, B, D 200 μm, C 50 μm.

Table 1. Taxon sampling for the phylogenetic analysis of *Neotroponiscus* and related isopods, with species codes, taxon name, geographical origins, and accession numbers. Brazil: BA, Bahia; ES, Espírito Santo; RJ, Rio de Janeiro; MG, Minas Gerais; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

Code	Species	Collection number	Location	Latitude	Longitude	COI	18S
Outgroup	*Trachelipus rathkii* (Brandt, 1833)	retrieved from GenBank				KT708241.1	AF279605.1
Outgroup	*Armadillidium vulgare* (Latreille, 1804)	retrieved from GenBank				AF255779.1	AJ287061.1
Outgroup	*Cubaris murina* Brandt, 1833	retrieved from GenBank				AB861533.1	AJ287064.1
Outgroup	*Platyarthrus hoffmannseggi* Brandt, 1833	retrieved from GenBank				KY020402.1	JN232927.1
Outgroup	*Porcellio scaber* Latreille, 1804	retrieved from GenBank				HQ978726.1	AJ287062.1
Outgroup	*Porcellionides pruinosus* (Brandt, 1833)	retrieved from GenBank				FN824140.1	KR424622.1
Outgroup	*Oniscus asellus* Linné, 1758	retrieved from GenBank				KU955994.1	AF255699.1
Outgroup	*Circoniscus bezzii* Arcangeli, 1931	UFRGS 5720	MG, São Roque de Minas	-20.3131	-46.5297	KJ814236.1	(X)
Outgroup	*Dubioniscus depressus* Cardoso et al 2016	UFRGS 6381	SP, Santo Antônio do Pinhal	-22.8276	-45.6359	(X)	(X)
Outgroup	*Trichorhina tomentosa* (Budde-Lund, 1893)		RS, Porto Alegre	-30.0680	-51.1212	KR424600.1	(X)
Outgroup	*Trichorhina bicolor* Araujo & Buckup, 1996		PR, Morretes	-25.5266	-48.7880	_	(X)
Outgroup	*Pudeoniscus birabeni* Vandel, 1963		SC, Itapoá	-25.9690	-48.6392	_	(X)
Outgroup	*Brasiloniscus* sp		RJ, Trindade	-23.3299	-44.7057	_	(X)
Outgroup	*Nagurus cristatus* (Dollfus, 1889)		SC, Joinville	-26.3219	-48.8636	_	(X)
N_RS1	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6447	RS, Porto Alegre	-30.0967	-51.1858	(X)	(X)
N_RS1F	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6447	RS, Porto Alegre	-30.0967	-51.1858	(X)	(X)
N_RS2	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6448	RS, Eldorado do Sul	-30.1003	-51.6944	(X)	(X)
N_RS2F	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6448	RS, Eldorado do Sul	-30.1003	-51.6944	_	
N_RS2F	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6454	RS, Viamão	-30.3836	-51.0206	(X)	(X)
N_RS5	*N. daguerrii* (Giambiage de Calabrese, 1939)	UFRGS 6448	RS, Eldorado do Sul	-30.1003	-51.6944	(X)	(X)
N_SC1	*N. argentinus* (Giambiagi de Calabrese, 1939)	UFRGS 6442	SC, Florianópolis	-27.6107	-48.5057	(X)	(X)
N_SC2	*N. argentinus* (Giambiagi de Calabrese, 1939)	UFRGS 6443	SC, Florianópolis	-27.6848	-48.5383	_	(X)
N_SC3	*Neotroponiscus* sp. 1	UFRGS 5587	SC, Blumenau	-27.0575	-49.0861	(X)	_
N_SC3M	*Neotroponiscus* sp. 1	UFRGS 5587	SC, Blumenau	-27.0575	-49.0861	(X)	(X)
N_SC3B	*Neotroponiscus* sp. 1	UFRGS 5587	SC, Blumenau	-27.0575	-49.0861	(X)	(X)
N_SC4	*N. argentinus* (Giambiagi de Calabrese, 1939)	UFRGS 6444	SC, Joinville	-26.3219	-48.8636	(X)	(X)
N_SC8	*N. argentinus* (Giambiagi de Calabrese, 1939)	UFRGS 5468	SC, São João Batista	-28.2644	-49.8533	(X)	(X)
N_SC9	*N. argentinus* (Giambiagi de Calabrese, 1939)		SC, Imbituba, Morro Mirim	-28.2445	-48.6983	_	(X)
N_SC10	N. plaumanni (Andersson, 1960)	UFRGS 6281	SC, Itajaí, Morro do Baú			_	_
N_PR1	*N. argentinus* (Giambiagi de Calabrese, 1939)		PR, Matinhos	-25.8356	-48.5707	_	(X)
N_MG8	*N. lobatus* Lemos de Castro, 1970	UFRGS 5127	MG, Matozinhos	-20.1520	-43.9716	_	_
N_SP4	N. lenkoi Lemos de Castro, 1970	UFRGS 6474	SP, Maresias	-23.8247	-45.5286	(X)	(X)
N_BA14	*Neotroponiscus carolii* Arcangeli,1936	UFRGS 6462	BA, Salvador	-12.7925	-38.4711	_	(X)
N_BA15	*Neotroponiscus carolii* Arcangeli,1936	UFRGS 6453	BA, Itajú	-15.0328	-38.9992	(X)	(X)
N_BA16	*Neotroponiscus* sp. 2		BA, Maraúvis	-14.1672	-38.9967	(X)	(X)
N_BA20	*Neotroponiscus carolii* Arcangeli,1936		BA, Ilheus, UESC	-14.7991	-39.1723	(X)	(X)
N_cilheus	*Neotroponiscus carolii* Arcangeli,1936	UFRGS 6461	BA, Ilheus, CEPLAC	-14.7573	-39.2332	_	(X)
N_F2BA	*Neotroponiscus carolii* Arcangeli,1936		BA, Ilheus, CEPLAC	-14.7573	-39.2332	KM200866	(X)
N_BAuna	*Neotroponiscus carolii* Arcangeli,1936	UFRGS 6468	BA, Una			(X)	(X)
N_RJ4A	*Neotroponiscus* sp. 3		RJ, Cabo Frio, Praia do Peró	-22.8671	-41.9850	(X)	(X)
N_RJ4B	*Neotroponiscus* sp. 3		RJ, Cabo Frio, Praia do Peró	-22.8671	-41.9850	(X)	(X)
N_RJ4M	*Neotroponiscus* sp. 3		RJ, Cabo Frio, Praia do Peró	-22.8671	-41.9850	(X)	_
N_RJ11	*Neotroponiscus* sp. 3		RJ, Buzius, Praia João Fernandes	-22.7394	-41.9850	_	(X)
N_ES1	N. perlatus Lemos de Castro, 1970	UFRGS 6180	ES, Santa Tereza	-19.9416	-40.5824	_	(X)
N_IP	*N. iporangaensis* Cardoso & Araujo, 2017	MZUSP 35062	SP, Iporanga			_	(X)
N_TU	*N. tuberculatus* Cardoso & Araujo, 2017	MZUSP 35063	MG, Brumadinho	-20.1520	-43.9716	_	_

Table 2. List of morphological characters, their states and origins.

Character (+ states)		Derivation of character
1	Dorsum, dorsal cuticular surface, plaques type: 0, low profile plaques; 1, semicircular with raised walls; 2, circular with raised walls (individualized); 3, circular with raised walls with polygonal pattern	New character
2	Dorsum, dorsal cuticular surface, scale-setae type: 0, piliform; 1, tricorns; 2, fan-shape; 3, tooth-shape	Adapted from Leistikow 2001, Schmidt 2002
3	Dorsum, noduli lateralis: 0, small, not discernible; 1, discernible	Adapted from Schmidt 2007
4	Dorsum, noduli lateralis, disposition, lateral margin: 0, 7 near lateral margin; 1, 6 near lateral margin (1 distant); 2, 5 near lateral margin (2 distant); 3, 4 near lateral margin (3 distant); 4, 3 near lateral margin (4 distant); 5, 2 near lateral margin (5 distant); 6, 1 near lateral margin (6 distant); 7, 0 near lateral margin (7 distant)	Adapted from Leistikow 2001
5	Dorsum, nodulus laterales 7, quantity: 0, one; 1, two	Adapted from Schmidt 2007
6	Dorsum, cephalothorax tuberculation: 0, absent; 1, present	Adapted from Schmidt 2002, Schmidt 2007
7	Dorsum, tegument tuberculation: 0, absent; 1, present	Adapted from Schmidt 2002, Schmidt 2007
8	Dorsum, tegument tubercle type: 0, granulation; 1, round; 2, spine; 3, rectangular (high); 4, rectangular (long); 5, stripes	Adapted from Schmidt 2002, Schmidt 2007
9	Dorsum, pleon median tuberculation: 0, absent; 1, present	Adapted from Schmidt 2002, Schmidt 2007
10	Dorsum, pleonite 1 paramedian ornamentation: 0, absent; 1, present	New character
11	Dorsum, pleonite 1 paramedian ornamentation: 0, absent; 1, present	New character
12	Dorsum, pleonite 3 paramedian ornamentation: 0, absent; 1, present	New character
13	Dorsum, pleonite 4 paramedian ornamentation: 0, absent; 1, present	New character
14	Dorsum, pleonite 5 paramedian ornamentation: 0, absent; 1, present	New character
15	Dorsum, pleotelson: 0, smooth; 1, vestigial carena; 2, carena; 3, tubercle	New character
16	Dorsum, pleotelson depression: 0, absent; 1, present	New character
17	Pereon, epimeron 1, development of anterior portion: 0, not reaching eyes; 1, reaching eyes; 2, surpassing eyes	New character
18	Pereon, epimeron 7, development of posterior corners relative to the pleon: 0, surpassing pleonite 2 but not surpassing pleonite 3; 1, surpassing pleonite 3 but not surpassing pleonite 4; 2, surpassing pleonite 4 but not surpassing pleonite 5	New character
19	Pereon, pereonite 1 epimeron, lateral groove: 0, absent; 1, present	Adapted from Schmidt 2007
20	Pereon, pereonite 1 epimeron, schisma: 0, absent; 1, present	Adapted from Schmidt 2007
21	Pereon, epimera, ventral lobe: 0, absent; 1, present	Adapted from Schmidt 2007
22	Pleonites, neopleura, shape: 0, triangular; 1, rectangular	Adapted from Leistikow 2001
23	Pleonite 5, neopleura, relative length with pleotelson: 0, shorter than distal margin; 1, reaching distal margin; 2, surpassing distal margin	Adapted from Leistikow 2001
24	Pleotelson, lateral margins, shape: 0, concave; 1, straight; 2, convex	Adapted from Leistikow 2001, Schmidt 2002
25	Pleotelson, lateral margins, orientation: 0, convergent; 1, parallel; 2, divergent	Adapted from Leistikow 2001, Schmidt 2002
26	Pleotelson, distal margin, shape: 0, rounded; 1, quadrangular (truncated); 2, acute	Adapted from Leistikow 2001, Schmidt 2002
27	Pleotelson, relative development (% width x length): 0, 30>60; 1, 60>90; 2, 90>120; 3, 120>	New character
28	Pleotelson, cover uropod protopod: 0, not covering; 1, covering	Adapted from Schmidt 2002
29	Pleotelson, length relative with uropod protopod: 0, shorter than protopod; 1, reaching protopod distal portion; 2, surpassing protopod; 3, surpassing protopod and reaching the tip o uropod exopod	Adapted from Schmidt 2002
30	Cephalothorax, frontal depression: 0, absent; 1, present	Adapted from Schmidt 2002
31	Cephalothorax, frontal line: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
32	Cephalothorax, frontal line, frontal lobe: 0, not developed; 1, developed	Adapted from Leistikow 2001, Schmidt 2002
33	Cephalothorax, frontal lobe, development relative to lateral lobes: 0, not reaching; 1, as long as lateral lobes; 2, surpassing	Adapted from Schmidt 2002
34	Cephalothorax, frontal lobe, shape: 0, triangular; 1, round; 2, oval; 3, ellipsoidal; 4, quadrangular; 5, trapezoidal; 6, pentagonal	Adapted from Schmidt 2002
35	Cephalothorax, dorsal view, frontal line, lateral lobes: 0, not developed; 1, developed	Adapted from Schmidt 2002
36	Cephalothorax, developed lateral lobes, shape: 0, rounded; 1, subquadrangular; 2, subtriangular	Adapted from Schmidt 2002
37	Cephalothorax, frontal shield: 0, absent; 1, present	Adapted from Schmidt 2002
38	Cephalothorax, suprantennal line: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
39	Antennula, aesthetascs arrangement: 0, in pairs, forming a stepped row; 1, tuft gathered apically; 2, medial tuft separated from an apical pair; 3, medial tuft; 4, in line	Adapted from Leistikow 2001, Schmidt 2007
40	Antennula, distal article, tip: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2007
41	Antennula, medial article dimension (width %): 0, 0-40; 1, 40-70; 2, 70-100; 3, 100-130; 4, 130>	Adapted from Leistikow 2001, Schmidt 2002
42	Antenna, 5º peduncle article, width in relation to length (%): 0, 0-20; 1, 20-40; 2, 40-60	New character
43	Antenna, flagellum, articles: 0, two; 1, three	Adapted from Leistikow 2001, Schmidt 2002
44	Antenna, flagellum triarticulated, articles relative length: 0, subequal; 1, distincts	New character
45	Antenna, flagellum biarticulated, articles relative length: 0, distal < proximal; 1, distal = proximal; 2, distal > 1x proximal; 3, distal > 2x proximal; 4, distal > 3x proximal; 5, distal > 4x proximal; 6, distal > 5x proximal	New character
46	Antenna, flagellum, relative legth x 5º peduncle article: 0, shorter; 1, subequal; 2, longer	New character
47	Mandibles, molar penicil composition: 0, single plumose seta; 1, tuft with 3-6 plumose setae; 2, tuft with 6-12 plumose setae; 3, tuft with more than 12 plumose setae	Adapted from Leistikow 2001
48	Maxillula, inner branch, distal tip: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
49	Maxillula, outer branch, outer set of teeth, number: 0, three; 1, four	Adapted from Leistikow 2001, Schmidt 2002
50	Maxillula, outer branch, inner set % of cleft teeth: 0, 100; 1, 75>; 2, 50>; 3, 25>; 4, 0	Adapted from Leistikow 2001

51	Maxillula, outer branch, inner set cleft type: 0, simple cleft; 1, trifurcate; 2, pectinate	Adapted from Leistikow 2001, Schmidt 2002
52	Maxilla, outer lobe, relative width with inner lobe: 0, wider; 1, subequal; 2, slender	Adapted from Leistikow 2001, Schmidt 2002
53	Maxilliped, palp, number of setae on first article: 0, one; 1, two	Adapted from Schmidt 2007
54	Maxilliped, endite, outer corner, lobes: 0, absent; 1, present	Adapted from Schmidt 2002
55	Maxilliped, endite, frontal face, penicil: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
56	Pereopod 1, Carpus, antennal brush, disposition: 0, transverse; 1, longitudinal	Adapted from Leistikow 2001, Schmidt 2002
57	Pereopod 1, Carpus, antennal brush, proportion in length: 0, 30-40; 1, 40-50; 2, 50-60; 3, 60-70; 4, 70-80; 5, 80-90	New character
58	Pereopod 1, carpus, width in relation to length (%): 0, 40-50; 1, 50-60; 2, 60-70; 3, 70-80; 4, 80-90	Adapted from Leistikow 2001
59	Pereopod 1, Carpus, distal seta, apex type; 0, double-fringe (2-1-2); 1, triple-fringe (3-1-3); 2, multiple-fringe	Adapted from Leistikow 2001
60	Pereopod 1 (males), Carpus, dense setae on sternal margin: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
61	Pereopod 2 (males), Carpus, dense setae on sternal margin: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002, Schmidt 2007
62	Pereopod 3 (males), Carpus, dense setae on sternal margin: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002, Schmidt 2007
63	Pereopod 4 (males), Carpus, dense setae on sternal margin: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
64	Pereopod 7 (males), base, distal margin, lateral depression: 0, absent; 1, present	Adapted from Schmidt 2007
65	Pereopod 7 (males), Ischium, concavity on sternal margin: 0, absent; 1, present	Adapted from Schmidt 2007
66	Pereopod 7 (males), Ischium, frontal view depression: 0, absent; 1, present	Adapted from Schmidt 2007
67	Pereopod 7, Dactylus, dactylar seta length versus outer claw: 0, dactylar seta > outer claw; 1, dactylar seta = outer claw; 2, dactylar seta < outer claw	Adapted from Leistikow 2001, Schmidt 2002
68	Pereopod 7, Dactylus, dactylar seta, shape: 0, simple; 1, enlarged; 2, with setules	Adapted from Leistikow 2001, Schmidt 2002
69	Pleopod 1 exopod (males), outer marginal setae: 0, absent; 1, present	Adapted from Schmidt 2002, Schmidt 2007
70	Pleopod 1 exopod (males), distal projection: 0, absent; 1, present	Adapted from Leistikow 2001
71	Pleopod 1 exopod (males), distal projection shape: 0, small projection; 1, round projection; 2, acute projection; 3, triangular projection; 4, quadrangular projection	Adapted from Leistikow 2001
72	Pleopod 1 exopod (males), lateral incision: 0, absent; 1, present	Adapted from Leistikow 2001
73	Pleopod endopod 1 (males), length relative to exopod: 0, short (less than twice of exopod length); 1, medium (2x exopod length); 2, long (3x exopod length); 3, very long (>3x exopod length)	Adapted from Leistikow 2001
74	Pleopod 1 endopod (males), distal portion, lobe: 0, absent; 1, present	Adapted from Leistikow 2001
75	Pleopod 1 endopod (males), apex ornamentation: 0, absent; 1, present	Adapted from Leistikow 2001
76	Pleopod 1 endopod (males), twisted distal apex: 0, absent; 1, present	Adapted from Leistikow 2001
77	Pleopod 2 endopod (males), length relative to the exopod: 0, short (as long as exopod); 1, medium (<2x exopod length); 2, elongated (>2x the exopod length)	Adapted from Leistikow 2001
78	Pleopod 5 exopod, dimension (relative length); 0, longer than wide; 1, as long as wide; 2, wider than long	Adapted from Leistikow 2001
79	Pleopods exopods, respiratory fields: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
80	Pleopods exopods, respiratory fields, type: 0, absent; 1, present	Adapted from Leistikow 2001, Schmidt 2002
81	Uropod, protopod, dimension (relative length): 0, longer than wide; 1, as long as wide; 2, wider than long	New character
82	Uropod, protopod, distal margin development: 0, absent; 1, present	Adapted from Schmidt 2002
83	Uropod, protopod, insertion of the endopod branch, relative to the exopod base: 0, proximal; 1, medial; 2, distal	New character
84	Uropod, exopod shape: 0, lanceolate; 1, plate-like	Adapted from Schmidt 2007
85	Uropod, exopod length, relative to the endopod: 0, 0-50; 1, 50-100; 2, 100-150; 3, 150-200; 4, 200-250	New character
86	Uropod, exopod length, relative to protopod: 0, 0-50; 1, 50-100; 2, 100-150; 3, 150-200; 4, 200-250; 5, 250-300	New character
87	Uropod, endopod branch, setae on margin, quantity: 0, sparse; 1, dense	Adapted from Schmidt 2002

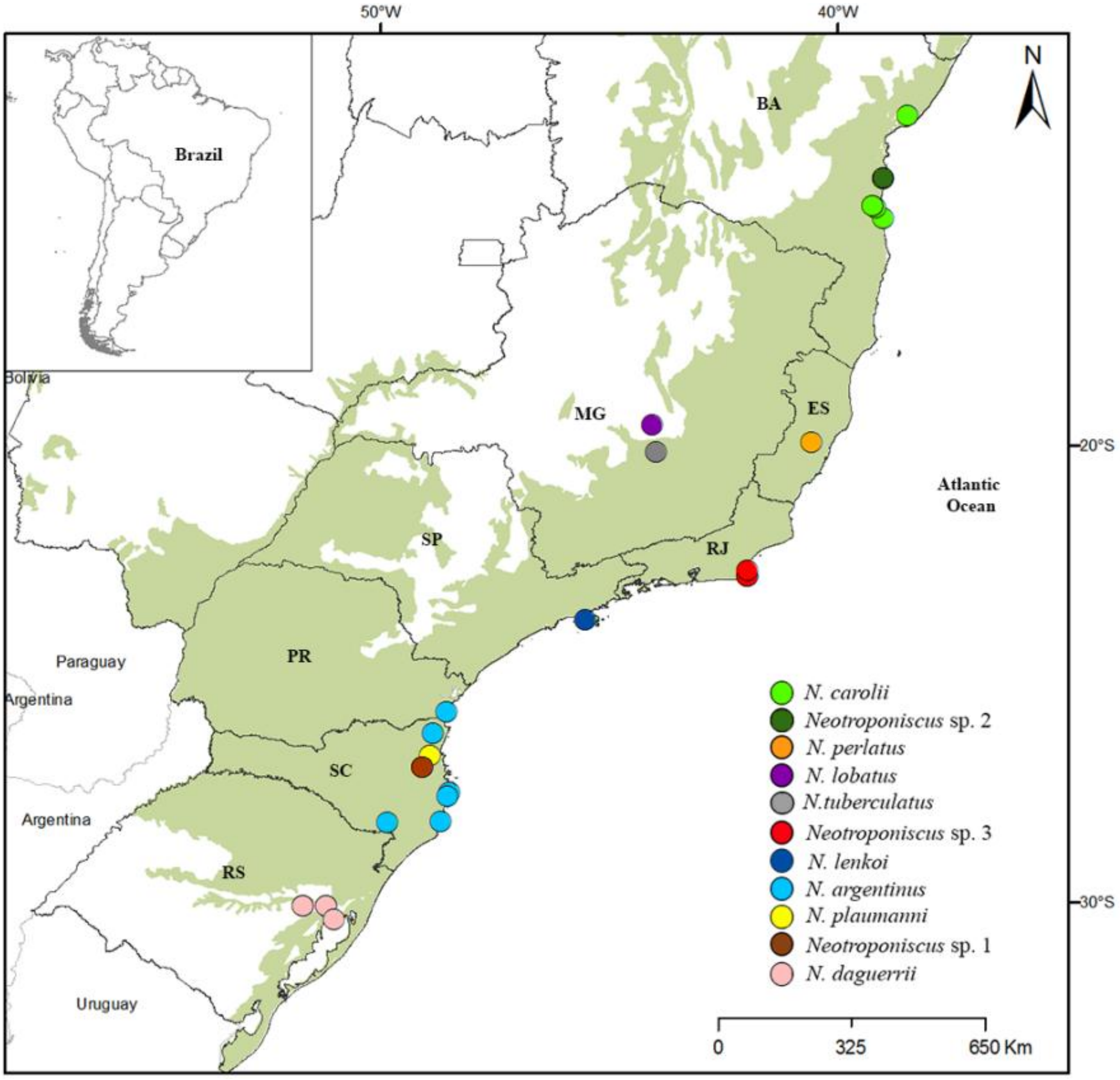

Figure 1. Sample species of *Neotroponiscus* along the Brazilian Atlantic Forest (in green). Brazil: BA, Bahia; ES, Espírito Santo; RJ, Rio de Janeiro; MG, Minas Gerais; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

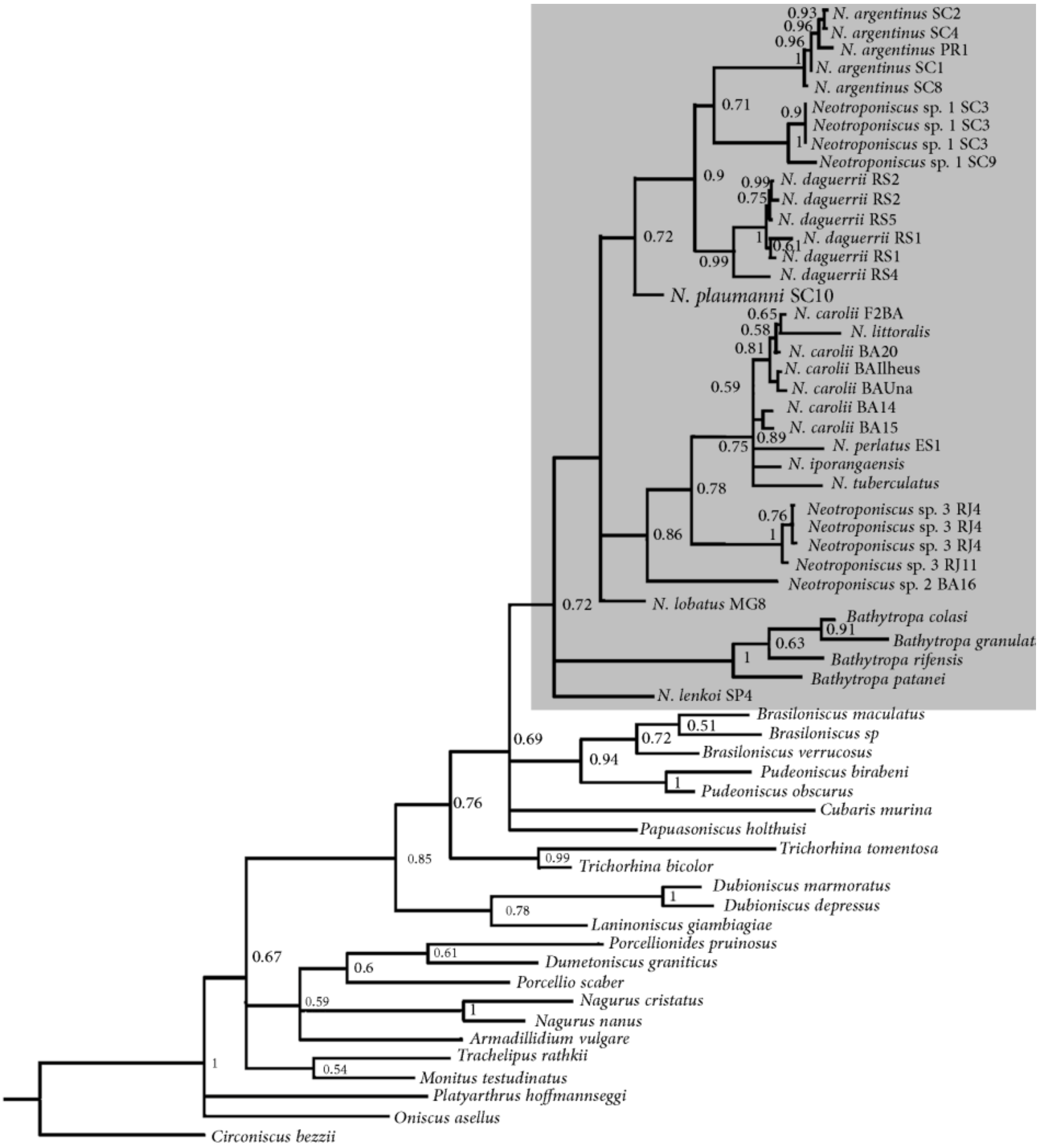

Figure 2. Bayesian inference consensus tree based on molecular markers and morphological characters for the complete taxon analyses with 63 terminals. Numbers close to nodes are Bayesian posterior probabilities (pp).

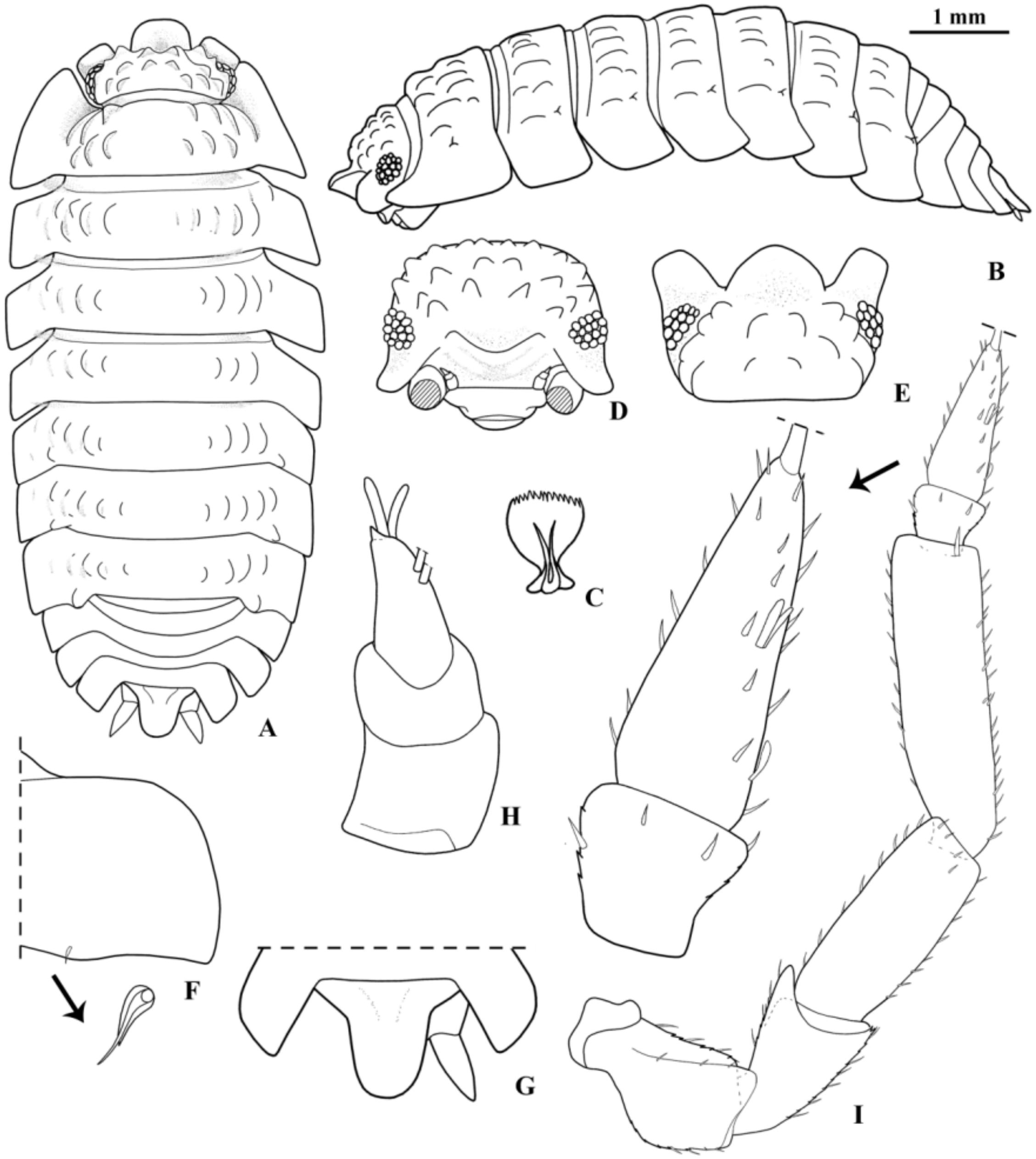

Figure 3. *Neotroponiscus* sp. 1. ♂ UFRGS 5587. A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, frontal view; E, cephalon, dorsal view; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

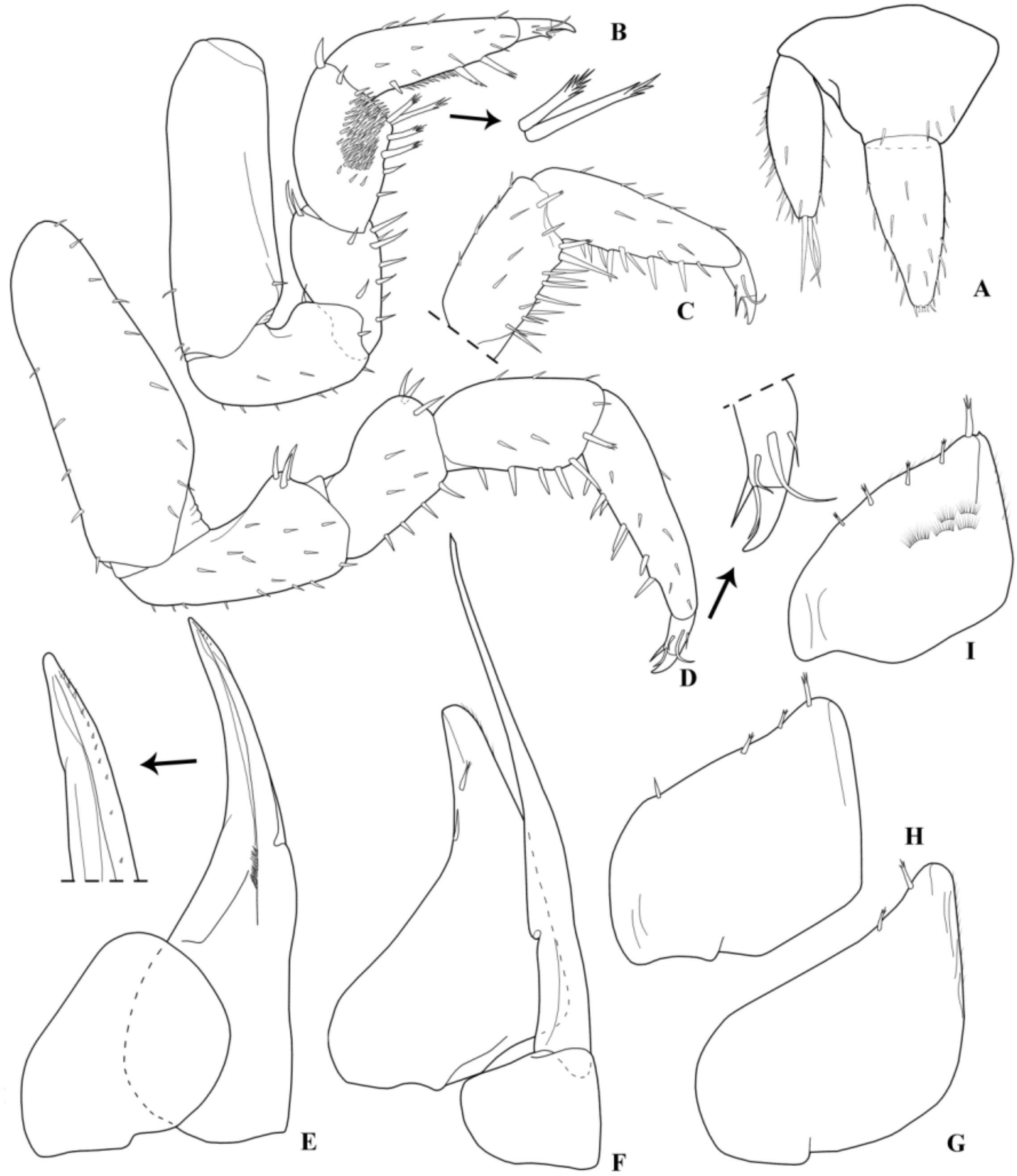

Figure 4. *Neotroponiscus* sp. 1. ♂ UFRGS 5587. A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

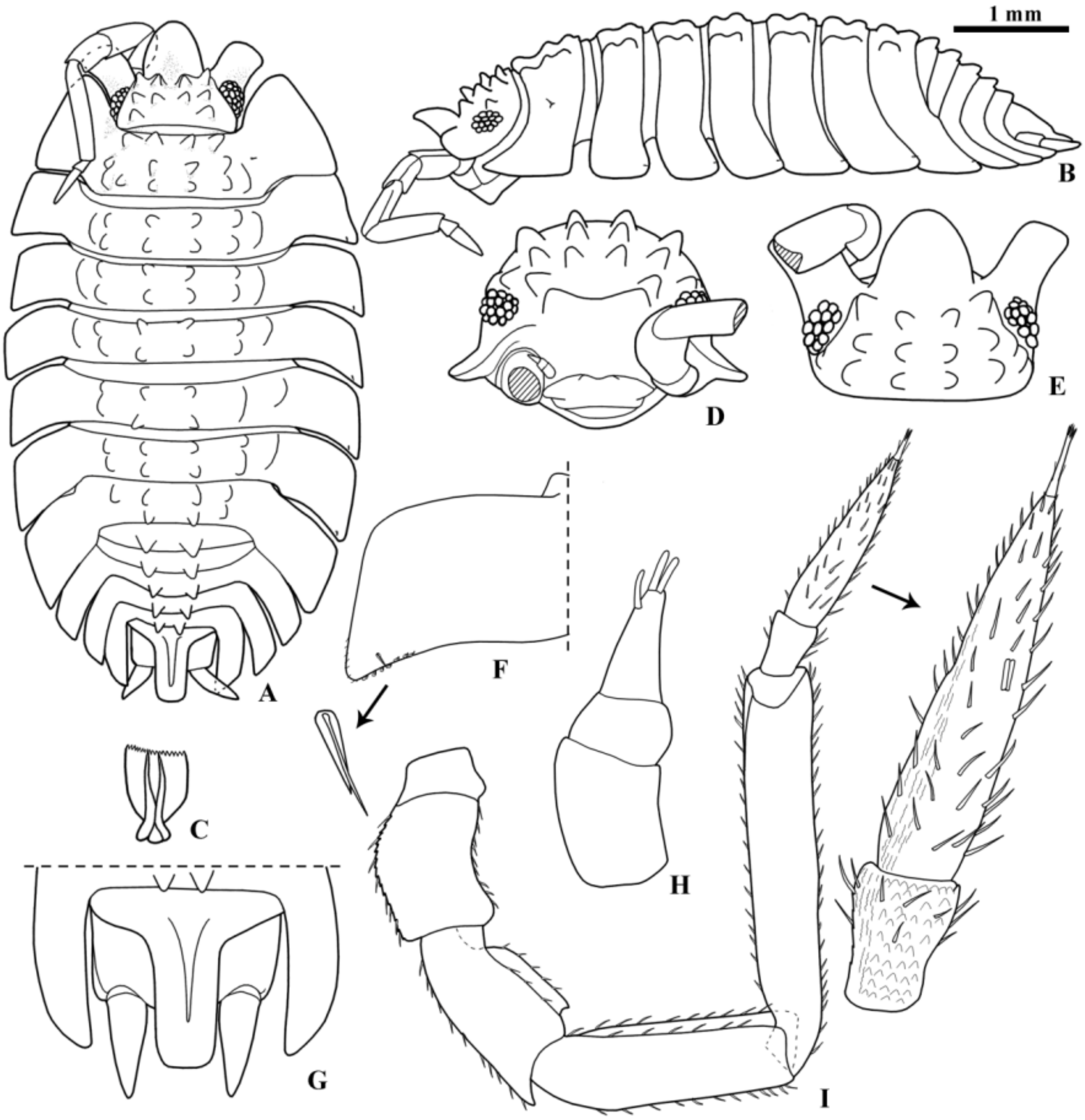

Figure 5. *Neotroponiscus* sp. 3. ♂ (MZUSP XXX). A, habitus, dorsal view; B, habitus, lateral view; C, scale-seta; D, cephalon, frontal view; E, cephalon, dorsal view;; F, pereonite 7; G, pleonite 5, telson and uropod, dorsal view; H, antennule; I, antenna.

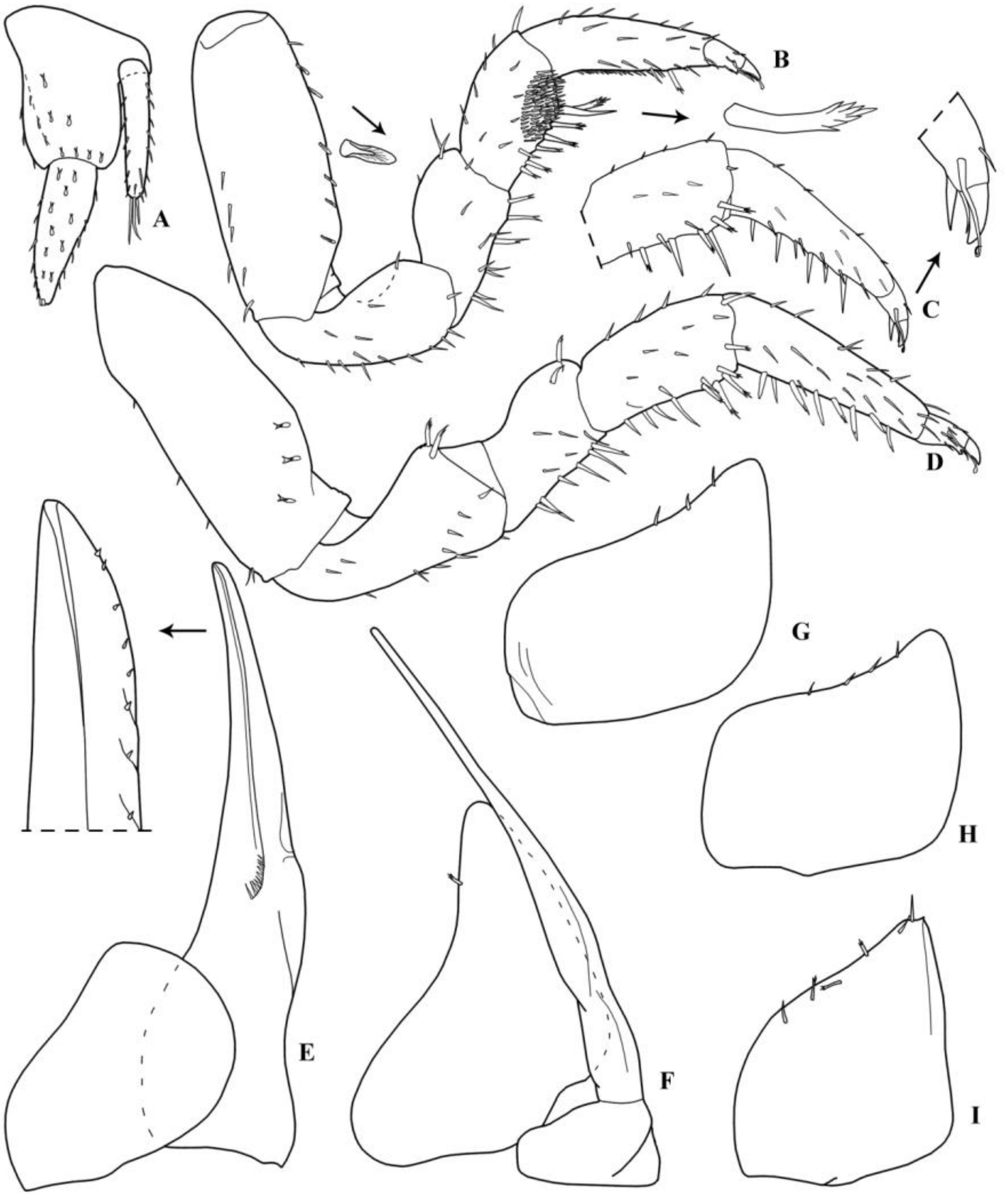

Figure 6. *Neotroponiscus* sp. 3 ♂ (MZUSP XXX). A, uropod; B, pereopod 1; C, pereopod 2; D, pereopod 7; E, pleopod 1; F, pleopod 2; G, pleopod 3 exopod; H, pleopod 4 exopod; I, pleopod 5 exopod.

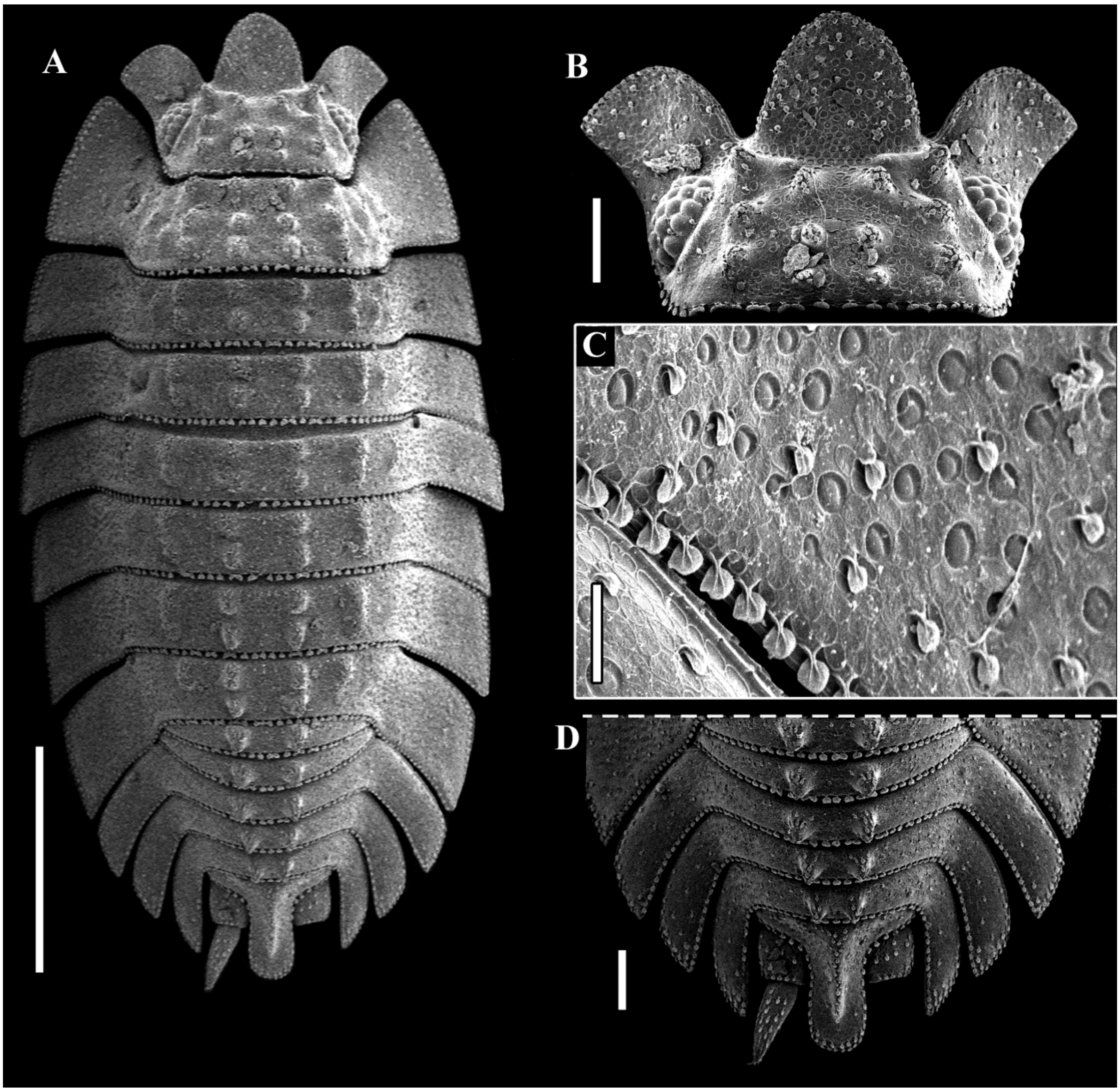

Figure 7. *Neotroponiscus* sp. 3 ♂ (MZUSP XXX). A, habitus, dorsal view; B, cephalon, dorsal view; C, dorsal surface on pereonite 7; D, pleon, telson and uropods, dorsal view. Scale bars: A 1mm, B, D 200 μm, C 50 μm.

Supporting Information

Appendix S1. Complete morphological data matrix.

```
MATRIX
C_bezzii        0?0--00-000000002001112200000010----1101210-
0020121000100100000010020131000010100120000
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2031110211114221111010201130001012112011110
C_murina        ?11700140000000020000112211030l0--0-1030210-403014-
01101310111000020113l0?0012110120100
D_marmoratus    1210000-00000000100000020200l110--1000012011-02014-
01001112000000020113000001210201045O
D_depressus     1210000-000000001000000202002110--1000011111-02014-
010010120000000201131100012102010351
P_hoffmannseggi  2317000-00000000-10000220200001123110120120-601114-
21101420000000020010020000?00-0000220
T_tomentosa     1217100-00000000000000110200000-----0110010-
3010020211001201111010000?100?000100-1010220
T_bicolor       1217000-0000000000000000010200000-----01200111-
011020011001201100000000012021001 20-2000430
P_birabeni      1017000-0000000120101102001020 10--1000001110-
120100011112320000001000100010012100100110
P_obscurus      1017001400000001201011020110201 0--1100001111-
121100011114220000001020101000012100100110
B_maculatus     ??17001400000001201111020110201 0--1100011110-
120110111112120000100001121000012100100000
B_verrucosus    2217011500000001201111020000201 0--1100001110-
02????????11200000000????????00?2100100??0
B_sp            3217000-00000001201111020010201 0--10000??211-
021110011114220000000021121000012100100001
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2031110211114101111001201120101012102000231
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4011110211113l0??????????????????2102000230
N_nanus         2113000-000000001000000202102011001000401l0-421114-2111131011000012000-
0000010102010330
P_scaber        11170110111111001000010202102011001100412 00-
2021130211014200000011201141101010111000340
P_pruinosus     ?117011000000000100000020200201 0--120131300-
00111100110120011100002011300010101120 00340
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L_giambiagiae   1217000-0000000000000000102002010--120101100-
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D_graniticus    ?112010000000000100000010210201110100101300-
2011110211112100000000000130000012 0-2000440
P_holthuisi     2?10000-000000002100010200202110--1100???10-400114-011-
112200000102001300011 1?0-2000220
M_testudinatus  ?????00-0000000021000102122020112612 00???01?-
001130?1????1?1110000??11200010?20-?1?03??
B_patanei       3117011510000000210001010011201124110011110-
50111202111044100000000000100001 0000-2010310
B_colasi        ??1701151111110020000101001120112611 00???10-
501?????1??034?00000102001000000 0?0-???0???
B_rifensis      ?117011511000000200001010011201115110010110-
41111302111033?0000000200100000000 0-2000??0
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30111300110122001000002001000000120-2000220
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N_RS5            221701120000000101000010211102011261000021?10-
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```
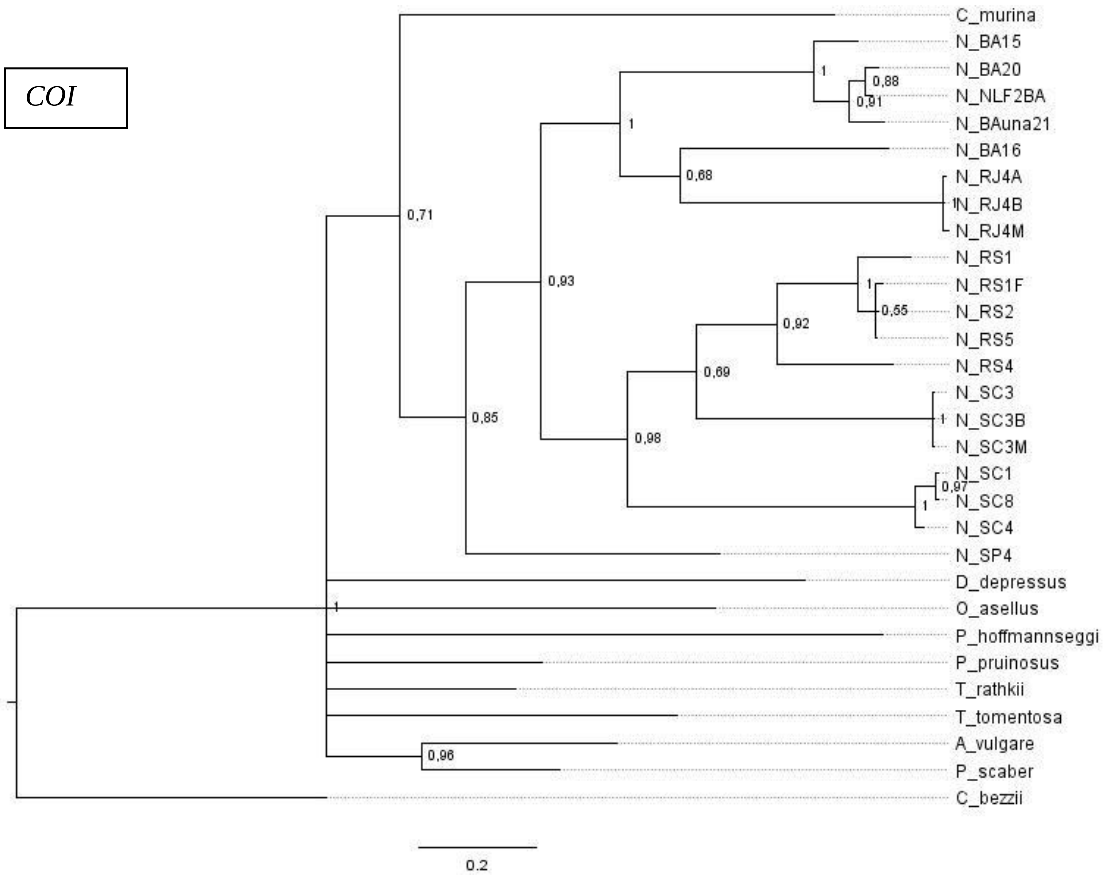
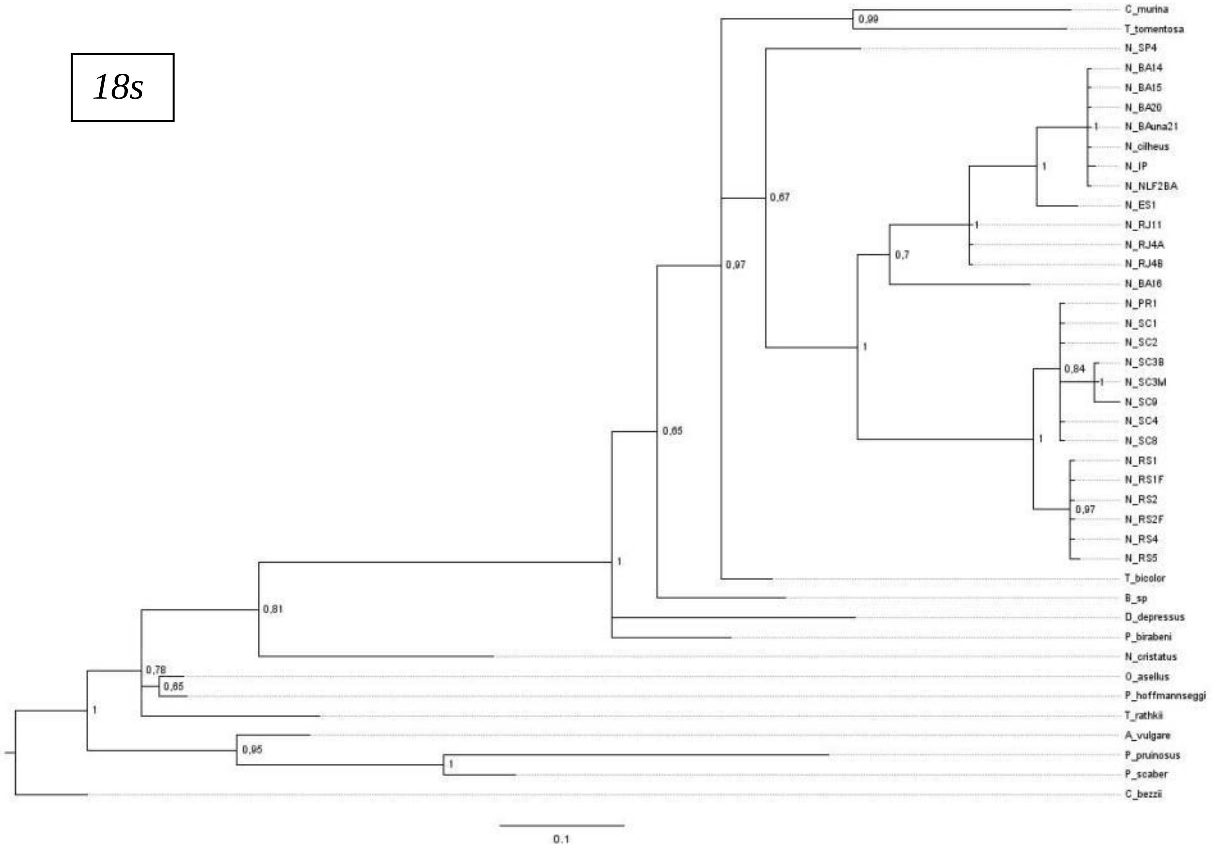

Appendix S2**.** Phylogenetic reconstruction for each partition separately [*cytochrome oxidase subunit I* (*COI*), *18s* rRNA (*18s*)], DNA concatenated, morphological and total evidence reduced datasets. In *COI*, *18S*, DNA concatenated and total evidence the numbers close to nodes are Bayesian posterior probabilities (pp). In the topology of the strict consensus tree for morphological data the values in nodes are Jacknife symmetrical resampling (SR) support. The second tree with morphological data show character changes: black circles indicate non-homoplastic synapomorphies; white circles indicate homoplastic synapomorphies.




18s
C_murina
T_tomentosa
N_SP4
N_BAI4
N_BAI5
N_BA20
N_BAuna21
N_cilheus
N_IP
N_NLF2BA
N_ES1
N_RJ11
N_RJ4A
N_RJ4B
N_BAI6
N_PR1
N_SC1
N_SC2
N_SC3B
N_SC3M
N_SC9
N_SC4
N_SC8
N_RS1
N_RS1F
N_RS2
N_RS2F
N_RS4
N_RS5
T_bicolor
B_sp
D_depressus
P_birabeni
N_cristatus
O_asellus
P_hoffmannseggi
T_rathkii
A_vulgare
P_pruinosus
P_scaber
C_bezzii
0,99
0,67
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0,78
0,65
0,95
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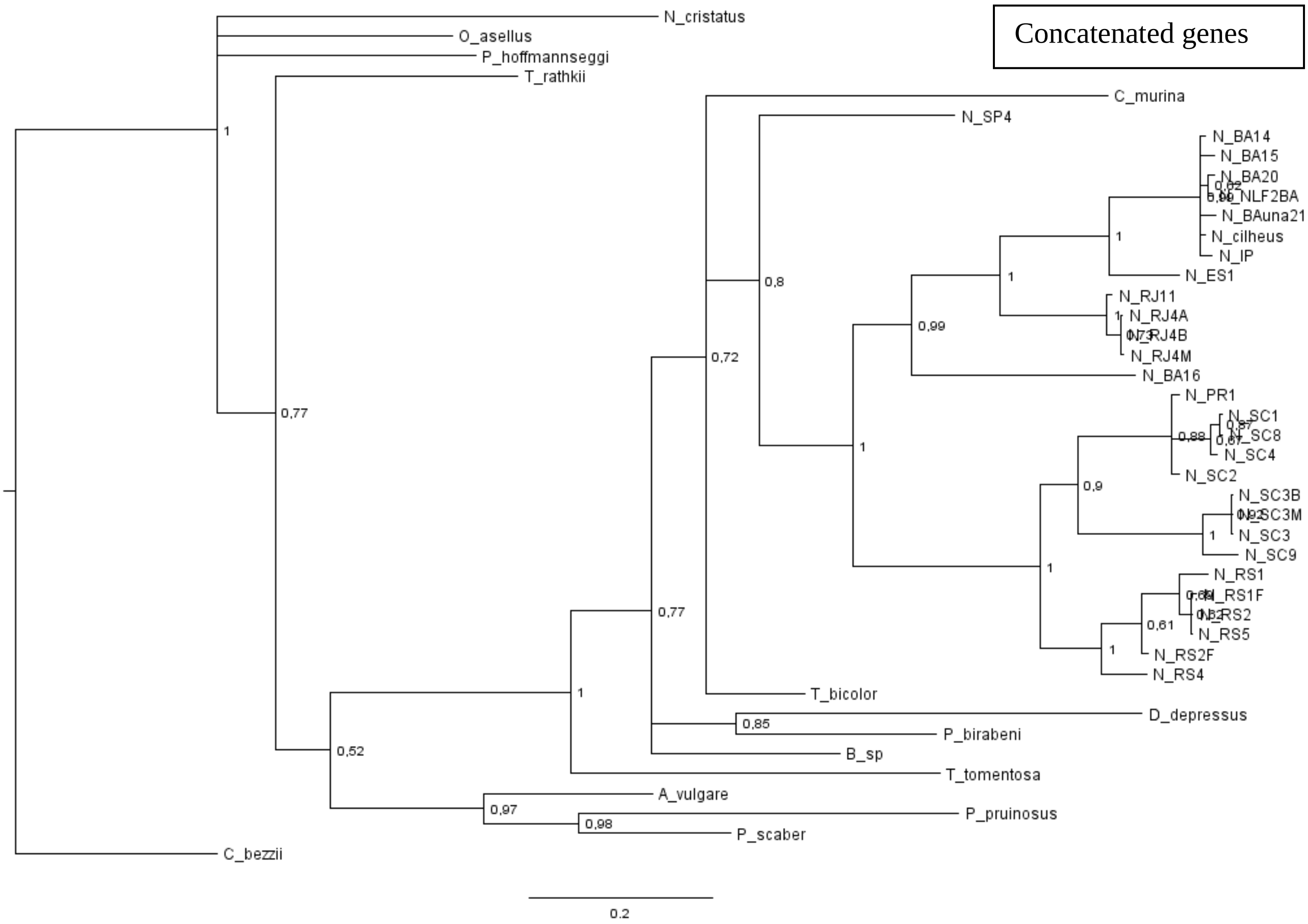
0.1


Concatenated genes
N_cristatus
O_asellus
P_hoffmannseggi
T_rathkii
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C_murina
N_SP4
N_BA14
N_BA15
N_BA20
0,62
0,99
N_NLF2BA
N_BAuna21
N_cilheus
N_IP
1
N_ES1
1
N_RJ11
1
N_RJ4A
0,73
N_RJ4B
N_RJ4M
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N_BA16
0,8
N_PR1
N_SC1
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0,88
N_SC8
0,67
N_SC4
N_SC2
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0,9
N_SC3B
0,92
N_SC3M
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N_SC3
N_SC9
0,72
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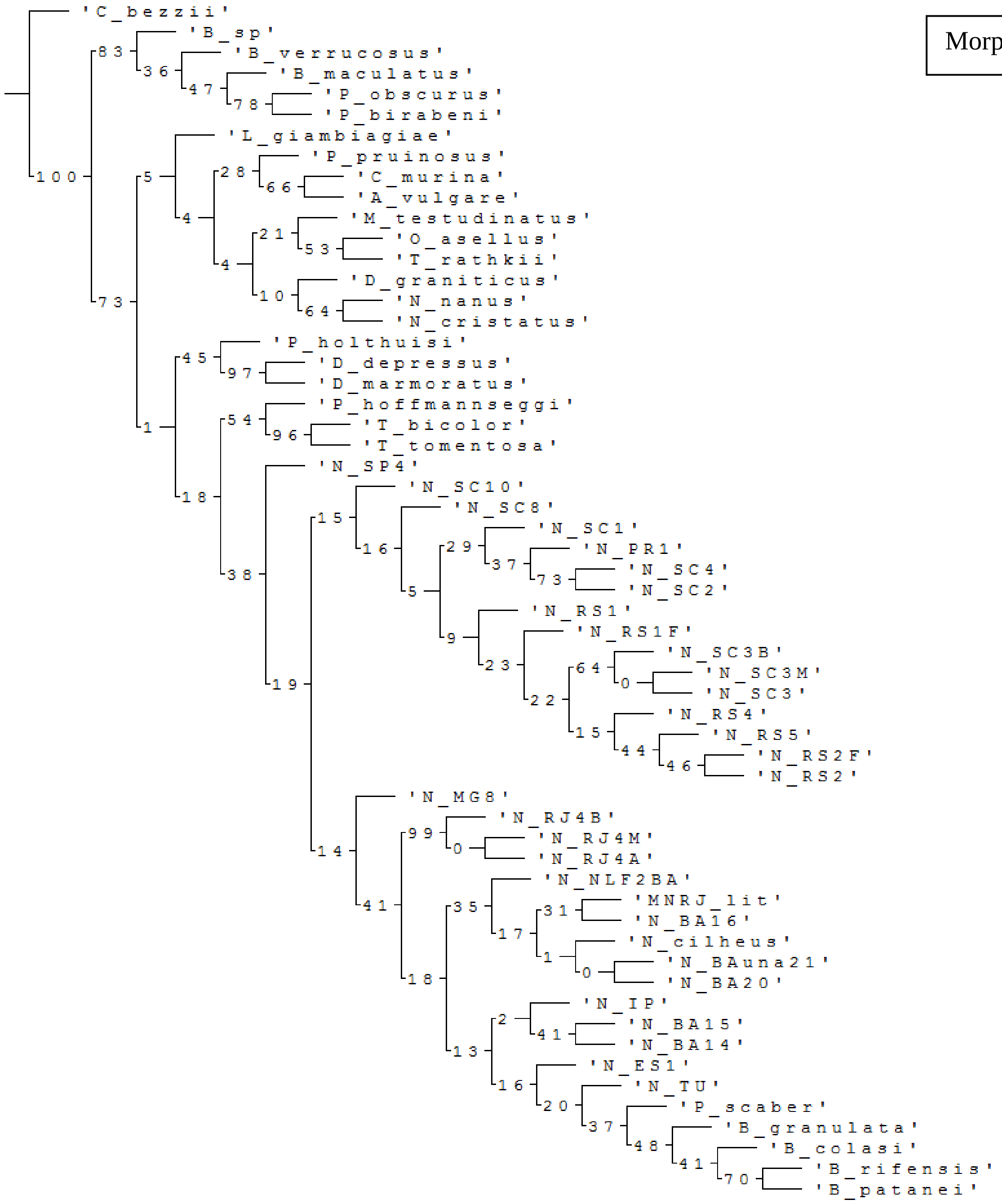
0,64
N_RS1F
0,62
N_RS2
N_RS5
0,61
1
N_RS2F
N_RS4
0,77
0,77
T_bicolor
1
0,85
D_depressus
P_birabeni
B_sp
0,52
T_tomentosa
A_vulgare
0,97
P_pruinosus
0,98
P_scaber
C_bezzii
0.2

Morphology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'O_asellus'
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'D_graniticus'
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'N_nanus'
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'D_depressus'
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'T_bicolor'
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'N_SC8'
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'N_IP'
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'N_BA14'
13
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16
'N_TU'
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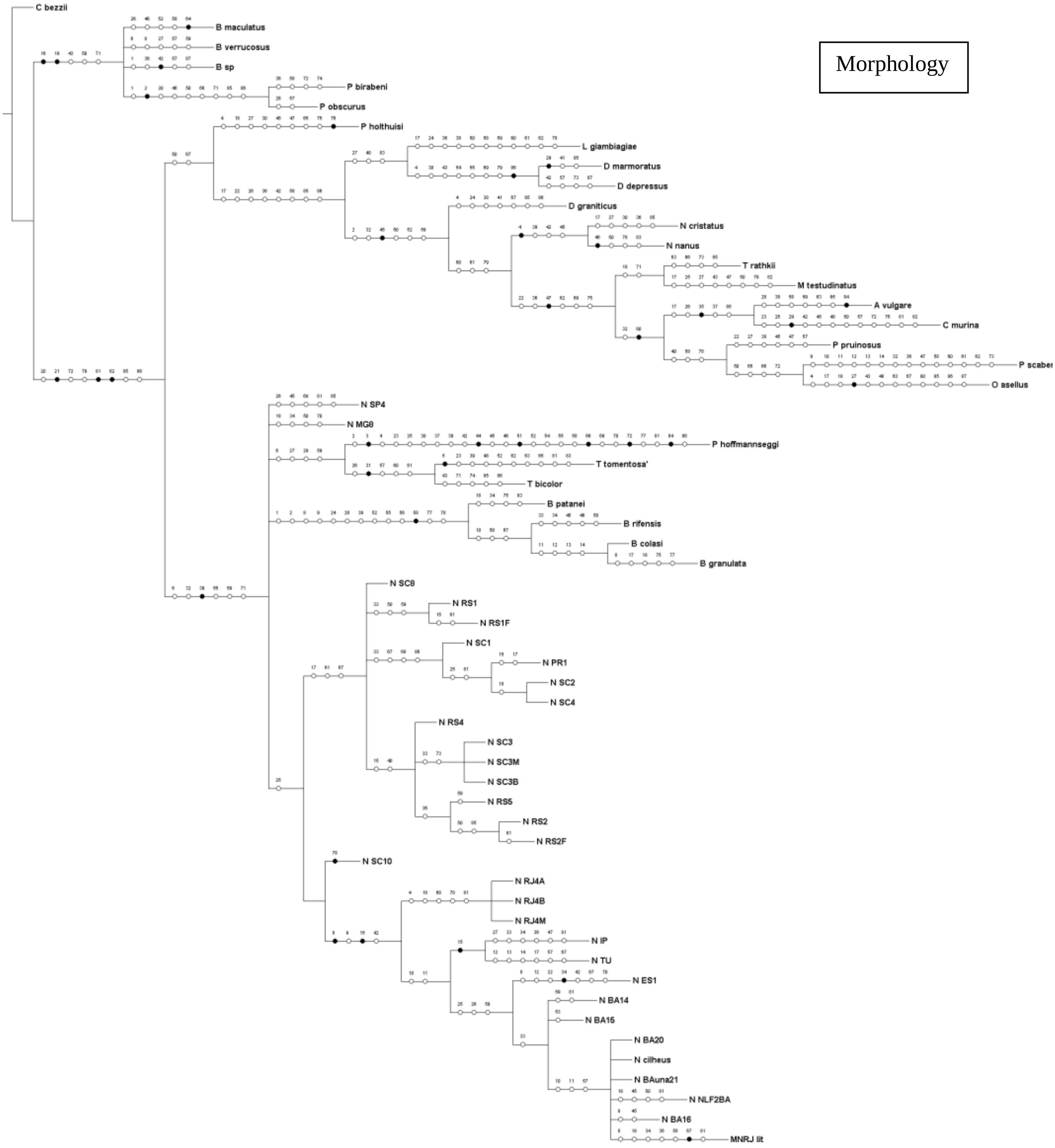
Morphology
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B verrucosus
B sp
P birabeni
P obscurus
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D depressus
D graniticus
N cristatus
N nanus
T rathkii
M testudinatus
A vulgare
C murina
P pruinosus
P scaber
O asellus
N SP4
N MG8
P hoffmannseggi
T tomentosa'
T bicolor
B patanei
B rifensis
B colasi
B granulata
N SC8
N RS1
N RS1F
N SC1
N PR1
N SC2
N SC4
N RS4
N SC3
N SC3M
N SC3B
N RS5
N RS2
N RS2F
N SC10
N RJ4A
N RJ4B
N RJ4M
N IP
N TU
N ES1
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N BA15
N BA20
N cilheus
N BAuna21
N NLF2BA
N BA16
MNRJ lit

Reduced analyse

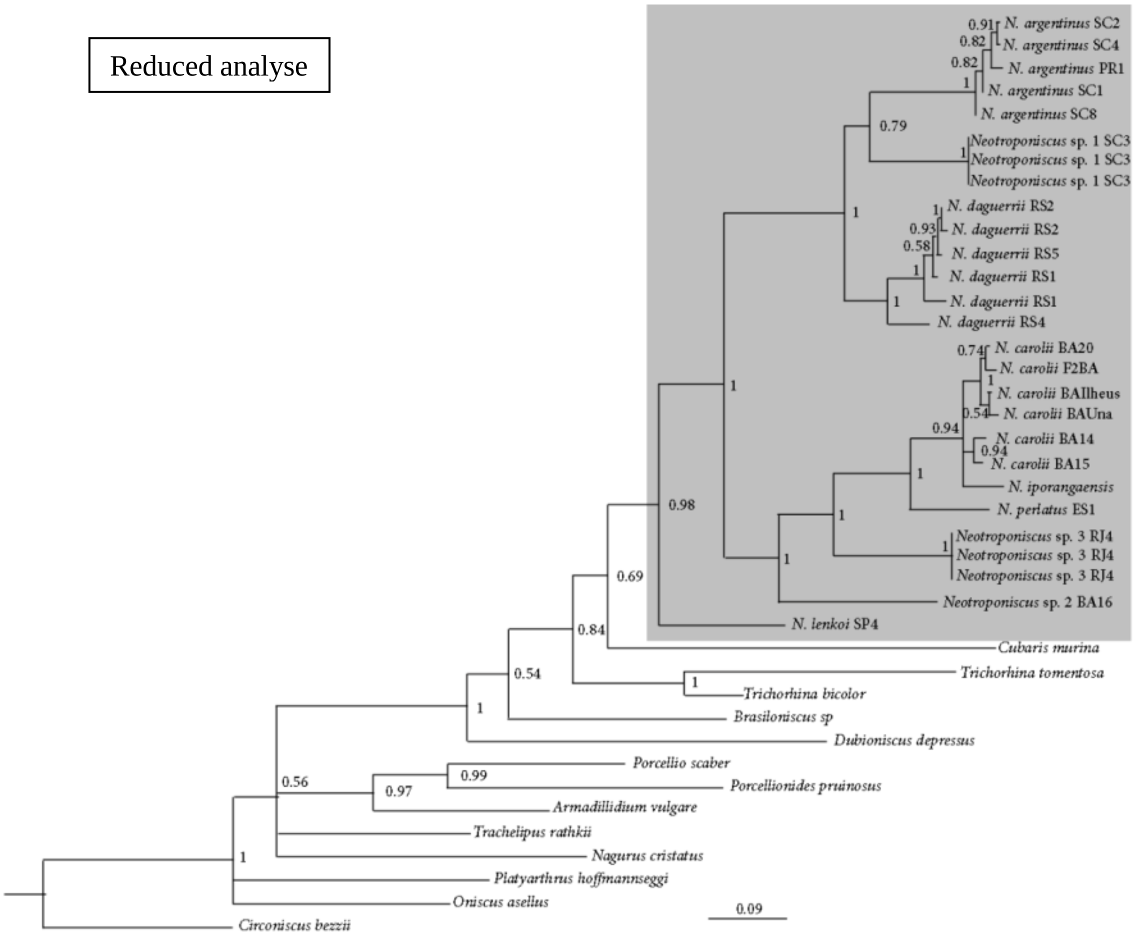

Table 3: Sequence divergence on citocromo c oxidase subunidade I (*COI*) gene between species, including outgroup.

	Avul	Cbez	Cmuri	Ddepr	NBA15	NBA16	NBA20	NBAun	NLF2BA	NRJ4A	NRJ4B	NRJ4M	NRS1	NRS1F	NRS2	NRS4	NRS5	NSC1	NSC3	NSC3B	NSC3M	NSC4	NSC8	NSP4	Oase	Phoffm	Pprui	Psca	Trath	Ttome
Avulgare		0.019	0.019	0.019	0.019	0.018	0.032	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.025	0.019	0.019	0.020	0.019	0.019	0.018	0.019	0.018	0.019	0.020	0.017	0.016	0.017	0.018
Cbezzii	0.265		0.021	0.020	0.020	0.020	0.030	0.020	0.020	0.020	0.020	0.020	0.020	0.019	0.020	0.025	0.020	0.019	0.020	0.019	0.019	0.019	0.019	0.019	0.020	0.021	0.019	0.019	0.019	0.021
Cmurina	0.250	0.297		0.020	0.019	0.019	0.032	0.020	0.019	0.020	0.020	0.020	0.019	0.019	0.019	0.024	0.019	0.019	0.020	0.019	0.019	0.019	0.019	0.019	0.020	0.020	0.020	0.019	0.019	0.020
Ddepress	0.204	0.268	0.281		0.020	0.019	0.031	0.020	0.020	0.020	0.020	0.020	0.020	0.019	0.020	0.025	0.020	0.020	0.021	0.020	0.020	0.019	0.020	0.019	0.020	0.021	0.019	0.019	0.018	0.020
NBA15	0.256	0.288	0.248	0.261		0.016	0.020	0.012	0.012	0.018	0.018	0.018	0.017	0.018	0.018	0.024	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.019	0.019	0.021	0.019	0.018	0.019	0.019
NBA16	0.239	0.267	0.239	0.240	0.186		0.026	0.017	0.017	0.018	0.018	0.018	0.017	0.017	0.017	0.023	0.016	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.019	0.018	0.018	0.018	0.018
NBA20	0.297	0.262	0.282	0.287	0.092	0.169		0.017	0.008	0.027	0.027	0.028	0.026	0.026	0.026	0.028	0.026	0.029	0.028	0.028	0.028	0.029	0.029	0.029	0.029	0.031	0.030	0.031	0.029	0.031
NBAuna	0.273	0.267	0.263	0.261	0.085	0.189	0.067		0.010	0.018	0.018	0.018	0.017	0.017	0.017	0.024	0.017	0.019	0.019	0.018	0.018	0.018	0.019	0.018	0.019	0.020	0.019	0.018	0.019	0.019
NLF2BA	0.261	0.261	0.261	0.261	0.083	0.176	0.015	0.053		0.018	0.018	0.018	0.017	0.017	0.017	0.024	0.017	0.019	0.019	0.018	0.018	0.019	0.019	0.018	0.019	0.020	0.019	0.019	0.018	0.019
NRJ4A	0.258	0.284	0.258	0.272	0.222	0.203	0.195	0.225	0.214		0.002	0.003	0.017	0.017	0.017	0.023	0.017	0.019	0.019	0.018	0.018	0.018	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.018
NRJ4B	0.256	0.282	0.256	0.270	0.220	0.201	0.190	0.222	0.212	0.002		0.003	0.017	0.017	0.017	0.023	0.017	0.018	0.019	0.018	0.018	0.018	0.018	0.019	0.019	0.019	0.019	0.019	0.019	0.018
NRJ4M	0.261	0.286	0.261	0.274	0.225	0.206	0.195	0.227	0.216	0.006	0.004		0.018	0.017	0.017	0.023	0.017	0.019	0.019	0.018	0.018	0.018	0.019	0.019	0.019	0.019	0.019	0.020	0.019	0.018
NRS1	0.252	0.265	0.246	0.249	0.212	0.184	0.179	0.206	0.199	0.201	0.199	0.203		0.011	0.010	0.021	0.010	0.018	0.017	0.017	0.017	0.018	0.018	0.018	0.018	0.021	0.018	0.018	0.019	0.018
NRS1F	0.254	0.271	0.250	0.236	0.210	0.182	0.179	0.206	0.203	0.197	0.195	0.199	0.064		0.004	0.020	0.004	0.018	0.017	0.016	0.016	0.018	0.018	0.018	0.019	0.020	0.018	0.019	0.018	0.018
NRS2	0.258	0.278	0.256	0.247	0.208	0.184	0.174	0.203	0.201	0.199	0.197	0.201	0.057	0.011		0.020	0.002	0.018	0.017	0.017	0.017	0.018	0.018	0.018	0.019	0.021	0.018	0.019	0.019	0.018
NRS4	0.283	0.290	0.259	0.283	0.239	0.212	0.205	0.239	0.229	0.229	0.226	0.232	0.152	0.148	0.145		0.020	0.024	0.022	0.022	0.022	0.023	0.024	0.024	0.025	0.026	0.025	0.025	0.026	0.026
NRS5	0.258	0.275	0.254	0.245	0.206	0.182	0.174	0.201	0.199	0.197	0.195	0.199	0.055	0.008	0.002	0.145		0.018	0.017	0.016	0.016	0.018	0.018	0.018	0.019	0.021	0.018	0.019	0.019	0.018
NSC1	0.261	0.261	0.250	0.259	0.220	0.222	0.226	0.244	0.242	0.222	0.220	0.225	0.197	0.197	0.195	0.215	0.193		0.019	0.018	0.018	0.007	0.003	0.019	0.020	0.020	0.018	0.019	0.019	0.020
NSC3	0.278	0.278	0.243	0.269	0.213	0.218	0.215	0.213	0.225	0.218	0.215	0.220	0.178	0.178	0.181	0.209	0.178	0.208		0.000	0.000	0.019	0.019	0.019	0.020	0.021	0.020	0.019	0.020	0.019
NSC3B	0.267	0.275	0.246	0.265	0.227	0.220	0.215	0.222	0.235	0.216	0.214	0.218	0.174	0.176	0.178	0.209	0.176	0.208	0.000		0.000	0.018	0.018	0.019	0.019	0.020	0.019	0.018	0.019	0.019
NSC3M	0.267	0.275	0.246	0.265	0.227	0.220	0.215	0.222	0.235	0.216	0.214	0.218	0.174	0.176	0.178	0.209	0.176	0.208	0.000	0.000		0.018	0.018	0.019	0.019	0.020	0.019	0.018	0.019	0.019
NSC4	0.248	0.261	0.256	0.249	0.210	0.216	0.215	0.237	0.229	0.210	0.208	0.212	0.193	0.197	0.195	0.205	0.193	0.030	0.211	0.212	0.212		0.008	0.019	0.019	0.020	0.018	0.019	0.019	0.020
NSC8	0.261	0.263	0.252	0.256	0.218	0.220	0.226	0.246	0.244	0.222	0.220	0.225	0.195	0.195	0.193	0.215	0.191	0.004	0.208	0.208	0.208	0.030		0.019	0.020	0.020	0.018	0.019	0.019	0.020
NSP4	0.239	0.258	0.254	0.236	0.227	0.212	0.231	0.222	0.212	0.242	0.239	0.244	0.206	0.220	0.225	0.242	0.222	0.233	0.238	0.242	0.242	0.220	0.231		0.018	0.020	0.019	0.018	0.017	0.019
Oasellus	0.254	0.299	0.288	0.277	0.254	0.231	0.262	0.248	0.248	0.258	0.256	0.261	0.242	0.250	0.248	0.320	0.246	0.288	0.259	0.261	0.261	0.280	0.288	0.246		0.020	0.018	0.018	0.019	0.018
Phoffman	0.286	0.294	0.301	0.320	0.307	0.290	0.303	0.305	0.303	0.288	0.286	0.290	0.301	0.303	0.307	0.330	0.307	0.309	0.294	0.297	0.297	0.297	0.307	0.278	0.307		0.019	0.020	0.019	0.019
Ppruinosus	0.191	0.252	0.265	0.245	0.244	0.220	0.251	0.258	0.242	0.252	0.250	0.254	0.225	0.229	0.231	0.276	0.229	0.233	0.264	0.261	0.261	0.231	0.235	0.218	0.231	0.280		0.017	0.017	0.019
Pscaber	0.153	0.265	0.235	0.227	0.235	0.214	0.267	0.235	0.231	0.246	0.244	0.248	0.237	0.237	0.244	0.290	0.242	0.246	0.245	0.244	0.244	0.244	0.248	0.227	0.227	0.282	0.180		0.017	0.018
Trathkii	0.186	0.261	0.261	0.195	0.229	0.220	0.226	0.216	0.212	0.248	0.246	0.250	0.242	0.233	0.239	0.296	0.237	0.244	0.271	0.261	0.261	0.242	0.246	0.189	0.239	0.284	0.180	0.178		0.019
Ttomen	0.248	0.305	0.284	0.288	0.269	0.233	0.282	0.263	0.269	0.246	0.244	0.248	0.231	0.231	0.231	0.310	0.229	0.282	0.259	0.254	0.254	0.286	0.284	0.258	0.244	0.280	0.244	0.218	0.237	

Table 4: Sequence divergence on citocromo c oxidase subunidade I (*COI*) gene between congeneric species of the *Neotroponiscus*.

COI	N_BA15	N_BA16	N_BA20	N_BAun	N_NLF2	N_RJ4A	N_RJ4B	N_RJ4M	N_RS1	N_RS1F	N_RS2	N_RS4	N_RS5	N_SC1	N_SC3	N_SC3B	N_SC3M	N_SC4	N_SC8	N_SP4
N_BA15		0.016	0.020	0.012	0.012	0.018	0.018	0.018	0.018	0.018	0.018	0.024	0.018	0.018	0.019	0.018	0.018	0.018	0.018	0.019
N_BA16	0.186		0.026	0.017	0.017	0.018	0.018	0.018	0.017	0.017	0.017	0.023	0.017	0.018	0.019	0.018	0.018	0.018	0.018	0.018
N_BA20	0.092	0.169		0.017	0.009	0.028	0.028	0.028	0.026	0.026	0.026	0.028	0.026	0.029	0.027	0.027	0.027	0.029	0.029	0.029
N_BAun	0.085	0.189	0.067		0.010	0.018	0.018	0.019	0.017	0.018	0.018	0.024	0.018	0.019	0.019	0.018	0.018	0.019	0.019	0.019
N_NLF2	0.083	0.176	0.015	0.053		0.018	0.018	0.018	0.017	0.017	0.017	0.023	0.017	0.019	0.019	0.018	0.018	0.019	0.019	0.018
N_RJ4A	0.222	0.203	0.195	0.225	0.214		0.002	0.003	0.017	0.017	0.017	0.023	0.017	0.018	0.019	0.018	0.018	0.018	0.018	0.019
N_RJ4B	0.220	0.201	0.190	0.222	0.212	0.002		0.003	0.017	0.017	0.017	0.023	0.017	0.018	0.019	0.018	0.018	0.018	0.018	0.019
N_RJ4M	0.225	0.206	0.195	0.227	0.216	0.006	0.004		0.018	0.017	0.017	0.023	0.017	0.019	0.019	0.018	0.018	0.018	0.019	0.019
N_RS1	0.212	0.184	0.179	0.206	0.199	0.201	0.199	0.203		0.011	0.010	0.021	0.010	0.018	0.018	0.017	0.017	0.018	0.018	0.018
N_RS1F	0.210	0.182	0.179	0.206	0.203	0.197	0.195	0.199	0.064		0.004	0.020	0.004	0.018	0.017	0.016	0.016	0.018	0.018	0.018
N_RS2	0.208	0.184	0.174	0.203	0.201	0.199	0.197	0.201	0.057	0.011		0.020	0.002	0.018	0.017	0.017	0.017	0.018	0.017	0.018
N_RS4	0.239	0.212	0.205	0.239	0.229	0.229	0.226	0.232	0.152	0.148	0.145		0.020	0.024	0.022	0.022	0.022	0.024	0.024	0.023
N_RS5	0.206	0.182	0.174	0.201	0.199	0.197	0.195	0.199	0.055	0.008	0.002	0.145		0.017	0.017	0.017	0.017	0.018	0.017	0.018
N_SC1	0.220	0.222	0.226	0.244	0.242	0.222	0.220	0.225	0.197	0.197	0.195	0.215	0.193		0.019	0.018	0.018	0.008	0.003	0.019
N_SC3	0.213	0.218	0.215	0.213	0.225	0.218	0.215	0.220	0.178	0.178	0.181	0.209	0.178	0.208		0.000	0.000	0.019	0.019	0.019
N_SC3B	0.227	0.220	0.215	0.222	0.235	0.216	0.214	0.218	0.174	0.176	0.178	0.209	0.176	0.208	0.000		0.000	0.018	0.018	0.019
N_SC3M	0.227	0.220	0.215	0.222	0.235	0.216	0.214	0.218	0.174	0.176	0.178	0.209	0.176	0.208	0.000	0.000		0.018	0.018	0.019
N_SC4	0.210	0.216	0.215	0.237	0.229	0.210	0.208	0.212	0.193	0.197	0.195	0.205	0.193	0.030	0.211	0.212	0.212		0.008	0.018
N_SC8	0.218	0.220	0.226	0.246	0.244	0.222	0.220	0.225	0.195	0.195	0.193	0.215	0.191	0.004	0.208	0.208	0.208	0.030		0.019
N_SP4	0.227	0.212	0.231	0.222	0.212	0.242	0.239	0.244	0.206	0.220	0.225	0.242	0.222	0.233	0.238	0.242	0.242	0.220	0.231	

Table 5: Sequence divergence on 18S ribosomal RNA (*18S*) gene between species, including outgroup.

18S	Avul	Cbez	Cmur	Ddepr	Ncris	Bra	Oase	Pbira	Pprui	Psca	Tbic	Trath	Phof	Ttom	SP4	BA14	BA15	BA16	BA20	Bau	ilheus	ES1	IP	F2BA	PR1	RJ11	RJ4A	RJ4B	RS1	RS1F	RS2	RS2F	RS4	RS5	SC1	SC2	SC3B	SC3M	SC4
Avulgare		0.015	0.018	0.019	0.018	0.018	0.013	0.018	0.019	0.015	0.017	0.018	0.013	0.017	0.018	0.019	0.019	0.018	0.020	0.019	0.019	0.019	0.019	0.019	0.019	0.018	0.018	0.018	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.022	0.018	0.019
Cbezzii	0.083		0.018	0.019	0.017	0.018	0.013	0.018	0.020	0.018	0.017	0.016	0.014	0.019	0.018	0.020	0.020	0.019	0.020	0.020	0.020	0.020	0.020	0.020	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.022	0.018	0.019
Cmurina	0.125	0.120		0.018	0.018	0.018	0.017	0.017	0.019	0.019	0.015	0.019	0.017	0.015	0.016	0.017	0.017	0.016	0.017	0.017	0.017	0.017	0.017	0.017	0.018	0.016	0.016	0.016	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.020	0.017	0.018
Ddepress	0.158	0.142	0.145		0.019	0.016	0.017	0.016	0.021	0.019	0.015	0.018	0.017	0.019	0.017	0.017	0.017	0.017	0.017	0.017	0.017	0.016	0.017	0.017	0.018	0.016	0.016	0.016	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.021	0.017	0.018
Ncristatus	0.133	0.115	0.135	0.153		0.017	0.015	0.018	0.020	0.017	0.018	0.018	0.015	0.018	0.018	0.019	0.019	0.019	0.020	0.019	0.019	0.020	0.019	0.019	0.019	0.019	0.019	0.019	0.020	0.020	0.020	0.020	0.020	0.020	0.019	0.019	0.022	0.018	0.019
Brasp	0.117	0.115	0.116	0.119	0.116		0.017	0.015	0.021	0.020	0.014	0.019	0.017	0.017	0.014	0.016	0.015	0.016	0.016	0.015	0.015	0.015	0.015	0.015	0.016	0.015	0.015	0.015	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.016	0.019	0.016	0.016
Oasellus	0.068	0.073	0.117	0.129	0.092	0.101		0.016	0.018	0.018	0.016	0.013	0.006	0.016	0.016	0.020	0.020	0.019	0.020	0.020	0.020	0.020	0.020	0.020	0.018	0.019	0.019	0.019	0.018	0.018	0.018	0.018	0.018	0.019	0.018	0.018	0.021	0.018	0.018
Pbirabeni	0.138	0.130	0.125	0.113	0.142	0.103	0.106		0.021	0.019	0.013	0.018	0.016	0.018	0.014	0.014	0.014	0.015	0.014	0.014	0.014	0.014	0.014	0.014	0.017	0.014	0.014	0.014	0.016	0.016	0.016	0.016	0.016	0.016	0.017	0.017	0.020	0.017	0.017
Ppruinos	0.155	0.168	0.174	0.204	0.181	0.198	0.147	0.202		0.018	0.021	0.020	0.017	0.020	0.020	0.022	0.022	0.021	0.022	0.022	0.022	0.022	0.022	0.022	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.021	0.024	0.020	0.021
Pscaber	0.088	0.151	0.154	0.182	0.135	0.165	0.136	0.174	0.142		0.018	0.019	0.018	0.019	0.020	0.020	0.020	0.020	0.021	0.020	0.020	0.021	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.023	0.019	0.020
Tbicolor	0.119	0.127	0.095	0.107	0.147	0.080	0.098	0.075	0.190	0.161		0.018	0.016	0.015	0.012	0.014	0.013	0.015	0.014	0.013	0.013	0.014	0.013	0.013	0.015	0.014	0.014	0.014	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.018	0.015	0.015
Trathkii	0.127	0.115	0.174	0.164	0.154	0.150	0.068	0.149	0.206	0.182	0.152		0.013	0.019	0.019	0.020	0.020	0.020	0.020	0.020	0.020	0.021	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.023	0.019	0.020
Phoffman	0.068	0.076	0.111	0.126	0.089	0.101	0.016	0.106	0.136	0.138	0.101	0.070		0.016	0.016	0.020	0.020	0.019	0.020	0.020	0.020	0.020	0.020	0.020	0.018	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.018	0.018	0.021	0.018	0.018
Ttomen	0.120	0.133	0.094	0.145	0.140	0.106	0.104	0.139	0.195	0.166	0.086	0.166	0.098		0.016	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.017	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.018	0.017	0.017	0.021	0.018	0.017
NSP4	0.133	0.131	0.102	0.133	0.148	0.088	0.112	0.101	0.205	0.190	0.066	0.191	0.109	0.104		0.014	0.014	0.016	0.015	0.014	0.014	0.015	0.014	0.014	0.014	0.014	0.014	0.014	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.017	0.014	0.014
NBA14	0.166	0.195	0.120	0.134	0.186	0.106	0.174	0.094	0.248	0.228	0.085	0.241	0.179	0.128	0.102		0.000	0.015	0.000	0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
NBA15	0.167	0.192	0.122	0.133	0.184	0.104	0.175	0.093	0.248	0.228	0.084	0.241	0.180	0.129	0.101	0.000		0.015	0.000	0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
NBA16	0.141	0.156	0.116	0.144	0.176	0.121	0.151	0.114	0.222	0.206	0.108	0.212	0.153	0.129	0.124	0.110	0.109		0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.014	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.018	0.015	0.015
NBA20	0.169	0.197	0.122	0.136	0.189	0.107	0.176	0.095	0.251	0.231	0.086	0.244	0.182	0.130	0.103	0.000	0.000	0.111		0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014
NBAuna	0.167	0.192	0.122	0.133	0.184	0.104	0.175	0.093	0.248	0.228	0.084	0.241	0.180	0.129	0.101	0.000	0.000	0.109	0.000		0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
Ncilheus	0.167	0.192	0.122	0.133	0.184	0.104	0.175	0.093	0.248	0.228	0.084	0.241	0.180	0.129	0.101	0.000	0.000	0.109	0.000	0.000		0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
NES1	0.172	0.204	0.122	0.133	0.191	0.104	0.192	0.095	0.256	0.239	0.095	0.254	0.195	0.132	0.103	0.042	0.041	0.116	0.042	0.041	0.041		0.009	0.009	0.014	0.009	0.009	0.009	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
NIP	0.164	0.190	0.119	0.130	0.182	0.104	0.172	0.090	0.245	0.225	0.082	0.239	0.177	0.126	0.099	0.002	0.002	0.106	0.002	0.002	0.002	0.043		0.002	0.014	0.009	0.009	0.009	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.013	0.014
NLF2BA	0.167	0.192	0.122	0.133	0.184	0.104	0.175	0.093	0.248	0.228	0.084	0.241	0.180	0.129	0.101	0.000	0.000	0.109	0.000	0.000	0.000	0.041	0.002		0.014	0.010	0.010	0.010	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.016	0.014	0.014
NPR1	0.148	0.149	0.130	0.146	0.159	0.108	0.136	0.125	0.218	0.188	0.099	0.192	0.136	0.126	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086		0.013	0.013	0.013	0.007	0.007	0.007	0.007	0.007	0.007	0.000	0.000	0.006	0.005	0.000
NRJ11	0.146	0.172	0.113	0.125	0.168	0.099	0.162	0.090	0.231	0.199	0.090	0.225	0.161	0.129	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076		0.000	0.000	0.014	0.014	0.014	0.014	0.014	0.015	0.013	0.013	0.016	0.013	0.013
NRJ4A	0.146	0.172	0.113	0.125	0.168	0.099	0.162	0.090	0.231	0.199	0.090	0.225	0.161	0.129	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076	0.000		0.000	0.014	0.014	0.014	0.014	0.014	0.015	0.013	0.013	0.016	0.013	0.013
NRJ4B	0.146	0.172	0.113	0.125	0.168	0.099	0.162	0.090	0.231	0.199	0.090	0.225	0.161	0.129	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076	0.000	0.000		0.014	0.014	0.014	0.014	0.014	0.015	0.013	0.013	0.016	0.013	0.013
NRS1	0.158	0.149	0.133	0.157	0.185	0.112	0.142	0.119	0.237	0.202	0.111	0.206	0.145	0.129	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095		0.000	0.000	0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007
NRS1F	0.158	0.149	0.133	0.157	0.185	0.112	0.142	0.119	0.237	0.202	0.111	0.206	0.145	0.129	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000		0.000	0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007
NRS2	0.158	0.149	0.133	0.157	0.185	0.112	0.142	0.119	0.237	0.202	0.111	0.206	0.145	0.129	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000		0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007
NRS2F	0.158	0.149	0.133	0.157	0.185	0.112	0.142	0.119	0.237	0.202	0.111	0.206	0.145	0.129	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000	0.000		0.000	0.003	0.007	0.007	0.010	0.008	0.007
NRS4	0.158	0.149	0.133	0.157	0.185	0.112	0.142	0.119	0.237	0.202	0.111	0.206	0.145	0.129	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000	0.000	0.000		0.003	0.007	0.007	0.010	0.008	0.007
NRS5	0.161	0.152	0.136	0.160	0.188	0.115	0.145	0.121	0.240	0.205	0.113	0.209	0.148	0.131	0.108	0.103	0.105	0.107	0.105	0.105	0.105	0.105	0.102	0.105	0.021	0.097	0.097	0.097	0.003	0.003	0.003	0.003	0.003		0.007	0.007	0.010	0.009	0.007
NSC1	0.148	0.149	0.130	0.146	0.159	0.108	0.136	0.125	0.218	0.188	0.099	0.192	0.136	0.126	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021		0.000	0.006	0.005	0.000
NSC2	0.148	0.149	0.130	0.146	0.159	0.108	0.136	0.125	0.218	0.188	0.099	0.192	0.136	0.126	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000		0.006	0.005	0.000
NSC3B	0.167	0.167	0.141	0.173	0.183	0.124	0.148	0.144	0.241	0.209	0.121	0.204	0.148	0.146	0.107	0.100	0.100	0.113	0.100	0.100	0.100	0.100	0.097	0.100	0.013	0.087	0.087	0.087	0.032	0.032	0.032	0.032	0.032	0.032	0.013	0.013		0.000	0.006
NSC3M	0.140	0.137	0.122	0.144	0.151	0.102	0.124	0.120	0.202	0.176	0.101	0.172	0.124	0.123	0.089	0.084	0.084	0.095	0.086	0.084	0.084	0.084	0.081	0.084	0.011	0.073	0.073	0.073	0.027	0.027	0.027	0.027	0.027	0.029	0.011	0.011	0.000		0.005
NSC4	0.148	0.149	0.130	0.146	0.159	0.108	0.136	0.125	0.218	0.188	0.099	0.192	0.136	0.126	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000	0.000	0.013	0.011	
NSC8	0.148	0.149	0.130	0.146	0.159	0.108	0.136	0.125	0.218	0.188	0.099	0.192	0.136	0.126	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000	0.000	0.013	0.011	0.000
NSC9	0.137	0.134	0.122	0.152	0.151	0.104	0.124	0.128	0.199	0.173	0.109	0.174	0.124	0.129	0.097	0.092	0.091	0.102	0.094	0.091	0.091	0.091	0.089	0.091	0.016	0.081	0.081	0.081	0.032	0.032	0.032	0.032	0.032	0.035	0.016	0.016	0.010	0.008	0.016

Table 6: Sequence divergence on 18S ribosomal RNA (*18S*) gene between congeneric species of the *Neotroponiscus*.

18S	N_SP4	N_BA14	N_BA15	N_BA16	N_BA20	N_Bauna	N_ilheus	N_ES1	N_IP	N_F2BA	N_PR1	N_RJ11	N_RJ4A	N_RJ4B	N_RS1	N_RS1F	N_RS2	N_RS2F	N_RS4	N_RS5	N_SC1	N_SC2	N_SC3B	N_SC3M	N_SC4	N_SC8	N_SC9
N_SP4		0.014	0.014	0.016	0.015	0.014	0.014	0.015	0.014	0.014	0.014	0.014	0.014	0.014	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.017	0.014	0.014	0.014	0.014
N_BA14	0.102		0.000	0.015	0.000	0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_BA15	0.101	0.000		0.015	0.000	0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_BA16	0.124	0.110	0.109		0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.014	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.018	0.015	0.015	0.015	0.016
N_BA20	0.103	0.000	0.000	0.111		0.000	0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_Bauna	0.101	0.000	0.000	0.109	0.000		0.000	0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_ilheus	0.101	0.000	0.000	0.109	0.000	0.000		0.009	0.002	0.000	0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_ES1	0.103	0.042	0.041	0.116	0.042	0.041	0.041		0.009	0.009	0.014	0.009	0.009	0.009	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_IP	0.099	0.002	0.002	0.106	0.002	0.002	0.002	0.043		0.002	0.014	0.009	0.009	0.009	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_F2BA	0.101	0.000	0.000	0.109	0.000	0.000	0.000	0.041	0.002		0.014	0.010	0.010	0.010	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.014	0.014	0.014	0.014
N_PR1	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086		0.014	0.014	0.014	0.007	0.007	0.007	0.007	0.007	0.007	0.000	0.000	0.006	0.005	0.000	0.000	0.006
N_RJ11	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076		0.000	0.000	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.013	0.014	0.014	0.014
N_RJ4A	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076	0.000		0.000	0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.013	0.014	0.014	0.014
N_RJ4B	0.091	0.045	0.045	0.087	0.046	0.045	0.045	0.043	0.043	0.045	0.076	0.000	0.000		0.015	0.015	0.015	0.015	0.015	0.015	0.014	0.014	0.016	0.013	0.014	0.014	0.014
N_RS1	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095		0.000	0.000	0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007	0.007	0.009
N_RS1F	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000		0.000	0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007	0.007	0.009
N_RS2	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000		0.000	0.000	0.003	0.007	0.007	0.010	0.008	0.007	0.007	0.009
N_RS2F	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000	0.000		0.000	0.003	0.007	0.007	0.010	0.008	0.007	0.007	0.009
N_RS4	0.106	0.103	0.102	0.105	0.105	0.102	0.102	0.102	0.100	0.102	0.018	0.095	0.095	0.095	0.000	0.000	0.000	0.000		0.003	0.007	0.007	0.010	0.008	0.007	0.007	0.009
N_RS5	0.108	0.103	0.105	0.107	0.105	0.105	0.105	0.105	0.102	0.105	0.021	0.097	0.097	0.097	0.003	0.003	0.003	0.003	0.003		0.007	0.007	0.010	0.009	0.007	0.007	0.009
N_SC1	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021		0.000	0.006	0.005	0.000	0.000	0.006
N_SC2	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000		0.006	0.005	0.000	0.000	0.006
N_SC3B	0.107	0.100	0.100	0.113	0.100	0.100	0.100	0.100	0.097	0.100	0.013	0.087	0.087	0.087	0.032	0.032	0.032	0.032	0.032	0.032	0.013	0.013		0.000	0.006	0.006	0.005
N_SC3M	0.089	0.084	0.084	0.095	0.086	0.084	0.084	0.084	0.081	0.084	0.011	0.073	0.073	0.073	0.027	0.027	0.027	0.027	0.027	0.029	0.011	0.011	0.000		0.005	0.005	0.004
N_SC4	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000	0.000	0.013	0.011		0.000	0.006
N_SC8	0.089	0.087	0.086	0.092	0.088	0.086	0.086	0.086	0.084	0.086	0.000	0.076	0.076	0.076	0.018	0.018	0.018	0.018	0.018	0.021	0.000	0.000	0.013	0.011	0.000		0.006
N_SC9	0.097	0.092	0.091	0.102	0.094	0.091	0.091	0.091	0.089	0.091	0.016	0.081	0.081	0.081	0.032	0.032	0.032	0.032	0.032	0.035	0.016	0.016	0.010	0.008	0.016	0.016	

Considerações Finais

A tese apresentada analisou a história evolutiva e as relações filogenéticas entre as espécies de *Neotroponiscus,* bem como com os outros componentes da família Bathytropidae. O uso de dados moleculares juntamente com aspectos morfológicos contribuiu para uma recuperação mais robusta dos relacionamentos filogenéticos para o as espécies de *Neotroponiscus*.

Para a análise filogenética, foi necessária a observação de diversas espécies provenientes de museus nacionais e internacionais, além da realização de coletas para obtenção de material fresco para o estudo genético. Durante análise dos espécimes percebeu-se a necessidade de caracteres morfológicos adequados ao diagnóstico das espécies, justificando a execução de um estudo taxonômico. Além disso, a escassez de estudos relacionados aos isopodos terrestres reforça a importâcia de investimentos taxonômicos. Potencialmente, a diversidade de outras famílias deve estar subestimada, assim como observado para as espécies descritas nesta tese.

No Capítulo I, o gênero *Levantoniscus* foi descrito com um material proveniente de Chipre. Este material ajudou a elucidar o *status* taxonômico de *Bathytropa wahrmanni*, outro táxon conhecido da região do mediterrâneo. As espécies novas compartilhavam caracteres anteriormente atribuídos ao gênero *Bathytropa*, tais como pulmões pleopodais, que diferem das outras espécies de *Bathytropa*.

No Capítulo II, o gênero americano *Dubioniscus* foi investigado e três espécies foram revisadas, duas delas são novas espécies descritas para o Brasil. Neste trabalho foi possível examinar o material da coleção de Vandel e notar a semelhança entre as espécies descritas por ele, sendo assim *Cubanoscia romanorum* foi sinomizada a *Dubioniscus negreae.*

No Capítulo III, duas novas espécies de *Neotroponiscus* foram descritas. A primeira foi coletada em cavernas de calcário localizado no Parque Estadual Turístico do Alto Ribeira (PETAR), enquanto a segunda espécie foi coletada em cavernas de minério de ferro do Quadrilátero de Ferro em Minas Gerais. Apesar das espécies não apresentarem características troglomórficas, ambas as espécies encontram-se ameaçadas de extinção, pois sofrem com os impactos do turismo e da mineração.

No Capítulo IV, as espécies de *Neotroponiscus* foram revisadas e novos caracteres foram levantados com o objetivo de proporcionar dados morfológicos detalhados para estudos filogenéticos para o grupo. Além disso, novos registros de ocorrência foram documentados para algumas espécies.

No último capítulo, as relações filogenéticas de *Neotroponiscus* foram analisadas com o auxílio de dados moleculares e morfológicos. O gênero foi recuperado como um grupo monofilético, concordando com a literatura, assim como seu parentesco com *Bathytropa*. A relação dos demais gêneros que compõe a família não pode ser definida, devido à necessidade de dados moleculares e adicionais táxons para determinar seu devido posicionamento em Crinocheta.

Os dados taxonômicos e moleculares obtidos nesta tese servirão como base para novas análises filogenéticas, além de contribuir para o conhecimento da diversidade deste táxon. Estudos futuros com uma abordagem biogeográfica serão importantes para elucidar os padrões de divergência na distribuição de Bathytropidae. Para as espécies de *Neotroponiscus*, uma análise semelhante também poderia esclarecer os padrões morfológicos encontrados entre os indivíduos localizados ao norte e sul do Brasil.

Anexos

Normas para a submissão da Revista

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Holotype. m, CAMEROON, Mount Koupé, 1600 m, rain forest, 8 February 1983, Bosmans & Bosselaers (sweep net), (MRAC).

Paratypes. Same data as for holotype, 4 mm 8ff W (MRAC).

Other material. Mount Koupé, 1300 m, rain forest, 1f, 31 January 1983 (pitfall trap); 1f, 2 February 1983 (sweep net) (MRAC Mount Koupé, 900 m, rain forest, 1 m (subadult) 2ff, 31 January 1983 (pitfall trap), Bosmans & Bosselaers (all MRAC).

Etymology. The name refers to the dark, reticulated marginal zone of the carapace.

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Description

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Phyllodoce badia Malmgren, 1867: 22, pl. II, fig. 6.

Anaitides citrina Bergström 1914: 140-141, fig. 41; Eliason 1962a: 18; Hartmann-Schröder 1971: 105-107, fig. 33D-F; Uschakov 1972: 136-137, pl. V, figs 5, 6.

Material examined. Phyllodoce citrina: 3 syntypes from Spitsbergen (SMNH type collection 2419 and 2420); 1 syntype from Spitsbergen (BMNH 1865.9.23.3); about 30 specimens from Wales, Shetland, western Norway, Spitsbergen, and Greenland (SMNH, MZB); about 10 specimens from the Arctic, Bering Sea and the Sea of Okhotsk (ZIL). *Phyllodoce badia*: several syntypes (at least 4 specimens and some fragments) from Bohuslän, Sweden (SMNH type collection 2423).

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