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IVANKLIN SOARES CAMPOS FILHO

ISÓPODOS TERRESTRES (CRUSTACEA, ONISCIDEA) DO BRASIL E ANÁLISE FILOGENÉTICA DE *BENTHANA* BUDDE-LUND, 1908 (PHILOSCIIDAE)

Tese de doutorado apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Departamento de Zoologia 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

Orientadora: Profª. Drª. Paula Beatriz de Araujo

Co-Orientador: Luiz Alexandre Campos

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ISÓPODOS TERRESTRES (CRUSTACEA, ONISCIDEA) DO BRASIL E ANÁLISE FILOGENÉTICA DE *BENTHANA* BUDDE-LUND, 1908 (PHILOSCIIDAE)

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Tese aprovada em 28/ 11/2014.

Dr Luiz Roberto Malabarba
Universidade Federal do Rio Grande do Sul

Dr Marcos Domingos Siqueira Tavares
Universidade de São Paulo

Dr Cristiana Serejo
Universidade Federal do Rio de Janeiro

Corpos em movimento
Universo em expansão
O apartamento que era tão pequeno
Não acaba mais

Vamos dar um tempo
Não sei quem deu a sugestão
Aquele sentimento que era passageiro
Não acaba mais

Quero explodir as grades
E voar
Não tenho pra onde ir
Mas não quero ficar

Novos horizontes
Se não for isso, o que será?
Quem constrói a ponte
Não conhece o lado de lá

Quero explodir as grades e voar
Não tenho pra onde ir
Mas não quero ficar
Suspender a queda livre
Libertar

O que não tem fim sempre acaba assim.

Novos Horizontes

Humberto Gessinger

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Prefácio

A ocupação e adaptação ao ambiente terrestre por vegetais e animais, constitui um dos maiores eventos evolutivos da história da vida na terra, o qual requereu muitas adaptações fisiológicas e morfológicas a fim de reduzir a dependência da água e suportar as novas condições ambientais, sendo estas integrantes fundamentais no processo de terrestrialização. Este processo possui uma história antiga, com provável origem no Pré-cambriano (Paleozoico) e ocorreu diversas vezes e em diferentes grupos durante o Paleozoico.

Dentre estes organismos que ocupam o ambiente terrestre, estão os crustáceos pertencentes à Subordem Oniscidea (Isopoda), popularmente conhecidos como "baratinhas da praia" e/ou "tatuzinhos de jardim"; Oniscidea inclui os representantes dentro de Crustacea com maior sucesso na conquista deste ambiente, com provável origem no Carbonífero Superior (326 Ma). Conhecer e compreender um pouco sobre a evolução deste grupo é um dos grandes objetivos desta tese e é essa história que ela conta. Claro, conta uma parte de uma grande história, mas para chegar a uma história robusta e inédita, foi necessária uma longa caminhada envolvendo uma série de estudos sobre o grupo, análise morfológica, fundamentos de taxonomia e estudar as diversas facetas que envolvem a análise filogenética. A tese inicia com uma introdução de cunho geral, para situar o leitor acerca dos isópodos terrestres e das temáticas abordadas nos capítulos subsequentes.

A seguir são apresentados sete capítulos na forma de artigos científicos. Os primeiros seis capítulos possuem cunho taxonômico e encontram-se publicados em periódicos especializados, e terão disponibilizado apenas a primeira página de acordo como publicados, respeitando os as normas e requisitos referentes aos direitos autorais cedidos aos periódicos.

O último capítulo será apresentado nas normas do periódico *Zoological Journal of the Linnean Society*, ao qual será submetido.

O primeiro capítulo, intitulado “Two new species of Scleropactidae (Crustacea: Isopoda: Oniscidea) from Pará, Brazil”, foi publicado no periódico de domínio aberto *Nauplius* no ano de 2011. Este capítulo tratou da descrição de duas novas espécies do gênero *Circoniscus* para a região de Canaã dos Carajás, Pará, Brasil.

O segundo capítulo, intitulado “A new species of *Atlantoscia* Ferrara & Taiti, 1981 (Oniscidea: Philosciidae) from Rio Grande do Sul, Brazil”, foi publicado no periódico de domínio aberto *Nauplius*, no ano de 2012. Neste estudo uma nova espécie do gênero *Atlantoscia* foi descrita, proveniente da Ilha dos Marinheiros, Rio Grande, Rio Grande do Sul, Brasil.

O terceiro capítulo, intitulado “Review of *Atlantoscia* Ferrara & Taiti, 1981 (Crustacea: Isopoda: Oniscidea: Philosciidae) with new records and new species”, foi publicado no periódico de cunho fechado *Organisms, Diversity and Evolution*, no ano de 2013. Neste capítulo, é abordada uma revisão do gênero *Atlantoscia* e a descrição de duas novas espécies provenientes dos estados da Bahia e São Paulo.

O quarto capítulo, intitulado “Two new species of *Benthana* Budde-Lund, 1908 (Crustacea: Isopoda: Philosciidae) from Brazil” foi publicado no periódico de domínio fechado *Tropical Zoology*, no ano de 2013. Aqui, duas novas espécies do gênero *Benthana* foram descritas e uma metodologia de análise do pleópodo do exópodo 1 dos machos foi proposta. Este estudo teve colaboração da aluna de graduação em ciências biológicas da Universidade Federal do Rio Grande do Sul, Silvana Leal Nunes Costa, como parte do programa de Iniciação Científica (CNPq, PROTAX).

O quinto capítulo, intitulado “New species and new records of *Benthana* Budde-Lund, 1908 (Isopoda: Oniscidea: Philosciidae) from southern Brazil”, foi publicado no periódico de domínio aberto *Papeis Avulsos de Zoologia*, no ano corrente. Neste estudo, uma nova espécie do gênero *Benthana* foi descrita e novos registros de ocorrência para outras espécies do gênero. Neste estudo a aluna de graduação em ciências biológicas da Universidade Federal do Rio Grande do Sul, Silvana Leal Nunes Costa, desenvolveu o trabalho com supervisão de Ivanklin. S. Campos Filho, e ambos supervisionados pela profª. Paula Beatriz de Araujo, e teve o estudo como parte do programa de Iniciação Científica da referida aluna (CNPq, PROTAX).

O sexto capítulo, intitulado "Terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Brazilian caves" foi publicado no periódico de domínio fechado *Zoological Journal of the Linnean Society*, no ano corrente. Este trabalho constituiu um dos primeiros esforços para o conhecimento da biodiversidade dos isópodos terrestres cavernícolas do Brasil, onde 3 gêneros novos foram propostos, 22 espécies foram reconhecidas, sendo 11 destas desconhecidas para a ciência.

Por fim, o sétimo e último capítulo, intitulado "Revisiting the phylogenetical relationships of Neotropical Philosciidae Kinahan, 1857 (Crustacea: Isopoda: Oniscidea) with emphasis on *Benthana* Budde-Lund, 1908: sensitivity analysis under different weighting schemes", o qual será submetido no periódico *Zoological Journal of the Linnean Society*, tem por finalidade testar as relações filogenéticas da família Philosciidae para os representantes Neotropicais, com ênfase no gênero *Benthana*.

Na seção de Considerações Finais, serão abordados os comentários gerais, conclusões e perspectivas.

Resumo

Os "tatuzinhos de jardim" são crustáceos pertencentes à ordem Isopoda, subordem Oniscidea, sendo esta, uma unidade monofilética, e uma das mais importantes por conter quase metade das espécies de isópodos conhecidos. Atualmente a Subordem Oniscidea possui cinco seções reconhecidas através de caracteres morfológicos: Ligiidae, Tylidae, Mesoniscidae, Synocheta e Crinocheta, esta última incluindo cerca de 80% da diversidade do grupo e os representantes com maiores adaptações ao ambiente terrestre. Atualmente para o Brasil são conhecidas aproximadamente 161 espécies de isópodos terrestres, incluindo os animais do ambiente cavernícola. Dentro de Oniscidea, a família Philosciidae possui distribuição conhecida para África, Ásia, Europa, Oceania e Américas, sendo um dos mais importantes grupos de Oniscidea em habitats tropicais. Filogeneticamente a família tem sido considerada parafilética, compartilhando características com as famílias Halophilosciidae e Scleropactidae. O gênero *Benthana* abrange 28 espécies localizadas apenas na America do Sul, e no Brasil possuem uma distribuição restrita para áreas de Mata Atlântica. Até o presente momento, alguns dos estudos sobre os isópodos terrestres ainda são insuficientes, logo, muitos grupos necessitam de revisão, para melhor compreensão das relações filogenéticas entre os táxons. O objetivo principal deste trabalho é proceder no inventariamento de isópodos terrestres do Brasil e revisitar as relações filogenéticas da família Philosciidae com ênfase no gênero *Benthana*. Para a taxonomia, o material utilizado neste trabalho foi obtido por empréstimo das coleções do Museu Nacional do Rio de Janeiro, Museu de Zoologia da Universidade de São Paulo e Coleção do Departamento de Zoologia da Universidade Federal do Rio Grande do Sul. Specimens were stored in 70% ethanol and descriptions were based on morphological characters. O material foi dissecado e seus apêndices montados em micropreparações. Os desenhos foram obtidos através de câmara clara. Os *noduli laterales* foram medidos de acordo com o método de Vandel (1962). Para representantes de *Benthana*, o exópodo do pleópodo 1 dos machos teve a taxa z:y medida segundo Araujo & Lopes (2003) e os níveis de reentrância do processo lateral de acordo com Campos-Filho *et al*. (2013). A matriz de caracteres foi baseada na literatura especializada bem como em exemplares de coleções cientificas. Os caracteres foram tratados como discretos e não ordenados; otimizações ACCTRAN/DELTRAN foram usadas para tratamento de ambiguidades. A matriz incluiu 123 terminais e 154 caracteres, com 4% de dados faltantes de e 9% inaplicáveis. Duas estratégias de busca foram adotadas, busca com pesos iguais e pesagem implícita. Para a segunda estratégia 25 valores de concavidade (*k*) foram adotados, sendo correlacionada com a análise de sensitividade. Jackknife foi adotado como medida de suporte. Taxonomia: Trinta e três especies de isópodos terrestres foram reconhecidas como pertencentes às famílias Trichoniscidae (1 spp.), Styloniscidae (2 spp.), Philosciidae (12 spp.), Scleropactidae (9 spp.), Dubioniscidae (3 spp.), Platyarthridae (4 spp.), Armadillidiidae (1 sp.), Armadillidae (3 spp.), três novos gêneros foram propostos, *Spelunconiscus* e *Xangoniscus* (Styloniscidae), e *Leonardoscia* (Philosciidae), 19 espécies foram reconhecidas como novas para a ciência: *Xangoniscus aganju* e *Spelunconiscus castroi* (Styloniscidae), *Atlantoscia ituberasensis, Atlantoscia petronioi*, *Atlantoscia sulcata*, *Benthana schmalfussi*, *Benthana guayanas*, *Benthana carijos*, *Leonardoscia hassalli*, *Metaprosekia quadriocellata* e *Metaprosekia caupe* (Philosciidae), *Amazoniscus leistikowi*, *Circoniscus buckupi* e *Circoniscus carajasensis* (Scleropactidae), *Novamundoniscus altamiraensis* (Dubioniscidae), *Trichorhina yiara*, *Trichorhina curupira* e *Trichorhina anhanguera* (Platyarthridae), e *Ctenorillo ferrarai* (Armadillidae), e quatro destas 19 espécies foram consideradas troglóbias: *Spelunconiscus castroi*, *Xangoniscus aganju*, *Leonardoscia hassalli* e *Amazoniscus leistikowi*.

Filogenia: A análise com pesos iguais resultou em 756 árvores igualmente parcimoniosas com 1.581 passos e o consenso resultou em 2.010 passos. A árvore de consenso estrito de pesos iguais muitas relações foram recuperadas dentro de uma grande politomia. A análise com pesagem implícita resultou em 35 árvores; a busca de SPR identificou a faixa de *k10* a *k15* com árvores mais similares (*k* médio = 11.5473). A família Philosciidae não teve monofilia recuperada. O gênero *Benthana* e diversos outros gêneros pertencentes à família Philosciidae amostrados se configuraram monofiléticos. As Tribos Prosekiini e Ischiosciini foram recuperadas como monofiléticas. Os gêneros *Alboscia* e *Leonardoscia* foram incluídos na tribo Prosekiini. As espécies *Prosekia albamaculata*, *P. lejeunei*, *P. rutilans* e *P. tarumae*, foram transferidas para o gênero *Androdeloscia*. Os gêneros *Nesophiloscia* e *Burmoniscus* não tiveram monofilias recuperadas. O gênero *Haloniscus* foi transferido para a família Philosciidae. O gênero *Oniscophiloscia* foi transferido para a família Balloniscidae. As famílias Halophilosciidae e Rhyscotidae apesar de terem sido recuperadas dentro de Philosciidae apresentaram alta estabilidade nas diferentes reconstruções.

Introdução

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1. Oniscidea: aspectos gerais

A Ordem Isopoda é uma das ordens da Superordem Peracarida mais diversa dentre os crustáceos, com mais de 10.300 espécies descritas e com uma ampla distribuição no globo, ocupando todos os habitats, desde regiões desérticas a mares profundos, até 7.280 metros de profundidade (exceto Antártica) (POORE & BRUCE, 2012). Dentre estas espécies, aproximadamente 60% são e marinhas ou estuarinas (POORE & BRUCE, 2012), 9% de águas continentais (WILSON, 2008), 7,7 % parasitas de outros crustáceos (WILLIAMS & BOYKO, 2012), e 40% terrestres (SCHMALFUSS, 2003; AHYONG *et al*., 2011).

A Ordem Isopoda constitui uma unidade monofilética (POORE, 2005; WILSON, 2009) e seus representantes compartilham diversas características morfológicas que definem o grupo: muda bifásica, presença de um marsupium para desenvolvimento da prole, um par de urópodos ligados ao pleotélson e pereópodos unirremes (POORE, 2005; WILSON, 2009; POORE & BRUCE, 2012). Atualmente a Ordem está dividida em 14 Subordens: Anthuridea, Asellota, Calabozoidea, Cymothoida, Flabellifera, Gnathiidea, Limnoriidea, Microcerberidae, Oniscidea, Phreatoicidea, Phroratopidea, Sphaeromatidea, Tainisopidea e Valvifera (WORMS, 2014).

A Subordem Oniscidea (isópodos terrestres) é única linhagem dentro de Crustacea que inclui representantes estritamente terrestres (BROLY *et al*., 2013), com aproximadamente 4 mil espécies descritas e encontradas nos mais variados ambientes, incluindo a zona litoral, campos, desertos, montanhas, cavernas, ninhos de formigas, bromélias e ambientes urbanos, onde muitas espécies são sinantrópicas (SCHMALFUSS, 2003; AHYONG, 2011).

Os isópodos terrestres tiveram sua monofilia confirmada através de estudos morfológicos e moleculares (SCHMALFUSS, 1974, 1989; WÄGELE, 1989; POORE, 2005;

WILSON 2009) e atualmente, cinco seções reconhecidas: Ligiidae, Tylidae, Mesoniscidae, Synocheta e Crinocheta (SCHMIDT, 2008).

As investigações sobre as diferentes maneiras pelas quais os isópodos se adaptaram à vida na terra têm apontado, basicamente, adaptações fisiológicas baseadas em modificações anatômicas e adaptações comportamentais (SCHMALFUSS, 1998; ZIMMER *et al.* 2002).

Uma das grandes modificações para a vida no ambiente terrestre está relacionada com o surgimento e desenvolvimento de estruturas especializadas para a respiração aérea, em substituição às brânquias das espécies aquáticas, os pulmões pleopodais. Esta estrutura varia desde uma simples área respiratória (Fig. 1A), devido a uma diminuição do espessamento da cutícula (LEISTIKOW & ARAUJO, 2001), a uma estrutura ramificada complexa e internalizada (Fig. 1B), que pode atingir a proximidades do coração (FERRARA *et al.*, 1994, 1996; PAOLI *et al.*, 2002).

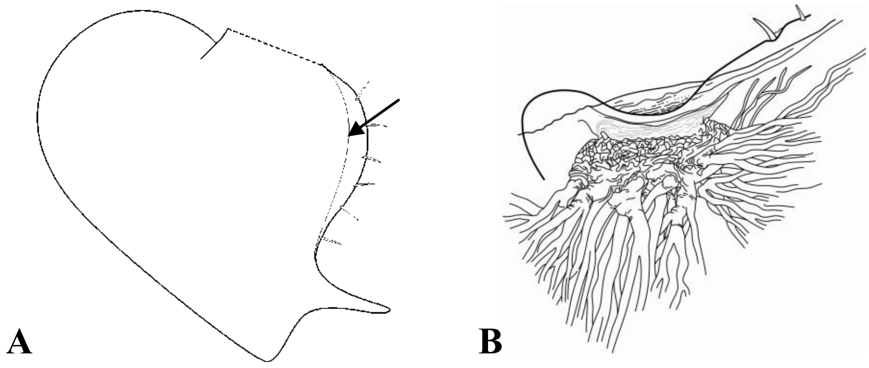

Figura 1. A. *Benthana longicornis* Verhoeff, 1941: exópodo do pleópodo 1, seta indicando área respiratória; **B**. *Periscyphis arabicus* Barnard, 1941: reconstrução de pulmão pleopodal derivado (Adaptada de FERRARA *et al.*, 1996).

Outra adaptação, característica de Peracarida, é a presença de um marsúpio para o desenvolvimento da prole (POORE & BRUCE, 2012). Em Oniscidea, o marsúpio possui uma função adicional de microaquário, que permite o desenvolvimento dos filhotes independentemente de uma fonte externa de água (Fig. 2) (HOESE, 1984; WIESER, 1984, Hoese & Janssen, 1989). O marsúpio é constituído por cinco pares de oostegitos sobrepostos, provenientes da base dos pereópodos 1-5, e sua sobreposição resulta em uma bolsa fechada onde a prole se desenvolve (Appel *et al*., 2011). Dois tipos de marsúpio são conhecidos: o do tipo anfíbio (Fig. 3A), encontrado em Ligiidae, aberto nas porções anterior e posterior, permitindo uma circulação de água absorvida por capilaridade pelo sexto e sétimo pereópodos (sistema condutor de água) ou por ação de corrente no sentido póstero-anterior; e o do tipo terrestre (Fig. 3B), encontrado nas formas mais derivadas, não havendo conexão com o sistema condutor de água ou meio externo, sendo a fêmea responsável pelo suprimento de água (Hoese, 1984).

Figura 2. *Porcellio scaber* Latreille, 1804, fêmea ovígera: imagem em estereomicroscópio ilustrando o marsúpio. Foto: Carina de Souza Appel.

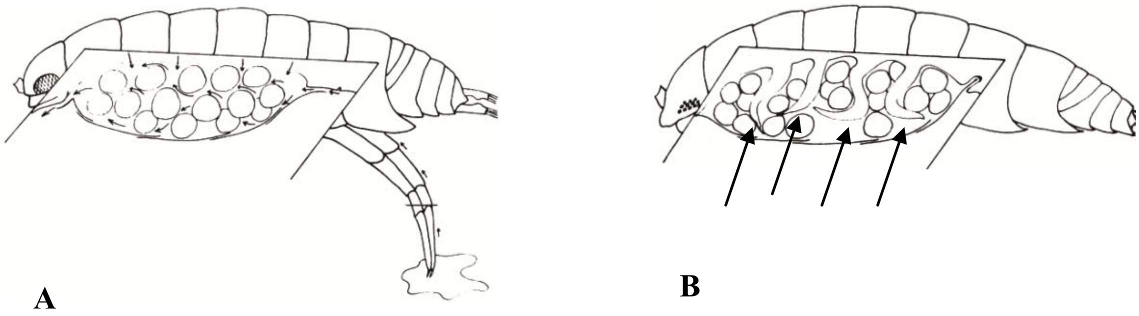

Figura 3. **A**. Marsúpio tipo anfíbio; **B**. Marsúpio tipo terrestre, setas indicando a presença de cotilédones. (Adaptadas de Hoese & Jassen, 1989).

Uma adaptação comportamental, diretamente correlacionada com aspectos morfológicos e fisiológicos, é a habilidade volvacional ou de se enrolar e formar uma bola (Fig. 4A). Esta habilidade está presente em algumas famílias de isópodos terrestres (e.g. Tylidae, Philosciidae, Scleropactidae, Eubelidae, Armadiliidae), e é em parte responsável pela resistência à perda de água (Wieser, 1963) e como estratégia de defesa contra predadores (Fig. 4B) (Schmalfuss, 1984).

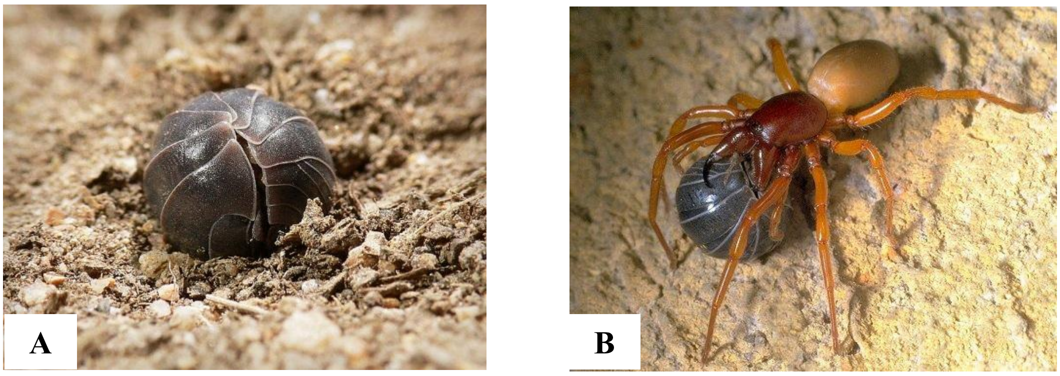

Figura 4. A. *Armadillidium vulgare* Brandt, 1833 (Foto de Wikipédia, 2014). **B.** Aranha, *Dysdera erythrina* (Walckenaer, 1802) predando isópodo terrestres *Armadillidium vulgare* (Foto de Roger Key, 2008).

Outra adaptação comportamental, importante na colonização do ambiente terrestre, é a agregação ou hábito de se agrupar (Alee, 1929). Tal comportamento é estimulado por feromônios de agregação ou de reprodução e captado por setas sensoriais específicas dispostas nas antenas e antênulas, a fim de reduzir a superfície corporal exposta sensível a transpiração, prevenindo a perda de água (Takeda, 1980, 1984; Schmalfuss, 1998). O hábito gregário também possui benefícios adicionais, relacionados com diferentes aspectos da história de vida dos isópodos terrestres, como redução do consumo de oxigênio, aumento do crescimento corporal, estímulos bióticos a reprodução e melhor acesso aos companheiros, possíveis defesas compartilhadas contra predadores, promoção da coprofagia como fonte secundária de alimento e aquisição de endossimbiontes (Broly *et al*. 2013).

A dieta dos oniscídeos consiste principalmente de matéria orgânica em decomposição como folhas, madeira, fungos e tapetes de bactérias, podendo predar alguns animais e ocasionalmente larvas de insetos, em pomares cítricos (PAOLETTI & HASSAL, 1999; ZIMMER & TOPP, 2000; FROUZ *et al.,* 2008). Assim, são considerados importantes detritívoros relacionados ao processo de decomposição, tendo sua dinâmica e densidade populacional influenciando este processo e afetando a composição física e química do solo (ZIMMER & TOPP, 2000; ZIMMER, 2005; FROUZ *et al.,* 2008). A capacidade dos oniscídeos digerirem celulose por liberação hidrolítica de glicose, tem sido observada como caráter evolutivo para a vida no ambiente terrestre, tendo dois cenários evolutivos possíveis: o primeiro, que esta habilidade foi adquirida simultaneamente com modificações fisiológicas que permitiram a colonização da terra, e o segundo, que esta habilidade foi um pré-requisito para a colonização da terra, sendo melhor suporte devido às espécies marinhas tidas como ancestrais terem a mesma capacidade. Outro fator relacionado com esta habilidade é a presença de microorganismos endosimbiontes nos hepatopâncreas e no tubo digestivo, contribuindo na digestão da celulose (ZIMMER & TOPP, 2000; ZIMMER *et al.,* 2002).

Muitos animais se alimentam de isópodos como outros artrópodos (aranhas, escorpiões, insetos) e vertebrados (anfíbios, répteis e mamíferos insetívoros) (WARBURG *et al.* 1984, HOPKIN 1991, ARAUJO, 1999). Porém, quando atacados, mostram diferentes formas de defesa, de acordo com a sua constituição corporal: (1) corredores – com pereópodos relativamente longos e fortes e tergitos planos; (2) aderentes – com corpo achatado, tergitos expandidos lateralmente e pereópodos curtos; (3) volvacionais – com tergitos convexos e capacidade de enrolar-se em bola, se ameaçados; (4) espiniformes – com espinhos tergais proeminentes; (5) rastejadoras – com tergitos providos de costelas longitudinais, pereópodos curtos e fracos; e (6) não conformistas – todas as espécies que não se encaixam dentro das cinco principais categorias (SCHMALFUSS 1984). Recentemente, duas outras características funcionais foram observadas, os saltadores (HASSALL *et al.*, 2006), registrada para um representante de *Burmoniscus* do Sabah, Malásia; e os nadadores (TAITI & XUE, 2012), com a base do maxílipodo distalmente alargada e pereópodos anteriores subquelados, presente em representantes cavernícolas e adaptados secundariamente ao ambiente aquático.

2. Filogenia

Os primeiros estudos sobre o grupo, os quais datam do final do séc. XIX e início do séc. XX, não possuíam uma abordagem filogenética e os autores utilizavam interpretações pessoais para agrupar os táxons. A partir de SCHMALFUSS (1989), Oniscidea foi configurado como um grupo monofilético (Fig. 5), com as seguintes sinapomorfias: (1) redução da primeira antena; (2) redução da maxílula; (3) alteração do tamanho do maxilípodo; e (4) presença de um complexo sistema condutor de água.

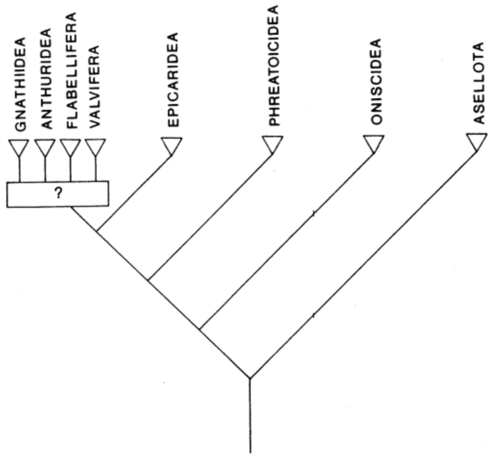

Figura 5. Cladograma apresentado por SCHMALFUSS (1989) para as relações em Isopoda.

No estudo de SCHMALFUSS (1989), Asellota foi utilizado como grupo irmão de Oniscidea por características plesiomórficas compartilhadas com *Ligia,* como por exemplo, modificação específica no artículo basal do endópodo do pleópodo 2. As infraordens Tylomorpha e Ligiamorpha foram invalidadas, por apresentarem relações parafiléticas.

Olibrinidae foi transferida de Crinocheta para Synocheta e Scyphacidae, Actaeciidae e Tylidae foram reunidas em um novo táxon, 'Scyphacoidea', e configuradas grupoirmão de Oniscoidea, por apresentar no sistema condutor de água, canais e setas especializadas alinhadas ao longo do basipodito do sétimo pereópodo. Synocheta e Crinocheta, grupos mais derivados, foram configurados gruposirmão por compartilharem a fusão da papila genital.

Simultaneamente, WÄGELE (1989) postulou Diplocheta (Ligiidae, Mesoniscidae e Tylidae) como grupo-irmão de Synocheta + Crinocheta, estes com vários ramos não resolvidos, devido aos poucos dados taxonômicos. A linhagem Crinocheta, se apresentou como mais derivada, concordando com SCHMALFUSS (1989), definida pelo desenvolvimento das áreas respiratórias dorsais nos exópodos dos pleópodos, onde a ausência indica um caráter plesiomórfico (Olibrinidae, Bathytropidae, Berytoniscidae, Halophilosciidae, Platyarthridae, Rhyscotidae e Scyphacidae). Contudo, esta ausência nas famílias Tendosphaeridae, Spelaeoniscidae, Stenoniscidae, Hekelidae, Irmaosidae e Scleropactidae, indicando uma perda secundária (SCHMIDT 2002).

Em sua análise sobre Oniscidea, ERHARD (1995, 1997, 1998) (Fig. 6), com base no exoesqueleto e musculatura do pleon, estabeleceu Ligiidae (Diplocheta) como grupoirmão de Holoverticata (Tylidae, Mesoniscidae, Synocheta e Crinocheta), onde Mesoniscidae forma um clado, Orthogonopoda, com Synocheta e Crinocheta, os quais formam o clado (Euoniscoida). Euoniscoida apresentou quatro autapomorfias, entre estas, a papila genital do macho totalmente fundida, com Synocheta possuindo fusão dos ductos genitais dentro da papila genital e Crinocheta pelos dois primeiros pares de pleópodos e a papila genital, concordando com os trabalhos de SCHMALFUSS (1989) e WILSON (1991).

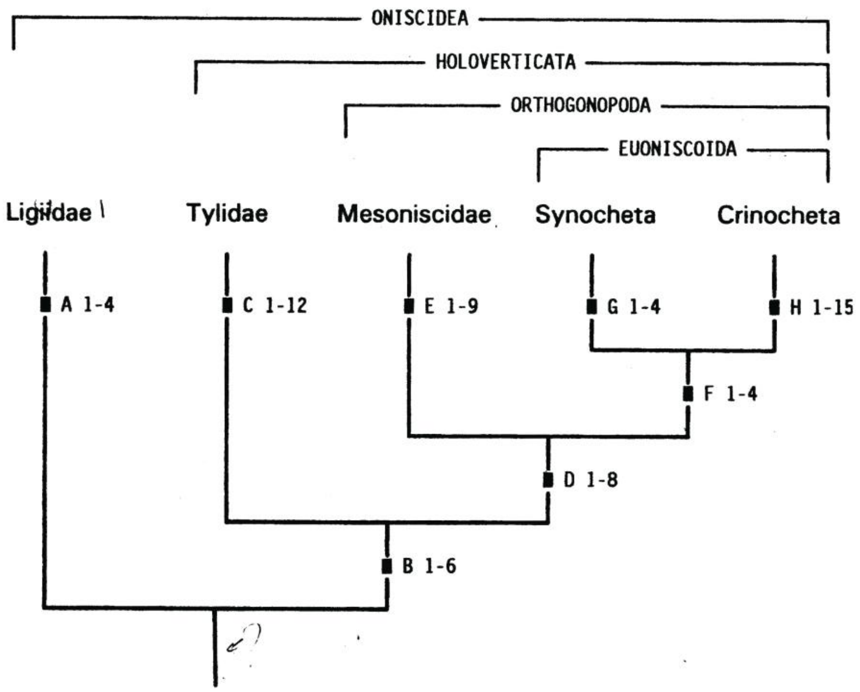

Figura 6. Cladograma apresentado por ERHARD (1998) para as relações em Oniscidea.

SCHMIDT (2002, 2003) construiu a filogenia das famílias de Crinocheta baseado em 15 autapomorfias, já registradas por WÄGELE (1989) e ERHARD (1995, 1997). Dentro do clado de Crinocheta, Philosciidae, Halophilosciidae e Scleropactidae se agruparam em uma politomia, pertencente à superfamília Oniscoidea, compartilhando 2 autapomorfias: (1) pereópodos 1-4 (ou menos) do macho com largas áreas contendo setas na face ventral do mero e carpo; e (2) cone apical da antena muito estreito, as vezes tão longo quanto o articulo flagelar apical, provido de um pequeno par de sensílios livres laterais (Fig. 7A, B).

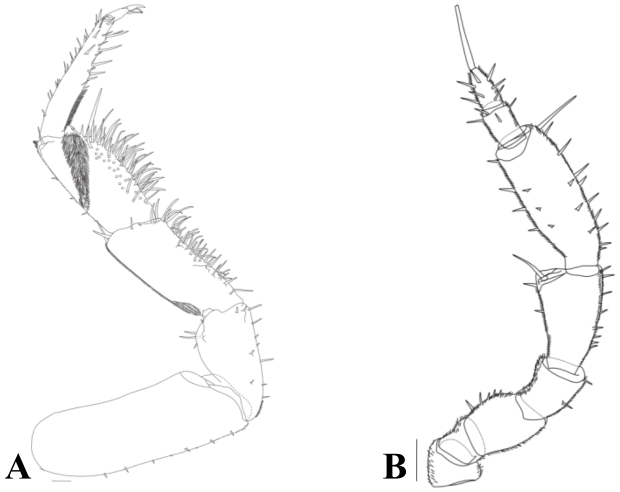

Figura 7. Ilustrações indicando os caracteres compartilhados pelo Táxon 3 de SCHMIDT (2002): *Benthana picta* (Brandt, 1833), macho: **A**. pereiópodo 1; *Circonoscus* sp., macho: **B**. antena. Escalas: 0.1mm.

Trabalhos utilizando técnicas moleculares vêm confirmando os resultados das análises morfológicas e gerando alguns conflitos, podendo indicar fatores como poucos dados, ou poucos representantes, ou ainda, caracteres homoplásticos, ou outras implicações não percebidas nas análises morfológicas e moleculares (MICHEL-SALZAT & BOUCHON, 2000; MATTERN & SCHLEGEL, 2001; WILSON, 2009).

3. Philosciidae: *Benthana* Budde-Lund, 1908[1]

Philosciidae Kinahan, 1857 abrange cerca 557 espécies distribuídas em 115 gêneros, entre estes, um gênero continua incerto (AHYONG, 2011; CAMPOS-FILHO *et al*., 2014; WORMS, 2014). A família tem ampla distribuição, ocorrendo na Austrália, sul da Ásia, África, Europa e Américas, sendo um dos mais importantes grupos de Oniscidea em habitats tropicais e zonas úmidas (LEISTIKOW, 2001).

A família Philosciidae tem sido considerada parafilética; inclui um grande número de gêneros e espécies unidos por caracteres plesiomórficos (LEISTIKOW, 2001; SCHMIDT, 2002,

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[1] Este tema foi amplamente abordado na dissertação de mestrado de Ivanklin Soares Campos Filho. Foi trazida de forma reduzida por ser considerado um tema relevante para a presente tese.

2008): corpo do tipo corredor, com superfície tergal suave e brilhosa e flagelo antenal com três artículos (LEISTIKOW, 2001a).

LEISTIKOW (2001) (Fig. 8) apresentou o agrupamento *Oxalaniscus* Leistikow, 2000 e *Quintanoscia* Leistikow, 2000 como grupo-irmão dos demais gêneros, agrupados em Nodilateralia (SCHMIDT 1999) com as sinapomorfias: (1) escudo ventral da papila genital esclerotizado (Fig. 9A), (2) flagelo da antena com três artículos e (3) órgão apical com estojo cuticular (Fig. 9B). *Benthana* Budde-Lind, 1908 encontra-se em uma politomia com Rhyscotidae e *Atlantoscia* Ferrara & Taiti, 1981, compartilhando o endito do maxílipodo sem setação nas margens (Fig. 10).

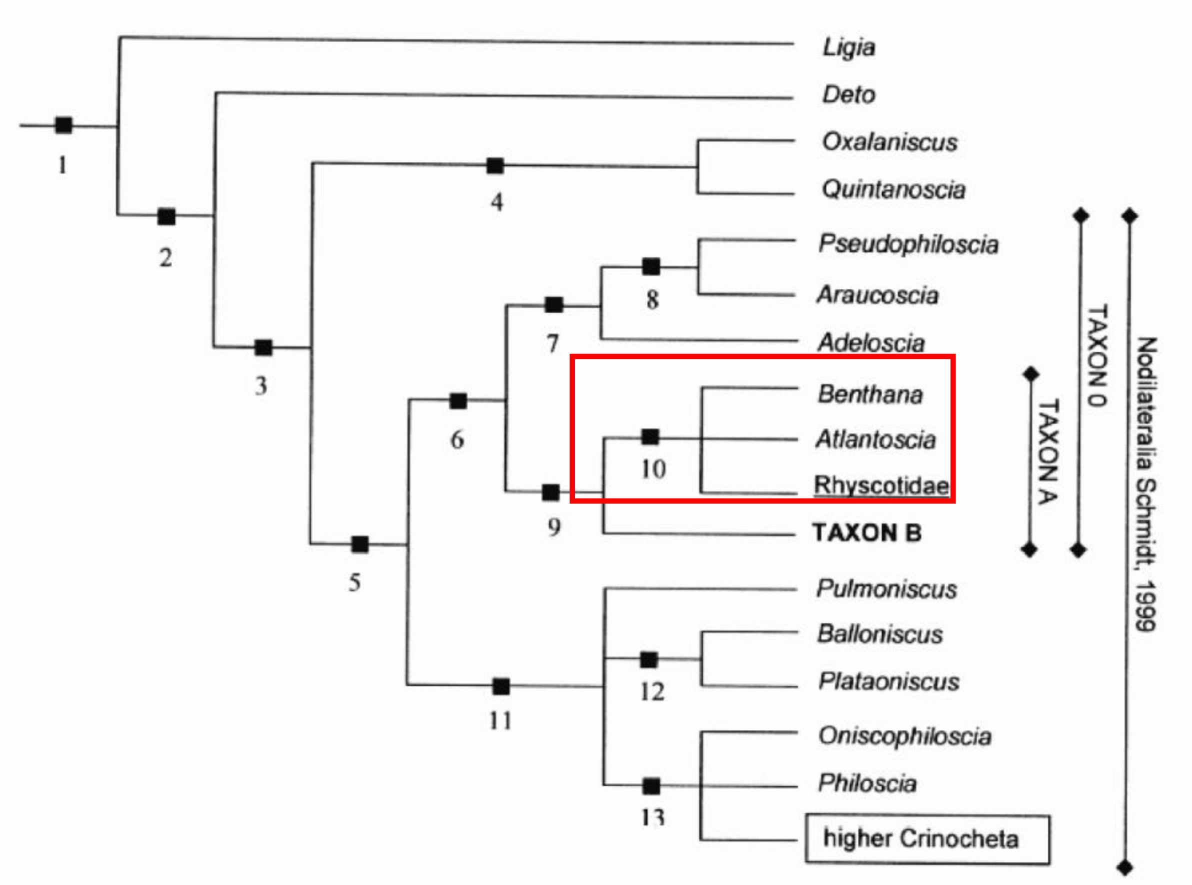

Figura 8. Dendrograma proposto por LEISTIKOW (2001).

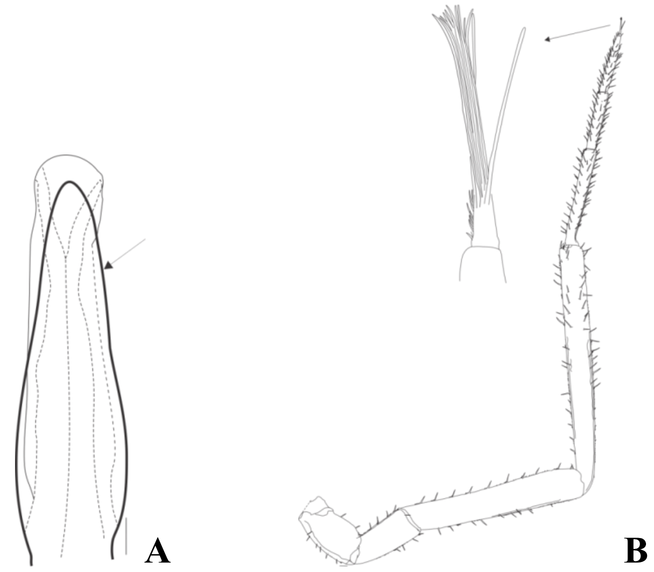

Figura 9. *Benthana picta*, macho: **A**. Papila genital com seta indicando o escudo ventral; **B**. antena, com destaque para o órgão apical. Escala: 0.1mm.

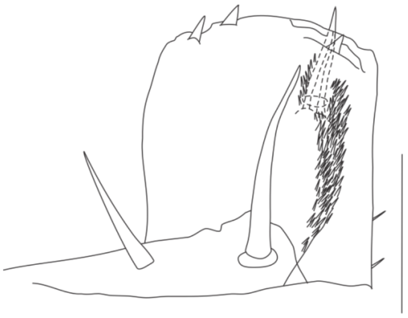

Figura 10. *Benthana picta*, macho: endito do maxílipodo (sem setação nas margens do endito). Escala: 0.1mm.

Dentro de Philosciidae, *Benthana* inclui 26 espécies, com duas espécies Chilenas, *B. angustata* (Nicolet, 1849) e *B. bilineata* (Nicolet, 1849), com posição de difícil afirmação devido à falta de exemplares-tipo, descrições e diagnoses e dados de localidade tipo; e um subgênero, *Benthanoscia* Lemos de Castro, 1958 com três espécies. Sua distribuição vai desde a porção tropical oeste e subtropical da América do Sul (LEMOS DE CASTRO, 1958a; LEISTIKOW, 2001; SCHMALFUSS, 2003; LEISTIKOW & ARAUJO, 2006).

O gênero é caracterizado por duas sinapomorfias: (1) exópodo do pleópodo 1 com formato cordiforme apresentando uma protrusão lateral dentiforme (Fig. 11A) e (2) carpo do pereópodo 1 com seta tipo mão (Fig. 11B) (LEISTIKOW, 2001).

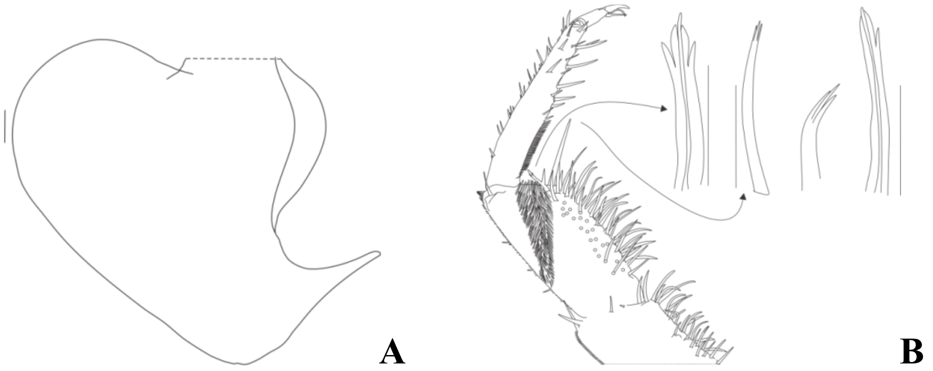

Figura 11. *Benthana picta* (Brandt, 1833), macho: **A.** exópodo do pleópodo 1: formato cordiforme e protrusão dentiforme. **B**. carpo do pereópodo 3, setas dentadas. Escalas: 0.1mm.

Sobre as contribuições para o gênero, muitos estudos apresentaram registros e descrições insuficientes (BRANDT, 1833; NICOLET, 1849; BUDDE-LUND, 1885; JACKSON, 1926; GIAMBIAGI DE CALABRESE, 1931; VAN NAME, 1936; CAMARGO, 1954).

VERHOEFF (1941) descreveu *B. longicornis* e estabeleceu *Benthana* como gênero.

GRUNER (1955) apresentou uma diagnose para o gênero com base na análise de exemplares depositados na coleção do Museu de História Natural de Berlim e coletados no Peru. O autor descreveu *B. sulcata* Gruner, 1955, para o Rio de Janeiro, *B. peruensis* Gruner, 1955, para Lima, Peru, e *B. pauper* Gruner, 1955, para Talcahuano, Valparaiso, Chile. LEMOS DE CASTRO (1958a) revisou o gênero e apresentou o primeiro histórico taxonômico para o mesmo. Criou um novo gênero, *Benthanoides*, para conter as espécies descritas por JACKSON (1926), *B. pauper*, *B. villosa*, e a espécie descrita por GRUNER (1955), *B. peruensis*. Ainda, descreveu sete novas espécies, *B. schubarti*, *B. convexa*, *B. albomarginata*, *B. werneri*, *B. santosi*, *B. longipenis* e *B. bocainensis*, e redescreveu *B. olfersii*, *B. sulcata*, *B. picta* e *B. longicornis*.

LEMOS DE CASTRO (1958b) propôs a criação do gênero *Benthanoscia*, para conter *B. longicaudata* Lemos de Castro, 1958, e elaborou uma diagnose para o gênero baseado em caracteres de forma do corpo, onde discutiu suas relações com *Benthana*, mas sendo distinta por características de coloração e forma do corpo.

ANDERSSON (1960) reilustrou *B. longicornis* e discutiu sua caracterização com base nos trabalhos de VERHOEFF (1941), GRUNER (1955) e LEMOS DE CASTRO (1958a). O autor também discutiu as relações para *B. picta*, onde discordou dos trabalhos de GRUNER (1955) e LEMOS DE CASTRO (1958a), devido à margem lateral externa do exópodo do pleópodo 1, descrita originalmente exibindo setas e ausente em seu trabalho. Também adicionou uma característica de dimorfismo sexual para o ísquio do pereópodo 7 não mencionada pelos autores anteriores. Por fim, neste trabalho *B. picta* teve registro de ocorrência para o Paraguai.

LENKO (1971) realizou o primeiro estudo de mirmercofilia, onde *B. convexa*, *B. olfersii*, *B. picta* e uma espécie não identificada de *Benthana*, foram registradas como hóspedes ocasionais em ninhos de *Camponotus rufipes* (Fabricius, 1775) (Hymenoptera: Formicidae) e *Odontomachus affinis* Guerin-Meneville, 1844 (Hymenoptera: Formicidae), devido a estes habitarem diferentes nichos ecológicos e os formigueiros apresentavam características ambientais favoráveis similares ao ambiente natural adequado.

LEMOS DE CASTRO (1985) descreveu *B. moreirai*, para São Paulo, e *B. dimorpha*, para o Espírito Santo. Neste trabalho, o autor comentou acerca do dimorfismo sexual encontrado nos ramos do urópodo.

A única espécie cavernícola para o gênero foi descrita por LIMA & SEREJO (1993), *B. iporangensis*, proveniente das cavernas Águas Quentes, Areias de Cima e Areias de Baixo, localizadas em Iporanga, SP.

ARAUJO & BUCKUP (1994), em seu estudo sobre os isópodos terrestres do Sul do Brasil, descreveram *B. taeniata* para o Rio Grande do Sul e Santa Catarina. Subsequentemente, ARAUJO *et al.* (1996) apresentaram novos registros de *B. picta* para a mesma área geográfica.

BOYKO (1997) elaborou um catálogo de isópodos depositados na coleção do Museu Americano de História Natural. Identificou *B. albomarginata*, coletada em Santa Tereza, Espírito Santo, e *Benthanoscia longicaudata* (= *B. (Benthanoscia) longicaudata)* coletada no Alto da Mosela, Petrópolis, Rio de Janeiro.

SOUZA-KURY (1998) elaborou um catálogo para as espécies de isópodo terrestres brasileiras e incluiu as 15 espécies de *Benthana* conhecidas até então.

ARAUJO & LEISTIKOW (1999) apresentaram uma diagnose mais detalhada do gênero *Benthana*, discutiram suas relações com *Ctenoscia*, *Benthanops* Barnard, 1932, *Benthanoides*, *Benthanoscia* e *Alboscia* Schultz, 1995 baseados no formato do endito externo da maxílula, a presença de dentes ctenados. Incluíram na discussão *Benthanoides*, com base no formato do exópodo do pleópodo 1 dos machos, e *Ischioscia* Verhoeff, 1928 sobre o formato das setas encontradas no carpo do pereiópodo 1. Ainda, redescreveram *B. convexa* com base em exemplar macho.

LEISTIKOW & WÄGELE (1999) elaboraram o catálogo para isópodos terrestres do Novo Mundo, registrando 19 espécies em *Benthana*, ainda incluindo *B. peruensis* e *B. villosa*.

LEISTIKOW & ARAUJO (2001), estudando a morfologia dos pulmões pleopodais de oniscídeos sul americanos, com base nas espécies *B. picta* e *Atlantoscia floridana* (Van Name, 1940), apresentaram o pulmão com uma área respiratória simples como caráter no seu estado mais primitivo (ver Fig. 1A), onde a cutícula teria sua espessura reduzida, visando facilitar a difusão do oxigênio.

ARAUJO & LOPES (2003) descreveram três novas espécies, *B. serrana*, *B. trinodulata* e *B. araucariana* e propuseram um método para caracterização do exópodo do pleópodo 1, se alargado ou alongado. Os autores também ampliaram os registros de *B. picta* e *B. taeniata* para o Rio Grande do Sul.

SCHMALFUSS (2003), em seu catálogo mundial sobre isópodos terrestres, incluiu 20 espécies de *Benthana*, ressaltando as duas espécies chilenas duvidosas descritas por NICOLET (1849).

LEISTIKOW & ARAUJO (2006), analisando a posição sistemática de *Benthanoscia*, redescreveram e ilustraram *B. taeniata* e baseados em uma exemplar fêmea, sugeriram a inclusão deste como subgênero de *Benthana*, juntamente com *B. sulcata* e *B. moreirai*, por compartilharem o dimorfismo sexual nos ramos do urópodo.

SOKOLOWICZ *et al*.,. (2008) *B. cairensis* para o Rio Grande do Sul e sugeriram a inclusão de *B. olfersii* no subgênero *Benthanoscia* por esta possuir dimorfismo sexual nos ramos do urópodo.

CAMPOS FILHO & ARAUJO (2011) descreveram uma nova espécie, *B. itaipuensis* para a região oeste do estado do Paraná.

CAMPOS-FILHO *et al*., (2013) descreveram duas novas espécies *B. schmalfussi* para o estado do Rio de Janeiro, e *B. guayanas* para o estado do Paraná. Ainda, os autores propuseram um método adicional para caracterização do processo lateral do exópodo do pleópodo 1 dos machos, os níveis de indentação.

COSTA *et al*., (2014) descreveram uma nova espécie, *B. carijos* para os estados de São Paulo e Santa Catarina, e ampliaram o registro de ocorrência para *B. cairensis*, *B. longicornis*, *B. moreirai*, *B. picta*, *B. serrana* e *B. taeniata* para a região sul do Brasil.

Recentemente CAMPOS-FILHO *et al*., (2014) no estudo sobre os isópodos terrestres cavernícolas do Brasil, registraram a ocorrência de *B. taeniata* em gruta localizada na Serra da Canastra, Minas Gerais.

Objetivos

Geral

O objetivo principal desta tese de doutorado é proceder no inventariamento de isópodos terrestres do Brasil e revisitar as relações filogenéticas da família Philosciidae com ênfase no gênero *Benthana*.

Específicos

- Descrever, quando possível, novas espécies de isópodos terrestres da fauna Brasileira, incluindo os representantes cavernícolas;
- Testa monofilia da família Philosciidae pra os representantes Neotropicais;
- Testar a monofilia do gênero *Benthana* e estabelecer uma hipótese de relações de parentesco dentre as espécies do gênero e dentre os representantes Neotropicais de Philosciiidae.

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Capítulo 1

Artigo:

Two new species of Scleropactidae (Crustacea: Isopoda: Oniscidea) from Pará, Brazil.

Autores:

Ivanklin Soares Campos-Filho e Paula Beatriz Araujo.

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil.

Periódico:

Nauplius.

Situação:

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Two new troglobitic species of Scleropactidae (Crustacea: Isopoda: Oniscidea) from Pará, Brazil

Ivanklin Soares Campos-Filho and Paula Beatriz Araujo

(ISCF, PBA) Laboratório de Carcinologia, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av Bento Gonçalves, 9500, 91510-070, Agronomia, Porto Alegre, Brasil. E-mail: (ISCF) ivanklin.filho@gmail.com; (PBA) pabearaujo@gmail.com

Abstract

The South America Scleropactidae includes 53 nominal species distributed in 14 genera. In Brazil, there are 16 species recorded in the north and southeast regions. Here, two new species of Scleropactidae are described based on material collected in caves in the state of Pará, both troglobitic and allocated in the genus *Circoniscus. Circoniscus buckupi* sp. nov. can be distinguished from its congeners by the long second article of antennal flagellum, inner endite of maxillula with a small hook-like spine at the apex, a long dactylar organ with pectinate apex conferring a knife-shaped appearance and the absence of schisma in adults. *Circoniscus carajasensis* sp. nov. can be distinguished from *Circoniscus buckupi* sp. nov. by the presence of schisma on pereionite 1 in adults and dactylar organ with a fringe appearance.

Key words: *Circoniscus*, cave, Neotropical.

Introduction

Approximately 300 troglobitic species of terrestrial isopods are recorded in 16 families (Taiti, 2004), including Scleropactidae. The South America Scleropactidae, to date, includes 53 nominal species distributed in 14 genera (Schmidt, 2007): *Amazoniscus* Lemos de Castro, 1967; *Caecopactes* Schmidt, 2007; *Circoniscus* Pearse, 1917; *Colomboniscus* Vandel, 1972; *Colomboscia* Vandel, 1972; *Globopactes* Schmidt, 2007; *Heptapactes* Schmidt, 2007; *Microsphaeroniscus* Lemos de Castro, 1984; *Neosanfilippia* Brian, 1957; *Richardsoniscus* Vandel, 1963; *Scleropactes* Budde-Lund, 1885; *Scleropactoides* Schmidt, 2007; *Sphaeroniscus* Gerstäcker, 1854 and *Spherarmadillo* Richardson, 1907. In Brazil, only the genera *Amazoniscus* (two species, one of them troglobitic), *Circoniscus* (eight species), *Heptapactes* (one species) and *Microsphaeroniscus* (five species) are recorded in the north and in the southeast regions (Souza and Lemos de Castro, 1991; Schmalfuss, 2003; Souza *et al.*, 2006; Schmidt, 2007).

The family Scleropactidae has been considered paraphyletic (Leistikow, 2001; Schmidt, 2002; 2003; 2007; 2008), sharing two synapomorphies with Halophilosciidae and Philosciidae: (1) male pereiopods 1-4 with large fields of scales on the ventral face of merus and carpus, and (2) second antenna apical cone very slender, often longer than the apical flagellar article, provided with a pair of small lateral free sensilla (Schmidt, 2003).

The genus *Circoniscus* was proposed by Pearse (1917) to include *C. gaigei*. Souza and Lemos de Castro (1991) described three new

Capítulo 2

Artigo:

A new species of *Atlantoscia* Ferrara & Taiti, 1981 (Oniscidea: Philosciidae) from Rio Grande do Sul, Brazil.

Autores:

Ivanklin Soares Campos-Filho, Suelen Goulart Contreira e Elis Regina Lopes-Leitzke.

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil.

Universidade Federal do Rio Grande, Instituto de Ciências Biológicas, Laboratório de Zoologia Geral.
Av. Itália, km 8, s/n, Vila Maria, 96203-900, Rio Grande, Rio Grande do Sul, Brasil.

Periódico:

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Situação:

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Nauplius 20(2): 137-144, 2012

A new species of *Atlantoscia* Ferrara & Taiti, 1981 (Oniscidea: Philosciidae) from Rio Grande do Sul, Brazil

Ivanklin Soares Campos-Filho, Suelen Goulart Contreira and Elis Regina Lopes-Leitzke

(ISCF) Laboratório de Carcinologia, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Agronomia, 91510-070, Porto Alegre, Rio Grande do Sul, Brazil. E-mail: ivanklin.filho@gmail.com
(SGC, ERLL) Laboratório de Zoologia Geral, Instituto de Ciências Biológicas, Universidade Federal do Rio Grande, Av. Itália, km 8, s/n, Vila Maria, 96203-900, Rio Grande, Rio Grande do Sul, Brazil. E-mails: (SGC) su_goulart@hotmail.com, (ERLL) elisleitzke@gmail.com

Abstract

To date the genus *Atlantoscia* Ferrara and Taiti, 1981 includes two species, *A. floridana* (van Name, 1940) and *A. rubromarginata* Araujo and Leistikow, 1999. The species *Atlantoscia petronioi* sp.n. is described on the basis of material collected in a coastal dune forest area of the southern Rio Grande do Sul state, Brazil. This new species is characterized by antenna with accentuate setose *sulcus* from the peduncle to the distal article of the flagellum, outer endite of maxillula with slender seta among the outer group teeth and accessory tooth, one trifid tooth in the inner group, and male pleopod 1 endopod with distal part pointed and subapically not swollen.

Key words: Neotropical, restinga, terrestrial isopods.

Introduction

The genus *Atlantoscia* Ferrara and Taiti, 1981 presently includes two species, *A. floridana* (van Name, 1940), with a distribution in coastal regions of Florida, Brazil, Argentina, and Ascension and Saint Helena islands; and *A. rubromarginata* Araujo and Leistikow, 1999, with records in Sergipe, Brazil (Araujo and Leistikow, 1999; Schmalfuss, 2003). The phylogenetic relationships of *Atlantoscia* are still obscure. Leistikow (2001) proposed a phylogeny of South American Philosciidae in which *Atlantoscia* shares a polytomy with *Benthana* Budde-Lund, 1908 and Rhyscotidae, based on the character "maxilliped endite without setation, distal margin transverse".

The present contribution describes a new species of *Atlantoscia*, based on material collected in a restinga (coastal dune forest) area of the Ilha dos Marinheiros, in the municipality of Rio Grande, state of Rio Grande do Sul, Brazil.

Material and Methods

The material examined herein is deposited in the Museu de Zoologia (MZUSP), Universidade de São Paulo, São Paulo; the Museu Nacional Rio de Janeiro (MNRJ), Rio de Janeiro; and the Coleção de Crustáceos of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brazil.

Capítulo 3

Artigo:

Review of *Atlantoscia* Ferrara & Taiti, 1981 (Crustacea: Isopoda: Oniscidea: Philosciidae) with new records and new species.

Autores:

Ivanklin Soares Campos-Filho, Jonathas Teixeira Lisboa e Paula Beatriz Araujo.

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil.

Universidade Estadual de Santa Cruz, Campus Soane Nazaré de Andrade.
Rodovia Ilhéus-Itabuna, KM 16, 45662-900 Ilhéus, Bahia, Brasil.

Periódico:

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REVIEW

ORGANISMS
DIVERSITY &
EVOLUTION

Review of *Atlantoscia* Ferrara & Taiti, 1981 (Crustacea: Isopoda: Oniscidea: Philosciidae) with new records and new species

**Ivanklin Soares Campos-Filho · Jonathas Teixeira Lisboa ·
Paula Beatriz Araujo**

Received: 20 July 2012 / Accepted: 3 January 2013 /

Abstract The neotropical genus *Atlantoscia* Ferrara & Taiti, 1981 includes three species, *A. floridana* Van Name, 1940, occurring in coastal regions of Florida (USA), Brazil, Argentina, and Ascension and Saint Helena islands, *A. rubromarginata* Araujo & Leistikow, 1999 and *A. petronioi* Campos-Filho, Contreira and Lopes-Leitzke, 2012 from Brazil. Two new species from Brazil are here described, one from the state of Bahia and one from the state of São Paulo. All the new species have respiratory areas on pleopods 1–5 exopods. The specimens were collected in areas of Atlantic Forest and in cocoa (*Theobroma cacao*) plantations. New records of *A. floridana* and *A. rubromarginata* and distribution maps are presented.

Keywords New species · Terrestrial isopods · Brazil · Neotropics

Introduction

The family Philosciidae Kinahan (1857) includes approximately 660 species placed among 114 genera (Schmalfuss 2003) widely distributed in Australia, southern Asia, Africa, Europe and the Americas. It is one of the most important groups of terrestrial isopods in tropical and wetlands habitats (Leistikow 2001). The family has been considered to be a paraphyletic assemblage owing to characters shared with Scleropactidae Verhoeff (1938) and Halophilosciidae Verhoeff (1908) (Leistikow 2001; Schmidt 2002, 2008).

The genus *Atlantoscia* Ferrara & Taiti, 1981 was erected to allocate the new species *A. alceui* from Ascension Island. This species was later considered to be a junior synonym of *A. floridana* (Van Name 1940), originally described from Winter Park, Florida, USA, and widely distributed in coastal regions of Florida (USA), Brazil, Argentina, and Ascension and St. Helena Islands (Schmalfuss 2003; Taiti and Ferrara 1991). Two more species of Atlantoscia are presently known: *A. rubromarginata* Araujo & Leitikow, 1999 from the state of Sergipe, Brazil (Araujo and Leistikow 1999) and *A. petronioi* Campos-Filho, Contreira & Lopes-Leitzke, 2012 from the state of Rio Grande do Sul, Brazil (Campos-Filho et al. 2012).

In the present contribution the taxonomy of all the species of *Atlantoscia* is revisited and two new species are described.

Systematic review

Moreira (1927) described *Philoscia paulensis* from São Paulo, Brazil, based on specimens donated by J. Schenck, but its description and illustrations are insufficient to recognize the species. Subsequently, Moreira (1931) published a French version of his previous work (Moreira 1927) adding some species and some remarks not mentioned in the original work. Van Name (1940) described *Philoscia floridana* from Florida, discussing its relationships with *Philoscia inquilina* [= *Formicascia inquilina* (Van Name 1936)]. Schultz (1964) described *Philoscia bonita* from Florida, probably the same species cited in previous articles as *Philoscia* sp. (Schultz 1961, 1963). Vandel (1963) examined Delamare Deboutteville's collection of terrestrial isopods

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I. S. Campos-Filho (✉) · P. B. Araujo
Laboratório de Carcinologia, Departamento de Zoologia,
Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves,
91510-070 Porto Alegre, Rio Grande do Sul, Brazil
e-mail: ivanklin.filho@gmail.com

J. T. Lisboa
Campus Soane Nazaré de Andrade, Universidade Estadual
de Santa Cruz, Rodovia Ilhéus-Itabuna, KM 16,
45662-900 Ilhéus, Bahia, Brazil

Capítulo 4

Artigo:

Two new species of *Benthana* Budde-Lund, 1908 (Crustacea: Isopoda: Philosciidae) from Brazil.

Autores:

Ivanklin Soares Campos-Filho, Silvana Leal Nunes Costa e Paula Beatriz Araujo.

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil.

Observações:

Trabalho com colaboração da estudante de graduação em Ciências Biológicas, Universidade Federal do Rio Grande do Sul, Porto Alegre, Silvana Leal Nunes Costa, como produção resultante da Iniciação Científica.

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Two new species of *Benthana* Budde-Lund, 1908 (Crustacea: Isopoda: Philosciidae) from Brazil

Ivanklin Soares Campos-Filho*, Silvana Leal Nunes Costa and Paula Beatriz Araujo

Laboratório de Carcinologia, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 91510-070 Porto Alegre, Rio Grande do Sul, Brazil

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Two new species of *Benthana* Budde-Lund, 1908 are described from material collected in the states of Rio de Janeiro and Paraná, Brazil. *Benthana schmalfussi* **n. sp.** is distinguished by the shape of the male pleopod 1 exopod, whereas *Benthana guayanas* **n. sp.** is distinguished by the *noduli laterales* d/c coordinates and shape of the male pleopod 1 exopod. A new method is given for defining the shape of the outer distal margin of the male pleopod 1 exopod.

http://zoobank.org/urn:lsid:zoobank.org:pub:A79EDB3B-F7AC-47A3-ADD8-DA00FFAD69CB

Keywords: neotropical; Oniscidea; terrestrial isopods; woodlice

Introduction

The family Philosciidae Kinahan, 1857, considered paraphyletic (Schmidt 2008), includes almost 600 species in 114 genera with a wide distribution (Leistikow 2001; Schmalfuss 2003). The genus *Benthana* Budde-Lund, 1908 includes 21 species (two dubious species from Chile excluded) (Schmalfuss 2003; Leistikow and Araujo 2006; Sokolowicz et al. 2008; Campos-Filho and Araujo 2011). All species are recorded from Brazil, and only one, *Benthana picta* (Brandt, 1833), is also found in Paraguay (Andersson 1960; Araujo et al. 1996; Schmalfuss 2003). In Brazil, members of *Benthana* occur from the state of Minas Gerais (19°32′S, 44°27′W) to the state of Rio Grande do Sul (29°52′S, 50°47′W). Several species, e.g. *B. picta*, are widely distributed and 12 species are known to occur only in the type-locality (including one from a cave).

The most important character in defining the genus *Benthana* is the presence of the dentiform protrusion on the male pleopod 1 exopod (see Leistikow 2001: 34). However, there is a wide variation in the shape of the exopod among the different species, but it is difficult to be defined in order to compare the species. In a first attempt to quantify the variation and erect a discrete character, which is important in a cladistic context (*sensu* Goloboff et al. 2006), Araujo and Lopes (2003: 2427) defined the shape of this appendage as elongated or rounded, based on the z:y ratio, measurement calculated by the distance between the maximum re-entrance point from the outer margin to the internal margin (**y**) in respect of central axis of the exopod (**e**), and the maximum height measured from the apex in relation to the axis (**z**).

Recently, we began a taxonomic revision of the genus with the examination of material deposited in Brazilian collections and material collected in recent expeditions in southern

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*Corresponding author. Email: ivanklin.filho@gmail.com

Capítulo 5

Artigo:

New species and new records of *Benthana* Budde-Lund, 1908 (Isopoda: Oniscidea: Philosciidae) from southern Brazil**.**

Autores:

Silvana Leal Nunes Costa, Ivanklin Soares Campos-Filho e Paula Beatriz Araujo.

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil.

Observações:

Trabalho desenvolvido pela estudante de graduação em Ciências Biológicas, Universidade Federal do Rio Grande do Sul, Porto Alegre, Silvana Leal Nunes Costa, como produção resultante da Iniciação Científica, supervisionado por Ivanklin Soares Campos Filho, ambos sob orientação da Prof. Drª Paula Beatriz de Araujo.

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NEW SPECIES AND NEW RECORDS OF *BENTHANA* BUDDE-LUND, 1908 (ISOPODA: ONISCIDEA: PHILOSCIIDAE) FROM SOUTHERN BRAZIL

SILVANA LEAL NUNES COSTA[1,2]
IVANKLIN SOARES CAMPOS-FILHO[1,3]
PAULA BEATRIZ ARAUJO[1,4]

ABSTRACT

The genus Benthana *includes 25 species with distribution in Brazil and Paraguay. In this paper we describe a new species from the state of Santa Catarina, southern Brazil, and provide new records for* Benthana cairensis *Sokolowicz, Araujo & Boelter, 2008,* Benthana longicornis *Verhoeff, 1941,* Benthana moreirai *Lemos de Castro, 1985,* Benthana picta *(Brandt, 1833),* Benthana serrana *Araujo & Lopes, 2003, and* Benthana taeniata *Araujo & Buckup, 1994.*

KEY-WORDS: Crustacea; Terrestrial isopods; Neotropical; Atlantic forest.

INTRODUCTION

The family Philosciidae Kinahan, 1857 includes almost 600 species in about 114 genera with a wide distribution (Ahyong *et al.,* 2011). The genus *Benthana* Budde-Lund, 1908 includes 25 species: 22 recorded from Brazil, one (*Benthana picta* (Brandt, 1833)) from Brazil and Paraguay, and two dubious species from Chile (*B. angustata* (Nicolet, 1849) and *B. bilineata* (Nicolet, 1849)) (Andersson 1960; Schmalfuss 2003; Leistikow & Araujo, 2006; Sokolowicz *et al.,* 2008; Campos-Filho & Araujo, 2011; Campos-Filho *et al.,* 2013). In southern Brazil eight species of *Benthana* are recorded: *B. araucariana* Araujo & Lopes, 2003, *B. guayanas* Campos-Filho, Costa & Araujo, 2013, *B. itaipuensis* Campos-Filho & Araujo, 2011, *B. longicornis* Verhoeff, 1941, *B. serrana* Araujo & Lopes, 2003, *B. taeniata* Araujo & Buckup, 1994, *B. trinodulata* Araujo & Lopes, 2003 and *B. picta* (Brandt, 1833).

The genus is characterized by the presence of the dentiform protrusion on the pleopod 1 exopod of male (Leistikow, 2001); additionally, in order to distinguish the species, two methods were proposed to analyze the appendage: the z:y ratio (see Araujo & Lopes, 2003), which classifies the exopod as elongated or rounded, and the levels of indentation (see Campos-Filho *et al.,* 2013), which categorizes the indentation of the distal margin of the dentiform protrusion as low, medium or high.

Recently we examined material collected during expeditions in southern Brazil and material deposited in the Coleção de Carcinologia, Universidade Federal do Rio Grande do Sul, Porto Alegre and Museu de Zoologia, Universidade de São Paulo (MZUSP) and identified one new species from the state of Santa Catarina, and new records for six species of *Benthana.*

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[1] Laboratório de Carcinologia, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS). Avenida Bento Gonçalves, 9.500, Agronomia, CEP 91501-970, Porto Alegre, RS, Brasil.

[2] E-mail: silvana.leal.87@gmail.com

[3] E-mail: ivanklin.filho@gmail.com

[4] E-mail: pabearaujo@gmail.com

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Capítulo 6

Artigo:

Terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Brazilian caves.

Autores:

Ivanklin Soares Campos-Filho, Maria Elina Bichuette, Eleonora Trajano, Stefano Taiti e Paula Beatriz Araujo

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil

Universidade Federal de São Carlos, Departamento de Ecologia e Biologia Evolutiva.
Rodovia Washington Luis, Km 235, 13565-905 São Carlos, São Paulo, Brasil

Universidade de São Paulo, Instituto de Biociências, Departamento de Zoologia.
Rua do Matão, trav.14, n°. 321, Cidade Universitária, 05508-090 São Paulo, Brasil

Istituto per lo Studio degli Ecosistemi, Consiglio Nazionale delle Ricerche.
Via Madonna del Piano 10, 50019 Sesto Fiorentino, Florença, Itália.

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Terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Brazilian caves

IVANKLIN SOARES CAMPOS-FILHO[1]*, PAULA BEATRIZ ARAUJO[1],
MARIA ELINA BICHUETTE[2], ELEONORA TRAJANO[3] and STEFANO TAITI[4]

[1]*Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia, Av. Bento Gonçalves, 9500, Agronomia, 91510-070 Porto Alegre, Rio Grande do Sul, Brazil*
[2]*Universidade Federal de São Carlos, Departamento de Ecologia e Biologia Evolutiva, Rodovia Washington Luis, Km 235, 13565-905 São Carlos, São Paulo, Brazil*
[3]*Universidade de São Paulo, Instituto de Biociências, Departamento de Zoologia, Rua do Matão, trav. 14, n°. 321, Cidade Universitária, 05508-090 São Paulo, Brazil*
[4]*Istituto per lo Studio degli Ecosistemi, Consiglio Nazionale delle Ricerche, Via Madonna del Piano 10, 50019 Sesto Fiorentino (Florence), Italy*

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To date, six species of terrestrial isopods were known from Brazilian caves, but only four could be classified as troglobites. This article deals with material of Oniscidea collected in many Brazilian karst caves in the states of Pará, Bahia, Minas Gerais, Mato Grosso do Sul, and São Paulo, and deposited in the collections of the Museu de Zoologia, Universidade de São Paulo, the Coleção de Carcinologia do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, and the collection of the Natural History Museum, Section of Zoology 'La Specola', Florence. Three new genera have been recognized: ***Spelunconiscus*** gen. nov. and ***Xangoniscus*** gen. nov. (Styloniscidae), and ***Leonardoscia*** gen. nov. (Philosciidae). Twenty-two species have been identified, 11 of which in the families Styloniscidae, Philosciidae, Scleropactidae, Plathyartridae, Dubioniscidae, and Armadillidae are new to science: ***Leonardoscia hassalli*** sp. nov., ***Metaprosekia quadriocellata* sp. nov.**, ***Metaprosekia caupe* sp. nov.**, ***Amazoniscus leistikowi* sp. nov.**, ***Novamundoniscus altamiraensis* sp. nov.**, ***Trichorhina yiara* sp. nov.**, ***Trichorhina curupira* sp. nov.**, and ***Ctenorillo ferrarai* sp. nov.** from Pará; ***Xangoniscus aganju* sp. nov.** from Bahia; and ***Spelunconiscus castroi* sp. nov.** and ***Trichorhina anhanguera* sp. nov.** from Minas Gerais. Four new species in the families Styloniscidae (***Spelunconiscus castroi* sp. nov.** and ***Xangoniscus aganju* sp. nov.**), Philosciidae (***Leonardoscia hassalli* sp. nov.**), and Scleropactidae (***Amazoniscus leistikowi* sp. nov.**) with highly troglomorphic traits can be considered as troglobitic, whereas all the remaining species are either troglophilic or accidentals. Brazilian caves are now under potential threat because of recent legislation, and the knowledge of the subterranean biodiversity of the country is thus of primary importance.

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ADDITIONAL KEYWORDS: cavernicolous fauna – Neotropical – new genera – new species.

INTRODUCTION

Terrestrial isopods (Oniscidea), widespread and abundant soil invertebrates, have great potential for successful colonization of subterranean habitats because of their detritivorous feeding habits and the availability of favourable substrates in caves throughout the world. Indeed, these animals have been recorded in all studied karst areas around the world as troglobites (species constituted by exclusively subterranean source populations), troglophiles (species with source populations in both hypogean and epigean habitats, with

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*Corresponding author. E-mail: ivanklin.filho@gmail.com, pabearaujo@gmail.com
ZOOBANK: urn:lsid:zoobank.org:pub:246C2229-308B-4A9B-A150-CE1D27D2EBD8.

Capítulo 7

Artigo:

Revisiting the phylogenetical relationships of Neotropical Philosciidae Kinahan, 1857 (Crustacea: Isopoda: Oniscidea) with emphasis on *Benthana* Budde-Lund, 1908: sensitivity analysis under different weighting schemes

Autores:

Ivanklin Soares Campos-Filho, Augusto Ferrari, Luiz Alexandre Campos e Paula Beatriz Araujo

Instituições:

Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia.
Av. Bento Gonçalves, 9500, Agronomia, 91501-970 Porto Alegre, RS, Brasil

Universidade Federal do Rio Grande – FURG, Instituto de Ciências Biológicas, Av. Itália, Km 8, s/n, Campus Carreiros, 96201-900, Prédio 6, Sala de Permanência 8, Rio Grande, RS, Brazil.

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Revisiting the phylogenetical relationships of Neotropical Philosciidae Kinahan, 1857 (Crustacea: Isopoda: Oniscidea) with emphasis on *Benthana* Budde-Lund, 1908: sensitivity analysis under different weighting schemes

I. S. CAMPOS-FILHO[1], A. FERRARI[2], L. A. CAMPOS[1] and PAULA BEATRIZ ARAUJO[1]

[1] Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Laboratório de Carcinologia, Av. Bento Gonçalves, 9500, Agronomia, 91510-070, Porto Alegre, Rio Grande do Sul, Brazil. E-mail: ivanklin.filho@gmail.com, pabearaujo@gmail.com, luizalexandre.campos@gmail.com.

[2] Augusto Ferrari, Universidade Federal do Rio Grande – FURG, Instituto de Ciências Biológicas, Av. Itália, Km 8, s/n, Campus Carreiros, 96201-900, Prédio 6, Sala de Permanência 8, Rio Grande, RS, Brazil. E-mail: ferrariaugusto@gmail.com.

SHORT RUNNING TITLE: Phylogenetic analysis of Neotropical Philosciidae with emphasis on *Benthana*

ABSTRACT

The suborder Oniscidea is considered monophyletic in which the family Philosciidae Kinahan, 1857 is paraphyletic. The family comprises about 114 genera worldwide distributed. The South American genus *Benthana* Budde-Lund, 1908 includes 28 species distributed in several Brazilian states, especially in Atlantic Forest areas. This work aims to revisit the phylogenetical relationships of the Neotropical Philosciidae with emphasis on *Benthana*, using a wide taxon sampling to construct the data matriz including several Philosciidae genera and other six families, Alloniscidae, Detonidae, Balloniscidae, Halophilosciidae, Rhyscotidae and Scyphacidae. The analysis is based on a matrix composed of 154 morphological characters and 123 terminal taxa. The 756 most parsimonious trees with 1581 steps were obtained with equally weghited characters. The implied weighting analysis produced 35 trees in 25 concavities regimes. The best *k* range chosen based on similarity coefficient through SPR analysis was defined in *10 – 15*. The best *k* value was defined in 11.5473. The topology presented as best value of *k* corresponds to the strict consensus of two trees recovered for the average value and are used as the hypothesis for the relationships within *Benthana* and among the Philosciidae genera. The monophyly of *Benthana* was recovered in both strategies as well as several genera within Philosciidae. The monophyletism of Philosciidae was not recovered. The relations of the Halophilosciidae and Rhyscotidae representatives were reconstructed. Lastly a taxonomic section based on the phylogenetical results provided new synonyms, new combinations and new arrangements.

ADDITIONAL KEYWORDS: Cladistics analysis – Neotropics – Implied Weighting – Halophilosciidae – Rhyscotidae.

INTRODUCTION

Terrestrial isopods represent one of the most successful evolutionary crustacean lineages adapted to terrestrial life. Along the evolutive pathway, in sense of space and time, they developed morphological, physiological and behavioural adaptations, and became independent from the aquatic environment for reproduction. To date, the group includes more than 4000 described species with a wide distribution in terrestrial habitats, from the coastal zone to arid environments (Schmalfuss, 2003; Ahyong *et al*., 2011).

Studies on the systematics of Oniscidea began in late 19th century, when the taxonomic groupings were based on personal interpretations, based especially on characters of general morphology (e.g. Jackson, 1926a; Van Name, 1936; Verhoeff, 1938). Despite the advent of cladistics, proposed by Hennig (1966), some studies on Oniscidea were still mostly based on the author's interpretations (e.g. Vandel, 1968, 1973a; Schutz, 1983, 1995). However, other studies made use of more consistent methods to infer phylogenetic relationships in Oniscidea, in particular the principles of Hennig (1966) (e.g. Schmalfuss, 1974, 1989; Wägele, 1989; Erhard, 1997; Leistikow, 2000, 2001a; Leistikow & Schmidt, 2002; Schmidt, 2002, 2008). Also, it is important to say that in these publications the data matrix is absent, thus making it difficult to repeat or re-interpret the results.

Schmalfuss (1974, 1989) and Wägele (1989) recognized Oniscidea as monophyletic taxa using morphological data. Later, studies with more comprehensive taxa sampling and employing molecular data, recovered the Oniscidea monophyly (Wilson, 2009). Within Oniscidea five sections are recognized: Ligiidae Leach, 1814, Tylidae Dana, 1854, Mesoniscidae Verhoeff, 1908, Synocheta and Crinocheta (Schmalfuss, 1989; Wägele, 1989; Erhard, 1997). Crinocheta includes the highest species richness of the group, approximately 80% of the total species, and had its phylogenetic relationships better explored (Leistikow, 2000, 2001a, 2001b; Leistikow & Schmidt, 2002; Schmidt, 2002, 2008).

The family Philosciidae Kinahan, 1857 (Crinocheta), considered paraphyletic by Schmidt (2002, 2008), includes about 115 genera distributed in Australia, southern Asia, Africa, Europe and the Americas (Ahyong *et al.*, 2011; Campos-Filho *et al.*, 2014), and constituting one of the most important Oniscidea representatives in tropical habitats (Leistikow, 2001b). The wide distribution of the family shows a remarkable morphological diversity (e.g. Vandel, 1963, 1968; Taiti & Ferrara, 1986a, 1986b), what can be related to adaptations to the kind of habitat.

Leistikow (2001b) studied the phylogenetic relationships of the Neotropical Philosciidae and found that the family is related to Halophilosciidae Verhoeef, 1908 and Scleropactidae Verhoeff, 1938. Later, in the first effort to reconstruct the phylogenetic relationships within Crinocheta, Schmidt (2002) found the same phylogenetic results as Leistikow (2001b), i.e. Philosciidae appeared again as paraphyletic closely related with Halophilosciidae and Scleropactidae, all grouped in an unresolved clade named Taxon 3 (see Schmidt, 2002). Subsequently, Schmidt (2008) combined the results of both authors and improved the resolution within Crinocheta. The result, however, still indicates paraphyly.

The Neotropical genus *Benthana* Budde-Lund, 1908 includes 28 species, four of which are placed in the subgenus *Benthanoscia* (Lemos de Castro, 1958). Nowadays, the records of *Benthana* are spread through several Brazilian states, especially in Atlantic Forest areas, as well as in Paraguay and Argentina (Campos-Filho *et al.*, submitted). Among the species of *Benthana*, *B. picta* (Brandt, 1833) and *B. taeniata* Araujo & Buckup, 1994 have a wider distribution, spanning across the known distribution of the genus, with the exception of Bahia and Espírito Santo states. *Benthana iporangensis* Lima & Serejo, 1993 is the sole troglobian species of *Benthana* recorded in the state of São Paulo. Recently, *B. taeniata* was recorded as accidental in cave environments in Minas Gerais State (Campos-Filho *et al.*, 2014).

The genus is characterized by the presence of the lateral process on pleopod 1 exopod of the male, and the dentiform protrusion, firstly observed by Verhoeff (1941) and confirmed as an autapomorphy by Leistikow (2001b). Pleopod 1 exopod of the males has a great morphological variability and is the main characteristic for species recognition and distinction (Campos-Filho *et al.*, submitted). In order to help species identification based on this appendage, two methods were proposed: the z:y ratio (see Araujo & Lopes, 2003), which classifies the exopod as elongated or rounded; and the levels of indentation (see Campos-Filho *et al.*, 2013b), which categorize the indentation of the distal margin of the dentiform protrusion as low, medium and high. Moreover, other characteristics support the recognition of species, such as: quantity of aesthetascs on the first antenna, number of denticles on proximal tooth of inner set of outer endite of first maxilla, the setation of the ventral margin of both merous and carpus of pereopods 1 to 4, the insertion levels and length of uropod branches, as well as the shape of the pleotelson (Campos-Filho *et al.*, submitted).

In the phylogenetic study of Leistikow (2001b), *Benthana* is place in an unresolved clade, named *Benthana*-group, with representatives of *Atlantoscia* Ferrara & Taiti, 1981 and *Ryscothidae* Budde-Lund, 1908. This clade has Taxon B as a sister group, the latter including the greatest diversity of taxa sampled by the author, with representatives of the Halophilosciidae and Scleropactidae. In a more comprehensive level, the *Benthana* group + Taxon B, called Taxon A, is considered as sister group to the clade that includes *Adeloscia* Vandel, 1977 (Australia) and *Pseudophiloscia* Budde-Lund, 1904 (Chile). Schmidt (2008) combined the results of Leistikow (2001b) and Schmidt (2002), and recovered the monophyly of *Benthana* (based on three species, without the type-species) and its relation as sister group to *Atlantoscia*. Unfortunately the author does not elucidate the methods for these results which make difficult its replicability.

This work aims to revisit the phylogenetical relationships of the Neotropical Philosciidae, with emphasis on *Benthana*, providing a modern view of cladistic methods. Secondarily, it provides new approaches to the relations in the Philosciidae, and tests the monophyly of several groups of the family that were sampled by us. We intended to make clear all the cladistic criteria of homology, character coding, outgroup choices and tests, support measures and optimization procedures. We also propose new characters and explore a wide range of taxa in order to provide more congruent and stable results.

MATERIAL AND METHODS

CLADISTIC CRITERIA

Topological similarity was defined as the criterion for primary homology (de Pinna, 1991; Agnarsson & Coddigton, 2008). Contingent coding (e.g. reductive coding) was defined as character coding (Pleijel, 1995; Kornet & Turner, 1999) as it has the benefit of allowing one to capture the grouping information implicit in the presence or absence of a feature, while simultaneously capturing the grouping information implicit in transformations of trait values (Brazeau, 2011). In order to clarify the character coding, the methodology of Sereno (2007) was adopted. The homoplastic condition was treated *ad hoc* by Hennig's Auxiliary Principle (see Wenzel, 1986) and ambiguous characters were analyzed individually *a posteriori* in order to make decisions about reversion or parallelism through the ACCTRAN and DELTRAN methodologies (Agnarsson & Miller, 2008). Fitch algorithm (Fitch, 1971) was chosen because the method greatly works symmetrically for unordered data sets, counting changes based on the information of the branches and closely related sister taxa to estimate the homologies, and does not take into account the states or numerical values of the nodes (see Felsenstein, 2004; Brazeau, 2011).

TAXON SAMPLING

Trying to increase the accuracy and stability of phylogenetic structure, a large taxon sampling has been conducted exploring a wide range of characters and possible combinations among them (Davis *et al*., 1993; Poe, 1998). Even though it may increase the homoplastic effect, missing data, and logical inapplicability, which can produce spurious results (Poe, 1998), such approach can have a high potential phylogenetic sign that will enable the testing of hypotheses of homology and construct more congruent phylogenetic results (Kearney, 2002; Fulton & Strobeck, 2006). The list of species, literature and distribution data used in the data matrix construction can be viewed in Table 1. The matrix includes 123 terminals with the root at *Deto marina* (Chilton, 1884), and it is available as a Mesquite extension file in the supporting material (Appendix 1) as well as online at TreeBase (ID: 16419).

CHARACTER SAMPLING

Characters were coded so as to include most of the morphological variations. Some characters were reinterpreted from Leistikow (2001b) and Schmidt (2002), but most are newly proposed. Autapomorphies were excluded to avoid the artificial inflation of the consistency index (Bryant, 1995). Missing data were coded as '?' and inapplicable characters as '-'. One behavioural character concerning the functional eco-morphological categories *sensu* Schmalfuss (1984) was included. The data matrix was built using Mesquite v.3.01 (build 658) (Maddison & Maddison, 2014) and evaluated *a priori* on Winclada (Nixon, 2002) to track and exclude uninformative characters.

PARSIMONY ANALYSES

Searches for the most parsimonious trees were conducted using two character-weighting methods. First, the characters were equally weighted. As suggested to multistate data matrices by Goloboff & Farris (2001), Ratch Parsimony (Nixon, 1999) was applied, thus exploring a wide range of most parsimonious trees into the tree space, increasing accuracy and reducing search time. Also, Ratch Parsimony was combined with Tree-Fusion and Tree Drifting algorithms in order to increase congruence (Goloboff, 1999, 2008). To reduce spurious results, the collapsing rule for zero-length branches was instructed to the software chosen to construct the phylogenetic inference (Brazeau, 2001). The search was conducted with New Technology Search in TNT v.1.1 (Goloboff *et al.*, 2003a, 2008a), with random seed = 1, and 100 hits (replications). The search parameters were conducted following Paladini *et al.* (2014), the Ratch algorithm has a perturbation phase in 25 for up-weighting and 5 for down-weighting, 20 interations, Tree-Fusion with 100 rounds, and Tree Drifting with 20 cycles.

The second search criterion was implemented by implied weighting (IW) (Goloboff, 1993, 1997; Goloboff *et al*., 2008b), minimizing the homoplastic effect (Nixon & Carpenter, 2012). In the implied weighting search, characters are analysed with weights inversely proportional to their level of homoplasy, determining how strong characters will be weighted against homoplasy (Goloboff, 1993). The IW search was done according to Mirande (2009), through the 'Implied.run' script (Appendix S2); the script attributes 25 values for *k* (concavity). The trees obtained through the IW analysis were compared by SPR distance (Goloboff, 2008), indicating the most similar trees groups in order to recognize the best *k* value (see also Teixeira *et al*., 2014; Paladini *et al*. 2014).

SENSITIVITY ANALYSIS AND STABILITY

According to Wheeler (2012) "There is no method to determine the 'true' values of the necessary parameters via observation in nature and no way to choose one set over another purely on their optimality values" (page 199).

Sensitivity analysis (Wheeler, 1995) was undertaken in order to assess clade support and stability of tree topologies and character congruence under different weighting regimes, trying to recognize where these different regimes support the most congruent trees, thus reducing the arbitrariness to interpret taxa and character evolution hypotheses (Donoghue & Ackerly, 1996; Simmons *et al*., 2008; Giribet & Wheeler, 2007). Weighting strategies have a high degree of descriptive efficiency and maximize the explanatory power of all lines of evidence, recognizing which weight regimes are incongruent among the data (Frost *et al*., 2001; Giribet, 2003; Simmons *et al*., 2008; Wheeler, 2012). Robustness can be defined as the stability of phylogenetic hypothesis to variations in phylogenetic inference procedures, including weighting regimes, and are often assessed via measures of node support, but rarely as the variation resulting from alternative tree constructing methodologies (Davis *et al*., 1993; Giribet, 2003; Egan, 2006; Simmons *et al*., 2008; Giribet & Wheeler, 2007).

The method proposed by Mirande (2009) for estimating the best *k* values according to the amount of homoplasy in an analysis of equal weights was interpreted here as a criterion for sensitivity analysis, and thereby evaluates how the *k* parameter influences the results, and determines in which *k* values the nodes are recovered (i.e. a measure of robustness). The choice for the best topological hypotheses generated from the 25 different implied weighting schemes was based on nodal stability, because all *k* parameters are independent of tree-construction (Giribet, 2003), and it could be defined as clade robustness (Monod & Prendini, 2014). Phylogenetic sensitivity analysis and tree comparison were represented graphically with Navajo boxes (Wheller, 2012) in 5 x 5 axes, representing the *k* range from 0 to 24 with highlights for most similar tree groups. In addition, clades found with equal weight search (EW) were also represented.

SUPPORT

Evaluation of group support is important in order to know how well supported are the groups obtained based on different perturbations, what favours the appearance of a given branch in a most-parsimonious topology (Egan, 2006; Freudenstein & Davis, 2010; Koupuchian & Ramírez, 2010).

Often, a support measure is mistaken as robustness of a phylogenetic hypothesis (Giribet, 2003), or considered as the relative explanatory power of a phylogenetic hypothesis; however, degree of support does not indicate the accuracy of the tree, because each measure describes different aspects of precision by assessing stability to perturbations relative to the data (Carpenter, 1992; Kluge, 1998; Shi *et al*., 2010). Nevertheless, quantifying and comparing support measures helps to discern implausible groups and improves phylogenetic structure (Judd, 1998; Kluge, 1998; Brower, 2006; Egan, 2006; Grant & Kluge, 2008).

Jackknife resampling (Efron, 1977; Lanyon, 1985) is used to estimate the variance of confidence intervals of branches, assessing the effect of taxon/character deletions on tree reconstruction, and detecting internal inconsistencies based in the comparison of pseudoreplications with the original phylogeny, plotting different scores on both poorly and strongly supported nodes (Lapoint *et al.*, 1994; Mort *et al.*, 2000). Sometimes jackknifing produces illogical results under weights or influence cost, because the asymmetry involved during the resampling results in values that may, or may not, correspond to the expected assessment of tree support, leading to wrong conclusions (Wheeler, 2010; Shi *et al.*, 2010).

As suggested by Goloboff *et al.* (2003b), in order to reduce spurious groups, the Jacknife symmetrical resampling (SR) was assumed as a support measure, because it eliminates the asymmetry caused by weights or costs, and gives each character equal probabilities in increasing and decreasing weights or costs. Additionally, the Jacknife Group present/Contradicted (GC) frequencies were used, in order to compare the frequency of supported groups with absolute jackknife resampling with the frequency of contradicted groups produced by different rearrangements. Jacknifing parameters were constructed with 5000 replicates, with 100 additional replicates and 10 trees saved per replicate with SPR+TBR swapping, performed with Traditional Search in TNT.

TAXONOMIC DECISIONS

Taxonomic and systematic assumptions based in phylogenetic studies involve congruence of results (Kluge, 1998). Cladograms can be interpreted as the result of taxonomic congruence and character interaction through the assessment of the hypothesis of homology (Davis *et al.*, 1993; Kluge, 1998). Sometimes taxa relationships can be difficult to interpret, because the interaction of characters might result in a complex scenario, since one character or a group of characters may influence these relations differently on cladograms (Davis *et al.*, 1993; Pol & Escapa, 2009). However, corroboration and refutation of hypotheses are simply alternative results from homology testing (Kluge, 1998).

In this study, systematic decisions were based on nodal stability through sensitivity analyses; nodal support values increased reliability in the assessment of phylogenetic inference. Moreover, morphology evidence was used to support our assumptions.

RESULTS

CHARACTER LIST

(Figures 1-5)

The data matrix includes 154 characters distributed in 13 groups:

(1) one character for the morphoecological category (*sensu* Schmalfuss, 1984);

(2) one character for the disposition of sexes;

(3) 6 characters for the pereon and related structures;

(4) 2 characters for the pleon and neopleurae;

(5) 3 characters for the pleotelson;

(6) 11 characters for the cephalothorax, including eyes;

(7) 10 characters for the first antennae;

(8) 5 characters for antennae;

(9) 36 characters for the buccal pieces;

(10) 35 characters for the pereopods, including dactylus;

(11) 2 characters for the genital papilla;

(12) 38 characters for pleopods 1, 2, 4 and 5;

(13) and, 4 characters for the uropods.

In addition, two of the four uropod characters were coded relative to the length of uropod branches regarding males and females, in order to test the subgenus *Benthanoscia* proposed by Leistikow & Araujo (2006).

The characters and their respective states were described according to the methodology proposed by Sereno (2007): locator, variable, variable qualifier and character state; for some characters the variable qualifier and/or the state of the character were suppressed when only the locator and variable were needed to describe the conditions of the character. For each character group, we provide a preliminary elucidation about its morphological aspects, its use in phylogenetic studies, the codification, and how they were constructed in this study.

MORPHOECOLOGICAL CATEGORY

001. *Ecological category*: (0) clinger, (1) runner, (2) roller, (3) creeper, (4) swimmer.

Character adapted from Schmidt (2002); and based on Schmalfuss (1989) Hassal *et al.* (2006), and Taiti & Xue (2012).

Based on morphology and behaviour, Schmalfuss (1984) presented six eco-morphological categories isopods have developed to reduce predator pressure and adapt to the abiotic factors of a micro-habitat: runners, clingers, rollers, creepers, spiny, and non conformists. Additionally, Hassall *et al.* (2006) observed a jumper isopod belonging to the genus *Burmoniscus* Collinge, 1914 from Sabah, Malaysia. There is also the swimmer, a recent category proposed by Taiti & Xue (2012). Despite the existence of eight eco-morphological categories, the spinyforms, non-conformists and jumpers were suppressed in the discussion here, since no terminal taxa were classified as belonging to these categories.

Runners (Schmalfuss, 1984; Schmitd, 2002) are characterized by a smooth dorsal surface, pleon narrower than pereon, and slender and elongated appendages (antennae and pereopods). This runner-habitus favours escapes at high speed and is found in species of Ligiidae, Olibrinidae Vandel, 1973, in several Philosciidae, Agnaridae Schmidt, 2003 and Porcellionidae Brandt, 1831 (Schmidt, 2002). Considering that Ligiidae is the most basal taxon in Oniscidea, and Olibrinidae is the most basal taxon in Crinocheta, the running-habitus is considered as a plesiomorphic condition for the Crinochetan lineages (see also Schmidt, 2002; Wilson, 2009).

Clingers (Schmalfuss, 1984; Schmidt, 2002) have broad tergites and enlarged epimera, forming a closed outline of tergal parts. When threatened, the species in this category remain motionless, holding tightly onto the substrate, and concealing the short pereopods under the tergites. The clinger-habitus seems to have evolved several times and is found in species of Ligiidae, Detonidae Budde-Lund, 1906, Philosciidae, Platyarthridae Vandel, 1946, Balloniscidae Vandel, 1963, Bathytropidae Vandel, 1952, Oniscidae Latreille, 1804, Trachelipodidae Strouhal, 1953, and Porcellionidae (Schmidt, 2002).

Rollers have evolved a body structure that rolls up into a ball, having the tergites and sternites disposed in a semi-circular cross-section, resulting in a completely circular cross-section when they roll up, preventing the access of predators to ventral parts and reducing water lost (Edney & Spencer, 1955; Edney, 1968; Schmalfuss, 1984; Appel *et al.*, 2011). The dorsal surface of roller animals can be smooth, as in runners (e.g. *Ethelum americanum* (Dollfus, 1896), Eubelidae Budde-Lund, 1904 (see Schmidt, 2003:101))), or tuberculate, as typical in clingers (e.g. *Armadilloniscus* Uljanin, 1875, Detonidae (see Schmidt, 2002:337)). The morphological modifications are quite large and evolved differently among and within families, since this functional category is commonly found in Scleropactidae, Pudeoniscidae Lemos de Castro, 1973, Tendosphaeridae Verhoeff, 1930, Eubelidae, Armadillidae Brandt, 1831 and Armadillidiidae Brandt, 1833, given the high probability of convergency or parallelism of different structures related with the conglobation ability and incongruence with other characters (see discussion on Schmidt, 2002:286-287).

Swimmer isopods, or amphibians, evolved secondarily from the terrestrial condition (Taiti & Xue, 2012), having a body shape that may classify them as runners or clingers, since these animals need a dynamic morphology to swim or hold their body onto the substrate. Vandel (1970) was the first to observe this condition in *Mexiconiscus laevis* (Rioja, 1956) (Trichoniscidae Sars, 1899). Recently, Taiti & Xue (2012) observed two species of *Trogloniscus* Taiti & Xue, 2012 having this specialized form, and related some morphological modifications such as the enlarged distal part of the maxillipedal basis and subchelate anterior male pereopod used to attach the body to the substrate or in reproduction (Taiti & Xue, 2012). This functional category is recognized in Synocheta, in few species of Trichoniscidae and one species of Styloniscidae (*Thailandoniscus annae* Dalens, 1989), all occurring in subterranean waters (see Taiti & Xue, 2012). In this study, the swimmer-habitus is present in species of *Haloniscus* Chilton, 1920.

When dealing with ecomorphological categories, Schmidt (2002) proposed a character with nine states, relating it to the runner, clinger and roller (conglobating) habitus. Two states were independently directed to the runner and clinger habitus, while the remaining states were coded to the roller habitus. By analysing the states proposed for the roller habitus, it is possible to observe distinct morphological characteristics together, as with the exoantennal conglobating ability correlated with the presence of a dorsal sulcus on cephalothoraxo allowing for the antennae to fit; such characteristics could have been treated as independent conditions, since that the dorsal sulcus only occurs in the Tendosphaeridae, while the exoantennal roller conditions is found in several groups.

In the present study, the morphological categories of runners and clingers were coded as independent conditions. Even though the roller condition is strongly present in more derived groups of Crinocheta, this characteristic was observed in species of *Armadilloniscus* (Detonidae), and is assumed as independent. Also, the functional categories of creepers and swimmers were coded in such a way that would allow for a first try of tracing the evolutionary routes of these habitus.

DISPOSITION OF SEXES

002. *Sexual character:* (0) separate sexes, (1) hermaphrodites.

Character coded as in Schmidt (2002).

In general, Oniscidea have separate sexes, exhibiting the typical morphological modifications on the first two pairs of male pleopods. Hermaphroditism occurs in Rhyscotidae, and adults without male genitalia are an exception.

Schmidt (2002) proposed one character to code this characteristic, which was also assumed here.

PEREON

003. *Pereon, tergo, dorsal surface*: (0) tuberculate; (1) smooth.

Character adapted from Leistikow (2001b) and Schmidt (2002).

004. *Pereon, tergo, tricorn-setae*: (0) not discernible; (1) discernible.

New character.

005. *Pereon, tergo, tricorn-setae, shape*: (0) piliform scale-seta; (1) fan-shaped scale-seta; (2) tricorn-seta; (3) arrow-shaped scale-seta; (4) crow-shape scale-seta; (5) double fringe-shaped.

Character adapted from Leistikow (2001b). New states proposed: 0, 3, and 4.

The dorsal surface of Oniscidea can exhibit distinct appearances, smooth as in Ligiidae, most Synocheta and several Crinocheta (e.g. *Atlantoscia* and *Benthana*), or tuberculate as in *Deto* Guérin-Meneville, 1836 and *Armadilloniscus*. Usually the dorsum bears small setae, named tricorn-setae or scale-seta (Holdich, 1984; Hadley & Hendricks, 1985). Since tricorn-setae are present on the cuticle of marine Isopods, the presence in Oniscidea can be regarded as plesiomorphic (Leistikow, 2001b; Schmidt, 2002). Occasionally tricorn-setae are not discernible, probably due to poor conservation conditions or manipulation, and sometimes not mentioned or illustrated in descriptions.

Tricorn-setae have mechanical and/or chemical functions in response to environmental conditions and micro-habitats (Schmalfuss, 1978; Holdich, 1984; Hadley & Hendricks, 1985) and may vary in shape. The elongated piliform scale-seta has a stout basis and slender distal portion. It is usually found in species that live in micro-habitats, like leaf-litter, that require mechanical responses to avoid the compression of the substrate. Piliform scale-setae are typical in *Androdeloscia* Leistikow, 1999, *Atlantoscia*, *Benthana* and *Colombophiloscia* Leistikow, 2000. The short tricorn-setae are typical in endogenous species confined to narrow spaces between the sediment particles where the permanent contact with the substrate allows for mobility, an increase in mechanical and chemical responses, and prevents the adherence of small particles or water to the cuticle. Fan-shaped tricorn-seta is found in *Caraiboscia* Vandel, 1968 and *Leonardoscia* Campos-Filho, Araujo & Taiti, 2014, the arrow-shape is found in *Littorophiloscia* Hatch, 1947, the peculiar crow-shape in *Pentoniscus vargasae* Leistikow, 1998, and the modified double fringe-shape in *Colombophiloscia alticola* Vandel, 1968 and *Haloniscus tomentosus* Taiti & Humpreys, 2001.

Leistikow (2001b) coded different textures of the dorsal surface based on the density of tricorn-setae. Differently, Schmidt (2002) proposed both characteristics as independent conditions, which is the interpretation used here.

PEREON: *NODULI LATERALES*

006. *Pereon, epimera, noduli laterales*: (0) not discernible; (1) discernible.

Character adapted from Leistikow (2001b) and Schmidt (2002).

007. *Pereon, epimera 1-6, nodulus lateralis, quantity*: (0) one on each side; (1) two on each side side.

New character.

008. *Pereon, epimera 7, noduli laterales, quantity*: (0) one; (1) two; (2) three; (3) four.

New character.

Among the dorsal tricorn-setae, a pair or more usually located on epimera 1-7 can be distinguished by shape and size, and are called *noduli laterales* (Verhoeff, 1907). They have a well-marked insertion on the dorsal surface of epimera, a stout basis, and a slender and elongated distal portion, such as found in several species of Philosciidae. As other dorsal tricorn-setae, the *noduli laterales* have mechanical and chemical sensorial response, directly correlated with the morphoecological category (Schmalfuss, 1984) and micro-habitat: long *noduli* are typical of runners and animals which live in leaf-litter, short *noduli* are commonly found in endogenous species, and a reduced form is found in rollers, e.g. species of Scleropactidae and Armadiliidae (see Schmidt, 2007; Taiti & Gruber, 2010).

The absence of *noduli laterales* is regarded as plesiomorphic, since this structure is not observed in marine isopods, in Ligidae, Tylidae, Mesoniscidae, Synocheta and basal families of Crinocheta (Olibrinidae, Detonidae, Scyphacidae Dana, 1854, and Alloniscidae Schmidt, 2003) (Leistikow, 2001b; Scmidt, 2002).

Vandel (1962) observed that the pereonites vary in length (c), the same happening for the position of the *noduli laterales* across the epimeron relative to the lateral (d) and proximal (b) margins. Moreover, the author observed that the ratio between epimera length and *noduli* position produced a x,y Cartesian Plan, closely resembling the original position at dorsum of the pereonites. This coordinates are often disposed in a diagram box in taxonomic studies or plotted directly in the illustrations of the dorsal habitus. This diagram box is useful in taxonomy, because of its stability within a given genus.

In Oniscidea the coordinates of the *noduli laterales* can exhibit similar patterns across different groups; for instance, the *nodulus* of the fourth pereonite inserted from the lateral margin, a common pattern in *Androdeloscia* and *Atlantoscia*, or the *noduli* of second and fourth pereonites shifted from lateral margin giving a ‘M’ appearance to the diagram box, a pattern found in *Afrophiloscia* Budde-Lund, 1908, *Burmoniscus* and *Renelloscia* Vandel, 1970.

The pattern of two *noduli* in one epimeron occurs in species of *Aphiloscia* Budde-Lund, 1908, *Tropiscia* Vandel, 1968, *Arcangeloscia* Schmalfuss & Ferrara, 1978, *Pagana* Budde-Lund, 1908 (Trachelipodidae), and some species of Armadillidae (Stefano Taiti, pers. comm.). Furthermore, only epimeron 7 may have two *noduli*, with the remaining epimera bearing one *nodulus*, as in *Benthana araucariana* and some species of *Hawaiioscia* Schultz, 1973. Epimera carrying several *noduli* is an uncommon condition present in species of *Halophiloscia* Verhoeff, 1908, with the exception of *Halophiloscia hirsuta* Verhoeff, 1928.

Leistikow (2001b) proposed four characters for the epimera and their dorsal structures. Among these characters, 2 were directed to the *noduli laterales*. For the first character, the author coded the absence/presence of *noduli* and the shape variation of the tricorn-setae when the *noduli* are absent; while the second character concerned the length of the *noduli* and their quantity and position relative to the lateral margins of epimera 2 and 4. When analysing the first character, the author treated the tricorn-setae and the *noduli laterales* as homologous, when in fact these are distinct structures. Since the homology of the *noduli laterales* has not been confirmed yet, their visual similarity to the tricorn-setae can lead to erroneous interpretations of hypothesis of homology. The groundpattern of Oniscidea lacks *noduli laterales* (Schmidt, 2002); here this condition is observed in Detonidae and Alloniscidae. On that matter, Leistikow (2001b) questions whether *noduli laterales* are primarily absent in several Philosciidae (e.g. *Ischioscia* Verhoeff, 1928) or if they are reduced, considering that the condition may have resulted from a reversion or modification (reduction) due to selective pressure. In the second character it is possible to observe a joint codification of independent characteristics, as with the quantity of *noduli* in each epimeron and the latter's position relative to the lateral margin; yet, it is noticeable that the author codified the relative displacement relative to the lateral margins of epimera 2 and 4 by correlating it with the patterns found in the genera. Independently, the conditions of absence or presence of the *noduli* may have been coded independently from the subsequente evolution of the character, and each epimeron may have been independently coded relative to the position of the *nodulus*, allowing the variation contained in the remaining epimera.

In this study, no particular position of the *noduli laterales* on the epimera was coded in order to respect the assumed homology criteria and to avoid misinterpretations or the overlap of conditions. This decision is based on the fact that several species exhibit one *nodulus* per epimera, and few species bear two or more, hampering the inclusion of the codification of the position of each *nodulus*. Taking the discussion on the evolution of the *noduli* into account, as well as the possible homology of this structure with tricorn-setae (Leistikow, 2001b), the terminology used to describe the absent and present states was avoided, specially because most of the data was recovered from literature, which sometimes is not mentioned in the descriptions and/or the illustrations, and due to the long preservation in ethanol. Within Philosciidae, species of *Ischioscia* and *Pentoniscus* Richardson, 1913 do not present *noduli laterales* (see Leistikow, 1998c, 2001g). This is considered as a secondary lost (Leistikow, 2001b; Schmidt, 2002).

PLEON

009. *Pleon, neopleura 3-5, diameter, development aspect relative to pereonite 7*: (0) progressive reduction appearance (1) reduced appearance.

Character adapted from Leistikow (2001b).

010. *Pleon, neopleura 3, development relative to neopleurae 4 and 5*: (0) reaching the midline of fourth neopleura, but not reaching the anterior margin of fifth neopleura; (1) reaching the anterior margin of fifth neopleura; (2) not reaching the midline of fourth neopleura.

New character.

In Oniscidea, the pleonites have a lateral development, the neopleurae, which may be clearly visible in dorsal view as with the broad neopleurae found in Tylidae, some Synocheta and several

Crinocheta; visible but not so developed as in Ligiidae, some Synocheta and several Crinocheta; or faintly visible or reduced as in Mesoniscidae and some Crinocheta (Gruner, 1966; Schmidt, 2003, 2007). According to Leistikow (2001), the body habitus depends on the extent of the coxal plates and neopleurae such as the plesiomorphic conditions present in the runner-type as in Ligiidae, which has both small neopleurae and coxal plates. Clingers and rollers, on the other hand, have enlarged epimera and neopleurae, resulting in a continuous appearance with the pereon or an ovate outline to the body, closing the gap between the fifth pleonite and pleotelson.

The character here was coded using the breadth of neuropleurae 3-5 in comparison with pereonite 7. Furthermore, it is assumed as an independent condition neopleurae 3-5 amplitude in relation to each other.

PLEOTELSON

011. *Pleotelson, lateral margins, shape*: (0) shallow-angled, almost 180°; (1) obtuse, more than 90°; (2) right-angled, equal or close to 90°.

New character.

012. *Pleotelson, distal margin, angle*: (0) obtuse, more than 90°; (1) right-angled, equal or close to 90°; (2) acute, less than 90°.

New character.

013. *Pleotelson, distal margin, shape appearance*: (0) rounded; (1) triangular.

Character adapted from Leistikow (2001b).

The telson in Oniscidea, as in all Isopoda, is the result of a fusion of the sixth pleonite with the telson, hence named pleotelson (Roman & Dalens, 1999). Generally the pleotelson of terrestrial isopods is triangular, but may vary in shape, as the square shape of Ligiidae and Tylidae, and the hourglass shape of the Armadiliidae. The pleotelson is useful in taxonomy due to shape stability within a genus. It may also bear particular features on the dorsum or on the outline of lateral and distal margins.

Leistikow (2001b) coded the outline of lateral and distal margins of the pleotelson, but the states were overlapped. In this study, variations of lateral and distal margins were treated as independent conditions based on the angles they form.

CEPHALOTHORAX

014. *Cephalothorax, nodulus lateralis*: (0) absent; (1) present.

New character.

015. *Cephalothorax, dorsal view, postfronts*: (0) not inflated; (1) inflated.

New character.

016. *Cephalothorax, dorsal view, lateral lobes*: (0) developed; (1) not developed.

Character adapted from Leistikow (2001b) and Schmidt (2002).

017. *Cephalothorax, frontal view, ommatidea field*: (0) projected, surpassing the outer margins of cephalon; (1) not projected.

Character adapted from Leistikow (2001b).

018. *Cephalothorax, frontal view, profrons shape appearance*: (0) projected subtriangular lobe inverted; (1) not projected.

Character adapted from Leistikow (2001b).

019. *Cephalothorax, linea supraantenalis*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Schmidt (2002).

020. *Cephalothorax, frontal view, linea supraantennalis, shape*: (0) straight; (1) bent downwards; (2) bent upwards.

New character.

021. *Cephalothorax, linea frontalis*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Scmhidt (2002).

022. *Cephalothorax, postfrons, lamina frontalis*: (0) absent; (1) present

New character.

023. *Cephalothorax, ommatidea*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Schmidt (2002).

024. *Cephalothorax, ommatidea number*: (0) 1; (1) 3; (2) 4; (3) 6; (4) 7; (5) 8; (6) 9; (7) 10; (8) 11; (9) 12; (10) 13; (11) 14; (12) 15; (13) 16; (14) 17; (15) 18; (16) 19; (17) 20; (18) 21; (19) 22; (20) 23; (21) 24; (22) 25; (23) 26; (24) 27; (25) 28; (26) 29; (27) 30.

Character adapted from Leistikow (2001b) and Schmidt (2002).

In arthropods, thoracic segments, and sometimes the appendages associated with them (such as crustacean's maxillipeds), were incorporated into the cephalothorax (e.g. Budd, 2002, 2008; Edgecomb, 2010). The morphology of the cephalothorax in Oniscidea was firstly studied by Jackson (1926b, 1928b), who introduced specific terminology to describe its different structures. Later, Vandel (1943, 1952) recognized and illustrated the *lamina frontalis* a small distinct area on the *postfrons* of *Ischioscia variegata* (Dollfus, 1893) inserted between the antennulae. Moreover, Schmalfuss (1974) and Erhard (1995, 1996, 1997) heavily studied the morphological and muscular structures of the isopod cephalothorax and made use of such data for phylogenetic studies.

Sometimes, the cephalothorax of the isopods presents modifications in its general shape. As an example is the flattened shape with protruding compound eyes, as seen in *Ischioscia* (Leistikow, 1999a).

As discussed above, the *noduli laterales* are located on epimera 1-7. Nevertheless, a very interesting feature is the presence of a pair of *nodulus lateralis* on the cephalothorax of species of *Aphiloscia*. This would be a remnant of the first segment of the pereon fused with the cephalon. This character, although present only in *Aphiloscia*, was coded here, in order to trace and discuss the evolution of *noduli laterales*, and also because this taxa has a very interesting variation of the pleopodal lungs (see discussion on pleopods section).

In dorsal view, the cephalothorax may present two prominent subquadrangular lateral structures, the lateral lobes. These are not developed in the plesiomorphic condition, such as in Ligiidae, Tylidae, and Mesoniscidae. The lateral lobes can accommodate the second antennae and are found in some Synocheta and in most Crinocheta (Schmidt, 2002).

The compound eyes are located dorsolaterally and are composed of several ommatidia as in *Ligia* spp., with up to 4,000 very small units (Schmalfuss, 1998; Schmidt 2002), few ommatidia, sometimes reduced to a single ommatidium as in *Trichorhina tomentosa* (Budde-Lund, 1893), or completely absent as in *Colombophiloscia alticola* or in endogenous or caverniculous species (Campos-Filho *et al.*, 2014). The eyes in Oniscidea are adapted to the effect of light and dark (Tuurala & Lehtinen, 1967; Edwards, 1969; Nemanic, 1977). With the exception of eyeless species, the taxa used in this study exhibited a wide variation in the number of ommatidia. For instance, four ommatidia in species of *Metaprosekia* Leistikow, 2000 and *Leonardoscia hassallii* Campos-Filho, Araujo & Taiti, 2014, and more than twenty in *Benthana* spp. In most families, the area where the eyes are disposed does not surpass the lateral margin of the cephalothorax, the exceptions being Detonidae, Philosciidae, Rhyscotidae and Armadillidae (Jackson, 1928; Schmidt, 2002, 2003).

Among the Philosciidae, this expanded area is clearly observable in *Ischioscia* and is commonly used as the first character for the recognition of the genus (see Lestikow, 1999a, 2000; Leistikow & Schmidt, 2002). However, the projected or expanded conditions of the eyes area was also observed for *Aphiloscia*, *Formicascia* Leistikow, 2001, *Mirtana* Leistikow, 1997, *Parischioscia* Lemos de Castro, 1967, *Pentoniscus*, *Portoricoscia* Leistikow, 1996, *Quintanoscia* Leistikow, 2000, *Roraimoscia* Leistikow, 2001, *Tropiscia* and *Xiphoniscus* Vandel, 1968.

Six structures can be recognized in the cephalothorax (seen in frontal view): *linea frontalis*, *profrons*, linea supraantennales, *postfrons*, clypeus and labrum (Jackson, 1928). The latter two were not discussed since they were not coded herein. The frontal line is absent in maritime isopods and is considered as a synapomorphy of Oniscidea; however, it can also be absent in some lineages of Crinocheta, such as in *Alloniscus oahuensis* Budde-Lund, 1885 (Alloniscidae), *Plataoniscus borellii* (Dollfus, 1897) (Balloniscidae) and *Benthana* (Philosciidae). The *linea supraantennalis* connects the superior portions of the antennal sockets, delimiting the profrons below and the postfrons above (Jackson, 1928). In the medium portion the *linea supraantennalis* may vary, directed downward as in *Atlantoscia* spp. and *Benthana* spp. or, upward as in species of *Rhyscotus* Budde-Lund, 1885 (Jackson, 1928, Campos-Filho *et al.*, 2013; Schmalfuss & Ferrara, 1978). In Crinocheta, the presence of the two lines is considered as a plesiomorphic condition, since both lines are present in Ligiidae (Schmidt, 2002).

The *postfrons* is a subrectangular transversal *lamina* placed between the *linea supraantennalis* and the clypeus, with the two pairs of antennae laterally inserted. In Rhyscotidae, the *postfrons* exhibits an interesting characteristic: a large anterior bulbous protuberance (Schmalfuss & Ferrar, 1978) that confers an inflated appearance to the *postfrons* and that can be observed in dorsal view. This large bulbous protuberance is bounded upwardly by the *linea supraantennalis*, and is diagnostic for the family (Schmidt, 2003). Between antennary sockets, some terrestrial isopods can have a mesial quadrangular lobe used to accommodate the second pair of antennae, not found in species of Ligiidae, Tylidae, Mesoniscidae, and Synocheta. In this study this quadratic lobe was found in some species of Detonidae and Philosciidae.

Leistikow (2001b) and Schmidt (2002) coded the development condition of the lateral lobes by correlating it with the absence/presence of the *linea frontalis* and *linea supraantennalis*. The absence/presence condition of the eyes was correlated with the number of ommatidea, which was proposed in interval groups.

In this study, morphological variations of the cephalothorax, including aspects of shape, lateral lobes development, prominent eyes area surpassing the outer margin of cephalothorax, absence/presence of *noduli laterales*, *linea frontalis*, *linea supraantennalis* and *lamina frontalis,* pattern of the *linea supraantennalis*, and *postfrons* developed in a bulbous lobe, were atomized into distinct and independent characters. Also, the number of ommatidea was assumed as an independent condition, in order to reduce arbitrariness and to avoid *a priori* ordering.

FIRST ANTENNA

025. *First antenna, articles, number*: (0) 3-jointed; (1) 2-jointed.

Character used by Schmidt (2002).

026. *First antenna, second article, setae*: (0) absent; (1) present.

Character adapted from Schmidt (2002).

027. *First antenna, distal article, proportion, width relative to length:* (0) as wide as long; (1) longer than wide;

New character.

028. *First antenna, distal article, flagelar seta:* (0) absent; (1) present.

New character.

029. *First antenna, distal article, setae*: (0) absent; (1) present.

New character.

030. *First antenna, third article, aestetascs position*: (0) occurring on lateral region and apex; restricted to apex.

Character adapted from Leistikow (2001b) and Schmidt (2002).

031. *First antenna, third article, lateral tufts position*: (0) continuous to apex set; (1) not continuous to apex set.

New character.

032. *First antenna, third article, set of lateral tufts*: (0) 1 set; (1) 2 sets; (2) 3 sets; (3) 4 sets; (4) 5 sets; (5) 6 sets; (6) 7 sets.

New character.

033. *First antenna, distal article, distal aesthetascs, number*: (0) three; (1) two; (2) one.

New character.

034. *First antenna, distal article, apical tip*: (0) absent; (1) present.

New character.

The first antenna of Oniscidea is composed of three articles, and this condition is considered a synapomorphy of the suborder (Schmalfuss, 1989). The first antenna may have a cylindrical or conical shape (Haug & Altner, 1984), where each article is moved by one muscle, and bears particular cylindric-shaped sensorial structures, the aesthetascs (Risler, 1977, 1978; Haug & Altner, 1984; Pynnönen, 1985; Hoese, 1989; Schmalfuss, 1998). Aesthetascs occur on the distal article, where they may appear as an apical tuft (e.g. *Rhyscotus sphaerocephalus* Budde-Lund, 1893), in a sequence of lateral rows plus an apical set (e. g. species of *Atlantoscia* and *Benthana*), disposed into two tufts independently arranged, one lateral and one apical (e.g. *Androdeloscia* and *Metaprosekia*), or as a continuous set arranged lateral-apically (e.g. *Yaerikima* Leistikow, 2001).

The first antenna may have two reductions, first the reduction of three to two articles by the fusion of the distal and middle articles, as Ligiidae, Mesoniscidae, Detonidae, Spelaeoniscidae Vandel, 1948, and Stenoniscidae, Verhoeff, 1908; and second, the reduction to one artice by the fusion of all articles, observed in Tylidae (Schmidt, 2002). Additionally, one or two plumose setae on middle article may be present as in *Armadilloniscus*, usually absent in Crinocheta (Schmidt, 2002).

Leistikow (2001b) coded the shape of first antenna correlated with the relative length of articles and the aesthetascs arrangement independently. Schmidt (2002) correlated the number of articles with absence/presence of aesthetascs, articles shape, and the absence/presence of plumose seta on middle article.

In this study morphological variations of the first antenna, including aspects of number or articles, shape, absence/presence of setae, flagelar seta and apical tip on second and distal articles, and aesthetascs arrangement and number, were atomized into distinct and independent characters.

SECOND ANTENNA

035. *Second antenna, flagellum, articles, number*: (0) 4; (1) 3; (2) 2.

Character used by Schmidt (2002).

036. *Second antenna, flagellum, apical organ, length relative to the third article of flagellum*: (0) subequal; (1) short, half or less from the length of third article; (2) long, more then 1 and 1/3 of the length of third article.

New character.

037. *Second atenna, flagellum, apical organ, sensilla*: (0) free sensilla; (1) enclosed by commom sheat.

Character adapted from Leistikow (2001b) and Schmidt (2002).

038. *Second antenna, apical organ, free sensilla, length relative to the base of the apical organ*: (0) > 3 times of the base diameter; (1) < 3 times of the base diameter.

Character adapted from Leistikow (2001b) and Schmidt (2002).

039. *Second antenna, apical organ, free sensila, insertion relative to the length of the apical organ*: (0) basal half part; (1) apical half part.

New character.

The Oniscidean second antenna groundpattern is a six-article peduncle and a multijointed flagellum, covered with tricorn-setae. In Oniscidea the first peduncle article is completely fused with cephalothorax and no more discernible. The flagellum has a tendency to diminish the number of articles: Ligiidae with 9-28 articles, Synocheta bearing 3-12 articles, and most Crinocheta with maximum of 4 articles, but usually having 3- or 2-jointed flagellum, with exception of *Olibrinus* Budde-Lund, 1913 with 7-18 articles. Moreover, an extreme flagellum reduction to a single article can be found in species of *Helleria* Ebner, 1968 (Schmalfuss, 1998, Leistikow, 2001b). The reduction of a multijointed condition to 4 articles, and from 4 to 3 articles probably occurred only once, but the 3-jointed evolved to 2-jointed several times by convergence, since both flagellar conditions occurs in Scleropactidae, Armadillidae and Eubelidae (Schmidt, 2002).

As first antenna, the second antennae are equipped with sensorial aesthetascs, located on the second and/or third flagellum articles (Alexander, 1977; Pynnönen, 1985; Hoese, 1989), with effective sense to be used for predation avoidance, intraespecific communication, and search for food and suitable microhabitats (Schmalfuss, 1998).

The apex of the antennal flagellum is equipped with a complex sensorial apparatus, the apical organ. The apical organ bears a tuft of long and thin setae, giving a hairy aspect to this structure. Setae on the apical organ may be freely arranged, as in Ligiidae, Tylidae, Mesoniscidae, Synocheta, and some Crinocheta (Olibrinidae and Detonidate), or enclosed by a commom sheath as in most Crinocheta. Laterally, two long sensory hair articulated with the central body arise from the apical organ, named free-sensilla. In general the free-sensilla are not discernible in species which display the apical organ with free sensory setae (Alexander, 1977; Seelinger, 1977). In relation to the distal article of flagellum, the apical organ can be shorter than the distal article bearing long free-sensilla (e. g. *Benthana* and *Plataoniscus* Leistikow, 2001), or longer than distal article bearing small free-sensilla (e. g. *Roraimoscia* and *Yaerikima*).

Leistikow (2001b) and Schmidt (2002) coded characters for the flagellum and apical organ, and considered them as independent. A sole aspect needs to be questioned, as both authors coded the size relation between the apical organ and the distal segment of the flagellum with the length of lateral sensilos, when they could have been dealt as independent. Still, both authors considered the multiarticulate flagellum as a plesiomorphic condition.

Here the morphological variations of second antenna were proposed regarding flagellum. They were re-coded based on both mentioned authors, including aspects of number of articles, apical organ length relative to the distal article of the flagellum, and free sensila insertion and length, were atomized into distinct and independent characters.

BUCCAL PIECES

040. *Mandibles, molar penicil, shape*: (0) simple; (1) dichotomized.

Characther adapted from Leistikow (2001b).

041. *Mandibles, molar penicil dichotomized, branches number*: (0) 3; (1) 4; (2) 5; (3) 6; (4) 7; (5) 8; (6) 9; (7) 10; (8) 11; (9) 12; (10) 13; (11) 14; (12) 15; (13) 17; (14) 20; (15) 28.

Characther adapted from Leistikow (2001b).

042. Mandibles, lacinia mobilis: (0) present; (1) absent.

Character adapted from Leistikow (2001b) and Schmidt (2002).

Mandibles in Oniscidea are asymmetrical and without palp In general the left mandible is stronger and the right mandible is ornamented. Na porção proximal interna das duas mandíbulas, existe uma developed area with a large masticatory surface, the pars molaris, and, distally have a strong sclerotized area, the incisor process. At the base of the incisor process there is a movable appendage of the mandibular gnathal edge, the *lacinia mobilis*, a synapomorphy of Peracarida (Boas, 1883; Hansen, 1893; Richter *et al.*, 2002; Richter & Kornicker, 2006). In Oniscidea, the *lacinia mobilis* when present, occurs on the left mandible. It is more visible in Ligiidae, Synocheta, and basal Crinocheta (Detonidae). On the other hand it is occasionally fused with an adjacent hairy lobe on the right mandible in the remaining Crinocheta (Schmidt, 2002). The pars molaris in Crinocheta is replaced by a molar penicil and consists in a tuft of one or several hairy setae inserted between pars molaris and incisor process (Richter *et al.*, 2002; Schmidt, 2002); probably the molar penicil is not homologous to the pars molaris, but with some setae inserted near of pars molaris (Richter *et al.*, 2002; Schmidt, 2002; Edgecomb *et al.*, 2003; Schmalfuss, 2005; Richter & Kornicker, 2006). In Philosciidae the molar penicil may vary from a single branch as found in species of *Colombophiloscia*, or composed of several and distinct branches as found in species of *Androdeslocia*, *Benthana,* and *Ischioscia*.

Leistikow (2001b) presented two characters for the mandibullae. In the first character, the author assumed a homology between the *pars molaris* and the molar penicil, because the coded the presence of the molar penicil instead of the structure of the *pars molaris*, the the presence of the *pars molaris* as a plesiomorphic condition, when Ligiidae was taken into account. In the second character, the amount of branches in the penicil molar was coded in value intervals, overlapping the simple condition with the dichotomized one.

Here the presence of *lacinia mobilis* was also assumed as plesiomorphic condition, regarding Detonidae. The morphological variations of of the molar penicil, including the conditions simple and dichotomized were treated as independent characters; in addition, for the dichotomized condition, the amount of branches was independently coded, thus reducing the arbitrariness of *a priori* codification and ordering.

043. *First maxilla, inner endite, apical tip*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Schmidt (2002).

044. *First maxilla, inner endite, penicils appearance:* (0) well developed; (1) not well developed.

New character.

045. *First maxilla, outer endite, outer margin, pilose length relative to outer margin:* (0) reaching the basal median portion (1) all margin; (2) reaching the first outer tooth.

New character.

046. *First maxilla, outer endite, teeth, composition*: (0) 5+6; (1) 4+4; (2) 4+5; (3) 4+6; (4) 4+7; (5) 4+3.

Character adapted from Leistikow (2001b) and Schmidt (2002).

047. *First maxilla, outer endite, inner set appearance*: (0) simple; (1) cleft; (2) pectinate.

Character adapted from Leistikow (2001b) and Schmidt (2002).

048. *First maxilla, outer endite, rostral seta*: (0) present; (1) absent.

Character adapted from Schmidt (2002).

049. *First maxilla, outer endite, rostral set appearance*: (0) hairy; (1) simple.

New character.

050. *First maxilla, outer endite, rostral seta, development*: (0) well developed; (1) reduced.

New character.

051. *First maxilla, outer endite, slender stalk between outer and inner set*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Schmidt (2002).

052. *First maxilla*, *outer endite, subapical tubercule*: (0) absent; (1) present.

Character adapted from Schmidt (2002).

The first maxilla or maxillule in Oniscidea is composed of two endites, the first one located on inner portion with slender shape and bearing apical hairy penicils; and the second, the outer endite, positioned adjacently to the inner endite, shows the outer lateral margin straight or sinuous bearing setae, and apically with strong teeth.

In the groundpattern of Oniscidea, the inner endite bears three hairy apical penicils, as found in Ligiidae, Tylidae, Synocheta, and only two in most Crinocheta; often in the place of the third penicil there is an acute angle or a lobe; and, rarely the inner endite bears 4-8 penicils, e. g. *Xeroporcellio* Strouhal, 1954 (Scleropactidae) (Ferrara & Taiti, 1983b; Schmalfuss, 1986, 1995; Leistikow, 2001b; Schmidt, 2002).

The outer endite is appicaly composed of two sets of teeth. The outer set bears 4-5 sclerotized teeth with simple apex, and the inner set bears of 3-7 slender teeth which may vary on apex, as the simple teeth of *Quintanoscia* and *Oxalaniscus* Leistikow, 2000, the cleft teeth of *Atlantoscia* and *Littorophiloscia*, and pectinate teeth of *Benthana* and *Ctenoscia* Verhoeff, 1928. Additionally, the outer endite can exhibit other four characteristics: the slender seta, when present is located between outer and inner teeth sets, has gustatory functions and is considered homologous to the hirsute setae founded in Synocheta; the triangular lobe, considered a vestigial tooth in the reduction of 5 to 4 teeth condition; the rostral setae, located subapically to the inner teeth set, resembling a tooth in size and shape, but usually reduced and simple; and the last one, the outer margin bearing thick long setae, which may be half or completely fitted in length (Leistikow, 2001b; Schmidt, 2002).

Leistikow (2001b) proposed three characters for the first maxilla; two of these are recoded and discussed here. In the first character, the author coded the number of penicils of the internal endite correlated with the presence of the apical tip; whereas in the second character, the composition of the inner teeth set of the external endite was correlated with the presence of a slender seta.

Schmidt (2002) proposed five characters for the fisrt maxilla, two of them considered here. One is seen on the inner endite, where the absence/presence and the number of apical hairy penicils were correlated with each other and the other is seen on the outer endite, where the teeth composition on inner set was correlated with absence/presence of slender seta, triangular lobe and rostral seta.

In this estudy, the presence of apical tip was assumed as condition to modify the shape of the distal margin of inner endite, because all taxa sampled which have an apical tip exhibited the distal margin straight. As Leistikow (2001b) and Schmidt (2002), the distal appearance of the inner teeth set of the external endite, the presence of particular structures of the slender seta, subapical tubercle and rostral seta on the outer endite, were coded as independent conditions.

053. *Maxilla, lobes, distal width relative to the base*: (0) subequal; (1) wider.

New character.

054. *Maxilla, lobes, appearance*: (0) distinct; (1) undistinct.

New character.

055. *Maxilla, outer lobe, distal margin shape*: (0) rounded; (1) sinuous; (2) pointed.

Character adapted from Schmidt (2002).

056. *Maxilla, outer lobe, width relative to inner lobe*: (0) wider; (1) narrow; (2) subequal.

Character adapted from Leistikow (2001b) and Schmidt (2002).

The second maxilla in Oniscidea is composed of two endites, fused from basis (sympodite) over most of their length, and is distally separated in two distinct lobes covered with sensilla on inner lobe and small setae on outer lober, the trichiform setae (Leistikow, 2001b; Schmidt, 2002). The second maxilla has clear sutures between lobes, always bearing 2 or 3 sensilla, and the sympodite suture are lacking; sometimes, for non taxonomists, these sutures are difficult to recognize, as in *Deto* and *Littorophiloscia*. The plesiomorphic condition in Oniscidea has the inner and outer lobe fused, resembling an unique structure, as found in *Ligia*. Most Crinocheta have the outer lobe broader and with clear sutures (Leistikow, 2001b), but Olibrinidae, the most basal lineages of Crinocheta (Schmidt, 2002), shows this condition.

Leistikow (2001b) proposed three independent states for the width relation between lobes in second maxilla. Schmidt (2002) proposed two characters, one relative to width relation between lobes correlated with shape of the distal margin of outer lobe, and the other to the distribution of sensilla on inner lobe. Schmidt (2002), no entanto, poderia ter codificado independentemente as características do primeiro caráter.

Here, the majority of sampled taxa presented the bilobed and covered in setae conditions; only a few taxa had a condition of difficult distinction among the lobes, even though it still did not configure a fusion between them. The reduction of the internal lobe, relative to the external lobe, was assumed as a derived condition *sensu* Leistikow (2001b).

057. *Maxilliped, base, outer distal margin, relative to the first palp article*: (0) not overpassing; (1) overpasssing.

New character.

058. *Maxilliped, base, outer distal margin, fringe*: (0) absent; (1) present.

New character.

059. *Maxilliped, palp, first article, appearance*: (0) simple; (1) hairy.

Character adapted from Leistikow (2001b) and Schmidt (2002).

060. *Maxilliped, palp, first article, setae, length*: (0) subequal; (1) distinct, one seta with 1/2 or less of the length of another seta.

Character adapted from Leistikow (2001b).

061. *Maxilliped, palp, distal articles, setae tufts regions*: (0) not restrict to the distal portions; (1) restrict to the distal portions; (2) reduced, weakly distinct.

Character adapted from Leistikow (2001b) and Schmidt (2002).

062. *Maxilliped, endite, length, relative to palp*: (0) subequal; (1) reaching 2/3 to the palp lenth.

New character.

063. *Maxilliped, endite, setose fields*: (0) discernible; (1) not discernible.

Character adapted from Leistikow (2001b) and Schmidt (2002).

064. *Maxilliped, endite, setose fields, distribution*: (0) along the endite; (1) a partir da porção medial até a margem distal; (2) restricted to the distal margin.

Character adapted from Schmidt (2002).

065. *Maxilliped, endite, inner distal margin, angle*: (0) obtuse, > 90°; right-angled, 90°.

New character.

066. *Maxilliped, endite, outer distal margin, angle*: (0) obtuse, > 90°; right-angled, 90°.

New character.

067. *Maxilliped, endite, distal margin, tubercule*: (0) absent; (1) present.

New character.

068. *Maxilliped, endite, distal margin, setae*: (0) absent; (1) present.

New character.

069. *Maxilliped, endite, sulcus marginalis, ornamentation*: (0) present; (1) absent.

New character.

070. *Maxilliped, endite, type of ornamentation on sulcus marginalis*: (0) penicil; (1) seta tooth-like.

Character adapted from Leistikow (2001b) and Schmidt (2002).

071. *Maxilliped, endite, inner distal margin, appearance*: (0) straight; (1) depressed.

Character adapted from Schmidt (2002).

072. *Maxilliped, endite, inner distal margin, tip*: (0) absent; (1) present.

Character adapted from Leistikow (2001b).

073. *Maxilliped, endite, outer distal margin, tip*: (0) absent; (1) present.

Character adapted from Schmidt (2002).

074. *Maxilliped, endite, medial seta*: (0) not discernible; (1) discernible.

New character.

075. *Maxilliped, endite, medial seta length, relative to the distal margin of the endite*: (0) short, not reaching the distal margin; (1) medium, reaching the distal margin; (2) long, surpassing the distal margin.

New character.

The maxilliped in Onsicidea consists of a small coxa, a large basis with an endite, a jointed palp and an endite. The maxilliped, as the other buccal appendages, is usefull in taxonomy, and exhibits a quite large morphological variation, usefull in phylogenetic studies (Leistikow, 2000c, 2001a, 2001b; Schmidt, 2002).

The maxilliped basis is commonly rectangular, bears sparsed tricorn-setae and has a ventral-lateral-groove, the so-called *sulcus lateralis* (Leistikow, 2001b). The lateral margins of maxilliped basis are often parallels, exhibiting subequal width, relative to the apical region (endite plus palp), but mostly broader in several taxa of Crinocheta. Furthermore, the basis can have distinct shapes, due to variations on proximal and distal portions, as the subtriangular basis of Rhyscotidae, or as an inverted subtriangular basis in *Trogloniscus*, a swimmer Oniscidea. Adjacent to the lateral margin of the base of the maxilipod we find a groove filled with thin setae, known as *sulcus lateralis* and that can stretch up to the endite.

The endite is a rectangular structure with a strong seta at the mediam portion and is rostrally covered with thin and small setae. The medial seta may vary in length when compared with the distal margin, shorter as in *Rhyscotus* and *Tropiscia*, or reaching the distal margin as in *Littorophiloscia*, or overpassing the distal margin as in *Benthana* and *Pulmoniscus* Leistikow, 2001. The endite have distally tubercles, as those found in *Aphiloscia* or, hook-like seate as in *Atlantoscia* and *Benthana*. The distal corners of endite may have a small tip as in *Floridoscia* Schultz & Johnson, 1984 and *Pseudophiloscia* Budde-Lund, 1904, or only in one of them, on inner corner as in *Balloniscus* Budde-Lund, 1908 and *Pulmoniscus*, or on outer corner as in *Adeloscia* Vandel, 1977 and *Androdeloscia*. The distal margin of endite may have a straight shaped as in *Deto*, or rounded as in *Atlantoscia*. Distally, the *sulcus lateralis* in Crinocheta may feature a smaller furrowed sensorial seta, known as knob-like penicil, or it can be absent, as in *Atlantoscia*. Taking into account this seta only *Benthana* exibits the modification from knob-like to tooth-like (Campos-Fiho *et al.*, 2014).

The maxilliped palp in the Oniscidea groundpatten is composed of five articles partially fused and bearing setal tufts on the edges of the articles; this condition is still present in Ligiidae, Synocheta and Olibrinidae, but reduced to 3 articles in most Crinocheta (Leistikow, 2001b; Schmidt, 2002). The basal article of palp usually bears 2 subequal or distinct in length setae, only one seta as in Scleropactidae or no seta at all; furthermore, this basal article may lacks setae, or have a reduction to one seta (Schmid, 2007). Nevertheless, all these conditions may vary in *Ligia*, which could be interpreted as convergent or parallel evolution within Crinocheta (Schmidt, 2002).

Leistikow (2001b) proposed five characters to describe the maxilliped, three of them with distinct characteristics coded together. The fisrt one is the basis width relative to the distal portion (palp plus endite) correlated with the absence/presence of thin setae on outer distal margin; the second is the number of articles of the palp correlated with the arrangement of setose areas; the third is the shape of the endite correlated with the absence/presence of particular structures (tubercles, distal hook-like seta, and tips on inner and outer corners).

Schmidt (2002) coded five characters to palp and endite, onde quatro destes poderiam ter sido codificados com maior independencia das condições, evitando ordenação *a priori*: the number of palp articles correlated with the disposition of setose areas and differences among the relation of setae length vs. width; the number of setae on basal article of palp correlated with the fusion of the basal article of palp with the basis of maxilliped; the shape of endite with the absence/presence and shape of the penicil at the end of *sulcus lateralis*; and the absence/presence of lobes on the outer corner of the endite correlated with the replacement of a lobe by seta-like structure, the knob-like penicil.

In this study we added two characters for the basis of the maxilliped regarding the distal outer margin, three characters for the maxilliped palp and 14 characters for the endite. The number of articles of the palp was not coded since most taxa sampled have three-articlulated palp, with only Detonidae having the four-article condition.

PEREOPODS

076. *Pereopod 1, carpus, relative length vs. width*: (0) twice longer than wide, transversal rectangular; (1) as wide as long, square; (2) twice wider than long, longitudinal rectangular.

New character.

077. *Pereopod 1, carpus, dorsal and ventral margins appearance*: (0) parallels; (1) convex.

New character.

078. *Pereopod 2, carpus, relative length vs. width*: (0) twice longer than wide, transversal rectangular; (1) as wide as long, square; (2) twice wider than long, longitudinal rectangular.

New character.

079. *Pereopod 2, carpus, dorsal and ventral margins appearance*: (0) parallels; (1) convex.

New character.

080. *Pereopod 1, propodus, dorsal and ventral margins appearance*: (0) parallels; (1) convex.

New character.

081. *Pereopod 2, propodus, dorsal and ventral margins appearance*: (0) parallels; (1) convex.

New character.

082. *Pereopods, ventral margin of merus, setae, setae fields*: (0) sparse; (1) dense.

Character adapted from Leistikow (2001b).

083. *Pereopods, ventral margin of carpus, setae*: (0) sparse; (1) dense.

New character.

084. *Pereopods, merus, wide field setae*: (0) absent; (1) present.

New character.

085. *Pereopod 1, merus, wide field setae composition*: (0) per. 1; (1) per. 2; (2) per. 3; (3) per. 4; (4) per. 5; (5) per. 6; (6) per. 7.

New character.

086. *Pereopods, merus, distribution of wide field seate*: (0) restricted to the margins; (1) not restricted.

New character.

087. *Pereopods, ventral margin of carpus, wide field setae*: (0) absent; (1) present.

New character.

088. *Pereopods, ventral margin of carpus, wide field setae compostion*: (0) per. 1; (1) per. 2; (2) per. 3; (3) per. 4; (4) per. 5; (5) per. 6; (6) per. 7.

New character.

089. *Pereopods, ventral margin of carpus with wide field setae, distribution*: (0) restricted to the margins; (1) not restricted.

New character.

090. *Pereopods, anterior margin of propodus, wide field setae*: (0) absent; (1) present.

New character.

091. *Pereopods, anterior margin of propodus, wide field setae*: (0) absent; (1) present.

New character.

092. *Pereopods, ventral margin of ischium, fringe setae*: (0) absent; (1) present.

New character.

093. *Pereopod 1, carpus, distal ornamental seta*: (0) double-fringe serrate; (1) hand-like; (2) tricorn-like; (3) clava-like; (4) leaf-like.

Character adapted from Leistikow (2001b).

094. *Pereopod 1, carpus, antennal brush, relative appearance*: (0) reduced; (1) well developed.

New character.

095. *Pereopod 1, carpus, antennal brush, disposition*: (0) longitudinal; (1) transverse.

Character adapted from Leistikow (2001b).

096. *Pereopod 1, carpus, antennal brush, relative longitudinal length vs. carpus length:* (0) not surpassing half of longitudinal carpus length; (1) surpassing half of longitudinal carpus length.

Character adapted from Leistikow (2001b).

097. *Pereopods, water conduction system*: (0) absent; (1) present.

Character adapted from Schmidt (2002).

098. *Pereopod 7, ventral margin of ischium, convex depression*: (0) absent; (1) present.

New character.

099. *Pereopod 7, dorsal margin of ischium, setae number*: (0) 1; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6; (6) 7; (7) 8; (8) 9; (9) 10; (10) 11; (11) 12.

New character.

100. *Pereopod 7, ventral margin of the merus, proximal lobe*: (0) absent; (1) present.

New character.

101. *Pereopod 7, ventral margin of the merus, distal lobe*: (0) absent; (1) present.

New character.

Pereopods can bear distinct structures, usefull in taxonomy, for example, the stermal lobes on merus of pereopods 7 as in *Androdeloscia* spp. and *Benthana* spp.. The pereopods are correlated with eco-morphological categories, runners have long and slender pereopods useful to escape, and clingers have short and robust pereopods, with higher functionality to attach their body in the substrate. Within Crinocheta, the carpus and propodus bears an apparatus for antenna-grooming and cleaning of the buccal pieces, the antennal-grooming brush (Verhoeff, 1908b). This apparatus is composed of a furrow on carpus rostral surface and fitted by cuticular scales, serving for cleaning the second antenna flagellum, which may vary in length and position (Leistikow, 2001b).

The ventral margin of merus to propodus bears long sensory setae, which may be sparsely arranged as in *Alboscia* Schultz, 1995 and *Roraimoscia*, or densely arranjed as in *Balloniscus* or *Benthana*. Sometimes, an intermediary condition of setation can be observed, as in *Colombophiloscia*. Distally on capus 1, independent of the sex, at least one sensory seta differs considerably from the others in the shape of apex, for example, *Atlantoscia* and *Littorohpiloscia* have the double-fringe serrate and *Benthana* and *Ischioscia* have the hand-like shaped seta (see also Leistikow, 2001).

Leistikow (2001b) founded a large amount of variation in pereopods, mostly coded as independents. Only two characters were presented with overlapped conditions, the absence/presence of particular structures on merus and capus 1 to 7 correlated among them, and the antennal-grooming brush on carpus 1 related to the absence/presence of distal hialyne scales. Schmidt (2002) coded few characters for pereopods but also with overlapped conditions, as the absence/presence of scales or spines on sternal and tergal margins of propodus 1-7 and the absence/presence of antennal-grooming brush on carpus 1 correlatead with the disposição of this structure on rostral surface (transverse or longitudinal).

In this study, the shape of carpus and propodus 1 and 2 were codified based on the relative appearance of sternal and tergal margins, since most taxa sampled have rectangular shape (straight margins), except *Ischioscia* and *Littorophiloscia,* which have enlarged carpus and propodus (convex margins), giving a rounded appearance. The setal area on sternal margins of pereopods were treated as independent among pereopods and pereopod subunits. The presence of particular structures were assumed as independent, since they do not represent an autapomorphic condition.

DACTYLUS

102. *Dactylus, dorsal margin, setose appearance*: (0) reduced setose appearance; (1) dense setose appearance.

New character.

103. *Dactylus, ventral margin, setose appearance*: (0) reduced setose appearance; (1) dense setose appearance.

New character.

104. *Dactylus, inner claw, length relative to the outer claw*: (0) short, less than 1/3 of outer claw length; (1) medium, reaching half of outer claw length; (2) long, subequals in length.

New character.

105. *Dactylus, ungual seta, length relative to the outer claw*: (0) reduced, less than 1/3 of outer claw length; (1) short, reaching half of length of outer claw; (2) medium, reaching the distal margin of the outer claw; (3) long, overpassing the outer claw distal margin.

New character.

106. *Dactylus, ungual seta, apex, shape*: (0) digitform; (1) spatulated; (2) pointed.

New character.

107. *Dactylus, dactylar organ, apex*: (0) cleft; (1) simple.

New character.

108. *Dactylus, dactylar organ, length relative to the outer claw*: (0) short, reaching outer claw insertion base; (1) medium, reaching half of length of outer claw; (2) long, reaching outer claw distal margin; (2) elongated, surpassing outer claw distal margin.

New character.

109. *Dactylus, dactylar organ with simple apex, shape*: (0) digitiform; (1) spatulated; (2) pointed; (3) arrow-shape.

New character.

110. *Dactylus, dactylar organ with simple apex, fringe ornamentation*: (0) absent; (1) present.

New character.

The dactilum is composed of two claws: the inner claw, thinner and located on the ventral portion, and the outer claw, highly developed and located on the dorsal portion; both claws are present in Oniscidea and are considered as a plesiomorphic condition inherited from the groundpattern of Oniscidea. Two distinct sensorial setae may be observed on the dactilum, one anterior to the outer claw, the dactylar organ, and a second one between the two claws, the ungual seta; both setae have different shape, length and, sometimes, associated structures in the lineages of Crinocheta, and are thus very useful for the taxonomical aspects that are discussed below.

Several scales or setae on both sternal and tergal margins may be present in the dactylus, providing the setose appearance typical in *Deto* and *Armadilloniscus*. The inner claw may vary in comparison with the outer claw within Crinocheta, from shorter as in *Deto*, reaching the medium portion of the outer claw as in *Alloniscus* Dana, 1854, or subequal in length as in *Atlantoscia* and *Benthana*.

The dactylar organ is simple in most Crinocheta, but can be bifurcate in two unequal branches as in Olibrinidae and Detonidae; may vary in length relative to the outer claw, from shorter (reaching the outré claw insertion base) as in *Burmoniscus* spp., a medium form (reaching the half portion of outer claw) as in several taxa sampled here, long forms (reaching the distal margin of outer claw) as in *Caraiboscia* spp. and *Colombophiloscia* spp., and longer (overpassing the distal margin of outer claw) as in *Ischioscia* spp., *Quintanoscia*, *Roraimoscia* and *Tropiscia*; and on apex bearing small thin setae, conferring the feathery aspect as in Detonidae, and some species of Philosciidae (e.g. *Cariboscia*, *Ischioscia* and *Pentoniscus*).

Between both claws there is the ungual seta (Taiti & Ferrara, 1986b). The length of the ungual seta relative to the outer claw may be: reduced in *Rhyscotus spp.*; reach the median portion of the outer claw as in *Haloniscus spp.* and *Ischioscia spp.*; subequal, such as seen in most taxa sampled here; or longer, surpassing the distal margin of the outer claw as seen in *Littorophiloscia spp.*. the shape of the apex of the ungual seta can also vary: from simple to the digitiform type; spatulated as in *Atlantoscia spp.* and *Hallophiloscia spp.*; or pointed as in species of *Andenoniscus* Verhoeff, 1941, *Tropiscia* and *Yaerikima*.

Leistikow (2001b) presented three characters for the dactylus: the inner claw length relative tothe outer claw, the shape of the ungual seta, and the shape of the dactylar organ. Schmidt (2002) proposed three characters regarding the dactylus, but the characteristics were coded as correlated: the absence/presence of inner claw correlated with development of outer claw; and, the dactilar organ apex simple or clef correlated with absence/presence small setae.

In this study morphological variations of the dactylus, including aspects of inner and outer margins, the inner claw, dactylar organ and ungual seta length, were atomized into distinct and independent characters.

111. *Genital papilla, ventral shield*: (0) absent; (1) present.

Character adapted from Leistikow (2001b) and Schmidt (2002).

112. *Genital papilla, ventral shield, relative length vs. width*: (0) long, longer than wide; (1) small, as wide as long.

Character adapted from Leistikow (2001b) and Schmidt (2002).

In Ligiidae and Tylidae a pair of genital papillae occurs in the middle of the hind margin of the sternite 8, while it is reduced in Mesoniscidae and fused in Synocheta and Crinhocheta (Schmidt, 2002). The genital papillae has insertion associated with the first pair of pleopods, usually having a sclerotized ventral shield, and surpassed by a cuticular lobe where are located the gonoducts orificies (Leistikow, 2001b). The genital papilla in Oniscidea contains two gonoducts, which are separated in Ligiidae and Tylidae, reduced in Mesoniscidae, and fused in Synocheta and Crinocheta. In Synocheta the gonoducts are partially fused, and in Crinocheta they are completely separated (Schmalfuss, 1989; Erhard, 1997; Schmidt, 2002). The ventral shield have a thickened cuticle in most Crinocheta and in some Synocheta (e.g. *Alpioniscus* Racovitza, 1908 e *Androniscus* Verhoeff, 1908), but also can be absent as in species of *Detonella* Lohmander, 1927. For the taxonomy, the genital papilla is an important actor in Synocheta, enabling the recognition of species of the families Styloniscidae and Trichoniscidae; within Crinocheta, the genital papilla has an important diagnostic character to recognize species of *Halophiloscia*, Halophilosciidae, usually with reduced ventral shield, and an elongated and bifurcate (Leistikow, 2001b; Schmidt, 2002).

Leistikow (2001b) and Schmidt (2002) proposed similar characters for the genital papilla, the absence/presence of the ventral shield, and relative length vs. width, both also assumed in the present study.

PLEOPODS

113. *Pleopods 1-5, exopods, respiratory fields*: (0) absent; (1) present.

Character adapted from Leistikow (2001b).

114. *Pleopods 1-5, exopods, type of respiratory fields*: (0) annulicornis-type; (1) rubromarginata-type; (2) fusca-type; (2) maculicornis-type.

New character.

115. *Pleopods, exopods, setae composition*: (0) 1-5; (1) 2-5; (2) 3-5).

New character.

116. *Pleopods, exopods, setae appearance*: (0) hairy; (1) simple.

New character.

117. *Pleopod 1 exopod, shape*: (0) ovoid; (1) triangular; (2) square-shaped; (3) heart-shaped; (4) cicle-shaped; (5) falciform-shaped.

New character.

118. *Pleopod 1 exopod, outer margin, shape based on angle*: (0) right-angled, 90°; (1) acute, less than 90°; (2) obtuse, more than 90°; (3) shallow, near of 180°.

New character.

119. *Pleopod 1 exopod, orientation*: (0) downwards; (1) outwards.

New character.

120. *Pleopod 1 exopod, distal margin, shape based on angle*: (0) obtuse, more than 90°; (1) right-angled, 90°; (2) acute, less than 90°; (3) shallow, near of 180°.

New character.

121 *Pleopod 1 exopod, heart-shaped, distal margin, apex shape*: (0) rounded; (1) triangular.

New character.

122. *Pleopod 1 exopod, heart-shaped, development of the inner proximal margin relative to the insertion margin*: (0) developed upwards; (1) not developed.

New character.

123. *Pleopod 1 exopod, heart-shaped, wricke-like depression*: (0) absent; (1) present.

New character.

124. *Pleopod 1 exopod, heart-shaped, outer margin, bulbous protrusion*: (0) absent; (1) present.

New character.

125. *Pleopod 1 exopod, heart-shaped, outer magin, lateral process*: (0) absent; (1) present.

New character.

126 *Pleopod 1 exopod, heart-shaped, lateral process, relative development related to the outer margin*: (0) lateral process shorter than outer margin; (1) lateral process reaching the outer margin; (2) lateral process surpassing the outer margin.

New character.

127. *Pleopod 1 exopod, heart-shaped, lateral process, orientation*: (0) downwards; (1) outwards; (2) upwards.

New character.

128. *Pleopod 1 exopod, heart-shaped, lateral process, indentation level*: (0) low; (1) medium; (2) high.

New character.

129. *Pleopod 1 exopod, heart-shaped, lateral process, z:y ration classification*: (0) rounded; (1) elongated.

New character.

130. *Pleopod 1 exopod, heart-shaped with lateral process, inner margin bearing lobe*: (0) absent; (1) present.

New character.

131. *Pleopod 1 exopod, heart-shaped with lateral process, inner lobe appearance*: (0) slender appearance, longer than wide; (1) enlarged appearance, as wide as long.

New character.

132. *Pleopod 1 endopod, length relative to exopod*: (0) short, less than twice of exopod length; (1) medium, twice of exopod length; (2) elongated, more than twice of the exopod length.

New character.

133. *Pleopod 1 endopod, half basal portion, width relative vs. half distal portion*: (0) subequal; (1) enlarged.

New character.

134. *Pleopod 1 endopod, distal portion, apex orientation* (0) outwards; (1) downwards.

New character.

135. *Pleopod 1 endopod, inner distal portion, scales*: (0) absent; (1) present.

Character modified from Leistikow (2001b).

136. *Pleopod 1 endopod, distal portion, minute setae*: (0) absent; (1) present.

New character.

137. *Pleopod 1 endopod, distal portion, minute setae, distribution*: (0) along of the inner margin; (1) restricted to the apex.

Character adapted from Leistikow (2001b).

138. *Pleopod 1 endopod, inner distal portion, ornamentation*: (0) absent; (1) present.

New character.

139. *Pleopod 1 endopod, outer distal portion, ornamentation*: (0) absent; (1) present.

New character.

140. *Pleopod 1 endopod, distal portion, lobe*: (0) absent; (1) present.

New character.

141. *Pleopod 1 endopod, outer median portion, ornamentation*: (0) absent; (1) present.

New character.

142. *Pleopod 1 endopod, distal median portion, crenulate plaque*: (0) absent; (1) present.

New character.

143. *Pleopod 2 exopod, outer margin, appearance relative to the angle*: (0) convex, more than 180°; (1) obtuse, more than 90° and less than 160°; (2) right-angled, 90°; (3) shallow, near of 180°.

New character.

144. *Pleopod 2, endopod, ornamentation*: (0) absent; (1) present.

New character.

145. *Pleopod 2 endopod, length relative to the exopod*: (0) short, less than twice of the exopod length; (1) medium, twice of exopod length; (2) elongated, more than twice of exopod length.

New character.

146. *Pleopod 4 exopod, distal portion, appearance*: (0) not elongated; (1) elongated.

New character.

147. *Pleopod 5 exopod, shape*: (0) rhomboid; (1) triangular; (2) ovoid; (3) rectangular; (4) square; (5) circle.

New character.

148. *Pleopod 5 exopod, outer margin, shape*: (0) sinuous; (1) straight; (2) convex.

Character adapted from Leistikow (2001b).

149. *Pleopod 5 exopod, distal portion, relative length with exopod*: (0) not elongated; (1) elongated in half of exopod length; (2) elongated, twice of exopod length.

New character.

Pleopods in Oniscidea are composed of five pairs located ventrally on pleon, and consisting of a broad sympodite and two plate-like structures, the exopods and the endopods (Schmidt, 2002). The male pleopods 1 and 2 endopods of all Crinocheta and some Synocheta are transformed to copulatory organs which interact with the genital papilla, with several interlocking structures, and 3 to 5 are similar in both sexes (Erhard, 1997; Leistikow, 2001b; Schmidt, 2002). Pleopods 1 and 2 exopods hardly display any sexual dimorphism other than shape (Schmidt, 2002).

In Oniscidea, the pleopod exopods played a very important function in the evolutionary transition from marine environmens to life on land. It was in the exopods that the development of respiratory organs, the pleopodal lungs took place (Schmidt & Wägele, 2001). In contrast with the thick cuticle of the dorsal surface, the exopods have a very thin cuticle devoted to gas exchange (Schmidt, 2002). These respiratory organs are located dorsally on outer margin of pleopod exopods having different levels of development, from a simple uncovered lung roughly semilunar in shape as in *Atlantoscia*, *Aphiloscia* and *Benthana*, and classified as *annulicornis*-type (Ferrara *et al.*, 1994); partially uncovered lung with many tubuliform folds arranged on more than one level which are connected together as found in *Aphiloscia*, *Balloniscus* and *Pulmoniscus*, the *fusca*-type (Ferrara *et al.*, 1994; Araujo & Leistikow, 1999; Lesitikow & Araujo, 2001); or the most derivate *maculicornis*-type, the real covered lung, consisting of many irregular branches which joint into an atrium opening to the outside through a narrow spiracle and arounded by a non-respiratory perispiracular area on dorsal surface (Ferrara *et al.*, 2004). Additionally, the exopods of Oniscidea have a very thin ventral integument than the dorsal cuticle and the haemolymph spaces are exposed to the ventral face, giving the implication that this is an additional area of gas exchange.

The exopods are inserted laterally on the posterior margin of the sympodite; their outer margin may bear some setae with feathery or simple aspect (Leistikow, 2001b; Schmid, 2002). The male pleopod 1 exopod may have various shapes, usefull in taxonomy.as the circular shape of *Adeloscia dawsoni* Vandel, 1977, or the hear-shaped of most taxa sampled. Furthermore, the male pleopod 1 exopod with heart-shaped may have some modifications, as the presence of the lateral protrusion on outer margin as found in *Benthana* and species of *Burmoniscus* and *Ischioscia*, or the typical wrinkle depression of *Ischioscia* giving the can-opener appearance to the pleopod exopod.

The male pleopod 1 endopod consists of a 2-jointed appendage with a dorsal spermatic furrow, commonly enlarged at the base and distally acute bearing dorsally a row of diminute setae along the medial margin, present in most Crinocheta with exception to *Olibrinus*; females lacks the endopod (Erhard, 1997; Schmidt, 2002). Furthermore, the endopod with one article condition is found in some Synocheta, and is considered as plesiomorphic condition (Schmidt, 2002). Compared with the exopod length, the endopod may be slightly longer as in *Alloniscus* and *Androdeloscia*, or distinctly longer as in most taxa sampled in this study. Moreover, the distal portion of the male endopod can bear peculiar structures as the typical fan-shape lobe of *Androdeloscia* or the crenulate plaque of *Atlantoscia*.

The male pleopod 2 exopod usually have a triangular shape and a convex outer margin bearing small feathery or small setae. The exopod may have a hairy sulcus onthe medial margin, funtioning as a resting placefor the endopod 1 (Schmidt, 2002). The male endopod 2 is a slender stick composed of two articles having a dorsal spermatic furrow. This shape favors the transport of the spermatophore distally; females have the endopod 2 small and conical (Schmidt, 2002). Uncommonly the endopod 2 may have particular structures, which allow for fast recognition of specific taxa, for example, the crenulate plaque found in *Atlantoscia rubromarginata* Araujo & Lesitikow, 1999 and *A. ituberasensis* Campos-Filoh, Lisboa & Araujo, 2013, or the complex distal ornamentation found in *Leornadoscia hassallii.*

The pleopod 5 exopod usually has a triangular shape as in most taxa, but can be rhomboid as in *Alloniscus*, *Balloniscus* and *Atlantoscia*, ovoid as in *Andricophiloscia pedisetosa* Taiti & Humpreys, 2001, rectangular as in *Burmoniscus andersoni* Taiti & Manicastri, 1988 square as in *Burmoniscus beroni* Taiti & Manicastri, 1988 and *B. gibbosus* Taiti & Manicastri, 1988 and round-shape as in *Halloniscus tomentosus* Taiti & Humpreys, 2001. Moreover, pleopods 3 to 5 endopods are characterized by a very thin cuticle and a thick epithelium with osmoregulation function (Kümmel, 1981, 1984; Wright & Machin, 1990; Wright & Ting, 2006).

Leistikow (2001b) proposed nine new pleopod characters, seven of which had characteristics overlapped in the codification: the absence/presence of a respiratory area in exopod 1; lungs of the semi-covered and covered types; the shape of exopod 1 correlated with the presence of a lateral incision; the absence/presence of a caudomedial strip of spines (smaller setae) correlated with the presence of a hyaline cuticullar lamel on the apex of the endopod; shape of endopod 2 correlated with the length of exopod 2; shape of exopod 5 correlated with the shape of the internal margin; and, shape of exopod 3 in females correlated with the layout of the structure.

Schmidt (2002) also proposed nine characters for the pleopods, but only three had overlapped characteristics in the codification: shape of the distal portion of endopod 1 correlated with the shape of the spermatic duct and the presence of setae or scales along the mesial margin of the endopod; shape of the basal portion of endopod 1 correlated with the quantity of strands in muscle M 47; and, thickness of exopod cuticle correlated with the presence of respiratory organs, as well as the type of organs and associated structures. However, it is possible to identify independent characteristics coded together; for instance, the absence/presence condition of respiratory organs was correlated with the type, associated structures and arragenment of these organs, and with shape of pleopod 1 and 2 endopods.

In this study morphological variations of the pleopods 1 and 2, pleopods 4 and 5 exopod, including aspects of shape, presence and type of respiratory organs, presence and type of setae on exopods, were atomized into distinct and independent characters.

UROPODS

150. *Uropod, protopod, insertion of the endopod branch, relative to the exopod base*: (0) distante to base; (1) subequal to base.

Character adapted from Leistikow (2001b) and Schmidt (2002).

151. *Uropod, endopod, inner margin, setae fringe*: (0) absent; (1) present.

Character adapted from Schmidt (2002).

152. *Male uropod, exopod branch, relative to endopod legth*: (0) subequals; (1) one third longer; (2) twice longer; (3) more than twice longer; (4) one third shorter.

New character.

153. *Female uropod, exopod branch, relative length to endopod*: (0) subequals; (1) one third longer; (2) twice longer; (3) more than twice longer.

New character.

The uropods in Oniscidea are inserted *juxtaposed* to the telson and composed of a proximal protopod bearing, the endopod and the exopod. Laterally, the uropod protopod can show a marked groove in which the pores of the repugnatory glands open, and the gland product is used to avoid predation (Gorvet, 1956; Gruner, 1966). Also, the uropod have a functional task in the mechanism of the water conducting system, both as removing the excess of water or as in the water uptake (Richardson & Araujo, 2014). Uropods are also correlated with eco-morphological categories: runners possuem os urópodos bem desenvolvidos e inseridos postero-lateralmente ao pleotélson, bem visíveis em vista dorsal, corroborando com a morfológica corporal adaptada para correr; clingers and rollers have well developed neopleurae and usually short uropods placed between the fifth neopleurae and telson, conferring a continuous appearance with the seventh pereonite. The branches may vary in length, subequal as in few species of *Benthana*, or easily distinct having exopod longer than endopod as in most taxa; sometimes the length is sexually dimorphic, often mentioned in descriptions, as in *Benthana* and *Porcellio* Latreille 1804. The insertion of the branches may be at the same level as in some *Benthana*, or having the endopod inserted proximally than the exopod as in *Caraiboscia*. In the Oniscidea groundpattern the uropod branches are inserted at the same level. Distally, the branch apex bears long sensorial setae, and sometimes the endopod bears a fringe of thin setae, as in *Benthana taeniata* Araujo & Buckup, 1994.

Leistikow (2001b) proposed three characters for the uropods: the level of the insertion of branches, relative length between branches, and protopod length relative to the telson, all treated as independents. Schmidt (2002) presented aditional characters for the uropods, such as: the shape of the pleotelson; development of the distal portion of the pleotelson relative to the uropod branches; shape of the protopod and exopod; absence/presence of setation on the internal margin of the endopod; and, protopod filling (or not) the gap between neopleura 5 and the pleotelson. Although very informative, these characters were not treated independently, caracterizing *a priori* order.

In this study morphological variations of uropod branches, including aspects of insertion level and absence/presence of frings of setae on the endopod, were atomized into distinct and independent characters. In order to test the subgenus *Benthanoscia* Lemos de Castro, 1958, which was originally proposed due to the sexual dimorphism of the uropod branches and the longer exopods in males (Leistikow & Araujo, 2006), the length of branches of male and females were coded independently.

CLADISTICS ANALYSIS

The 123 selected terminal taxa enabled to survey 154 characters. The missing data had the percentage ratio of 4% and the inapplicable characters of 9% (see Appendix 1).

The equal weights analysis produced 756 equally parsimonius trees, with length of 1581 steps (CI = 0.13; RI = 0.56), and the strictus consensus resulted in a tree with length 2010 steps, forming a large comb, with few groups recovered as monophyletic (Figs 1, 2).

In the analysis with the implied weighting schemes for each one of the 25 *k* values chosen one or two cladograms with the hightest fit value were obtained (Table 2). The best *k* range chosen based on similarity coefficient through SPR analysis for the data matrix presented here was *10 – 15* (see Table 3). The best *k* value was defined in 11.5473 (Table 2). The topology presented as best value of *k* corresponds to the strict consensus of two trees recovered for the average value. (Figs 3-6), and are used as the hypothesis for the relationships within *Benthana* and among the Philosciidae genera sampled here.

RELATIONS AT EQUAL WEIGHTS SEARCH

(Figures 6 and 7)

At equal weights search the monophyly of *Benthana* was not recovered, although 17 species were recovered in 5 clades with unsolved relations. The monophyly of the subgenus *Benthanoscia* was not recovered.

The monophyly of Philosciidae was not recovered here, although some relationships were reconstructed: *Quintanoscia* and *Oxalaniscus* were recovered with close relations and as basal clade of the family. The genera *Anchiphiloscia*, *Aphiloscia*, *Atlantoscia*, *Caraiboscia*, *Erophiloscia* Vandel, 1972, *Haloniscus*, *Oniscophiloscia*, *Pseudophiloscia*, and *Pentoniscus* were recovered with unsolved relations.

The species *Nesophiloscia culebroides* (Van Name, 1924) and *Metaprosekia caupe* Campos-Filho, Araujo & Taiti, 2014 had relations recovered with Halophilosciidae (except for *Littorophiloscia denticulata*). Both Philosciidae genera demonstrated polyphyletic origin.

The genera *Alboscia*, *Andricophiloscia* Vandel, 1973, *Caraiboscia*, *Colombophiloscia*, the species *Nesophilsocia* sp. and *Metaprosekia nodilinearis* Lesitikow, 2000, and the monotypic genera *Abebaioscia* Vandel, 1973, *Adeloscia*, *Ctenoscia*, *Floridoscia*, *Formicascia*, *Mirtana*, *Paraguascia*, *Parischioscia*, *Portoricoscia*, *Roraimoscia*, and *Yaerikima* were reconstructed with unsolved relations. Moreover, the genus *Ischioscia* had relations recovered with the monotypic genera *Leonardoscia* and *Tropiscia*.

The genus *Burmoniscus* demonstrates polyphyletic origin. *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978) was recovered with unsolved relations with *Andenoniscus*, *Androdeloscia*, *Metaprosekia quadriocelata* Campos-Filho, Araujo & Taiti, 2014, *Xiphoniscus* and *Erophiloscia*.

Moreover, most representatives of *Burmoniscus* were recovered in unsolved relations with *Anchiphiloscia*, and *Androdeloscia hamigera* had relations recovered with *Andenoniscus*.

The monophyly of the families Halophilosciidae and Rhyscotidae were not recovered. For Halophilosciidae, the representatives of *Halophiloscia* were recovered with close relations, and *Littorophiloscia* was recovered as polyphyletic.

The relations of the families Alloniscidae and Balloniscidae were recovered with the Philosciidae genera *Oniscophiloscia* and *Aphiloscia* with unsolved relations, not confirming here the monophyly of these families.

RELATIONS AT IMPLIED WEIGHTING SEARCH

(Figures 8-11)

PHILOSCIIDAE KINAHAN, 1857

(Figure 8)

Concavities values constructed: *0* to *15*.

Exclusive Synapomorphies: runner *sensu* Schmalfuss (1984) [001 – 1], neopleurae 3-5 not developed, giving to the pleon a narrow appearance relative to pereonite 7 [009- 1].

Additional Synapomorphies: ventral margin of merus and carpus of pereopods with sparse setae [081 – 0, 082 – 0], carpus of pereiopod 1 with transverse antennal-grooming brush [095 -1], pleopod 2-5 exopods bearing setae on outer margin [115 – 1], and pleopod 1 exopod heart like [117 – 3].

The family Philosciidae Kinahan, 1857 has several genera with confuse taxonomy, probably related with the morphologic diversity; since the family has representatives adapted from high moisture conditions (e.g. *Atlantoscia*, *Androdeloscia*, and *Bentahana*) to dry regions (*Aphiloscia*) (for more detais see Schmidt, 2003). The descriptions of several genera were based in general morphogy and their relations discussed based on author´s interpretations only.

Within Philosciidae several genera are united by plesiomorphic characters related with the runner-type category, which is inherited from the groundpattern of Oniscidea, and still present in Ligiidae, Synocheta, and some Crinocheta (Schmalfuss, 2003).

A remarkable character in some genus is the presence of pleopodal lungs, which evolved differently among the genera, from a simple respiratory area as in *Atlantoscia* spp. (Campos-Filho *et al*., 2013a) and *Benthana* (Campos-Filho *et al*., submitted) to very complex structures as in *Aphiloscia*, which shows all stages of evolution to this structure (Ferrara *et al*., 1994). Schmidt (2003) commented that Vandel (1963) based on the presence of respiratory structures proposed the family Balloniscidae to erecte the genus *Balloniscus*, but this solution did not solve the systematic position of this genus, although Schmidt (2002) not sampled representatives of Balloniscidae. Leistikow (2001b) recovered *Balloniscus* and *Plataoniscus* Leistikow, 2001c in a closely related clade to the Philosciid genera *Oniscophiloscia* Warberg, 1922, *Philoscia* Latreille, 1804 and *Pulmoniscus*. In addition, the complex lungs are also present in derivate lineages of Oniscidea (*sensu* Schmidt, 2002), explained by convergence evolution to attend habitat conditions. Nevertheless, the relations of the clades *Oniscophiloscia*, Balloniscidae and Philosciidae will be discussed later.

In this study the Philosciidae clade is supported by two characters closely related and hystorically postulated to the family representatives: the runner habitus and the pleon narrower than pereon. The additional synapomorphies, ventral margin of merus and carpus of pereopods bearing sparse setae could be assigned as additional characters for the family. On the other hand, the shape variation of male pleopod 1 exopod is sometimes difficult to be quantified and described due to the wide morphological variation within the family. Taking this in consideration, the heart-like shape of male pleopod 1 exopod should be interpreted more carefully, because this structure it is correlated with reproduction and varies in morphology among the genera and species. The condition recovered here for the male pleopod 1 exopod could be explained by convergence, because the species are distant related and occupy different habitats. Although a plesiomorphic hypothesis can not be discharded and further analyses exploring the family diversity may help to elucidate this question

CLADE A

Pseudophiloscia Budde-Lund, 1904, _Aphiloscia_ Budde-Lund, 1908 and _Benthana_ Budde-Lund, 1908

(Figure 9)

Concavities values constructed: *10* to *16*.

Synapomorphies: maxilla lobes wider than base [053 – 1], and carpus 1 with apex of distal seta hand-like [093 – 1].

Leistikow´s (2001b) reconstructed closely relathionships among *Pseudophiloscia*, *Araucoscia* and *Adeloscia*, supported by dense setae on ventral margin of pereopods, and shape of carpus and outer tooth of outer set of outer endite of first maxilla. The author also recovered *Benthana* in a clade, supported by the shape of maxilliped endite, but with unsolved relations with *Atlantoscia* and Rhyscotidae.

Among the synapomorphies presented for the reconstructed groups here, some considerations can be made. The maxilliped endite with tubercle on distal margin is also found in *Philoscida muscorum* (Scopoli, 1763) (not sampled here), and the distal seta of carpus 1 with apex hand-like is shared here with *Caraiboscia microphthalma*, *Ischioscia*, *Leonardoscia*, *Metaprosekia caupe*, *M. quadriocelata*, *Oniscophiloscia*, *Parischioscia*, *Portoricoscia*, *Pseudophiloscia*, and *Tropiscia*. Both conditions can be explained by convergence, because these taxa are distantly related phylogeneticaly and occur in distinct habitats.

Benthana Budde-Lund, 1908

(Figure 9)

Type species. *Benthana picta* (Brandt, 1833) by subsequent designation (Van Name, 1936).

Concavities values constructed: *0* to *24*.

Exclusive synapomorphy: maxilliped endite with tooth-like ornamentation at the end of *sulcus marginalis* [069 – 0, 070 – 1].

Additional synapomorphies: first maxilla outer endite with inner set of pectinate teeth [047 – 2], pleopod 1 exopod heart-like shaped with lateral process on outer margin [121 – 3, 129 – 1].

The monophyly of *Benthana* was recovered in all weighting regimes and its internal relationships demonstrated stabily in the different arrangementss.

Analisando as construções nos diferentes regimes de pesagem, except to the best *k* value, *Benthana* was recovered with *Adeloscia*, *Alboscia*, *Caraiboscia*, *Colombophiloscia*, *Floridoscia* and *Leonardoscia* in the values *0* to *4*; with several genera in the values *5* to *9*; with *Atlantoscia*, *Aphiloscia*, *Balloniscus*, *Oniscophiloscia*, *Paraguascia*, *Plataoniscus* and *Pulmoniscus* in the values *17* to *22*; with the last seven genera plus *Alloniscus* in the concavity *23*; and, lastly, with the last eight genera and plus Rhyscotidae in the value *24* (see trees on supplementar material). These reconstructions indicate *Benthana* close related with South American genera. The relations with *Aphiloscia* within the best *k* value may be interpreted here as an artefact of taxon sampling. Futher analyses including higher diversity of Philosciidae should helps to elucidate and intepretate these relations with more congruence.

The exclusive synapomorphy of *Benthana* is shared with the Chilean genus *Benthanoides* Lemos de Castro, 1958a (not sampled here), which support the probable relations between *Benthana* and South American genera, sharing common biogeographic history.

The pectinate shape of outer set of teeth of outer endite of first maxilla was often used to define *Benthana* (Budde-Lund, 1908; Van Name, 1936; Gruner, 1955 Lemos de Castro, 1958).

Here this character is shared with *Armadilloniscus* (Detonidae), *Abebaioscia*, *Alboscia*, *Ctenoscia*, and *Ischioscia*. As discussed in 'Charaters section', the pectinate teeth are regarded as a plesiomorphic condition for Crinocheta, because it is present in Ligiidae. In this study this characteristic was confirmed as synapomorphy of *Benthana* and can be interpreted in two ways: by retention of plesiomofphic condition or, secondary reversion.

Other characteristic very usefull to define *Benthana* is located in the male pleopod 1 exopod, the lateral process or dentiform protrusion (e.g. Lima & Serejo, 1993; Araujo & Buckup, 1994; Campos-Filho *et al*., submitted). Leistikow (2001b) confirmed this characteristic as synapomorphy of *Benthana*, and in addition, proposed the distal seta of carpus 1 with apex hand-like as synapomorphy (discussed previously). In this study, the presence lateral process on male pleopod 1 exopod is shared with *Burmosniscus* spp. and *Ischioscia* spp., and can be explained by convergence, because these taxa are distant related phylogeneticaly and biogeographically.

The subgenus *Benthanoscia* was proposed by Leistikow & Araujo (2006) based on sexual dimorphism in the uropod branches length, with exopod longer than endopod in males. However, this homology hypothesis was tested and rejected here, not confirming the monophyly of the subgenus in any weighting strategy.

Analysing the weighting regimes in the topology presented here for the best *k* value within *Benthana*, six clades were recovered as follow:

(1) Clade *Benthana albomarginata*, *Benthana* n. sp. 2 and *Benthana* n. sp. 4 - supported by one exclusive synapomorphy: pleopod 4 exopod with distal margin elongated [151 – 1]; and one additional synapomorphy: setae of first article of maxilliped palp distinct in length [60 – 1].

(2) Clade *Benthana bocainensis* and *B. serrana* - supported by four synapomorphies: maxilliped endite with inner distal margin right-angled [065 – 1], ischium 7 dorsal margin with 5 setae [099 – 4], pleopod 1 exopod with proximal portion not developed upwards relative to the insertion margin and lateral process shorter than outer margin [126 – 1, 130 – 0].

(3) Clade *Benthana sulcata*, *B. schmalfussi*, *B. longicornis*, *B. longicaudata*, *B. cairensis* and *B. werneri* - supported by three synapomorphies: antennal-grooming brush overpassing the median portion of carpus 1 [096 – 1], pleopods 1 – 5 exopods bearing setae on outer margin [119 – 0], and pleopod 1 exopod with high indentation level [132 – 2], except to *B. longicaudata* and *B. werneri* wihich shows medium indentation level. Moreover, the relations of *Benthana sulcata*, *B. schmalfussi*, *B. longicaudata* and *B. longicornis* were supported by one synapomorphy: inner margin of male pleopod 1 exopod without lobe [130 – 0]. This character condition is explained by reversion.

(4) Clade *Benthana moreirai* and *B. picta* - reconstructed in almost all concavitites, except for *23* and supported by one synapomorphy: antennal grooming brush overpasing the median portion or carpus 1 [096 – 1].

(5) Clade *Benthana itaipuensis*, *B. santosi*, *B. convexa*, and *B. longipenis* - supported by two synapomorphies: outer margin of pleopod 1 exopod right-angled [118 – 0], and inner margin of uropod protopod with fringe of setae [152 – 1].

In addition, the clade *B. itaipuensis* and *B. santosi* was supported by four synapomorphies: distal margin of maxilla outer lobe rounded [055 – 0], pereopods with ventral margin of merus bearing sparsed setae [082 – 0], male and female uropod exopod twice longer than endopod [153 – 2, 154 – 2]. The relations between *B. convexa* and *B. longipenis* were supported by two synapomorphies: pleopod 1-5 exopods with setae on outer margin [115 – 0], and outer margin of pleopod 5 exopod straight [149 – 1].

(6) Clade *B. araucariana*, *B. trinodulata*, *B. dimorpha* and *Benthana* n. sp. 1 - supported by two synapomorphies: male pleopod 1 exopod with proximal portion not developed upwards relative to the insertion margin and z:y ratio rounded [121 – 0, 129 – 1].

The species *Benthana* n. sp. 3 was recovered as most basal species, and *B. taeniata*, *B. olfersii*, *B. iporangensis* and *B. guayanas* were recovered as individual branches in different weighting regimes.

Within *Benthana*, the merus of pereopod 7 with ventral lobe on proximal portion [100 – 1], is recorded in *B. olfersii*. However, here this character is shared with *Benthana* n. sp. 2, *Aloniscus oahuensis* (Alloniscidae), *Anchiphiloscia aelleni*, *Androdeloscia formosa*, *Burmoniscus comtus*, and *Ischioscia curvaculeus*, and explained by convergence, possibly related to reproductive morphological adaptations.

The presence of fringe of setae on inner margin of uropod protopod and endopod is related with the water system conduction (Richardson & Araujo, 2014). Here, this character is shared with *B. taeniata*, *Ischioscia amazonica*, *I. sturmi*, and *Quintanoscia cotoyensis*, explained by convergence since these taxa are distant related.

The lobe on inner margin of male pleopod 1 exopod occurs exclusively in *Benthana*, probably evolved to hold the endopod 1 in resting position. The lobe occurs in *B. taeniata*, *B. bocainensis*, *B. serrana*, *B. cairensis*, *B. werneri*, *B. olfersii*, *B. iporangensis* and *B. guayanas*. Its presence can be explained in two ways: by convergence, since some of these species have a wide distribution or, by common origin, taking into consideration a possible ancestral area and posterior speciation. Furture biogeography analyses must be conduced to confirm these hypotheses.

Pseudophiloscia **Budde-Lund, 1904**

(Figure 9)

Type species: *Pseudophiloscia inflexa* Budde-Lund, 1904 by subsequente designation Leistikow (1998a).

Concavities values constructed: *0* to *24*.

Synapomorphies: neopleurae 3 not reaching the middline of the pleonite 4 [010 – 2], teeth of inner set of maxillula outer endite with simple apex [047 – 0], setae of maxillied palp distinct in length [060 – 1], inner and outer margins of maxilliped endite with apical tip [072 – 1, 073 – 1], dactylus inner claw length less than one third of the outer claw and ungual seta short, reaching the median portion of the outer claw [104 – 0, 105 – 1], dactylar organ elongated, overpassing the outer claw distal margin [108 – 3], pleopod exopods without respiratory area [113 – 0], pleopod 1 exopod with distal margin acute [120 – 2], and pleopod 1 exopod with wricke-like depression [123 – 1].

The genus *Pseudophiloscia* is recorded from Australia, Chile, Japan, New Zeland and Sumatra (Schmalfuss, 2003). It is characterized by two *noduli laterales* per side per epimera, first maxilla inner endite with apical tip and outer endite with 10 teeth wit apex simple, dactylus with inner claw short and dactilar organ overpassing the distal margin of outer claw and pleopod exopods without respiratory area (Leistikow, 1998a).

The genus has taxonomic history confuse regarding the genera *Araucoscia* and *Paraphiloscia* Stebbing, 1990 due to morphologicalsimilatiries of buccal pieces and pereopods (for more details see Leistikow, 1998a, 2001b).

The relations between the South American and Australian *Paraphiloscia* and *Pseudophiloscia* were discussed by Leistikow (1998a), who postulated a Transantartic conexion, with the relations with East Asia a relict of wide distribution.

Leistikow (2001b) has found closely relatationships between *Pseudophiloscia* and *Araucoscia* Verhoeff, 1939, supported by narrow epimerae, with two *noduli laterales* per side and wihthout *sulcus marginalis*, and outer endite of first maxilla composed of 4 + 6 teeth. Later, Leistikow (2001i) considered *Araucoscia* as junior synonym of *Pseudophiloscia* based on character proposed by Leitikow (2001b).

Here *Pseudophiloscia* was recovered with *Aphiloscia*, not corroboratig Leistikow´s (2001b) results. The genus *Aphiloscia* was not sampled by Leistikow (2001b) and the results recovered herein are probably linked with taxon sampling. Futher analyses with wide taxa sampling will elucidate the relations of both genera. Moreover, the taxonomic characters proposed by Leistikow (1998a) as genus diagnosis were confirmed as synapomorphies. In addition, the presence of wricke-like depression [123 – 1] is commonly found in *Ischioscia* spp., and probably associated with reproductive aspects. Here, this condition is explained by convergence, because these taxa are distant related.

Aphiloscia **Budde-Lund, 1908**

(Figure 9)

Type species: *Aphiloscia annulicornis* (Budde-Lund, 1885) by subsequent designation Taiti & Ferrara (1984).

Concavities values constructed: *0* to *24*.

Exclusive Synapomorphy: cephalothorax with a pair of *nodulus lateralis* [014 – 1].

Additional synapomorphies: seven additional synapomorphies: dorsal tricorn-like setae *sensu* Holdich (1984) [005 – 2], distal margin of pleotelson triangular-shaped [012 – 0], *linea supraantennalis* straight [020 – 0], mandibles with molar penicil simple {040 – 0], pereopods with dense setae on ventral margin of carpus and distal seta of carpus 1 with tricorn-like apex [083 – 1, 093 – 2], and pleopod 1 endopod with distal portion directed outwards [134 – 0].

The African genus *Aphiloscia* is well defined and easily recognized among Philosciidae by a series of characteristics such as the two *noduli* on cephalothorax, unique to this genus, and the double series of *noduli laterales* per side of pereonites (Ferrara *et al*., 1994). This genus has one of the most remarkble characteristics known in Oniscidea, which are strictly involved in the terrestrialization process, the presence of respiratory organs. These organs occur in *Aphiloscia* from a simple respiratory area, present in other Philosciids as *Philoscia* Latreille, 1804, *Atlantoscia* spp. or *Benthana* spp., to a very complex structure branched and internalized on pleopod exopods, as in *Porcellio* Latreille, 1804 (Porcellionidae) or in species of Eubelidae.

Within Oniscidea the *noduli laterales* are exclusive characteristics of Crinocheta, which arises in lineages with unsoloved relations of Philosciidae, Halophilosciidae, Scleropactidae, Stenoniscidae and derivative clades (Schmidt, 2002). The presence of *noduli* on cephalothorax may have many hypotheses. Here, the lost of *noduli* on cephalothorax could be interpreted as a derivative condition within Crinocheta, and secondarily the presence would be explained here by reversion. Furthermore, pouco se sabe sobre a evolução e função destas estruturas, sendo necessários estudos mais aprofundados.

CLADE B

Atlantoscia Ferrara & Taiti, 1981

(Figure 10)

Type species: *Atlantoscia alceui* Ferrara & Taiti, 1981 by monotypy.

Concavities values constructed: *0* to *17*.

Exclusive Synapomorphy: pleopod 1 endopod with a crenulate plaque on distal portion (except to *A. rubromarginata*) [142 – 1].

Additional synapomorphies: maxilliped base without fringe of setae on distal outer margin, except in *A. floridana* and *A. petronioi* [058 – 0], dactylus innner claw reaching the distal margin of the outer claw, except in *A. ituberasensis* [104 – 2], and the pleopod 1 exopod directed outwards (except in *A. floridana*) [119 – 1].

The genus *Atlantoscia* has occurs in South America, except *A. floridana* which occurs also in Florida, USA (Campos-Filho *et al*., 2013a). New species in the genus have been recently described (Campos-Filho *et al*., 2013a), and the relations among all *Atlantoscia* species have been demosntrated trhough morphological and molecular data (B. L. Zimmermann *et al*. submitted.).

The genus is characterized by *noduli laterales* coordinates with maximum distance from lateral margin at *nodulus* 4, shape of buccal pieces and male pleopods 1 and 2 (Araujo & Leistikow, 1999; Campos-Filho *et al*., 2013b).

Leistikow (2001b) recovered *Atlantoscia* in a clade with unsolved relations with *Benthana* and Rhyscotidae. Also, the author commented about similarities in the structures of cephalothorax with the genera *Androdeloscia*, *Erophiloscia* Vandel, 1972 and *Xiphoniscus* Vandel, 1968, and with *Benthana* in the shape of maxilliped. However, the shape of cephalothorax and the maxilliped of *Atlantoscia* are common within Philosciidae.

In this study *Atlantoscia* was recoved in a clade with stability in their relations. The species *A. rubromarginata* was recovered as most basal species of the genus, and *A. floridana* and *A. petronioi* were recovere with close relations. Interestingly these relations were also recovered with molecular data (Zimmermann *et al.*, submitted), which supports the monophyly of the genus. Comparing our results with Leistikow´s (2001b), *Atlantoscia* has close relations with the *Benthana*, *Pseudophiloscia* and *Aphiloscia*, and with *Paraguascia*.

***Paraguascia* Schultz, 1995**

(Figure 10)

Type species. *Paraguascia pigmentata* Schultz, 1995 by original designation.

Concavities values constructed: *13* and *14*.

Synapomorphies: presence of *linea frontalis* [021 – 1]; mandibles with molar penicil of three branches [041 – 0]; outer endite of maxillula with teeth composition 4 + 5 [046 – 2]; outer distal margin of maxilliped base overpassing the first article of palp [057 – 1]; maxilliped endite with medial seta not discernible [074 – 0]; carpus 1 with longitudinal antennal grooming-brush [095 – 0]; and pleopod 1 exopod directed downwards.

The monotypic genus *Paraguascia* was proposed by Schultz (1995) to include *P. pigmentata*. The author mentioned that the genus is close related of *Prosekia* (Vandel, 1968), probably because of *noduli laterales* coordinates, disposition of aesthetascs on first antenna and shape of buccal pieces. The author also mentioned that the genus could be distinguished by few aesthetascs on first antenna, mandibles with dichotomized molar penicil, maxilliped endite without peniciliate seta and uropod branches inserted at the same level. However, these characteristics are present in several Philosciidae.

Independently of our phylogenetical results, the close relations of both taxa are not confirmed here. The species of *Prosekia* (=*Androdeloscia*) share a complex apparatus on male pleopod 1 endopod, which is used as first diagnostic character. This characteristic is not present in *P. pigmentata* (see Schultz, 1995). Analysing the morphology of *P. pigmentata* (Schultz, 1995), it is possible to recognize similarities with *Atlantoscia*, is special with *A. floridana* and *A. petronioi*, such as dactylar organ with apex spatuled, and shape of pleopods 1 and 2. However, only the examination of the type material can assures the position of this taxon.

Within the best k value analysis *Paraguascia* was recovered as an individual branch inside Clade B. In the other weighting regimes the genus was recovered with *Altantoscia* in the concavities *18* to *24*, and recovered with different genera in the remaining weighting strategies, which probably indicates an unstable taxon.

Adeloscia **Vandel, 1977 and** ***Floridoscia*** **Schultz & Johnson, 1984**
(Figure 10)

Type species. *Adeloscia dawsoni* Vabdel, 1977 by monotypy and original designation; *Floridoscia fusca* Schultz & Johnson, 1984 by monotypy and original designation.

Concavities values constructed: *0* to *14*.

Synapomorphies: apical organ of second antenna with free sensilla inserted in the half apical portion [039 – 1], and mandibles with molar penicil simple [040 – 0].

Vandel (1977) described the New Zeland species *A. dawsoni* and based on the simple molar penicil of mandibles commented about a possible convergence between *Adeloscia* and *Paraphiloscia* Stebbing, 1900. Later, the phylogenetic relations of *Adeloscia* were evaluated by Leistikow

(2001b), who found close relations with *Pseudophiloscia,* as mentioned. Differently, the monotypic genus *Floridoscia* has never been was evaluated in a phylogenetic context.

The relations proposed here do not agree with the topology presented by Leistikow (2001). The first synapomorphy here is shared with *Andricophiloscia pedisetosa*, *Littorophiloscia insularis* and *Roraimoscia roraimae*, which coul be explained by convergence since these taxa are distant related and occur in different habitats. The second synapomorphy is share with several taxa within Philosciidae, and probably evolved by convergence.

Tribe Prosekiini Leistikow, 2001b

(Figure 10)

Concavities values constructed: *10* to *16*, *18* and *23*.

Synapomorphies: distal article of first antenna as wide as long [027 – 0], distal article of first antenna with aesthetascs occurring on lateral and distal margins [030 – 0].

To date the tribe Prosekiini includes the genera *Prosekia*, *Metaprosekia*, *Xiphoniscus*, *Andenoniscus*, *Androdeloscia* and *Erophiloscia* which shares the shape of first antenna and the aesthetascs disposed in two tufts, one lateral and other distal as synapomorphies (Leistikow, 2001b). Leistikow (2001b) recovered the group with unsolved relations with *Burmoniscus* and *Chaetophiloscia* Verhoeff, 1908c (not sampled here), sharing the position of *nodulus lateralis* 4 shifted from lateral margin.

The same relations proposed by Leistikow (2001b) were recovered here, except for *Prosekia* (not sampled in this study). In addition, the genera *Alboscia* and *Leonardoscia*, the species *M. caupe* Campos-Filho, Araujo & Taiti, 2014 and *M. quadriocellata* Campos-Filho, Araujo & Taiti, 2014 and *Burmoniscus kohleri* were recovered with close relations.

The genus *Prosekia* spp. has a confuse taxonomy involving the genera *Androdeloscia*, *Chaetophiloscia* and *Littorophiloscia* (Halophilosciidae), with most species transferred to *Androdeloscia*. However, only a taxonomic revision will solve these relations.

Taking into account the synapomorphy of Prosekiini and the relations recovered here, the clade *Alboscia* and *Leonardoscia* and the clade *Metaprosekia caupe* and *M. quadriocellata* must be included within the tribe. The case of *Burmoniscus kohleri* will be discussed further in the *Burmoniscus* section.

***Leornardoscia* Campos-Filho, Araujo & Taiti, 2014 and *Alboscia* Schlutz, 1995**

(Figure 10)

Type species. *Leonardoscia hassalli* Campos-Filho, Araujo & Taiti, 2014 by monotypy and original designation; *Alboscia elongata* Schultz, 1995 by original designation.

Concavities values constructed: *0* to *23*.

Synapomorphies: ecomorphological category creeper [0 – 3], outer distal margin of maxilliped base overpassing the first article of palp [057 – 1], maxilliped endite without ornamentation at the end of *sulcus marginalis* [069 - 1], and male pleopod 1 endopod more than twice longer than exopod [132 - 2].

The monotypic genus *Leonardoscia* was recently described by Campos-Filho *et al*. (2014) with occurrence to the Brazilian state of Pará. The authors commented that the genus shows affinities with the tribe Prosekiini (according Leistikow, 2001b) in the disposition of aesthetascs of first antenna, with *Caraiboscia* and *Colomboscia* by the shape of dorsal scale seta, and with *Metaprosekia* in the position of the *noduli laterales*.

The genus *Alboscia* includes four species distributed to Paraguay and in the Brazilian state of Rio Grande do Sul. In general the species of the genus are regarded as creeper (sensu Schmalfuss, 1984) and shows many particular characteristics which probably evolved in responde to this condition, e.g. reduction of body size, colorless, and eyes lacking or reduced to 1-3 ommatidea. A close relationship with *Benthana* and *Benthanops* Barnard, 1932 was postulated by Taiti & Ferrara (1980). Leistikow (2001b) commented that the genus probably is related with the tribe Prosekiini by the pectinate shape of outer set of teeth of outer endite of first maxilla. However, *Alboscia* has never been evaluated with cladistic methods.

The relations recovered here give supports to Leistikow´s (2001b) hypothesis, in which both taxa are related to the tribe Prosekiini (futher discussed herein).

Moreover, *Alboscia* spp. were recovered in the concavities *10* to *23*, supported by many synapomorphies: maxillula outer endite with teeth composition of 4 + 5 [046 – 2], outer distal margin of maxilliped base with fringe of setae, and endite setose fields not discernible along the structure and without ornamentation at the end of the *sulcus marginalis* [058 – 1, 063 – 1, 069 – 1], and pleopod 1 exopod with ovoid shape [117 – 0], except to *A. ornata* which shows the pleopod 1 exopod triangular [117 – 1].

***Metaprosekia* Leistikow, 2000c**

(Figure 10)

Type species. *Metaprosekia nodilinearis* Leistikow, 2000c by monotypy.

The genus *Metaprosekia* includes three species with records in Venezuela and the Brazilian state of Pará (Leistikow, 2000c; Campos-Filho *et al.*, 2014). The genus shows affinities with *Prosekia*, *Androdeloscia* and *Andenoniscus* in the shape of *noduli laterales* and first antenna (Leistikow, 2000c). Leistikow (2001b) recovered *Metaprosekia* (*M. nodilinearis*) related with the Prosekiini group based on the shape of first antenna and postulated two synapomorphies to the genus, eyes composed of three ommatidia and *noduli laterales* at same distance from lateral margin of epimera.

Here, the characteristic of eyes with three ommatidia was confirmed only for *Metaprosekia nodilinearis*, although it is shared with *Alboscia* spp. and *Nesophiloscia*, and the other two species of the genus shows eyes with four ommatidia. This condition can be explained by convergence in response of habitat conditions.

Regarding the position of *nuduli laterales*, as mentioned in character section, their positions were not coded here to reduce arbitrariness, and to avoid coding genera diagrams, which could generate misinterpretations.

In this study the monophyly of *Metaprosekia* was not confirmed. Moreover, the species *M. caupe* and *M. quadriocelata* were recovered in the concavities *5* to *24*, except to *17*, and with close relations with *Leonardoscia* and *Alboscia*, Differently *M. nodilinearis* was recovered with *Xiphoniscus* and *Erophiloscia* in the concavities *5* to *24*, except to *23*. These relations indicate that the first two species probably not belongs to *Metaprosekia*. Nevertheless, molecular analysis will elucidate this relation.

Xiphoniscus **Vandel, 1968 and** ***Erophiloscia*** **Vandel, 1972**

(Figure 10)

Type species. *Xiphoniscus mirabilis* Vandel, 1968 by monotypy and original designation; *Erophiloscia longistyla* Vandel, 1972 by original designation.

Concavities values constructed: *2* to *22*, and *24*.

Synapomorphies: *postfrons* with *lamina frontalis* [022 – 1] except to *E. acanthifera*, inner endite of first maxilla without apical tip [043 – 1] except to *E. acanthifera* [043 – 0].

The monotypic genus *Xiphoniscus* has records only in Ecuador, and shows a unique character among the Oniscidea, the epimeron 2 prolongated in the male (Leistikow, 2011b), not coded here because this characteristic is an autapomorphy and would represent an informative character. As mentioned, the taxon belongs to the tribe Prosekiini and had relations with *Andenoniscus*, *Androdeloscia* and *Erophiloscia* supported by the elongated length of *noduli laterales* and male pleopod exopods rounded (Leistikow, 2001b, 2001e).

The Neotropical *Erophiloscia* has recordsin Ecuador and Peru. The genus is remarkable distinguished from the other genera of Prosekiini by the male pleopod 2 endopod elongated and shape of pleopod 5 exopod with distal portion extremely elongated (Leistikow, 2001e).

The genus *Erophiloscia* was recovered in all concavities, supported by five synapomorphies: pleotelson with distal margin obtuse [012 – 0], *linea supraantennalis* medially bent downwards [020 – 1], pleopod 1 endopod with more than twice of the exopod length [132 – 2], pleopod 1 endopod without complex ornamentation [138 – 0, 139 – 0], except to *E. acanthifera*, and pleopod 5 exopod with inner distal portion elongated [150 – 1, 2], also present in *Androdeloscia hamigera*.

In this study, the elongation of male pleopod 1 and 2 endopod probably evolved to attend reproductive functions. In addition, it is well known for terrestrial isopods that the male pleopod 5 exopod has a lateral groove along the inner margin, in order to accommodate the endopod 2. Within *Erophiloscia* the elongated shape of inner distal portion of male pleopod 5 exopod probably envolved together with the pleopod 2 endopod elongation process. However, this condition is observed only in *Erophiloscia* spp. and *Androdeloscia* spp., which indicates a probable common history.

The condition of male pleopod 1 and 2 endopod elongated in *Erophiloscia* is shared here with Detonidae, Alloniscidae, Rhyscotidae and some Philosciidae (*Alboscia* spp., *Andricophiloscia pedisetosa*, *Benthana* n. sp. 1, *Burmoniscus* spp., *Colombophiloscia alticola*, *Ctenoscia minima*, *Leonardoscia* and *Nesophiloscia*), and also found in basal groups of Oniscidea (e.g. Ligiidae and Synocheta). This condition here could be explained by convergence, because these animals are phylogeneticatly distants and occurs in different habitats.

***Androdeloscia* Leistikow, 1999 and *Andenoniscus* Verhoeff, 1941**

(Figure 10)

Type species. *Androdeloscia hamigera* (Vandel, 1952) by original designation (Leistikow, 1999b); *Andenoniscus silvaticus* Verhoeff, 1941 by monotypy and original designation.

Concavities values constructed: *2* to *24*.

Exclusive synapomorphy: median portion of male pleopod 1 endopod ornamented [141 – 1].

Additional synapomorphy: first antenna without tip on distal article [034 – 0], except to *Andenoniscus schmalfussi*.

The genus *Androdeloscia* has wide distribution with records from southern Mexico, Central America and South America, including Galapagos (Leistikow, 1999b; 2001b; Schmalfuss, 2003; Schmidt & Leistikow, 2005; Campos-Filho & Taiti, in preparation). The genus has a long taxonomic history including the genera *Chaetophiloscia* and *Prosekia* (to more details see Leistikow, 1999b; Schmidt & Leistikow, 2005). The genus was erected to separate *Prosekia hamigera* (=*Androdeloscia hamigera* (Vandel, 1952)) and *P. silvatica* Lemos de Castro & Souza, 1986 (=*Androdeloscia silvatica* (Lemos de Castro & Souza, 1986)) based on the peculiar shape of male pleopod 1 endopod (Leistikow, 1999b). Subsequently several species of *Prosekia* have been transferred to *Androdeloscia* based on the shape of male pleopod 1 endopod (Leistikow, 1999b; Campos-Filho & Taiti, in preparation), and only *P. insularis* is considered *Littorophiloscia* (Halophilosciidae) (Lestikow, 2001b).

In the original description and illustrations of *Prosekia albomaculata* Lima, 1996, *P. lejeunei* Lemos de Castro & Souza, 1986 and *P. tarumae* Lemos de Castro, 1984 from the Brazilian states of Amazonia and Pará, and *P. rutilans* (Vandel, 1952) from Venezuela, many affinities with *Androdeloscia* are observed, such as *noduli laterales* coordinates (when available), shape of first antenna and arrangement of distal aesthetascs (characteristic of Prosekiini), second antenna with apical organ elongated and reduced free sensilla, shape of buccal pieces (molar pecil dichotomized, first maxilla outer endite with outer set of teeth cleft), and specially the complex shape of male pleopod 1 endopod, tipical of *Androdeloscia* (Vandel, 1952; Lemos de Castro, 1984; Lemos de Castro & Souza, 1986; Lima, 1996; Leistikow, 1999b; Schmidt & Leistikow, 2005). These informations provide enough support to transfer the mentioned species to *Androdeloscia*. Lastly, only *Prosekia pearsi* (Vandel, 1952) cannot be included in *Androdeloscia* since the description and illustrations of male pleopod 1 endopod provided by Vandel (1952) do not shows any complex shape. However, as happened to *P. insularis* (=*Littorophiloscia insularis* (Lemos de Castro & Souza, 1986)), this species shows similarities on male pleopods 1 and 2 with representatives of *Littorophiloscia*. Further examination of type material of *P. pearsi* and use of molecular techniques should confirm this.

The genus *Andenoniscus* Verhoeff, 1941 includes three species with records from Panama, Peru and Ecuador (Schmalfuss, 2003). The shape of the first antenna and buccal pieces, and male pleopod 1 endopod characterize the genus.

Andenoniscus has a confuse taxonomy. Vandel (1968) described *A. narcissi* and *A. tropicalis* based on female specimens and erroneously referenced Verhoeff (1951) as author of the genus. Later, Vandel (1972) transferred both species to *Erophiloscia*. Leistikow (1998b) commented that Vandel (1972) never examined a specimen of *Andenoniscus* and both species were transfer randomly to *Erophiloscia*, because Vandel (1972) did not analysed the shape of male pleopod 1 and 2 endopods of *Andenoniscus*, which shows the main characteristic of the genus. Neverthless, since both taxa were describes based on females, the real position of these taxa within *Andenoniscus* will be doubtfull. As suggested by Leistikow (1998b) both species should be treated as *nomia dubia* until males can be described.

As mentioned, the male pleopod 1 endopod with a complex apparatus is typical of *Androdeloscia* spp. (see Leistikow, 1999b). Here, this complex structure is present in *Andenoniscus*, which probably evolved in both taxa in response of reproductive patterns.

The morphology of *Andenoniscus* shows many affinities with *Androdeloscia*, such as, the *noduli laterales* coordinates, shape and arrangenment of aesthetascs of first antenna, second antenna with apical organ elongated and reduced free sensilla, first maxillula with tip on inner endite and outer endite with outer set of teeth cleft, maxilliped endite with an apical tip on outer distal margin and knob-like penicil at the end of *sulcus lateralis*, carpus of pereiopod 1 with antennal-grooming brush short and distal seta with apex serrate, and shape of pleopod 1 exopod (see Leistikow, 1998b, 1999a, 1999b, 2000b).

Leistikow (2001b) recovered both taxa as close related, supported by characteristics on maxilliped and shape of male pleopod 5 exopod. Here, the same relations between both taxa were recovered, mainly supported by the shape of male pleopod 1 endopod. About these relations, three hypotheses might explain it. In the first hypothesis, the male pleopod 1 endopod evolved by convergence in response of reproduction. Second, both taxa share a common biogeographic history, since these species occur in biogeographic areas close related and well known to other taxa (see Nihei & Carvalho, 2007; Morrone, 2013). The last hypothesis, based on the morphology previously discussed, the genus *Andenoniscus* is in fact *Androdeloscia*.

***Abebaioscia* Vandel, 1973, *Anchiphiloscia* Stebbing, 1908 and *Burmoniscus* Collinge, 1914 (Figure 10)**

Type species. *Abebaioscia troglodytes* Vandel, 1973 by monotypy; *Anchiphiloscia karongae* Stebbing, 1908 by original designation; *Burmoniscus moulmeinus* Collinge, 1914 (=*Philoscia coeca* Budde-Lund, 1895) by original designation.

Concavities values constructed: *10* to *24*.

Synapomorphies: first antenna with distal article of flagellum and apical organ subequal in length [036 – 0], and pleopod 1 exopod directed downwards [119 – 0].

The monotypic genus *Abebaioscia* was proposed to include the cavernicolous species *A. troglodytes* Vandel, 1973 from Pannikin cave, Australia. The genus is characterized by the *noduli laterales* coordinates, pleon narrower than pereon, mandibles with molar penicil dichotomized, outer set of outer endite of first maxilla with cleft teeth, and maxilliped endite with knob-like penicil at the end of *sulcus marginalis* (Vandel, 1973). However, the *noduli laterales* diagram box provided by Vandel (1973), contradicts the original description. The author described the maximum distance from the lateral margin of epimera for the fourth *nodulus lateralis*, but this condition is observed in the third *nodulus*. Furthermore, looking the illustrations produced by the author some diagnostic chacateristics can be added: pleotelson with distal margin rounded, distal article of first antenna with two sets of two aesthetascs disposed on lateral margins plus apical pair, second antenna with distal article of flagellum and apical organ ssubequal in length, distal margin of maxilliped endite with two setae hook-like, male pleopod 1 exopod falciform shaped and endopod 1 stout on basis, and male pleopod 2 exopod triangular, outer margin concave bearing three setae and longer than endopod 2.

The genus *Anchiphiloscia* Stebbing, 1908 includes 21 species distributed in Africa and southern Asia (Schmalfuss, 2003), and was erected to include *A. karongae* Stebbing, 1908 from Malawi and *A. cunningtoni* (= *Aphiloscia c* (Stebbing, 1908)) from Zambia. The genus has a large taxonomic history related to the genera *Aphiloscia*, *Afrophiloscia* (=*Anchiphiloscia*), *Philoscia* and *Setaphora* Budde-Lund, 1908 (for more details see Ferrara & Taiti, 1986). The genus is characterized by the *noduli laterales* coordinates (peaks on epimera 2 and 4), cephalothorax with *linea supraantennalis*, mandibles with molar penicil simple, first maxillula inner endite with a tip on distal margin and outer endite with teeth composed of 4 + 6 (five teeth cleft), pleopod exopods without respiratory areas and uropod branches inserted at similar level (Ferrara & Taiti, 1986).

The genus *Burmoniscus* comprises more than 80 described species distributed in southern Asia, Australia, Afro-tropical regions, Seychelles and Micronesia archipelagos (Schmalfuss, 2003). Only *B. kohleri* Schmalfuss & Ferrara, 1978 and *B. meeusei* are recorded in the Americas (Schmalfuss, 2003; Leistikow, 2001b), and probably introduced by human activity (Araujo *et al*., 1996; Taiti & Ferrara, 1991b). The genus has beed revised and defined by Taiti & Ferrara (1986), and was configured as paraphyletic united by plesiomorphic characters (Leistikow, 2001).

The genera *Abebaoioscia* and *Anchiphiloscia* have never beee evaluated into a phylogenetic account. Here, both taxa were close related with *Burmoniscus*, except to *B. kohleri*. Moreover, a quite interesting question regarding the method assumed here arises and will be discussed further after taxa relationships.

The genus *Abebaioscia* is supported by six synapomorphies: pleotelson with distal margin obtuse [012 – 0], mandibles with molar penicil of four branches [023 – 1], maxilliped endite without setose fileds discernible [063 – 1], dorsal margin of ischium 7 with one seta [099 – 0], and male and female uropod exopod with more than twice of endopod length [153 – 3, 154 – 3]. The shape of pleotelson and mandibles with molar penicil unbranched, used in taxonomy, were confirmed here as synapomorphies. Moreover, these characteristics are present in several groups of Philosciidae.

The genus *Anchiphiloscia* was recovered in all weighting regimes, supported by eight synapomorphies: apical organ shorter than distal artigle of flagellum and freee sensilla three times longer than the base of the apical organ [036 – 1, 038 – 0], maxilliped endite with outer distal margin obtuse and *sulcus marginalis* without ornamentation [066 – 1, 069 – 1], carpus 2 enlarged with margins showing convex appearance [079 – 1], merus and carpus of pereopods with setae in wide fieds [084 – 1, 087 – 1], and distal seta of carpus 1 with apex clava-like shape [093 – 3].

The pereopods with robust carpus, and sometimes propods, bearing extra setae in wide fields are typically found in *Ischioscia* spp. and *Littorophiloscia* spp. (see Taiti & Ferrara, 1986b; Leistikow, 2001g), remembering that this type of setae are different from those long setae found on ventral margin of pereopods merus and carpus, and these seate are located surrounding those long setae. Here, this condition of robust carpus 2 is also shared with *Burmoniscus* spp. and *Halophiloscia couchii*, which could be explained by convergence related with habitat conditions.

The monophyly of *Burmoniscus* was not recovered here (Fig. 9). Only *B. kohleri* and *Anchiphiloscia* share the depression on inner distal margin of maxilliped endite and *B. kohleri* was recovered within the Prosekiini tribe, with good stability. Leistikow (2001b) recovered *Burmoniscus*, including *B. kohleri* and *B. meeusei*, with unsolved relations with Prosekiini and *Chaetophiloscia*. Nevertheless, the author sampled only two species of *Burmoniscus*, probably because these species are recorded in Americas. Therefore, the relations of *B. kohleri* within Prosekiini should be treated carefully. The shape of first antenna and arrangement of aesthetascs of *B. kohleri* differs from the Prosekiini, and the relations recovered here could be an artefact of sampling. Further analyses including higer diversity of the genus and use of molecular methods will confirm the hypothesis recovered herein.

Burmoniscuis meeusei demonstrates close relations with *Anchiphiloscia*, supported by one exclusice synapomorphy: maxilliped endite with depression on inner distal margin [071 – 1]; and six additional synapomorphies: maxilliped base with fringe of setae on outer distal margin [058 – 0], maxilliped palp with setae subequals in length on first article [060 – 0], carpus of pereiopod 1 robust, giving to the margins a convex appearance [077 – 1], ventral margin of pereopods with wide field setae [087 – 1], ischium 7 dorsal margin with three setae [099 – 2], and pleopod 1 exopod outer margin with right-angled [118 – 0].

The results between both taxa are quite unespected, since *B. meeusei* was closely related with Prosekiini and *Chaetophiloscia* (Leistikow, 2001b). However, some comments can be made here. *Burmoniscus meeusei* was first described as *Chaetophiloscia meeusei* by Houthuis (1947), and later transferred to *Burmoniscus* by Taiti & Ferrara (1991b). Historically, the gerena *Anchiphiloscia*, *Burmoniscus*, *Chaetophiloscia* (not sampled), *Philoscia* (not sampled) and *Setaphora* Budde-Lund, 1908 (not sampled) have a con fuse taxonomy (Taiti & Ferrara, 1986), although these taxonomic studies reveal some level of relations. Furthermore, our results indicate some levels of relations between *Anchiphiloscia* and *Burmoniscus*, as postulated through taxonomic studies. However, higher taxon sampling including the metioned genera will elucidate and confirm this hypothesis recovered here.

The remaining species *Burmoniscus* were recovered in the concavities *5* to *24*, except in the values *15* and *16*. Leistikow (2001b) commented that the genus não teve nenhuma sinapomorfia recuperada. Unfortunatly our results also not recovered any synapomorphy to the clade including more species of the genus.

CLADE C

(Figure 11)

Concavities values constructed: *10* to *14*.

Synapomorphies: maxilliped endite with setose fields discernible from the half portion to the distal margin of endite [063 – 0, 064 – 1], and medial seta reaching the distal margin of endite [075 – 1].

The Clade C includes the Philosciidae genera *Andricophiloscia*, *Caraiboscia*, *Colombophiloscia*, *Ctenoscia*, *Formicascia*, *Haloniscus*, *Ischioscia*, *Mirtana*, *Nesophiloscia*, *Oxalaniscus*, *Parischioscia*, *Pentoniscus*, *Portoricoscia*, *Quintanoscia*, *Roraimoscia*, *Tropiscia*, and *Yaerikima*, and the families Halophilosciidae and Rhyscotidae.

Leistikow (2001b) recovered close relations between *Roraimoscia*, *Formicascia*, *Portoricoscia*, *Parischioscia* and the tribe Ischiosciini, which was named as *Roraimoscia*-group, supported by *profrons* without depression to fit the second antenna, no lateral lobes and *linea frontalis* reduced. Moreover, Ischiosciiini included *Oreades* (Vandel, 1968), *Ecuadoroniscus* (Vandel, 1968), *Mirtana* Leistikow, 1997, *Tropiscia* and *Ischioscia* Verhoeff, 1928 (Leistikow, 2001b), the first two genera were not sampled here, supported by proximal article of first antenna with distal shield-like protrusion and pleotelson with ventral semicircular pit apically (leistikow, 2001b). Athough, some comments should be made it here. Analysing the illustrations of *Formicascia* (see Table 1 to references) is possible recognize the depressions to fit the second antenna, and the *linea frontalis* reduced is a modified present condition, misinterpretate in the author character codding (see Characters section herein). In addition, the Ischiosciini characters are really difficult to observe, since was not illustrated by the author, and not observed in the descriptions and illustrations.

Independently, our results showed a quite similar topology with Leistikow´s (2001b) results.

***Andricophiloscia* Vandel, 1973, *Oxalaniscus* Leistikow, 2000b and *Quintanoscia* Leistikow, 2000b.**

(Figure 11)

Type species. *Andricophiloscia melanesiensis* Vandel, 1973 by original designation and monotypy; *Philoscia ctenoscoides* Mulaik, 1960 by monotypy; *Philoscia contoyensis* Mulaik, 1960 by monotypy.

Concavities values constructed: *5* to *14*.

Synapomorphies: maxilliped endite with medial seta not discernible [074 – 0], distal seta of carpus of pereiopod 1 with apex tricorn [093 – 2], and dactilar organ with apex spatulated [109 – 1].

The genus *Andricophiloscia* Vandel, 1973 was created to include *Andricophiloscia melanesiensis* from New Guinea. Later, Taiti & Humphreys (2001) described two new species from Australia, *A. pedisetosa* Taiti & Humpreys, 2001 and *A. stepheni* (Nicholls & Barnes, 1926). The genus is characterized by the *noduli laterales* coordinates inserted more or less at the same distance from the lateral margin, outer endite of first maxilla with outer set composed of 4 + 6 simple teeth, shape of male pleopods 1 and 2 (endopods very long), and uropods branches inserted almost in same level (Vandel, 1973; Taiti & Humpreys, 2001). Taiti & Humprey (2001) commented that the elongated male pleopod endopods of *Andricophiloscia* can be also found in *Chaetophiloscia* and *Natalscia* Verhoeff, 1942 (not sampled).

The monophyly of *Andricophiloscia* was not recovered here. The genus was recovered in unsolved clade with unsolved *Oxalaniscus* Leistikow, 2000b and *Quintanoscia* Leistikow, 2000b. The hypotheses of very long male pleopod 1 and 2 endopods were rejected as synapomorphies to *Andricophiloscia*,. In this study, as metioned in 'Character' section, the length of male pleopod 1 and 2 endopods were atomized in two different characters. The very long male endopod 1 is shared with Denotidae, Rhyscotidae spp., *Adeloscia*, *Alboscia* spp., *Colombophiloscia* spp., *Ctenoscia* Verhoeff, 1928, *Erophiloscia*, *Leonardoscia*, and *Nesophiloscia*; and the endopod 2 shared with

Detonidae, *Benthana* n. sp. 1, *Burmoniscus* spp., *Erophiloscia* spp., and *Leonardoscia*. This condition is explained by convergence, and related with reproduction aspects.

Leistikow (2000b) revised the Mexican species described by Mulaik (1960), *Philoscia ctenoscoides* from Chiapas, and *P. contoyensis* from Contoy Island, Quintana, and ereceted the genera *Oxalaniscus* and *Quintanoscia* to allocate both species respectivally. Later, Leistikow (2001b) recovered both taxa as close related and as basal clade of Philosciidae, supported by the reduction of the *linea fontalis*, molar penicil with three branches, first maxilla outer endite composed of 4 + 6 teeth and inner set of teeth with apex simple.

Here the relations between *Oxalaniscus* and *Quintanoscia* were recovered in almost all concavities, except to *15* and *16*. The clade was supported by many synapomorphies: neopleurae 3-5 with progressive reduction relative to the pereonite 7 [009 – 0], *post-frons* with *lamina frontalis* [022 -1], mandibles with molar penicil of three branches [041 – 0], maxilliped palp with distal tufts of setae not restricted [061 – 0], antennal-grooming brush longitudinal disposed [095 – 0], dactilar organ long, reaching the distal margin of outer claw [108 – 2], male pleopod 1 exopod with distal margin right-angle [144 – 1], male pleopod 5 exopod rhomboid-shaped with outer margin sinuous [148 – 0, 149 – 0].

***Haloniscus* Chilton, 1920, *Ctenoscia* Verhoeff, 1928, *Nesophiloscia* Vandel, 1968 and Rhyscotidae Budde-Lund, 1908**

(Figure 11)

Type species. *Haloniscus searlei* Chilton, 1920 by monotypy; *Ctenoscia minima* (Dollfus, 1892) by subsequent designation (Verhoeff, 1928), and *Philoscia culebroides* Van Name, 1924 by subsequent designation (Vandel, 1968).

Concavities values constructed: *0* to *23*, except in the values *15*, *16* and *24*.

Synapomorphy: absence of eyes [023 – 1], and first antenna with aesthetacs inserted distally [030 – 1].

The genus *Haloniscus* was erected by Chilton (1920) to include *H. searlei* from Australia. Taiti *et al*. (1995) described the new species *H. anophthalmus* from New Caledonia, commented that the genus shows affinities with *Alloniscus* Dana, 1854 by the absence of *noduli laterales*, flagellum of three articles, shape of buccal appendages and uropod protopod flattened without groove on outer margin, and suggested move the genus to the family Scyphacidae. Later, Taiti & Humpreys (2001) revised and redefined the genus, and described three new species *H. longiantennatus*, *H. stylifer* and *H. tomentosus*, all with records to Australia.

Haloniscus was originally included in the family Oniscidae by Chilton (1920). Green (1971) commented the genus shares morphological similarities with the sub-families Schyphacinae (=Scyphacidae Schimdt, 2002) and Philosciinae (=Philosciidae). Taiti *et al*. (1995) based in the previous characteristics mentioned, suggested include in the family Scyphacidae, also followed by Taiti & Humpreys (2001). Lastly, Schmalfuss (2003) considered the family as *incert sedis*. Nowdays *Alloniscus* belongs to the family Alloniscidae (see Schmidt, 2002).

The relations of the genus within Crinocheta have been discussed based on morphology and has never been evaluated in a phylogenetic Here the genus demonstrated close relations with Philosciidae. Moreover *Haloniscus* was recovered in all concavities, supported by one exclusive synapomorphy: ecomorphological category swimmer *sensu* Taiti & Xue (2012) [001 – 4]; and four additional synapomorphies: *noduli laterales* not discernible [006 – 0], apical organ with sensilla free [037 – 0], ischium 7 with three dorsal setae [099 – 2], pleopod 2 exopod with outer margin convex [143 – 0], and pleopod 5 exopod ovoid shaped [148 – 2].

The swimmer habitus is a quite interesting issue in Oniscidea. Vandel (1970) based in *Mexiconiscus laevis* (Rioja, 1956) collected from subterranean water of Mexican caves, considered the aquatic way of life as primitive, as a marine ancestral retained condition. Nowdays it is well known that this way of life is widespread in the family Trichoniscidae (Synocheta) (Taiti & Xue, 2012) and also reported within Crinocheta (Taiti & Ferrara, 2004), and considered a specialized form secondarily derivative from terrestrial condition (Tabacaru, 1999). Based on the relations recovered here, this condition is confirmed as derivative in Philosciidae facies.

As postulated by Leistikow (2001b) the absence of *noduli* is considered a drivative condition, also confirmed here, regarding the derived clades of *Haloniscus* and *Ischioscia* (further discussed), explained by convergence which probably evolved in response of habitat pressure.

The apical organ of second antenna is one of the characteristics which could be interpratate here as reversion to plesiomorphic condition, shared with Detonidae and Alloniscidae. Lastly, the shape of pleopod 1-5 exopods probably evolved to attend the swimmer condition, since they are large with pilose margins.

The relations recovered here suggest that *Haloniscus* is a Philosciidae representative, and for the moment the genus should be placed within the family.

Ctenoscia **Verhoeff, 1928c and** ***Nesophiloscia*** **Vandel, 1968**

(Figure 11)

Concavities values constructed: *0* to *22*, except in the values *15*, *16* and *24*.

Synapomorphies: male pleopod 1 endopod with diminute setae restricted to the apex [137 – 1].

The genus *Ctenoscia* has confuse taxonomic history involving the genera *Benthana*, *Chaetophiloscia* and *Philoscia* (see Schmalfuss, 2003 for references), Moreover the genus *Nesophiloscia* was recently revised and defined by Campos-Filho & Taiti (submitted). However, both taxa have never been evaluated in a phylogenetic contextand here is the first attempt to recover their history within Philosciidae.

The monophyly of *Nesophiloscia* was not recovered here, since the genus demonstrated close relations with *Ctenoscia* and with the family Halophilosciidae (further discussed).

Yaerikima **Leistikow, 2001f,** ***Pentoniscus*** **Richardson, 1913,** ***Colombophiloscia*** **Leistikow, 2001d and** ***Caraiboscia*** **Vandel, 1968**

(Figure 11)

Type species. *Philoscia kartaboana* (Van Name, 1936) by monotypy; *Pentoniscus pruinosus* Richardson, 1913 by monotypy and original designation; *Colombophiloscia alticola* Vandel, 1968 by subsequent designation (Leistikow, 2001d); *Caraiboscia microphthalma* Vandel, 1968 by motype and original designation.

Concavities values constructed: *10* to *15*.

Synapomorphies: pleotelson with distal margin obtuse [012 – 0], distal article of first antenna with lateral aesthetascs continuous disposed with distal aesthetascs [031 – 0], and male and female uropod exopod one third as long as endopod length [153 – 1, 154 – 1].

The genus *Yaerikima* was erected by Leistikow (2001f) to allocate *Philoscia kartaboana* described by Van Name (1936) from Kamakusa, Guyana. The genus differs of *Philoscia* by the absence of *noduli laterales*, epimera with subrectangular margins, cephalothorax *profrons* with two sinuous lines dorsally on atennal sockets, and clypeus with distal part narrower than basis (Leistikow, 2001b, 2001f).

Leistilow (2001b) recovered *Yaerikima* close related with *Pentoniscus* Richardson, 1913 and *Roraimoscia*-group (both taxa discussed ahead), supported by the absence of lateral lobes on cephalothorax, commented about morphological affinities between *Yaerikima* and the genera *Atlantoscia*, *Burmoniscus* and *Formicascia* in the shape of male pleopod 1 exopod, and suggested close relations with Prosekiini tribe in basis of flagelliform shape of male endopod 2 and shape of first antenna. Although, *Yaerikima* is distinguish from those genera in the shape of cephalothorax and second antenna flagellum with apical organ very long. Moreover, the relations between *Yaerikima* and Prosekiini are not assured because of the aesthetascs arrangement (see Leistikow, 2001b, 2001f).

Our topological results show some level congruence with the topology proposed by Leistikow (2001b). The genus *Yaerikima* was close related with *Pentoniscus*, *Colombophiloscia* Leistikow, 2001d and *Caraiboscia* Vandel, 1968 within the best *k* value. The relation hypothesis with Prosekiini was not supported herein because the aesthetascs arragement on distal article of first antenna diverges from those found within Prosekiini.

The genus *Pentoniscus* was recently revised and defined by Leistikow (1998c). The genus is characterized by mandibles with molar penicil simple, pereopods 2 and 3 with quadrangular scales and rhomboid shape of plepod 5 exopod (Leistikow, 2001b). As mentioned,

Leistikow (2001b) recovered close relations of *Pentoniscus* with *Yaerikima* and *Roraimoscia*-group, supported by pleopod 5 exopod with three sinuous rows of fringed scales. Here *Pentoniscus* was close recovered with *Colomboscia* and *Cariboscia* in the concavities *10* to *15*, supported by outer endite of first maxilla with 4 + 5 teeth [046 – 2], maxilla basis subequals in width with lobes [053 – 0], first article of maxilliped palp with setae subequals in length [060 – 0], and male pleopod 1 exopod circle-shaped [117 – 4]. These recovered relations differ of Leistikow (2001b). However, the teeth number on outer endite of first maxillula and shape of male pleopod 1 exopod corrobores with taxonomy *sensu* Leistikow (1998c).

The Philosciidae genera *Colombophiloscia* Leistikow, 2001d and *Caraiboscia* Vandel, 1968 are very distinct within Philosciidae. These taxa show some morphological variations linked with endogeous life which are different from the typical philosciid runners: dorsal slender habitus and tegument covered modified tricorn-seta with leaf-like appearance, reduced compound eyes, short pereopods and slow moving (Schmalfuss, 1977, 1984; Leistikow, 2001d). Although, these characteristics can be found in other Philosciidae sampled here (e.g. *Metaprosekia*, *Leonardoscia* and *Pentoniscus*) and in other families within Oniscidea (e.g. Dubioniscidae Schultz, 1995 and Plathyarthridae Verhoeff, 1949).

Leistikow (2001b) recovered *Colombophiloscia* and *Caraboscia* in a clade with close relations with Prosekiini, supported by dorsal tricorn-setae leaflet, compound eyes reduced to 4 ommatidia, first antenna with a single row of erected aesthetascs and first maxillula outer endite with outer set of teeth with simple apex.

Here the relations between both taxa were recovered in the concavities *0* to *15*, supported by creeper ecomorphological category *sensu* Schmalfuss (1984) and rhomboid shape of pleopod 5 exopod. Since the creeper functional category is present in other taxa here, this condition can be explained by convergence, because these taxa are geographically distant. Although, futher analyses with biogeographyc methods will test this hypothesis.

Roraimoscia-group Leistikow, 2001b

(Figure 11)

Concavities values constructed: *10* to *23*.

Synapomorphy: Cephalothorax with ommatidia field projected [017 – 0].

The *Roraimoscia*-group includes the Neotropical genera *Formicascia*, *Parischioscia*, *Portoricoscia*, *Roraimoscia* and the tribe Ischiosciini Leistikow, 2001b (further discussed). The clade was supported by the cephalothorax *profons* without depressions to hold the second antenna, no lateral lobes and *linea frontalis* reduced (Leistikow, 2001b). Only *Formicascia* shows cephalothorax *profons* with slight depressions (see Leistikow, 2001f).

Leistikow (2001b) recovered close relations between these taxa. The genera *Roraimoscia* and *Formicascia* were close related, supported by female pleopod 3 exopod with medial part elongated and pleotelson with lateral margins bearing two concavities; *Portoricoscia*, *Parischioscia* and Ischiosciini demonstrated close relations, supported by molar penicil partially fused and composed of maximmally 7 branches; and moreover *Parischioscia* and Ischiosciini had relations supported by first antenna proximal article with slight shield-like lobe and carpus 1 with distal seta hand-like (Leistikow, 2001b).

The ommatidia field projected outwards of lateral margins of cephalothorax is typically found in *Ischioscia* and often used as diagnostic. The character shield-like lobe on first antenna proposed by Leistikow (2001b) could not be tested here, because was not recognized neither in specimens nor species illustrations. The carpus 1 with distal seta hand-like had homology hypothesis rejected, since is present in other taxa sampled here (e.g. *Benthana*, *Metaprosekia* spp., *Oniscophiloscia*, *Parischioscia*, *Portoricoscia*, *Pseudophiloscia* and *Tropiscia*). The projected ommatidia field is interpreted here as synapomorphy of the *Roraimoscia*-group.

In this study, the topology recovered to the *Roraimoscia*-group, show similarities with the results of Leistikow (2001b), despite some characters proposed by the authro not being assumed and coded here. The relations of the group will be discussed ahead following the recovered topology (see Fig. 9).

***Roraimoscia* Leistikow, 2001f**

(Figure 11)

Type species. *Philoscia roraimae* Van Name, 1936 by monotypy.

Concavities values constructed: *10* to *23*.

Synapomorphies: caphalothorax *postfrons* with *lamina frontalis* [022 – 1], apical organ of second antenna flagellum with free sensilla inserted in half apical part [039 – 1], male pleopod 1-5 exopods with setae on outer margin [115 – 0], and male pleopod 1 endopod with distal inner and outer margins ornamented [138 – 1, 139 – 1].

The monotypic genus *Roraimoscia* was erected to include *Philoscia roraimae* described by Van Name (1936) from Venezuela. Leitikow (2001b) characterized the genus by waxy plates covering the groove of the basis of pereopods, prominent sensory seta on ventral margin of ischium, pleopod exopods with two rows of setae on outer margin, and male genital papilla with pectinate scales.

The synapomorphies founded here corroborates with taxonomy characteristics *sensu* Leistikow (2001f).

Formicascia Leistikow, 2001f

(Figure 11)

Type species. *Philoscia inquilina* van Name, 1936 (by monotypy).

Concavities values constructed: *10* to *15* and *18* to *23*.

Synapomorphies: neopleurae 3 well developed, reaching the mediam margin of four pleonite [010 – 0], pleotelson with distal margin acute [012 – 2], first antenna second article with setae [026 – 1], first maxillula outer endite with subapical tubercle [052 – 1], maxilliped endite with medial seta reaching the distal margin of endite [075 – 1], carpus 1 with antennal grooming brush reduced [092 – 1], dactilar organ reaching the half portion of outer claw and without fringe of diminute setae [108 – 1, 110 – 0], male pleopod 1 exopod falciform-shaped and directed outwards, and endopod with lobe on distal part [117 – 5, 119 – 1, 140 – 1], male pleopod 2 endopod twice as long as exopod [146 – 1], and pleopod 5 exopod rhomboid-shaped [148 – 0].

The mototypic genus *Formicascia* was erected by Leistikow (2001f) to include *Philoscia inquilina* originally described by Van Name (1936) from Guyana. Leistikow (2001b) configured two autapomorphies to the genus, epimera withour *sulcus marginalis* with distal edges broadly rounded, and genital papilla short with vasa deferentia much inflated on proximal portion. These characteristics were not coded herein. Although, the characters proposed here are shared with other taxa sampled here and could be interpreted as additional synapomorphies to the genus. Further species recognition will provides better supports for these characters.

Parischioscia **Lemos de Castro, 1967**

(Figure 11)

Type species. *Philoscia omissa* (Van Name, 1936) by monotypy.

Concavities values constructed: *8* to *15* and *18* to *23*.

Exclusive synapomorphy: maxilla outer lobe distally pointed [055 – 2].

Synapomorphies: eyes with three ommatidia [024 – 0], and ischium 7 with dorsal margin bearing 3 long setae [099 – 2].

Lemos de Castro (1967) erected the genus *Parischioscia* to include *Philoscia omissa* described by Van Name (1936) from Guyana, on the basis of the prominent compound eyes and postulated close relations with *Ischioscia*. As metioned, Leistikow (2001b) recovered *Parischioscia* close related with Ischiosciini, and proposed two autapomorphies for the genus: male pereopods 1-5 with transverse groove on carpus proximally boardered by cuticle of hyaline scales, and cephalothorax with ommatidia field prominent.

Regarding *Ischioscia*, Leistikow (2001b) considered *Parischioscia* as more primitive in basis of absence of pereopods 1 to 3 have no carpus enlarged with prominent setae fields, typically found in *Ischioscia*. However, the author considerated doubtful the relations between both taxa, because have no supported synapomorphy. Moreover, the author commented that three characteristics could support these relations, the cephalothorax with prominent ommatidia fields, the shape of proximal article of first antenna and the distal seta of carpus 1 with hand-like apex. These shared characters could be explained by convergence.

Leistikow (2001b) proposed the cephalothorax laterally expanded as synapomorphy of the genera *Ischioscia*, *Mirtana* and *Tropiscia*. Although, this characteristic was observe here in the other genera of *Roraimoscia*-group (see illustrations on Leistikow, 1997, 1999c, 2001a, 2001f, 2001h, 2001h). The distal seta of carpus 1 with han-like apex is shared with other taxa sampled here (e.g. *Atlantoscia* spp., *Benthana*, *Ischioscia*, *Portoricoscia*).

The most peculiar characteristic is the pointed shape of maxilla outer lobe, exclusive of *Parischioscia*. Leistikow (2001b) postulated a reduced maxilla outer lobe as derivate condition within Philosciidae. Moreover, further diversity investigation of Oniscidea at Amazonia region should recognize more specimens to the genus, which will elucidate if this pointed shape of maxilla outer lobe is a synapomorphy of the genus.

***Portoricoscia* Leistikow, 1999c**

(Figure 11)

Type species. *Philoscia richmondi* Richardson, 1901 by monotypy.

Concavities values constructed: *6* to *15* and *18* to *23*.

Synapomorphies: pleotelson with distal margin obtuse [012 – 0], apical organ longer than distal article of flagellum [036 – 2], first maxilla inner endite with apical tip and outer endite composed of 4 + 5 teeth [043 – 1, 046 - 2], maxilla lobes with undistinct appearance [054 – 1], pereiopod 3 and 4 with merus bearing wide field of setae not restricted to the margins [085 – 2, 3; 086 – 1], dactilar organ reaching the median portion or outer claw [108 – 1], male pleopod 1 exopod square-shaped and endopod ornamented on outer portion [117 – 2, 139 – 1].

The monotypic *Portoricoscia* was ereceted by Leistikow (1999c) to include *Philoscia richmondi* described by Richardson (1901) from Greater Antiles, Puerto Rico. The genus was revised and redefined by Leistikow (1999c).

Leistikow (2001b) proposed four autapomorphies: cephalothorax higher than broad, second antenna slender with very long apical organ, propodus and carpus 2 to 7 with very long distal seta, and merus 1 to 5 with medial brushs of cuticular scales. The author suggested the brush of cuticular scales on merus probably evolved to attend reproduction

Leistikow (2001b) on the basis of absence of *nuduli laterales* and gland pores on epimerae, and rounded shape of distal margin of pleotelson, postulated that the genus belongs to basal lineages of Crinocheta. However, the topology recovered by the author and here contradicts this assumption. Probably the lack of *noduli* represents a derivate condition which evolved in response to habitat pressure. Other hypotheses can not be discarded are the *noduli laterales* could be reduced or evolved to seta-like structure. Although further investigations are necessary in order to elucidate the role of *noduli laterales* on the biology of Crinocheta.

Tribe Ischiosciini Leistikow, 2001b

(Figure 11)

Concavities values constructed: *6* to *24*.

Synapomorphy: neopleurae 3 reaching the middline of fouth pleonite [010 – 0], pleotelson with lateral margins obtuse [011 – 1], cephalothorax with *linea supraantennalis* straight and *lamina frontalis* [020 – 0, 022 – 1], pereopods with ventral margins bearing wide setae fields [087 – 0], and male and female uropod exopod longer than endopod [153 – 1, 154 – 1].

The tribe Ischiosciini includes the genera *Ecuadoroniscus* Vandel, 1968 (not sampled), *Ischioscia*, *Mirtana*, *Oreades* Vandel, 1968 (not sampled), and *Tropiscia*, supported by first antenna proximal article with shield-like protrusion and pleotelson with ventral semicircular pit apically (Leistikow, 2001b).

The shield-like protrusion is interpreted by the author as development of the distal portion of proximal article of first antenna. Although, these character was not code here because difficulties to interpretate the illustrations, which could be misisterpreted because of draw position. The genera *Ischioscia* and *Mirtana* share the male pleopod 1 exopod with lateral process and slight incision on outer margin, not observed in *Tropiscia*. The illustrations of *Tropiscia* provided by Leistikow (2001a) show the male exopod 1 with a bulbous protrusion on outer margin. Analysing species within *Ischioscia* (see Leistikow 1999a; 2001g, 2001h) and *Mirtana* (see Leistikow, 1997) is possible observes the presence of this bulbous protrusion, e.g. *Ischioscia fasciifrons* Leistikow, 2001g and *Mirtana costaricensis* Leistikow, 1997. Considering these informations, two hypotheses could be given, these genera share a common evolutive history or, *Mirtana* and *Tropiscia* belongs to *Ischioscia*. Our results recovered close relations between *Tropiscia* and *Ischioscia* (including *Mirtana*) supporting partially the second hypothesis and will be further discussed. Lastly, the characters proposed here are assumed as additional synapomorphies to the tribe.

***Tropiscia* Vandel, 1968**

(Figure 11)

Type species. *Tropiscia flagellata* Vandel, 1968 by monotypy and original designation.

Concavities values constructed: *0* to *22*, except in the values *15*, *16* and *24*.

Synapomorphies: epimera with *noduli lateralis* [006 – 1], eyes with four ommatidia [024 – 1], first antenna with lateral aesthetascs inserted continuous with the apex set [031 – 0], molar penicil of mandibles composed of five branches [041 – 2], ischium 7 with four dorsal long setae [099 – 3], dactylus ungual seta with poited apex [106 – 2], and male pleopod 1 exopod with bulbous protrusion on outer margin, and endopod twice as long as exopod with minute seate restricted to the apex [124 – 1, 132 – 1, 137 – 1].

The monotypic genus *Tropiscia* was erected by Vandel (1968) to include the Ecuadorian species *T. flagellata*. The genus was revised and redefined by Leistikow (2001a), who postulated three autapomorphies: reduction of the longitudinal row of spines on male pleopod 1 endopod, reduction of *linea frontalis* and two flageliform tricorn-setae on epimera, *noduli laterales* sensu Vandel (1968). The genus is close related with *Ischioscia* by the flattened shape of cephalothorax with compound eyes protruding giving T-shaped in frontal view, and male pleopod 1 exopod with bulbous protrusion on outer margin (Leistikow, 2001a, 2001b; Lesitikow & Schmidt, 2002).

As mentioned previously the genus could have a common history with *Ischioscia* or, belongs to it. Analysing the description and illustrations provided by Leistikow (2001a), many affinities could be recognized, supporting these conjectures, the flattened shape of cephalothorax, reduced *linea frontalis*, presence of *lamina frontalis*, pleotelson with ventral apical pit on distal portion, shape and aesthetascs arrangement on first antenna, second antenna with apical organ very long, shape of buccal appendages, merus and carpus 1 with wide field of setae (surroudind the antennal grooming brush on carpus 1), distal seta of carpus 1 with hand-like apex, and male pleopod 1 exopod with bulbous protrusion on outer margin.

Leisitkow (2001a) postulated few different characteristics in the comparison among *Tropiscia* and *Ischioscia*, shorter inner claw, male pleopod 1 endopod acute, and pereopods without specializations. Therefore, other species of *Ischioscia* show pereopods without striking specialization, e.g. *Ischioscia zebricolor* Leistikow, 1999a.

The most interesting question regarding the relations between both taxa is the presence of *noduli laterales* in *Tropiscia sensu* Vandel (1968), not observed in *Ischioscia* (Leistikow, 2001b). As mentioned previously the absence of *noduli laterales* is regarded as plesiomorphic condition (Leistikow, 2001b). Vandel (1968) recognized to *Tropiscia* the elongated tricorn-like structure as *noduli laterales*. Based on Vandel (1968), a reduction or modification of this structure can not be discarded, and further investigations need to be evaluated within *Ischioscia*, in order to recognized possible *noduli laterales* and test the hypothesis of *Tropiscia* as representative of *Ischioscia*. Independently, our results reinforce the relations between both taxa.

Ischioscia **Verhoeff, 1928b**

(Figure 11)

Type species. *Ischioscia lobifera* Verhoeff, 1928b by monotypy; synonym of *Philoscia variegate* Dollfus, 1893 (non Dollfus, 1898).

Concavities values constructed: *0* to *24*.

Synapomorphy: carpus of pereiopod 1 enlarged, conferring plate-like appearance [077 – 1].

The genus *Ischioscia* has been discussed in several contributions (Schmalfuss, 1980; Leistikow, 1997, 1999a, 2000a, 2001b, g; Leistikow & Schmidt, 2002a, b). The genus is regarded as Neotropical representative and characterized by symplesiomorphies: male carpus of pereiopod 1 enlarged to a plate-like extension, scale fields of male pereiopod 1 covering frontal side of the merus, carpus and propodus, male pereiopod 7 ischium with ventral field of of hair-like scales, and catylus with long inner claw (Leistikow & Schmidt, 2002a).

The monotypic *Mirtana* was recently proposed by Leistikow (1997) to include the species *M. costaricensis* from Costa Rica. The genus shows many affinities with *Ischioscia*, such as presence of *linea frontalis*, no *noduli laterales*, pleotelson with distal ventral apical pit, shape of and aesthetascs arrangement on first antenna, second antenna flagellum with apical organ long, shape of buccal appendages, pereopods with wide setae fields, dactylus with long inner claw and and dactilar organ, and shape of male pleopod 1 exopod. Moreover, the genus shows particular characters which probably evolved convergently to attend habitat pressure and could be mentioned here as autapomorphies, such as dorsum tegument slightly granulate with short tricorn scale-seta, and neopleurae well developed confering the pleon a continuous aspect with pereon.

The monophyly of *Ischioscia* was recovered herein, as in the studies of Leistikow (2001b) and Leistikow & Schmidt (2002a). Our results not recovered the same charaters proposed by the author, probably because of the low taxon sampling and coding method. Based in the relations recovered here and those mentioned affinities between *Ischioscia* and *Mirtana*, the genus should be placed within *Ischioscia* until further diversity investigations and phylogenetic analyses will be conduced. In addition, other characters supports the placement of *Mirtana* within *Ischioscia*, the triangular shape of distal par of pleotelson [013 – 0], presence of setae on second article of first antenna [026 – 1], and male pleopod 1 exopod with lateral process on outer margin, and endopod ornamented on outer distal portion [125 – 1, 139 – 1].

Halophilosciidae Kesselyák, 1931

(Figure 11)

Concavities values constructed: *0* to *24*.

Synapomorphies: dorsal tricorn scale-setae arrow-shaped [005 – 3], maxilla lobes with undistinct appearance, and outer and inner lobes subequals [054 – 1, 056 – 2], dactylus with long ungual seta, overpassing the distal margin of outer claw [105 – 3], male epleopod 1 endopod with setae resctricted to the apex [137 – 1], and pleopod 5 exopod with outer margin sinuous [149 – 0].

To date the family Halophilosciidae comprises three genera: *Halophiloscia*, *Littorophiloscia* and *Stenophiloscia* Verhoeff, 1908b (not sampled here).

Leistikow (2001b) recovered the family close related with Philosciidae, supported by male pereiopod 1 carpus and propodus enlarged, ungual seta strong and apically spatuliform and vasa deferentia run from the genital papilla in pereonite 7 rostrally and bend two times caudally and again rostrally. Schmidt (2003) recovered Halophilosciidae in an unsolved clade with the families Philosciidae and Scleropactidae, supported by second antenna with apical organ longer than distal article of flagellum, with sensory hairs enclosed in a common sheath and lateral free sensila reduced in size.

In this study the Halophilosciidae genera were recovered with close relations and will be further discussed. In addition the characters proposed here are in accordance with taxonomic studies of Taiti & Ferrara (1986b) and Leistikow (2001b).

As mentioned previously the genus *Nesophilsocia* demonstrated close relations with the family. Here *N. culebroides* was recovered in all weighting strategies with Halophilsociidae.

The characters recovered here to *N. culebroides* show many affinities with the Halophilosciidae genera, such as the reduced and arrow-like shape of dorsal tricorn scale-seta, shape of maxilla lobes and very long ungual seta, commonly observed in *Littorophiloscia* (see Taiti & Ferrara, 1986b). Moreover, in the study of Campos-Filho & Taiti (in preparation) *N. culebroides* demonstrate other similarities with *Littorophiloscia* in the *noduli laterales* inserted at similar distance from lateral margin, pleotelson appicaly rounded, maxilliped endite setose with penicil knob-like, uropod exopod twice longer than endopod, and shape of genital papilla.

In basis of recovered topology and morphological affinities with *Littorophiloscia*, the *Nesophiloscia culebroides* should be place into the family Halophilosciidae until further analyses will be conduce. Independently, as mentioned by Leistikow (2001b), the family Halophilosciidae needs a revision in worldwide scale.

***Halophiloscia* Verhoeff, 1908 and *Littorophiloscia* Hatch, 1947**

(Figure 11)

Type species. *Halophiloscia couchii* (Kinahan, 1857) and *Philoscia richardsonae* Holmes & Gay, 1904.

Concavities values constructed: *0* to *24*.

Exclusive Synapomorphy: ungual seta of dactylus appicaly spatulated [106 – 1].

Additional synapomorphy: pereopods with ventral margin of carpus with wide field of setae [087 – 1].

The genus *Halophiloscia* comprises 18 species reported to Mediterranean, coast of eastern Altantic, southern Caribbean and Neotropics, including Galapagos (Schmalfuss, 2003; Campos-Filho & Taiti, in preparation). The genus is mainly recognized by the apical bifurcate shape of genital papilla lamella (Leistikow, 2001b). Schmidt (2003) commented that the bifurcate tip of the male genital papailla evolved in response of vasa deferentia evolution, and postulated that the family probably is close related of Philosciidae. Leistikow (2001b) discussed the relations between *Halophiloscia* and *Stenophiloscia*, which both taxa exhibit similarities in bifurcate tip of genital papailla and complex arrangenment of vasa deferentia, and presence of many *noduli laterales* by epimeron.

The genus *Littorophiloscia* was revised by Taiti & Ferrara (1986b) and redefined by Leistikow (2001b). The genus is characterized by many morphological characteristics, such as short neopleurae, dorsal tricorn scale-setae cordiform-shaped, pleotelson with distal margin rounded and lateral margins concaves, first maxilla outer endite composed of 4 + 6 (outer set cleft), maxilliped endite hairy bearing penicil knob-like, pereiopod 1 carpus and propodus (sometimes pereiopod 2) enlarged with wide field of setae, dactylus with long and enlarged apex of ungual seta and cordiform shape of male pleopod 1 exopod.

Leistikow (2001b) recovered the relations between *Halophiloscia* and *Littorophiloscia* based in the shape of vasa deferentia, more complex in *Halophiloscia*. Here the relations between both taxa were recovered and the character proposed here are in accordance with taxonomy (see Taiti & Ferrara, 1986b, Leistikow, 2001b, and Schmidt, 2003).

The very complex shape of vasa deferentia was postulated as autapomorphy of *Halophiloscia* by Leistikow (2001b). Schmidt (2003) also recognized this character as autapomorphy and proposed four additional characters: genital papilla with bifurcated tip, spermatozoa arranged in 'tortilla-like' *sensu* Vandel (1962), male pleopod 1 endopod enlarged and maxilliped palp with tufts of setae with fringed appearance.

Here the genus was recovered in all weighting strategies, supported by one exclusive synapomorphy: the genital papilla with ventral shield as wide as long [112 – 1]; and four additional synapomorphies: mandibles with molar penicil composed of 10 branches [041 – 7], first maxilla outer endite composed of 5 + 6 teeth [046 – 0], male pleopod endopod with inner distal portion ornamented [138 – 1], male uropod exopod very long, more than twice as long as endopod [123 – 3]. These characteristics also corrobores with taxonomy (see Schmidt, 2003)

Rhyscotidae Budde-Lund, 1908

(Figure 11)

Concavities values constructed: *0* to *24*.

Exclusive Synapomorphies: hermaphrodites [002 – 1], and cephalothorax *postfrons* inflated [015 – 1].

To date the family Rhyscotidae comprises two genera with about 25 species reported to Central and South America and Africa (Schmidt, 2003). The family shows some unique characters within Oniscidea, the inflated appearance of the head and the hermaphroditism (Schmidt, 2003). The family was redefined and discussed in Crinocheta facies by Schmidt (2003).

As mentioned, Leistikow (2001b) recovered the family with unsolved relations with *Atlantoscia* and *Benthana*. Differently, Schmidt (2003, 2008) recovered the family as monophyletic and close related with Squamiferae clade (including Dubioniscidae, Platyarthridae and Spelaeniscidae).

The relations recovered here are probably an artefact of taxon sampling. Probably a wide sampling including higher diversity within Crinocheta lineages will produce better resolution to the family.

Balloniscidae Vandel, 1963

(Figure 8)

The family Balloniscidae was erected by Vandel (1963) to include the genera *Balloniscus* and *Plataoniscus* based on the presence of pleopodal lungs in all pleopod exopods. The author also commented about the differences on cephalothorax and lung structure between both taxa.

Leistikow (2001b) recovered the Balloniscidae genera *Balloniscus*, *Plataoniscus* and *Pulmoniscus* in an unsolved clade with Philosciidae and ‘higer Crinocheta’. Strangely, Schmalfus (2003) in his catalog assumed *Pulmoniscus* as a genus of Philosciidae, probably based on the relations recovered by Leistikow (2001b). However, in the latter author never postulated them as belonging to Philosciidae. Moreover, the author discussed close relations with Agnaridae based on the similar structure of pleopodal lungs. Lastly, *Pulmoniscus* is assumed here as Balloniscidae.

***Balloniscus* Budde-Lund, 1908**

(Figure 8)

Type species. *Philoscia sellowii* Brandt, 1833.

Concavities values constructed: *0* to *14*.

Synapomorphies: pleotelson appicaly acute [012 – 2], first maxilla outer lobe with subapical tubercle [052 – 1], pereopod 7 ischium with a ventral depression [098 – 1], dactylus inner claw reaching the distal margin of outer claw and dactylar organ pointed [104 – 1, 109 – 2], and male pleopod 1 exopod with distal margin straight [120 – 3].

To date the genus *Balloniscus* includes six species with records in South America (Schmalfuss, 2003). Araujo & Leistikow (1999) based on the shape of the first antennae and aesthetascs arrangement, shape of antennal grooming-brush of carpus 1 and type of ventral setae on merus and carpus of pereopods, discussed the relations between *Balloniscus* and the South America Philosciidae genera *Atlantoscia* and *Benthana*, and commented that these characters could support a common ancestry. Moreover, the authors commented that *Balloniscus* have more derivative characters linked with clinger habits, which contradicts the close relations with the runners *Atlantoscia* and *Benthana*.

Leistikow (2001b) redefined the genus and postulated two autapomorphies: presence of semi-covered pleopodal lungs and male pleopod 1 exopod subquadrangular-shaped.

Contrary to the hypotheses of Araujo & Leistikow (1999), Leistikow (2001b) recovered *Balloniscus* close related with *Plataoniscus* (further discussed), supported by the reduction of setae on carpus 1. Therefore, the relationships of both taxa were recovered in an unsolved clade with *Philoscia* and derivative lineages of Crinocheta. However, a comparisonbetween *Balloniscus* and

Philoscia may result in recovered relations as a result of artefact of sampling, since *Philoscia* shows many distinct characteristics, such as presence of *linea frontalis*, first antenna with aesthetascs appicaly inserted, first maxilla inner endite with apical tip, second maxilla with subequal lobes, maxilliped endite with apical tubercle and inner margin distally depressed, dactylar organ longer than outer claw, shape o male pleopod 1 and the presence of *Onyscus*-type lungs.

Our results are similar with those found by Leisitkow (2001b). The genus *Balloniscus* was recovered as monophyletic and close of Balloniscidae lineages and the characters corroborates taxonomy (see Araujo & Zardo, 1995; and Araujo & Leistikow, 1999). The homology hypothesys of partially uncovered pleopodal lungs *maculicornis*-type *sensu* Ferrara *et al.* (1994) was not confirmed here, since this structure occurs in other taxa sampled here. Furthermore, our results indicate that the pleopodal lungs evolved convergently within Crinocheta to meet environmental conditions imposed to respiration. Further analyses including higher taxa diversity within Crinocheta will elucidade the relations of the genus within Balloniscidae.

***Oniscophiloscia* Wahrberg, 1922**

(Figure 8)

Type species. *Philoscia* (*Oniscophiloscia*) *mirifica* Wahrberg, 1922 by monotypy and original designation.

Concavities values constructed: *13* to *22*.

Exclusive synapomorphies: *profrons* with inverted triangle-shaped lobe [018 – 0], and outer endite of first maxilla with teeth composition 4 + 7 [046 – 4].

Additional synapomorphies: pleotelson with distal margin triangular [013 – 1], maxillula outer endite with teeth composition 4 + 7 and inner set with apex simple [046 – 4, 047 – 0], pleopods exopods without repiratory area [106 – 0], pleopod 1 endopod bearing scales on inner distal portion and having a complex ornamented structure [135 – 1, 138 – 1, 139 – 1].

The genus *Oniscophiloscia* occurs only in Juan Fernández Islands and is considered an isolated representative of Crinocheta (Leistikow, 2001b). As in other Crinocheta, this taxon shows morphological characters adapted to the clinger functional category, such as strong pereopods and well developed neopleurae.

Leistikow (2001b) recovered *Oniscophiloscia* with unsolved relations with *Balloniscus*, *Plataoniscus* and *Pulmoniscus* (Balloniscidae), *Philoscia* (Philosciidae) (not sampled here), and derivative lineages within Crinocheta, supported by dorsal scale-seta as tricorn-like *sensu* Holdich (1984), and ischium 7 with more than 5 dorsal setae. Here, *Oniscophiloscia* configured the most basal clade of Balloniscidae, not in accordance with Leistikow (2001b). Among the characters proposed by Leistikow (2001b), or the relations between *Oniscophiloscia* and Balloniscidae, *Philoscia* and derivative Crinocheta, the presence of dorsal scale-seta tricorn-like *sensu* Holdich (1984) was confirmed here. In addition, the clinger condition was recovered as synapomorphy for the clade, except for *Balloniscus* + Philosciidae, which appear in the runner condition. Although the clinger condition is considered here as doubtful for *Balloniscus* and will be further discussed.

The inverted subtriangular lobe on cephalothorax and male pleopod 1 endopod distally ornamented are assumed here as synapomorphies of *Oniscophiloscia*. Regarding the taxonomic studies, the first maxilla outer endite with 4 + 7 teeth and pleopods exopods without respiratory areas were confirmed here as synapomorphies.

As mentioned in the character section, the clinger category as well as the related morphological adaptations probably evolved togheter and many times within Crinocheta, explained by convergence to meet the habitat conditions and reduce predator pressure.

Based on the relations recovered here and in the morphological affinities with Balloniscidae, the genus *Oniscophiloscia* should be placed into the family until further analyses can be conduced.

Plataoniscus Leistikow, 2001b and *Pulmoniscus* Leistikow, 2001b

(Figure 8)

Type species. *Plataoniscus borelli* by original designation and *Balloniscus insularuminfraventum* (Vandel, 1952) by monotypy.

Concavities values constructed: *13* and *14*.

Synapomorphies: first maxilla outer endite with outer set of teeth pectinate [047 – 2], pleopods exopods with pleopodal lungs *maculicornis*-type [113 – 3], and pleopod 2 exopod outer margin with shallow-angle (~180°) [143 – 3].

The genus *Plataoniscus* was first erected by Vandel (1963) without type species designation. Leistikow (2001b) re-examined the species described by Vandel and designated *P. borellii* (Dollfus, 1897) as the type of the genus. The author redefined the genus and postulated four autaomorphies: pleopod 1 and 2 exopods with monospiracular lungs and pleopod 3 to 5 multispiracular, perispiracular area with triangular or three-tipped cuticular scales as derivates of pectinate scales, pleopod exopods with central row of setae in apical region, and male pleopod 5 exopod with medial furrow of caudal surface.

The monotypic genus *Pulmoniscus* was erected by Leistikow (2001b) to include *P. insularuminfraventum*, originally described by Vandel (1952) as *Balloniscus* representative. The genus was redefined by Leistikow (2001b) and four autapomorphies were proposed: cephalothorax with lateral lobes, first maxilla outer endite with outer set of teeth crow-shaped 3-tipped, pleopod exopods with covered lungs and spiraculum opening distally at more than one third of lateral length. In addition, the author discussed the close relations with *Agnara* Budde-Lund, 1908 based on the shape of male pleopods.

As previously mentioned, Leistikow (2001b) recovered *Plataoniscus* close related to *Balloniscus*; the genus *Pulmoniscus* was recovered with unsolved relations with Balloniscidae, Philoscia and derivative Crinocheta.

Here both taxa demonstrated to be closely related. Despite the recovered relationships among them has not being built within a broader system of weighting, taxon showed close relationships with *Balloniscus* and *Oniscophiloscia*. Another hypothesis which could not be discharded is the family Balloniscidae belongs to Philosciidae. This idea can be discussed based onmorphology, in which all characters such as clinger habits, second antennae flagellum composed of three articles and apical organ shorter than distal article, shape of buccal appendages and derivative pleopodal lungs, also occurs in Philosciidae. However, further analyses including worldwide scale taxa sampling and molecular thecniques are necessary to confirm this hypothesis.

CLADISTC ANALYSES: IMPLIED WEIGHTING STRATEGY

The comparison of phylogenetic trees arises when alternative phylogenies are obtained using different phylogetic methods to access the stability of reconstruction methods and their different results (Alberich *et al*., 2009; Mir & Rosseló, 2010). In our case this comparison is given by different weighting regimes *sensu* Wheller (1995), and appears in the relations of *Abebaioscia*, *Anchiphiloscia* and *Burmoniscus,* in which a quite unespected result has arised: the non recovered node relationships in any searched weighting regime (see Fig. 10). The search of best *k* values *sensu* Mirande (2009) and the recognition of the most similar tree groups through SPR analyses should respect the metricity rule of triangle inequality *sensu* Wheeler (2012). In order to respect this rule, all tree groups recovered here in all concavities have similar distance. The result recovered for this clade does not indicate a spurious result, on the contrary, indicates that the tree space is wider. The Table 2 shows the best *k* value ranging from *10* (=9.381) to 15 (14.072) concavities, recognized by SPR analyses (Table 3). The SPR demonstrates that these concavites have the most similar tree topology, respecting the rule and keeping similar distance in the remaining concavity trees.

The best *k* value defined herein (=11.5473) and the non recovered cluster for the relations among *Abebaioscia*, *Anchiphiloscia* and *Burmoniscus*, indicate that this reconstruction is an additional tree, clearly observed trhough the concavity values of the Table 2. Each value constructs a different topology with similar distance among them. Our results suggest that the search of the best *k* value still has to be explored, in order to access more topologies within the best *k* value range. In addition, supporting this hypothesis in the clade recovered here (Figs 8-11) it is possible to observe that when the concavities *13* and *14* are recovered, the first three concavities are not, and the other way around. This is easily explained by the best *k* value (11.5473), which is more similar with the *13* and *14* concavities, but also respecting the triangle inequality rule, since it occurs within the best range.

JACKNIFE SUPPORTS

The jackknifing had not good measures for some clades and sometimes the jackknife CG showed high measures. However, these measures probably were influencied by the costs and the multistate matrix data as commented by Goloboff *et al.* (2003b).

TAXONOMY

Family Balloniscidae Vandel 1963

Genus *Oniscophiloscia* Warberg, 1922

Type species.

Philoscia (*Oniscophiloscia*) *mirifica* Wahrberg, 1922 by monotypy and original designation.

Diagnosis.

Leistikow (2001b).

Composition.

Oniscophiloscia anomala (Dollfus, 1980), *Oniscophiloscia kuscheli* Strouhal, 1961 and *Oniscophiloscia mirifica* Warberg, 1922.

Family Philosciidae Kinahan, 1857

Genus *Haloniscus* Chilton, 1920

Type species.

Haloniscus searlei Chilton, 1920 by monotypy.

Diagnosis.

Taiti & Humpreys (2001).

Composition.

Haloniscus anophthalmus Taiti, Ferrara & Iliffe, 1995, *Haloniscus longiantennatus* Taiti & Humphreys, 2001, *Haloniscus searlei* Chilton, 1920, *Haloniscus stylifer* Taiti & Humphreys, 2001 and *Haloniscus tomentosus* Taiti & Humphreys, 2001.

***Roraimoscia*-group Leistikow, 2001**

Tribe Ischiosciini Leistikow, 2001

Genus *Ischioscia* Verhoeff, 1928

Type species.

Ischioscia lobifera Verhoeff, 1928b by monotypy; synonym of *Philoscia variegate* Dollfus, 1893 (non Dollfus, 1898).

Diagnosis.

Leistikow (2000a, 2001b, g; Leistikow & Schmidt, 2002a).

Ischioscia costaricensis (Leistikow, 1997) n. comb.

Mirtana costaricensis Leistikow, 1997:119, plates I-VI; Leistikow & Wägele, 1999:19; Schmalfuss, 2003:146.

Diagnosis and description.

Leistikow (1997).

Distribution.

Cerro, Zurqui, Heredia, Costa Rica.

Tribe Prosekiini Leistikow, 2001

Genus *Alboscia* Schultz, 1995

Type species.

Alboscia elongata Schultz, 1995 by original designation.

Diagnosis.

Schultz (1995) and Araujo (1999).

Composition.

Alboscia elongata Schultz, 1995, *Alboscia itaipuensis* Araujo & Quadros, 2005, *Alboscia ornata* Araujo, 1999 and *Alboscia silveirensis* Araujo, 1999.

Genus *Androdeloscia* Leistikow, 1999

Type species.

Androdeloscia hamigera (Vandel, 1952) by original designation (Leistikow, 1999b).

Diagnosis.

Leistikow (1999b) and Schmidt & Leistikow (2005).

Androdeloscia albamaculata **(Lima, 1996) n. comb.**

Prosekia albamaculata Lima, 1996: 102, figs. 1-17; Souza-Kury, 1998:661; Leistikow & Wägele, 1999: 22; Schmalfuss, 2003:216.

Diagnosis and description.

Lima (1996).

Distribution.

Amazonia, Brazil.

Androdeloscia lejeunei **(Lemos de Castro & Souza, 1986) n. comb.**

Prosekia lejeunei Lemos de Castro & Souza, 1986, 432, figs 13-26; Souza-Kury, 1998:662; Leistikow & Wägele, 1999: 22; Schmalfuss, 2003:216.

Diagnosis and description.

Lemos de Castro & Souza (1986).

Distribution.

Pará, Brazil.

Androdeloscia tarumae **(Lemos de Castro, 1984) n. comb.**

Prosekia tarumae Lemos de Castro, 1984: 442, figs. 1-12; Souza-Kury, 1998:662; Leistikow & Wägele, 1999: 22; Schmalfuss, 2003:217.

Diagnosis and description.

Lemos de Castro (1984).

Distribution.

Amazonia, Brazil.

Androdeloscia rutilans **(Vandel, 1952) n. comb.**

Chaetophiloscia rutilans Vandel, 1952: 124, figs 39-41; Leistikow & Wägele, 1999: 22; Schmalfuss, 2003:217.

Prosekia rutilans; Leistikow, 2001j: 112, figs 1-6..

Diagnosis and description.

Leistikow (2001j).

Distribution.

El Junquito, Venezuela.

Genus *Leonardoscia* Campos-Filho, Araujo & Taiti, 2014

Type species.

Leornadoscia hassalli Campos-Filho, Araujo & Taiti, 2014 by monotypy and original designation.

Diagnosis.

Campos-Filho *et al*. (2014).

Distribution.

Pará, Brazil.

Genus *Metaprosekia* Leistikow, 2000

Type species.

Metaprosekia nodilinearis Leistikow, 2000c by monotypy.

Diagnosis.

Leistikow (2000c) and Campos-Filho *et al*. (2014).

Metaprosekia caupe Campos-Filho, Araujo & Taiti, 2014

Metaprosekia caupe Campos-Filho *et al.*, 2014:387, figs 20-22 and 40.

Diagnosis and description.

Campos-Filho *et al*. (2014).

Distribution.

Brazil, state of Pará.

Metaprosekia quadriocelata Campos-Filho, Araujo & Taiti, 2014

Metaprosekia quadriocelata Campos-Filho *et al.*, 2014:383, figs 17-19 and 40.

Diagnosis and description.

Campos-Filho *et al*. (2014).

Distribution.

Pará, Brazil.

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Figure Captions

Figure 1. *Benthana picta* (Brandt, 1833): A, Habitus, dorsal; B, cephalothorax, frontal; C, piliform scale-seta; D, pleotelson. *Androdeloscia galapagensis* (Anderson, 1960): E, Habitus, dorsal; F, cephalothorax, frontal; G, piliform scale-seta; H, pleotelson. *Nesophiloscia culebroides* (Van Name, 1924): I, Habitus, dorsal; J, cephalothorax, frontal; K, arrow-like scale-seta; L, pleotelson. *Atlantoscia sulcata* Campos-Filho, Lisboa & Araujo, 2013: M, Habitus, dorsal; N, cephalothorax, frontal; O, *nodulus lateralis*; P, piliform scale-seta; Q, pleotelson. Scale bar: 1 mm.

Figure 2. First and second antennae, male. A, B, *Benthana picta* (Brandt, 1833); C, D, *Littorophiloscia denticulata* (Ferrara & Taiti, 1982); E, F, *Ischioscia amazonica* Lemos de Castro, 1955; G, H, *Androdeloscia galapagensis* (Anderson, 1960).

Figure 3. *Benthana* n. sp. 3: A, left mandible; B, right mandible. *Benthana picta* (Brandt, 1833): C, left mandible, D, right madible; E, first maxilla; H, second maxilla; K, maxilliped, arrow indicating tooth-like ornamentation. *Leonardoscai hassalli* Campos-Filho, Araujo & Taiti, 2014: F, first maxilla. *Littorophiloscia denticulata* (Ferrara & Taiti, 1982): G, first maxilla; I, second maxilla. *Ischioscia amazonica* Lemos de Castro, 1955: J, second maxilla. *Nesophiloscia culebroides* (Van Name, 1924): L, maxilliped, arrow indicating penicil knob-like. *Atlantoscia petronioi* Campos-Filho, Contreira & Lopes-Leitzke, 2012: M, maxilliped.

Figure 4. Pereopod 1, dactylus and uropod, male. A, B, *Benthana picta* (Brandt, 1833); C, D, *Ischioscia amazonica* Lemos de Castro, 1955; E, F, *Littorophiloscia denticulata* (Ferrara & Taiti, 1982); G, H, *Androdeloscia galapagensis* (Anderson, 1960).

Figure 5. Pleopods 1 and 2, pleopod 5 exopod and genital papilla, male. *Benthana picta* (Brandt, 1833): A, pleopod 1; B, pleopod 2; C, pleopod 5 exopod; D, genital papilla. *Androdeloscia galapagensis* (Anderson, 1960): E, pleopod 1; F, pleopod 2; G, pleopod 5 exopod. Littorophiloscia culebroides (Van Name, 1924): H, pleopod 1; I, pleopod 2; J, pleopod 5 exopod; K, genital papilla.

Figure 6. Strict consensus tree from equal weigths analysis, part A.

Figure 7. Strict consensus tree from equal weigths analysis, part B.

Figure 8. Strict consensus tree of two cladograms resulting from best *k* value for the morphological data with the implied weighting scheme. Navajo rug (on left) of 5 x 5 axis representing all concavities analyzed. Green highlights the most similar tree groups recognized thought SPR analysis. Dashed clades indicate weighting regime recovered. EW indicate clades also recovered with equal weights analysis. Jacknife SR/GC resampling represented in the upper portion of the nodes.

Figure 9. Clade A representing the recovered relations with best *k* value for *Aphiloscia* Budde-Lund, 1908, *Benthana* Budde-Lund, 1908 and *Pseudophiloscia* Budde-Lund, 1904.

Figure 10. Clade B representing the recovered relations with best *k* value for *Abebaioscia* Vandel, 1973, *Adeloscia* Vandel, 1977, *Alboscia* Schultz, 1995, *Anchiphiloscia* Stebbing, 1908, *Andenoniscus* Verhoef, 1941, *Androdeloscia* Leistikow, 1999, *Atlantoscia* Ferrara & Taiti, 1981,

Burmoniscus Collinge, 1914, *Erophiloscia* Vandel, 1972, *Floridoscia* Schultz & Johnson, 1984, *Leonardoscia* Campos-Filho, Araujo & Taiti, 2014, *Metaprosekia* Leistikow, 2000, *Paraguascia* Schultz, 1995 and *Xiphoniscus* Vandel, 1968.

Figure 11. Clade C representing the recovered relations with best *k* value for *Andricophiloscia* Vandel, 1973, *Caraiboscia* Vandel, 1968, *Colombophiloscia* Leistikow, 2001, *Ctenoscia* Verhoeff, 1928, *Formicascia* Leistikow, 2001, *Haloniscus* Chilton, 1920, *Ischioscia* Verhoeff, 1928, *Mirtana* Leistikow, 1997, *Nesophiloscia* Vandel, 1968, *Oxalaniscus* Leistikow, 2000, *Parischioscia* Lemos de Castro, 1967, *Pentoniscus* Richardson, 1913, *Portoricoscia* Leistikow, 1999, *Quintanoscia* Leistikow 2000, *Roraimoscia* Leistikow 2001, *Tropiscia* Vandel, 1968 and *Yaerikima* Leistikow, 2001 and the families Halophilosciidae and Rhyscotidae.

Table 1. List of terminal taxa, literature and distribution. Abbreviations: AL, Alagoas; AM, Amazônia; AP, Amapá; BA, Bahia; DF, Distrito Federal; ES, Espírito Santo; MG, Minas Gerais; PA, Pará; PR, Paraná; SC, Santa Catarina; SE, Sergipe; SP, São Paulo; RJ, Rio de Janeiro; RS, Rio Grande do Sul.

Taxon	Literature	Distribution
Scyphacidae Schmidt, 2002		
Haloniscus Chilton, 1920		
H. longiantennatus Taiti & Humphreys, 2001	Taiti & Humphreys (2001).	Australia: Murchison region.
H. tomentosus Taiti & Humphreys, 2001	Taiti & Humphreys (2001).	Australia: Murchison region.
H. stilifer Taiti & Humphreys, 2001	Taiti & Humphreys (2001).	Australia: Murchison region.
Detonidae Budde-Lund, 1906		
Armadilloniscus Uljanin, 1875		
A. caraibicus Paoletti & Stinner, 1989	Paoletti & Stinner (1989), Schmidt (2002).	Venezuela.
A. conglobator Taiti & Ferrara, 1989	Taiti & Ferrara (1989).	New Caledonia.
A. lamellatus Taiti & Ferrara, 1989	Taiti & Ferrara (1989).	Somalia, Malaysia, Indonesia and Philippines.
Deto Guerin-Meneville, 1836		
D. marina (Chilton, 1885)	Chilton (1885) and Schimidt (2002).	Australia.
D. echinata Guerin-Meneville, 1836	Budde-Lund (1906), Chilton (1915), Coleman & Leistikow (2001) and Leistikow (2001b).	Namibia and South Africa.
Alloniscidae Schmidt, 2003		
Alloniscus Dana, 1854		
A. oahuensis Budde-Lund, 1885	Ferrara & Taiti (1983a) and Schultz (1984).	Littoral from Indian and Pacific Ocean.

A. perconvexus Dana, 1854	Schultz (1984).	EUA: California and Vancouver island, and ?Japan.
A. pigmentatus Budde-Lund, 1885	Schmidt (2003).	Madagascar, Aldabra island, Chagos, Comoro, Mozambique and China.
Rhyscotidae Budde-Lund, 1908		
Rhyscotus Budde-Lund, 1885		
R. sphaerocephalus Budde-Lund, 1893	Schmalfuss & Ferrara (1978) and Schmidt (2003).	Ecuador (Galapagos islands), and Venezuela
Rhyscotoides Arcangeli, 1949		
R. parallelus (Budde-Lund, 1893)	Vandel (1952) and Mulaik (1960).	Mexico, Ecuador (Galapagos islands), Venezuela and Angola.
Balloniscidae Vandel, 1963b		
Balloniscus Budde-Lund, 1908		
B. glaber Araujo & Zardo, 1996	Araujo & Zardo (1996).	Brazil (RS).
B. sellowii (Brandt, 1833)	Araujo & Leistikow (1999), Leistikow & Araujo (2001) and Schmidt & Wägele (2001).	Brazil (SC and RS), Uruguay, and Argentina: Buenos Aires.
Plataoniscus Leistikow, 2001		
P. borellii (Dollfus, 1897)	Arcangeli (1958), Vandel (1963) Leistikow (2001b).	Bolivia and Argentina.
Halophilosciidae Kesselyák, 1930		
Halophiloscia Verhoeff, 1908a		
H. couchi (Kinahan, 1858)	Ferrara & Taiti (1978) and Schmidt (2003).	Coasts of the Atlantic from Senegal to the British Isles, Atlantic islands, Mediterranean

		and Black sea, introduced in Americas and Australia.
Halophiloscia sp.	Campos-Filho & Taiti, in preparation.	Ecuador: Galapagos islands.
Littorophiloscia Hatch, 1947		
L. culebroides (Van Name, 1924)	Van Name (1924) and Campos-Filho & Taiti (in preparation).	Ecuador: Galapagos islands.
L. denticulata (Ferrara & Taiti, 1982)	Ferrara & Taiti (1982b), Taiti & Ferrara (1986b) and Leistikow (2000b).	Andaman Islands, Guatemala, and Brazil (BA).
L. insularis (Lemos de Castro & Souza, 1986)	Lemos de Castro & Souza (1986) and Leistikow (2001b).	Brazil (BA) and Venezuela.
Philosciidae Kinahan, 1857		
Abebaioscia Vandel, 1973		
A. troglodytes Vandel, 1973	Vandel (1973).	Australia: Pannikin cave, Nullabor Plain.
Adeloscia Vandel, 1977		
A. dawsoni Vandel, 1977	Vandel (1977) and Leistikow (1998a).	New Zealand: North island.
Alboscia Schultz, 1995		
A. elongata Schultz, 1995	Schultz (1995).	Paraguay: Concepcion.
A. itapuensis Araujo & Quadros, 2005	Araujo & Quadros (2005).	Brazil (RS).
A. ornata Araujo, 1999	Araujo (1999).	Brazil (RS).
A. silveirensis Araujo, 1999	Araujo (1999).	Brazil (RS).
Anchiphiloscia Stebbing, 1908		
A. aelleni (Ferrara & Taiti, 1982)	Ferrara & Taiti (1982a, 1986).	Kenia: Shimoni cave; and Tanzania: Tanga.

A. karongae Stebbing, 1908	Stebbing (1908) and Ferrara & Taiti (1986).	Malawi: Kabwe.
A. pilosa (Budde-Lund, 1913)	Ferrara & Taiti (1986).	Chagos Archipelago; Salomon Island; Malaysia; Indonesia: Java and Bali; Krakatau and Hawaii.
A. suarezi (Dollfus, 1895)	Ferrara & Taiti (1986).	Madagascar; Comoro Islands: Pomoni and Mirontsi (Anjouan) and Grande Comore; and Seychelles: Coetivy, Félicité and Poivre Islands (Amirantes).
Andenoniscus Verhoef, 1941		
A. schmalfussi Leistikow, 1999	Leistikow (1999a).	Panama.
A. silvaticus Verhoeff, 1941	Verhoeff (1941) and Leistikow (1998b).	Peru: Sivia.
Andricophiloscia Vandel, 1973		
A. pedisetosa Taiti & Humpreys, 2001	Taiti & Humpreys (2001).	Australia: Lake way, Murchison region.
A. stepheni (Nicholls & Barnes, 1926)	Taiti & Humpreys (2001).	Australia: Tenidewa and Geraldton areas.
Androdeloscia Leistikow, 1999		
A. formosa (Mulaik, 1960)	Mulaik (1960) and Leistikow (2000b).	Mexico: Tabasco; and Guatemala: Petén.
A. hamigera (Vandel, 1952)	Vandel (1952) and Leistikow (1999b).	Venezuela: Caripe and Penisula de Paria.
A. valdezi Leistikow, 2000	Leistikow (2000b).	Guatemala: Petén and Zacapa.

Aphiloscia Budde-Lund, 1908		
A. annulicornis (Budde-Lund, 1885)	Ferrara *et al*. (1994).	Madagascar, Comoro, Mauritius, Réunion and Seychelles.
A. cunningtoni (Stebbing, 1908)	Ferrara & Taiti (1986).	Zambia.
A. fusca Ferrara, Paoli & Taiti, 1994	Ferrara *et al*. (1994).	Madagascar.
A. maculicornis (Budde-Lund, 1898)	Taiti & Ferrara (1980) and Ferrara *et al*. (1994).	Kenya, Uganda, Tanzania, Zaire, Zambia, Malawi and Zimbabwe.
A. rwandaensis Ferrara, Paoli & Taiti, 1994	Ferrara *et al*. (1994).	Rwanda: Kigali.
Atlantoscia Ferrara & Taiti, 1981		
A. ituberasensis Campos-Filho, Lisboa & Araujo, 2011	Campos-Filho *et al*. (2013a).	Brazil (BA).
A. floridana (Van Name, 1940)	Taiti & Ferrara (1991a), Araujo & Leistikow (1999), Leistikow & Araujo (2001) and Campos-Filho *et al*. (2013a).	EUA: Florida; from nothern to southern Brazil, Argentina, and Ascension and St. Helena islands
A. petronioi Campos-Filho, Contreira & Lopes-Leitzke, 2012	Campos-Filho *et al*. (2012).	Brazil (RS).
A. rubromarginata Araujo & Leistikow, 1999	Araujo & Leistikow (1999) and Campos-Filho *et al*. (2013a).	Brazil (AL, SE and BA).
A. sulcata Campos-Filho & Araujo, 2013	Campos-Filho *et al*. (2013a).	Brazil (SP).
Benthana Budde-Lund, 1908		
B. albomarginata Lemos de Castro, 1958	Lemos de Castro (1958a).	Brazil (ES and SP).
B. araucariana Araujo & Lopes, 2003	Araujo & Lopes (2003).	Brazil (RS).
B. bocainensis Lemos de Castro, 1958	Lemos de Castro (1958a) and Campos-Filho *et al*. (submitted).	Brazil (RJ and SP).
B. cairensis Sokolowicz, Araujo & Boelter, 2008	Sokolowcz *et al*. (2008) and Campos-Filho *et al*. (submitted).	Brazil (PR, SC and RS).
B. carijos Costa, Campos-Filho & Araujo, 2014	Costal *et al*. (2014).	Brazil (SP and SC).
B. convexa Lemos de Castro, 1958	Lemos de Castro (1958a) and Araujo & Leistikow (1999).	Brazil (MG, RJ, SP and SC).
B. dimorpha Lemos de Castro, 1985	Lemos de Castro (1985) and Campos-Filho *et al*. (submitted).	Brazil (ES).

B. guayanas Campos-Filho, Costa & Araujo, 2013	Campos-Filho *et al*. (2013b).	Brazil (SP and PR).
B. iporangensis Lima & Serejo, 1993	Lima & Serejo (1993) and Campos-Filho *et al*. (submitted).	Brazil (SP).
B. itaipuensis Campos-Filho & Araujo, 2011	Campos-Filho & Araujo (2011).	Brazil (PR).
B. longicaudata (Lemos de Castro, 1958)	Lemos de Castro (1958b) and Leistikow & Araujo (2006).	Brazil (MG, RJ and SP).
B. longicornis Verhoeff, 1941	Campos-Filho *et al*. (submitted).	Brazil (DF, SP, PR and SC).
B. longipenis Lemos de Castro, 1958	Lemos de Castro (1958a) and Campos-Filho *et al*. (submitted).	Brazil (MG, RJ, SP and RS).
B. moreirai Lemos de Castro, 1985	Lemos de Castro (1985) and Campos-Filho *et al*. (submitted).	Brazil (SP and SC).
B. olfersii Lemos de Castro, 1958	Lemos de Castro (1958a) and Campos-Filho *et al*. (submitted).	Brazil (RJ and SP).
B. picta (Brandt, 1833)	Campos-Filho *et al*. (submitted).	Brazil (MG, ES, RJ, SP, PR, SC and RS), and Paraguay: Villarica.
B. santosi Lemos de Castro, 1958	Lemos de Castro (1958a) and Campos-Filho *et al*. (submitted).	Brazil (MG, RJ, SP and SC).
B. schmalfussi Campos-Filho, Costa & Araujo, 2013	Campos-Filho *et al*. (2013b).	Brazil (RJ).
B. schubarti Lemos de Castro, 1958	Lemos de Castro (1958a) and Campos-Filho *et al*. (submitted).	Brazil (MG, RJ and SP).
B. serrana Araujo & Lopes, 2003	Araujo & Lopes (2003) and Campos-Filho *et al*. (submitted).	Brazil (RJ and SP).
B. sulcata Gruner, 1955	Campos-Filho *et al*. (submitted).	Brazil (RJ, SP and PR).
B. taeniata Araujo & Buckup, 1994	Leistikow & Araujo (2006).	Brazil (DF, MG, RJ, SP, PR, SC and RS).
B. trinodulata Araujo & Lopes, 2003	Araujo & Lopes (2003) and Campos-Filho *et al*. submitted.	Brazil (RS).
B. werneri Lemos de Castro, 1958	Lemos de Castro (1958) and Campos-Filho *et al*. submitted.	Brazil (SP).
B. aimorés Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. submitted.	Brazil (ES).
B. goitacás Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. submitted.	Brazil (ES).
B. tupinambá Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. submitted.	Brazil (BA).
B. canastraensis Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. submitted.	Brazil (MG).
Burmoniscus Collinge, 1914		
B. andersoni Taiti & Manicastri, 1988	Taiti & Manicastri (1988).	Sri Lanka.
B. beroni Taiti & Manicastri, 1988	Taiti & Manicastri (1988).	Sri Lanka: Kuruvita

		(Sabaragamuwa).
B. coecus (Budde-Lund, 1894)	Taiti & Ferrara (1986a).	Burma: Moulmein.
B. comptus (Budde-Lund, 1894)	Taiti & Ferrara (1986a).	Burma: Monti Carin.
B. gibbosus Taiti & Manicastri, 1988	Taiti & Manicastri (1988).	Sri Lanka: Kuruvita (Sabaragamuwa) and Yakkala (Yongammulla).
B. kohleri (Schmalfuss & Ferrara, 1978)	Schmalfuss & Ferrara (1978) and Leistikow (2000b).	Cameroon: Victoria; São Tomé Island; and Guatemala: Izabal region.
B. meeusei (Holthuis, 1947)	Taiti & Ferrara (1991b) and Araujo *et al*. (1996).	England; Hawaii: Kalapana; Brazil (SC); and Taiwan.
B. ocellatus (Verhoeff, 1928a)	Taiti & Ferrara (1986a).	China, Hong Kong and Taiwan.
B. stilifler Taiti & Manicastri, 1988	Taiti & Manicastri (1988).	Sri Lanka: Karagala and Kuruvita (Sabaragamuwa).
Caraiboscia Vandel, 1968		
C. christiani Leistikow, 2001	Leistikow (2001d).	Venezuela: Peninsula de Paria.
C. microphthalma Vandel, 1968	Vandel (1968) and Leistikow (2001d).	Guadaloupe: Goubeyre.
Colombophiloscia Leistikow, 2001		
C. alticola Vandel, 1968	Vandel (1968) and Leistikow (2001d).	Ecuador: Baños.
C. naevigesta Vandel, 1968	Vandel (1968).	Ecuador: Santa Cruz Island (Galapagos).
Ctenoscia Verhoeff, 1928		
C. mínima (Dollfus, 1892)	Jackson (1926a), Verhoeff (1928c), Vandel (1946) and Rodriguez & Barrientos (1993).	Canary Islands, Portugal, Spain, Menorca Island and La Galite

		Archipelago.
Erophiloscia Vandel, 1972		
E. acanthifera Leistikow, 2001	Leistikow (2001e).	Peru: Huanuco.
E. recurvata Leistikow, 2001	Leistikow (2001e).	Peru: Huanuco.
E. waegelei Leistikow, 2001	Leistikow (2001e).	Colombia.
Floridoscia Schultz & Johnson, 1984		
F. fusca Schultz & Johnson, 1984	Schultz & Johnson (1984).	EUA: Crandon Park, Florida.
Formicascia Leistikow, 2001		
F. inquilina (Van Name, 1936)	Van Name (1936) and Leistikow (2001f).	Guyana.
Ischioscia Verhoeff, 1928		
I. amazonica Lemos de Castro, 1955	Lemos de Castro (1955) and Leistikow & Schmidt (2002a, 2002b).	Brazil (AM).
I. bolivari Vandel, 1968	Vandel (1968) and Leistikow & Schmidt (2002a).	Brazil (AM).
I. colorata Leistikow, 2001	Leistikow (2001g) and Leistikow & Schmidt (2002a).	Venezuela.
I. curvaculeus Leistikow, 2001	Leistikow (2001h) and Leistikow & Schmidt (2002a).	Colombia.
I. cadoangelis Leistikow, 2000	Leistikow (2000a).	Costa Rica.
I. sturmi (Vandel, 1972)	Vandel (1972) and Leistikow & Schmidt (2002a, 2002b).	Colombia.
Leonardoscia Campos-Filho, Araujo & Taiti, 2014		
L. hassali Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. (2014).	Brazil (PA).
Metaprosekia Leistikow, 2000		
M. caupe Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. (2014).	Brazil (PA).
M. nodilinearis Leistikow, 2000	Leistikow (2000b).	Venezuela.

M. quadriocelata Campos-Filho, Araujo & Taiti, 2014	Campos-Filho *et al*. (2014).	Brazil (PA).
Mirtana Leistikow, 1997		
M. costaricensis Leistikow, 1997	Leistikow (1997).	Costa Rica.
Nesophiloscia Vandel, 1968		
Nesophiloscia sp.	Campos-Filho & Taiti (in preparation).	Ecuador: Galapagos islands.
Oniscophiloscia Wahrberg, 1922		
O. anomala (Dollfus, 1890)	Van Name (1936), Strouhal (1961) and Leistikow (2001b).	Chile: Juan Fernández islands.
O. mirifica Wahrberg, 1922	Van Name (1936), Strouhal (1961) and Leistikow (2001b).	Chile: Juan Fernández islands.
Oxalaniscus Leistikow, 2000		
O. ctenoscoides (Mulaik, 1960)	Mulaik (1960) and Leistikow (2000b).	Mexico: Chiapas.
Paraguascia Schultz, 1995		
P. pigmentata Schultz (1995)	Schultz (1995).	Paraguay: Misiones.
Parischioscia Lemos de Castro, 1967		
P. omissa (Van Name, 1936)	Van Name (1936), Lemos de Castro (1967) and Leistikow (2001f).	Guyana, French Guyana, and Brazil (AP).
Pentoniscus Richardson, 1913		
P. pruinosus Richardson, 1913	Van Name (1936), Schultz (1969) and Leistikow (1998c).	Costa Rica.
P. vargasae Leistikow, 1998	Leistikow (1998c).	Costa Rica.
Portoricoscia Leistikow, 1999		
P. richmondi (Richardson, 1901)	Van Name (1936) and Leistikow (1999c).	Puerto Rico.

Pseudophiloscia Budde-Lund, 1904		
P. chilenica (Verhoeff, 1939)	Verhoeff (1939), Leistikow (1998a, 1998b) and Leistikow (2001i).	Chile.
P. inflexa Budde-Lund, 1904	Budde-Lund (1904), Leistikow (1998a) and Leistikow (2001i).	Chile.
Pulmoniscus Leistikoiw, 2001		
P. insularuminfraventum (Vandel, 1952)	Vandel (1952) and Leistikow (2001b).	Venezuela: Windward islands.
Quintanoscia Leistikow 2000		
Q. contoyensis (Mulaik, 1960)	Mulaik (1960) and Leistikow (2000b).	Mexico: Yucatán Peninsuka.
Roraimoscia Leistikow, 2001		
R. roraimae (Van Name, 1936)	Van Name (1936) and Leistikow (2001f).	Venezuela.
Tropiscia Vandel, 1968		
T. flagellata Vandel, 1968	Vandel (1968) and Leistikow (2001a).	Ecuador: province Oriente.
Xiphoniscus Vandel, 1968		
X. mirabilis Vandel, 1968	Vandel (1968) and Leistikow (2000c).	Ecuador: Puyo.
Yaerikima Leistikow, 2001		
Y. kartaboana (Van Name, 1936)	Van Name (1936) and Leistikow (2001f).	Guyana.

Table 2. Implied results. Highlight to indicate the concavity range for the *kē* value.

k	**Distortion (%)**	***k* Ref**	**Tree length**	**Trees**	**Fit**	**difspr**	**agree**	**nodcons**
k0	50	4.691	1672	2	72.335	0	0	0
k1	51.667	5.014	1672	2	70.724	0	122	120
k2	53.333	5.361	1668	2	69.096	3	119	115
k3	55	5.733	1668	2	67.449	0	122	120
k4	56.667	6.134	1668	2	65.783	0	122	120
k5	58.333	6.567	1652	1	64.093	14	74	93
k6	60	7.036	1652	1	62.369	3	116	114
k7	61.667	7.546	1652	2	60.619	0	121	119
k8	63.333	8.102	1652	2	58.84	0	121	119
k9	65	8.711	1643	2	57.025	5	113	109
k10	66.667	**9.381**	1632	1	55.173	9	99	102
k11	68.333	**10.122**	1632	1	53.265	0	123	121
k12	70	**10.945**	1632	1	51.316	0	123	121
k13	71.667	**11.865**	1627	2	49.321	6	109	112
k14	73.333	**12.899**	1627	2	47.274	0	122	120
k15	75	**14.072**	1628	1	45.173	16	96	93
k16	76.667	15.412	1605	1	43.001	28	59	78
k17	78.333	16.958	1608	1	40.747	29	48	79
k18	80	18.763	1607	1	38.425	13	98	101
k19	81.667	20.895	1606	1	36.009	5	100	112
k20	83.333	23.453	1606	1	33.507	0	123	121
k21	85	26.58	1606	1	30.908	0	123	121
k22	86.667	30.489	1604	1	28.198	2	121	119
k23	88.333	35.515	1596	1	25.357	15	80	83
k24	90	42.216	1596	1	22.37	20	85	75
kē		**11.5473**	**1629**					

Table 3. SPR comparison results. Total amount highlighted to indicate the most similar tree groups, indicating the *k* range to calculate the *kē*. Legend: *k*, concavity; *kē*, medium value from most congruent concavity.

SPR	***k0***	***k1***	***k2***	***k3***	***k4***	***k5***	***k6***	***k7***	***k8***	***k9***	***k10***	***k11***	***k12***	***k13***	***k14***	***k15***	***k16***	***k17***	***k18***	***k19***	***k20***	***k21***	***k22***	***k23***	***k24***
k0	**0**	0	9	9	14	14	23	23	27	30	30	30	30	30	30	30	41	44	44	45	45	44	45	49	49
k1	0	**0**	9	9	14	14	23	23	27	30	30	30	30	30	30	30	41	44	44	45	45	44	45	49	49
k2	9	9	**0**	0	8	8	15	15	25	29	28	28	28	28	28	28	35	38	38	38	38	39	38	43	43
k3	9	9	0	**0**	8	8	15	15	25	29	28	28	28	28	28	28	35	38	38	38	38	39	38	43	43
k4	14	14	8	8	**0**	0	15	15	26	31	30	30	30	30	30	30	37	39	39	43	41	40	41	45	45
k5	14	14	8	8	0	**0**	15	15	26	31	30	30	30	30	30	30	37	39	39	41	41	40	41	45	45
k6	23	23	15	15	15	15	**0**	0	14	19	20	20	20	20	20	20	27	29	29	41	41	41	41	45	45
k7	23	23	15	15	15	15	0	**0**	14	19	20	20	20	20	20	20	27	29	29	41	41	41	41	45	45
k8	27	27	25	25	26	26	14	14	**0**	14	15	15	15	15	15	15	27	29	29	42	42	43	42	44	44
k9	30	30	29	29	31	31	19	19	14	**0**	1	1	1	1	1	1	21	24	24	38	38	40	38	41	41
k10	30	30	28	28	30	30	20	20	15	1	**0**	0	0	0	0	0	20	23	23	37	37	39	37	40	40
k11	30	30	28	28	30	30	20	20	15	1	0	**0**	0	0	0	0	20	23	23	37	37	39	37	40	40
k12	30	30	28	28	30	30	20	20	15	1	0	0	**0**	0	0	0	20	23	23	37	37	39	37	40	40
k13	30	30	28	28	30	30	20	20	15	1	0	0	0	**0**	0	0	20	23	23	37	37	39	37	40	40
k14	30	30	28	28	30	30	20	20	15	1	0	0	0	0	**0**	0	20	23	23	37	37	39	37	40	40
k15	30	30	28	28	30	30	20	20	15	1	0	0	0	0	0	**0**	20	23	23	37	37	39	37	40	40
k16	41	41	35	35	37	37	27	27	27	21	20	20	20	20	20	20	**0**	3	3	23	23	19	23	25	25
k17	44	44	38	38	39	39	29	29	29	24	23	23	23	23	23	23	3	**0**	0	20	20	16	20	22	22
k18	44	44	38	38	39	39	29	29	29	24	23	23	23	23	23	23	3	0	**0**	20	20	16	20	22	22
k19	45	45	38	38	41	41	41	41	42	38	37	37	37	37	37	37	23	20	20	**0**	0	5	2	10	10
k20	45	45	38	38	41	41	41	41	42	38	37	37	37	37	37	37	23	20	20	0	**0**	5	0	10	10
k21	44	44	39	39	40	40	41	41	43	40	39	39	39	39	39	39	19	16	16	5	5	**0**	5	12	12
k22	45	45	38	38	41	41	41	41	42	38	37	37	37	37	37	37	23	20	20	0	0	5	**0**	10	10
k23	49	49	43	43	45	45	45	45	44	41	40	40	40	40	40	40	25	22	22	10	10	12	10	**0**	0
k24	49	49	43	43	45	45	45	45	44	41	40	40	40	40	40	40	25	22	22	10	10	12	10	0	**0**
total	735	735	636	636	679	679	598	598	630	543	**528**	**528**	**528**	**528**	**528**	**528**	592	614	614	722	720	735	722	800	800

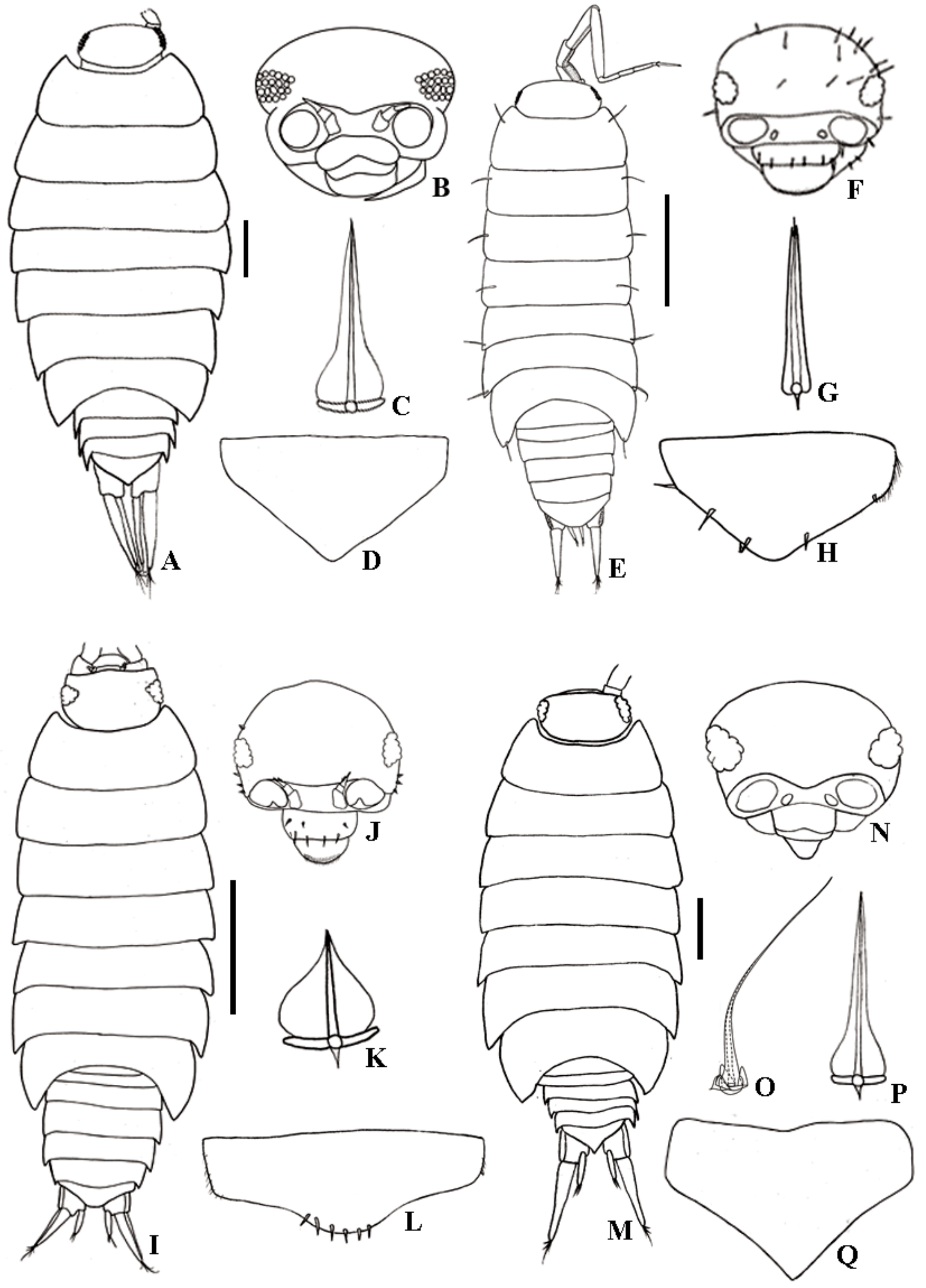


Figure 1

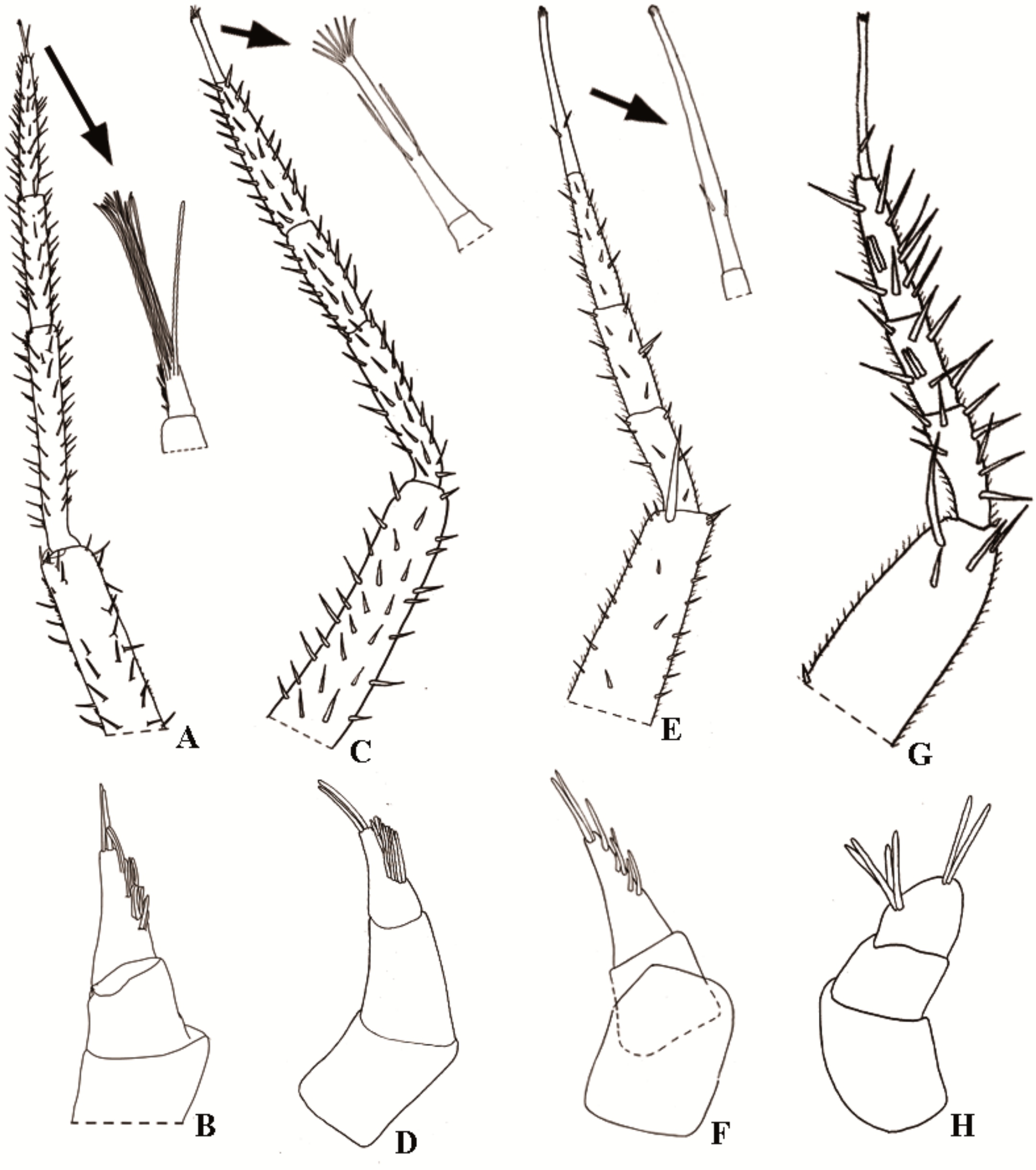


Figure 2

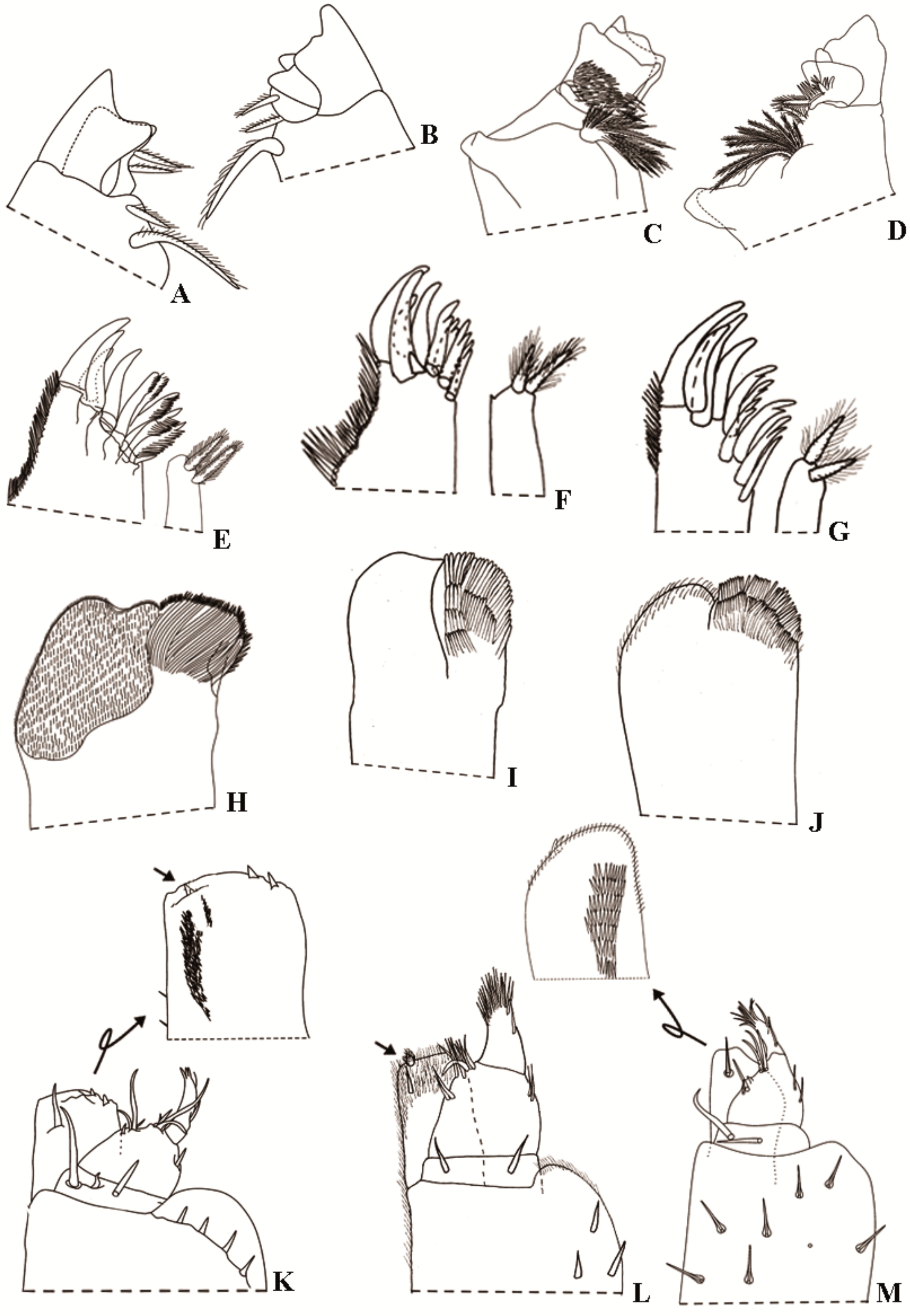


Figure 3

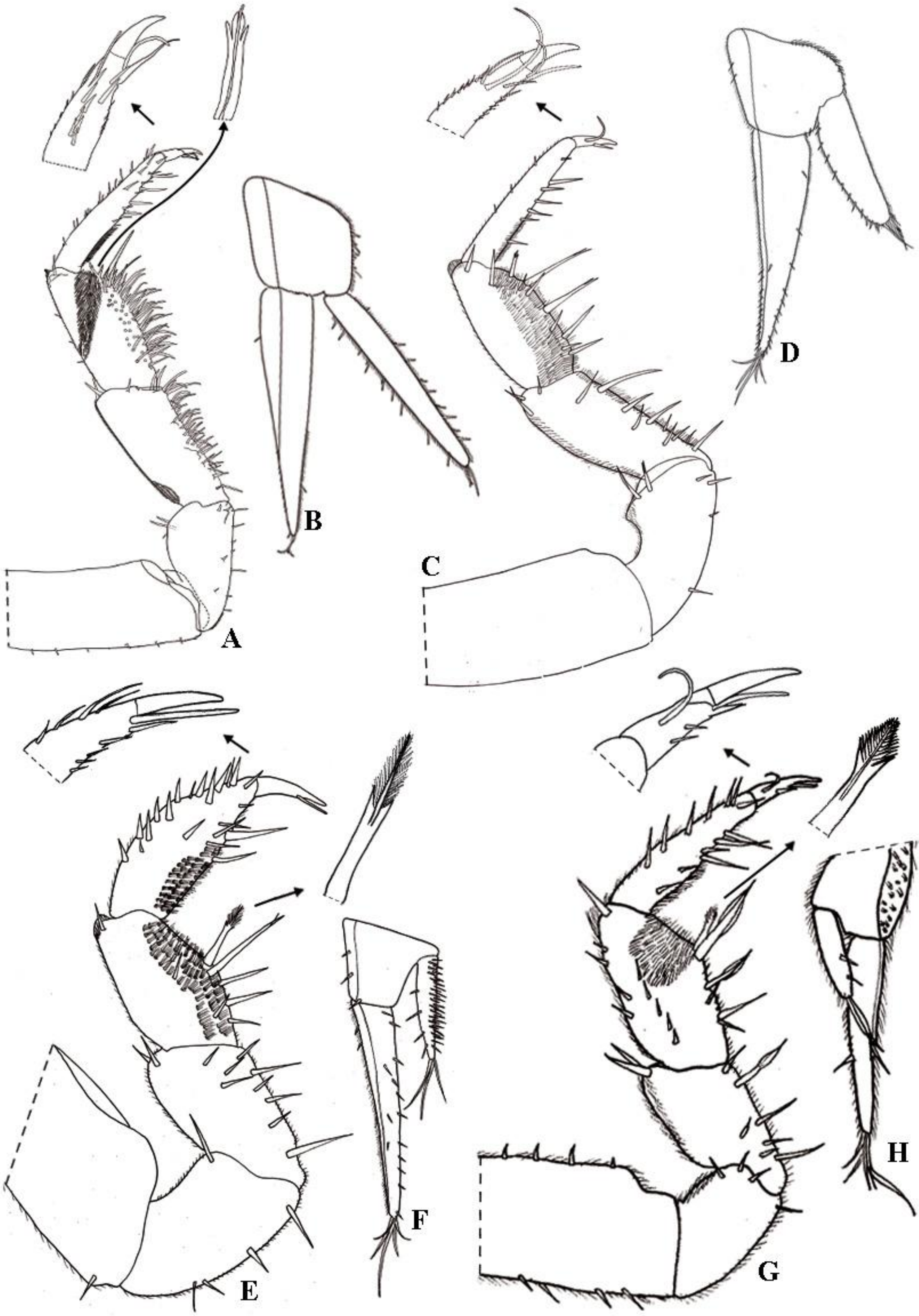


Figure 4

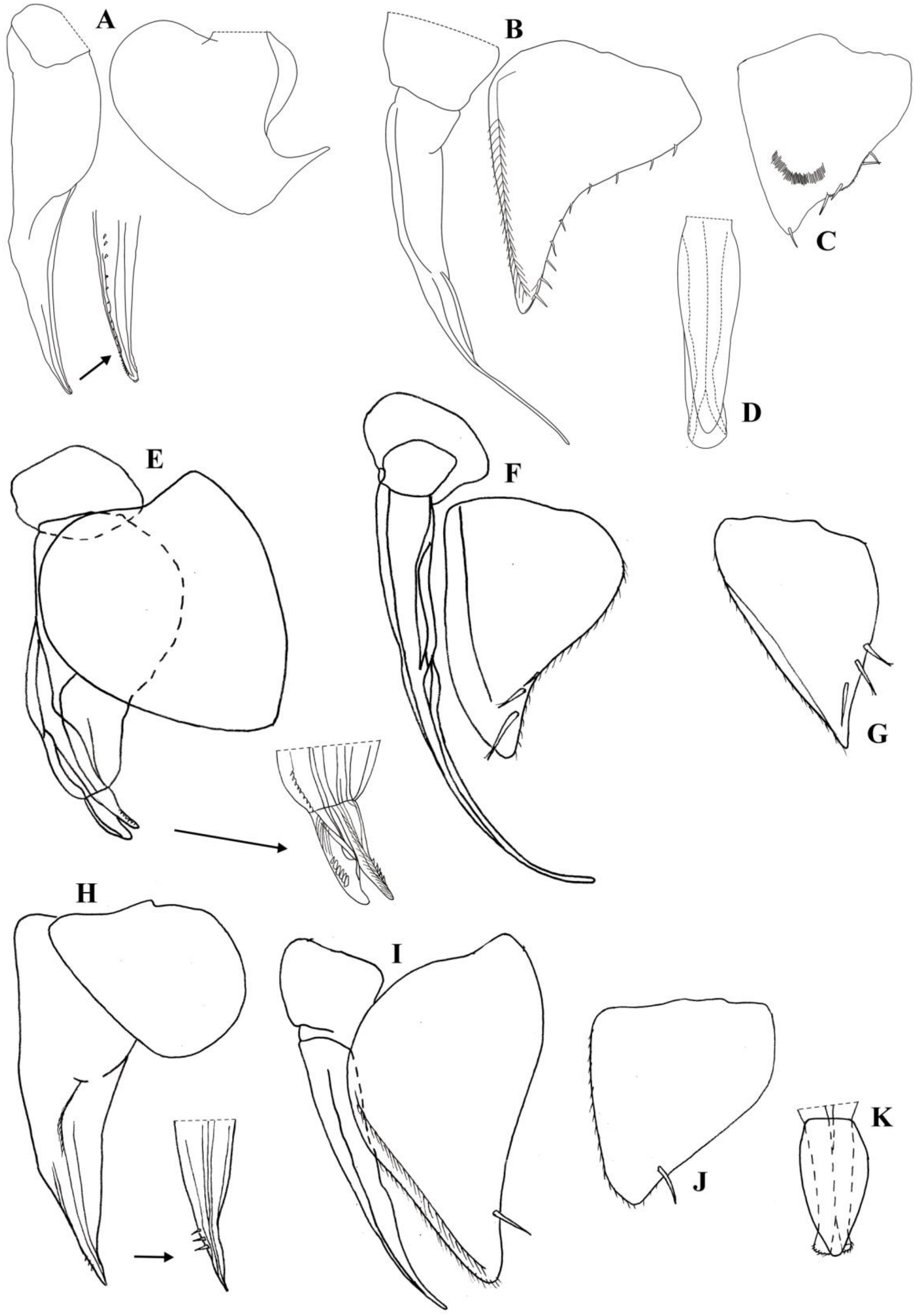
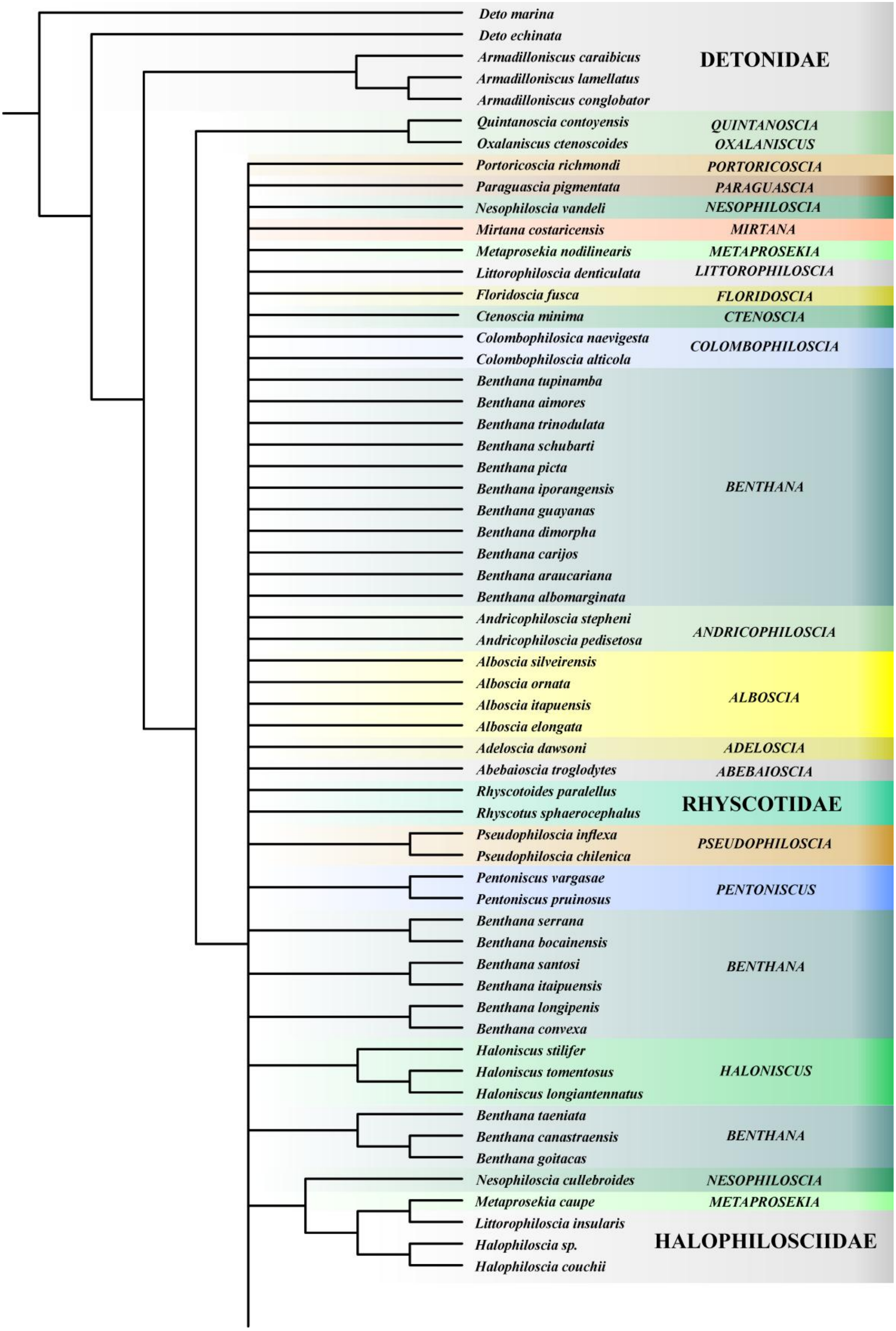


Figure 5


Deto marina
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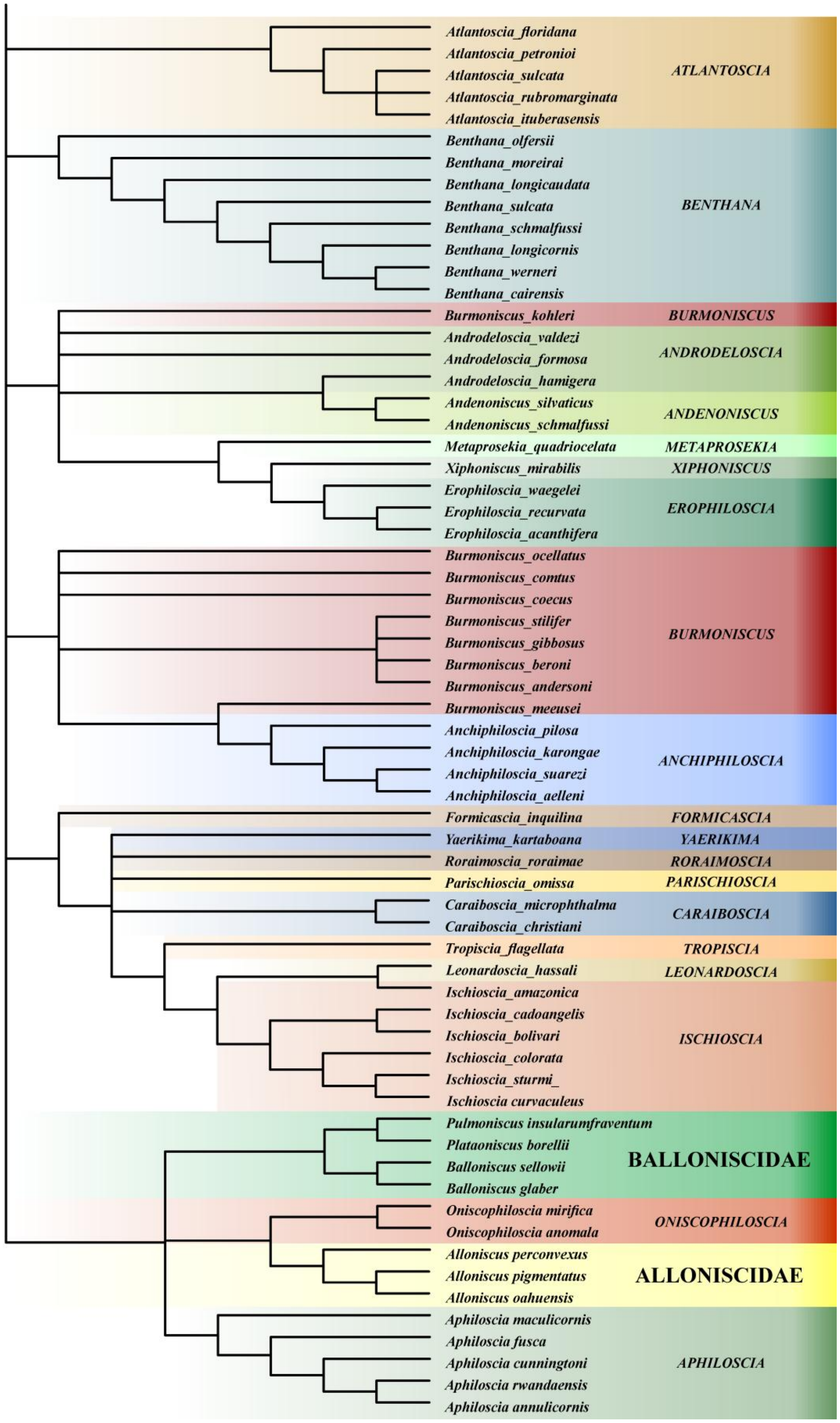
Armadilloniscus lamellatus
Armadilloniscus conglobator
DETONIDAE
Quintanoscia contoyensis
Oxalaniscus ctenoscoides
QUINTANOSCIA
OXALANISCUS
Portoricoscia richmondi
PORTORICOSCIA
Paraguascia pigmentata
PARAGUASCIA
Nesophiloscia vandeli
NESOPHILOSCIA
Mirtana costaricensis
MIRTANA
Metaprosekia nodilinearis
METAPROSEKIA
Littorophiloscia denticulata
LITTOROPHILOSCIA
Floridoscia fusca
FLORIDOSCIA
Ctenoscia minima
CTENOSCIA
Colombophilosica naevigesta
Colombophiloscia alticola
COLOMBOPHILOSCIA
Benthana tupinamba
Benthana aimores
Benthana trinodulata
Benthana schubarti
Benthana picta
Benthana iporangensis
Benthana guayanas
Benthana dimorpha
Benthana carijos
Benthana araucariana
Benthana albomarginata
BENTHANA
Andricophiloscia stepheni
Andricophiloscia pedisetosa
ANDRICOPHILOSCIA
Alboscia silveirensis
Alboscia ornata
Alboscia itapuensis
Alboscia elongata
ALBOSCIA
Adeloscia dawsoni
ADELOSCIA
Abebaioscia troglodytes
ABEBAIOSCIA
Rhyscotoides paralellus
Rhyscotus sphaerocephalus
RHYSCOTIDAE
Pseudophiloscia inflexa
Pseudophiloscia chilenica
PSEUDOPHILOSCIA
Pentoniscus vargasae
Pentoniscus pruinosus
PENTONISCUS
Benthana serrana
Benthana bocainensis
Benthana santosi
Benthana itaipuensis
Benthana longipenis
Benthana convexa
BENTHANA
Haloniscus stilifer
Haloniscus tomentosus
Haloniscus longiantennatus
HALONISCUS
Benthana taeniata
Benthana canastraensis
Benthana goitacas
BENTHANA
Nesophiloscia cullebroides
NESOPHILOSCIA
Metaprosekia caupe
METAPROSEKIA
Littorophiloscia insularis
Halophiloscia sp.
Halophiloscia couchii
HALOPHILOSCIIDAE

Figure 6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Atlantoscia_petronioi
Atlantoscia_sulcata
Atlantoscia_rubromarginata
Atlantoscia_ituberasensis
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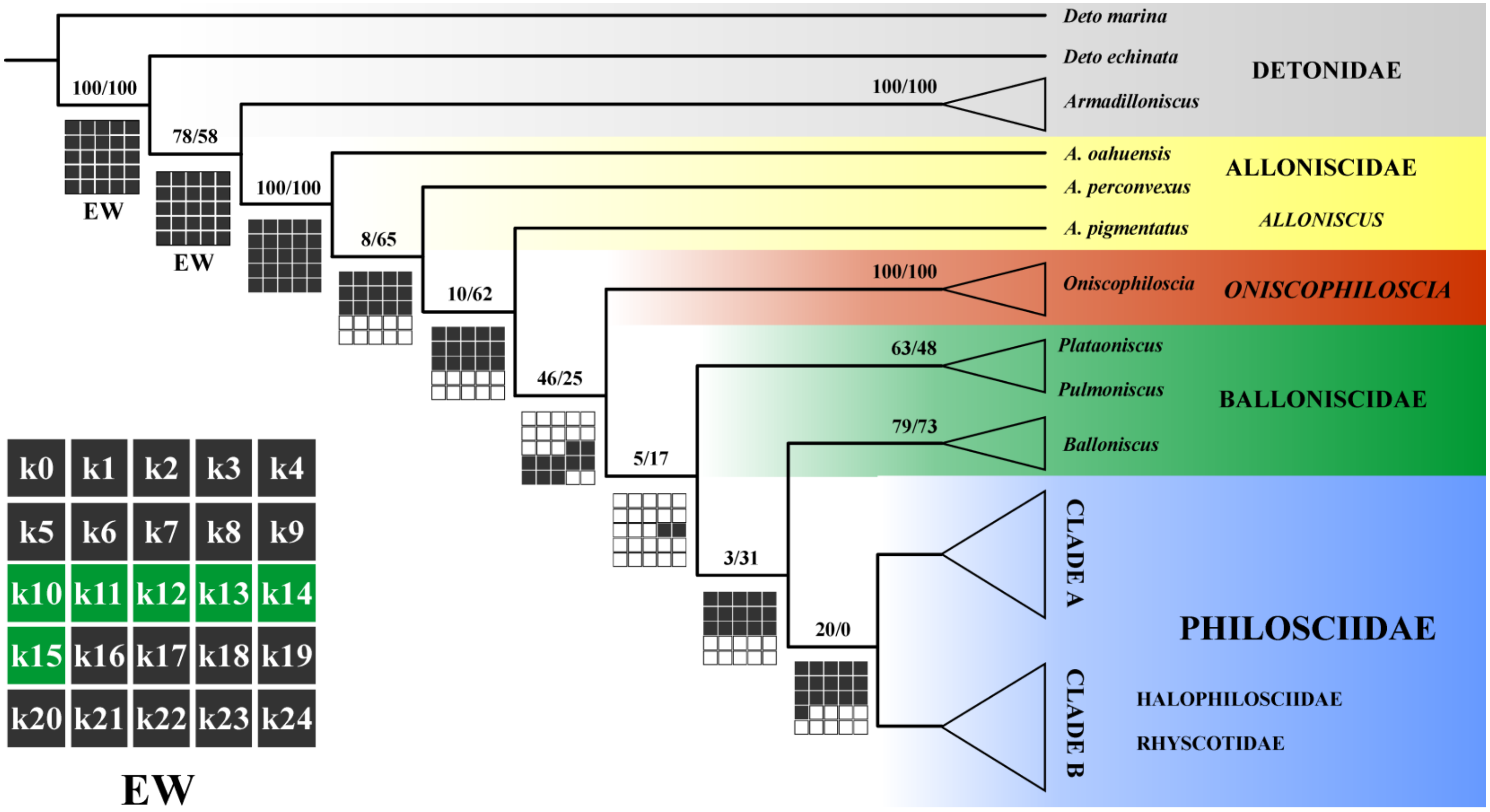
Benthana_olfersii
Benthana_moreirai
Benthana_longicaudata
Benthana_sulcata
Benthana_schmalfussi
Benthana_longicornis
Benthana_werneri
Benthana_cairensis
BENTHANA
Burmoniscus_kohleri
BURMONISCUS
Androdeloscia_valdezi
Androdeloscia_formosa
Androdeloscia_hamigera
ANDRODELOSCIA
Andenoniscus_silvaticus
Andenoniscus_schmalfussi
ANDENONISCUS
Metaprosekia_quadriocelata
METAPROSEKIA
Xiphoniscus_mirabilis
XIPHONISCUS
Erophiloscia_waegelei
Erophiloscia_recurvata
Erophiloscia_acanthifera
EROPHILOSCIA
Burmoniscus_ocellatus
Burmoniscus_comtus
Burmoniscus_coecus
Burmoniscus_stilifer
Burmoniscus_gibbosus
Burmoniscus_beroni
Burmoniscus_andersoni
Burmoniscus_meeusei
BURMONISCUS
Anchiphiloscia_pilosa
Anchiphiloscia_karongae
Anchiphiloscia_suarezi
Anchiphiloscia_aelleni
ANCHIPHILOSCIA
Formicascia_inquilina
FORMICASCIA
Yaerikima_kartaboana
YAERIKIMA
Roraimoscia_roraimae
RORAIMOSCIA
Parischioscia_omissa
PARISCHIOSCIA
Caraiboscia_microphthalma
Caraiboscia_christiani
CARAIBOSCIA
Tropiscia_flagellata
TROPISCIA
Leonardoscia_hassali
LEONARDOSCIA
Ischioscia_amazonica
Ischioscia_cadoangelis
Ischioscia_bolivari
Ischioscia_colorata
Ischioscia_sturmi_
Ischioscia curvaculeus
ISCHIOSCIA
Pulmoniscus insularumfraventum
Plataoniscus borellii
Balloniscus sellowii
Balloniscus glaber
BALLONISCIDAE
Oniscophiloscia mirifica
Oniscophiloscia anomala
ONISCOPHILOSCIA
Alloniscus perconvexus
Alloniscus pigmentatus
Alloniscus oahuensis
ALLONISCIDAE
Aphiloscia maculicornis
Aphiloscia fusca
Aphiloscia cunningtoni
Aphiloscia rwandaensis
Aphiloscia annulicornis
APHILOSCIA

Figure 7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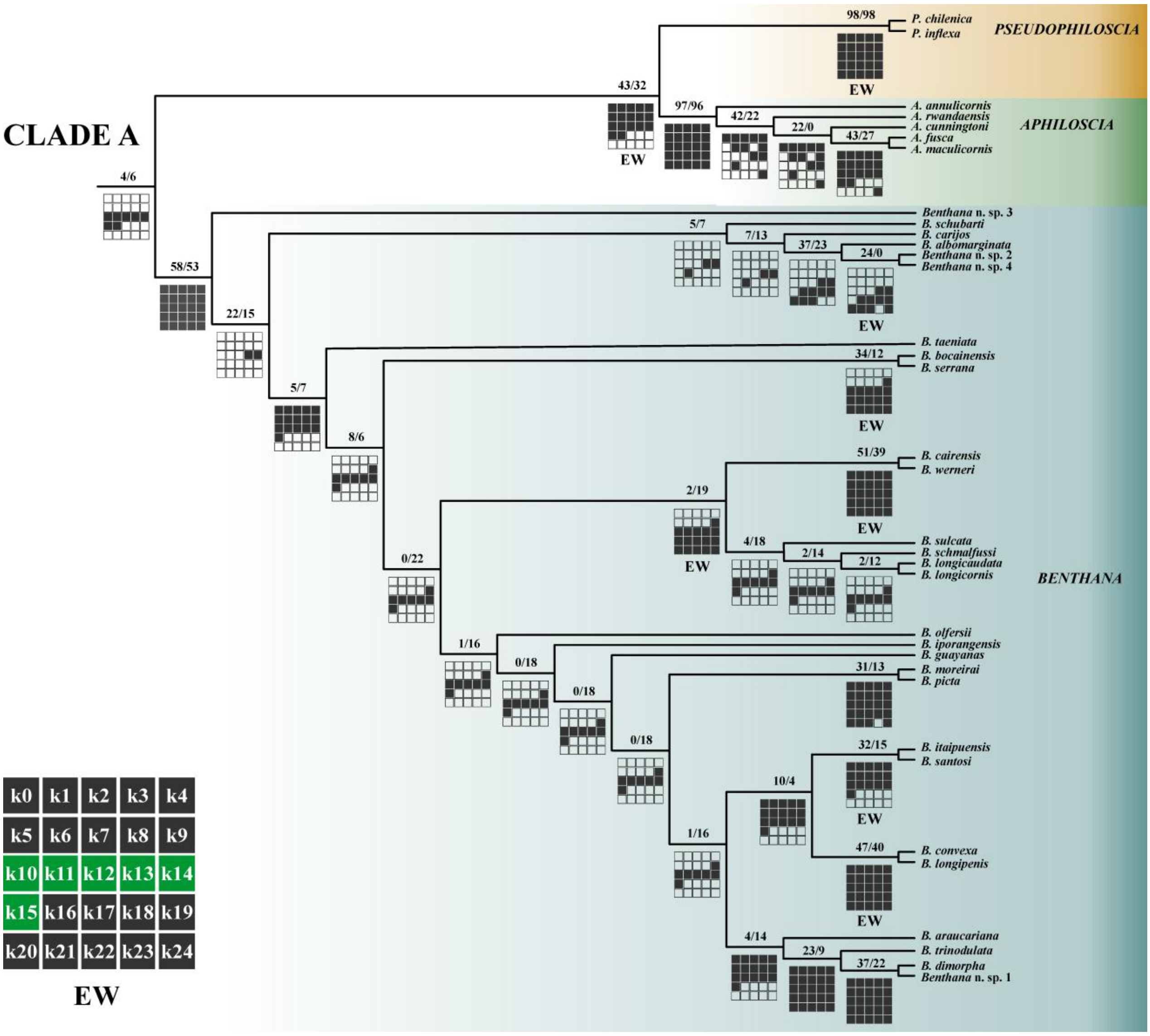
Armadilloniscus
100/100
78/58
EW
EW
100/100
A. oahuensis
ALLONISCIDAE
A. perconvexus
A. pigmentatus
ALLONISCUS
8/65
10/62
100/100
Oniscophiloscia
ONISCOPHILOSCIA
63/48
Plataoniscus
Pulmoniscus
BALLONISCIDAE
46/25
79/73
Balloniscus
5/17
CLADE A
3/31
PHILOSCIIDAE
20/0
CLADE B
HALOPHILOSCIIDAE
RHYSCOTIDAE
k0
k1
k2
k3
k4
k5
k6
k7
k8
k9
k10
k11
k12
k13
k14
k15
k16
k17
k18
k19
k20
k21
k22
k23
k24
EW

Figure 8


CLADE A
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58/53
43/32
EW
98/98
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P. inflexa
PSEUDOPHILOSCIA
EW
97/96
42/22
22/0
43/27
A. annulicornis
A. rwandaensis
A. cunningtoni
A. fusca
A. maculicornis
APHILOSCIA
22/15
5/7
7/13
37/23
24/0
EW
Benthana n. sp. 3
B. schubarti
B. carijos
B. albomarginata
Benthana n. sp. 2
Benthana n. sp. 4
5/7
8/6
B. taeniata
34/12
B. bocainensis
B. serrana
EW
0/22
2/19
EW
51/39
B. cairensis
B. werneri
EW
4/18
2/14
2/12
B. sulcata
B. schmalfussi
B. longicaudata
B. longicornis
BENTHANA
1/16
0/18
0/18
0/18
B. olfersii
B. iporangensis
B. guayanas
31/13
B. moreirai
B. picta
1/16
10/4
32/15
B. itaipuensis
B. santosi
EW
47/40
B. convexa
B. longipenis
EW
4/14
23/9
37/22
B. araucariana
B. trinodulata
B. dimorpha
Benthana n. sp. 1
k0
k1
k2
k3
k4
k5
k6
k7
k8
k9
k10
k11
k12
k13
k14
k15
k16
k17
k18
k19
k20
k21
k22
k23
k24
EW

Figure 9

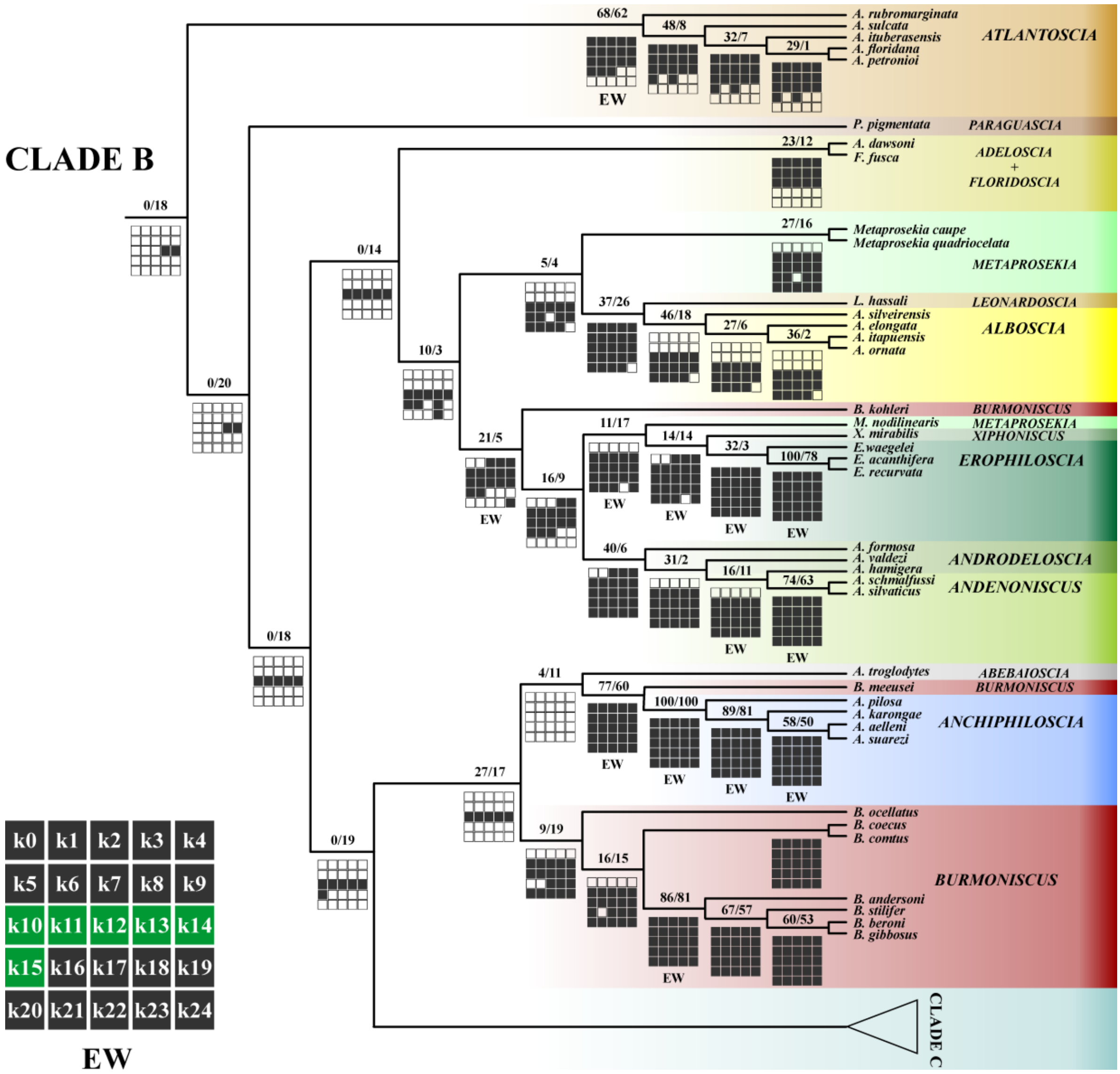
CLADE B
0/18
0/20
0/18
0/14
0/19
10/3
5/4
21/5
16/9
27/17
4/11
9/19
68/62
48/8
32/7
29/1
EW
A. rubromarginata
A. sulcata
A. ituberasensis
A. floridana
A. petronioi
ATLANTOSCIA
P. pigmentata
PARAGUASCIA
23/12
A. dawsoni
F. fusca
ADELOSCIA
+
FLORIDOSCIA
27/16
Metaprosekia caupe
Metaprosekia quadriocelata
METAPROSEKIA
37/26
46/18
27/6
36/2
L. hassali
LEONARDOSCIA
A. silveirensis
A. elongata
A. itapuensis
A. ornata
ALBOSCIA
B. kohleri
BURMONISCUS
11/17
14/14
32/3
100/78
M. nodilinearis
METAPROSEKIA
X. mirabilis
XIPHONISCUS
E.waegelei
E. acanthifera
E. recurvata
EROPHILOSCIA
40/6
31/2
16/11
74/63
A. formosa
A. valdezi
ANDRODELOSCIA
A. hamigera
A. schmalfussi
A. silvaticus
ANDENONISCUS
A. troglodytes
ABEBAIOSCIA
77/60
B. meeusei
BURMONISCUS
100/100
89/81
58/50
A. pilosa
A. karongae
A. aelleni
A. suarezi
ANCHIPHILOSCIA
16/15
86/81
67/57
60/53
B. ocellatus
B. coecus
B. comtus
BURMONISCUS
B. andersoni
B. stilifer
B. beroni
B. gibbosus
CLADE C
k0 k1 k2 k3 k4
k5 k6 k7 k8 k9
k10 k11 k12 k13 k14
k15 k16 k17 k18 k19
k20 k21 k22 k23 k24
EW

Figure 10

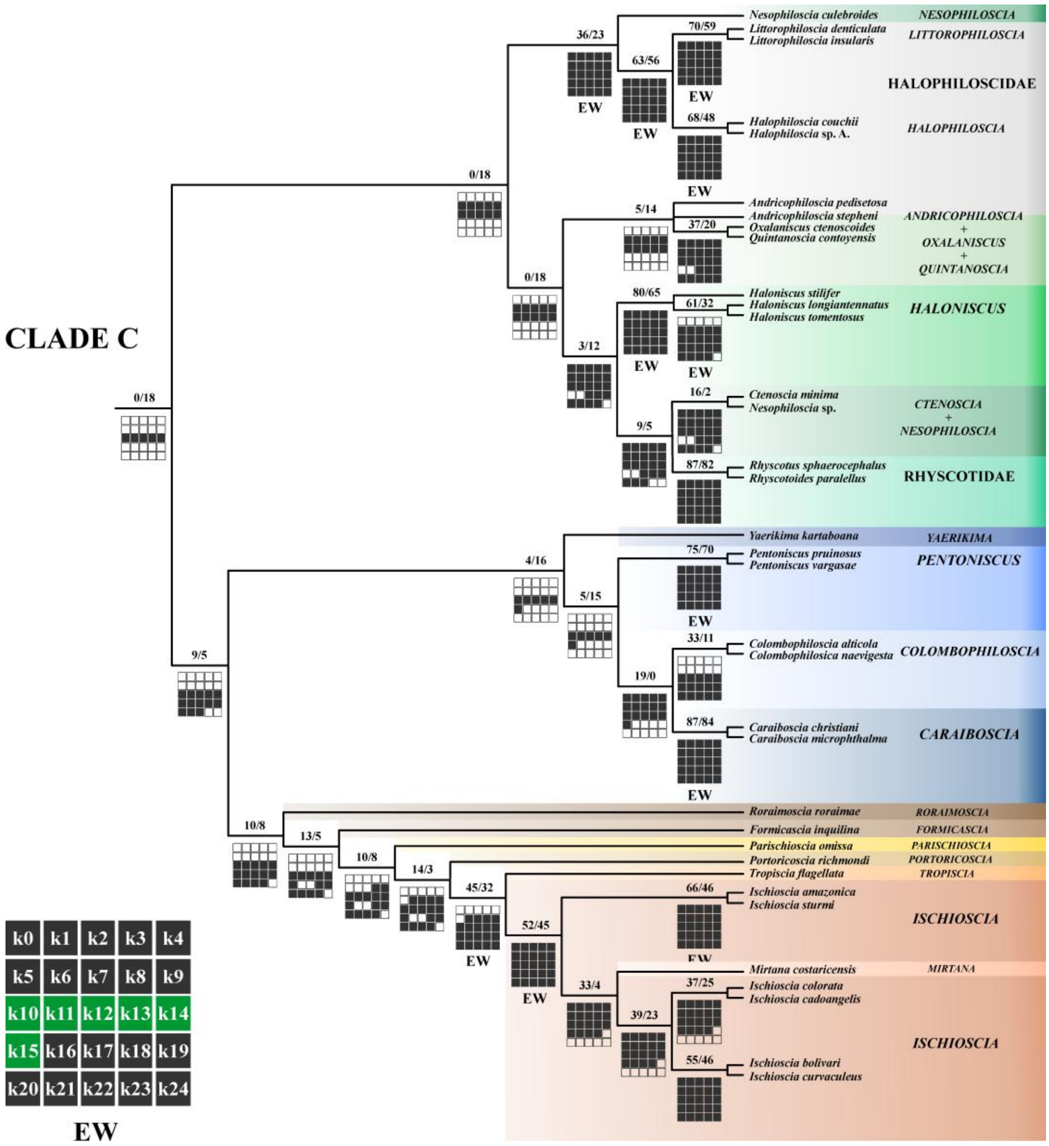
CLADE C
0/18
0/18
36/23
EW
63/56
EW
70/59
EW
68/48
EW
Nesophiloscia culebroides
NESOPHILOSCIA
Littorophiloscia denticulata
Littorophiloscia insularis
LITTOROPHILOSCIA
HALOPHILOSCIDAE
Halophiloscia couchii
Halophiloscia sp. A.
HALOPHILOSCIA
0/18
5/14
37/20
Andricophiloscia pedisetosa
Andricophiloscia stepheni
Oxalaniscus ctenoscoides
Quintanoscia contoyensis
ANDRICOPHILOSCIA
+
OXALANISCUS
+
QUINTANOSCIA
3/12
80/65
EW
61/32
EW
Haloniscus stilifer
Haloniscus longiantennatus
Haloniscus tomentosus
HALONISCUS
9/5
16/2
Ctenoscia minima
Nesophiloscia sp.
CTENOSCIA
+
NESOPHILOSCIA
87/82
Rhyscotus sphaerocephalus
Rhyscotoides paralellus
RHYSCOTIDAE
9/5
4/16
Yaerikima kartaboana
YAERIKIMA
5/15
75/70
EW
Pentoniscus pruinosus
Pentoniscus vargasae
PENTONISCUS
19/0
33/11
Colombophiloscia alticola
Colombophilosica naevigesta
COLOMBOPHILOSCIA
87/84
EW
Caraiboscia christiani
Caraiboscia microphthalma
CARAIBOSCIA
10/8
13/5
10/8
14/3
45/32
EW
52/45
EW
Roraimoscia roraimae
RORAIMOSCIA
Formicascia inquilina
FORMICASCIA
Parischioscia omissa
PARISCHIOSCIA
Portoricoscia richmondi
PORTORICOSCIA
Tropiscia flagellata
TROPISCIA
66/46
EW
Ischioscia amazonica
Ischioscia sturmi
ISCHIOSCIA
33/4
39/23
Mirtana costaricensis
MIRTANA
37/25
Ischioscia colorata
Ischioscia cadoangelis
55/46
Ischioscia bolivari
Ischioscia curvaculeus
ISCHIOSCIA
k0 k1 k2 k3 k4
k5 k6 k7 k8 k9
k10 k11 k12 k13 k14
k15 k16 k17 k18 k19
k20 k21 k22 k23 k24
EW

Figure 11