

PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
FACULDADE DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**ANÁLISE CLADÍSTICA DAS SUBFAMÍLIAS DE HAHNIIDAE BERTKAU, 1878
(ARACHNIDA, ARANEAE)**

Nancy França Lo Man Hung

DISSERTAÇÃO DE MESTRADO

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2013

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Dissertação apresentada como requisito para obtenção do título de Mestre em Zoologia pelo Curso de Pós-Graduação de Zoologia da Pontifícia Universidade Católica do Rio Grande do Sul.

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WARNING

This dissertation is not valid as publication, as described in the chapter 3 of the International Code of Zoological Nomenclature. Therefore, taxonomic changes and/or new names proposed here are not valid for nomenclatural or priority purposes.

ADVERTÊNCIA

Esta dissertação não é válida como publicação, conforme capítulo 3 do Código Internacional de Nomenclatura Zoológica. Portanto, os novos nomes e/ou as mudanças taxonômicas propostas aqui não tem validade para fins de nomenclatura ou prioridade

Numquam ponenda est pluralitas sine necessitate

Pluralidades não devem ser postas sem necessidade

William de Ockham, século XIV

Ao meu pai (*in memoriam*) que sempre incentivou os estudos. A minha mãe, Peter e Grace como forma de compensar pelo tempo que me afastei do convívio familiar, absorvida neste estudo. Ao David com amor, admiração e gratidão por seu incansável apoio em todos os momentos. Ao Eric com sua mania de sorrir e alegrar meu dia.

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Meu interesse por hahniideos começou muito antes, mas intensificou-se há aproximadamente um ano antes de começar o mestrado, morava em Belém (PA) e frequentava como bolsista o Museu Paraense Emílio Goeldi, auxiliava na curadoria das coleções de invertebrados não insetos, sob orientação do Alexandre Bonaldo, e por conta das minhas funções percebi a necessidade de identificação de alguns exemplares de Hahniidae, um grupo relativamente abundante na coleção mas, com pouquíssima informação taxonômica. Surgia então o desejo de reverter essa situação. Perguntei para outros pesquisadores se havia alguém trabalhando com o grupo e o que eles achavam de eu me embrenhar pelos caminhos da sistemática. Tive então, ótimos conselhos e ajuda de David Candiani, Adalberto Santos, Alexandre Bonaldo, Ana Tourinho, Antonio Brescovit, Cris Rheims, Ricardo Ott, inclusive o Adal repassou cópia da tese do Catley, que em 1996 trabalhou com espécimes da região sul temperada. Posteriormente, precisava pensar em um projeto para desenvolver durante o mestrado, o grupo é grande e assim também são as várias lacunas no conhecimento, tive inúmeras sugestões de Bruno Rodrigues, Cida Marques, Emanuel Cafofo, Erica Buckup, Laura Miglio, Lina Almeida, Maria Rita Poeta, Rafael Francisco, Rafael Indicatti, Renato Teixeira, Regiane Saturnino, Williams Paredes, além dos pesquisadores já citados acima e, durante as disciplinas do mestrado obtive sugestões de Pedro Gnaspini e Roberto Reis. Minhas primeiras investidas no desejo de concorrer ao mestrado na PUCRS foi amplamente auxiliada por Estevam Silva, que na ocasião, sanou várias de minhas dúvidas. Posso dizer que toda ajuda do Professor Arno Lise foi fundamental, pois intercedeu na pós graduação para que a prova de seleção do mestrado fosse aplicada em Belém, bem como o auxílio na documentação enquanto morava longe, sua orientação e zelo durante o mestrado foi essencial neste estudo, lamento apenas não ter tido mais oportunidade (devido a falta de tempo) de aprender a desenhar com um dos maiores ícones do desenho científico, mas guardo comigo alguns de seus conselhos feitos nos meus esboços. Janael Ricetti intercedeu para que minha visita ao Museu Capão da

Imbuia (PR) tivesse êxito. Sobre a pós-graduação, obtive bolsa integral do CNPq (130775/2011-8), desenvolvi minha pesquisa no laboratório de Aracnologia do Museu de Ciência e Tecnologia da PUCRS, contei com total (e essencial) apoio do Centro de Microscopia e Microanálises, excelente apoio de Luana Santos, dos professores e durante a minha fase como representante discente, obtive ajuda de inúmeros amigos da pós graduação. Minha estadia em Porto Alegre foi amplamente auxiliada por D. Vanir e Sr. Luiz, com certeza, eles são grandes responsáveis por eu ter tido uma ótima impressão da hospitalidade da cidade. Bem próximo de terminar o prazo padrão (24 meses) do mestrado, já em São Paulo, nasceu meu filhinho Eric, o CNPq concedeu a licença maternidade (quatro meses), que passou muito rápido, mas que foi muito importante para uma mãe de primeira viagem e, nessa fase, a ajuda que obtive da família foi mais que importante para a finalização desta dissertação. A instituição, ao órgão de fomento, a todos citados e, aqui incluo o pessoal dos laboratórios pelos quais passei, quero registrar o meu sincero agradecimento, por todas essas andanças (São Paulo, Belém, Porto Alegre) saibam que vocês ajudaram muito e deixarão saudades.

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RESUMO

O presente trabalho visou estudar as relações filogenéticas e testar o monofiletismo das subfamílias de Hahniidae. Sendo assim, este trabalho foi dividido em duas partes: a primeira é uma apresentação geral composta por uma breve revisão literária sobre Hahniidae e a segunda parte é um artigo, redigido em inglês, e em formato de artigo para publicação: **Artigo:** *Cladistic analysis of the subfamilies of the comb-tailed spider (Araneae: Hahniidae)*, artigo será submetido para a revista *Zoologica Scripta* (Fator 2.913 – A1). No artigo foi realizada uma análise de parcimônia com buscas heurísticas, caracteres não ordenados e com pesos iguais para todos os caracteres, resultando em uma hipótese de relacionamento (L= 412, CI= 37, RI= 53) entre 30 terminais e 106 caracteres morfológicos, sendo 63 somáticos, 42 sexuais e um comportamental. Esta é a primeira hipótese filogenética para a família baseada em caracteres morfológicos e composta por integrantes das três subfamílias de Hahniidae. O grupo interno foi composto por 14 espécies de Hahniinae, cinco espécies de Cybaeolinae, cinco espécies de Cryphoecinae, duas espécies *incertae sedis* e, o grupo externo composto por integrantes de Dictynidae, Cybaeidae, Agelenidae e Amaurobidae. Nesta hipótese, Hahniidae como está atualmente delimitada, não é um agrupamento monofilético, Cryphoecinae é monofilético e parece relacionada com Cybaeidae e Dictynidae, os demais hahniideos aparecem como grupo irmão de Dictynidae. Tanto Cybaeolinae quanto Hahniinae não formam um grupo monofilético. Cybaeolinae parece ser composta apenas pelo gênero *Cybaeolus*, enquanto que para Hahniinae são necessários mais estudos para definir os relacionamentos entre os gêneros que compõem esta subfamília, especialmente uma revisão extensiva do gênero *Hahnia*.

ABSTRACT

The present work aimed to study the phylogenetic relationships and test the monophyly of the subfamilies of Hahniidae. Thus, this study was divided into two parts: the first is an introduction consisting of a brief literature review on Hahniidae and, the second part is written manuscript for publication in English: **Article:** Cladistic analysis of the subfamilies of the comb-tailed spider (Araneae: Hahniidae), manuscript will be submitted to *Zoologica Scripta* (Factor 2913 - A1). In the manuscript we performed a parsimony analysis with heuristic search, characters unordered and with equal weights for all characters, resulting in relationship hypothesis (L = 412, CI = 37, RI = 53) between 30 terminals and 106 morphological characters, 63 somatic, 42 sexual and one from behavior. This is the first phylogenetic hypothesis for the family based on morphological characters and composed of members of all three subfamilies of Hahniidae. The ingroup was composed of 14 species of Hahniinae, five species of Cybaeolinae, five species of Cryphoecinae, two species *incertae sedis*, and the outgroup composed of members of Dictynidae, Cybaeidae, Agelenidae and Amaurobidae. In this hypothesis, Hahniidae as is currently defined, is not a monophyletic group, Cryphoecinae is monophyletic and related with Cybaeidae and Dictynidae, other hahniids appear as the sister group to Dictynidae. Both, Cybaeolinae and Hahniinae are not a monophyletic group. Cybaeolinae seems to be composed only by gender *Cybaeolus*, while for Hahniinae more studies are needed to define the relationships between the genera that comprise this subfamily, especially an extensive review of the genus *Hahnia*.

APRESENTAÇÃO

1. Taxonomia

Hahniidae é composta por aranhas com tamanho reduzido (de 1 a 6 mm), entelegineas e escribeladas. Normalmente habitam a serapilheira ou são encontradas sob pedras e troncos, onde podem construir pequenos refúgios com folhas e/ou teias (Opell & Beatty 1976). Apresentam ampla distribuição geográfica, ocorrendo em todos os continentes exceto Antártica (Platinick 2013). A família é facilmente reconhecida pelo arranjo transversal dos três pares de fiandeiras e pela presença de um espiráculo traqueal (Bertkau 1878; Opell & Beatty 1976).

Em 1841, Carl Ludwig Koch decidiu homenagear o pesquisador alemão Carl Wilhelm Hahn, autor das quatro primeiras obras de *Die Arachniden* (1831-1848) (Figura 1) com o nome genérico: *Hahnia*, no qual, anos mais tarde, foi baseado o nome da família: Hahniidae Bertkau, 1878.



Figura 1. A) Carl Ludwig Koch (1778-1857); **B)** Carl Wilhelm Hahn (1786-1836); **C)** *Die Arachniden* (1841).

Desde que Bertkau (1878) estabeleceu a família, alguns posicionamentos taxonômicos foram propostos para o grupo. Primeiramente foi alocada em subfamílias dentro de Agelenidae por Emerton (1890) e Simon (1892). Entretanto, Petrunkevitch (1933) removeu o grupo do clado artificial (i.e. um grupo sem critérios filogenéticos) Quadrostiatae, com base na redução do número de ostíolos cardíacos (dois pares), e elevou-a novamente

à categoria de família, distante taxonomicamente de Agelenidae. Com base no sistema traqueal que avança até o cefalotórax, Gerhardt e Kaestner (1938) e Kaston (1948) alocaram Hahniidae na superfamília Lycosoidea. Posteriormente, Lehtinen (1967) propôs outra classificação, alocando algumas espécies da tribo Cryphoeceae, Ageleninae (Simon, 1897), e parte de Cybaeinae, como subfamílias de Hahniidae (i.e., Cryphoecinae e Cybaeolinae), além de alocar Hahniidae dentro da superfamília Amaurobioidea. Forster (1970) apoiou em parte a classificação de Lehtinen (1967), entretanto, seguindo uma visão mais ampla da delimitação de Hahniidae, ou seja, apenas gêneros que demonstrassem arranjos transversais dos três pares de fiandeiras, decidiu alocar Hahniidae dentro da superfamília Dictynoidea, devido aos membros desse grupo compartilharem traqueias medianas fortemente ramificadas ou divididas (Figura 2), diferente de Amaurobioidea, cujos membros compartilham traqueias delgadas não ramificadas (Forster 1970; Bromhall 1987).

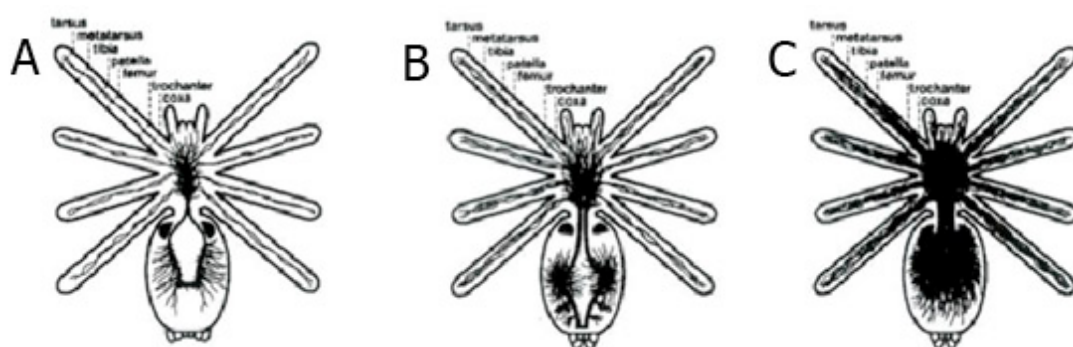


Figura 2. Estruturas respiratórias. **A)** *Hahnia* (Hahniidae); **B)** *Dictyna* (Dictynidae); **C)** *Argyroneta* (Cybaeidae) modificado a partir de Bromhall (1987).

A primeira revisão relacionando todas as famílias de Araneomorphae foi proposta por Coddington & Levi (1991). Nesta hipótese (Figura 3), Hahniidae está posicionada de Dictynoidea, no clado *Retrolateral Tibial Apophysis* (RTA). Neste estudo, os autores argumentam que, provavelmente, Hahniidae deve compartilhar sinapomorfias, nas estruturas dos palpos, com Dictynidae e Cybaeidae, e que, possivelmente, a condição ramificada da traqueia em Dictynoidea indica o monofiletismo do grupo.

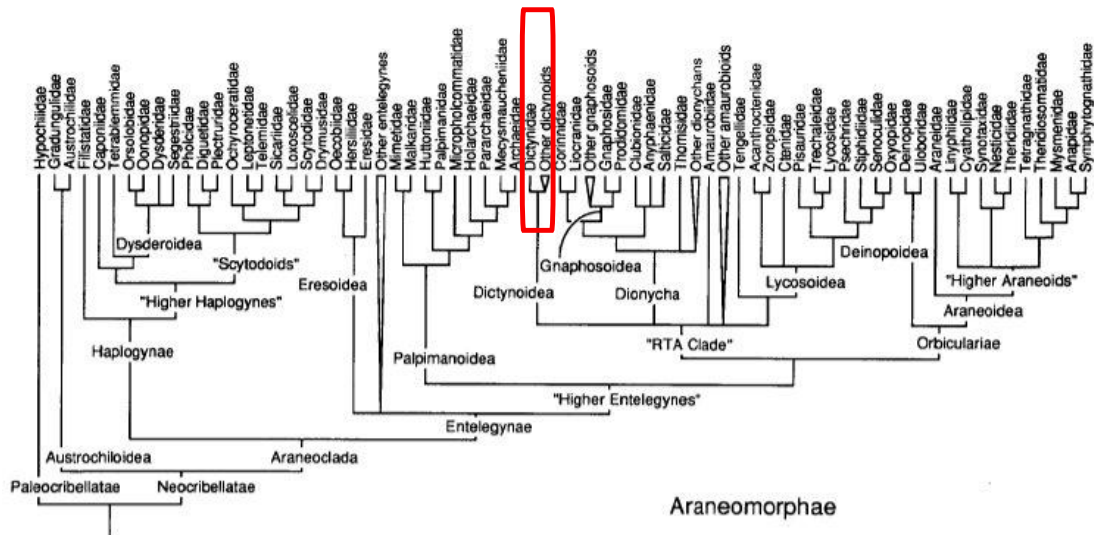


Figura 3. Relacionamento de Araneomorphae proposto por Coddington & Levi (1991). Em destaque no retângulo a superfamília Dictynoidea, onde Hahniidae está posicionada atualmente.

A família Hahniidae é composta atualmente por 250 espécies distribuídas em 27 gêneros amplamente distribuídos (Platnick 2013; Zhang *et al.* 2013).

Hahnia C. L. Koch, 1841 tem como espécie-tipo *H. pussila* C. L. Koch, 1841, descrita com base em macho e fêmea, para a região Paleártica. Atualmente é o gênero mais diverso da família, com 98 espécies descritas, amplamente distribuídas. Na região Neotropical há 11 espécies descritas, sendo que seis delas foram baseadas apenas em exemplares fêmeas da Costa Rica, Panamá, Porto Rico, Argentina e Brasil

Cryphoeca Thorell, 1870 tem como espécie-tipo *C. silvicola* (C. L. Koch, 1834), descrita com base em macho e fêmea para a região Paleártica. Atualmente o gênero conta com 13 espécies descritas para as regiões Paleártica, Oriental, Australiana e Neártica.

Iberina Simon, 1881, espécie-tipo *I. mazarredoi* Simon, 1881 descrita com base em macho e fêmea. Atualmente o gênero possui duas espécies descritas, com ocorrência na França e Rússia.

Cybaeolus Simon, 1884, espécie-tipo *C. pussillus* Simon, 1884 descrita com base em macho e fêmea para o Chile e Argentina. Inclui atualmente três espécies exclusivamente Neotropicais.

Tuberta Simon, 1884, espécie-tipo *T. maerens* (O.P.-Cambridge, 1863) descrita com base em macho e fêmea. Atualmente o gênero conta com duas espécies distribuídas pela Europa e Azerbaijão.

Scotospilus Simon, 1886, espécie-tipo *S. bicolor* Simon, 1886 descrita com base em macho e fêmea para a Tasmânia. Atualmente o gênero conta com oito espécies descritas para as regiões Australiana e Oriental.

Alistra Thorell, 1894, espécie-tipo *A. longicauda* Thorell, 1894 descrita com base em fêmea da Sumatra. Atualmente o gênero conta com 18 espécies descritas para as regiões Australiana, Oriental e Etiópica.

Antistea Simon, 1898, espécie-tipo *A. elegans* (Blackwall, 1841) descrita com base em macho e fêmea para a região Paleártica. Atualmente o gênero conta com três espécies descritas para o Canadá, Estados Unidos e região Paleártica.

Neohahnia Mello-Leitão, 1917 atualmente conta com quatro espécies descritas, todas endêmicas da região Neotropical. O gênero possui como espécie-tipo *N. sylviae* descrita com base em exemplar jovem do Rio de Janeiro, Brasil (ver, Moreira *et al.* 2010). Neste mesmo trabalho Mello-Leitão (1917) também descreve *N. palmicola* e ao contrário do que pressuposto por Moreira *et al.* (2010) esta espécie também é descrita com base em exemplar jovem, coletado na mesma localidade-tipo de *N. sylviae*. Outras duas espécies estão alocadas no gênero: *N. ernsti* (Simon, 1897), descrita originalmente em *Hahnia*, com base em macho e fêmea de Saint Vincent, Venezuela e transferida posteriormente para *Neohahnia* por Lehtinen (1967); e *N. chibcha* Heimer & Müller, 1988 descrito com base em macho e fêmea da Colômbia. A diagnose do gênero proposta por Mello-Leitão (1917) apresenta caracteres de pouco valor diagnóstico, ou seja, relativamente comuns entre as espécies como: olhos médios anteriores contíguos, mas separados dos laterais por um diâmetro ou mais; olhos posteriores de tamanho semelhante, entre si, e cílios de altura muito maior que as interdistâncias dos olhos médios anteriores.

Neoaviola Butler, 1929 é atualmente um gênero monotípico que inclui a espécie *N. insolens* Butler, 1929; descrita com base em fêmea para Victoria, Austrália.

Neoantistea Gertsch, 1934, espécie-tipo *N. agilis* (Keyserling, 1887) descrita com base em macho e fêmea para a região Neártica. Atualmente, o gênero conta com 23 espécies descritas para as regiões Neártica, Paleártica e oito espécies com distribuição Neotropical.

Calymmaria Chamberlin & Ivie, 1937, espécie-tipo *C. monicae* Chamberlin & Ivie, 1937 descrita com base em macho e fêmea para Santa Monica, Los Angeles, California. Atualmente, o gênero conta com 31 espécies com distribuição no Canadá, Estados Unidos e México.

Ethobuella Chamberlin & Ivie, 1937, espécie-tipo *E. tuonops* Chamberlin & Ivie, 1937 descrita com base em macho e fêmea. O gênero conta com duas espécies descritas para o Canadá e Estados Unidos.

Austrohahnia Mello-Leitão, 1942 um gênero monotípico que inclui a espécie *A. praestans* Mello-Leitão, 1942 descrita com base em fêmea da Argentina.

Dirksia Chamberlin & Ivie, 1942, espécie-tipo *D. cinctipes* (Banks, 1896) descrita com base em macho e fêmea para a região Neártica. O gênero abriga uma segunda espécie *D. pyrenaea* (Simon, 1898) com distribuição na França.

Amaloxenops Schiapelli & Gerschman, 1958, espécie-tipo *A. vianai* Schiapelli & Gerschman, 1958 descrita com base em ambos os sexos. Atualmente, o gênero abriga duas espécies (*A. vianai* Schiapelli & Gerschman e *A. palmarum* (Schiapelli & Gerschman, 1958)) endêmicas da Argentina.

Intihuatana Lehtinen, 1967 é atualmente um gênero monotípico composto pela espécie *I. antarctica* (Simon, 1902) descrita com base em macho e fêmea para a Argentina.

Lizarba Roth, 1967 é atualmente um gênero monotípico que inclui a espécie *L. separata* Roth, 1967 descrita com base em fêmea para o Brasil.

Kapanga Forster, 1970, espécie-tipo *K. wiltoni* Forster, 1970 descrita com base em macho e fêmea. Atualmente, o gênero conta com 10 espécies distribuídas na região Australiana.

Neocryphoeca Roth, 1970, espécie-tipo *N. gertschi* Roth, 1970. Atualmente, o gênero conta com duas espécies com descrições baseadas em fêmeas com distribuição nos Estados Unidos.

Rinawa Forster, 1970, espécie-tipo *R. otagoensis* Forster, 1970 descrita com base em macho e fêmea. Atualmente, o gênero conta com quatro espécies com distribuição na região Australiana.

Harmiella Brignoli, 1979 é atualmente um gênero monotípico que inclui a espécie *H. schiapelliae* Brignoli, 1979 descrita com base em exemplar macho coletado na serapilheira do solo em Nova Teutônia (município Seara), Santa Catarina, Brasil. O gênero é diagnosticado pela ausência de olhos, clípeo baixo, ausência de fôvea torácica e ausência de órgão estridulatório na face externa das quelíceras.

Willisus Roth, 1981 é atualmente um gênero monotípico que inclui a espécie *W. gertschi* Roth, 1981 descrita com base em macho e fêmea para os Estados Unidos.

Porioides Forster, 1989, espécie tipo *P. rima* (Forster, 1970) descrita com base em macho e fêmea. Atualmente, o gênero conta com duas espécies de distribuição na Nova Zelândia.

Asiohahnia Ovtchinnikov, 1992, espécie-tipo *A. alavica* Ovtchinnikov, 1992 descrita com base em macho e fêmea. Atualmente, o gênero conta com cinco espécies com distribuição Paleártica.

Cryphoecina Deltshv, 1997 é atualmente um gênero monotípico que inclui a espécie *C. deelemana* Deltshv, 1997 descrita com base em macho e fêmea para a região Paleártica.

Pacifantistea Marusik, 2011 é atualmente um gênero monotípico que inclui a espécie *P. ovtchinnikovi* Marusik, 2011 descrita com base em macho e fêmea para a região Paleártica.

2. Hipóteses de relacionamento entre os gêneros

Em 1967, quando Lehtinen transferiu alguns gêneros de Agelenidae para Hahniidae, ele alocou os representantes da família em três subfamílias: Cryphoecinae, Cybaeolinae e Hahniinae (Tabela 1).

Cryphoecinae (*sensu* Lehtinen) é composta por *Calymmaria*, *Cryphoeca*, *Ethobuella* e *Tuberta*, amplamente distribuídas na região Neártica e Paleártica. Cryphoecinae e Hahniinae foram transferidas de Agelenidae por Lehtinen (1967) mas consideradas possíveis integrantes de Dictynidae por Wunderlich (1995) e Wunderlich & Hansen (1995). Entretanto, Lehtinen apoia

que as similaridades entre as espécies de Cryphoecinae com as espécies de Hahniinae são coerentes, haja vista que algumas espécies (por exemplo de, *Cryphoeca*) foram primeiramente registradas dentro do gênero *Hahnia* (ver Platnick 2013).

Tabela 1. Classificação atual dos gêneros de Hahniidae (Lehtinen 1967; Marusik 2011).

Hahniinae	Cybaeolinae	Cryphoecinae	<i>Incertae sedis</i>
<i>Alistra</i>	<i>Austrohahnia</i>	<i>Calymmaria</i>	<i>Asiohahnia</i>
<i>Amaloxenops</i>	<i>Cybaeolus</i>	<i>Cryphoeca</i>	<i>Cryphoecina</i>
<i>Antistea</i>	<i>Lizarba</i>	<i>Dirksia</i>	<i>Harmiella</i>
<i>Hahnia</i>		<i>Ethobuella</i>	<i>Kapanga</i>
<i>Iberina</i>		<i>Tuberta</i>	<i>Neocryphoeca</i>
<i>Intihuatana</i>			<i>Porioides</i>
<i>Neoantistea</i>			<i>Rinawa</i>
<i>Neoaviola</i>			<i>Willisus</i>
<i>Neohahnia</i>			
<i>Pacifantistea</i>			
<i>Scotospilus</i>			

Cybaeolinae (*sensu* Lehtinen) possui espécies exclusivamente da Região Neotropical, apresentando estruturas reprodutivas bastante similares a Hahniinae (*sensu* Lehtinen), não apresentando, porém um condutor funcional distinto, mas sim um tégulo em forma de disco e com função semelhante a de condutor envolto pelo êmbolo (Lehtinen 1967) (Figura 4).

Hahniinae (*sensu* Lehtinen) apresenta ampla distribuição de espécies em todo o mundo e possuem os mesmos padrões básicos de apófise tibial e patelar encontrados nos machos de Cybaeolinae (Lehtinen 1967) (Figura 4), entretanto, segundo Lehtinen (1967) a maioria das espécies de Hahniinae apresenta redução da apófise média, sendo que o condutor embolar do palpo dos machos de Hahniinae consiste de um sulco na margem cimbial em casos onde o condutor verdadeiro esteja totalmente reduzido (ou ausente).

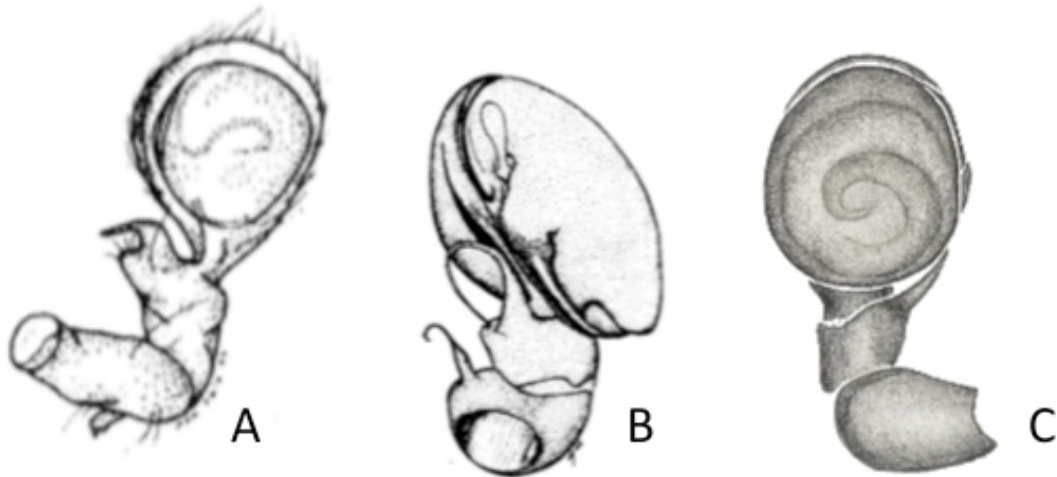


Figura 4. Palpo do macho. **A)** *Cybaeolus pusillus* (Cybaeolinae) por Lehtinen (1967); **B)** *Hahnia pusilla* (Hahniinae) por Lehtinen (1967); **C)** *Neohahnia ernsti* (Hahniinae) por Lo-Man-Hung *et al.* (em prep.)

Lehtinen (1967) considerou que, provavelmente, as espécies de *Hahnia* são as mais basais do grupo, devido a uma distinta apófise média em forma de “colher” presente nas espécies do gênero (exceto em algumas espécies orientais que apresentam apenas uma apófise mediana rudimentar).

Segundo Lehtinen (1967) há três grupos de espécies em Hahniinae: algumas espécies de *Hahnia* constituem um grupo natural e *Iberina* parece ser um derivado deste grupo. *Intihuatana*, *Amaloxenops* e outras espécies Neotropicais e orientais vinculadas a estes gêneros, bem como as *incertae sedis* genéricas devem compor este grupo. O segundo grupo de espécies seria composto por *Neoantistea*, *Neohahnia* e algumas espécies de *Hahnia*, sendo que *Antistea* é provavelmente um grupo derivado deste. *Alistra* e algumas espécies de *Hahnia* formariam o terceiro grupo de espécies, caracterizados pelas longas fiandeiras, muitas macrocerdas nas pernas e especialmente pela simplicidade das estruturas copulatórias.

Segundo observações de Lehtinen (1967) provavelmente a apófise média de Hahniidae foi reduzida na maioria das linhas evolutivas do grupo, o que pode ser observado dentro de Cryphoecinae, em *Tuberta*, em que a apófise média é totalmente reduzida, e em *Cryphoeca*, em que é bem pequena e quase escondida abaixo do condutor (Lehtinen 1967).

Atualmente, para estudos de relacionamento com Hahniidae, destacam-se três estudos, a tese de Catley (1996) que abordou as espécies de Hahniidae da Zona Temperada Sul em uma revisão taxonômica e análise filogenética com base em caracteres morfológicos e dois trabalhos que abordaram indiretamente algumas espécies de Hahniidae em análises filogenéticas moleculares: Spagna & Gillespie (2008) e Miller *et al.* (2010).

Catley (1996) objetivou estabelecer os limites de Hahniidae e delimitar o grupo irmão da família, para isso realizou em sua tese de doutorado uma revisão taxonômica e análise filogenética (Figura 5) para as espécies de Hahniidae distribuídos na Zona Temperada Sul, com ênfase nas espécies do Chile, sua análise filogenética abordou 53 caracteres e 30 terminais compostos de quatro gêneros descritos e cinco gêneros não descritos, incluindo Hahniinae e Cybaeolinae.

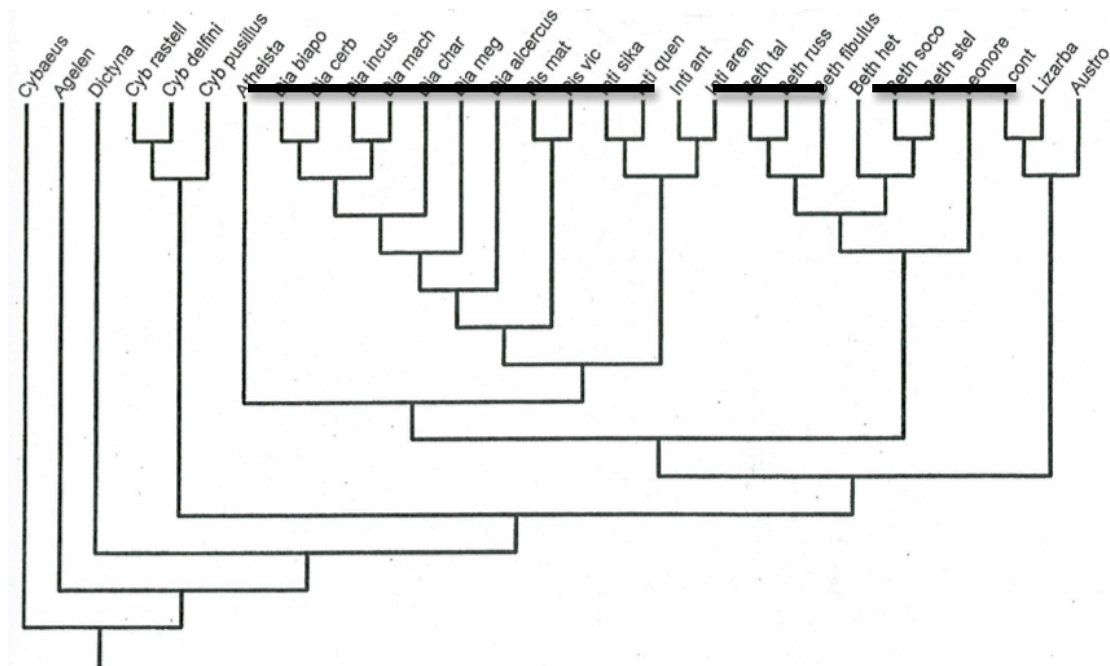


Figura 5. Hipótese filogenética com base em caracteres morfológicos (L=211, CI = 33, RI =55) apresentada por Catley (1996) para as espécies de Hahniidae da Zona Sul Temperada. Barra preta sobre as espécies não descritas.

Segundo revisão de Catley (1996), Cryphoecinae apresenta condição ramificada da traqueia média, retendo uma simples traqueia lateral (característica tida como perdida em Hahniidae), além disso, o sistema traqueal não se estenderia até o cefalotórax, como normalmente ocorre em

Hahniidae e, portanto, sua inclusão nesta família não seria justificada. Para Catley (1996) Cybaeolinae (*sensu* Lehtinen) seria parafilético pois, *Lizarba* e *Austrohahnia* perteceriam a Hahniinae (Figura 5), *Cybaeolus* seria monofilético e seu status como subfamília redefinido e estabelecido como grupo irmão de Hahniinae.

Spagna & Gillespie (2008) utilizaram dados moleculares de genes nucleares (DNA ribossomal 18S, 28S e codificador de proteína H3), assim como o Citocromo oxidase I, para sugerir uma hipótese filogenética para as aranhas que possuem três unhas do “clado RTA” (Coddington & Levi 1991). Nesse estudo, com análise bayesiana, Hahniidae aparece como um grupamento não monofilético. A hipótese proposta por Spagna & Gillespie (2008) aloca *Neoantistea agilis* (Keyserling, 1887) (Hahniidae: Hahniinae) como grupo irmão de *Megadictyna thilenii* Dahl, 1906 (Nicodamidae) e Cryphoecinae (Hahniidae) *sensu* Lehtinen, no clado (*Cryphoeca* + (*Cybaeus* + *Calymmaria*)) (Figura 6) (Spagna & Gillespie 2008).

Segundo Spagna & Gillespie (2008) o agrupamento (*Cryphoeca* + (*Cybaeus* + *Calymmaria*)) parece um possível candidato a grupo irmão dos Agelenidae da Região Holártica e, apesar deste clado possuir representantes de duas famílias (*Cryphoeca* e *Calymmaria* pertencem a Hahniidae e *Cybaeus* pertence a Cybaeidae) estes foram previamente classificados em Agelenidae (Lehtinen 1967; Roth & Brane 1972; Platnick 2013).

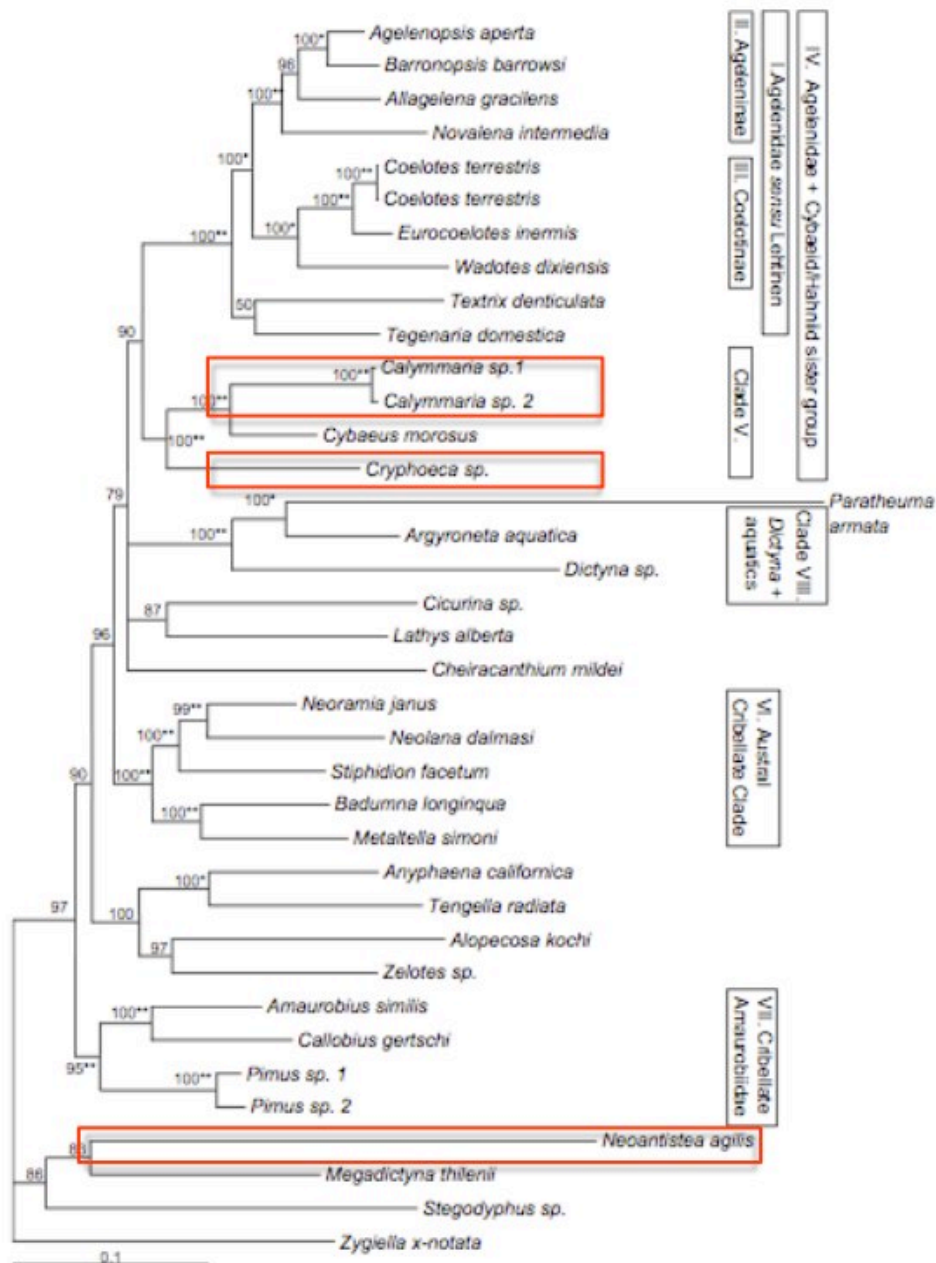


Figura 6. Análise bayesiana de dados combinados (18S + 28S + COI + H3) proposta por Spagna & Gillespie (2008). Em destaque nos retângulos os representantes de Hahniidae.

Miller *et al.* (2010) propuseram uma hipótese filogenética com base em dados moleculares (18S, 28S, H3, COI) das aranhas entelegíneas, incluindo neste estudo representantes das três subfamílias de Hahniidae (Hahniinae, Cybaeolinae e Cryphoecinae). Assim como no estudo feito por Spagna & Gillespie (2008), na maioria das análises bayesianas feitas por Miller *et al.* (2010) o monofiletismo de Hahniidae só foi recuperado com a adição de *Cybaeus* (Cybaeidae) (Figura 7).

A hipótese de Miller *et al.* (2010) (Figura 7), também indica que o monofiletismo de Hahniinae só pode ser recuperado com a adição de *Cybaeolus* (Cybaeolinae). Os autores justificam que apesar de *Cybaeolus* possuir arranjos de fiandeiras mais típico, assim também o possuem alguns representantes de Hahniinae, como algumas espécies do gênero *Hahnia*, que possuem tanto arranjo de fiandeiras transversais, como arranjo de fiandeiras não modificado (Lehtinen 1967).

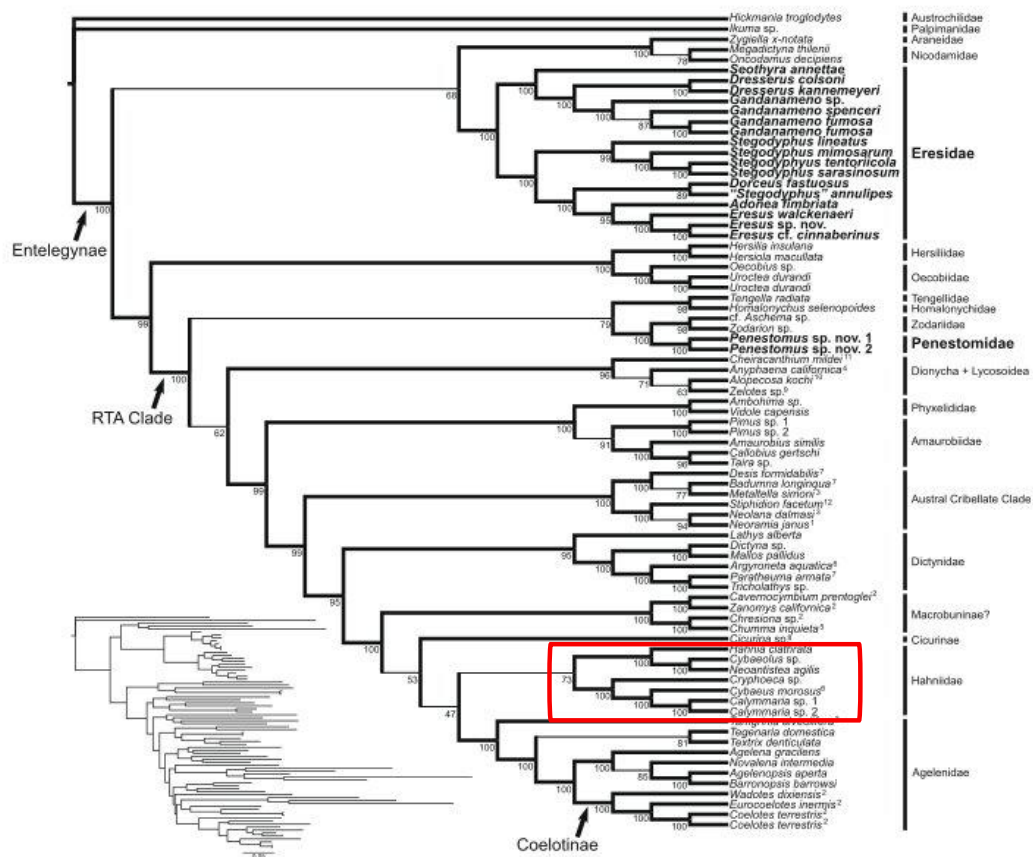


Figura 7. Análise bayesiana de dados combinados (18S + 28S + COI + H3) proposta por Miller *et al.* (2011). Em destaque no retângulo representantes de Hahniidae.

As três análises citadas acima sugerem a necessidade de uma nova delimitação de Hahniidae. Entretanto, Catley (1996) não utilizou as três subfamílias em sua análise filogenética, assim também como Spagna & Gillespie (2008) em sua análise molecular e, mesmo Miller *et al.* (2010) que representou as três subfamílias em sua análise molecular não conseguiu uma definição completa do relacionamento destas, possivelmente devido a critérios de alinhamento e otimização de sua análise molecular.

Sendo assim, o presente trabalho visou estudar as relações filogenéticas e testar o monofiletismo das subfamílias de Hahniidae. Definir as relações entre as subfamílias é necessário para tornar possível um acréscimo de informações que possibilitem futuras revisões dos gêneros e espécies do grupo. Para tanto, este trabalho foi dividido em duas partes: esta apresentação/revisão em português e um capítulo redigido em inglês e em formato de artigo para publicação: *Cladistic analysis of the subfamilies of the comb-tailed spider (Araneae: Hahniidae)*: artigo em formato para submissão da revista *Zoologica Scripta* (Factor 2.913 – A1), normas (instruções para autores) no final do manuscrito.

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ARTICLE

**Cladistic analysis of the subfamilies of the comb-tailed spider
(Araneae: Hahniidae)***

*Manuscrito formatado para submissão ao *Zoologica Scripta*

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**Cladistic analysis of the subfamilies of the comb-tailed spider
(Araneae: Hahniidae)**

NANCY F. LO-MAN-HUNG

Running head:

Cladistic analysis of Hahniidae

N.F. Lo-Man-Hung

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Since Bertkau established Hahniidae, many taxonomic changes were proposed for the group. Indeed, even now, no such consensus for the relationships between subfamilies of the Hahniidae or their related groups. Therefore, this study tested the three subfamilies placement within the Hahniidae and providing a first cladistic analysis of Hahniidae based on morphological characters including the three subfamilies. The character matrix comprised 30 terminal taxa coded for 106 characters. Characters were treated as unordered and equally weighted. A parsimony analysis estimated by heuristic search found one shortest tree (L = 412, CI = 37, RI = 53). This tree shows that Hahniidae is not a monophyletic group but comprises two distinct lineages, one composed by genera of the subfamily Cryphoecinae arising in more basal nodes on the cladogram and, the other one includes the remaining hahniids as sister-group of Dictynidae, comprising both Cybaeolinae and Hahniinae as non-monophyletic groups. Cybaeolinae seems to be composed only by the genus *Cybaeolus*. Regarding for Hahniinae, formal subdivisions should not be made until genera are revised, but at least the delimitation of *Hahnia* is quite necessary.

Introduction

In 1841, C. L. Koch honored the German researcher Carl Wilhelm Hahn, author of the first four volumes of *Die Arachniden* (1831-1848), with the genus name *Hahnia*, which, years later, was chosen as the type-genus of the family Hahniidae Bertkau, 1878. The family includes small spiders easily recognized by the transverse arrangement of three pairs of spinnerets and the presence of a tracheal spiracle on the middle of the abdomen or near the spinnerets (Bertkau 1878; Opell & Beatty 1976).

Since Bertkau (1878) established the family, many taxonomic changes were proposed for the group. It was first allocated as a group within Agelenidae by Emerton (1890) and Simon (1892). However, Petrunkevitch (1933) removed the group from the clade Quadrostiatae based on reduction of cardiac ostia (two pairs) and ranked it again to family status. Gerhardt & Kaestner (1938) and Kaston (1948), based on the tracheal system that advances to the cephalothorax, allocated Hahniidae in the superfamily Lycosoidea. Thereafter, Lehtinen (1967) proposed another classification, allocating some species of the tribe Cryphoeceae, of the subfamily Ageleninae (Simon, 1897), and part of the subfamily Cybaeinae as subfamilies (i.e., Cryphoecinae and Cybaeolinae) within Hahniidae, which was allocated within the superfamily Amaurobioidea. Forster (1970) partly supported Lehtinen's classification, however, following a limited view of Hahniidae definition (i.e., just genera recognized by transverse arrangement of the three pair of spinnerets), he decided to allocate Hahniidae within the superfamily Dictynoidea, even more because the members of this group share median strongly branched or divided tracheae, unlike Amaurobioidea, whose members share thin unbranched tracheae (Forster 1970; Bromhall 1987).

The family Hahniidae currently comprises 27 genera and 250 species with a wide distribution throughout the world (Platnick 2013; Zhang *et al.* 2013). It includes three subfamilies, Cryphoecinae (*sensu* Lehtinen) that comprises genera widely distributed by Nearctic and Palaeartic regions, the median apophysis can be fully reduced or very small and almost hidden below the

conductor, Cybaeolinae (*sensu* Lehtinen) is endemic to Neotropical Region and share reproductive structures very similar to Hahniinae (*sensu* Lehtinen), although the absence of conductor distinct and functional, Cybaeolinae genera have a disc-shaped tegulum surrounded by a circular embolus with similar function as conductor and Hahniinae (*sensu* Lehtinen) comprises genera widely distributed around the world, genera share the same tibial and patellar apophysis basic patterns of Cybaeolinae males, however, most species have reduced median apophysis and have a cymbial border furrow if the true conductor is reduced or absent (Lehtinen 1967).

Coddington & Levi (1991) placed Hahniidae in the superfamily Dictynoidea, in the *Retrolateral Tibial Apophysis* (RTA) clade, following Forster's classification (1970). After that, Catley (1996) aimed to establish the limits of Hahniidae and delimit the sister group of the family, his phylogenetic analysis based on morphological characters to species distributed in South Temperate Zone addressed 53 characters and 30 terminals, including Hahniinae and Cybaeolinae. Catley (1996) study the tracheal systems of some species of Cryphoecinae and reported that they show a branched condition of median tracheae and retain simple lateral tracheae unlike the other hahniids. Furthermore, phylogenetic analysis provides both Hahniinae and Cybaeolinae paraphyletic because *Lizarba* and *Austrohahnia* would belong to Hahniinae (Catley 1996). Afterwards, newly released two papers dealing with phylogenetic relationships at the molecular level within the Hahniidae, Spagna & Gillespie (2008) and Miller *et al.* (2010). Both studies shared similar results, in most Bayesian analysis there are no support for the monophyly of Hahniidae unless the genus *Cybaeus* L. Koch (Cybaeidae) is added to the family.

Despite the studies cited above claim for a new delimitation of Hahniidae, Catley (1996) did not use the three subfamilies in their phylogenetic analysis, so as Spagna & Gillespie (2008) in their molecular analysis and, even Miller *et al.* (2010) could not delimited the family as because it was not the goal of their study as some alignment (most Hahniidae species) appear consistent with the phenomenon of long-branch attraction. Hence, this article provided the first

morphological cladistic analysis to test the three subfamilies placement within the Hahniidae.

Materials and Methods

Specimens

Specimens examined are deposited in the following institutions (abbreviations and curators in parentheses): American Museum of Natural History, New York, New York (AMNH, N.I. Platnick); Instituto Butantan, São Paulo, São Paulo (IBSP, D.M. Barros-Battesti); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCTP, A.A. Lise); Museo de La Plata, La Plata, Buenos Aires (MLP, L.A. Pereira); Museu Paraense Emílio Goeldi, Belém, Pará (MPEG, A.B. Bonaldo).

Morphological abbreviations

Abbreviations used in the text and figures, as follows:

ALE Anterior lateral eyes; **ALS** Anterior lateral spinnerets; **AME** Anterior median eyes; **mAP** minor ampullate gland spigot; **MAP** major ampullate gland spigot; **PI** piriform gland spigot; **PLE** Posterior lateral eyes; **PLS** Posterior lateral spinnerets; **PME** Posterior median eyes; **PMS** Posterior median spinnerets.

Laboratory procedures

All morphological measurements and color patterns were based on specimens immersed in 80% alcohol, examined using a stereomicroscopy ZEISS SV11. The measurements were taken with an ocular micrometer and were used a conversion factor from the known measurement to convert the physical length of the marks on the scale in millimeters. Male palp examination were mostly based on left pedipalp, female genitalia was first dissected

following Levi (1965) then, it was submitted to trypsin enzyme (for digesting internal soft tissues) following a modified protocol of Álvarez-Padilla & Hormiga (2007) and immersed in clove oil to examination of internal structures. For the scanning electron micrographs (SEM), the structures were cleaned for 3 min in alcohol in an ultrasonic bath (Ultrasonic Cleaner USC 700) with water, then structures were submitted to dehydration by crescent alcohol concentration series (3 series: 85%, 90%, 96%) passed after to acetone 100% and then they were critical-point dried from CO₂ using a critical point dryer (Bal-Tec CPD 030 Critical Point Dryer) for 2h. The dried structures were fixed to aluminum stubs with double-sided adhesive carbon tape and, sometimes, the pieces were mounted on the top of entomological pins. The stubs were then sputter coated with gold in a Bal-Tec SCD 005 Sputter Coater and placed in a vacuum desiccator until examination under a Philips XL 30 scanning electron microscope operated at 20kV. All the SEM protocol and images were made at Centro de Microscopia e Microanálises (CEMM) of Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS). SEM images were processed with open source image editing Gimp 2.6 (GNU Image Manipulation Program) and the final plates were edited with open source vector graphics editor Inkscape 0.48.

Taxon choice

The ingroup included representatives of all the three subfamilies of Hahniidae and some *incertae sedis* specimens as currently known (Appendix 1). Whenever possible the analyses were made by study specimens of type genera of these subfamilies. The dataset comprises 13 representatives of Hahniinae, four of Cybaeinae, five of Cryphoecinae and two *incertae sedis*. *Hahnia heterophtalma* Simon, 1905 and *Intihuatana antarctica* (Simon, 1902) were scored using literature sources (Simon 1902; Catley 1996).

Outgroup choice

The outgroup included representatives of the superfamily Dictynoidea, following Coddington and Levi (1991) as Dictynidae and Ageleniidae plus representatives of related families as Cybaeidae (Appendix 1). To root the cladogram it was used a representative of Amaurobiidae, because it is the family more closely related and most basal among the groups discussed (Miller *et al.* 2010). Males of *Coelotes terrestris* (Wider, 1834) and *Amaurobius ferox* (Walckenaer, 1830) were scored using literature sources (Roberts 1985; Silva 2003; Jocqué & Dippenaar-Schoeman 2006).

Character selection

Morphological characters were scored based on examination at stereomicroscopy, SEM images, bibliographical references or other observations. Characters and their respective character states are defined and described in Appendix 2. Characters were described following the character statement proposed by Sereno (2007). Throughout the text, figures cited from literature are listed as “fig.” and those appearing in this paper as “Fig.”

Cladistic analysis

The character matrix was edited using the software Mesquite version 2.74 (Maddison & Maddison 2010). The resulting data matrix was analyzed using parsimony method performed using the software TNT version 1.1 (Goloboff *et al.* 2008). Maximum parsimony analysis were estimated using the heuristic search option and to ensure that minimum length is hit independently several times, a series of searches with either number of replications and number of trees saved per replication changed were performed. Thus, parsimonious trees was assessed by performing with 5000 replicates of stepwise random addition holding 100 trees at each step and tree bisection reconnection (TBR), subtree pruning and regrafting (SPR) branch swapping algorithms. In order to explore the result the tree retained was also start an additional branch swapping. Characters were all treated as unordered and

equally weighted, the software MacClade version 4.08 (Maddison and Maddison 2005) was used to analyze patterns of evolution using character-state optimization, in tracing character evolution tool. Node robustness of the tree topology obtained was estimated through Goodman-Bremer Support metric (Goodman *et al.* 1982; Bremer 1988, 1994; Grant and Kluge 2008a) values and were calculated for each node in TNT using a manual command when progressively larger number of suboptimal trees is retained (i.e. mult 20; sub 1; hold 2000; bsupport;... mult 20; sub 2; hold 4000; bsupport;... increasing successively until Goodman-Bremer support is achieved). It was also calculated the Ratio of Explanatory Power (REP), support (Grant and Kluge 2007) a measurement across datasets that allows comparison of support across datasets (Grant and Kluge 2007, 2008b).

Results

In total, 30 terminal taxa were coded for 106 characters (Appendix 3). Characters were coded from male and female genitalia (33 male and nine female), 63 characters were based on other structures (carapace, abdomen, legs) and one was coded from behavior data (Appendix 2). One shortest tree (Fig. 1) was found by heuristic search (L = 412, CI = 37, RI = 53).

In this hypothesis Hahniidae is not monophyletic. Cybaeidae is the sister group of Cryphoecinae + Dictynidae + remaining hahniids, this node is supported by three non-ambiguous synapomorphies: a thickened and flattened embolus shape at the base (26:4), absence of cephalothorax markings (40:1), absence of cribellum (74:0) and one homoplastic synapomorphy: an oval tegulum shape (31:0). Cryphoecinae arises as monophyletic group and is supported by three homoplastic synapomorphies: absence of loop of ejaculatory duct (30:0), dark pigmentation around eyes (56:1) and presence of colulus (75:1) and, it is a sister group of Dictynidae + remaining hahniids with three homoplastic synapomorphy: carapace and abdomen both mottled (44:3), chelicerae not tumid (48:1) and absent of muscle dots on dorsum of abdomen (81:0). Dictynidae emerges as sister group of the remaining hahniids and this

clade is supported by two non-ambiguous synapomorphies: a simple and long embolus (26:0), contiguous ALE-PLE interdistance (60:0) and two homoplastic synapomorphies: a short terminal part above the bulbus (23:0), embolus base free (25:1). Hahniidae (except Cryphoecinae) is supported by five unambiguous (one non-homoplastic) synapomorphies: presence of retrolateral patellar apophysis (14:1), labium length wider than long (36:1), carapace color lighter than abdomen (44:0), unpigmented spinnerets (69:0), transverse spinneret topology (70:2). *Harmiella schiapelliae* + *Pacifantistea ovtchinnikovi* are basal species of the clade composed by remaining hahniids (Hahniidae except Cryphoecinae) and it is supported by two homoplastic synapomorphy: presence of cymbial furrow (24:1) and presence of tarsal spines (91:1). *Cybaeolus* is defined as a monophyletic clade with a better supported clade (i.e., Goodman-Bremer support value greater than 12, Fig. 1) and, it is supported by four non-ambiguous synapomorphies: embolus shape is a simple median spine (26:7), ALE and PLE with dark pigmentation (56:2), semi-transverse spinneret topology (70:1), elongate tarsal organ (95:2) and five homoplastic synapomorphy: distal shape of retrolateral tibial apophysis in straight angle (5:2), absence of longitudinal fovea groove (45:0), conical shape of ALS (65:0), tracheal spiracle at the base of spinnerets (79:0), absence of femoral spines (97:0). *Cybaeolus* arises here as a sister group of apical *Hahnia* species, this clade is supported by one non-ambiguous synapomorphy: a small median apophysis (2:0); and two homoplastic synapomorphies: presence of stridulatory ridges in retrolateral face of male chelicerae (51:1) and presence of dorsum abdomen muscle dots not round (81:2). Indeed, *Hahnia* as currently recognized seems to be polyphyletic comprised at least of five related clades with six other genera seem to be interspersed between them (*Austrohahnia*, *Intihuatana*, *Lizarba*, *Neoantistea*, *Neocryphoeca*, *Neohahnia*). *Neoantistea* genus is supported by two non-ambiguous synapomorphies: presence of tracheal spiracle twice as far from de base of spinnerets (79:3), presence of stridulatory organ on abdomen (80:1) and five homoplastic synapomorphies: presence of small patellar spur on males (20:1), a long terminal part (above the bulbus) (23:1), presence of muscle

dots not rounded on the dorsum of abdomen (81:2), long insemination ducts (88:1) and presence of long recurved ventral setae in all male legs (105:1).

Discussion

This is the first cladistic analysis of Hahniidae as a whole based on morphological characters. The hypothesis reported (Fig. 1) here highlight a number of important systematic issues pertaining to Hahniidae and related families. Not surprisingly, Hahniidae is not a monophyletic group (Catley 1996; Spagna and Gillespie 2008; Miller *et al.* 2010). Likewise, the close relationship between Dictynidae, Cybaeidae and Hahniidae was previously hypothesized (Coddington and Levi 1991).

An unmodified spinneret topology treated here consists in a basic pattern observed in most Araneomorphae, with PMS located posteriorly more closely to the PLS than to the ALS and, PLS close to ALS (70:0, Fig. 2A). Modified spinneret topology must represent an unique non-ambiguous synapomorphy for Hahniidae *sensu stricto* in this analysis, at least three stages of modification were observed in the specimens studied. A semi-transverse spinneret topology was based in observation of migration anteriorly of PMS and laterally of PLS in relation to ALS, resulting in PMS more closely to ALS than PLS, this state is shared by *Cybaeolus* (70:1, Fig. 2B). A transverse spinneret topology condition is where the PMS and PLS migrated even more to almost be parallel with ALS (70:2, Fig. 2C). At last, it was observed a third state of modified spinneret topology, between semi-transverse and transverse spinneret topology that evolved independently in *Neocryphoea gertschi* Roth, 1970, *Lizarba separata* Roth, 1967 and *Coelotes terrestris* (Wider, 1834) (70:3, Fig. 1).

Cryphoecinae (*sensu* Lehtinen) is composed of five genera: *Calymmaria*, *Cryphoea*, *Dirksia*, *Ethobuella* and *Tuberta* with wide distribution through Nearctic and Palearctic regions. Two genera were used to represent this subfamily in the analysis (*Calymmaria* and *Dirksia*), cladistics result suggest that Cryphoecinae is monophyletic group however must be removed from Hahniidae because they are not members of this family as defined herein due

Cryphoecinae members present unmodified spinneret topology. Indeed, both Spagna and Gillespie (2008) and Miller *et al.* (2010) corroborated similar results, in most Bayesian analysis representatives of Cryphoecinae were considered more closely related to Cybaeidae, the causes of this phylogenetic conflict may be due members of subfamily Cryphoecinae that shared a more typical spinneret arrangement like *Cybaeus* L. Koch (Miller *et al.* 2010). However, despite the shared characters between Cybaeidae and Cryphoecinae there is no strong evidence that they are related in this present study. More needs to be done in order to test their hypothesis, e.g. more exemplar species of Cybaeidae and Cryphoecinae, especially type taxa (i.e. *Cybaeus* L. Koch, 1868 and *Cryphoeca* Thorell, 1870, respectively) should be included in the analysis (see, Prendini 2001, for strategy for exemplar choice in phylogenetic analysis), even more considering the relative uncertainty placement of *Argyroneta aquatica* Clerck, 1757, several authors placed within Cybaeidae (Selden 2002; Jocqué and Dippenaar-Schoeman 2006; Platnick 2013) against molecular phylogeny where the species is placed within Dictynidae (Spagna and Gillespie 2008; Miller *et al.* 2010).

Cybaeolinae (*sensu* Lehtinen) included *Austrohahnia*, *Cybaeolus* and *Lizarba* genera, to diagnose the subfamily the following characters were proposed by Lehtinen (1967): absence of a distinct functional conductor and a disc-shaped tegulum surrounded by a circular embolus with similar function as conductor. Whereas in this hypothesis (Fig. 1), the monotypic genera *Austrohahnia* and *Lizarba* do not seem to share characters with *Cybaeolus* leading Cybaeolinae as currently known, a non monophyletic group supporting Catley's study (1996), in fact, even Lehtinen (1967: 368) considered which at least relationship of *Austrohahnia* and *Cybaeolus* remained obscure.

Morphological phylogenetic analysis for this study supports as well as Catley (1996), however, the monophyly of the Neotropical *Cybaeolus* and so, suggest to recognize the subfamily Cybaeolinae as valid, comprised only by this genus. Four non-ambiguous and five homoplastic synapomorphies support this clade (Fig. 1). Lehtinen (1967) observed that some features could be shared by both cybaeolines and hahniines like the same tibial and patellar apophysis

basic patterns in males. However, he could not be sure if these features were result of parallel evolution. Similar to Lehtinen (1967), in this present hypothesis *Cybaeolus* also share some characters with hahniines, especially apomorphic *Hahnia* (i.e., *H. nava*, *H. pusilla*, *H. helveola*, *H. cinerea*, *H. ononidum*, Fig. 1) including a non-ambiguous synapomorphy: presence of a small median apophysis (2:0) and two homoplastic synapomorphies: stridulatory ridges in retrolateral face of male chelicerae (51:1) and presence of abdominal muscle dots (81:2).

Hahniinae (*sensu* Lehtinen) comprises genera widely distributed globally and, most species with reduced median apophysis and a cymbial border furrow in the case of true conductor is reduced or absent. Lehtinen (1967) did not use phylogenetic analysis to describe the relationships, but he clearly believed that Hahniinae must be separated in tribes, then, he recognized three groups within Hahniinae, as follow: a group with a spoon-shaped median apophysis should consist by part of *Hahnia* species, *Iberina*, *Intihuatana*, *Amaloxenops* and some Neotropical and Oriental species; a second group based on closely resemble of female genitalia would consist by part of *Hahnia* species, *Neoantistea*, *Neohahnia* and *Antistea* and, a third group characterized by very long spinnerets, features on leg spines and simple genitalia would consist by part of *Hahnia* species and *Alistra*. The hypothesis reported here could not support Lehtinen's grouping, first of all because Hahniinae is a non monophyletic group in this analysis, and so even if, for example, the clade ((*Neoantistea agilis*, *Neoantistea magna*) (*Hahnia montana*, *Neohahnia ernsti*)) is supported by two homoplastic synapomorphies: sternum wider than long (39:1) and long PLS in relation to ALS (66:0), meaning a mixture of second and third Lehtinen's grouping. Further investigation by Lehtinen (1967) suggests that the shape of median apophysis in most *Hahnia* species could indicate this genus as a most basal within Hahniinae. The hypothesis reported here find strong evidence that *Hahnia* as current known, is a polyphyletic group comprised at least five related clades with six other genera seems to be interspersed between them (*Austrohahnia*, *Intihuatana*, *Lizarba*, *Neoantistea*, *Neocryphoeca*, *Neohahnia*).

To date, these five clades do not coincide with groups previously established by Lehtinen (1967).

Overall, the hypothesis present here has shown important and emerging issues related to Hahniidae as currently known and families related. Hahniidae is not a monophyletic group but comprises two distinct lineages: one related to genera of the subfamily Cryphoecinae and its closely relationship to Cybaeidae and/or Dictynidae would be possible to test with a more appropriate phylogenetic analysis with more included species; other one is related to remaining hahniids as sister group of Dictynidae, comprising both Cybaeolinae and Hahniinae not monophyletic group. Cybaeolinae seems to be comprised only by *Cybaeolus* genus. While for Hahniinae, as Lehtinen (1967) stated the still uncertain position of many genera and the limits of this analysis could not define any prepositions about Hahniinae's groups, at least, the delimitation of *Hahnia* genus is quite necessary.

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Figure 1. Phylogeny of Hahniidae subfamilies based on evolution of 106 morphological characters defined in Appendix 2 and 3, L = 412, CI = 37, RI = 53. Only characters changing unambiguously on branch, tracing character evolution are represented by symbols, see legend for means. Goodman-Bremer support and REP values given near nodes, on the left and right sides, respectively. Labels of subfamilies follow Lehtinen (1967) and Marusik (2012)

Figure 2. A-F: **A.** *Cybaeolus delfini*, female, chelicerae. **B.** *Cybaeolus delfini*, female, rastellum. **C.** *Cybaeolus rastellus*, female, chelicerae. **D.** *Cybaeolus rastellus*, female, rastellum. **E.** *Dirkisia cintipes*, male, metatarsus II, tarsal organ. **F.** *Dirkisia cintipes*, female, tibia III, trichobotrial, base.

Figure 3. A-F: **A.** *Hahnia pusilla*, female, chelicerae lateral. **B.** *Hahnia pusilla*, female, stridulatory ridges. **C.** *Cybaeolus rastellus*, male, chelicerae lateral. **D.** *Cybaeolus rastellus*, male, stridulatory ridges. **E.** *Cybaeolus delfini*, female, chelicerae lateral. **F.** *Cybaeolus delfini*, female, stridulatory ridges.

Figure 4 A-F: **A.** *Calymmaria monicae*, male, spinneret topology. **B.** *Cybaeolus pusillus*, male, spinneret topology. **C.** *Neohahnia ernsti*, male, spinneret topology. **D.** *Calymmaria monicae*, male MLS. **E.** *Cybaeolus rastellus*, male ALS. **F.** *Neohahnia ernsti*, male, ALS.

Figure 1.

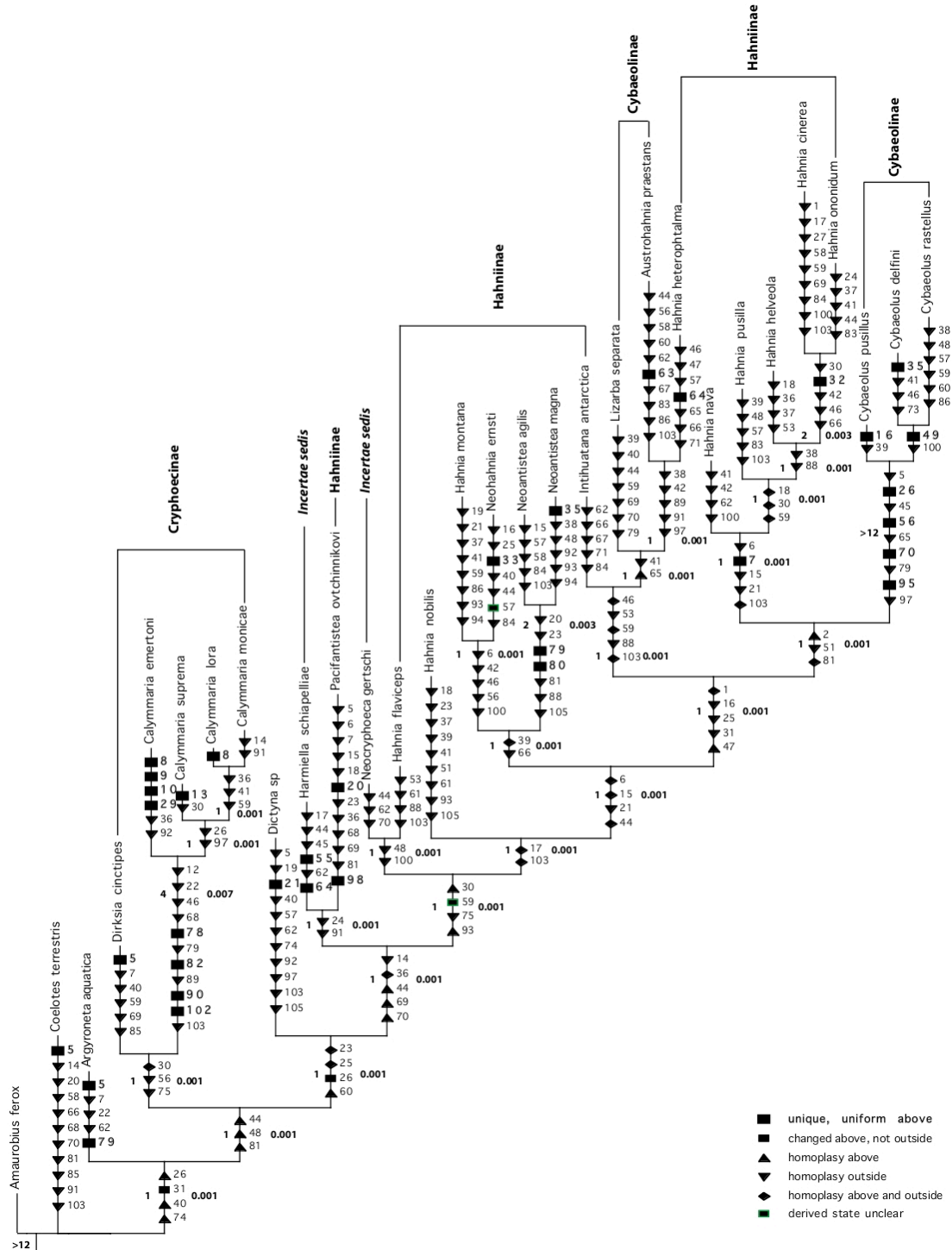


Figure 2.

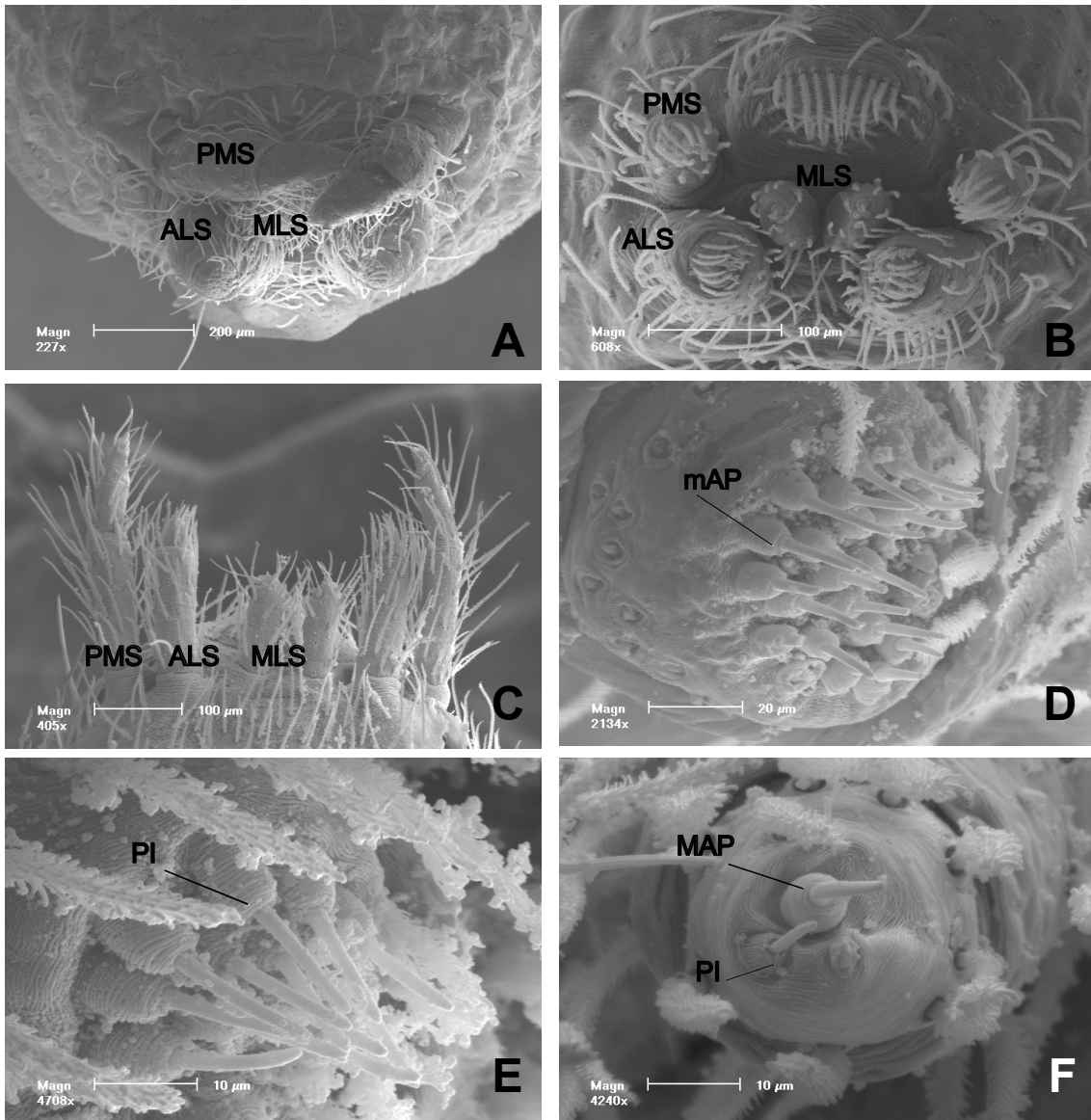


Figure 3.

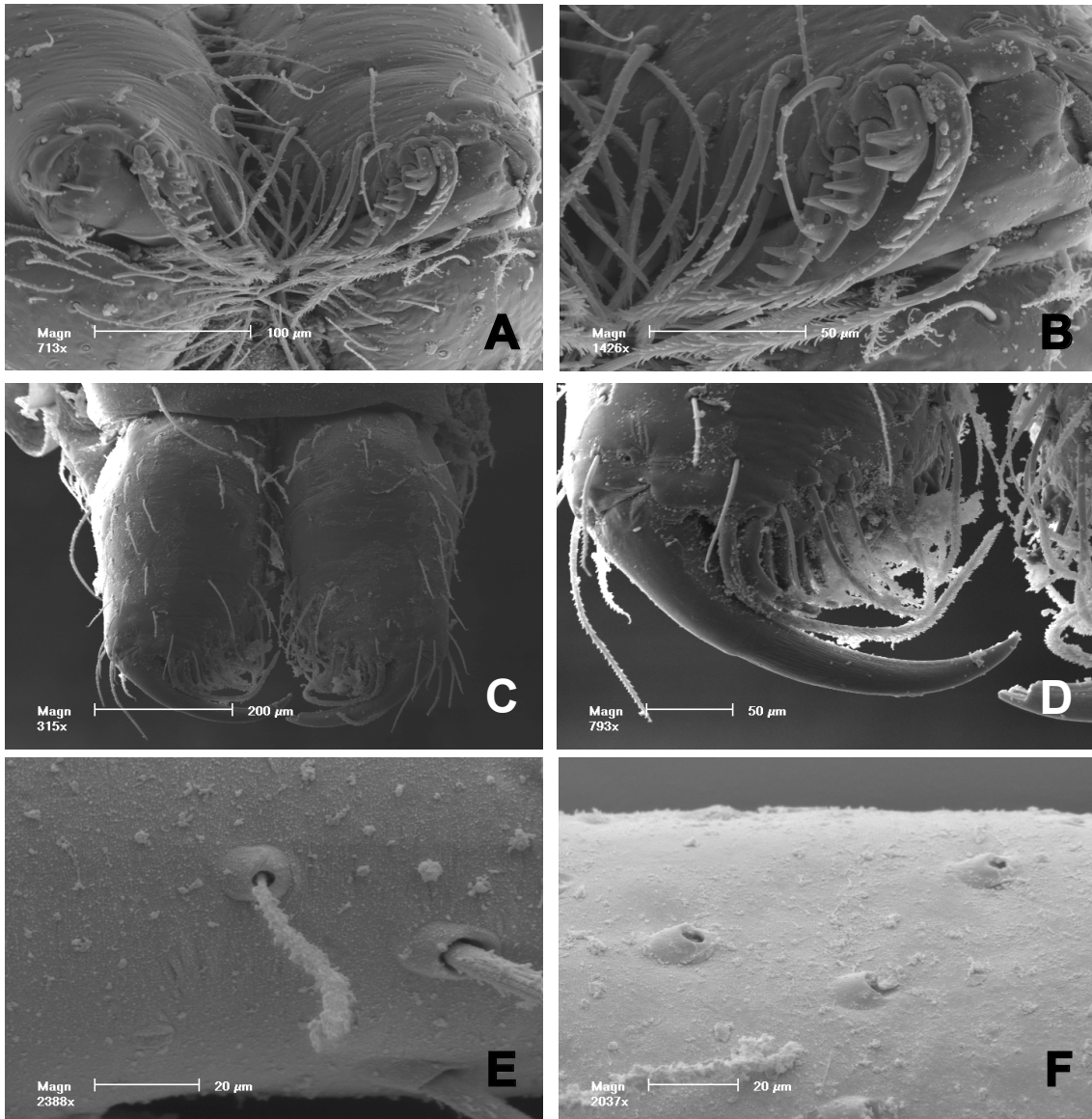
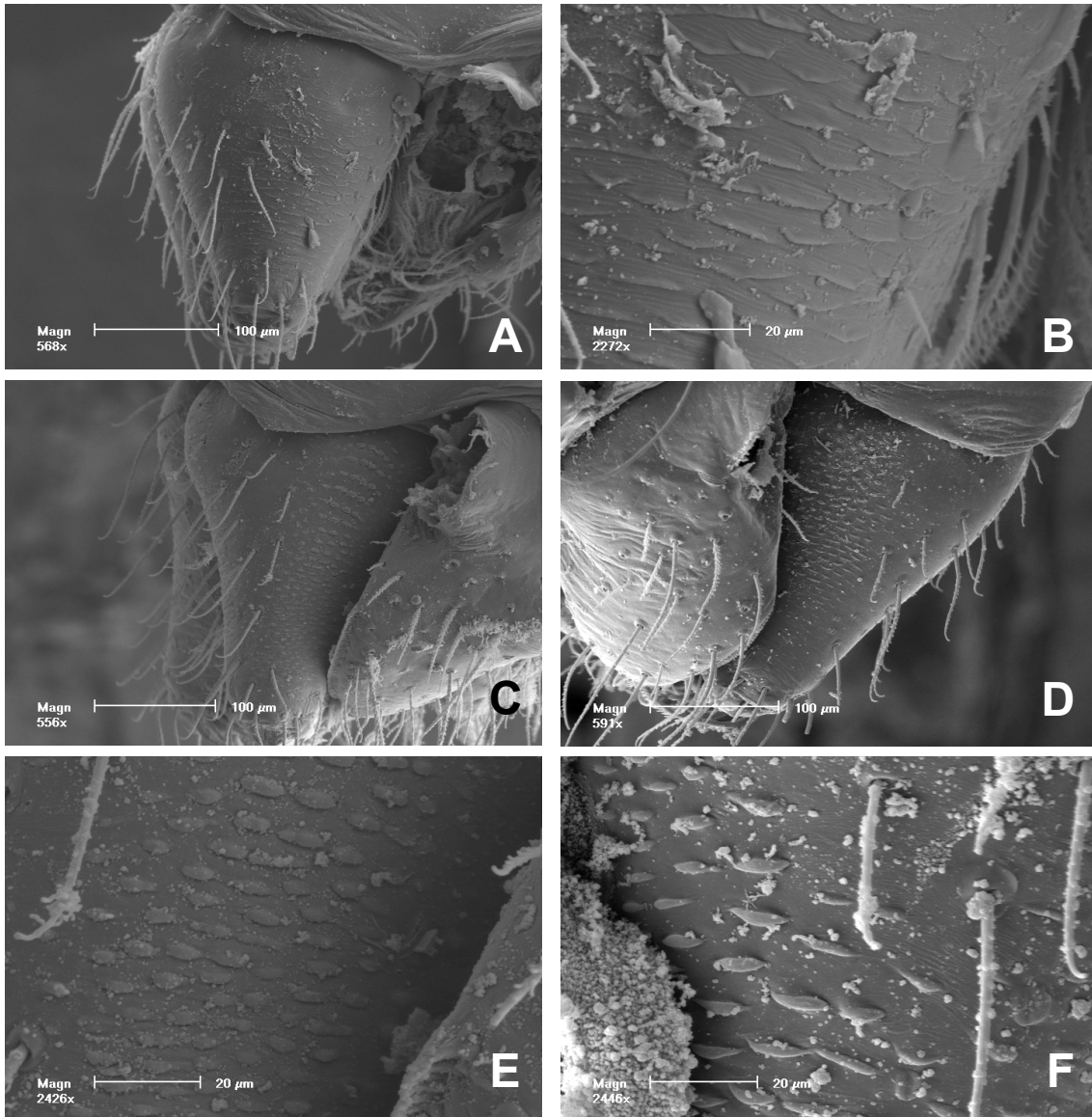


Figure 4.



Supporting Informations

Appendix S1. List of terminals, with collecting and deposition data examined in the cladistic analyses. Vouchers were labeled as “Hahniidae Phylogeny”.

Ingroup

HAHNIIDAE

Cybaeolinae (*sensu* Lehtinen)

Austrohahnia praestans Mello-Leitão, 1942. ARGENTINA: *Santiago del Estero* (Colonia Dora), XI.1940, J.W. Abalos, 2♀ Syntypes (MLP 15590).

Cybaeolus delfini (Simon, 1904). CHILE: *Chiloé* (Isla Chiloé, Guabún: N of Ancud), 13-15.I.1980, L.E. Peña, 1♀ (AMNH).

Cybaeolus pussillus Simon, 1884. CHILE: *Osorno* (Region X (Los Lagos): Osorno: hills S Maicolpue elev. 50m), 19.II.1992, N. Platnick, P. Goloboff and M. Ramirez, 1♀ (AMNH).

Cybaeolus pussillus Simon, 1884. CHILE: *Aisén* (Region XI (Aisén): reserva Nacional Río Simpson, 37km W Coihaique 20m, wet forest), 20.I.1986, N.I. Platnick, P.A. Goloboff and R.T. Schuh, 1♂ (AMNH).

Cybaeolus rastellus (Roth, 1967). CHILE: *Bío-Bío* (Region del Bío-Bío (VIII): El Manzano, nr Cotulmo), 15.XII.1985, L.E. Peña, 1♂1♀ (AMNH).

Lizarba separata Roth, 1967. BRAZIL: *Río de Janeiro*: Teresópolis (Est. Rio, 1600-1800m elev.), 16.III.1946, H. Sick, Holotype, 1♀ (AMNH).

Hahniinae (*sensu* Lehtinen)

Hahnia cinerea Emerton, 1890. USA: *Arizona* (Graham Mt.), 13.IX.1950, W.J. Gertsch, 2♂1♀ (AMNH).

Hahnia flaviceps Emerton, 1913. USA: *Louisiana* (Madison Parish Tallulah), 13.II.1935, J.A. Beatty, 1♂3♀ (AMNH).

Hahnia helveola Simon, 1875. ENGLAND: *Hampshire* (Beaulieu Rd Station), 17.X.1954, 1♂1♀ (AMNH).

Hahnia montana (Blackwall, 1841). AUSTRALIA: *Perth* (Blackwood, alt 900m), 5.IX.1965, 1♂1♀ (AMNH).

Hahnia nava (Blackwall, 1841). ENGLAND: *Cunberland* (Grimmer Crag), 4.VI.1950, J.A.L.C., 1♀ (AMNH).

Hahnia nava (Blackwall, 1841). ENGLAND: *Hampshire* (Needs oar poinst Harts), 9.IV.1955, J.A.L.C, 1♂ (AMNH).

Hahnia nobilis Opell & Beatty, 1976. MEXICO: *Hidalgo* (5mi. N. Encarnacion (6000')), 20°55'N 99°12'W, 28.VII.1966, J and W. Ivie, Paratypes, 1♂1♀ (AMNH).

Hahnia onoidum Simon, 1875. SWITZERLAND: *Basel* (Mergei Kerlez), 3♂2♀ (AMNH).

Hahnia pusilla C.L. Koch, 1841. ENGLAND: *Surrey*, 1♂1♀ (AMNH).

Neoantistea agilis (Keyserling, 1887). USA: (WV Preston County, WV University Forest Chestnut Ridge. Mixed Oak-Hardwood), 19-26.VI.1990, D.T. Jennings, 1♂1♀ (AMNH).

Neoantistea magna (Keyserling, 1887). USA: *Maine* (Piscataquis County, Wels 1.9km SSE of Soubunge Mtn.), 27.VII.1977, D.T.J., 1♂1♀ (AMNH).

1♂1♀ (AMNH).

Neohahnia ernsti (Simon, 1897). BRAZIL: *Pará*: Bragança, II.2007, D.F. Candiani and N.F. Lo-Man-Hung, 1♀ (MPEG 13490).

Neohahnia ernsti (Simon, 1897). BRAZIL: *Piauí*: José de Freitas (Fazenda Nazareth), 4°47'58.1"S 42°37'48.8"W, 1♂ (MPEG).

Pacifantistea ovtchinnikovi Marusik, 2011. RUSSIA: (Far east, Sakhalin Area, Moneron Isl., SE shore near Vostochnyve Isles), 46°14.387'N 141°15'W, 23.VIII.2011, Yu.M. Marusik, Paratypes, 1♂1♀2j (AMNH).

Cryphoecinae (*sensu* Lehtinen)

Calymmaria emertoni (Simon, 1897). CANADA: *British Columbia*: (Vancouver Is., Tofino), 10-31.V.1950, R. Guppy, 1♀ (AMNH).

Calymmaria emertoni (Simon, 1897). CANADA: *British Columbia*: (Vancouver Is., Wellington), IX.1950, R. Guppy 1♂ (AMNH).

Calymmaria lora Chamberlin & Ivie, 1942. USA: *California*: (Shaver Lake), IX.1959, 1♂ (AMNH).

Calymmaria lora Chamberlin & Ivie, 1942. USA: *California*: (Sequoia Nat. Pk.-3700 near Ash Mt. Entrance), 5.VII.1956, W. Gertsch and R. Roth, 1♀ (AMNH).

Calymmaria monicae Chamberlin & Ivie, 1937. USA: *California*: (2mi. No. Bolinas, Marin Co.), W122.42: N37.54, 27.IX.1963, Jean & Wilton Ivie, 1♂2♀ (AMNH).

Calymmaria suprema Chamberlin & Ivie, 1937. USA: *California*: (Ben Lomond), 6.VII.1956, V. Roth and W. Gertsch, 1♂2♀ 3j (AMNH).

Dirksia cinctipes (Banks, 1896). CANADA: *British Columbia*: (Tofino, Vancouver Is.), 7-15.VIII.1953, R. Guppy, 1♀ (AMNH).

Dirksia cinctipes (Banks, 1896). CANADA: *British Columbia*: (Kyuquot, Spring Is.), 21.VII.1959, S.L. Neave, 1♂ (AMNH).

Incertae sedis

Neocryphoeca gertschi Roth, 1970. USA: *Arizona* (Mt. Lemmon (vic. Summerhaven)), 21.V.1963, 1♀ (AMNH).

Harmiella schiapelliae Brignoli, 1979. BRAZIL: *Santa Catarina* (Rio Molha, Urussanga), 28°31'S 49°19'W, 21-28.VIII.2007, R. Teixeira, 1♂ (IBSP 129808)

Outgroup

Coelotes terrestris (Wider, 1834) (AGELENIDAE). GERMANY: (Neverbürg Baden-wurtemberg), 10.IV.1993, A.D. Brescovit, 1♀ (MCTP 4561).

Amaurobius ferox (Walckenaer, 1830) (AMAUROBIIDAE). GERMANY: (Neverbürg Baden-wurtemberg), 10.IV.1993, A.D. Brescovit, 1♀ (MCTP 4559).

Argyroneta aquatica (Clerck, 1757) (CYBAEIDAE). GERMANY: (Plön – Scheswig - Holstein), 13.V.1993, A.D. Brescovit, 1♂1♀ (MCTP 3209).

Dictyna sp. (DICTYNIDAE). BRAZIL: *Rio Grande do Sul* (Capão Grande), 27.VIII.1992, R.G. Buss, 2♂1♀1j (MCTP 3258).

Appendix S2. Characters description surveyed for the cladistic analysis of the subfamilies within the Hahniidae.

Male genitalia

- 1 *Median apophysis*: (0) absent; (1) present.
- 2 *Median apophysis, size*: (0) small; (1) large.
- 3 *Retrolateral tibial apophysis*: (0) absent; (1) present.
- 4 *Tibial apophysis, number*: (0) one; (1) two, one retrolateral + one accessory apophysis; (2) three, distal, medial and basal apophysis (Heiss and Draney 2004: figs 6-7).
- 5 *Retrolateral tibial apophysis, distal, direction angle*: (0) recurved (obtuse angle); (1) curved (acute angle); (2) right angle; (3) straight angle; (4) divided, anterior straight and posterior curved (acute angle); (5) border.
- 6 *Retrolateral tibial apophysis, distal, length*: (0) short; (1) median; (2) long.
- 7 *Distal tibial apophysis, direction*: (0) upwards, directed against the patellar apophysis; (1) downwards, directed towards the patellar apophysis; (2) sideways.
- 8 *Medial retrolateral tibial apophysis, shape*: (0) flat, wide from above; (1) thick at base and pointed upward; (2) knob-like; (3) flat.
- 9 *Basal retrolateral tibial apophysis, shape*: (0) thick; (1) rounded at tip.
- 10 *Basal retrolateral tibial apophysis, length*: (0) all long; (1) from above long.
- 11 *Membranous finger-like process at base of retrolateral tibial apophysis, distal* (Catley 1996: char. 6): (0) absent; (1) present (Catley 1996: figs 297, 307).
- 12 *Ventral patellar apophysis*: (0) absent; (1) present.
- 13 *Ventral patellar apophysis, shape*: (0) rounded; (1) knob-like.
- 14 *Retrolateral patellar apophysis*: (0) absent; (1) present.
- 15 *Retrolateral patellar apophysis, teeth*: (0) absent; (1) present.
- 16 *Retrolateral of patellar apophysis, teeth number*: (0) one; (1) two; (2) three, four.
- 17 *Retrolateral patellar apophysis, position*: (0) basal; (1) distal-lateral; (2) medial-basal.

- 18** *Retrolateral patellar apophysis, orientation* (Catley 1996: char. 4): (0) upwards; (1) downwards; (2) sideways.
- 19** *Patella, shape* (Catley 1996: char. 5): (0) globose; (1) regular.
- 20** *Patellar spur*: (0) absent; (1) thin; (2) strong; (3) strong as large as the tibial apophysis. In *Pacifantistea* the patellar spur is strong, as large as the tibial apophysis, while in *Neoantistea* it is smaller or absent (Marusik 2011) and, *Hahnia flaviceps* maybe be the only North American species of the genus with a double patellar spur (Opell and Beatty 1976).
- 21** *Cymbium, shape* (Catley 1996: char. 38): (0) reniform (Catley 1996: fig151); (1) longer than wide (Catley 1996: fig 230); (2) obtuse (Catley 1996: fig 175); (3) extended distally (Catley 1996: fig 260); (4) acute.
- 22** *Cymbium, tip*: (0) absent; (1) present. This is a synapomorphy of *Calymmaria* (Heiss and Draney 2004: figs 6-7) also present in *Argyroneta aquatica* by parallelism.
- 23** *Cymbium, terminal part above the bulb, length*: (0) short; (1) long.
- 24** *Cymbium, furrow*: (0) absent; (1) present. In *Cybaeolus* the RTA seems lay in cymbial furrow.
- 25** *Embolus, base* (Catley 1996: char. 40): (0) fixed (held in close proximity to the tegulum after its point of origin, Catley 1996: fig 70); (1) free (extends away from the tegulum after its point of origin, Catley 1996: fig 138).
- 26** *Embolus, shape*: (0) a simple long thin spine-like; (1) flat; (2) round; (3) with an ectal tooth; (4) thickened and flattened at the base; (5) thickened along its entire length; (6) bifurcate; (7) a simple median spine. The embolus in *Calymmaria* may be a simple, long, spine-like, round (considered plesiomorphic state) or may be thickened and flattened at the base, thickened along its entire length, bifurcate, or with an ectal tooth (apomorphic state) (Heiss and Draney 2004).
- 27** *Conductor*: (0) absent; (1) present.
- 28** *Conductor, modifications*: (0) simple; (1) well developed in many distal lobes Usually conductor is unmodified and is considered plesiomorphic and the form modified into lobes is considered apomorphic (Heiss and Draney 2004).

29 *Conductor, basal lobe*: (0) absent; (1) present/sclerotized; (2) present/not sclerotized. In *Calymmaria* the conductor is well developed with many distal lobes and sometimes a basal lobe sclerotized or not sclerotized (Heiss and Draney 2004: fig 6). In *Amaurobius ferox* the conductor can be partly hyaline and partly sclerotized but always has a hyaline base (Silva 2003: fig 12a).

30 *Ejaculatory duct, loop*: (0) absent; (1) present, a small (shallow) loop; (2) present, strong (deep). The absence of the loop of the ejaculatory duct is considered the plesiomorphic state, its presence apomorphic (Heiss and Draney 2004). The seminal duct can form a shallow or deep loop on the retrolateral side in the proximal region of the tegulum. In *Pacifantistea* (Marusik 2011: fig 4) the loop of the ejaculatory duct is small and shallow, unlike all species of *Neoantistea* (see e.g., *N. magna* (Keyserling, 1887) in Marusik 2011: fig 31; *N. quelpartensis* Paik, 1958 in Marusik 2011: fig 38).

31 *Tegulum, shape*: (0) oval; (1) circular; (2) irregular.

32 *Tegulum, setae*: (0) absent; (1) present.

33 *Palpal tarsal, trichobothria* (Griswold *et al.* 2005: char. 7): (0) absent; (1) present.

Carapace

34 *Endite, length*: (0) wider than long; (1) longer than wide.

35 *Endite, shape*: (0) rounded; (1) trapezoid; (2) rectangle; (3) irregular.

36 *Labium, length*: (0) longer than wide; (1) wider than long; (2) as long as wide.

37 *Labium, shape*: (0) square; (1) rectangle; (2) trapezoid; (3) triangle; (4) oval; (5) mushroom.

38 *Sternum, shape* (Catley 1996: char. 9): (0) truncate posteriorly; (1) with "neck".

39 *Sternum, length*: (0) longer than wide; (1) wider than long; (2) as long as wide.

40 *Cephalothorax, color markings* (modified from Catley 1996: char. 10): (0) dark medially (cephalic and median area dark brown, pale yellow laterally); (1)

unicolorous; (2) pale medially (cephalic median area and laterally pale yellow laterally, thoracic area dark brown).

41 *Cephalothorax, color border* (Catley 1996: char. 11): (0) with black border; (1) without black border.

42 *Cephalothorax, dark lateral markings* (Catley 1996: char. 44): (0) absent; (1) present.

43 *Carapace, shape*: (0) longer than broad; (1) broader than long.

44 *Carapace, color in relation abdomen*: (0) lighter in color than the abdomen; (1) darker than abdomen; (2) same color; (3) both mottled.

45 *Longitudinal thoracic fovea groove*: (0) absent; (1) present.

46 *Pars cephalica mark, dark asymmetrical marking in cephalic region* (modified from Catley 1996: char. 13): (0) absent; (1) present.

47 *Cheliceral proximal condyle* (Catley 1996: char. 18): (0) absent; (1) present.

48 *Chelicerae tumid proximally* (Catley 1996: char. 22): (0) tumid; (1) not tumid.

49 *Rastellum*: (0) absent; (1) present (Fig. 3A-D). *Cybaeolus pusillus* differs from that of *C. delfini* (Fig. 3A-B) and *C. rastellus* (Fig. 3C-B) by the absence of a rastellum on the female chelicera (Roth 1967).

50 *Rastellum, base* (Catley 1996: char. 19): (0) projecting anteriorly; (1) not projecting. (*Cybaeolus delfini* in Catley: 1996: figs.74 and 109; *C. rastellus* in Catley: 1996: fig 110)

51 *Stridulatory ridges, on the lateral face chelicerae*: (0) absent; (1) present (Fig. 3). Stridulating ridges on the chelicerae are described for Sicariidae (Simon 1893), Mimetidae (Machado 1941), Diguettidae and Scytodidae (Legendre 1963), Ochyroceratidae, Pholcidae and Caponiidae (Brignoli 1975; 1977), Amaurobiidae (GRISWOLD 1990), Zodariidae (Jocqué 2005), Linyphiidae (Hormiga 1994). For Hahniidae, some authors stated the presence of stridulatory organ in *Neoantistea* (Gertsch 1934; Opell and Beatty 1976) and *Antistea* (Opell and Beatty 1976), Brignoli (1978) mentioned that some *Hahnia* from Bhutan have the chelicerae provided with stridulatory file; Jocqué and Bosmans (1982) examined 16 *Hahnia* species and at least the males examined proved to have a stridulatory file on the chelicerae. In *Pacifantistea* a stridulatory organ is absent (Marusik 2011). In *Cybaeolus* is present (Fig. 3).

52 Stridulatory ridges, on lateral face of chelicerae, type: (0) row of simple more or less parallel ridges (Fig. 3B); (1) groups of scales, arranged roughly in parallel rows on the lateral side of the chelicera (Fig. 3D,F). From 16 *Hahnia* species examined by Jocqué and Bosmans (1982) the stridulatory type like most linyphiids (row of simple parallel ridges) were found in *H. montana* (Blackwall, 1841) (Jocqué and Bosmans 1982: fig 9) and *H. candida* Simon, 1875, also it can be groups of scales (parallel rows on the lateral side of the chelicerae) found in *H. helveola* Simon, 1875 (Jocqué and Bosmans 1982: fig 6), *H. vangoethemi* Benoit, 1978, *H. schubotzi* Strand, 1913 and *H. tabulicola* Simon, 1898, be arranged in straight lines on the lateral side of the chelicera (*H. spinata* Benoit, 1978, Jocqué and Bosmans 1982: fig 7), the stridulating ridges of the lateral side can merge into in front and on the back of the chelicerae (*H. benoit* Bosmans & Thijs, *H. breviducta* Bosmans & Thijs, *H. inflate* Benoit, *H. major* Benoit, *H. ononidum* Simon, *H. pusilla* C. L. Koch, *H. nava* (Blackwall) (Jocqué and Bosmans 1982: fig 8). These several different types of stridulating files could represent parallel evolution of chelicerae stridulating ridges and, probably the pronounced reticulations are more primitive type than as found in most linyphiids (Jocqué and Bosmans 1982). Stridulatory ridges formed by two patches of setae on the carapace's posterior surface was described for Gertsch (1934) to *Neoantistea*, a stridulatory organ is formed by two patches of setae lying dorsal and lateral to the petiole in *Antistea* and *Neoantistea* (Opell and Beatty 1976), however, Jocqué and Bosmans (1982) do not believe this feature can be regarded as a synapomorphy due its independently evolution in many families.

53 Clypeus (Catley 1996: char. 41): (0) deep (3 or >X diameter of AME); (1) shallow (<3 X diameter of AME). Mello-Leitão (1917) used differ *Hahnia* (clypeus as same wide than AME) to *Neohahnia* (clypeus much wider than AME), but this character seems to be less informative to define genera. In *Pacifantistea* clypeus low (Marusik 2011: fig 11), less than diameter of the anterior lateral eyes. In *Neocryphoeca gertschi*, AME are in the carapace border, clypeus is quite low.

54 *Stridulatory ridges, on carapace*: (0) absent; (1) present. First found in *Antistea elegans* by Simon (1897).

Eyes

55 *Eyes*: (0) absent; (1) present.

56 *Eyes, pigmentation around* (modified from Catley 1996: char. 14): (0) absent; (1) present all eyes; (2) present, on ALE with PLE, few in PME and AME.

57 *Eyes, size of AME* (modified from Catley 1996: char. 15): (0) small; (1) large; (2) same. AME \leq 75% the size of ALE was considered small whereas AME $>$ 76% the size of ALE were coded as large.

58 *AME-AME, interdistance* (Catley 1996: char. 42): (0) contiguous; (1) separate (0.02-0.05); (2) widely separate ($>$ 0.05).

59 *PME-PME, interdistance* (Catley 1996: char. 16): (0) $>$ than diameter of PME; (1) $<$ diameter of PME; (2) same.

60 *ALE-PLE, interdistance*: (0) contiguous; (1) separate (0.02-0.05); (2) widely separate ($>$ 0.05).

61 *ALE-PLE-PME, interdistance*: (0) contiguous; (1) separate.

Abdomen

62 *Opisthosomal, color pattern* (Catley 1996: char. 25): (0) dictynid-like; (1) unicolors (pale); (2) chevrons; (3) mottled (without chevrons); (4) anterior median stripe.

63 *Ventral patch of modified setae on venter* (Catley 1996: char. 26): (0) absent; (1) present. Modified setae near spiracle (Catley 1996: fig 259).

64 *Spinnerets, distal segment of ALS, length* (modified from Catley 1996: char. 31): (0) short; (1) long (when proximal segment $<$ X4 distal); (2) median.

65 *ALS, shape* (Catley 1996: char. 32): (0) drop; (1) cylindrical; (2) conical.

66 *PLS, length* (Catley 1996: char. 33): (0) long ($>$ X1 length of ALS); (1) short ($<$ X1 length of ALS).

67 *PLS, distal segment, length* (Catley 1996: char. 33): (0) long (if proximal $>$ X4 distal); (1) short (if proximal $<$ X4 distal).

- 68** *PLS, distal segment, shape* (Catley 1996: char. 33): (0) rounded; (1) oblique; (2) wedge-shaped.
- 69** *Spinneret, pigmentation* (modified from Catley 1996: char. 36): (0) unpigmented; (1) some segments pigmented; (2) all segments pigmented. In *Calymmaria*, spinneret pigmentation is the same color patterns of abdomen, Dorsal dark and ventral more pale. Usually, in most species analyzed ALS are pigmented, but in *Lizarba*, ALS and PMS are pigmented, PLS unpigmented.
- 70** *Spinneret, topology* (modified from Catley 1996: char. 37): (0) unmodified (Catley 1996: fig 5A; Fig. 2A); (1) semi-transverse (Catley 1996: fig 5B; Fig. 2B); (2) transverse (Catley 1996: fig 5C; Fig. 2C); (3) between semi-transverse and transverse.
- 71** *Conspicuous basal lateral setae, ALS* (Catley 1996: char. 43): (0) absent; (1) present.
- 72** *Piriform spigots, ALS, number* (Catley 1996: char. 47): (0) five and less (Fig. 2F); (1) nine and above (Fig. 2E).
- 73** *Cylindrical spigots, PMS, number* (Catley 1996: char. 48): (0) one; (1) two; (2) three.
- 74** *Cribellum*: (0) absent; (1) present.
- 75** *Colulus*: (0) absent; (1) present.
- 76** *Colulus, division*: (0) divided; (1) not divided.
- 77** *Colulus, shape*: (0) longer than wide; (1) wider than long.
- 78** *Colulus, setae*: (0) less than 14 setae; (1) 15 to 20 setae.
- 79** *Tracheal spiracle, position*: (0) at the base of spinnerets; (1) rather at a distance from spinnerets; (2) midway between spinnerets and epigastric fold; (3) twice as far from base of spinnerets as from epigastric furrows; (4) close to epigastric furrow. In *Cybaeolus* the tracheal spiracle is placed at the base of spinnerets rather than *Hahnia* that has at a distance from them (Roth 1967). In *Pacifantistea* the spiracle placed midway between spinnerets and epigastral fold (Marusik 2011).
- 80** *Stridulatory organ, abdomen*: (0) absent; (1) present. First found in *Antistea elegans* by Simon (1897). Stridulatory ridges are present in *Antistea* and *Neoantistea* even in juveniles (see Marusik 2011: fig 10).

81 Muscle dots, dorsum of abdomen: (0) absent; (1) present, round; (2) present, not rounded. In *Neoantistea*, in both sexes have muscle dot not round (see Marusik 2011: figs 26-27).

Female genitalia

82 Midpiece: (0) absent; (1) present (Heiss and Draney 2004: fig 4-5).

83 Secondary spermathecae: (0) absent; (1) present.

84 Copulatory ducts, open, position (Catley 1996: char. 29): (0) posterior; (1) anterior; (2) lateral; (3) central. Posterior (Catley 1996: fig 309), anterior (Catley 1996: fig 178).

85 Epigyne, atrium, ventral view: (0) absent; (1) present.

86 Copulatory ducts, open (Catley 1996: char. 30): (0) medially; (1) laterally. Medially (Catley 1996: fig 144), laterally (Catley 1996: fig 122).

87 Fertilization ducts: (0) absent; (1) present (Heiss and Draney 2004: fig 5).

88 Fertilization ducts, length: (0) very short; (1) very or rather long. In *Pacifantistea* the fertilization ducts are very short against the Holarctic genera of Hahniinae: *Hahnia sensu lato*, *Antistea*, *Neoantistea*, *Asiohahnia* where the ducts are very or rather long (Marusik 2011).

89 Lateral duct: (0) absent; (1) present (Heiss and Draney 2004: fig 5).

90 Blind duct: (0) absent; (1) present (Heiss and Draney 2004: fig 5).

Leg

91 Tarsal spines: (0) absent; (1) present (Marusik 2011: fig 6b).

92 Tarsal trichobothria (Griswold *et al.* 2005: char. 3): (0) absent; (1) present (Griswold *et al.* 2005: fig 147E).

93 Tarsal trichobothria, number (Catley 1996: char. 39): (0) one; (1) two; (2) more than two.

94 Tarsal trichobothrial, rows (Griswold *et al.* 2005: char. 4): (0) one (a single line, Griswold *et al.* 2005: fig 147E); (1) two or more (an arrangement forming two or more rows, Griswold *et al.* 2005: fig 141D).

95 Tarsal organ, morphology (Catley 1996: char. 45): (0) round (Catley 1996: fig 240; Fig. 2E); (1) semi-elongate (cylindrical) (Catley 1996: fig 196); (2) elongate (fusiform) (Catley 1996: fig 82).

96 Trichobothrial, base, morphology (Catley 1996: char. 46): (0) with slight depression (Catley 1996: fig 268); (1) Strong depression (Catley 1996: fig 302); (2) very strong depression (Catley 1996: fig 239; Fig. 2F).

97 Femoral spines: (0) absent; (1) present.

98 Femoral outgrowth, lack: (0) absent; (1) present.

99 Metatarsal spines: (0) absent; (1) present.

100 Metatarsal trichobothria (Griswold *et al.* 2005: char. 4): (0) one or two; (1) three or more.

101 Trochanter notch: (0) absent; (1) present.

102 Patellar fracture line: (0) absent; (1) present (Heiss and Draney 2004: fig 3). Present in *Calymmaria* on all legs, but absent from most Nearctic agelenid and all other hahniid genera (Heiss and Draney 2004). In Heiss and Draney (2004) *Calymmaria* shares a dorsal patellar fracture line with *Willisus*, *Blabomma*, *Yorima*, *Cybaeota*, and *Cybaeina* and this six genera were hypothesized to form a monophyletic lineage (Heiss and Draney 2004: fig 134), although the authors suggest that is quite possible that this single apomorphic character was a case of homoplasy.

103 Patela plus the tibia on the first pair of legs, length: (0) short patela-tibia; (1) very long in relation to the length of the carapace; (2) same length.

104 Setae, between the claws: (0) normal; (1) oval.


105 Recurved ventral hairs, male leg I: (0) absent; (1) present in all legs; (2) present in tibia. In *Neoantistea* are very characteristic recurved ventral setae (see Marusik 2011: fig 29).

Behavior

106 Web architecture (modified from Catley 1996: char. 52): (0) arboreal sheet-web with tangle above (Catley 1996: fig.2); (1) sheet-web; (2) veil-web; (3) tangled-web among rock; (4) web retreats under rock; (5) small funnel like web.

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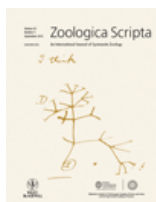
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Sundberg, P. (2010) Ribbon worm (Nemertea) systematics in the 21st century. *Zoologica Scripta*, 00, 000-000.
Systematic developments in the phylum Nemertea are reviewed and shown to ... *Per Sundberg, Department of Zoology, University of Gothenburg, P.O. Box 463, SE-405 30 Gothenburg, Sweden. E-mail per.sundberg@zool.gu.se (<mailto:per.sundberg@zool.gu.se>)*

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Genus *Pachygnatha* Sundevall, 1823

Pachygnatha atromarginata sp. n. (Figs 100-111)

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

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

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

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

Diagnosis. This species can be distinguished by the shape of the paracymbium (Fig. 103) and the vulvar morphology (Fig. 111) in the female.

Description

Male (holotype). Total body length 2.38mm, 1 car 1.15mm, 1 stern 0.66 mm, 1 abd

1.45 mm, w car 0.93 mm ...
Female (paratype). Total body length 3.03mm ...

The complete data of the holotype and paratypes, and the institutions in which they are deposited, must be recorded in the original description. All material examined should be listed in similar format: localities should be cited in order of increasing precision as in the examples; names of countries should be in capitals. Sex symbols will be used in the journal; abbreviations used to indicate sex must be clearly stated in the manuscript.

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Family PHYLLODOCIDAE

Genus *Phyllodoce* Lamarck, 1818

Phyllodoce citrina Malmgren, 1865: Fig. 2.

Phyllodora citrina Malmgren, 1865: 95-96, pl. XIII, fig. 24.

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

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

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

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Book

Parenti, L. R. & Ebach, M. (2009). *Comparative biogeography*. Berkely: University of California Press.

Article in book

Andrew, C. J. (2007). The grid and biodiversity informatics. In G. B. Curry & C. J. Humphries (Eds) *Biodiversity databases. Techniques, politics and applications* (pp. 83-82). Boca Raton: CRC Press.

Computer programs

Swofford, D. L. 1993. PAUP - *Phylogenetic Analysis Using Parsimony. Ver. 3. 1.* [Computer software and manual]. Champaign, Illinois: Illinois Natural History Survey.

On-line source

Eriksson, T. (1996, June). AutoDecay version 2.9.2. Available via <http://www.botan.su.se/systematik/Folk/Torsten.html>

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