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UNIVERSIDADE DE SÃO PAULO

Thalles Platiny Lavinscky Pereira

Análise cladística das moscas parasitoides de formigas dos gêneros *Neodohrniphora* Malloch 1914, *Cremersia* Schmitz 1924 e *Eibesfeldtphora* Disney 2009 (Diptera, Phoridae, Metopininae)

Cladistics analysis of the ant-parasitoid flies of the genera *Neodohrniphora* Malloch 1914, *Cremersia* Schmitz 1924 and *Eibesfeldtphora* Disney 2009 (Diptera, Phoridae, Metopininae)

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Prof(a). Dr(a).

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Orientador

Dedicatória

Dedico a todos os pesquisadores

viventes e em memória

do Museu Nacional

#museunacionalvive

Quem costuma vir de onde eu sou

Às vezes não tem motivos pra seguir

[...]
Irmão, você não percebeu

Que você é o único representante

Do seu sonho na face da terra

Se isso não fizer você correr, chapa

Eu não sei o que vai

(Compositores: Beatnick, / K-Salaan,israel Feliciano,Leandro

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Resumo

Os dípteros da família Phoridae possuem grande diversidade, bem como apresentam entre seus gêneros e espécies uma das maiores plasticidades de papeis no ecossistema, atuando como herbívoros, decompositores, polinizadores, parasitoides etc.. Alguns grupos são conhecidos como parasitoides de formigas como os gêneros *Cremersia* Schmitz 1924, *Eibesfeldtphora* Disney 2009 e *Neodohrniphora* Malloch 1914. Em termos filogenéticos, a primeira hipótese cladistica proposta recuperou *Cremersia* Schmitz e *Neodohrniphora* Malloch como gêneros irmãos. Posteriormente, *Neodohrniphora* foi classificado em três subgêneros: *N.* (*Eibesfeldtphora* Disney), *N.* (*Neodohrniphora* Malloch) e *N.* (*Wallerphora* Disney). Mais recentemente, o subgênero *Eibesfeldtphora* foi elevado ao nível de gênero e os gêneros *Cremersia* e *Neodohrniphora* foram sinonimizados como único grupo, baseado em análises morfológicas. Tais mudanças foram justificadas com base nas características do ovipositor. Portanto, os objetivos do presente trabalho foram no **capítulo 1**, reconstruir as relações filogenéticas entre os gêneros *Cremersia*, *Eibesfeldtphora* e *Neodohrniphora* revisando amplamente os caracteres morfológicos de genitália e estudar as relações coevolutivas com seus hospedeiros, e no **capítulo 2** revisar taxonomicamente o gênero *Neodohrniphora*. A maior parte do material estudado e analisado morfologicamente foi proveniente principalmente das coleções LACM (Los Angeles – EUA) e MZSP (São Paulo – Brasil). O resultado da análise filogenética recuperou os gêneros como monofiléticos e a presença de traços coevolutivos entre os parasitoides e os hospedeiros. No segundo capítulo sete novas espécies foram descritas para o gênero *Neodohrniphora.* Esse estudo confirma a importância de estudos de genitália feminina para os grupos de parasitóides, tanto para informações taxonômicas como para filogenéticas. Trabalhos futuros serão importantes para elucidar melhor esses mecanismos de oviposição dos forídeos, como o estudo da musculatura do abdômen e a observação em campo do ataque dos parasitóides às formigas.

Abstract

The Phoridae have a great diversity, as well as presenting one of the largest plasticides of roles in the ecosystem, acting as herbivores, decomposers, pollinators, parasitoids, etc. Some groups are known as ant parasitoids like the genera *Neodohrniphora* Malloch 1914,. *Cremersia* Schmitz 1924 and *Eibesfeldtphora* Disney 2009. In phylogenetic studies, the first proposed cladistic hypothesis recovered *Cremersia* Schmitz and *Neodohrniphora* Malloch as sister genera. Subsequently, *Neodohrniphora* was classified into three subgenus: *Eibesfeldtphora*, *Neodohrniphora* and *Wallerphora*. More recently, the subgenus *Eibesfeldtphora* was raised to the genus level and the genera *Cremersia* and *Neodohrniphora* were synonymized, based on morphological analyzes. The synonym was justified based on the characteristics of the ovipositor. The objective of the present work was to reconstruct the phylogenetic relationships between the genera *Cremersia, Eibesfeldtphora* and *Neodohrniphora,* revising extensively the morphological characters of genitalia and to study the coevolutionary relations with their hosts, and in chapter 2 make a revision of the genus *Neodohrniphora*. Most of the material studied and analyzed morphologically came from the LACM (Los Angeles - USA) and MZSP (São Paulo - Brazil) collections. The result of the phylogenetic analysis recovered the genera as monophyletic and the presence of coevolutionary traits between the parasitoids and the hosts. This study confirms the importance of studies of female genitalia for groups of parasitoids, both for taxonomic and phylogenetic information. Future works will be important to elucidate better the oviposition mechanisms of parasitoids, as the study of the musculature of the abdomen and the field observation of the attack of the parasitoids to the ants.

Classificação de Phoridae

Phoridae é uma família da ordem Diptera constituída por espécimes de tamanho pequeno, entre 0,4 e 6 mm de comprimento, geralmente com corpo compacto e frequentemente rico de cerdas. Possui venação característica, com veias costal e radiais espessas, sem veias transversais (Brown, 2009). A família distribui-se por todas as regiões biogeográficas e reúne 4.000 espécies em 289 gêneros (Thompson, 2008), e no Brasil são conhecidas aproximadamente 850 espécies (Ament & Pereira, 2018).

Levando em consideração os hábitos de vida conhecidos das espécies de Phoridae, podemos afirmar que a maior parte dos forídeos são parasitoides, depois de Tachinidae e Bombyliidae eles são o terceiro maior grupo (Brown, 2018).

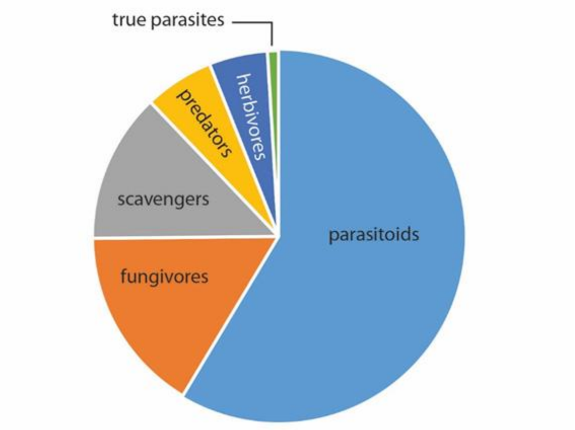


Figura 1. Hábitos de vida conhecidos entre os forídeos (retirado de Brown 2018, baseado em Disney, 1994).

Três classificações de Phoridae são propostas na literatura. Brown (1992) propôs uma divisão em cinco subfamílias - Hypocerinae, Phorinae, Aenigmatiinae, Conicerinae, e Metopininae. Por outro lado, Disney (1994) preserva fundamentalmente a divisão proposta por Schmitz (1929, 1951) com as subfamílias Phorinae, Metopininae, Aenigmatiinae, Thaumatoxeninae e Termitoxeniinae. Mais recentemente, uma terceira classificação proposta por Brown (2015) e corroborada por Ament (2017) baseada em filogenia morfológica recuperou as subfamílias Sciadocerinae, Chonocephalinae, Termitoxeniinaae, Metopininae e Phorinae. Outras publicações recentes, incluindo dados moleculares, além de reunir uma amostragem maior de gêneros e espécies começaram a propor soluções para resolver essas divergências (Cook *et al.* 2004 e Brown & Smith 2010), mas sem proposições taxonômicas.

Classificação de Metopininae

A subfamília Metopininae contém a maior parte dos gêneros e espécies descritos, incluindo o vasto e possivelmente parafilético gênero *Megaselia* Rondani com 1600 espécies (Brown, 1992). É a única subfamília de Phoridae que não difere consideravelmente na sua delimitação segundo as diferentes classificações (Brown, 1992; Disney 1994; Brown, 2015), apesar da amostragem relativamente baixa considerando o tamanho da subfamília. Está dividida em duas tribos, Beckerinini e Metopinini (Brown, 1992), sendo a última caracterizada pela presença de quatro cerdas supra-antenais, embora existam grupos com a reversão desse caráter.

A tribo Metopinini está dividida em dois grupos de gêneros, *Metopina* e *Megaselia,* neste ultimo estão incluídos os indivíduos com glândula de Dufour presente nas fêmeas (se ausente, esternito oito alongado) e segmento sete modificado como um estilete para perfurar (Brown, 1992).

Muitos gêneros do grupo-*Megaselia* são de parasitoides, com segmento sete modificado para posicionamento do ovipositor ou escleritos abertos e esternito oito modificado como um estilete para perfurar.

Inserida nesse grupo de gêneros está a série-*Apocephalus* (Figura 2), monofilética *sensu* Brown (1992), abrange os gêneros cujas fêmeas possuem o segmento VII modificado para o parasitismo, com um mecanismo de perfuração utilizado para facilitar a deposição dos ovos nos hospedeiros (Figura 2, caráter 5)., ficando esse segmento retraído dentro do abdomen em repouso (Figura 2, caráter 6). (Brown, 1992).

Na série-*Apocephalus* estão incluídos, os gêneros *Apocephalus* Coquillett, *Auxanommatidia* Borgmeier, *Cremersia* Schmitz, *Dacnophora* Borgmeier; *Eibesfeldtphora* Disney, *Lecanocerus* Borgmeier, *Menozziola* Schimitz, *Microselia* Schimitz, *Myrmosicarius* Borgmeier, *Neodohrniphora* Malloch, *Pseudacteon* Coquillett, *Trucidophora* Brown.

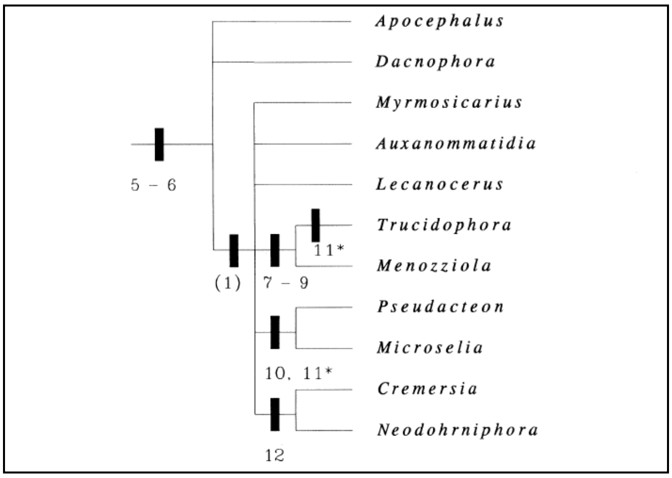


Figura 2 – Relações filogenéticas da série-*Apocephalus* (retirada de Brown, 1992).

A maioria desses gêneros é conhecida por serem parasitoides de formigas, sendo estudadas para o controle biológico dos gêneros *Atta*, *Acromyrmex* e principalmente *Solenopsis* (Orr, 1992; Tonhasca Jr & Bragança, 2000). O gênero *Eibesfeldtphora* ataca exclusivamente as formigas do gênero *Atta* (Uribe *et al.*, 2014), o gênero *Neodohrniphora* ataca exclusivamente o gênero *Acromyrmex* e o gênero *Cremersia* gêneros de formigas de correição não-*Eciton*.

O gênero *Neodohrniphora* (*sensu* Disney, 2009, *i.e.*, incluindo *Cremersia*) possui 23 espécies com distribuição no continente americano, desde os EUA (Califórnia, Texas, Novo México), passando pelo México, Panamá, Costa Rica, Equador e Brasil (AM, RO, GO, MG, RJ, SP, PE, SC, PA) até a Argentina (Malloch, 1912, 1914; Schmitz, 1924; Borgmeier, 1925, 1928, 1961, 1963, 1971; Prado, 1976; Disney, 2007, 2008, 2009). Possui como hospedeiros as formigas cortadeiras dos gêneros *Acromyrmex* e *Atta*, e já foram encontrados associados às formigas de correição do gênero *Labidus* (Disney, 2009). O último estudo taxonômico com esse grupo foi de Disney (2009), que descreveu duas espécies novas e forneceu chave para as espécies; no entanto, as 21 espécies restantes foram descritas quase que majoritariamente por Borgmeier e necessitam ser revisadas e redescritas.

Eibesfeldtphora (*sensu* Disney, 2009, *i.e.*, incluindo *Wallerphora*) possui 21 espécies de distribuição neotropical, desde o México Equador, Colômbia, Costa Rica, Guiana, Panamá, Guatemala, Brasil, até Argentina (Malloch, 1912, 1914; Schmitz, 1924; Disney, 1996; Brown, 2001; Disney, 2009; Brown, 2012; Uribe *et al.*, 2014). É encontrado associado a nove espécies de *Atta* (Hymenoptera: Formicidae) (Uribe *et al.*, 2014). Os estudos taxonômicos mais recentes foram: Brown (2001) com uma revisão do gênero e Uribe *et al.* (2014) com descrição de 2 novas espécies e chave de identificação.

Todos esses gêneros são conhecidos por serem parasitoides de Formicidae, sendo estudadas para o controle biológico dos gêneros *Atta* e *Acromyrmex* (Orr, 1992; Tonhasca Jr & Bragança, 2000). O gênero *Eibesfeldtphora* ataca exclusivamente as formigas do gênero *Atta* (Uribe *et al.*, 2014).

Uma hipótese filogenética incluindo os gêneros *Cremersia*, *Eibesfeldtphora* e *Neodohrniphora*, além de analisar a proposta de sinonímia recentemente feita por Disney (2009) irá também esclarecer quanto à sua delimitação e composição taxonômica, poderá também trazer cenários interessantes no que diz respeito às estreitas interações coevolutivas aparentemente presentes nas relações parasita-hospedeiro entre estes gêneros de Phoridae e formigas-cortadeiras.

Os processos de coespeciação entre parasitas e hospedeiros ocorrem de forma análoga à especiação por vicariância entre duas espécies, quando uma espécie é separada de outra geograficamente pode haver especiação, no processo de parasita hospedeiro os hospedeiros se comportam como massas terrestres em vicariância, podendo provocar especiação entre os hospedeiros. Nesse processo, a coespeciação ocorre exatamente quando o processo de cladogênese do parasita acompanha o processo do hospedeiro (Page, 2003) Com a filogenia dos parasitoides será possível testar se a lei se aplica nessa relação, uma vez que é amplamente conhecida a filogenia para Formicidae (Ward, 2010) e para *Atta* e *Acromyrmex* (Schultz & Meier, 1995; Wetterer *et al*., 1998; Bacci *et al.*, 2009; Cristiano *et al.*, 2013), gêneros de formigas com maior número de espécies de *Cremersia*, *Eibesfeldtphora* e *Neodohrniphora* associados (Disney, 2009).

Objetivos

Levando em consideração toda a discordância presente na nomenclatura e delimitação dos gêneros e das espécies do grupo estudado, o objetivo geral dessa tese foi entender as mudanças taxonômicas e históricas ocorridas nas delimitações genéricas, e a partir de uma análise cladística morfológica, propor uma hipótese de relacionamento.

No capítulo UM analisamos profundamente a morfologia dos gêneros parasitoides abordados e com ferramentas para análise cladística, inferimos o relacionamento filogenético entre as espécies e gêneros. Encontramos como resultado os três gêneros como três clados monofiléticos, e com o suporte de caracteres sinapormórficos e homoplásticos pudemos propor uma hipótese mais rebuscada, quando comparada a inferências feitas por análises empíricas, porém com agrupamentos intuitivos sem uma metodologia objetiva e robusta.

No capítulo DOIS utilizando os resultados do primeiro capítulo e tratando os gêneros como monofiléticos fizemos a revisão do gênero *Neodohrniphora*, propondo hipóteses de limitação específica e fazendo mudanças nomenclaturas. Isso foi efetivado levando em consideração principalmente a morfologia da genitália. A partir disso foi possível identificar divergências e semelhanças entre as espécies já descritas e na proposição de novas.

Chapter 1

Cladistics analysis of the ant-parasitoid flies of the genera *Neodohrniphora* Malloch 1914, *Cremersia* Schmitz 1924 and *Eibesfeldtphora* Disney 2009 (Diptera, Phoridae, Metopininae)

Abstract

Phoridae flies present great diversity, as well as one of the largest plasticity of ecological roles among their genera and species, acting as herbivores, decomposers, pollinators, parasitoids etc. The genera *Cremersia* Schmitz 1924, *Neodohrniphora* Malloch 1914 and *Eibesfeldtphora* Disney 2009 are parasitoids of army ants and leafcutter ants. These genera have undergone several taxonomic changes including: allocation of species to other genera (eg *Apocephalus*), proposal of species-groups and subgenres, synonyms of subgenera, subgenera raised to genus rank, and finally synonyms between the genera. The objective of this work is to propose a hypothesis of phylogenetic relationship between the genera, as well as to attempt to unravel the historical association and interactions between Phoridae and their ant's hosts.

Introduction

"Diptera as parasitoids" is how Feener and Brown (1997) begin their paper, which tries to convince and prove to its readers that Diptera order is as parasitoidic as Hymenoptera (possibly more).

The Phoridae family has around 4,340 species (PCAT, 2019) throughout the world. In Brazil, it is the largest Diptera family with about to 850 species (Ament & Pereira, 2019). More than 60% (which we know about the biology) are parasitoids (Disney, 1994; Brown 2018), and after Tachinidae and Bombyliidae the family is the third largest group of parasitoids (Brown, 2018).

The genera of the *Apocephalus*-series are included in this family and many are known as ant parasitoids (Brown, 1992). Recent studies have revealed great advances in the biology of this group and some species have been used as biological control for fire and leaf-cutting ants (Refs). Regarding *Apocephalus*-series systematics, there are many problems to be solved, including generic delimitations and relationships between these genera.

The phylogenetic hypothesis by Brown (1992) indicated *Cremersia* and *Neodohrniphora* as sister genera, sustained by the presence of distinctive, hook-shaped seta on female ovipositor ventrally. After Disney (1996) classified *Neodohrniphora* in three subgenera, *Neodohrniphora, Eibesfeldtphora* and Wallerphora. Brown (2001) considered the subgenus *Wallerphora* as part of the subgenus *Eibesfeldtphora*.

Recently, after analysis and comparison of the ovipositor, Disney (2009) raised the subgenus *Eibesfeldtphora* to genus rank and synonymized the genera *Neodohrniphora* and *Cremersia*, justifying the separation by the differences in the ovipositor of *Cremersia* and *Eibesfeldtphora*.

Neodohrniphora and *Cremersia* include 24 species with distribution in the Americas; from USA (California, Texas, New Mexico), Mexico, Panama, Costa Rica, Ecuador, Brazil (AM, RO, GO, MG, RJ, SP, PE, SC, PA), to Argentina (Malloch, 1912, 1914; Schmitz, 1924; Borgmeier, 1925, 1928, 1961, 1963, 1971; Prado, 1976; Disney, 2007, 2008, Disney *et al.*, 2009). The last work with this group was that of Disney *et al.* (2009), which also describe new species and provide an identification key.

Eibesfeldtphora includes 21 species with neotropical distribution from Mexico Ecuador, Colombia, Costa Rica, Guyana, Panama, Guatemala, Brazil, to Argentina (Malloch, 1912, 1914; Schmitz, 1924; Disney, 1996; Brown, 2001; Disney, 2009; Brown, 2012; Uribe et al,. 2014). The last taxonomic studies were: Brown (2001) with generic revision and Uribe *et al.* (2014) with new species and key identification.

The objective of this work is to propose a hypothesis of phylogenetic relationship between the genera, as well as try to unravel the historical association and interactions between Phoridae and their ants hosts. A phylogenetic hypothesis including *Cremersia*, *Eibesfeldtphora* and *Neodohrniphora* will figure out about the synonymy proposed by Disney et al. (2009) and verify their generic delimitation and taxonomic compositiom.

Materials and methods

This analysis deals exclusively with female specimens. The specimens examined were mainly from the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM) and the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZSP). Additional material from the following museums was examined: Instituto Nacional de Bioversidad, Heredia, Costa Rica (INBio), Museum of Zoology, University of Cambridge, Cambridge, UK (MZUC) and Academy of Natural Sciences, Philadelphia, USA (ANSP). List of the examined material – Appendix 1.

The genitalia were treated for 15 minutes in each of the following steps: KOH 10% in water bath 50 ºC; rinsed in acetic acid 10%; water; dehydrated in alcohol 70%; alcohol PA and placed in a vial with glycerin.

The photographs and stacking were made in the LACM using Keyence VHX 5000 digital microscope. Scanning electron microscopy was performed at LACM. Images were edited in the softwares GIMP version 2.10.8 and Inkscape version 0.91.

Taxon sampling

The ingroup consisted of all species of the genera *Neodohrniphora*, *Cremersia* (except *C. pernambucana*) and *Eibesfeldtphora*. The outgroup consisted of representatives of some genera of the *Apocephalus* series (sensu Brown, 1992): *Apocephalus* Coquillett, *Pseudacteon* Coquillett and *Myrmosicarius* Borgmeier (all three parasitoids of ants). In addition, based on Brown (1992)'s phylogeny, a species of the genus *Myriophora* (parasitoid of myriapods) was also added as outgroup and a species of *Megaselia* was chosen to root the cladogram.

Morphological characters and homologies

General terminology follows Cumming & Wood (2017). The female terminalia were named according to Nakayama (2007). The parasitoid genitalia are usually complex and very different from the Phoridae ground plan. This study proposes different nominated genitalia parasitoid structures from some Phoridae papers, realizing a comparison between the genera, while at the same time tracing hypotheses of homology.

The homology criteria used were based on structure and position. Some of the constructed characters were based on previous studies, which are referenced to below the character. Most genitalia character homology is proposed for the first time for the different genera.

Characters were constructed following Sereno (2007), and in the character coding the contingent coding was preferred (Forey & Kitching, 2000).

Phylogenetic analyses

The analysis and results were divided into two parts, the first one with the analysis using equal weighting of characters, presenting and discussing the results of the clades of strict consensus with optimizations of ambiguous characters. In the second, we verified the data matrix under implied weighting of characters (Goloboff, 1993) with different values of concavity (k =1,2,3,4,5,10 and 20), to figure out about the similarities and differences on topologies, synapomorphies and homoplasies. Since there is no consensus in the literature on the choice of K value (Goloboff, 1993, 1997, 2008b), we chose the tree based on the search for characters that better explained the support of the clade. The value chosen was K =2 for this discussion.

The polarization was conducted using the method of outgroup comparison (Nixon & Carpenter, 1993). The matrix was built in Mesquite version 3.04 software (Maddison & Maddison, 2015) and analyzed in TNT version 1.1 (Goloboff *et al.*, 2008a). To make a robust and exhaustive analysis, we implemented New Technology tree searches, with 100 replications, holding 10000 trees, using the default except for: in the Sectorial Search parameters we added exclusive sectorial search; Ratched with 200 of numbers of interactions; Drift with 50 cycles; Tree fusing with 20 rounds; Find min. length 50 times; and Collapsing trees after search. Furthermore, we doubled and tripled those values in other analyses.

Bremer support values were calculated in TNT (Bremer, 1994). Ambiguous characters were optimized in Winclada (Nixon, 2002) using the algorithms ACCTRAN (Farris, 1970) and DELTRAN (Swofford & Maddison, 1987). In this study, both optimizations were applied individually for each character, as Amorim (2002) suggests, the selection result is discriminated on the character. All characters were treated as non-ordered and non-additive

Host Data

The information about host associations was obtained based on labels and papers (Disney *et al.*, 2009; Uribe *et al.*, 2014).

Host–parasite cophylogeny

We created a host tree of the ant genera from the phylogeny inferred by Moreau & Bell (2013). This phylogeny was chosen because it contains all the genera parasitized by *Cremersia, Eibesfeldtphora* and *Neodhorniphora*, in addition to an extensive sampling of the formicoid clade. We pruned the host tree to remove outgroups and duplicates using the R (R version 3.5.2) package “ape” (version 5.2; Paradis *et al.*, 2004; Popescu *et al.*, 2012; Paradis & Schliep 2018). The R package “phytools” (version 0.6-60; Revell 2012) was used to produce a tanglegram, which shows the generic phylogeny of the parasitoids in relation to the generic phylogeny of the ants.

To evaluate the cophylogenetic patterns between Phoridae genera (*Cremersia, Eibesfeldtphora* and *Neodhorniphora*) and host ants, we used the R implementation of PARAFIT (Legendre *et al.*, 2002) in the package "ape". The ParaFit was ran for 100,000 permutations with Cailliez correction for negative eigenvalues and testing for the contribution of each individual link using the ParaFitLink1 and ParaFitLink2 tests. We corrected individual link p-values using the Bonferroni correction. PARAFIT tests for evidence of congruency between host and parasite trees, calculating a global measurement of congruency and individual links. The null hypothesis (H0) of the global test was that the relationship pattern of the two groups has been independent. Individual links were evaluated to determine how much each contributes to the global test statistic (Legendre *et al.*, 2002).

Results and Discussion

List of Characters

In total, more than 200 characters were analyzed, mainly from the studies Brown et al 2015, Ament (2017) and Hash *et al* (2017). However, the focus and the samplings of these studies were different: Phorinae in Ament (2017) and Brown *et al.* 2015, and one different parasitoid genera in Hash *et al.* (2015). Thereby, we did not use most of these characters, as there was no character-state variation and they were not informative for the specimens of the matrix studied herein. It is likely that with a larger sampling of Metopininae, such characters could be used. Some putative characters proposed by Brown (2001) were also used.

A total of 95 characters were used: 11 from the head, 6 from the thorax, 10 from the abdomen, and 68 from terminalia.

Head

1. Frons, supra-antennal setae (L= 1; CI=100; RI=100):

(0) absent

(1) present

Ament (2017, character 8) presents an extensive commentary about this character and concludes, through comparisons of different studies (Brown 1992, Brown *et al.* 2015), that the presence of supra antennal setae could be at the base of Metopininae + Phorinae, with reversions in both subfamilies. We found the absence of supra-antennal setae (reversion) as a synapormophy of the clade *Cremersia* (*Neodohrniphora,* *Eibesfeldtphora*). With a larger sampling of Metopininae, as well of *Apocephalus* group parasitoids, we will probably be able to determine where the reversions exist in the entire family.

2. Frons, supra-antennal setae, number (L=1; CI= 100; RI=100):

    (0) 2
    (1) 4

3. Frons, supra-antennal setae, position (L= 2; CI=50; RI=0) (DELTRAN):

    (0) supra-antennal more anterior than frontorbital
    (1) supra-antennal and frontorbital aligned

4. Frons, supra-antenal setae, chaetotaxy (L=1; uninformative) (DELTRAN):

    (0) lower spant the same size of spant
    (1) lower spant smaller than spant

5. Frons, interfrontal ventral setae, position (L=7; CI=28; RI=82) (DELTRAN):

    (0) close to orbital position (very distant from each other)
    (1) distant from midline (distant from each other)
    (2) close to midline (close to each other)

6. Frons, frontal dorsal row of setae, position (L=3; CI=66; RI=96) (DELTRAN=ACCTRAN):

    (0) interfrontals more anterior than fronto-orbitals
    (1) interfrontals more posterior than fronto-orbitals
    (2) interfrontals and fronto-orbitals aligned

This character corresponds to character 13 of Ament. (2017), with modifications. The phylogeny recovers the state (0) as synapomorphic for the genera *Cremersia*.

7. Frons, additional frontal setulae (L=2; CI=50; RI=0) (DELTRAN):

    (0) absent
    (1) present

This character corresponds to character 14 of Ament. (2017).

8. Frons, area above the ventral interfontral setae, surface (L=3; CI=33; RI=92) (ACCTRAN):

(0) bare
(1) setulose

9. Antennae, antennal first flagellomere, shape (L=2; CI=100; RI=100):

(0) globular
(1) conical
(2) conical-elongated

This character corresponds to character 18 of Ament. (2017).

10. Gena, chaetotaxy (L=7; CI=42; RI=83) (DELTRAN=ACCTRAN):

(0) without or with very small setulae
(1) one parafacial and one small genal setulae
(2) one parafacial and one genal medium setulae
(3) many genal medium setulae

This character corresponds to character 23 of Ament. (2017).

11. Palpus, shape (L=2; CI=50; RI=0):

(0) cylindrical, short
(1) flattened, of medium length

This character corresponds to character 24 of Ament. (2017).

Thorax

12. Foretarsomer 5, apex, shape (L=15; CI=26; RI=47):

(0) truncate (Fig. 50)
(1) round (Fig. 49)
(2) elongate (Fig. 47)
(3) bacilliform (Fig. 48)
(4) conical

13. Proepisternum, medio-dorsal part, surface (L=4; CI=100; RI=100) (DELTRAN=ACCTRAN):

(0) with setae and setulae spaced out

(1) with longitudinal setae row

(2) bare

(3) with two or three setae anterior to the spiracle

(4) with two setulae anterior to the spiracle

The presence of larger, stronger dorsal proepisternal setae is considered a synapomorphy of Metopininae + Phorinae in Briown *et. al.* 2015 (character 27), who considered the absence of the character secondarily lost in groups like termitophilous phorines, which may have happened with *Cremersia*.

14. Foreleg, tibia, dorsal, chaetotaxy (L=2; CI=100; RI=100) (DELTRAN=ACCTRAN):

(0) with longitudinal palisade row and setulae

(1) with setulae only

(2) with longitudinal spines row

This was a putative character previously proposed by Brown (2001) as “Foreleg, Dorsal longitudinal palisade row on fore tibia”. The state 0 was recovered as synapomorphic for the clade (*Eibesfeldtphora* spp.).

15. Foreleg, tarsomer 5 relative to the 4, topology (L=1; CI=100; RI=100):

(0) non fused

(1) fused

This was a putative character previously proposed in Brown 2001 as “Fore tarsomeres 4 and 5 fused to form single segment (five separate segments in outgroups)”. The state 1 was recovered as synapomorphic for the clade (*Eibesfeldtphora mexicanae* (*Eibesfeldtphora* spp.)).

16. Wing, C vein, setae, number (L=2; CI=50; RI=96):

(0) <35

(1) >40

17. Halter, apex, relative colour (L=3; CI=33; RI=93) (ACCTRAN):

(0) concolor to the rest of the halter (Fig. 2-3)

(1) with an apical rounded macula(Fig. 4)

This character corresponds to character 89 of Ament. (2017).

Abdomen

18. Tergite 1, posterior margin, chaetotaxy (L=1; CI=100; RI=100):
    (0) with small setulae
    (1) with microtrichia/bare

19. Tergite 2, posterior margin, chaetotaxy (L=3; CI=66; RI=97):
    (0) with setae and setulae spaced out across margin
    (1) with small setulae
    (2) with microtrichia/bare

20. Sternite 3, chaetotaxy (L=2; CI=50; RI=0):
    (0) with microtrichia or bare
    (1) with setulae

21. Tergite 3, posterior margin, chaetotaxy (L=4; CI=50; RI=94):
    (0) with setae and setulae spaced out
    (1) with small setulae
    (2) with microtrichia or bare

22. Sternite 3, chaetotaxy (L=13; CI=15; RI=8):
    (0) with setae and setulae spaced out
    (1) with setulae
    (2) with microtrichia or bare

23. Tergite 4, posterior margin, chaetotaxy (L=3; CI=66; RI=97):
    (0) with setae and setulae spaced out across margin
    (1) with small setulae
    (2) with microtrichia or bare

24. Sternite 4, chaetotaxy (L=10; CI=20; RI=55) (ACCTRAN):
    (0) with thick setae
    (1) with setulae

(2) with microtrichia or bare

25. Tergite 5, posterior margin, chaetotaxy (L=5; CI=60; RI=94):

(0) with setae and setulae spaced out across margin

(1) with small setulae

(2) with microtrichia or bare

(3)with setae and setulae spaced out across margin and thick setae on the lateral

26. Sternite 5, posterior margin, chaetotaxy (L=6; CI=33; RI=83):

(0) with thick setae

(1) with setulae

(2) with microtrichia or bare

27. Sternite 5, shape (L=1; CI=100; RI=100):

(0) single piece

(1) divided medially

Terminalia

28. Tergite 6, posterior margin, chaetotaxy (L=7; CI=42; RI=87):

(0) with setae and setulae spaced out across margin

(1) with small setulae

(2) with microtrichia or bare

(3)with thick setae

29. Sternite 6, posterior margin, chaetotaxy (L=5; CI=80; RI=96):

(0) with setae and setulae spaced out across margin

(1) with tranversal row of long filamentous setae

(2) with microtrichia or bare

(3)with small setulae

(4) with thick setae

30. Segment 6, mid third, membrane between St6 and Tg6, appearance (L=2; CI=100; RI=100) (DELTRAN=ACCTRAN):

(0) fully membranous (Fig. 3)
(1) sclerotized, ring-shape (Fig. 4)
(2) sclerotized, C shape (Fig. 1)

31. Segment 6, posterior third, membrane between St6 and Tg6, appearance (L=3; CI=66; RI=96) (ACCTRAN):

(0) fully membranous (Fig. 2)
(1) sclerotized, C shape (Fig. 1)
(2) sclerotized, ring-shaped (Fig. 4

32. Segment 6, sternite, surface (L=6; CI=83; RI=97):

(0) bare
(1) with setula
(2) with setulae and setae
(3)with setae, setula and major sensilla (Fig. 37)
(4) with thick setae
(5)with setae

33. Sternite 6, appearance (L=11; CI=18; RI=67):

(0) membranous
(1) with a sclerotized plate
(2) with an elongated sclerotized plate
(3)with anterior part membranous and posterior sclerotized (Fig 11)

34. Sternite 6, shape (L=13; CI=38; RI=60) (DELTRAN):

(0) quadrangular
(1) rectangular
(2) round
(3)elongate
(4) triangular
(5) concave (Fig 11)

35. Segment 6, sternite, membranous anteroventral margin (L=11; CI=18; RI=57):

(0) bare

(1) with transverse row with distinctly sclerotized insertion points (Fig. 11)

(2) with setulae and setae

This was a putative character previously proposed in Brown 2001 as “1 - Series of long lateral setae on abdominal segment 6 (absent in outgroups). This character unifies the subgenus *Neodohrniphora*.”

The state 1 was recovered as synapomorphic for the genus *Neodohrniphora*, which demonstrates the importance of assuming putative characters in taxonomic papers.

36. Segment 7, sclerites, appearance (L=1; Uninformative) (DELTRAN=ACCTRAN):

(0) largely membranous (Fig. 41 -43)

(1) both sclerotized and modified for parasitism (oviscape) (Figs. 2-40)

This character corresponds to character 5, with modifications, in Brown 1992 (table 10) and 32 in Hash (2017).

37. Tergite 7, apex, shape (L=1; CI=100; RI=100):

(0) symmetrical (Fig. 36, a)

(1) asymmetrical (Fig. 7-9)

38. Tergite 7, dorso anterior apex, shape (L=3; CI=66; RI=0):

(0) truncate

(1) elongated

(2) round

39. Segment 7, mid third, dorsal, shape (L=3; CI=66; RI=50) (DELTRAN):

(0) concave

(1) flattened laterally

(2) flattened dorsoventrally

40. Tergite 7, posterior margin, apex, surface (L=5; CI=80; RI=88) (DELTRAN=ACCTRAN):

(0) with setae and setulae spaced out

(1) pair of short spine (1x2 – dimensions)

(2) pair of long spine (1x5 – dimensions)

(3)bare

(4) pair of setae

41. Tergite 7, dorso-lateral part, surface (L=2; CI=100; RI=100):

(0) bare

(1) With parallel row of setae

(2) With parallel row of setulae

42. Segment 7, anterior third, membrane between St7 and Tg7, appearance (L=5; CI=40; RI=87) (DELTRAN):

(0) fully membranous

(1) partially membranous and bearing a sclerotized longitudinal strip

(2) sclerotized, ring-shaped

43. Segment 7, mid third, membrane between St7 and Tg7, appearance (L=5; CI=40; RI=85) (DELTRAN):

(0) fully membranous

(1) partially membranous and bearing a sclerotized longitudinal strip

(2) sclerotized, ring-shaped

44. Segment 7, posterior third, membrane between St7 and Tg7, appearance (L=4; CI=50; RI=90):

(0) fully membranous

(1) partially membranous and bearing a sclerotized longitudinal strip

(2) sclerotized, ring-shaped

45. Tergite 7, right side, apex, shape (L=14; CI=28; RI=16):

(0) elongated cylindrical

(1) short pointed

(2) flattened dorsoventrally

(3) Flattened laterally

(4) digitiform

46. Tergite 7, dorsal center, surface (L=7; CI=28; RI=28):

(0) bare
(1) with spines
(2) with setulae

47. Tergite 7, right side, apex, surface (L=15; CI=33; RI=9):
(0) one long spine (Fig. 51, arrow)
(1) two long spines (Fig. 53, red arrow)
(2) two short spine (Fig 7)
(3) one short spine
(4) two long and curved spines (Fig. 52, red arrow)
(5) bare

48. Tergite 7, composition (L=1; uninformative):
(0) single piece (Figs 1 – 32)
(1) divided into two sclerites, anterior and posterior (37,38)

49. Sternite 7, composition (L=2; CI=100; RI=100):
(0) entire (Fig 42)
(1) divided into two sclerites (Fig 38, c)
(2) divided into three sclerites (Fig 12,c)

50. Tergite 7, tegument, appearance (L=1; CI=100; RI=100):
(0) smooth (Fig. 54, arrow)
(1) with deep streaks (Fig. 53,white arrow)

Character 51 – 65 see Fig A, Chapter 2.

51. Sternite 7, globular lobe, appearance (L=1; uninformative) (DELTRAN=ACCTRAN):
(0) membranous
(1) sclerotized

52. Sternite 7, globular lobe, shape (L=5; CI=20; RI=20) (ACCTRAN):
(0) lobed (Chapter 2, fig 15)
(1) bilobed (Chapter 2, fig 13)

(2) globose (Chapter 2, fig 18)

53. Sternite 7, lobe arm, position on globular lobe, (L=3; CI=33; RI=50):

(0) dorsal (Chapter 2, fig 21)

(1) ventral(Chapter 2, fig 20)

54. Sternite 7, lobe arm, appearance (L=1; uninformative) (DELTRAN=ACCTRAN):

(0)partially membranous and partially sclerotized

(1) fully sclerotized

55. Sternite 7, lobe arm, shape (L3=; CI=100; RI=100) (DELTRAN=ACCTRAN):

(0) cylindrical short (1x1 dimensions) (Chapter 2, fig 17)

(1) cylindrical long (1x2 dimensions) (Chapter 2, fig 15)

(2) flattened (Chapter 2, fig 21)

(3) globose (Chapter 2, fig 18)

56. Sternite 7, lobe arm, apex, curvature (L=5; CI=60; RI=33) (DELTRAN):

(0) straight

(1) inward

(2) downward

(3) inward and downward

57. Sternite 7, lobe arm, apex, shape (L=3; CI=66; RI=50):

(0) pointed

(1) flattened

(2) truncated

58. Sternite 7, lobe arm, angle in relation to lateral part of sternite 7 (L=1; CI=100; RI=100):

(0) ~90º

(1) ~180º

59. Sternite 7, movable lateral plate, appearance (L=1; uninformative):

(0) weakly sclerotized
(1) sclerotized

60. Sternite 7, movable lateral plate, number of processes (L=3; CI=33; RI=0):
(0) one
(1) two

61. Sternite 7, movable lateral plate, shorter processes, position (L=1; uninformative):
(0) dorsal
(1) ventral

62. Sternite 7, movable lateral plate, chaetotaxy (L=4; CI=50; RI=33):
(0) with setae forming rows, not in combs
(1) with setae in combs
(2) with spines in combs

63. Sternite 7, movable lateral plate, dorsal process, apex, shape (L=4; CI=75; RI=0):
(0) digitiform
(1) truncate
(2) bilobed
(3)triangular and acute

64. Sternite 7, movable lateral plate, ventral process, apex, shape (L=4; CI=50; RI=0) (DELTRAN):
(0) digitiform
(1) triangular and acute
(2) round

65. Sternite 7, dorsal base, shape (L=3; CI=66; RI=66) (DELTRAN=ACCTRAN):
(0) round
(1) triangular
(2) keel-shaped

66. Sternite 8, process (L=1; CI=100; RI=100):

(0) absent
(1) present

67. Sternite 8, process, position (L=1; uninformative):
(0) ventral (Chapter 2, fig 19)
(1) dorsal (Chapter 2, fig 20)

68. Sternite 8, apex, shape (L=2; CI=100; RI=100):
(0) round
(1) acute
(2) flattened dorsoventrally

69. Tergite 8, composition (L=2; CI=50; RI=96):
(0) entire (Fig, 10,b)
(1) divided into two sclerites (Fig. 14, b)

70. Sternite 8, composition (L=1; uninformative):
(0) entire
(1) divided into two sclerites

71. Segment 8, tergite, position (L=3; CI=100; RI=100) (DELTRAN=ACCTRAN):
(0) disjoint from tergite 7 (Fig. 43, b)
(1) fused to the apex of tergite 7 (Fig. 44b; 39,b; 40,b; 35,b)
(2) fused to the side of tergite 7 (fig. 16,17)
(3) withdrawn into segment 7 (Fig. 15)
(4) fused to lateral margin of tergite 7 (Fig. 38b)

As character 35, this is a putative character previously proposed in Brown (2001) as “2- Lateral lobe present on ovipositor (absent in subgenus *Neodohmiphora* and outgroups). This character unifies the subgenus *Eibesfeldtphora*”

The state 2 was recovered as synapomorphic for the clade *E. mexicanae* + *Eibesfeldtphora* spp.

72. Segment 8, sternite, position (L=2; CI=100; RI=100) (DELTRAN=ACCTRAN):
(0) disjoint from tergite 7

(1) fused to the apex of sternite 7

(2) withdrawn into segment 7

73. Sternite 8, shape (L=3; CI=100; RI=100) (DELTRAN):

(0) membranous or with a sclerotized plate

(1) hook (Fig. 11,e)

(2) ring (Fig 14, e)

(3) shoe spatula (Fig, 31 red arrow)

(4) elongate plate (Fig, 9,e)

74. Tergite 8, lobes, shape (L=1; uninformative) (DELTRAN=ACCTRAN):

(0) with single, broad, concave lobe (Fig. 16,b)

(1) with two or three defined lobes (Fig 17,b)

This is a putative character previously proposed in Brown (2001) as “Lateral lobe subdivided into dorsal and ventral lobes (single lobe in *N. mexicanae*)”. State 0 was recovered as autopomorphic for *Eibesfeldtphora mexicanae*, state 1 synapormophic for the clade *Eibesfeldtphora* spp.

75. Tergite 8, dorsal part, shape (L=10; CI=20; RI=11):

(0) flattened laterally

(1) flattened dorsoventrally

(2) cylindrical

76. Tergite 8, dorsal part, apex, shape (L=10; CI=30; RI=0) (DELTRAN=ACCTRAN):

(0) digitiform (Fig, 17,b)

(1) round

(2) truncate (Fig 16,b)

(3)triangular

77. Tergite 8, ventral part, shape (L=11; CI=18; RI=10):

(0) flattened laterally

(1) flattened dorsoventrally

(2) cylindrical

78. Tergite 8, ventral part, apex, shape (L=8; CI=37; RI=0) (DELTRAN=ACCTRAN):

(0) digitiform
(1) round
(2) truncate
(3) triangular

79. Tergite 8, distance between the dorsal and ventral parts (L=9; CI=33; RI=0) (DELTRAN=ACCTRAN):

(0) widely separated
(1) close together
(2) adjacent each other, appearing as a single structure
(3) fused

80. Tergite 8, dorsal part, arrangement of setae (L=5; CI=20; RI=0):

(0) just at the apex
(1) more than the apex

81. Tergite 8, ventral part, arrangement of setae (L=8; CI=12; RI=12) (DELTRAN=ACCTRAN):

(0) just at the apex
(1) more than the apex

82. Tergite 8, central part, surface (L=2; CI=50; RI=0) (DELTRAN=ACCTRAN):

(0) bare
(1) with setae
(2) with setulae

83. Tergite 8, dorsal part in relation to ventral part, size (L=10; CI=10; RI=0) (DELTRAN):

(0) equal
(1) dorsal bigger than ventral
(2) ventral bigger than dorsal

84. Tergite 8, dorsal part in relation to ventral part, thickness (L=10; CI=20; RI=11) (DELTRAN=ACCTRAN):

(0) equal

(1) dorsal thicker than ventral

(2) ventral thicker than dorsal

85. Segments 9 and 10, position relative to the 8 (L=1, uninformative) (DELTRAN=ACCTRAN):

(0) at the apex

(1) withdrawn into segment 8

86. Tergite 9 and tergite 10, topology (L=2; CI=50; RI=96):

(0) fused (Fig, 18, f)

(1) non fused (Fig 20,j)

87. Sternite 9, position relative to the tergite 10 (L=2; CI=50; RI=95):

(0) internal to tergite10 (Fig, 12, 23, 24)

(1) ventral to tergite10 (Fig, 18, I; 21 red,

88. Sternite 9, posterior process, topology (L=3; CI=33; RI=86) (DELTRAN):

(0) fused

(1) non fused

89. Sternite 9, anterior, topology (L=2; CI=50; RI=0) (DELTRAN):

(0) fused

(1) non fused

90. Sternite 9, anterior apex, curvature (L=1; CI=100; RI=100):

(0) straight (Fig. 24, pink;

(1) convex (Fig.20, h; 23, pink;)

91. Tergite 10, processes, composition (L=3; CI=100; RI=100) (DELTRAN):

(0) three pieces (anterior + ventral/lateral + posterior) (Fig. 18,20,21, 23)

(1) one single piece (anterior and posterior fused) (Fig 24)

(2) two pieces (anterior + ventral/lateral) (Fig 22)
(3) one single piece (anterior)

92. Tergite 10, posterior process, shape (L=3; CI=100; RI=100) (DELTRAN=ACCTRAN):

(0) cone (Fig. 18,d)
(1) tubular (Fig 20, g)
(2) braided (Fig 10,d)
(3) claw (1fig 19,g)

93. Tergite 10, anterior process, shape (L=3; CI=66; RI=95) (DELTRAN=ACCTRAN):

(0) sheath, involving the tergite 9 and sternite 9
(1) elongated
(2) semi-sheath - involving the tg9 and st9

94. Tergite 10, apex, direction (L=3; CI=100; RI=100):

(0) parallel with sternite apex
(1) down curved
(2) up curved
(3) curved laterally

95. Oviposition mechanisms (L=4; CI=75; RI=95) (DELTRAN=ACCTRAN):

(0) lay eggs
(1) perforation, with partial eversion of tergite 9 + 10 of segment 7
(2) perforation, with total eversion of tergite 9 + 10 of segment 7
(3) perforation, with partial eversion of tergite 9 + 10 of segment 8

This character was observed based on the internal and external morphology. The size and shape of sclerites were considered, and some specimens were found in different stages of oviscape evertion. (fig 25-32). Oviposition *Neodohrniphora:*figs 25-26. Oviposition *Eibesfeldtphora:* Fig. 27 and 28 protated, 29-30parcially everted and 31 and 32 totally everted.

Comparative morphology and homology proposals

This study was done based on comparative morphological analysis including more than two genera of parasitoids (*Neodohrniphora*, *Cremersia, Eibesfeldtphora, Apocephalus, Pseudacteon*, *Myrmosicarius* and *Myriophora*). Herein, we propose some homologies (Figs 7-24 ; 33-46)

Segments 7 and 8

Segment seven was considered to be that after segment six. When the segment was not clearly defined (sometimes presented as internal to segment six), we differentiated it from segment eight by an unsclerotized gap (Fig x and y). When a fold was visible in the structure, it was considered the same segment seven (fig *Pseudacteon*) instead of the eight. In general, the sclerotization, the number and position of segments were crucial factors for determining the structure. Occasionally, Segment 8 was not clearly separated from segment seven, but sometimes presented one or two pieces, and was internal to segment seven (Fig x and y).

Segment 9 and 10

Tergites and sternites 9 and 10 are present in the ground pattern of Diptera. However, the trend within the Diptera order is to reduce or merge these sclerites. In most Cyclorrhapha, only one ventral sclerite and one dorsal sclerite are present in the region between segment 8 and the cerci (Kotrba, 2000).

In Phoridae, the characterization of these segments has been widely discussed by Disney (1988) and Brown (1992). Nakayama (2007) suggests the female segmentation as in illustration (x) and we use such interpretation to propose in this study that: when two segments are present S9 and T9+T10 (fused), when 3 different segments are present we identify stenite 9, tergite 9 and 10. The separation of T10 and T9 is also present in parasitoids of the Family Pipunculidae (Kehlmaier & Assmann, 2008).

With the comparative analysis, we noticed that these two segments are elongated and sometimes form a tube at the posterior apex in parasitoidic phorids. Remembering Bernoulli’s Principle, decreased thickness of tubular systems causes an increase in velocities of the flow inside them, we can understand why oviposition is often so fast inside the hosts (Porter, 1998).

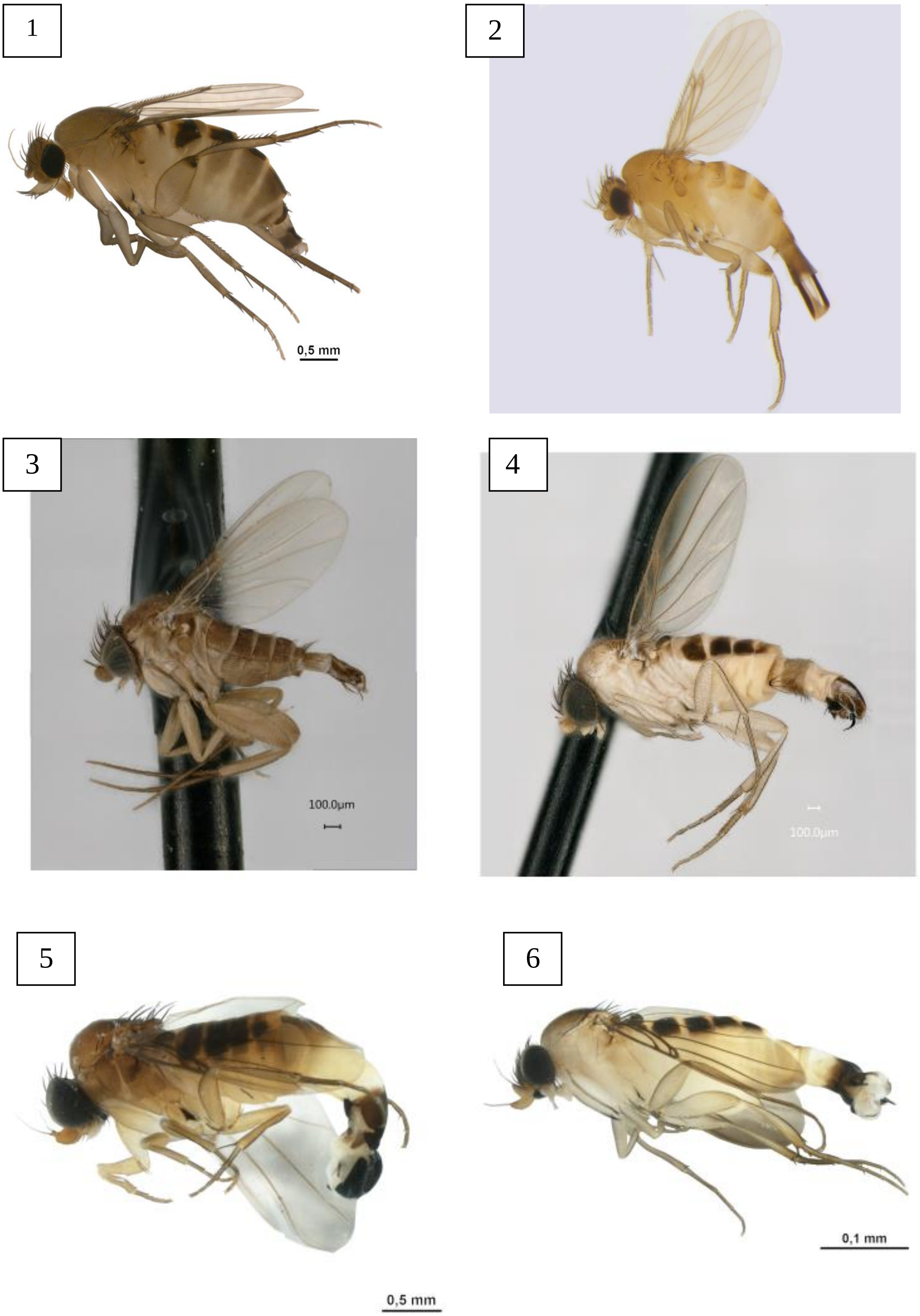


Fig 1–6. Habitus images (left lateral), females. 1. *Megaselia scalaris.* 2. *Myriophora* sp.. 3. *Cremersia australis.* 4. *Neodorniphora* sp. nov.5. 5. *Eibesfeldtphora inornata.* 6. *Eibesfeldtphora elongata*.

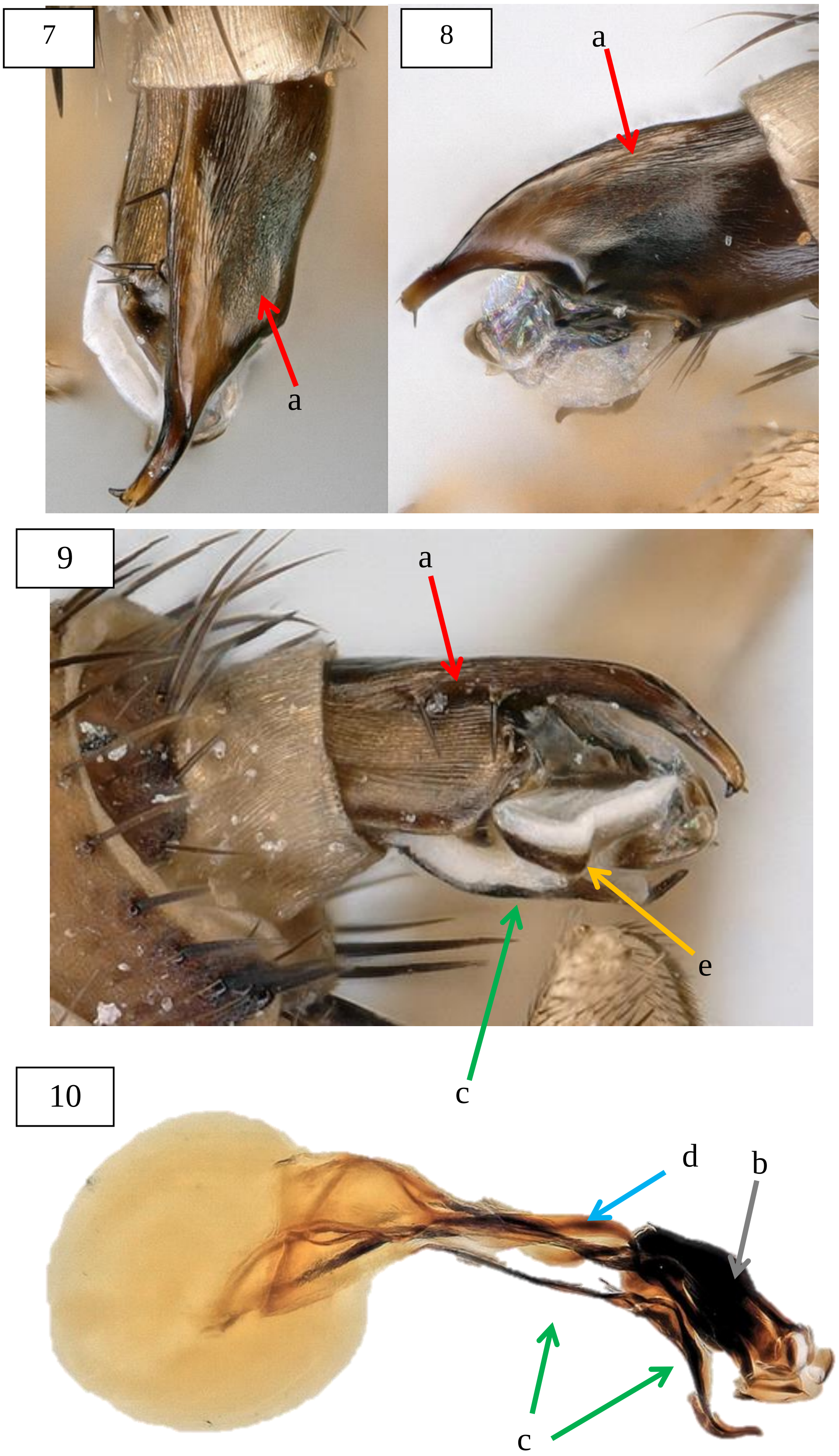


Fig. 7 – 10 Ovipositor of *Cremersia salesiana*. 7.Dorsal view. 8. Right lateral view. 9. Left lateral view. 10. Left lateral view. a, tergite 7; b, tergite 8; c, sternite 7; d, tergite 10. . e, esternite 8.

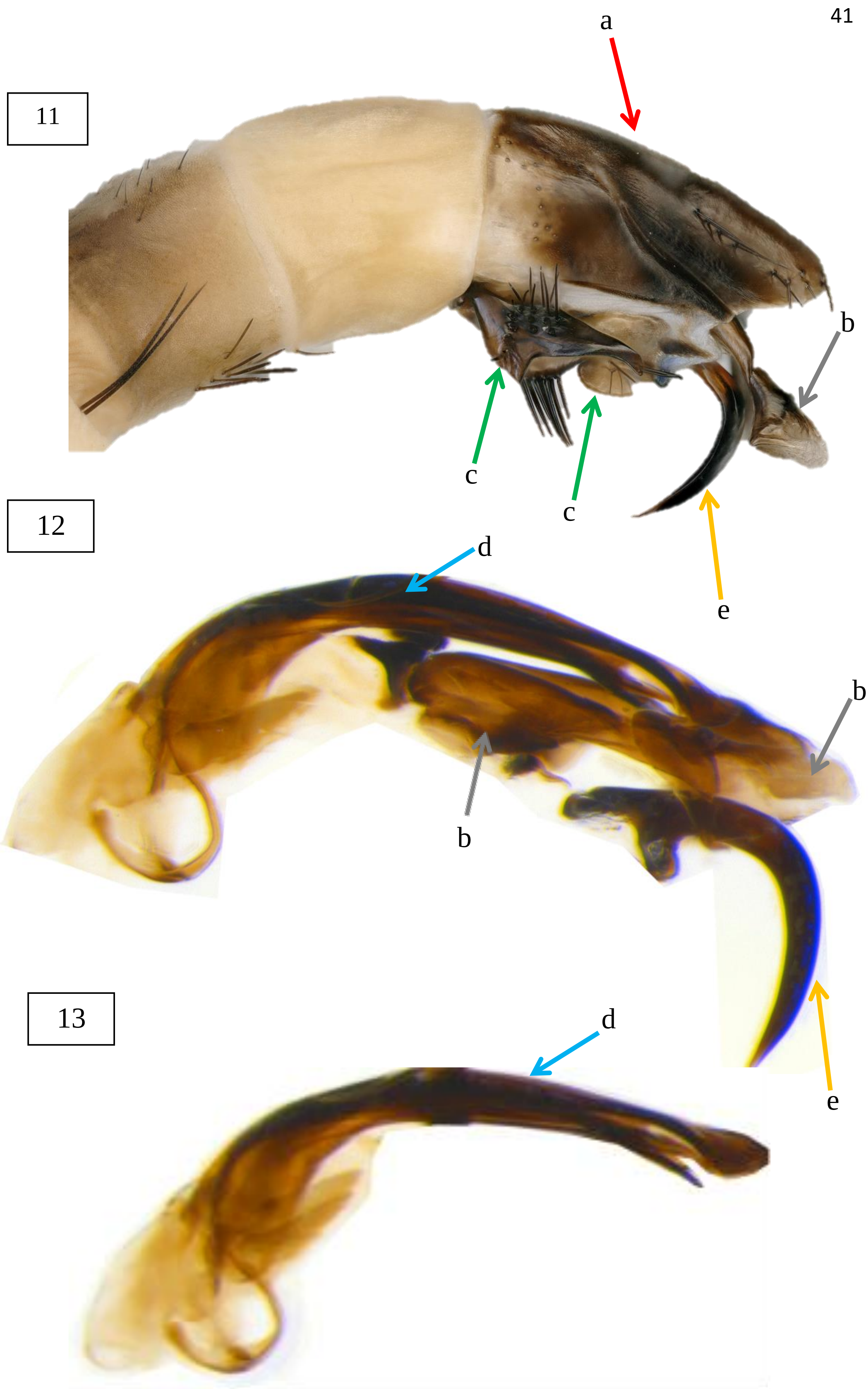


Fig. 11 – 13 Ovipositor of *Neodohrniphora gigantea*.. left lateral view. a, tergite 7; b, tergite 8; c, sternite 8; d, tergite 10. e, esternite 8.

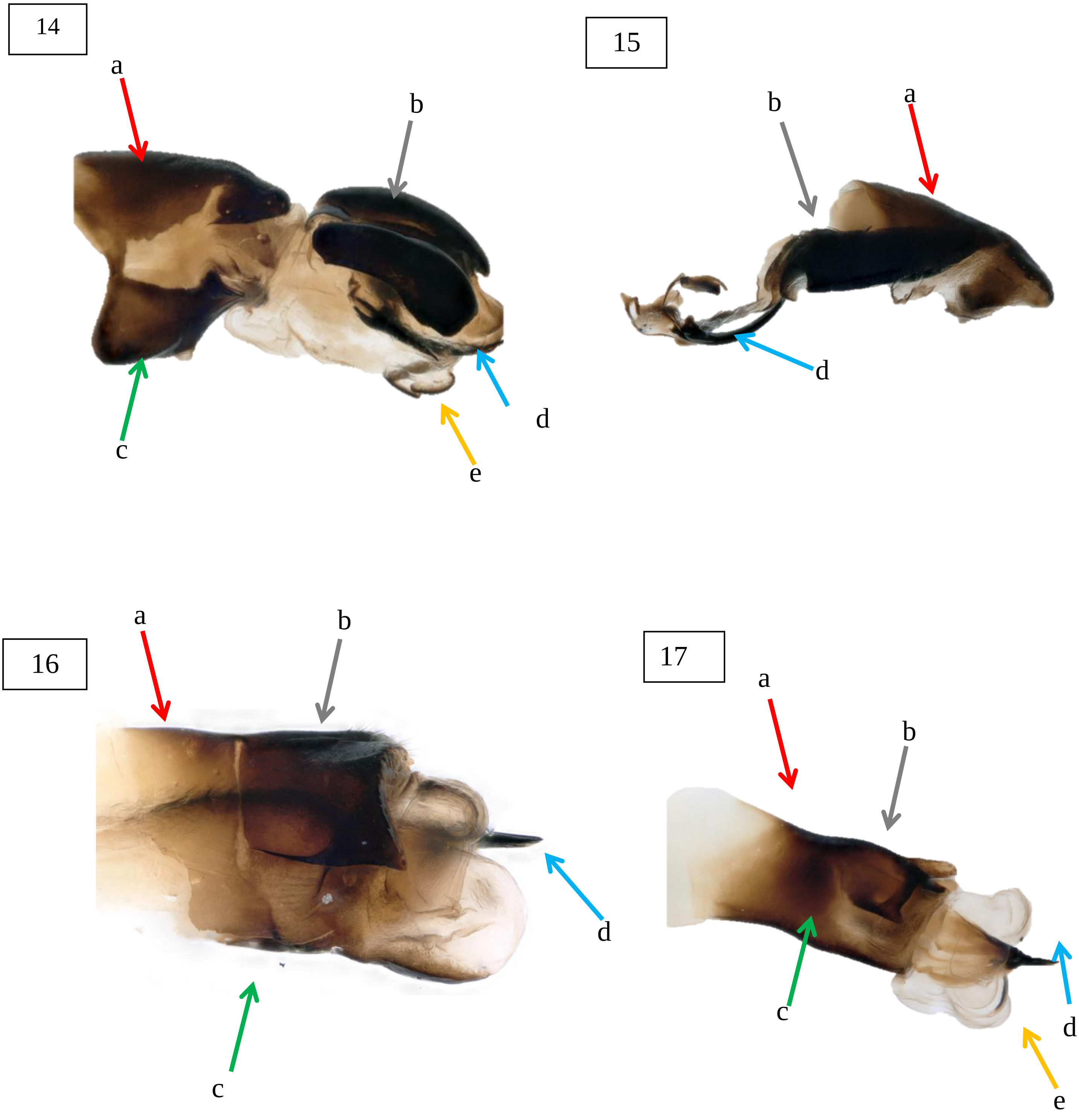


Fig. 14 – 17 Ovipositor in left lateral view.14-15. *Eibesfeldtphora inornata;* 14. everted ovipositor; 15. inverted ovipositor. 16. *Eibesfeldtphora mexicanae.* 17. *Eibesfeldtphora curvinervis.* a, tergite 7; b, tergite 8; c, sternite 8; d, tergite 10. e, esternite 8.

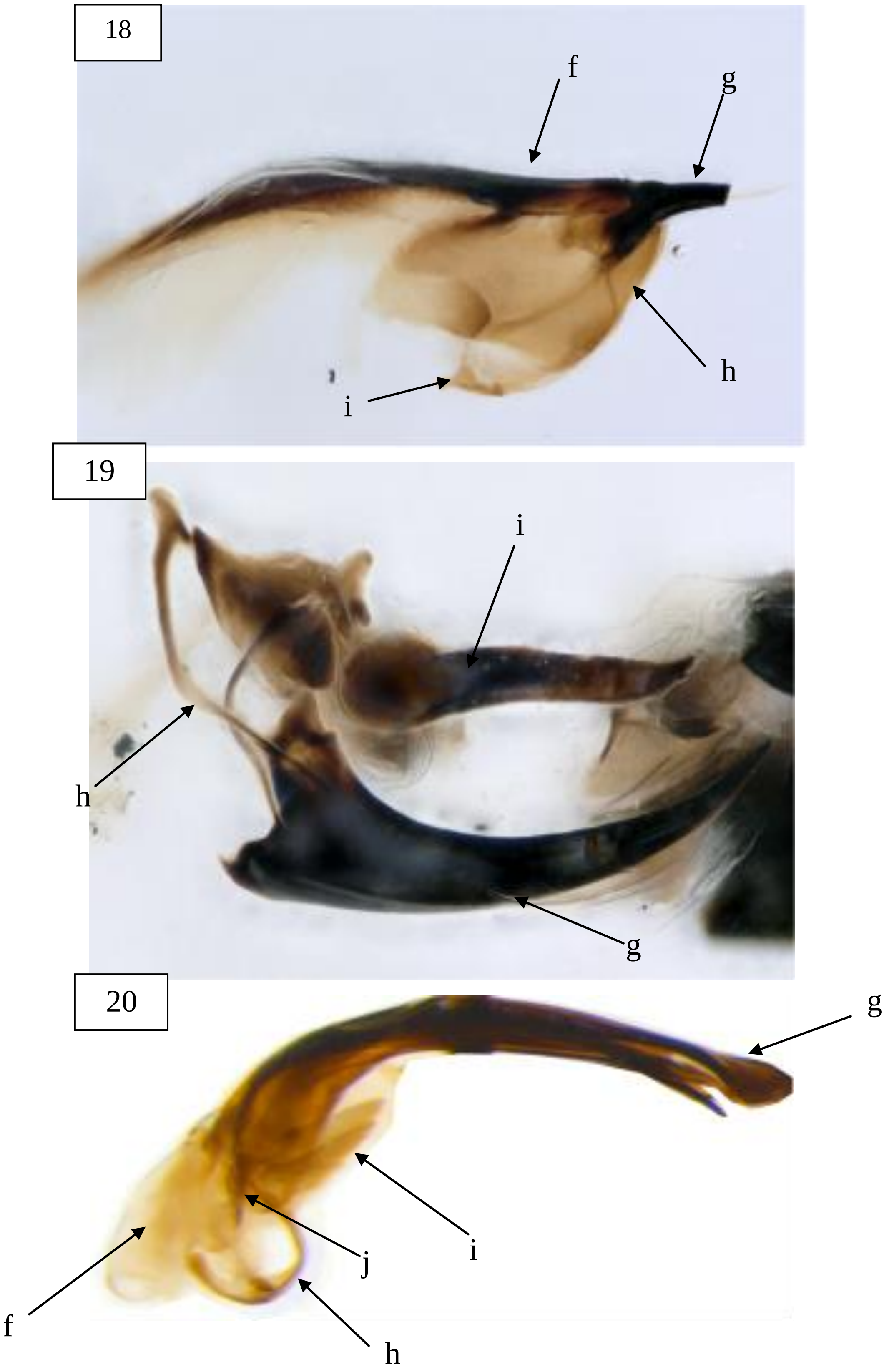
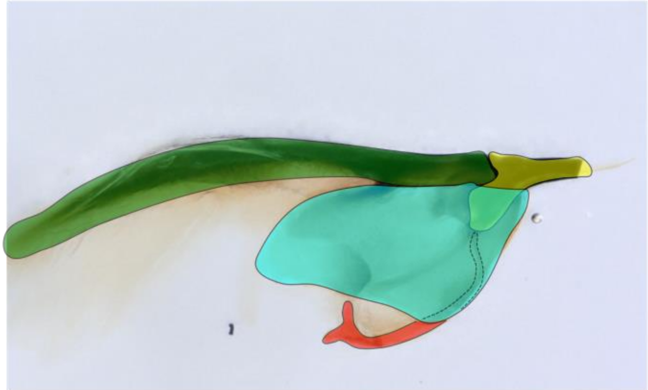


Fig. 18 – 20 Ovipositor in left lateral view.18. *Eibesfeldtphora mexicanae,* 19. *Eibesfeldtphora inornata;* 20. *Neodohrniphora gigantea*, f+g+i, tergite 10; h, sternite 9; j, tergite 9;

21



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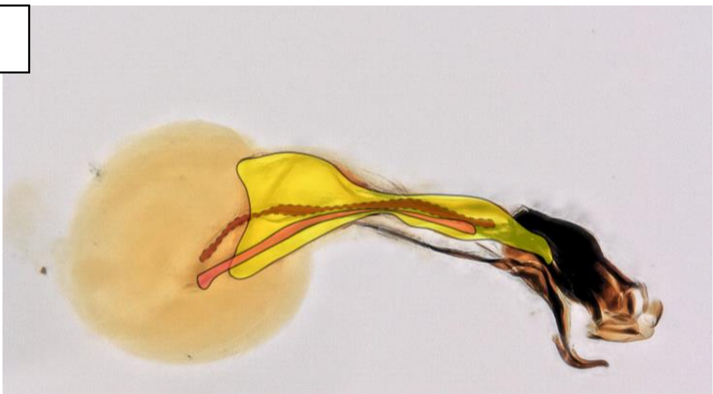


Fig. 21 – 24 Ovipositor in left lateral view.21. *Eibesfeldtphora mexicanae,* 22. *Eibesfeldtphora inornata;* 23. *Neodohrniphora* sp nov. 1; 24. *Cremersia salesiana;* yellow, blue and green, tergite 10; red sternite 9; wine, tergite 9; pink, sternite 9.

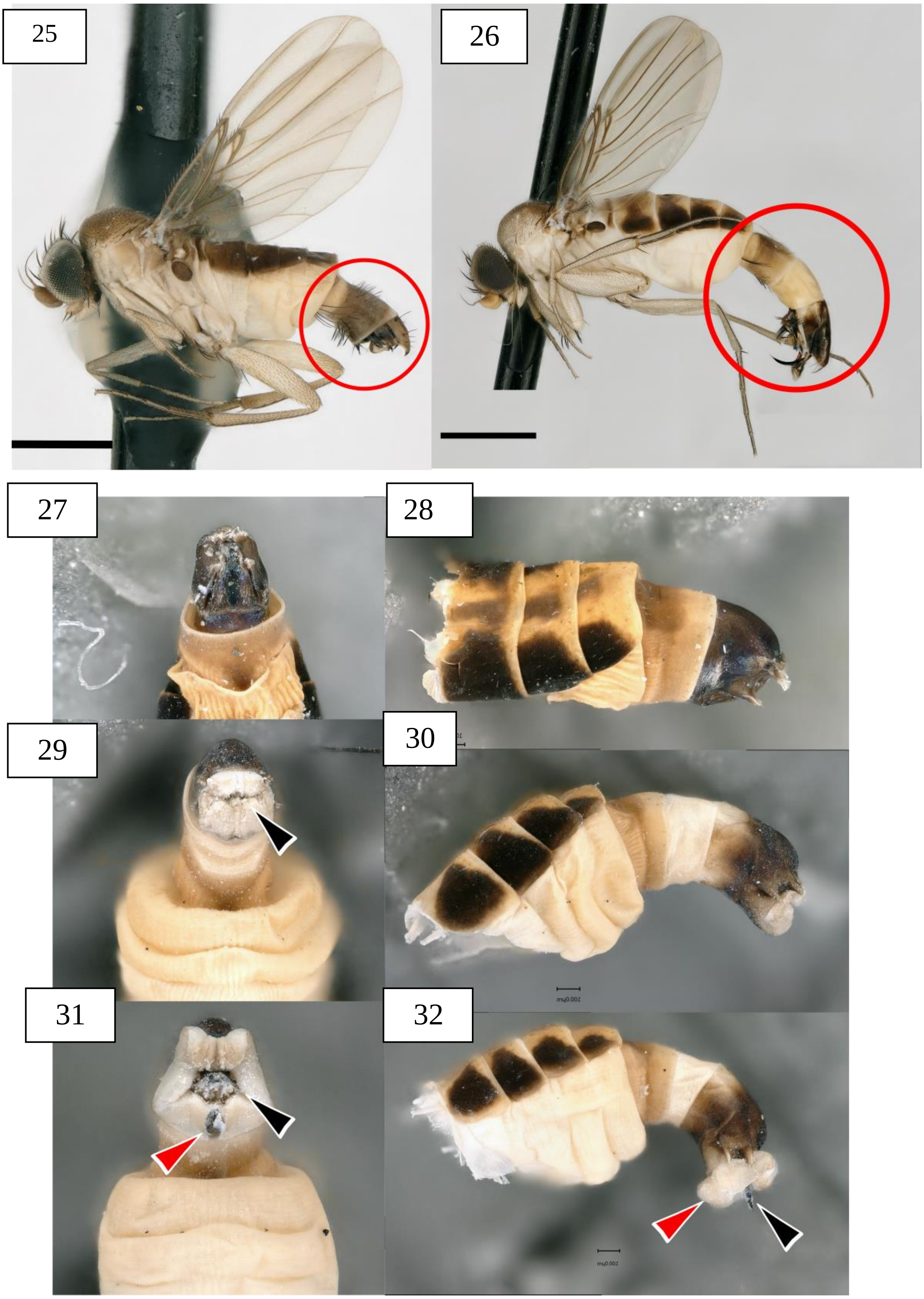


Fig. 15-32. 25-26 Habitus images (left lateral), females, 25. *Neodohniphora calverti;*. red circle, inverted ovipositor. 26. *Neodohniphora* sp. nov.1. red circle, everted ovipositor. Figs. 27-32.*Eibesfeldtphora declinata.* Fig. 27,29,31. posterior view; Fig. 28,30,32. left lateral view. Black arrow. Tergite 10. Red arrow. sternite 8.

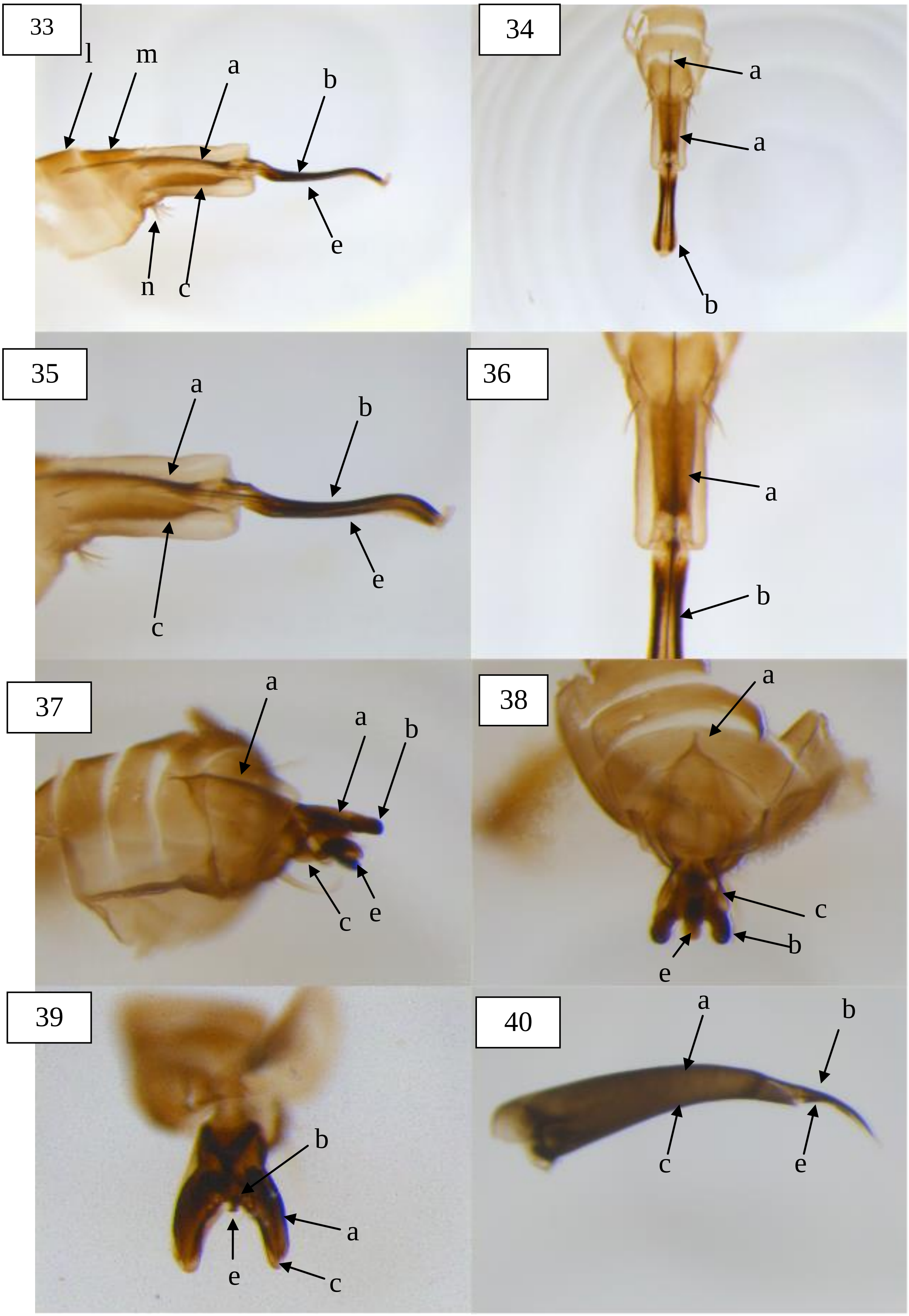


Fig. 33 – 40. 33, 35, 37, 40. Ovipositor left lateral view. 34,36,38, 39. Ovipositor dorsal view. 33-36. *Apocephalus attophius*. 37-38. *Pseudacteon wasmanni*. 39.

Pseudacteon browni. 40. *Myrmosicarius grandicornis*. a, tergite 7; b, tergite 8; c, sternite 8; d, tergite 10. e, esternite 8. l. tergite 5; m. tergite 6; n. sternite 6;

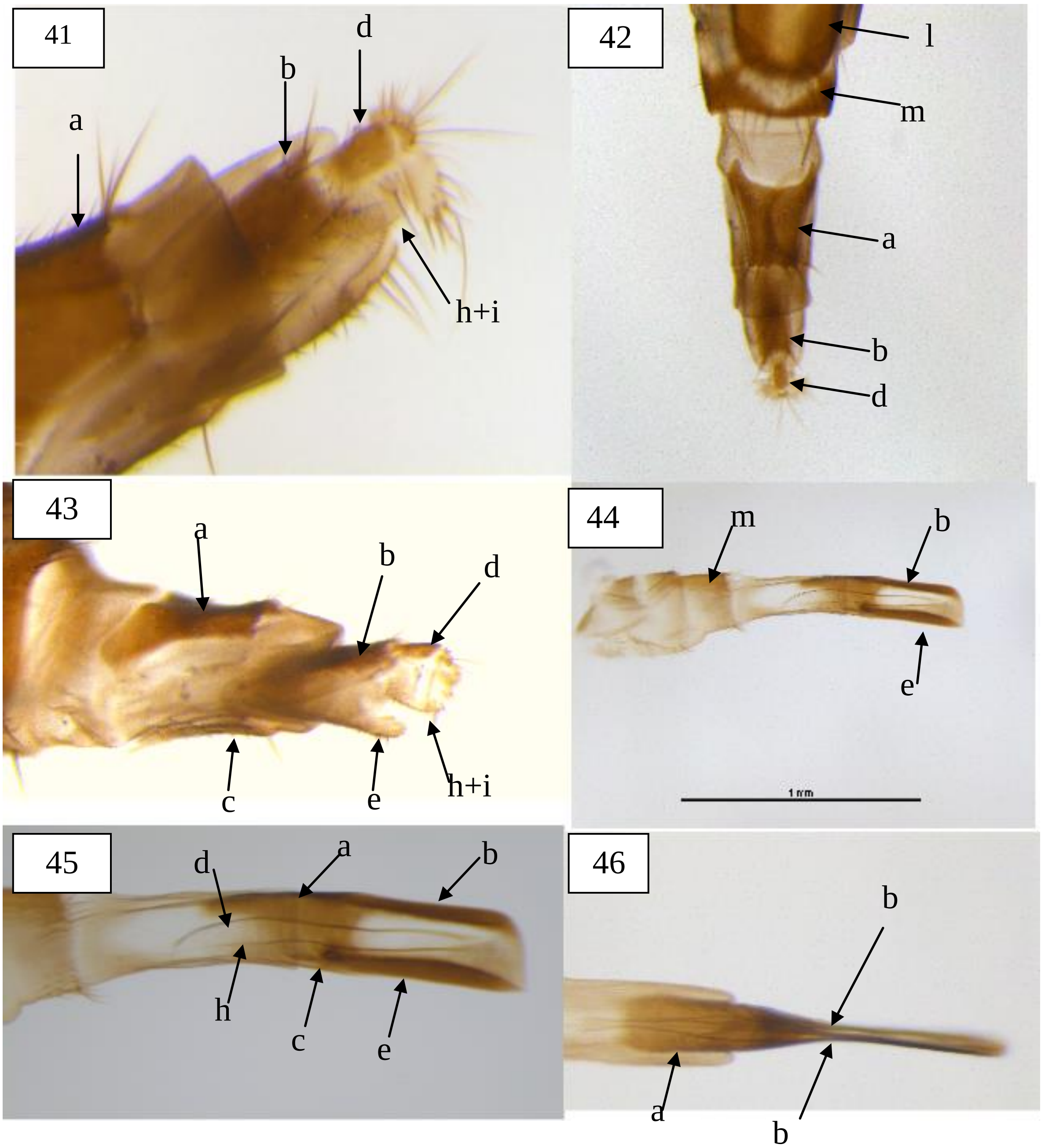


Fig. 41 – 46. 41, 43-45 Ovipositor left lateral view. 42, 46. Ovipositor dorsal view. 41-43. *Megaselia scalaris.* 44-46. *Myriophora* sp. a, tergite 7; b, tergite 8; c, sternite 8; d, tergite 10. e, esternite 8. l. tergite 5; m. tergite 6; n. sternite 6; h, sternite 9; j, tergite 9;

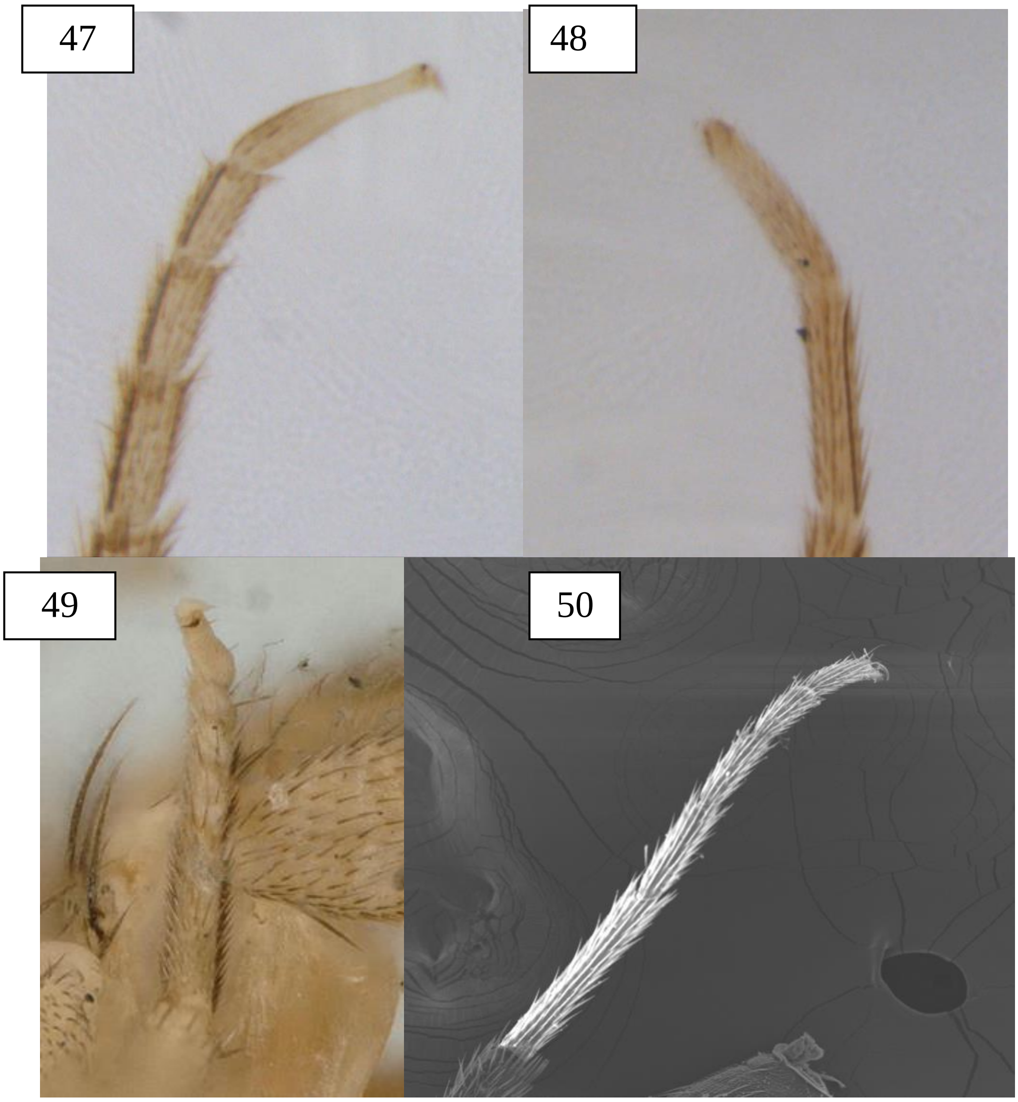


Fig. 47 – 50. Foretarsomer. 47. *Cremersia longipes.* 48. *Cremersia brasiliensis* 49. *Cremersia zikani* 50. *Neodorniphora* sp. nov 5.

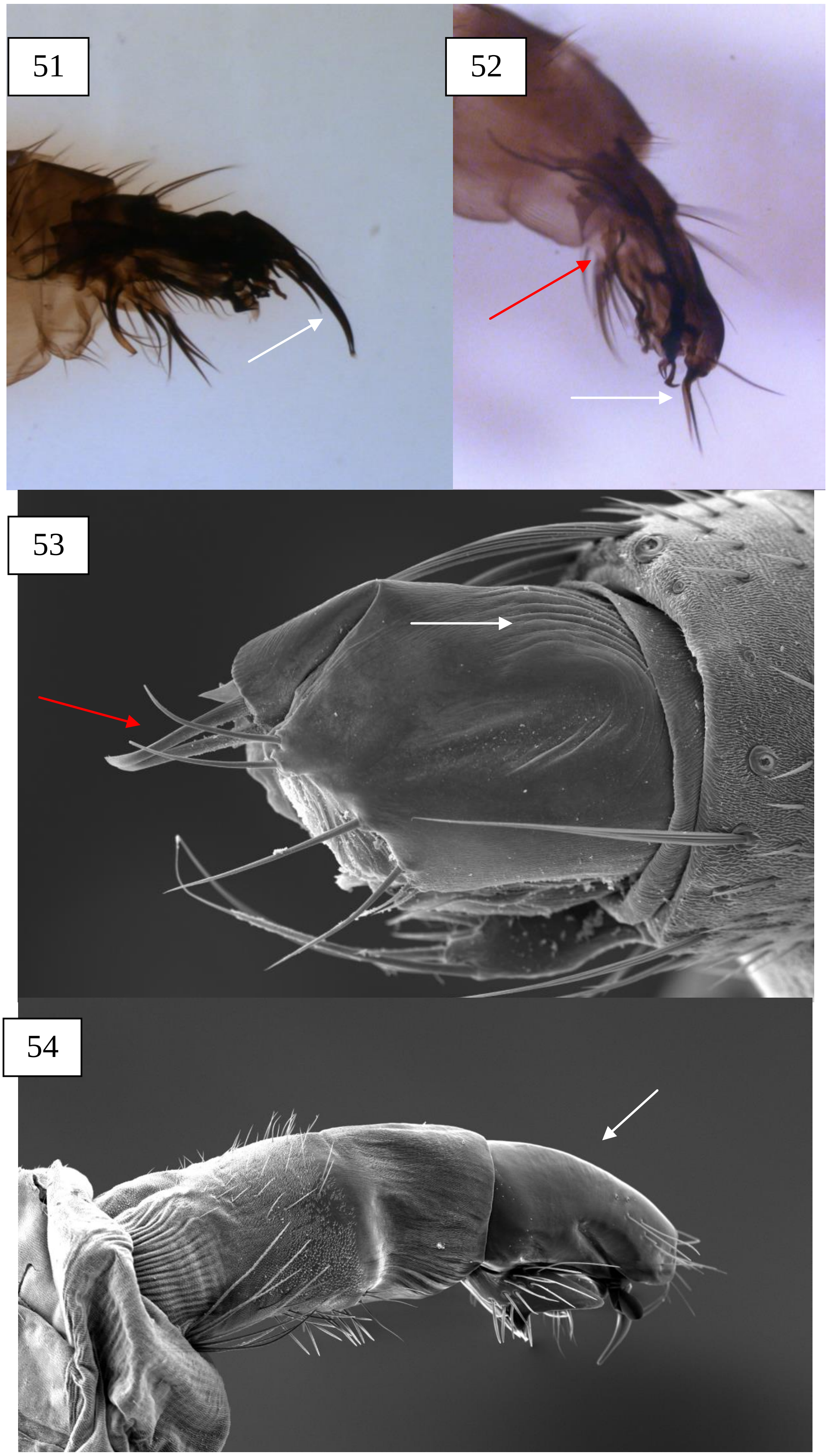


Fig. 51,52,54 Ovipositor left lateral view. 53 42, Ovipositor right dorsolateral view. 51. *Cremersia spinicauda*. 52. *Cremersia lonigipes*. 53. *Cremersia spinicosta*. 54. *Neodohrniphora* sp. nov.5.

Phylogenetic analyses

The equal weighting (EW) analysis resulted in 902 most parsimonious trees, with the best score of 305 steps, Ci=60, Ri=90 (Fig. X). When we increased the parameters two and three times, we found a higher number of trees with 2,678 and 5,660, respectively, but the best score and the consensus tree were maintained. The level of resolution is extremely low, with the three genera *Neodohrniphora*, *Cremersia* and *Eibesfeldtphora* monophyletic and well supported (synapomorphies and branch support), but the internal relationships are not resolved.

Characters that support the *Neodohrniphora* genus in the equal weighting analysis are:

Table 1. Exclusive synapomorphies for the clade

Character	**Optimization**	Character-state
29. Sternite 6, posterior margin, chaetotaxy		(1) with transversal row of long filamentous setae
30. Segment 6, second third, membrane between St6 and Tg6, appearance	DELTRAN =ACCTRN	(1) sclerotized, ring-shaped
35. Segment 6, sternite, membranous anteroventral margin		(1) with transverse row with distinctly sclerotized insertion points
41. Tergite 7, dorso-lateral part, surface		(1) with parallel row of setae
49. Sternite 7, composition		(2) divided into three sclerites
73. Sternite 8, shape	DELTRAN	(1) hook
90. Sternite 9, anterior apex, curvature		(1) convex
.94. Tergite 10, apex, direction		(1) down curved

Characters that support the *Cremersia* genus in the equal weighting analysis are:

Table 2. Exclusive synapomorphies for the clade

Character	**Optimization**	**Character-state**
6. Frons, frontal dorsal row	DELTRAN=ACCTRAN	(0) interfrontals more

of setae, position		anterior than fronto-orbitals
13. Proepisternum, medio-dorsal part, surface	DELTRAN=ACCTRAN	(3) with two or three setae anterior to the spiracle
19. Tergite 2, posterior margin, chaetotaxy		(0) with setae and setulae spaced out across margin
21. Tergite 3, posterior margin, chaetotaxy		(0) with setae and setulae spaced out
23. Tergite 4, posterior margin, chaetotaxy		(0) with setae and setulae spaced out across margin
37. Tergite 7, dorso anterior apex, shape		(1) asymmetrical
50. Tergite 7, tegument, appearance		(1) with deep streaks
73. Sternite 8, shape	DELTRAN	(4) elongate plate
91. Tergite 10, processes, composition	DELTRAN	(1) one single piece (anterior and posterior fused)
92. Tergite 10, posterior process, shape	DELTRAN=ACCTRAN	(2) braided
94. Tergite 10, apex, direction		(3) curved laterally

Characters that support the *Eibesfeldtphora* genus in the equal weighting analysis are:

Table 3. Exclusive synapomorphies for the clade

Character	**Optimization**	**Character-state**
9. Antennae, antennal first flagellomere, shape		(2) conical-elongated
28. Tergite 6, posterior margin, chaetotaxy		(2) with microtrichia or bare
95. Oviposition mechanisms	(DELTRAN=ACCTRAN):	(2) perforation, with total eversion of tergite 9 + 10 of segment 7

The analyses applying implied weighting (IW) of characters resulted in a smaller number of trees (Table 4). Different concavity values (k) produced different number of trees and topologies. With the k value (k=2) we had only 21 trees, and the strict consensus is mostly resolved (Fig. 63 cladogram with k=2), with some significant polytomies in *Cremersia* only. The same is observed in the strict consensus trees with other k values (Figs 64-68 cladograms with k3-20). In the strict consensus for k=20, the tree is almost fully resolved (Fig 68 cladogram with k=20). As expected, the topology under k=20 resembles that of EW analysis, but the tree is resolved, not fully polytomic as in EW analysis. In all analyses using implied weighting, the three genera *Neodohrniphora*, *Cremersia* and *Eibesfeldtphora* are recovered monophyletic and well supported.

Cremersia in the IW analyses is supported by a varying number of synapomorphies from 9 (with k1-3) to 11 (with k4-20). The synapomorphies supporting *Neodohrniphora* also varied in the IW analyses, from 7 (k1-3) to 8 (k4-10). On the other side, for *Eibesfeldtphora*, the IW analyses were completely convergent with the EW results, indicating the same three synapomorphies for the genus, even when applying different k values (k1-20).

Table 4. Results of the phylogenetic analysis using implied weighting of characters under different concavity (k) values.

K	**N° trees**	**Fit**
1	23	35.03333
2	21	26.48961
3	45	21.50357
4	325	18.16984
5	243	15.72650
10	322	9.44594
20	188	5.28347

Relations with the outgroup genera.

In all analyses (EW and IW with k1-20), we recovered the clade C*remersia* (*Neodohrniphora*, *Eibesfeldtphora*) as a sister group of *Myrmosicarius*, the Bremer support value was 3 in the EW analysis. Six characters (EW) are supporting this clade, four homoplasies (characters 6, 8, 24 and 39) and two synapormophies (characters 13 and 86), but not exclusive. Among these, the state 2 in character 13 was recovered as synapomorphic with a reversion to state 3 on *Cremersia,* also the state 1 in character 86 was recovered as synapomorphic with a reversion to state 0 on *Eibesfeldtphora*. In the IW analysis, only two characters supports this clade under k1-3 (characters 6 and 86), however under k=20 five of the six characters abovementioned support the clade (except for character 8).

Although species of *Myrmosicarius* are parasitoids of leaf-cutter ants and army ants (Disney *et al*., 2008), there are not enough sampling of *Pseudacteon* (two out of 72) and *Apocephalus* (one out of 343) species to support any inference, but by including more species such scenario could change. The same justification can be used to explain the paraphyletic *Pseudacteon* in the EW tree. In the IW trees with k1-3 *Pseudacteon* was recovered monophyletic.

In his analysis, Brown (1992) found the same topology with *Apocephalus* as a sister genera of *Pseudacteon, Myrmosicarius Cremersia* and *Neodohrniphora* (+*Eibesfeldtphora*). Except for *Cremersia* (whose developmental biology of larva unknown), these genera share the characteristic of larval development inside ant heads (Disney, 1994).

Monophyly of Neodohrniphora, Cremersia *and* Eibesfeldtphora

The monophyly of the three genera in all analyses were recovered and well supported (Figs. 54-57, 62-68, Tables 1-3), refuting Disney's (2009) hypothesis of *Cremersia* and *Neodohrniphora* synonymy, and supporting his hypothesis of *Eibesfeldtphora* raised to the genus rank. Also, we recovered *Neodohrniphora* as a well-supported sister group of *Eibesfeldtphora,* and such clade as a sister group of *Cremersia*. For this clade the Bremer support value was 4.

Five characters (EW) are supporting the clade of these three genera, one homoplasy and four synapormophies, two exclusive: the state 0 in character 1 (already discussed below the character) and, the state 2 in character 72. The evolution of these character 72 can demonstrate that the sternite eigth first was fused at the apex of the sternite seven, and the common ancestral of *Cremersia* (*Neodohniphora, Eibesfeldtpohra*) shared the internalization of this segment into segment seven. In the

IW analysis with k1-10, the same five characters appear supporting this clade, and with k=20, a sixth characters is also present (homoplasic character 26).

Ten characters (EW) are supporting clade A (*Neodohrniphora, Eibesfeldtphora*) (fig 57), six homoplasies (characters 5, 10, 16, 17, 26 and 69) and four synapormophies (characters 31, 32, 33 and 91), of these one exclusive: the state 3 in character 33. Besides this, the state 2 in character 31 was recovered as synapomorphic with a reversion to state 0 on *Eibesfeldtphora inornata*. Also the state 0 in character 91 was recovered as synapomorphic with a reversion to state 2 on *E. inornata*. For this clade the Bremer support value was 5. In the IW with k=20, there are five characters supporting clade A (homoplasic 10, 16 and 69, and synapomorphic 32 and 33).

Cremersia clades

Monophyly of clade B (*Neodohrniphora setifemur*,*Cremersia spnicosta*) (fig 58) was recovered and five characters (EW) support this clade, all homoplasies. The state 2 in character 10, in *Cremersia* only occurs in this clade, and is shared with *Neodohrniphora* and *Eibesfeldtphora*. Besides this, the other homoplasies occur differently in several species in *Cremersia*. For this clade, the Bremer support value was 1. The species *N. setifemur* was described after the synonymy of *Neodohrniphora* and *Cremersia* (Disney 2009), and, after a morphology analysis of these two species that also lacks autopormophies, we suggest synonymizing them. In the IW analyses with all k values (k1-20), only character 10 supports the clade.

Monophyly of clade C ((*Cremersia salesiana*, *C.* sp. nov.2)(*C. crassipina*, *C. pilosa*)) (Fig. 58) was recovered and five characters (EW) are supporting this clade, three homoplasies (24, 34 and 46) and two exclusive synapomorphies (26 and 32). The homoplasies occur differently in several species in *Cremersia* and in diferent genera. The synapomorphies are, the state 2 in character 26, and the state 4 in character 32. For this clade the Bremer support value was 1. In *Cremersia* only 5 species have as exclusive genus ant host *Nomamyrmex,* these four from clade C and *C. brasiliensis*. In the IW analyses with k1-3 and k20, only three of those characters support clade C (characters 26, 32 and 46), while with k4, 5 and 10, character 34 also appears.

For all clades in *Neodohrniphora* the Bremer support value was 1 in the EW analysis.

Monophyly of clades D and E (Fig. 59), was recovered and one character is supporting clade D and seven are supporting clade E. The clade D has the state 2 in character 32. All IW analyses (with all k values) are convergent and indicates character 32 as well. The clade E has only one homoplasy and six synapomorphies, of these are no exclusive synapomorphies and occur in different states in several species. Despite of the characters with Bremer support 1 in the groups, taxonomically they were important in the classification of the species.

Monophyly of clade F and G (fig 59), was recovered and one character (EW and all IW analyses) is supporting clade F and three (EW) are supporting clade G. The clade F has a synapomorphy of the state 0 in character 68 with a reversion to state 2 on *N.* sp.nov.6. Clade G has two exclusive synapomorphies, the state 0 in character 55 and the state 0 in character 58. This clade presents the species that occur in the Brazilian Atlantic forest, except for *Neodohrniphora* sp. nov. 5. All IW analyses (k1-20) recovered two characters supporting clade G (synapomorphies 56 and 58).

Monophyly of clade H (fig 59), was recovered by one homoplasic character (EW and all IW analyses) is supporting this clade, the state 0 in character 28. In chapter two they will have their synonymy properly explained.

Eibesfeldtphora clades

The evolution of the position and shape of tergite eigth (characters 71 and 74 in the EW analysis) in this clade follow the steps, firstly the ancestor had tetgite 8 internal to the sternite seven, posteriorly this change in a single piece fused to sternite seven (Clade I) and in the next clade (J) after fused, the division of this segment into lobes.

Eibesfeldtphora inornata has four autapomorphies: the state 2 in character 73, the state 2 in character 91, the state 3 in character 92, and the state 2 in character 94. For the clade *Eibesfeldtphora*, the Bremer support value was 5, in clade I was 3 and 1 in clade J.

We considered the internal genitalia morphology species *E. inornata* very different from the others *Eibesfeldtphora* species (Fig. 60, clade I). Future analyzes, could resolving the relation between species of Clade I and a evaluating of the support, and problable will elucidate if is necessary the separation of this species of the genus.

Monophyly of clade L (fig 60) was recovered and four homoplasies (EW) are supporting clade L. The state 2 in character 75, the state 2 in character 77, the state 1 in character 81, and the state 0 in character 84. Bremer support value was 1. In the IW analyses, the different k values varies in the number of characters supporting clade L. With k1-5, characters 79 and 81 support the clade, and with k10-20, only character 75 is present. These species have in common the host *Atta sexdens*.

New classification proposal

Neodohrniphora Malloch, 1914 (11)
N. acromyrmecis Borgmeier, 1925
N. calverti Malloch 1914 [Type species]
N. cognata Prado. 1976
N. wasmanni Borgmeier
N. sp nov. 1
N. sp nov. 2
N. sp nov. 3
N. sp nov. 4
N. sp nov. 5
N. sp nov. 6
N. sp nov. 7
Cremersia Schmitz 1924 **stat. reval. comb. nov**. (24 species)

C. adunca (Borgmeier) 1961 **stat. reval. comb. nov**
C. australis (Borgmeier) 1928 **stat. reval. comb. nov**
C. brasiliensis (Borgmeier) 1928 **stat. reval. comb. nov**
C. coecum (Greene) 1938 **stat. reval. comb. nov.**
C. costalis (Borgmeier) 1925 **stat. reval. comb. nov**
C. crassicostalis (Disney) 2008 **stat. reval. comb. nov**
C. crassispina (Borgmeier) 1928 **stat. reval. comb. nov**
C. longipes (Borgmeier) 1971 **stat. reval. comb. nov**
C. pernambucana (Borgmeier) 1925 **stat. reval. comb. nov**
C. pilipes (Borgmeier) 1961 **stat. reval. comb. nov**

C. pilosa (Borgmeier) 1928 **stat. reval. comb. nov**

C. salesiana (Borgmeier) 1928 **stat. reval. comb. nov**

C. setitarsus (Borgmeier) 1971 **stat. reval. comb. nov**

C. spinicauda (Borgmeier) 1961 **stat. reval. comb. nov**

C. spinicosta (Malloch) 1912 **stat. reval. comb. nov**

C. spinosissima (Borgmeier) 1925 **stat. reval. comb. nov**

C. zikani (Schmitz) 1924 [Type species] **stat. reval. comb. nov**

C. sp. nov 1

C. sp. nov 2

C. sp. nov 3

C. sp. nov 4

C. sp. nov 6

C. sp. nov 7

C. sp. nov 10

Eibesfeldtphora Disney 2009 (21 species)

E. arcuata (Brown) 2001

E. attae (Disney) 1996

E. bragancai (Brown) 2001

E. breviloba Brown 2012

E. cumsaltensis Disney 2009

E. curvinervis (Malloch) 1914 [Type species]

E. declinata (Brown) 2001

E. digitata Brown 2012

E. dissita (Brown) 2001

E. elongata (Brown) 2001

E. erthali (Brown) 2001

E. inferna (Brown) 2001

E. inornata Uribe & Brown 2014

E. isomorpha (Brown) 2001

E. leei (Brown) 2001

E. mexicanae (Disney) 1996

E. pala (Brown) 2001

E. prolixa (Brown) 2001

E. tonhascai (Brown) 2001
E. trifurcata Uribe & Brown 2014
E. trilobata Disney 2009

Host associations

The cophylogenetic analysis was done at the generic level, since no resolution was found in clades of *Cremersia* and *Eibesfeldtphora*. ParaFit provided significant support for congruence between host–parasite topologies, rejecting the global null hypothesis (P = 0.000001; Table 5). However, it is important to note that only the individual links between *Cremersia* and its hosts contributed significantly to the global test. Furthermore, *Cremersia* contains three of the five links present in the analysis. Based on the small number of hosts, parasites, and individual links, as well as the presence of associations concentrated in only one terminal, we may be dealing with a type I error because of lack of power (Legendre *et al.*, 2002).

Although we must carefully interpret the result obtained by the ParaFit analysis, the examination of the tanglegram (Fig. 61, 55) can help clarify the association between the groups. At first glance, due to the sampling disparity between the two topologies, the tanglegram may not appear to show any obvious congruence between topologies. However, some enlightenment can be obtained by grouping ant genera into subfamilies. In this way, *Cremersia* (parasite of *Labidus*, *Neivamyrmex and Nomamyrmex*) is restricted to Dorylinae, whereas *Neodohrniphora* and *Eibesfeldtphora* (parasites of *Acromyrmex* and *Atta*, respectively) are restricted to Myrmicinae. Combining the subfamilies into clades, the host tree can be divided into two main clades: 1) (((Pseudomyrmicinae, Myrmeciinae),(Dolichoderinae, Aneuretinae)) Dorylinae) in which *Cremersia* is restricted; and 2) (((Ectatomminae, Heteroponerinae) Myrmicinae) Formicinae) in which *Neodohrniphora* and *Eibesfeldtphora* are restricted. If we assume that associations above the species level can represent deeper evolutionary history (Segraves, 2010), we can speculate from the association pattern found that the evolutionary history of the two groups may not be independent.

In a study about another group of ant parasites, Murray *et al.* (2013) used tree reconciliation and event-based reconstruction to obtain an association hypothesis between the wasp family Eucharitida and its ant hosts. As we did in the present study, they reduced the datasets of ants and eucharitids down to the generic level to perform the analysis. They found that host-parasite evolutionary histories were more similar than expected at random, and that host–parasitoid relationships at the subfamily and generic level showed a conserved pattern of host use within major clades of the wasp family. On the other hand, Eucharitidae exhibit a general trend of ant subfamily host-switching at an early time period, followed by high host conservatism at the ant-subfamily level in extant lineages. According to Murray *et al.* (2013), the results suggest that the host use may not be determined by the host phylogeny, but by ecological constraints, while the host switches by ecological fitting. Our findings present some similarities with those described by Murray *et al.* (2013), as the conserved pattern of host use above the species level, which makes us wonder if there could be any agreement between the history of the two groups of ant parasites. However, this needs to be assessed in light of biogeographic patterns, the timing of key evolutionary events, and the co-phylogeny reconstruction of both at the species level and in a more comprehensive way, contemplating all Phoridae genera that parasitize ants.

Table 5. ParaFit tests including three Phoridae genera and ants hosts. Probabilities were computed after 100000 random permutations. Global tests and individual associations with $P < 0.05$ are shown in bold. The ParaFit test is based on topology of the trees.

Parasite	Host	*p-value*
Cremersia	*Nomamyrmex*	**9.9999E-06**
Cremersia	*Labidus*	**9.9999E-06**
Cremersia	*Neivamyrmex*	**9.9999E-06**
Eibesfeldtphora	*Atta*	0.0992
Neodohrniphora	*Acromyrmex*	0.1001
Global Test		**9.9999E-06**

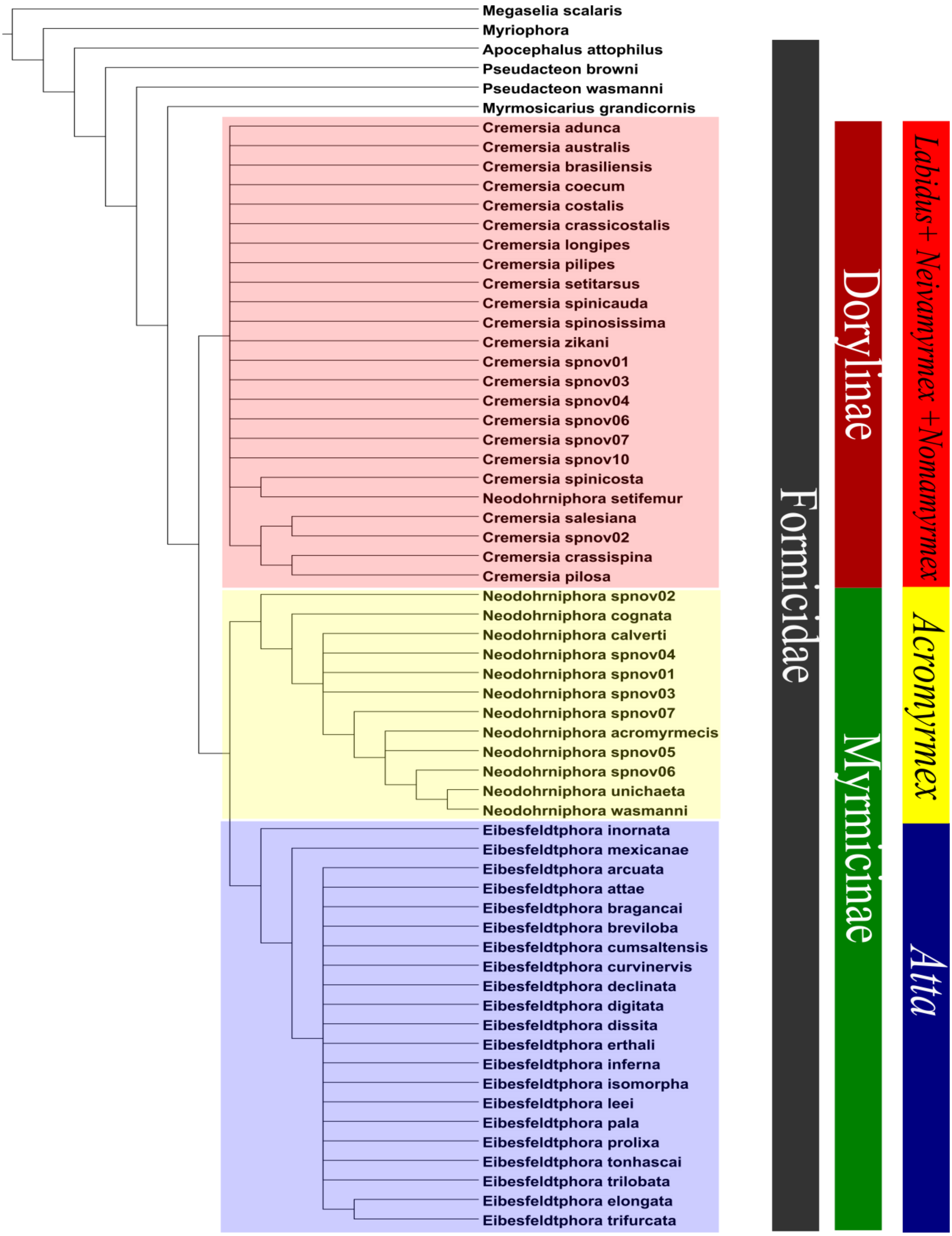


Fig 55. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Bremer support values above the clades. Relation of the parasitoids (tree) with the hosts (gray, red, yellow, green to blue rectangles)

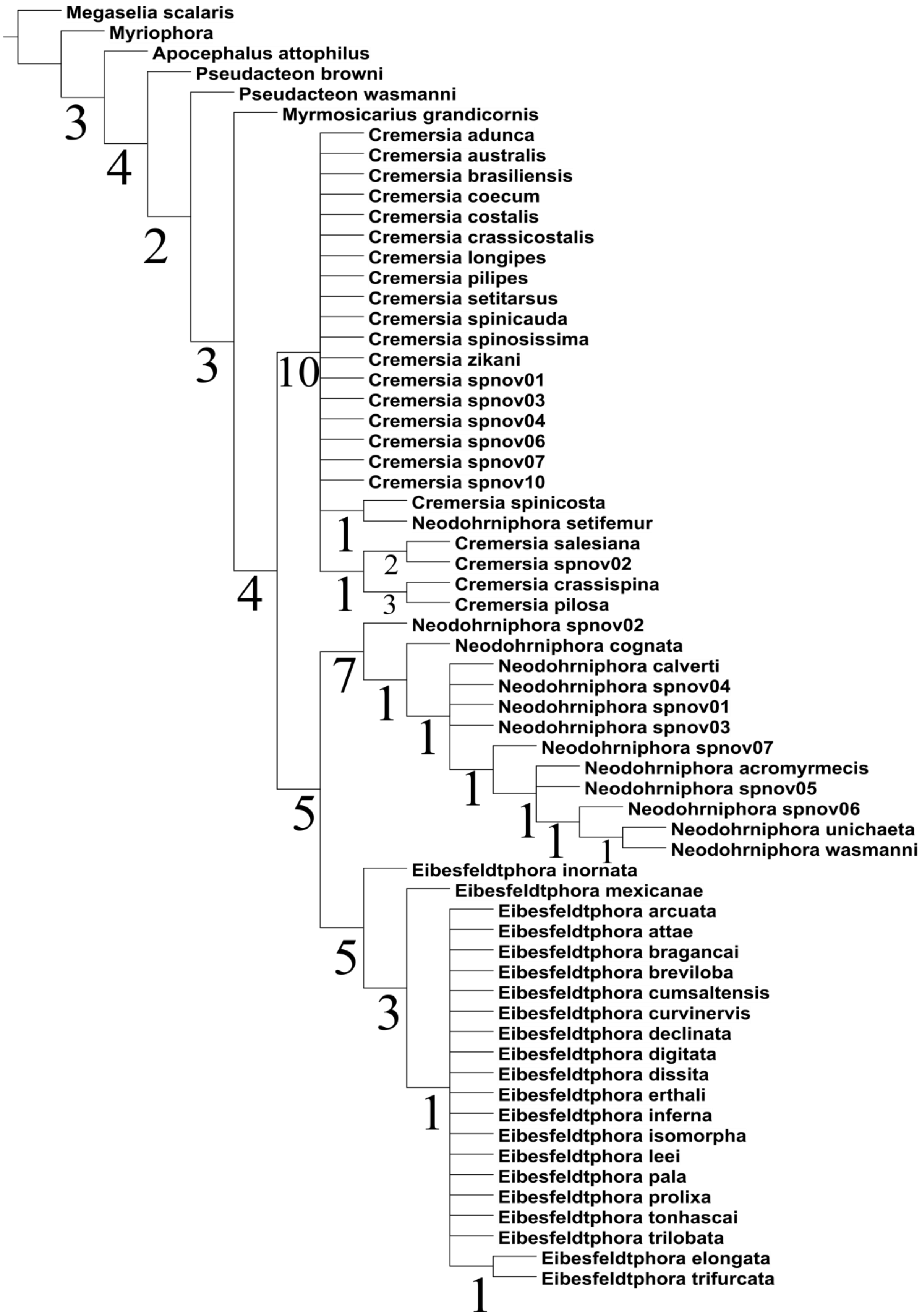


Fig 56. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Bremer support values above the clades.

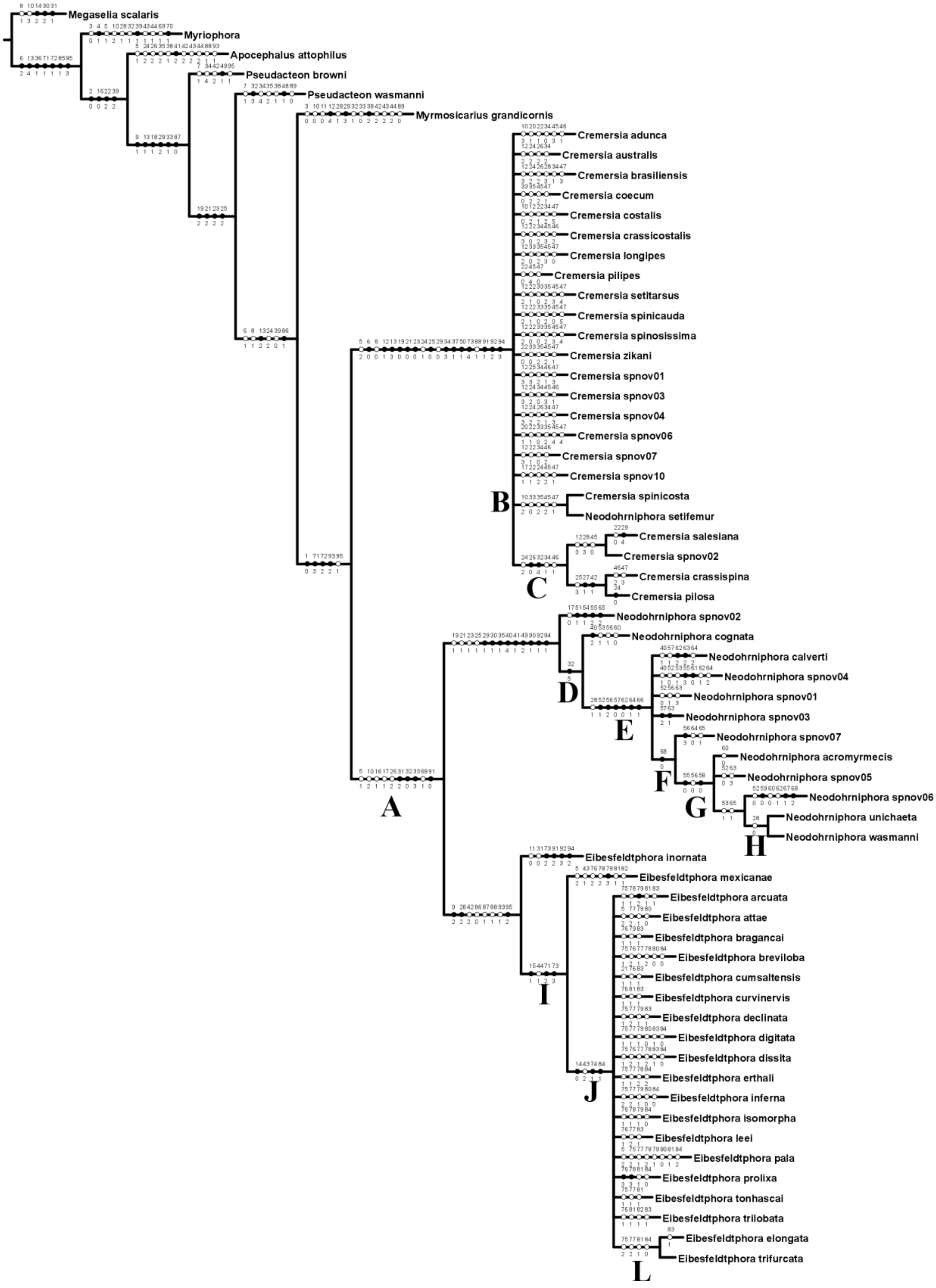


Fig 57. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black synapomorphies. Letters below the clade are for explaining results.

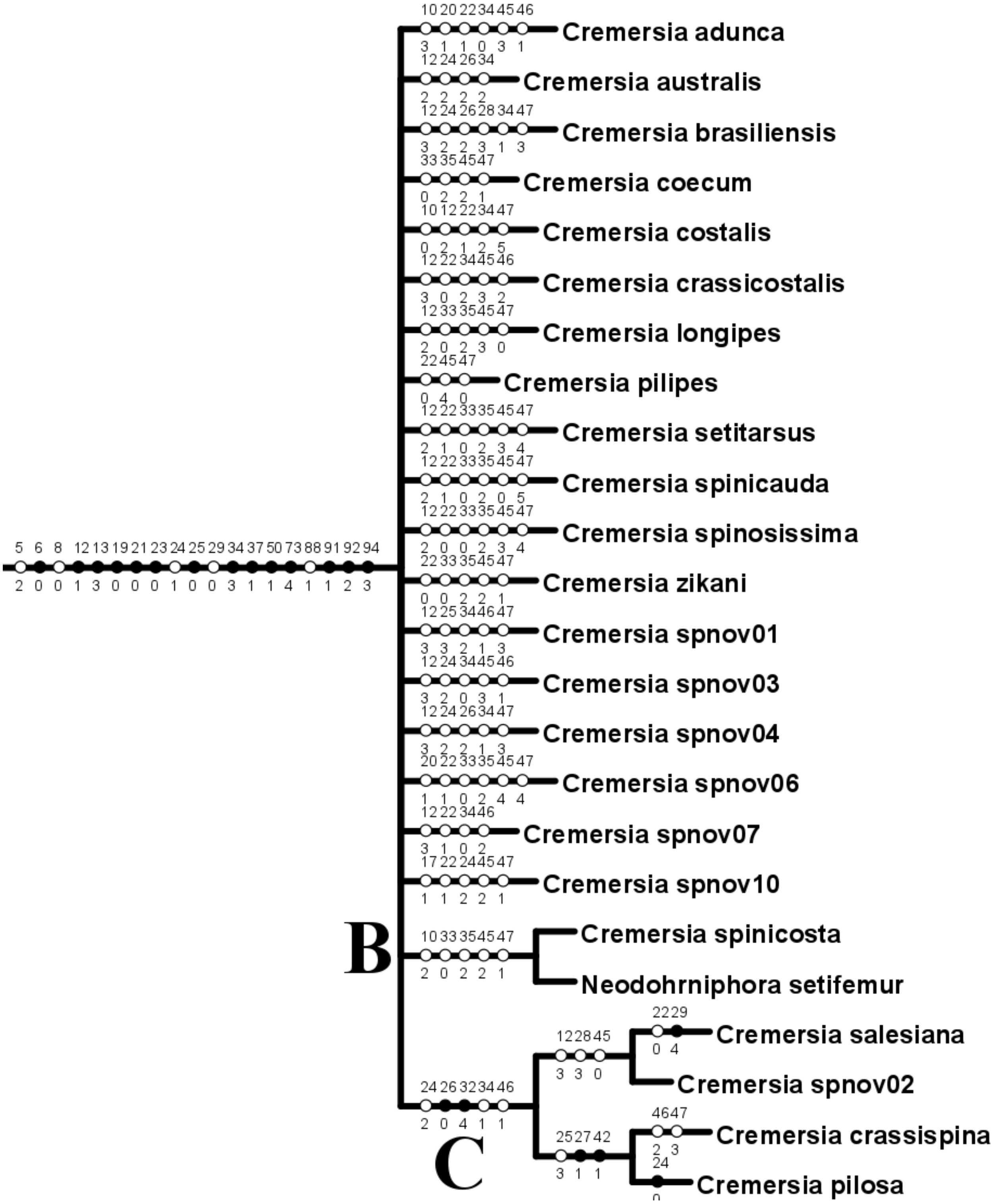


Fig 58. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Numbers above the clade refer to the character, numbers below the clade refer to the state of the character, white circles homoplasy and black circles synapomorphies. Letters below the clade are for explaining results.

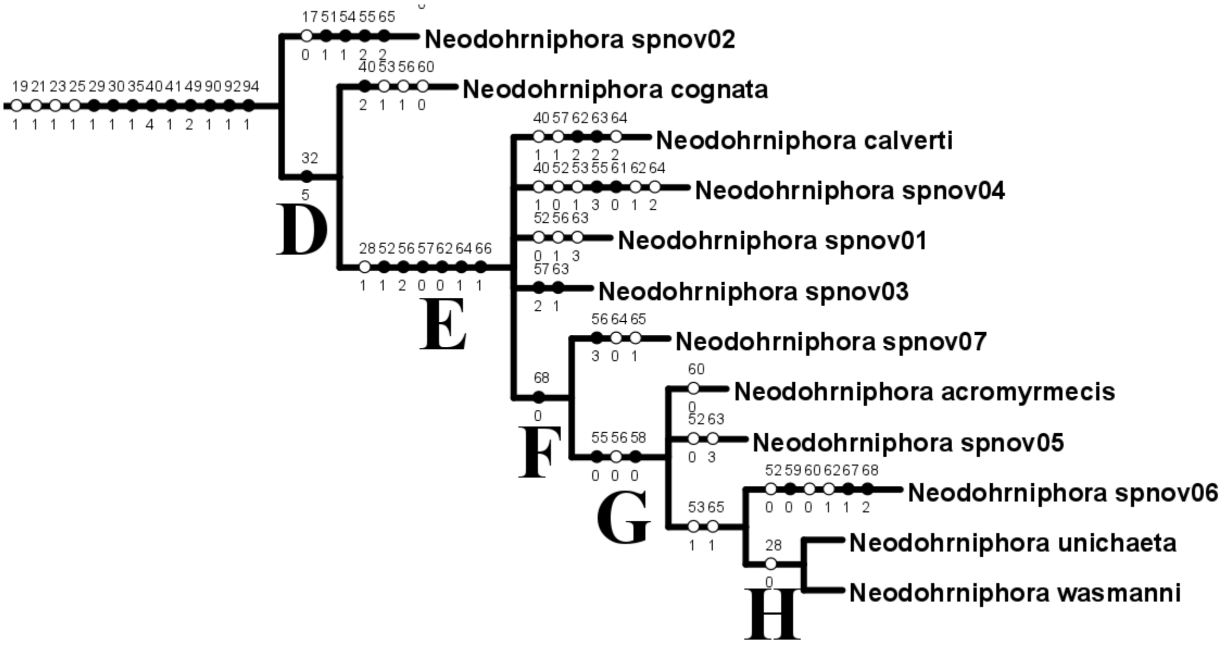


Fig 59. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies. Letters below the clade are for explaining the results.

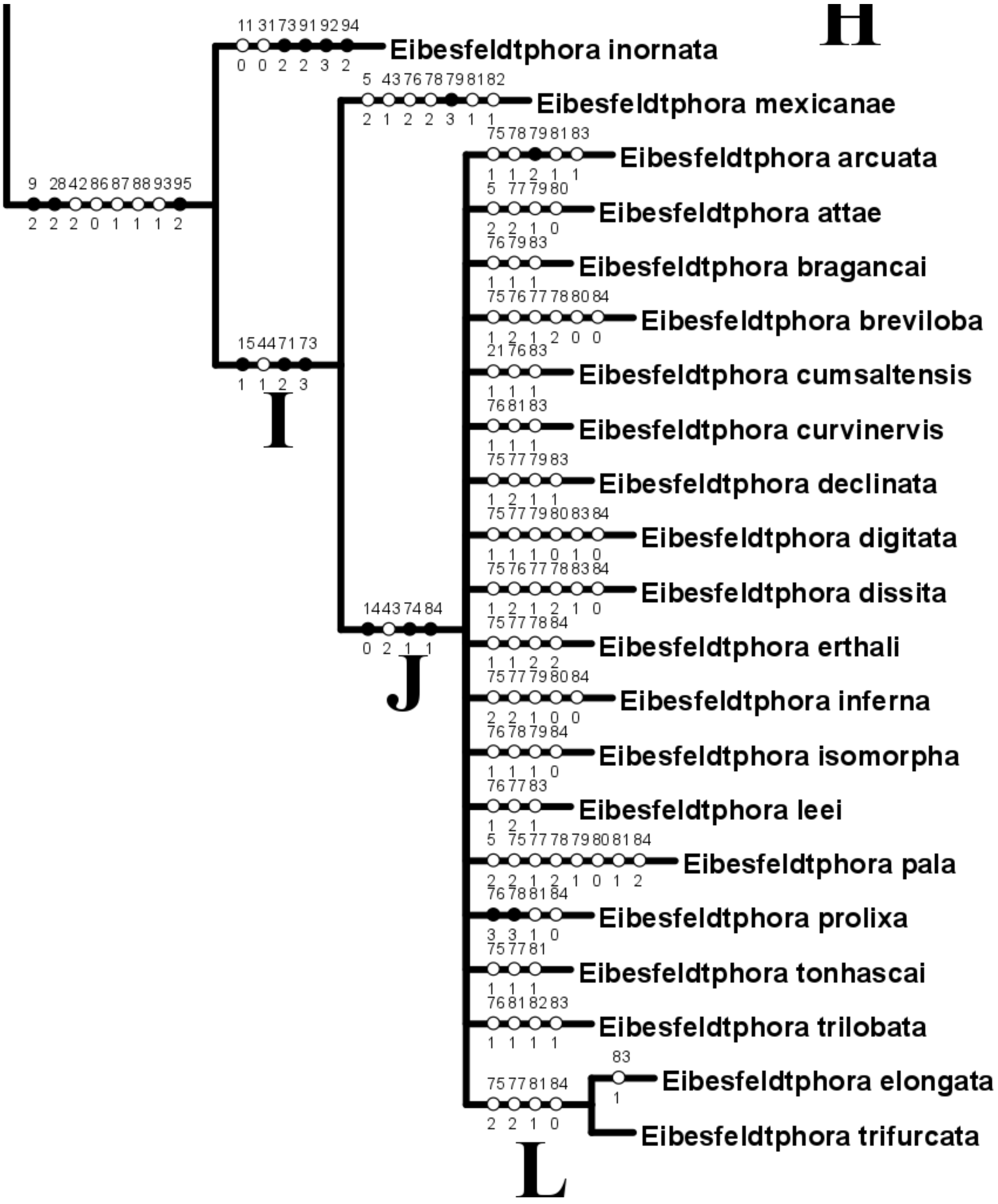


Fig 60. Tree based on strict consensus cladogram of the 902 most parsimonious trees. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies. Letters below the clade are for explaining the results

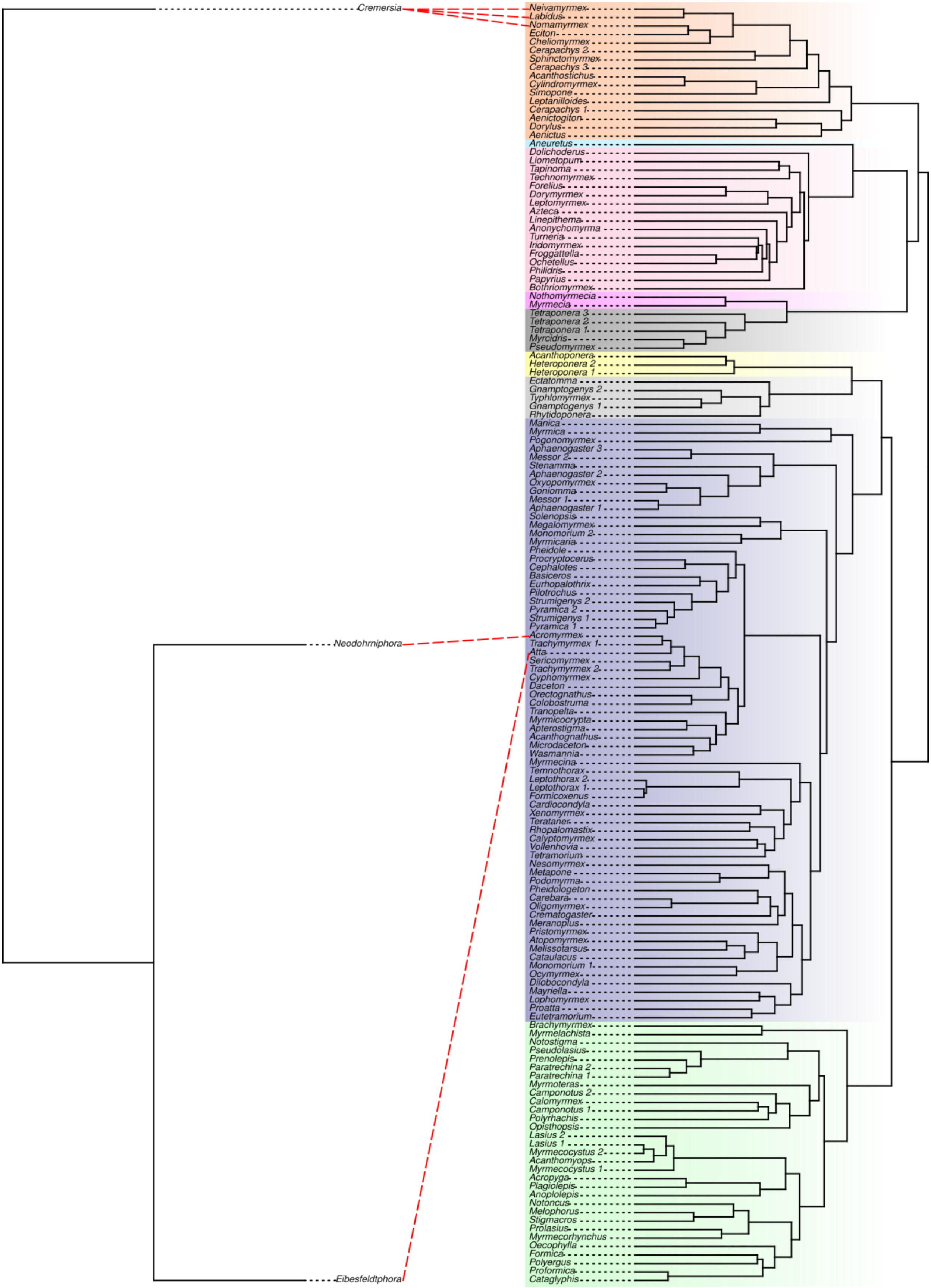


Fig 61. Tanglegram shows the genera phylogeny of the parasitoids relative to the genera phylogeny of the ants. Highlighted in orange = Dorylinae and blue = Myrmicinae

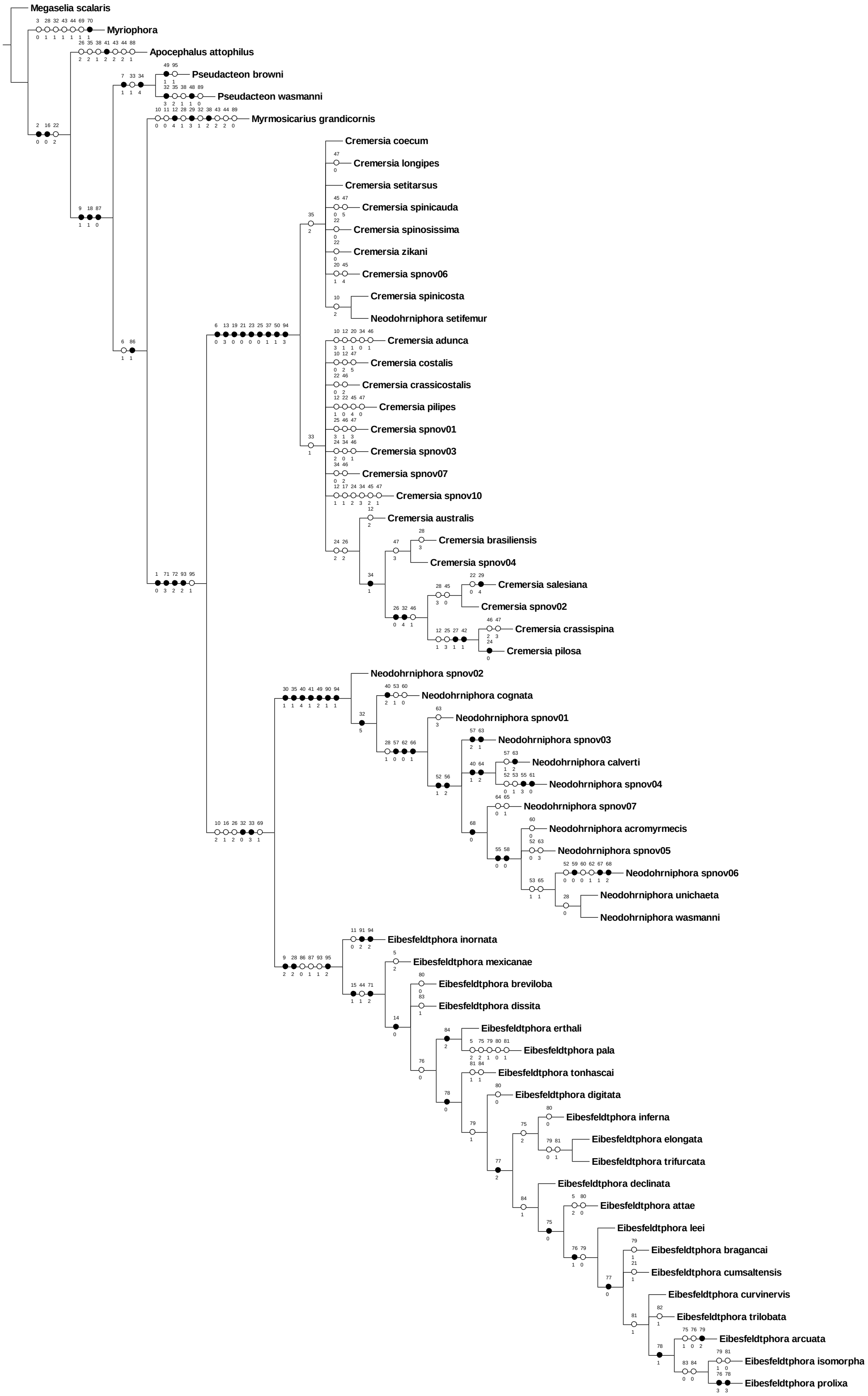


Fig 62. Tree based on strict consensus cladogram of the 23 most parsimonious trees. IW, K=1 Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

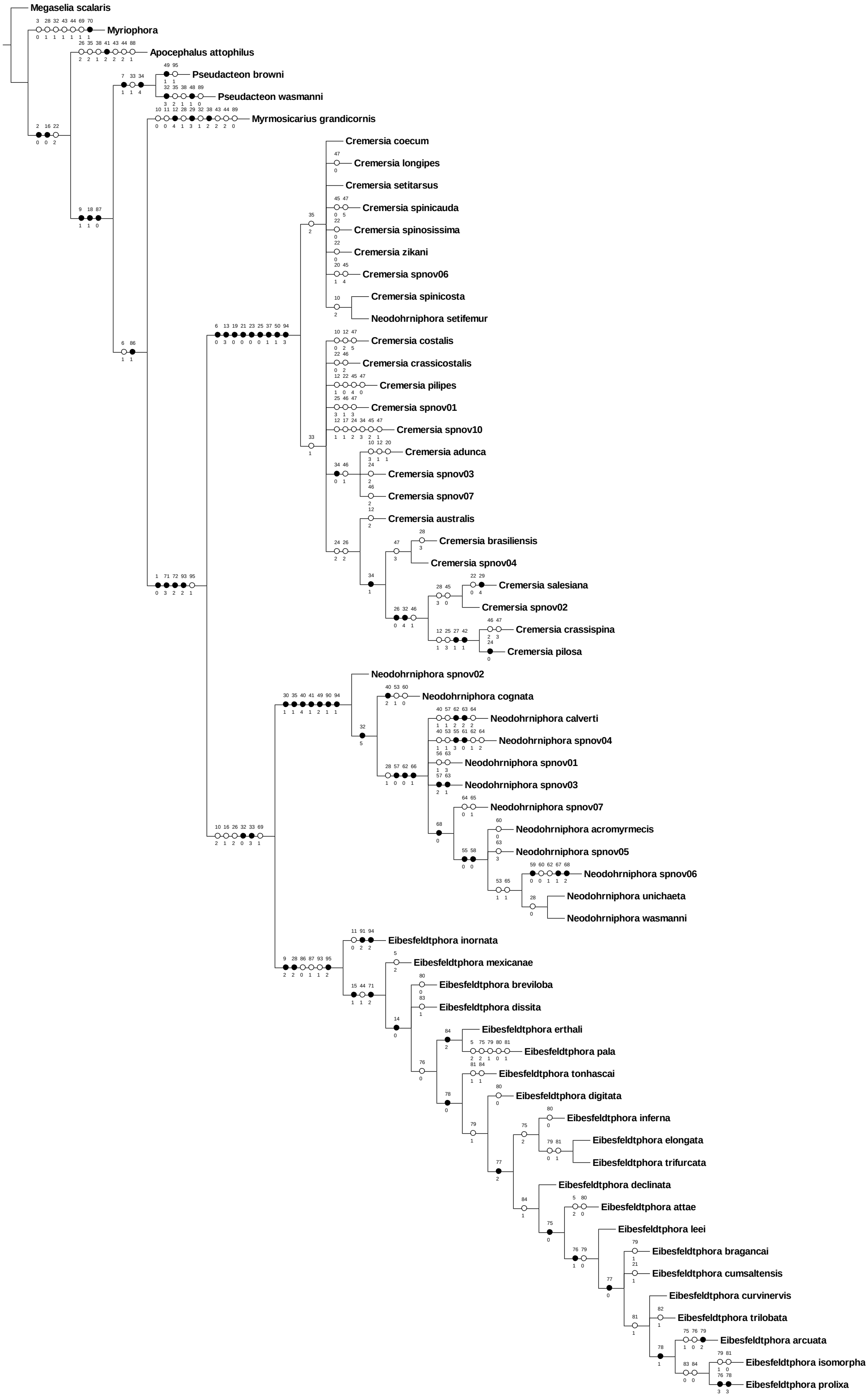


Fig 63. Tree based on strict consensus cladogram of the 21 most parsimonious trees. IW, K=2. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

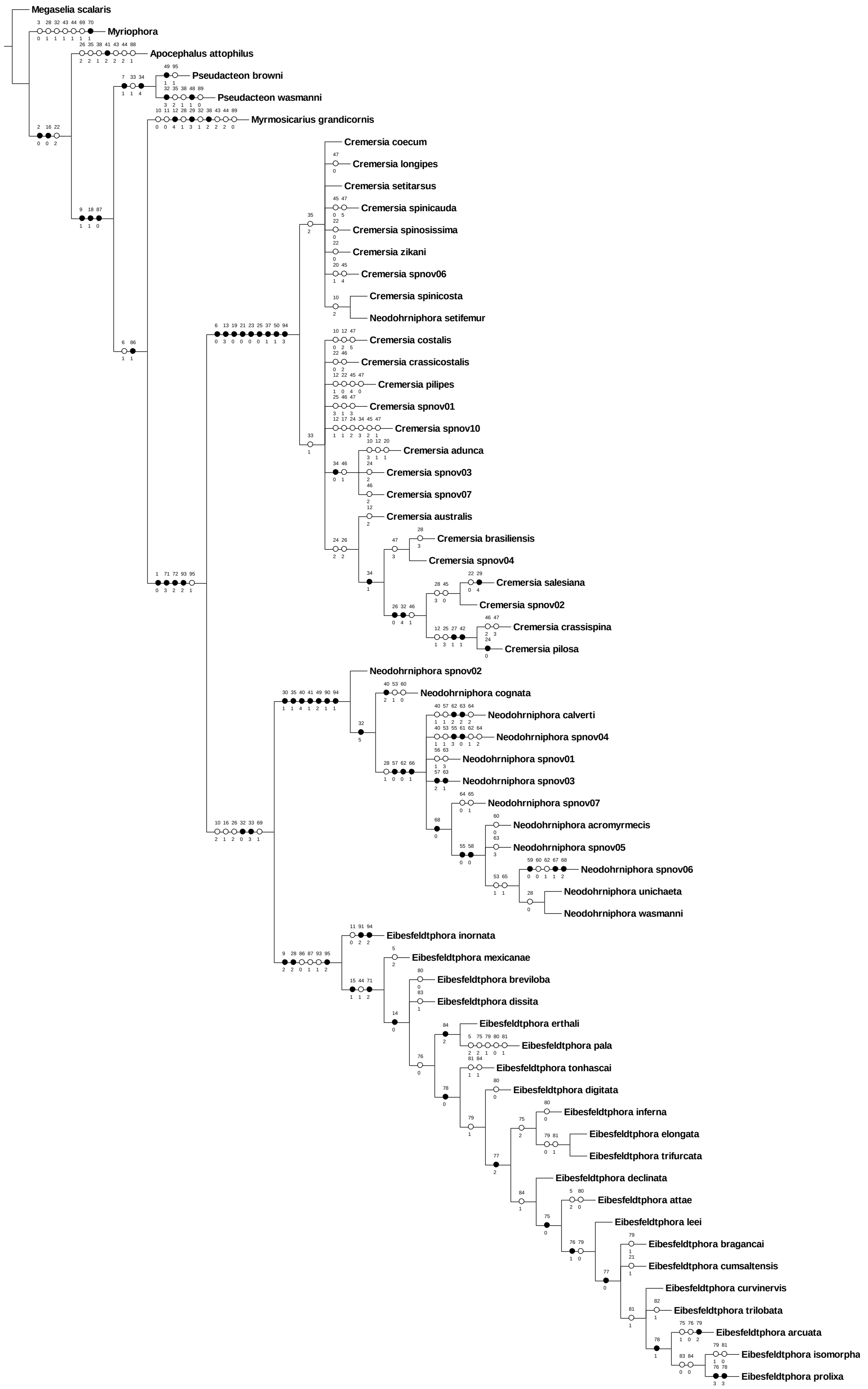


Fig 64. Tree based on strict consensus cladogram of the 45 most parsimonious trees. IW, K=3. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

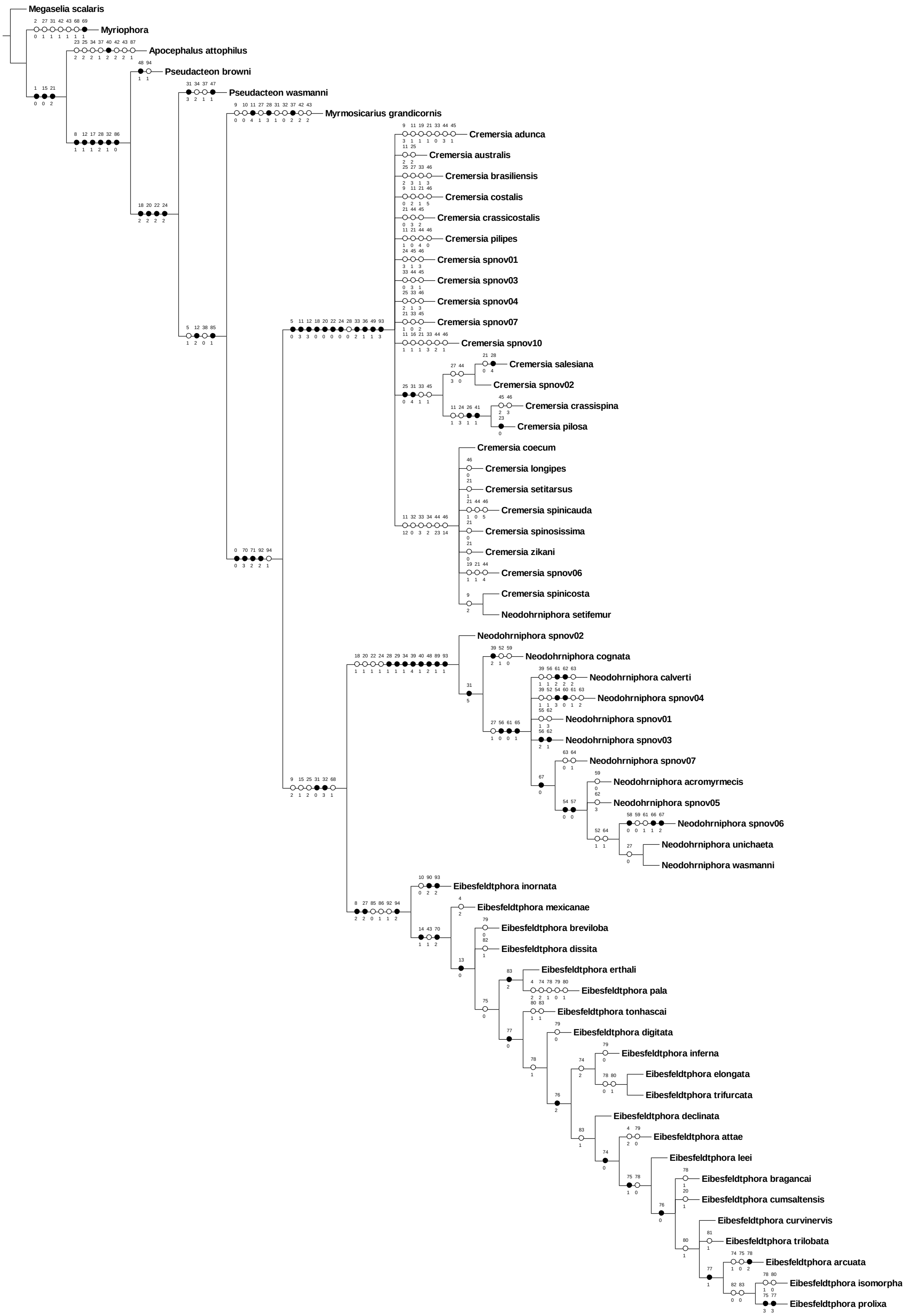


Fig 65. Tree based on strict consensus cladogram of the 325 most parsimonious trees. IW, K=4. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

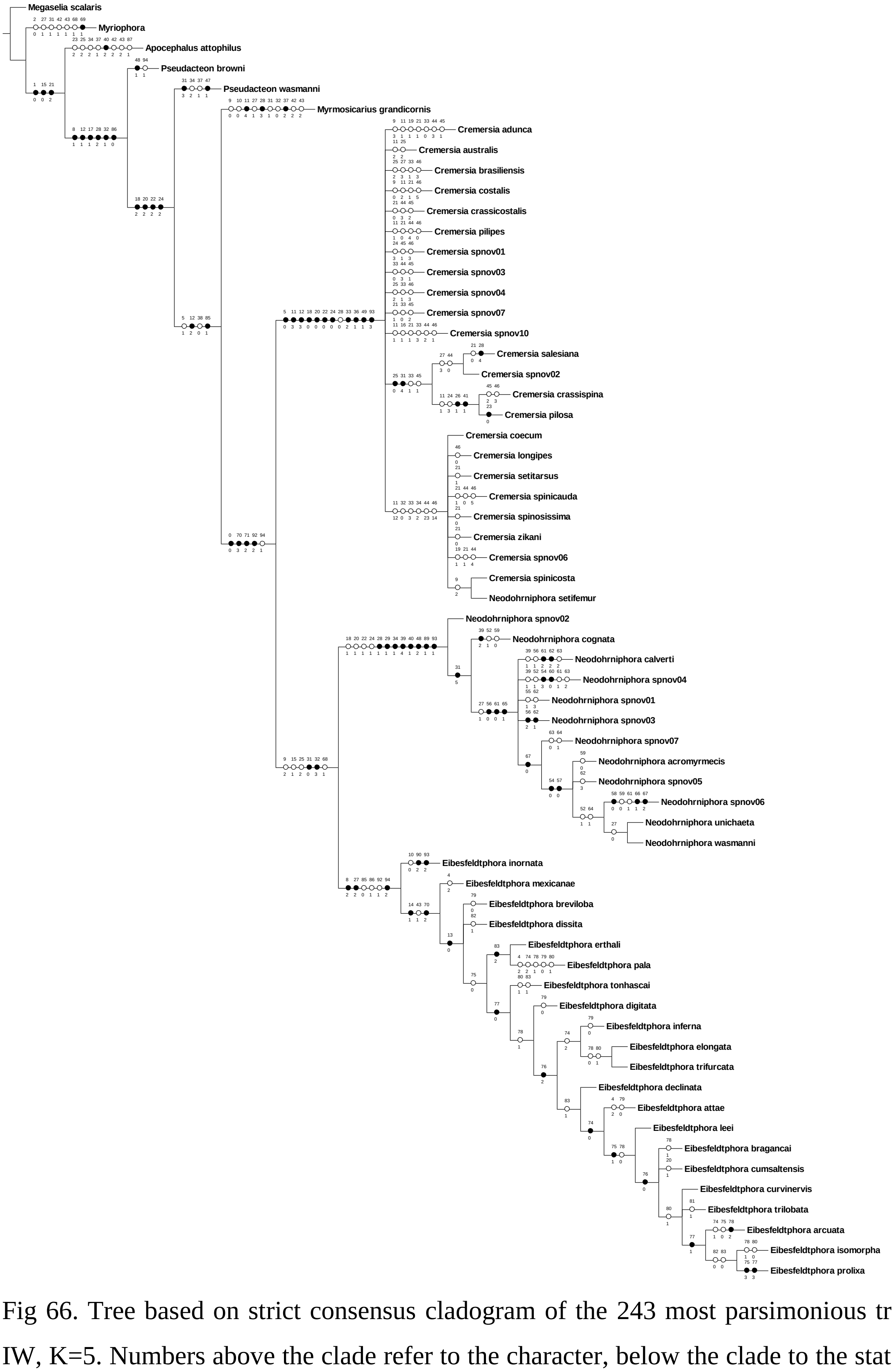


Fig 66. Tree based on strict consensus cladogram of the 243 most parsimonious trees. IW, K=5. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

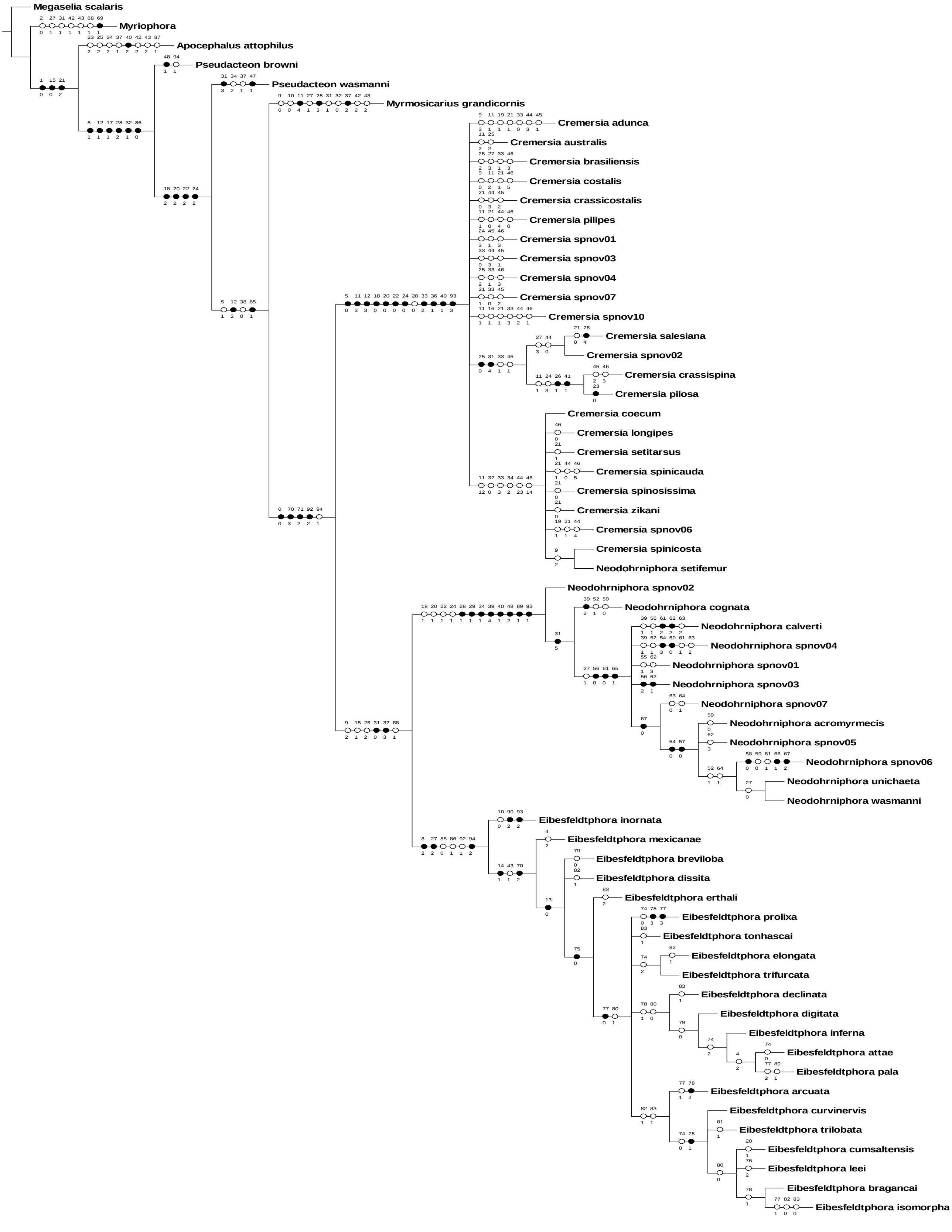


Fig 67. Tree based on strict consensus cladogram of the 322 most parsimonious trees. IW, K=10. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

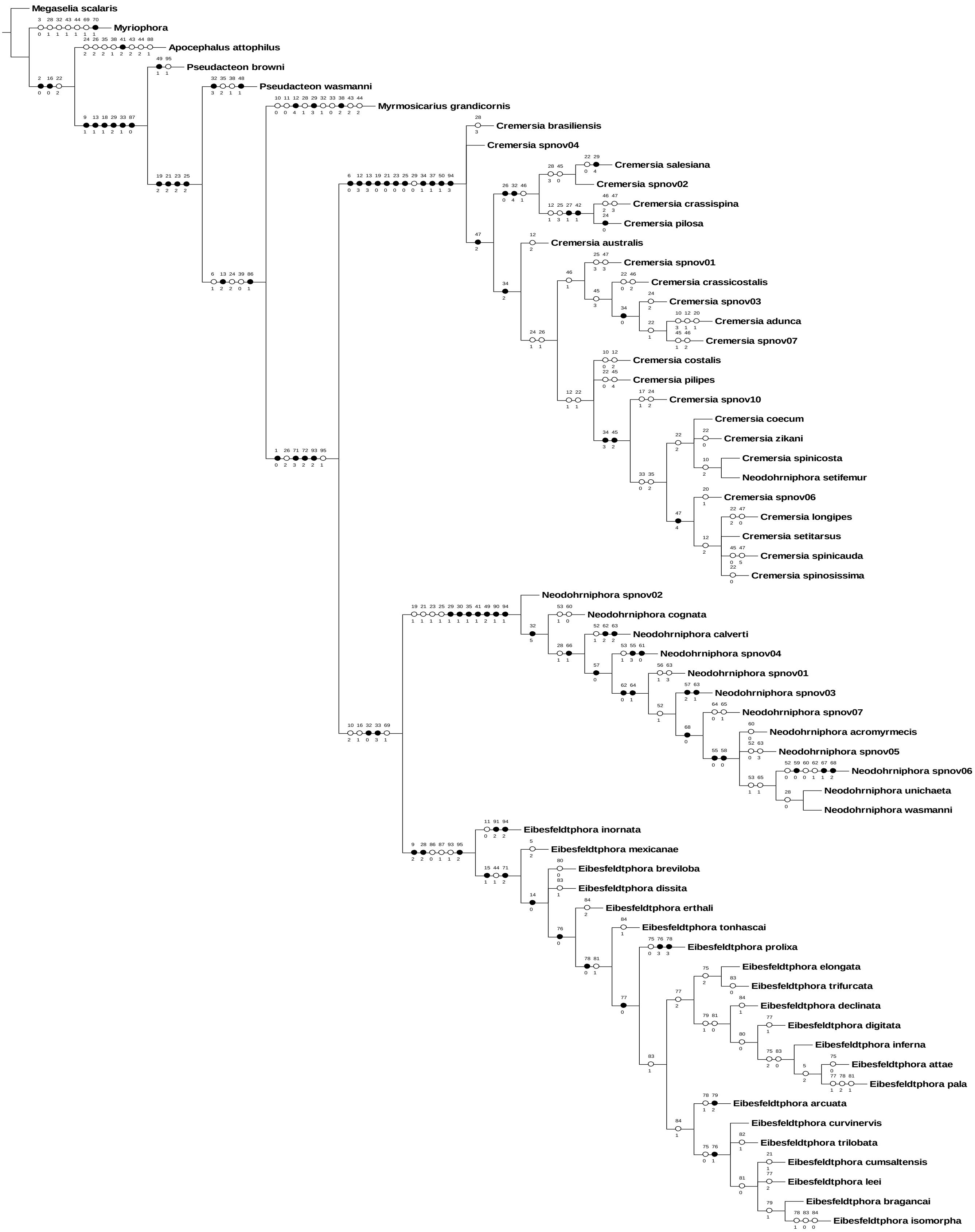


Fig 68. Tree based on strict consensus cladogram of the 188 most parsimonious trees. IW, K=20. Numbers above the clade refer to the character, below the clade to the state of the character, white circles homoplasy and black circles synapomorphies.

Conclusions

Cladistic analysis often result in trees with good support of synapomorphic and homoplastic characters, allowing more sophisticated hypotheses to be proposed based on these results. When compared to inferences made by empirical analysis, but with intuitive groupings without an objective and robust methodology, this study allowed a basis for taxonomic decisions and classification of the studied genera. The genera *Neodohrniphora*, *Cremersia* and *Eibesfeldtphora* were recovered as monophyletic and valid genera, rejecting earlier proposal of Disney *et al.* (2009) synonymizing *Cremersia* and *Neodohrniphora*. A new classification proposal is proposed here and recognized these three as valid genera. Furthermore, adding more species of *Pseudacteon* and *Apocephalus*, and other genera of parasitoids (Brown, 1992) could further clarify the relations between the genera of the *Apocephalus* Group.

This work was an important in the comparative understanding and a detailed analysis of parasitoid phorids' female genitalia structures. Significant progress has been made towards the understanding and proposal of homologies for the female terminalia of Phoridae based on careful examining of *Neodohrniphora*, *Cremersia* and *Eibesfeldtphora* herein.

Another barrier to be overcome in the future is with regard to males, a detailed study integrating morphology, molecular and morphometry probably will illuminate the uncertainties that exist about couples' pairing. After that, new steps can be taken in the study and use of males to obtain characters for phylogeny.

References

Ament, D. C. (2017). Phylogeny of Phorinae sensu latu (Diptera: Phoridae) inferred from a morphological analysis with comprehensive taxon sampling and an uncommon method of character coding. *Zoological Journal of the Linnean Society*, *181*(1), 151-188.

Ament, D.C & Pereira, T.P.L. 2019. Phoridae *In: Catálogo Taxonômico da Fauna do Brasil*. PNUD. Available in: <http://fauna.jbrj.gov.br/fauna/faunadobrasil/183530>. Accessed in: January/2019

Amorim, D.S. (2002) *Fundamentos de sistemática filogenética*, 2nd Edition. Holos, Ribeirão Preto.

Borgmeier, T. 1925. Novos subsidios para o conhecimento da familia Phoridae. *Archivos do Museu Nacional do Rio de Janeiro,* 25, 85–281, pls. I–X4I.

Borgmeier, T. 1928. Investigacoes sobre Phorideos Myrmecophilos (Diptera-Phoridae). *Archivos do Instituto Biologico de Defesa Agricola e Animal São Paulo,* 1, 159–192.

Borgmeier, T. 1961. Weitere Beitraege zur Kenntnis der neotropischen Phoriden, nebst Beschreibung einiger *Dohrniphora*–Arten aus der indo–australischen Region (Diptera, Phoridae). *Studia Entomologica*, 4, 1–112.

Borgmeier, T. 1963. Revision of the North American Phorid Flies. Part 1. (Dipt. Phoridae). *Studia Entomologica,* 6, 1–256.

Borgmeier, T. 1971. Further studies on phorid flies, mainly of the Neotropical Region (Diptera, Phoridae). *Studia Entomologica*, 14, 1–172.

Bremer, K. R. (1994). Branch support and tree stability. Cladistics, 10(3), 295-304.

Brown, B.V. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea). *Memoirs of the Entomological Society of Canada*, 164, 1–144.

Brown, B.V. 2001. Taxonomic revision of *Neodohrniphora*, subgenus *Eibesfeldtphora* (Diptera: Phoridae). *Insect Systematics Evolution*, 32 (4), 393–409. http://dx.doi.org/10.1163/187631201x00272

Brown, B.V. 2004. Revision of the subgenus *Udamochiras* of *Melaloncha* bee–killing flies (Diptera: Phoridae: Metopininae). *Zoological Journal of the Linnean Society*, *140*(1), 1–42.

Brown, B.V. 2010. Phoridae. 725–761. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M. & Zumbado, M.A. (Eds.): *Manual of Central American Diptera*, *Volume 1,* NRC Research Press, Ottawa, Canada, 729 pp.

Brown, B.V., Braganca, M.A.L., Gomes, D.S., Queiroz, J.M. & Teixeira, M.C. 2012. Parasitoid phorid flies (Diptera: Phoridae) from the threatened leafcutter ant Atta robusta Borgmeier (Hymenoptera: Formicidae). *Zootaxa,* 3385, 33–38.

Brown, B. V., Souza Amorim, D., & Kung, G. A. 2015. New morphological characters for classifying Phoridae (Diptera) from the structure of the thorax. *Zoological Journal of the Linnean Society,* 173(2), 424-485.

Cumming, J.M & Wood, D.M. (2017) 3. Adult Morphology and Terminology. *In*: Kirk–Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. *Volume 1. Introductory chapters and keys to Diptera families*. Suricata 4. SANBI Graphics & Editing, Pretoria, pp. 69–88.

Disney, R.H.L. 1994. *Scuttle flies: the Phoridae*. Chapman and Hall, London, xii + 467 pp.

Disney, R.H.L. 1996. A key to *Neodohrniphora* (Diptera: Phoridae), parasites of leaf–cutter ants (Hymenoptera: Formicidae). *Journal of Natural History*, 30(9), 1377–1389.

Disney, R. H. L. Unusual costal chaetotaxy in the phylogenetically interesting Ironomyiidae and Sciadoceridae (Diptera). In: **Annales Entomologici Fennici.** p. 19-20. 1988.

Disney, R.H.L. 2007. New species and revisionary notes on scuttle flies (Diptera: Phoridae) associated with Neotropical army ants (Hymenoptera: Formicidae). *Sociobiology*, 49 (3), 1–58.

Disney, R. H. L. & Franquinho Aguiar, A. M. 2008. Scuttle flies (Diptera: Phoridae) of Madeira. *Fragm. Faun. Warsaw*. 51: 23-62.

Disney, R.H.L., Elizalde, L. & Folgarait, P.J. 2009. New species and new records of scuttle flies (Diptera: Phoridae) that parasitize leaf–cutter and army ants (Hymenoptera: Formicidae). *Sociobiology*, 5 (2), 601–632.

Farris, J.S., 1970. Methods for computing Wagner trees. *Systematic Zool*ogy, 19, 83–92

Forey, P.L. & Kitching, I.J. (2000) Experiments in coding multi–state characters. *Homology and Systematics: Coding Characters for Phylogenetic Systematics* (ed by R. Scotland & R. T. Pennington), pp. 54 –80. New York, Taylor & Francis.

Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–91.

Goloboff, P. A. (1997). Self-weighted optimization: tree searches and character state reconstructions under implied transformation costs. *Cladistics*, 13(3), 225-245

Goloboff, P.A.; Farris, S. & Nixon, K. (2008a) TNT, a free program of phylogenetic analyses. *Cladistics*, 24, 774–786.

Goloboff, P. A., Carpenter, J. M., Arias, J. S., & Esquivel, D. R. M. (2008b). Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, 24(5), 758-773.

Hash, John Mark. *Systematics and Natural History of the Millipede-Parasitic Genus Myriophora Brown (Diptera: Phoridae*). University of California, Riverside, 2015.

Kehlmaier, C., Assmann, T. (2008). The European species of Chalarus Walker, 1834 revisited (Diptera: Pipunculidae).*Zootaxa,1936*, 1-39.

Kotrba, M. Morphology and terminology of the female postabdomen. *Contributions to a Manual of Palaeartic Diptera (with special reference to flies of economic importance),* v. 1, p. 75-84, 2000.

Legendre, P., Desdevises, Y., & Bazin, E. (2002). A statistical test for host–parasite coevolution. *Systematic biology*, *51*(2), 217-234

Maddison, W.P. & D.R. *Maddison. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04* (available in: http://mesquiteproject.org).

Malloch, J.R. 1914. Costa Rican Diptera collected by Philip P. Calvert, Paper I. A partial report on the Borboridae, Phoridae and Agromyzidae, by J. R. Malloch. *Transactions of the American Entomological Society*, 40, 8–36, 1 plate. [1914.03.23].

Moreau, C.S. & Bell, C.D. 2013. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, *67*(8), 2240-2257.

Murray, E. A., Carmichael, A. E., & Heraty, J. M. (2013). Ancient host shifts followed by host conservatism in a group of ant parasitoids. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1759), 20130495.

Nakayama, H. (2007). Systematic and morphological studies of the genus Chaetopleurophora Schmitz (Diptera: Phoridae) occurring in Japan. *Entomological science*, 10(4), 395-406.

Nixon, K.C. 2002. *WinClada, version 1.00.08*. Program and distribution by author, Cornell University, Ithaca, New York.

Nixon, K.C. & Carpenter, J.M. (1993) On outgroups. *Cladistics*, 9, 413–426.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289-290.

Paradis, E., & Schliep, K. (2018). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*. https://doi.org/10.1093/bioinformatics/bty633

PCAT – Phorid Catalog – Online data for phorid flies. Available in: < http://www.phorid.net/pcat/> Accessed in: January/2019

Powell, S. & Clark, E. (2004). Combat between large derived societies: a subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insectes Sociaux*, *51*(4), 342–351.

Popescu, A.A., Huber, K.T. & Paradis, E. (2012). ape 3.0: New tools for distance-based phylogenetics and evolutionary analysis in R. *Bioinformatics*, *28*(11), 1536-1537

Porter, S. D. (1998). Biology and behavior of Pseudacteon decapitating flies (Diptera: Phoridae) that parasitize Solenopsis fire ants (Hymenoptera: Formicidae).*Florida Entomologist*, 292-309.

Prado, A.P. do. 1976. Records and descriptions of phorid flies, mainly of the Neotropical Region (Diptera; Phoridae). *Studia Entomologica*, Petropolis, 19, 561–609."

Revell, L. J. (2012), phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3: 217–223. doi:10.1111/j.2041-210X.2011.00169.x

Schmitz, H. 1927. Revision der Phoridengattungen, mit Beschreibung neuer Gattungen und Arten. *Natuurhistorisch maandblad*. 16: 30–40., 45–50, 59–65, 72–79, 92–100, 110–116, 128–132, 142–148, 164, 176, figs.

Segraves, K.A. Evo Edu Outreach (2010) 3: 62. https://doi.org/10.1007/s12052-009-0199-z

Sereno, P.C. (2007) Logical basis for morphological characters in phylogenetics. *Cladistics*, **23**, 565–587.

Swofford, D.L. & Maddison, W.P. 1987. Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci*., 87, 199– 229.

Uribe, S., Brown, B.V., Braganca, M.A., Queiroz, J.M. & Nogueira, C.A. 2014. New species of *Eibesfeldtphora* Disney (Diptera: Phoridae) and a new key to the genus. *Zootaxa*, 3814(3), 443–450.

Appendix

Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Megaselia scalaris	1	1	1	0	0	1	0	1	0	3	1	0	0	2	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	2	1	2	0	5	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	0
Myriophora	1	1	0	1	1	2	0	0	0	2	1	0	4	1	0	1	0	0	1	0	1	1	1	1	1	1	0	1	0	0	0	1	0	5	0	1	0	0	1	3	0	0	1	1	-	-	-	0	0	0
Apocephalus attophilus	1	0	1	-	1	2	0	0	0	1	1	0	4	1	0	0	0	0	1	0	1	2	1	2	1	2	0	0	0	0	0	2	0	5	2	1	0	1	2	3	2	2	2	2	-	-	-	0	0	0
Pseudacteon browni	1	0	1	-	0	2	1	0	1	1	1	0	1	1	0	0	0	1	1	0	1	2	1	1	1	1	0	0	2	0	0	2	1	4	0	1	0	0	2	3	0	2	0	0	-	-	-	0	1	0
Pseudacteon wasmanni	1	0	1	-	0	2	1	0	1	1	1	0	1	1	0	0	0	1	2	0	2	2	2	1	2	1	0	0	2	0	0	3	1	4	2	1	0	1	2	3	0	0	0	0	-	-	-	1	0	0
Myrmosicarius grandicornis	1	0	0	-	0	1	0	1	1	0	0	4	2	1	0	0	0	1	2	0	2	2	2	2	2	1	0	1	3	0	0	1	0	5	0	1	0	2	0	3	0	2	2	2	-	-	-	0	0	0
Eibesfeldtphora arcuata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora attae	0	-	-	-	2	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora bragancai	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora breviloba	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora cumsaltensis	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	1	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora curvinervis	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora declinata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora digitata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora dissita	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora elongata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora erthali	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora inferna	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora inornata	0	-	-	-	1	1	0	1	2	2	0	0	2	1	0	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	0	0	3	5	0	1	0	0	0	3	0	2	0	0	-	-	-	0	0	0
Eibesfeldtphora isomorpha	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora leei	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora mexicanae	0	-	-	-	2	1	0	1	2	2	1	0	2	1	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	1	1	-	-	-	0	0	0
Eibesfeldtphora pala	0	-	-	-	2	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora prolixa	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora tonhascai	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora trifurcata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Eibesfeldtphora trilobata	0	-	-	-	1	1	0	1	2	2	1	0	2	0	1	1	1	1	2	0	2	2	2	2	2	2	0	2	2	0	2	0	3	5	0	1	0	0	0	3	0	2	2	1	-	-	-	0	0	0
Cremersia adunca	0	-	-	-	2	0	0	0	1	3	1	1	3	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	2	1	0	0	1	1	0	0	-	0	0	0	0	3	1	2	0	0	1
Cremersia australis	0	-	-	-	2	0	0	0	1	1	1	2	3	1	0	0	0	1	0	0	0	2	0	2	0	2	0	0	0	0	0	2	1	2	0	1	1	0	0	-	0	0	0	0	1	0	2	0	0	1
Cremersia brasiliensis	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	2	0	2	0	2	0	3	0	0	0	2	1	1	0	1	1	0	0	-	0	0	0	0	1	0	3	0	0	1
Cremersia coecum	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	2	0	1	0	0	1
Cremersia costalis	0	-	-	-	2	0	0	0	1	0	1	2	3	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	1	2	0	1	1	0	0	-	0	0	0	0	1	0	5	0	0	1
Cremersia crassicostalis	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	2	1	2	0	1	1	0	0	-	0	0	0	0	3	2	2	0	0	1
Cremersia crassispina	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	0	0	2	0	2	3	0	1	0	0	0	0	4	1	1	0	1	1	0	0	-	0	1	0	0	1	2	3	0	0	1
Cremersia longipes	0	-	-	-	2	0	0	0	1	1	1	2	3	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	3	0	0	0	0	1
Cremersia pilipes	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	2	1	?	0	1	1	0	0	-	0	0	0	0	4	0	0	0	0	1
Cremersia pilosa	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	0	0	2	0	0	3	0	1	0	0	0	0	4	1	1	0	1	1	0	0	-	0	1	0	0	1	1	2	0	0	1
Cremersia salesiana	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	0	0	2	0	0	0	3	4	0	0	4	1	1	0	1	1	0	0	-	0	0	0	0	0	1	2	0	0	1
Cremersia setitarsus	0	-	-	-	2	0	0	0	1	1	1	2	3	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	3	0	4	0	0	1
Cremersia spinicauda	0	-	-	-	2	0	0	0	1	1	1	2	3	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	0	0	5	0	0	1
Cremersia spinicosta	0	-	-	-	2	0	0	0	1	2	1	1	3	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	2	0	1	0	0	1
Cremersia spinosissima	0	-	-	-	2	0	0	0	1	1	1	2	3	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	3	0	4	0	0	1
Cremersia zikani	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	2	0	1	0	0	1
Neodohrniphora setifemur	0	-	-	-	2	0	0	0	1	2	1	1	3	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	2	0	1	0	0	1
Cremersia spnov01	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	2	0	1	3	1	0	0	0	0	0	2	1	2	0	1	1	0	0	-	0	0	0	0	1	1	3	0	0	1
Cremersia spnov02	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	2	0	2	0	0	0	3	0	0	0	4	1	1	0	1	1	0	0	-	0	0	0	0	0	1	2	0	0	1
Cremersia spnov03	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	2	0	2	0	1	0	0	0	0	0	2	1	0	0	1	1	0	0	-	0	0	0	0	3	1	2	0	0	1
Cremersia spnov04	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	2	0	2	0	2	0	0	0	0	0	2	1	1	0	1	1	0	0	-	0	0	0	0	1	0	3	0	0	1
Cremersia spnov06	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	2	0	3	2	1	1	0	0	-	0	0	0	0	4	0	4	0	0	1
Cremersia spnov07	0	-	-	-	2	0	0	0	1	1	1	3	3	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	1	0	0	1	1	0	0	-	0	0	0	0	1	2	2	0	0	1
Cremersia spnov10	0	-	-	-	2	0	0	0	1	1	1	1	3	1	0	0	1	1	0	0	0	1	0	2	0	1	0	0	0	0	0	2	1	3	0	1	1	0	0	-	0	0	0	0	2	0	1	0	0	1
Neodohrniphora unichaeta	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	0	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora acromyrmecis	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora calverti	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	1	1	0	0	0	-	-	-	0	2	0
Neodohrniphora cognata	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	0	1	1	2	5	3	5	1	1	0	0	0	2	1	0	0	0	-	-	-	0	2	0
Neodohrniphora wasmanni	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	0	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov04	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	1	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov01	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov05	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov07	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov06	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov02	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	0	1	1	0	1	2	1	2	1	2	0	0	1	1	2	0	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0
Neodohrniphora spnov03	0	-	-	-	1	1	0	1	1	2	1	0	2	1	0	1	1	1	1	0	1	2	1	2	1	2	0	1	1	1	2	5	3	5	1	1	0	0	0	4	1	0	0	0	-	-	-	0	2	0

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
Megaselia scalaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	3	-	-	0	0
Myriophora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	0	1	0	3	-	-	0	3
Apocephalus attophilus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	1	0	3	-	1	0	3
Pseudacteon browni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	1	0	3	-	0	0	1
Pseudacteon wasmanni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	3	-	0	0	3
Myrmosicarius grandicornis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	0	0	3	-	0	0	3
Eibesfeldtphora arcuata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	0	0	1	2	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora attae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	0	2	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora bragancai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	0	0	1	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora breviloba	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	2	1	2	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora cumsaltensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora curvinervis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora declinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	0	2	0	1	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora digitata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	0	1	0	1	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora dissita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	2	1	2	0	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora elongata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	2	0	2	0	0	1	1	0	1	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora erthali	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	0	1	2	0	1	0	0	0	2	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora inferna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	2	0	2	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora inornata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	3	2	2	-	-	-	-	-	-	-	-	-	-	-	1	0	1	1	1	0	2	3	1	2	2
Eibesfeldtphora isomorpha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora leei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	2	0	0	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora mexicanae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	0	-	2	-	2	3	1	1	1	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora pala	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	2	0	1	2	1	0	1	0	0	2	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora prolixa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	3	0	3	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora tonhascai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	1	0	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora trifurcata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	2	0	2	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	0	2
Eibesfeldtphora trilobata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	2	3	1	0	1	0	0	0	1	1	1	1	1	1	0	1	1	1	0	0	0	1	0	2
Cremersia adunca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia brasiliensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia coecum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia costalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia crassicostalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia crassispina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia longipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia pilipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia pilosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia salesiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia setitarsus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spinicauda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spinicosta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spinosissima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia zikani	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Neodohrniphora setifemur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Cremersia spnov10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	3	2	4	-	-	-	-	-	-	-	-	-	-	-	1	1	0	1	1	0	1	2	2	3	1
Neodohrniphora unichaeta	0	1	1	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora acromyrmecis	0	1	0	0	0	0	0	0	1	0	-	0	-	-	0	1	0	0	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora calverti	0	1	0	0	1	2	1	1	1	1	1	2	2	2	0	1	0	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora cognata	0	0	1	0	1	1	1	1	1	0	-	1	-	-	0	0	-	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora wasmanni	0	1	1	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov04	0	0	1	0	3	2	0	1	1	1	0	1	0	2	0	1	0	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov01	0	0	0	0	1	1	0	1	1	1	1	0	3	1	0	1	0	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov05	0	0	0	0	0	0	0	0	1	1	1	0	3	1	0	1	0	0	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov07	0	1	0	0	1	3	0	1	1	1	1	0	0	0	1	1	0	0	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov06	0	0	1	0	0	0	0	0	0	0	-	1	-	-	1	1	1	2	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov02	1	0	0	1	2	0	1	1	1	1	1	1	0	0	2	0	-	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1
Neodohrniphora spnov03	0	1	0	0	1	2	2	1	1	1	1	0	1	1	0	1	0	1	1	0	3	2	1	-	-	-	-	-	-	-	-	-	-	-	1	1	0	0	1	1	0	1	2	1	1

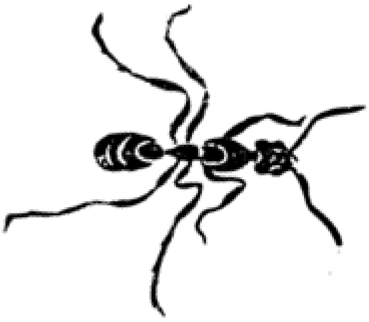
Examined Material

Barcode	Owner	Note	*Genus*	Species	Locality	Country	State
	LACM		*Megaselia*	*scalaris*	Viçosa	Brazil	Minas Gerais
	MZSP		*Myriophora*	sp.	Itariri	Brazil	São Paulo
	MZSP		*Pseudacteon*	*wasmanni*	Itariri	Brazil	São Paulo
	MZSP		*Pseudacton*	*browni*	Itariri	Brazil	São Paulo
	MZSP		*Apocephalus*	*attophilus*	Florestal	Brazil	Minas Gerais
	MZSP		*Myrmosicarius*	*grandicornis*	Florestal	Brazil	Minas Gerais
LACM ENT 003365	LACM	PT	*Cremersia*	*adunca*	Kerrville	USA	Texas
LACM ENT 349977	LACM	PT	*Cremersia*	*adunca*	Kerrville	USA	Texas
MZSP EDP 00050	MZSP	PT	*Cremersia*	*adunca*	Kerrville	USA	Texas
MZSP EDP 00051	MZSP	PT	*Cremersia*	*adunca*	Kerrville	USA	Texas
MZSP EDP 00052	MZSP	PT	*Cremersia*	*adunca*	Kerrville	USA	Texas
LACM ENT 049774	LACM		*Cremersia*	*australis*	Cruce de Mono	Panama	Darien
LACM ENT 349984	LACM		*Cremersia*	*australis*	Rd. to Rincon, 24mW, Pan-American Hwy	Costa Rica	Puntarenas
LACM ENT 239371	LACM		*Cremersia*	*australis*	Arroyo Tuhiri, Mapiri	Bolivia	La Paz
LACM ENT 055403	LACM		*Cremersia*	*australis*	16km W Guapiles	Costa Rica	Limon
MZSP EDP 00028.9	MZSP		*Cremersia*	*brasiliensis*	Campinas, Goiânia	Brazil	Goiás
MZSP EDP 00029	MZSP	PT	*Cremersia*	*brasiliensis*	Campinas, Goiânia	Brazil	Goiás
MZSP EDP 00049	MZSP		*Cremersia*	*brasiliensis*	Campinas, Goiânia	Brazil	Goiás
MZSP EDP 00066	MZSP		*Cremersia*	*coecum*	Kerrville	USA	Texas
MZSP EDP 00067	MZSP		*Cremersia*	*coecum*	Kerrville	USA	Texas
MZSP EDP 00068	MZSP		*Cremersia*	*coecum*	Kerrville	USA	Texas
MZSP EDP 00069	MZSP	PT	*Cremersia*	*coecum*	Uvalde	USA	Texas
LACM ENT 034672	LACM		*Cremersia*	*costalis*	3km SW Rincon	Costa Rica	Puntarenas
LACM ENT 153456	LACM		*Cremersia*	*costalis*	PNN Utria, Visitor Center	Colombia	Choc??
MZSP EDP 00012	MZSP	PT	*Cremersia*	*costalis*	Rio Negro	Brazil	Paraná
MZSP EDP 00012.1	MZSP	PT	*Cremersia*	*costalis*	Rio Negro	Brazil	Paraná
MZSP EDP 00031	MZSP		*Cremersia*	*crassipina*	Inhumas	Brazil	Goiás
MZSP EDP 00031.1	MZSP		*Cremersia*	*crassipina*	Inhumas	Brazil	Goiás
MZSP EDP 00005	MZSP	PT	*Cremersia*	*longipes*	Barro Colorado Island	Panama	Canal Zone
MZSP EDP 00005.1	MZSP	PT	*Cremersia*	*longipes*	Barro Colorado Island	Panama	Canal Zone
MZSP EDP 00043	MZSP	PT	*Cremersia*	*pilipes*	Kerrville	EUA	Texas
LACM ENT 220525	LACM		*Cremersia*	pilosa	PNN Tayrona, Pueblito	Colombia	Magdalena
LACM ENT 132435	LACM		*Cremersia*	pilosa	PNN Tayrona, Pueblito	Colombia	Magdalena
MZSP EDP 00010.2	MZSP		*Cremersia*	*pilosa*	São Gabriel da Cachoeira	Brazil	Amazonas
MZSP EDP 00021	MZSP	PT	*Cremersia*	*pilosa*	Campinas, Goiânia	Brazil	Goiás
MZSP EDP 00022	MZSP		*Cremersia*	*pilosa*	Campinas, Goiânia	Brazil	Goiás
MZSP EDP 00090	MZSP		*Cremersia*	*salesiana*	Monte Negro, Linha C25, Setor Chacareiro	Brazil	Rondônia
LACM ENT 228287	LACM		*Cremersia*	setitarsus	Mocagua, PNN Amacayacu	Colombia	Amazonas
MZSP EDP 00002.2	MZSP	PT	*Cremersia*	*setitarsus*	Barro Colorado Island	Panama	Canal Zone
MZSP EDP 00037.4	MZSP		*Cremersia*	*spinicauda*	Nova Teotônia	Brazil	Santa Catarina
MZSP EDP 00070	MZSP	HT	*Cremersia*	*spinicauda*	Nova Teotônia	Brazil	Santa Catarina
MZSP EDP 00071	MZSP	PT	*Cremersia*	*spinicauda*	Nova Teotônia	Brazil	Santa Catarina
MZSP EDP 00072	MZSP		*Cremersia*	*spinicauda*	Nova Teotônia	Brazil	Santa Catarina
MZSP EDP 00040	MZSP	PT	*Cremersia*	*spinicosta*	São José	Costa Rica	
MZSP EDP 00040.1	MZSP	PT	*Cremersia*	*spinicosta*	São José	Costa Rica	
LACM ENT 237955	LACM		*Cremersia*	spinosissima	PNN Farallones de Cali, La Meseta	Colombia	Valle de Cauca
LACM ENT 035826	LACM		*Cremersia*	*spnov01*	Sacha Lodge	Ecuador	Sucumbios
LACM ENT 039507	LACM		*Cremersia*	*spnov02*	35km SSE Flor de Oro	Bolivia	Santa Cruz
LACM ENT 133280	LACM		*Cremersia*	*spnov02*	Serra do Cipó	Brazil	Minas Gerais
LACM ENT 052289	LACM		*Cremersia*	spnov03	Patagonia	USA	Arizona
LACM ENT 187262	LACM		*Cremersia*	*spnov04*	SFF Colorados, El Mirador	Colombia	Bolivar
LACM ENT 206759	LACM		*Cremersia*	spnov06	San Antonio de Cumbaza	Peru	San Martin
LACM ENT 206762	LACM		*Cremersia*	spnov06	San Antonio de Cumbaza	Peru	San Martin
LACM ENT 291108	LACM		*Cremersia*	spnov06	PNN Gorgona, El Helechal	Colombia	Cauca
LACM ENT 305123	LACM		*Cremersia*	spnov07	Lençóis, Rio Mucugezinho	Brazil	Bahia
LACM ENT 305127	LACM		*Cremersia*	spnov07	Lençóis, Rio Mucugezinho	Brazil	Bahia
LACM ENT 305121	LACM		*Cremersia*	spnov07	Lençóis, Rio Mucugezinho	Brazil	Bahia
LACM ENT 305115	LACM		*Cremersia*	spnov07	Lençóis, Rio Mucugezinho	Brazil	Bahia
LACM ENT 004805	LACM		*Cremersia*	spnov10	3km SW Rincon	Costa Rica	Puntarenas
MZSP EDP 00007	MZSP		*Cremersia*	*zikani*	Butantan, Horto O. Cruz	Brazil	São Paulo

Barcode	**Owner**	**Note**	***Genus***	**Species**	**Locality**	**Country**	**State**
MZSP EDP 00039	MZSP	PT	*Cremersia*	*zikani*	Petropolis	Brazil	Rio de Janeiro
LACM ENT 291300	LACM		*Neodohrniphora*	mokana	SFF Los Colorados, Alto El Mirador	Colombia	Bolivar
LACM ENT 232503	LACM	HT	*Neodohrniphora*	rapunzel	PNN Cueva de Los Guácharos, Mirador	Colombia	Huila
LACM ENT 349980	LACM	PT	*Neodohrniphora*	rapunzel	2km S. Baeza	Ecuador	Napo
LACM ENT 349987	LACM?	HT	*Neodohrniphora*	truncata	14km S Cañas	Costa Rica	Guanacaste
LACM ENT 349981	LACM?	PT	*Neodohrniphora*	truncata	14km S Cañas	Costa Rica	Guanacaste
MZSP EDP 00092	MZSP	HT	*Neodohrniphora*	*calverti*	Near Hacienda El Brazil, one mile north of the Alajuela city	Costa Rica	Alajuela
Prado 1976			*Neodohrniphora*	*calverti*	La Suiza	Costa Rica	Cartago
LACM ENT 147218	LACM	PT	*Neodohrniphora*	gigantea	Barro Colorado Island	Panama	Canal Zone
LACM ENT 228851	LACM	PT	*Neodohrniphora*	gigantea	SFF Colorados, El Mirador	Colombia	Bolivar
LACM ENT 349990	LACM		*Neodohrniphora*	*cognata*	Pakitza	Peru	Madre de Dios
LACM ENT 018019	LACM		*Neodohrniphora*	*cognata*	Sacha Lodge	Ecuador	Sucumbios
MZSP EDP 00079	MZSP		*Neodohrniphora*	*cognata*	Belém	Brazil	Pará
MZUC, 39-42	MZUC	PT	*Neodohrniphora*	*wasmanni*	Santa Fe	Argentina	San Cristóbal
LACM ENT 217319	LACM		*Neodohrniphora*	*wasmanni*	Reserva Vida Silvestre Urugua-í	Argentina	Misiones
LACM ENT 217529	LACM		*Neodohrniphora*	*wasmanni*	Reserva Vida Silvestre Urugua-í	Argentina	Misiones
LACM ENT 234122	LACM		*Neodohrniphora*	canina	Patawa, Kaw Mountain	French Guiana	Regina
LACM ENT 186000	LACM		*Neodohrniphora*	*pseudoacromyrmecis*	Reserva Vida Silvestre Urugua-í	Argentina	Missiones
LACM ENT 216193	LACM		*Neodohrniphora*	*acromyrmecis*	Reserva Vida Silvestre Urugua-í	Argentina	Missiones
MZSP EDP 00094	MZSP	HT	*Neodohrniphora*	*acromyrmecis*	Rio Negro	Brazil	Paraná
MZSP EDP 00078	MZSP		*Neodohrniphora*	*acromyrmecis*	Aquidauana, Res. Ecolo. UEMS, Mata ciliar, Córrego Fundo	Brazil	Mato Grosso do
MZSP EDP 00080	MZSP		*Neodohrniphora*	*acromyrmecis*	Ribeirão Preto, Campus USP	Brazil	São Paulo
MZSP EDP 00082	MZSP		*Neodohrniphora*	*acromyrmecis*	Ribeirão Preto, Campus USP	Brazil	São Paulo
MZSP EDP 00087	MZSP		*Neodohrniphora*	*acromyrmecis*	Nova Teotônia	Brazil	Santa Catarina
MZSP EDP 00105	MZSP	PT	*Neodohrniphora*	*acromyrmecis*	Rio Negro	Brazil	Paraná
MZSP EDP 00074	MZSP		*Neodohrniphora*	*queirozi*	Cachoeiras de Macacu, Regua	Brazil	Rio de Janeiro
MZSP EDP 00075	MZSP		*Neodohrniphora*	*queirozi*	Cachoeiras de Macacu, Regua	Brazil	Rio de Janeiro
MZSP EDP 00089	MZSP		*Neodohrniphora*	*queirozi*	Vassouras	Brazil	Rio de Janeiro
MZSP EDP 00112	MZSP		*Neodohrniphora*	*queirozi*	Cachoeiras de Macacu, Regua	Brazil	Rio de Janeiro
MZSP EDP 00114	MZSP		*Neodohrniphora*	*queirozi*	Cachoeiras de Macacu, Regua	Brazil	Rio de Janeiro
LACM ENT 23227	LACM	PT	*Eibesfeldtphora*	*arcuata*	Yasuni Biological Research Station	Ecuador	Napo
LACM ENT 22975	LACM		*Eibesfeldtphora*	*attae*	PNN Tayrona, Pueblito	Colombia	Magdalena
LACM ENT 12653	LACM		*Eibesfeldtphora*	*bragancai*	Viçosa	Brazil	Minas Gerais
LACM ENT 30511	LACM	PT	*Eibesfeldtphora*	*breviloba*	Rio de Janeiro	Brazil	Rio de Janeiro
INBIOCRI0022748	LACM	PT	*Eibesfeldtphora*	*curvinervis*	La Selva Biological Station	Costa Rica	Heredia
LACM ENT 22835	LACM		*Eibesfeldtphora*	*declinata*	Presidente Figueiredo, REBio Uatumã, Ilha Y	Brazil	Amazonas
LACM ENT 30510	LACM		*Eibesfeldtphora*	*digitata*	Presidente Figueiredo, REBio Uatumã, Ilha Y	Brazil	Amazonas
LACM ENT 23272	LACM	HT	*Eibesfeldtphora*	*dissita*	Presidente Figueiredo, REBio Uatumã, Ilha Y	Brazil	Amazonas
LACM ENT 24065	LACM	PT	*Eibesfeldtphora*	*elongata*	Viçosa	Brazil	Minas Gerais
LACM ENT 09405	LACM		*Eibesfeldtphora*	*erthali*	Viçosa	Brazil	Minas Gerais
LACM ENT 05742	LACM	PT	*Eibesfeldtphora*	*inferna*	La Selva Biological Station	Costa Rica	Heredia
INBIOCRI0022726	LACM	HT	*Eibesfeldtphora*	*isomorfa*	La Selva Biological Station	Costa Rica	Heredia
LACM ENT 08277	LACM		*Eibesfeldtphora*	*isomorfa*	La Selva Biological Station	Costa Rica	Heredia
LACM ENT 08277	LACM		*Eibesfeldtphora*	*inornata*	Viçosa	Brazil	Minas Gerais
LACM ENT 23526	LACM	PT	*Eibesfeldtphora*	*leei*	PNN Gorgona, Alto el Mirador	Colombia	Cauca
LACM ENT 04745	LACM		*Eibesfeldtphora*	*leei*	El Saman, PNN Gorgona	Colombia	Cauca
LACM ENT 00174	LACM	HT	*Eibesfeldtphora*	*mexicanae*	Catemaco	Mexico	Veracruz
LACM ENT 36565	LACM	PT	*Eibesfeldtphora*	*mexicanae*	Catemaco	Mexico	Veracruz
LACM ENT 23585	LACM		*Eibesfeldtphora*	*pala*	San Martin, PNN Amacayacu	Colombia	Amazonas
LACM ENT 12035	LACM		*Eibesfeldtphora*	*pala*	San Martin, PNN Amacayacu	Colombia	Amazonas
LACM ENT 22371	LACM	PT	*Eibesfeldtphora*	*prolixa*	Cuyabeno	Ecuador	Sucumbios
LACM ENT 11150	LACM		*Eibesfeldtphora*	*prolixa*	Cuyabeno	Ecuador	Sucumbios
LACM ENT 24066	LACM	PT	*Eibesfeldtphora*	*tonhascai*	Viçosa	Brazil	Minas Gerais
LACM ENT 12646	LACM		*Eibesfeldtphora*	*tonhascai*	Viçosa	Brazil	Minas Gerais
LACM ENT 23398	LACM	PT	*Eibesfeldtphora*	*trifurcata*	Manaus, PDBFF Reserve 1210	Brazil	Amazonas
LACM ENT 36565	LACM		*Eibesfeldtphora*	*trifurcata*	Manaus, PDBFF Reserve 1210	Brazil	Amazonas
LACM ENT 25496	LACM		*Eibesfeldtphora*	*trilobata*	Reserva Vida Silvestre Urugua-í	Argentina	Misiones
LACM ENT 25496	LACM		*Eibesfeldtphora*	*trilobata*	Reserva Vida Silvestre Urugua-í	Argentina	Misiones

Chapter 2

Revision of the ant-parasitic genus *Neodohrniphora* Malloch (Diptera: Phoridae)



Abstract

The ant-parasitic genus *Neodohrniphora* Malloch is revised based on female specimens. Herein, eleven species are studied, seven of which are new to science: *N. canina* **sp. nov.,** *N. gigantea* **sp. nov.,** *N. mokana* **sp. nov.,** *N. pseudoacromyrmecis* **sp. nov.,** *N. queirozi* **sp. nov.,** *N. rapunzel* **sp. nov.,** and *N. truncata* **sp. nov.** *Neodohrniphora wasmanni* Borgmeier is **revalidated** and two new synonymies are proposed: *N. similis* Prado is synonymized with *N. acromyrmecis* Borgmeier, and *N. unichaeta* Disney is synonymized with *N. wasmanni* Borgmeier**.** Unfortunately, the unique type material (holotype) of *N. cognata* has been lost or destroyed. In order to provide stability and a necessary standard for comparison, a **neotype** for *N. cognata* is designated based on material collected from the same type locality, data, and collector. A new key for all the females of *Neodohrniphora* is provided.

Key words: *Acromyrmex,* Leaf-cutting ant, parasitoid, phorid flies.

Introduction

The genus *Neodohrniphora* Malloch, 1914 (Diptera, Phoridae) is known for its leaf-cutting ant parasitic flies (Borgmeier 1925, 1929, 1961; Prado 1976; Disney 1996, Disney *et al*. 2008). Its species has been recorded parasitizing 5 ant species, all from the genera *Acromyrmex* Mayr. The genus has a Neotropical distribution with records from nine countries (Argentina, Brazil, Bolivia, Peru, Ecuador, French Guiana, Colombia, Panama and Costa Rica).

In this paper, seven new species are described, taxonomic acts and a new key for all the *Neodohrniphora* females are provided.

Taxonomic history

(Fig. B)

Malloch (1914) established *Neodohrniphora* genus from a new Costa Rican species, *N. calverti,* based on a male. In the same paper, he described *A. curvinervis* in the genus *Apocephalus* Coquillett.

Borgmeier (1925 and 1929) described 5 new species from Brazilian localities: *N. acromyrmecis* (#f), *N. montana* (#m), *N. robusta* (#m), *N. declinata* (#f) and *N. wasmanni* (#f). Additionally, Borgmeier transferred *A. curvinervis* Malloch to *Neodohrniphora* (Schimitz,1927, considered this species *incertae sedis*, and Schmitz, 1929, doubtfully placed it in the genus *Myrmosicarius* Borgmeier).

Borgmeier (1961) reasserted the assignment of *A. curvinervis* to *Neodohrniphora*, and considered both *N. declinata* and *Apocephalus fontalis* Curran, 1964 as synonym of *A. curvinervis*

Borgmeier (1966) described *N. arnaudi* from USA (California), which he doubtfully placed in *Neodohrniphora* (Brown 1997, synonymized *N. arnaudi* with *Apocephalus horridus* Borgmeier, 1963). And, besides *N. declinata* already synonymized in 1961, all other species described by him in 1925 and 1929, namely *N. acromyrmecis, N. montana, N. robusta* and N. *wasmanni*, were here synonymized with the type-species *N. calverti*.

Borgmeier (1968) in the world catalog mentions the species *N. arnaudi*, *N. calverti* and *N. curvinervis* and maintaining the synonymies.

Prado (1976) studied the type material of Borgmeier species from Brazilian and Costa Rican material, deposited at the MZSP. He reinstated *N. acromyrmecis* and *N. declinata,* revalidated *N. frontalis*, proposed two new species *N. cognata* and *N. similis,* from Brazil, and illustrated *N. calverti*'s female terminalia. Also he synonymized N. montana, *N. robusta* and *N. wasmanni* with *N. acromyrmecis*. In this study, Prado proposed the classification of two species-groups: *calverti*-group (with *N. calverti*, *N. acromyrmecis, N. cognata,* and *N. similis*) and *curvinervis*-group (with *N. curvinervis, N. frontalis,* and *N. declinata).*

Disney (1996) concluded that the *curvinervis*-group constituted a distinct subgenus and described then the subgenus *Eibesfeldtphora,* while the *calverti*-group was placed in the subgenus *Neodohrniphora* and described the subgenus *Wallerphora*. He also described *Neodohrniphora* (*Eibesfeldtphora*) *attae* and *Neodohrniphora* (*Wallerphora*) *mexicanae*.

Brown (2001) revised the subgenus *Eibesfeldtphora* and did not recognize the subgenus *Wallerphora*, transferring *Neodohrniphora* (*Wallerphora*) *mexicanae* to subgenus *Eibesfeldtphora*. He suggested putative synapomorphies for the subgenera *Neodohrniphora* and *Eibesfeldtphora*.

Disney *et al*. (2009) synonymized *Cremersia* with *Neodohrniphora,* described *N. unichaeta,* and the subgenus *Eibesfeldtphora* was raised to genus level.

Brown (2010), Zuha & Disney (2018), the on line Phorid Catalog (PCAT, 2019) and Ament & Pereira (2019) considered *Cremersia* and *Neodohrniphora* as different genera.

Material and methods

This revision dealt exclusively with female specimens. Currently, new males and females cannot be associated unless they are collected in copula or have molecular sequence data.

The specimens examined were mainly from the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM). Additional material was examined from the following museums: Instituto Nacional de Bioversidad, Heredia, Costa Rica (INBio), Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZSP), Museum of Zoology, University of Cambridge, Cambridge, UK (MZUC) and Academy of Natural Sciences, Philadelphia, USA (ANSP), Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso” (ZUEC).

The sections of the examined material were produced using AutoMatEx (Brown 2013). The genitalia were treated for 15 minutes in each of the following steps: KOH 10% in water bath 50 ºC; rinsed in acetic acid 10%; water; dehydrated in alcohol 70%; alcohol PA and placed in a vial with glycerin. The wings were mounted between two round glass cover slips with Canada balsam and glued onto cardboard paper (Riccardi P. pers. comm.). The terminalia and wing mountings were pinned together with the respective specimens.

During the “water” step, the genitalia were protracted using two thin tweezers, one to hold the genitalia and the other to push the genitalia internally to simulate the oviposition movement.

Morphological terminology followed Cumming & Wood (2017). The female terminalia were named according to Nakayama (2007). For genitalia descriptions, we used specific morphological terminology for this genus, which is described in this paper in the glossary below. Body length: front of head to posterior apex of segment 5. Costal length: apex of basicosta to apex of costa. Wing length: apex of basicosta to apex of wing (Brown, 2004).

Glossary and abbreviations

Until now, no other genera have presented the same morphological pattern in the female genitalia; therefore, we proposed the following terminology (Fig. A). The position and shape of segments were considered to propose this terminology.

Tg – Tergite

St – Sternite

mov lat pl – Movable lateral plate: part of St7.

dor bas – Dorsal base: anterior dorsal part of St7.

glb lob – Globular lobe : posterior dorsal part of St7.

lob arm – Lobe arm: structure on Globular lobe .

ho – Hook, modified St 8.

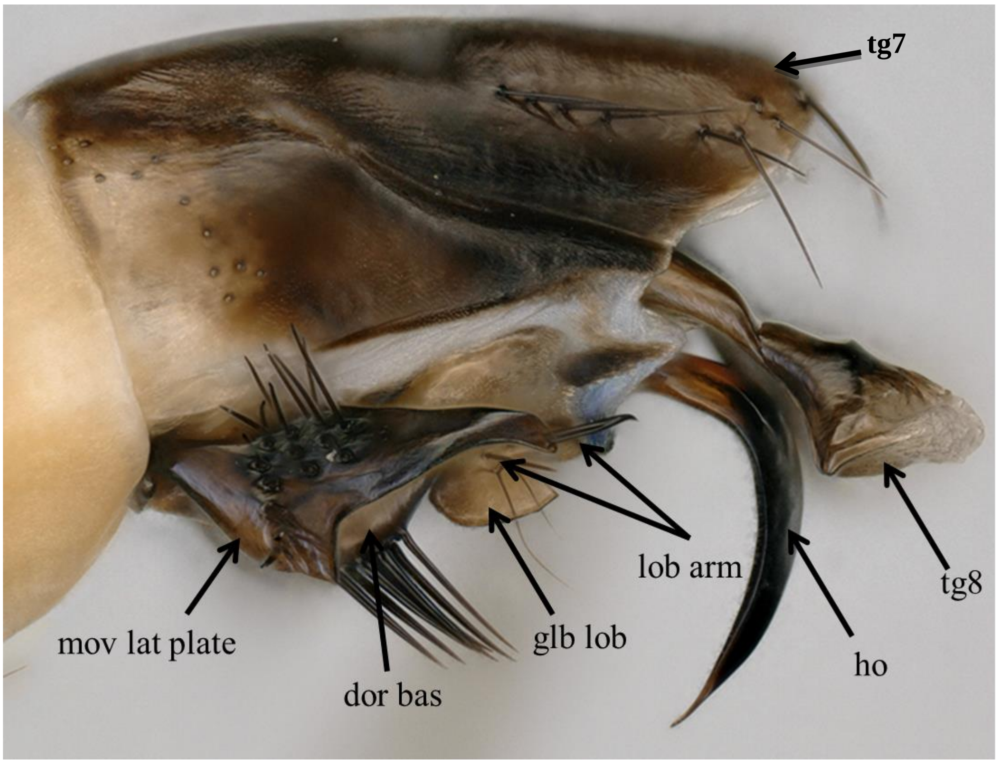


Fig A. Oviscape, segment 7 (left lateral) of female *Neodohrniphora gigantea*.

Results

Taxonomy

Genus *Neodohrniphora*

Neodohrniphora Malloch, 1914: 24. Holotype male, Borgmeier, 1925: 213; 1929: 496; 1962: 478; 1966:140; 1968: 228 (cat.). Brown, 1992a: 84.

Type species: *Neodohrniphora calverti* Malloch, 1914.

Diagnosis. Female. Head. Frons with 2–4–4–4 setae, without supra–antennal setae. Position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae and presence of setulae on frons. Antenna flattened, flagellomere 1 with arista subapical. Palpus with distinct apical setae. **Thorax.** Scutum with one postpronotal seta, two notopleural setae, one intra–alar seta, one postalar seta and one pre–scutellar dorsocentral seta. Scutellum with an anterior and posterior pairs of setae. Wing. With > 50 Costal cilia. Sc not reaching vein 1. Halter knob brown. **Abdomen**. First abdominal segment shorter than the others. Tergites 3–5 subequal in length. Sternites 1–5 unsclerotized. Segment 6 ring shape, with dorsal setulae and each side of the anteroventral part with long setae in a transverse row and with distinctly sclerotized insertion points, and filamentous setae on posteroventral part. **Oviscape** (Fig. A) (Table 1). Heavily sclerotized, dark brown, with parallel dorsal row of setae. Tg7 connected to St7 by membrane. St7 divided into three portions, two movable lateral plates and a central portion with the following structures: dorsal base, globular lobe, and a lobe arm. Sternite 8 modified like a hook. Tg8 divided into two segments.

Synapomorphies for the genera based on females (Chapter 1):

TABLE 1. Exclusive synapomorphies for the genus *Neodohrniphora*.

Character	Character-state
29. Sternite 6, posterior margin, chaetotaxy	(1) with tranversal row of long filamentous setae
30. Segment 6, second third, membrane between St6 and Tg6, appearance	(1) sclerotized, ring-shaped
35. Segment 6, sternite, membranous anteroventral margin	(1) with transverse row with distinctly sclerotized insertion points
41. Tergite 7, dorso-lateral part, surface	(1) with parallel row of setae
49. Sternite 7, composition	(2) divided into three sclerites
73. Sternite 8, shape	(1) hook

90.	Sternite 9, apex,	anterior curvature	(1) convex	
.94.	Tergite 10, direction	apex,	(1) down curved	

Segment 6 on anteroventral part with long setae in a transverse row and with distinctly sclerotized insertion points; (also present in Brown 2001)

Oviscape with Tg7 with parallel dorsal row of setae.

St7 divided into three segments: two movable lateral plates and a central segment with the following structures: dorsal base, globular lobe, and a lobe arm.

Sternite 8 modified like a hook.

***Neodohrniphora acromyrmecis* Borgmeier,** 1925

(Figs 1, 14, 24, 36)

Neodohrniphora acromyrmecis Borgmeier,1925:216. Holotype female (MZSP). Type-locality: Rio Negro, Paraná, Brazil. Borgmeier, 1929: 214 (key); 1929: 498 (list); Borgmeier, 1966: 140 (as synonym of *calverti*); Prado, 1976: 589 (revalidation).

Neodohrniphora montana Borgmeier, 1925: 217, fig. 37, pl. 9, fig. 44. Holotype male. (MZSP). Type-locality: Petrópolis, Rio de Janeiro, Brazil. Prado, 1976: 590 (syn.).

Neodohrniphora robusta Borgmeier, 1925: 219, pl. 9, fig. 43. Holotype male. Type-locality: Petrópolis, Rio de Janeiro, Brazil. Prado, 1976: 590 (syn.).

Neodohrniphora similis Prado, 1976:595, figs. 68–69. Holotype female. Type-locality: Vilhena, Rondônia, Brazil **(N. Syn.).**

Diagnosis. Movable lateral plate triangular, short and compact, less than half the length of Tg7. Globular structure bilobed, the posterior one is more sclerotized and pointed than the anterior one. Lobe arm shorter than globular lobe and sclerotized part ventrally directed.

Redescription. Female. Oviscape. Movable lateral plate short and triangular with 10–13 setae. Dorsal base with 5 thick setulae. Globular structure bilobed, the posterior is more sclerotized and pointed. Lobe arm shorter than globular lobe, unsclerotized part with 5 filamentous setulae and short sclerotized part ventrally directed. Hook shorter than movable lateral plate and acuminate. Tg8 with round apex.

Type Material examined Holotype [wing] f# of *acromyrmecis*. **BRAZIL**: **Paraná**: Rio Negro, 26.083°S, 49.6876°W, 28.ii.1924, W. Frey col.; wing mounted on slide (MZSP) [MZSP EDP 00094]. Paratype f# of *acromyrmecis*. **BRAZIL**: **Paraná**: Rio Negro, 26.083°S, 49.6876°W, 28.ii.1924, W. Frey col. (MZSP).

Other material examined. ARGENTINA: **Missiones**: Reserva Vida Silvestre Uruguaí, 25.97°S, 54.11°W, 1f#, 10–12.xii.2003, B. Brown, G. Kung col., Malaise #5 (LACM). **BRAZIL**: **Mato Grosso do Sul**: Aquidauana, Res. Ecol. UEMS, Mata ciliar, Córrego Fundo, 20.4344°S, 55.6558°W, 1f#, 27.viii–11.ix.2011, Lamas, Nihei eq. Col., Malaise 07 – Sisbiota-CNPq/FAPESP (MZSP); **Santa Catarina**: Nova Teotônia, 27.1833°S, 52.3833°W, 1f#, no date (MZSP); **São Paulo**: Ribeirão Preto, Campus USP, 21.1638°S, 47.8612°W, 2f#, 29.X–06.xi.2013, Martins, Ignacio, Fachin, Porto col., Malaise (MZSP).

Distribution. From northern Argentina to southern Brazil.

Remarks. After dissecting the *N. acromyrmecis* paratype and *N. wasmanni* from Borgmeier’s material, which he identified himself, and comparing to Borgmeier's descriptions and drawings, we figured out that *N. wasmanni* is not the same species as *N. acromyrmecis*. *Neodohrniphora similis* was described based on misidentification by Prado (1976; he also designated a lectotype for *N. acromyrmecis*, but the holotype already existed, represented by only the wing slide).

Neodohrniphora montana and *N. robusta* are known only from male specimens, and this synonymy can only be explored when a revision of *Neodohrniphora* males is feasible.

Neodohrniphora calverti **Malloch**

(Figs 2, 15, 25, 34)

Neodohrniphora calverti Malloch, 1914: 25. Holotype male. Type-locality: Alajuela, Costa Rica. Brues, 1915: 111 (Cat.); Borgmeier, 1966: 140 (synonymized *N. montana*, *N. robusta* and *N. wasmanni* with *N. calverti*); Borgmeier, 1968: pag (cat.); Prado, 1976: 590 figs. 64–65 (Female description, from La Suiza, Costa Rica; synonymized *N. montana*, *N. robusta* and *N. wasmanni* under *N. acromyrmecis*).

Diagnosis Female. Movable lateral plate with two processes, both on posterior part, one short and the other divided at the posterior. Lobe arm longer than globular lobe, with sclerotized part of the apex facing outwards. Hook shorter than movable lateral plate.

Redescription. Female. Oviscape. Movable lateral plate with two processes, both in the posterior part, one dorsal short and the other ventral divided at the posterior part, with 3 thin lateral setae and 3 dorsal thick setae. Dorsal base with 5 thick setulae. Globular lobe round. Lobe arm longer than globular lobe, with 5 filamentous setulae, the same size on unsclerotized part and short sclerotized part with the apex outwards directed. Hook shorter than movable lateral plate. Tg8 with round apex.

Material examined: Holotype m#. **COSTA RICA: Alajuela**: Near Hacienda El Brazil, one mile north of the Alajuela city, 10.0576°N, 84.1754°W, 1000m, 15.xi.1909, P. P Calvert col. (ANSP) [ANSP Type No 6037]; wing mounted on slide (MZSP) [MZSP EDP 00092].

Other material examined. COSTA RICA: Alajuela: Penãs Blancas Valey, 10.1169°N, 84.6701°W, 700m, 1f#, 10.X.1987, E. Cruz col., Malaise (LACM).

Distribution. Costa Rica.

Remarks: Regarding the wing of *N. calverti* holotype at MZSP, Borgmeier (1962) visited the Academy of Natural Sciences (Philadelphia) in May 1961, where he examined the holotype and wrote "Der Fluegel liegt mir im Praeparat vor." We are unsure if this statement meant that he was able to bring the mounted wing slide to Brazil, although it is currently deposited at the MZSP.

Neodohrniphora cognata Prado

(Figs 3, 16, 26, 35)

Neodohrniphora cognata Prado, 1976: 591, fig 72. Holotype female (probably lost). Type-locality: Belém, Pará, Brazil. Prado, 1976: 590 fig.72; Brown 2009: 739, fig. 52.49.

Diagnosis. Movable lateral plate with only one long process, knife shape. Lobe arm larger than globular, with sclerotized part inwards directed and parallel to the dorsal part of Tg7.

Redescription. Female. Oviscape. Movable lateral plate with only one long process, knife shape, with 7 lateral thin setae, dorsal base with 7 thick setulae. Globular structure bilobed; lobe arm longer than globular lobe with three short setae and two filamentous setae on unsclerotized part and long sclerotized part facing inwards and parallel to the dorsal part of Tg7. Hook shorter than movable lateral plate. Tg8 with rounded apex.

Type material examined. Neotype f# **BRAZIL**: **Pará**: Belém, 1.43°S, 48.42°W, 10m, 1f#, vii.1965, H.S.Lopes **new designation.**

Other material examined. ECUADOR: **Sucumbios**: Sacha Lodge, 0.5°S, 76.5°W, 270m, 1f#, 3–13.iv.1994, P. Hibbs, Malaise (LACM), 1f#, 21.xi–01.vii.1994, P. Hibbs, Malaise (LACM). **PERU**: **Madre de Dios**: Pakitza, 11.94°S, 71.28°W, 356m, 1f#, 15.ii.1992, B. Brown, D. Feener, Over *Acromyrmex octospinosus* (LACM), 7f#, 15.ii.1992, B.Brown, D.Feener, attacking *Acromyrmex octospinosus* (LACM), 1f#, 18.ii.1992, B.Brown,D.Feener, over *Acromyrmex octospinosus* (LACM), 6f#, 24.ii.1992, B.Brown, D.Feener, over *Acromyrmex octospinosus* (LACM), 5f#, 7.iii.1992, B.Brown, D.Feener, over *Acromyrmex octospinosus* (LACM), Tambopata Research Center, 13.14°S, 69.61°W, 1f#, 22–25.viii.2001, B. Brown, G. Kung, Malaise (LACM).

Distribution Peru, Ecuador, and North Brazil.

Remarks: Examined material and type-series of Prado were not found at MZSP, or at the ZUEC, where he retired, thus in order to provide stability to identity of *N. cognata*, we decided to designate a neotype with the same data as holotype, from the type locality, and same data and collector.

As well as Pereira *et al*. (2015) found in the association between *Pseudacteon arcuatus* (Phoridae) and their host *Solenopsis geminata* (Formicidae), it is possible that *N. cognata* presents the same geographical distribution as the host *Acromyrmex octospinosus* (Golçalves 1961; Janicki *et al*. 2016; Guénard *et al*. 2017) (Table2).

Neodohrniphora wasmanni Borgmeier, stat. revalidated.

(Figs 4, 17, 27, 36)

Neodohrniphora wasmanni Borgmeier, 1928: 121. Holotype female. Type-locality: Tapera, São Lourenço da Mata, Pernambuco, Brazil. Borgmeier, 1929: 498, figs 3–5; 1965: 140 (as syn. Of *N. calverti*); Prado, 1976: 590 (as syn. of *N. acromyrmecis*)

Neodohrniphora unichaeta Disney, 2009: 620, figs 38–39. Holotype female. Type-locality: Parque Nacional Copo. Santiago del Estero, Argentina. (**N. Syn.).**

Diagnosis: Movable lateral plate with two processes, one ventral ventrally directed and the other dorsal long, with setae on anterior and posterior half. Lobe arm shorter than globular lobe with the sclerotized part ventrally directed.

Redescription. Female. Oviscape. Movable lateral plate with two processes, one ventrally directed, and the other dorsal long with setae only on anterior half. Dorsal base with 7 thick setulae. Globular structure bilobed. Lobe arm shorter than globular lobe, with two short setae and one filamentous setulaeon unsclerotized part, long sclerotized part ventrally directed. Hook acuminate and shorter than movable lateral plate. Tg8 with rounded apex.

Type material examined: Holotype f#. **BRAZIL**: **Pernambuco**: Tapera, São Lourenço da Mata, 8.0451°S, 34.9757°W, vi.1928, Pickel, Dom Bento (MZSP) [wing on slide, MZSP EDP 00093]. Paratype f# of *N. unichaeta*. **ARGENTINA: San Cristóbal:** Santa Fe, 30.2°S, 61.15°W, 73m, 1f#, 2.4II.2006, L. Elizalde, reared from Acromyrmex heyeri in lab (MZUC 39–42) .

Other material examined. **ARGENTINA**: **Misiones**: Reserva Vida Silvestre Uruguaí, 25.97°S, 54.11°W, 400m, 5f#, B. Brown, G. Kung, Malaise (LACM), 1f#, 7–8.vii.2003, B.Brown, G. Kung, Malaise trap #4 (LACM), 3f#, 10–12.xii.2003, B.Brown,G.Kung, Malaise trap #6 (LACM), 1f#, 7–9.xii.2004, B. Brown, G. Kung, Malaise (LACM), 2f#, 14.xii.2003, G.Kung, Over ant hosts (LACM); **BOLIVIA**: **La Paz**: Rio Merke, 3km NW Mapiri, 15.31°S, 68.23°W, 500m, 1f#, 09.iv.2001, G. Kung, Over *Acromyrmex* (LACM). **BRAZIL**: **Mato Grosso do Sul**: Porto Murtinho, 21.6833°S, 57.7785°W, 1f#, 26.xii–10.i.2012, Lamas, Nihei eq. Col., Malaise 31 – Sisbiota-CNPq/FAPESP (MZSP), Porto Murtinho Faz. Retiro Conceição – Trilha da Espinhadeira, 21.6833°S, 57.7785°W, 1f#, 29. iii–18.iv.2012, Lamas, Nihei eq. Col., Malaise 31 – Sisbiota-CNPq/FAPESP (MZSP); **Rio de Janeiro**: Vassouras, 22.216°S, 43.633°W, 1f#, ii.2012, L. Elizalde (MZSP); **Santa Catarina**: Nova Teotônia, 27.1833°S, 52.3833°W, 1f#, v.1952, F. Plaumann (MZSP), 11f#, (MZSP), Nova Teotônia, 27.1833°S, 52.3833°W, 500m, 1f#, v.1952, F. Plaumann (MZSP), 11f#, (MZSP).

Distribution. Northern Argentina, Brazil, and Bolivia.

Remarks. After we dissected the *N. acromyrmecis* paratype and *N. wasmanni* from Borgmeier's material, compare to species' descriptions, and examined Borgmeier's drawings, we figured out that *N. wasmanni* is not the same species as *N. acromyrmecis*.

Summary of the main taxonomic changes

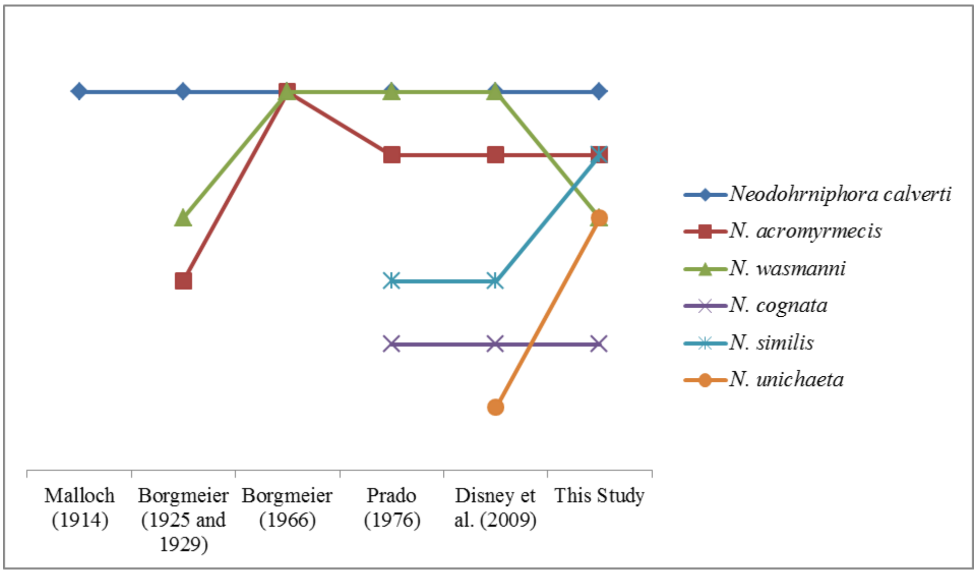


Fig B. Summary of the main taxonomic changes of described species, from their respective papers.

New species

***Neodohrniphora canina* sp.nov.** (as sp. nov. 4 in chapter 1)

(Figs 5, 18, 28, 35)

Diagnosis. Tg7 each side with a tooth posteriorly, close to apex (Fig. 18 – arrow). Movable lateral plate with two processes, the shorter in the dorsal part, chela crab-like. Lobe arm larger than globular lobe and sclerotized part in the shape of a hook, touching each other.

Description. Female. Body length 2.5 mm . **Head**. Frons brown dark, with 2–4–4–4 setae, without supra antennal setae. Position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae, and presence of setulae on frons. Antenna flattened, flagellomere 1 with arista subapical. Palpus yellow with distinct apical setae, 2 shorter setae, and two setulae rows. **Thorax**. yellow, being darkest on top. Thoracic scutum with one postpronotal seta, two notopleural setae, one intra-alar seta, one postalar seta and one pre-scutellar dorsocentral seta. Scutellum with an anterior posterior pair of setae. **Wing.** 2.04 mm long, 0.8 mm wide. Costal vein 0.85 mm. Costal ratios : 7.3:2.5:1. Around 50 costal cilia. Sc not reaching vein 1. Axillary ridge: alula with 4 setae, upper calyptra with 6. Basicosta with 3 setae and tegula with 6. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, Tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, with dorsal setula, and each side of the anteroventral part with 10 long feathered setae in a transverse row and with distinctly sclerotized insertion points; ventral part with 10 thick setae; and three filamentous setae on posteroventral part. Tg 2–5 Dark brown. **Oviscape**. Heavily sclerotized, dark brown. Tg7 each side with a tooth posteriorly and two irregular dorsal rows of 10 feathered macrosetae. In the posterior apex, two enlarged conical setae ventrally directed. S7 movable lateral plate with two processes, chela crab-like with 4 thin setae on dorsal part and 2 thick on ventral part. Dorsal base with 11 thick setulae. Globular lobe sclerotized with pointy posterior apex. Lobe arm bigger than globular lobe with 5 filamentous setae on unsclerotized part and long sclerotized part in the shape of a hook, touching each other. Hook shorter than movable lateral plate. Tg8 with rounded apex.

Distribution: Known from one site in French Guiana.

Etymology: The species is named after the presence of a structure tooth-like, or canine tooth, at the posterior part, close to the apex.

Material examined: Holotype f#. **FRENCH GUIANA**: **Regina**: Patawa, Kaw Mountain, 4.54°N, 52.15°W, 400m, i.2006, J.Cerda, Malaise trap[LACM ENT 234122].

Neodohrniphora gigantea **sp. nov.** (as sp. nov. 1 in chapter 1)

(Figs 5, 22, 29, 35)

Diagnosis. Movable lateral plate with two triangular processes, one short process directed downwards and the other long backward with apex inwards directed. Lobe arm longer than globular lobe, with a long sclerotized part facing backward.

Description. Female. Body length 2.8–3.0 mm . **Head.** Frons brown dark, with 4–4–4 setae, without supra antennal setae, position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae, and presence of setulae on frons. Antenna flagellomere 1 with arista subapical. Palpus yellow with distinct apical setae, 2 shorter setae, and two rows of setulae. **Thorax.** Yellow. Scutum with one postpronotal seta, two notopleural setae, one intra-alar seta, one postalar seta and two pre-scutellar dorsocentral setae, an anterior pair of long setae, and a posterior pair of setulae. Scutellum with an anterior pair of setulae and a posterior pair of long setae. **Wing.** 2.5 –2.6 mm long, 1.0 –1.2 mm wide. Costal vein 1.0–1.2 mm. Costal ratios 8.3:3:1. Around 65 costal cilia. Sc not reachinging vein 1. Axillary ridge: alula with 5 setae, upper calyptra with 6. Basicosta with 2 setae, tegula with 5 setae. Haltere knob brown. **Abdomen**. First abdominal tergite shorter than the others, second one elongated, and tergites 3–5 subequal in length. Sternites 1–5 unsclerotized. Segment 6 ring shape, with dorsal setula and each side of the segment with anteroventral region with 2–3 long feathered setae in a transverse row and with distinctly sclerotized insertion points; midventral region with 6–7 thick setae; and one filamentous setae on posteroventral region. Tergites 2–5 dark brown. **Oviscape**. Heavily sclerotized, dark brown. Tg7 with a parallel dorsal row of 8–10 feathered macrosetae on each side, in the apex with two setae ventrally directed. S7 with movable lateral plate with two triangular processes, one ventral short process downwards and the other dorsal long process backward, apex facing inwards, with 13 thick setae. Dorsal base with 7 thick setulae. Globular lobe with acuminate apex. Lobe arm longer than globular lobe, with one short seta and two filamentous setae on unsclerotized part and long sclerotized part facing backward. Hook longer than movable lateral plate. Tg8 with triangular apex.

Distribution: Colombia, Panama and Costa Rica,

Etymology: Named for the large dimensions of oviscape.

Material examined: Holotype f#. **COLOMBIA**: **Bolivar**: SFF Colorados, El Mirador, 9.9°N, 75.13°W, 400m, 3–18.viii.2001, E. Deulufeut col, CAP-2048, Malaise trap, (LACM) [LACM ENT 186482].

Paratypes. **COLOMBIA**: **Bolivar**: SFF Colorados, Alto El Mirador, 9.9°N, 75.13°W, 180m, 2f#, 26.xii–10.i.2002, E. Deulufeut col, CAP-2934, Malaise trap SFF Colorados, Alto El Mirador, 9.9°N, 75.12°W, 180m, 2f#, 26.xii–10.i.2002, E. Deulufeut col, CAP-2934, Malaise trap SFF Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 1f#, 6 – 24.x.2001, E. Deulufeut col, Malaise (LACM), 5f#, 3–18.ix.2001, E. Deulufeut col, CAP-2162, Malaise trap (LACM), 1f#, 3–18.ix.2001, E. Deulufeut col, CAP-2162, Malaise trap (LACM), 3f#, 3–18.viii.2001, E. Deulufeut col, CAP-2048, Malaise trap (LACM), 12f#, 18.viii–3.ix.2001, E. Deulofeut, CAP-2051, Malaise trap (LACM), SFF Los Colorados, Alto El Mirador, 9.54°N, 75.7°W, 400m, 1f#, 18.vii–3.viii.2001, E. Deulufeut col, Malaise (LACM), 2f#, 18.vii–3.viii.2001, E. Deulufeut col, Malaise (LACM). **COSTA RICA**: **Limon**: 16km W Guapiles, 10.15°N, 83.92°W, 400m, 1f#, iii–v.1990, P. Hanson col, Malaise (LACM); **Puntarenas**: 5km SW Rincon, Tropical Youth Center, 8.7°N, 83.51°W, 40m, 1f#, 31.v–7.vi.1998, B. Brown, V. Berezovskiy, Malaise trap #3 (LACM). **PANAMA**: **Canal Zone**: Barro Colorado Island, 9.17°N, 79.83°W, 1f#, 2–9.vi.1993, J. Pickering col, Malaise (LACM), 1f#, 7–21.ix.1994, J. Pickering col, Malaise trap #2441 (LACM).

Other material examined. **COLOMBIA**: **Bolivar**: SFF Colorados, Alto El Mirador, 9.9°N, 75.12°W, 180m, 1f#, 26.xii–10.i.2002, E. Deulufeut col, CAP-2934, Malaise trap SFF Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 8f#, 18.viii–3.ix.2001, E. Deulofeut, CAP-2051, Malaise trap (LACM), 10f#, 3–18.ix.2001, E. Deulufeut col, CAP-2162, Malaise trap (LACM), 1f#, 6–24.x.2001, E. Deulufeut col, CAP-2417, Malaise trap (LACM), 4f#, 22.ix–7.x.2001, E. Deulufeut col, CAP-2165, Malaise trap (LACM), 1f#, 3–18.viii.2001, E. Deulufeut col, CAP-2048, Malaise trap (LACM), SFF Los Colorados, Alto El Mirador, 9.54°N, 75.7°W, 400m, 9f#, 18.vii–3.viii.2001, E. Deulufeut col, Malaise (LACM). **COSTA RICA**: **Heredia**: La Selva Biological Station, 10.43°N, 84.02°W, 40m, 1f#, 15.xi.1993, ALAS, Malaise trap M/08/270 (LACM), 1f#, 15.vii.1993, ALAS, Malaise trap M/12/162 (INBC), 1f#, 1.vi.1993, ALAS, Malaise trap M/12/118 (LACM), 1f#, 1–15.iv.1993, ALAS, Malaise trap M/16/079 (INBC), 1f#, 1.vii.1993, ALAS, Malaise trap M/12/146 (INBC), 1f#, 14.vi.1993, ALAS, Malaise trap M/02/125 (INBC), 1f#, 14.vi.1993, ALAS, Malaise trap M/12/134 (INBC), 1f#, 2.vi.1993, ALAS, Malaise trap M/15/121 (INBC); **Puntarenas**: 5km W Piedras Blancas, 8.77°N, 83.28°W, 100m, 1f#, i.1993, P. Hanson col, Malaise trap (LACM). **PANAMA**: **Canal Zone**: Barro Colorado Island, 9.17°N, 79.83°W, 2f#, 1–8.ix.1994, J. Pickering col, Malaise trap #1695 (LACM), 2f#, 12–19.v.1993, J. Pickering, Malaise trap #942 (LACM), 1f#, 7–14.vii.1993, J. Pickering col, Malaise trap #974 (LACM), 2f#, 7–21.ix.1994, J. Pickering col, Malaise trap #2441 (LACM), 2f#, 2–9.vi.1993, J. Pickering col, Malaise trap #945 (LACM), 1f#, 2–9.x.1996, J. Pickering col, Malaise trap #6942 (LACM), 1f#, 18–25.xi.1992, J. Pickering col, Malaise trap #727 (LACM), 2f#, 28.vii–4.viii.1993, J. Pickering col, Malaise trap #991 (LACM).

***Neodohrniphora* mokana** (as sp. nov. 5 in chapter 1)

(Figs 7, 23, 30, 35)

Diagnosis. Tg7 with two parallel dorsal rows of feathered macrosetae on each side; Movable lateral plate with two triangular processes, one short process ventrally directed, and the other long facing posteriorly with apical facing backward. Dorsal base with thick setulae. Globular lobe without pointy posterior apex. Lobe arm shorter than globular lobe with one short setae and two filamentous setae on unsclerotized part and sclerotized part ventrally directed.

Description. Female. Body length 1.8–2.1 mm. **Head**. . Frons brown, with 4–4–4 setae, without supra antennal setae, position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae, and presence of setulae on frons. Antenna. Flagellomere 1 with arista subapical (Fig. 1). Palpus yellow with distinct apical setae, 2 shorter setae, and two setulae rows. **Thorax.** Yellow, being darkest on top. Thoracic scutum with one postpronotal seta, two notopleural setae, one intra-alar seta, one postalar seta and one pre-scutellar dorsocentral seta. Scutellum with an anterior pair of setulae (subequal to acrostichal hair) and a posterior pair of long setae. **Wing.** 1.7–2.0 mm long, 0.6–0.7 mm wide. Costal vein 0.7 mm. Costal ratios : 6.9:3.9:1. Around 50 costal cilia. Sc not reaching vein 1. Axillary ridge: alula with 5 setae, upper calyptra with 5. Basicosta with 3 setae and tegula with 3. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, with dorsal setula and each side of the segment: anteroventral part with 5–6 long feathered setae in a transverse row and with distinctly sclerotized insertion points; ventral part with 10–15 thick setae; and four filamentous setae on posteroventral part. Tergite 2–5 dark brown with sides darker than the center. **Oviscape.** Heavily sclerotized, dark brown. Tg7 with two parallel dorsal rows of 10–12 feathered macrosetae on each side, in the posterior apex two different setae ventrally directed. S7 with movable lateral plate with two triangular processes, one short process ventrally directed and the other long facing posteriorly with apical facing backward, with 10 thick setae. Dorsal base with 8 thick setulae. Globular lobe without pointy posterior apex. Lobe arm shorter than globular lobe with one short setae and two filamentous setae on unsclerotized part and sclerotized part ventrally directed. Hook shorter than movable lateral plate. **Tg8** with rounded apex.

Distribution: Known from Colombia.

Etymology: Named after the Mokaná indigenous people, who inhabits in the Department of Bolivar, Colombia, where most oftype material was collected.

Material examined: Holotype. f#. **COLOMBIA**: **Bolivar**: SFF Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 3–18.ix.2001, E. Deulufeut col, CAP-2162, Malaise trap, (LACM) [LACM ENT 186350].

Paratypes. **COLOMBIA**: **Bolivar**: PNN Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 1f#, 3–18.ix.2001, E. Deulufeut col, Malaise (LACM), SFF Colorados, Alto el Mirador, 9.9°N, 75.12°W, 180m, 1f#, 22.xii.2001–10.i.2002, E. Deulufeut col, CAP-2165, Malaise trap (LACM), SFF Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 4f#, 14–30.i.2002, E. Deulufeut col, Malaise trap CAP-2935 (LACM), 4f#, 22.ix–7.x.2001, E. Deulufeut col, CAP-2165, Malaise trap (LACM), 6f#, 18.viii–3.ix.2001, E. Deulofeut, CAP-2051, Malaise trap (LACM), 1f#, 18.viii–3.ix.2001, E. Deulufeut col, Malaise (LACM), 1f#, 3–18.viii.2001, E. Deulufeut col, CAP-2048, Malaise trap (LACM), 1f#, 18.vii–3.viii.2001, E. Deulofeut, CAP-2051, Malaise trap (LACM), 5f#, 3–18.ix.2001, E. Deulufeut col, CAP-2162, Malaise trap (LACM), SFF Los Colorados, Alto el Mirador, 9.54°N, 75.7°W, 400m, 1f#, 18.vii–3.viii.2001, E. Deulofeut, CAP-1725, Malaise trap (LACM); **Magdalena**: PNN Tayrona, Gairaca, 11.33°N, 74.03°W, 5m, 1f#, 22.ii–5.iii.2001, R. Henriquez col, CAP-1350, Malaise trap (LACM), 1f#, 22.ii–5.iii.2001, R. Henriquez col, Malaise (LACM), PNN Tayrona, Neguanje, 11.33°N, 74.03°W, 10m, 1f#, 21.ii–15.iii.2001, R. Henriquez col, CAP-1351, Malaise trap (LACM).

Other material examined. COLOMBIA: **Bolivar**: PNN Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 15f#, 3–18.ix.2001, E. Deulufeut col, Malaise (LACM), SFF Colorados, Alto El Mirador, 9.9°N, 75.12°W, 180m, 7f#, 22.xii.2001–10.i.2002, E. Deulufeut col, CAP-2934, Malaise trap (LACM), 9f#, 14–30.i.2002, E. Deulufeut col, Malaise trap CAP-2935 (LACM), SFF Colorados, Alto El Mirador, 9.9°N, 75.12°W, 400m, 7f#, 22.xii.2001–10.i.2002, E. Deulufeut col, CAP-2934, Malaise trap (LACM), 9f#, 14–30.i.2002, E. Deulufeut col, Malaise trap CAP-2935 (LACM), SFF Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 18f#, 18.viii–3.ix.2001, E. Deulufeut col, Malaise (LACM), 4f#, 3–18.viii.2001, E. Deulufeut col, CAP-2048, Malaise trap (LACM), SFF Colorados, La Suiris, 9.9°N, 75.12°W, 126m, 2f#, 16–31.xii.2000, E. Deulufeut col, CAP-948, Malaise trap (LACM), SFF Colorados, La Yaya, 9.9°N, 75.12°W, 280m, 1f#, 22.ix–7.x.2001, E. Deulufeut col, Malaise (LACM), SFF Los Colorados, Alto El Mirador, 9.54°N, 75.7°W, 400m, 6f#, 18.vii–3.viii.2001, E. Deulufeut col, Malaise (LACM), 3f#, 22.v–7.vi.2001, E. Deulofeut, CAP-1725, Malaise trap (LACM), SFF Los Colorados, Alto el Mirador, 9.9°N, 75.12°W, 400m, 6f#, 18.vii–3.viii.2001, E. Deulufeut col, Malaise (LACM), 3f#, 22.v–7.vi.2001, E. Deulofeut, CAP-1725, Malaise trap (LACM), SFF Los Colorados, El Mirador, 9.9°N, 75.12°W, 400m, 24f#, 22.ix–7.x.2001, E. Deulufeut col, Malaise (LACM), 9f#, 3–18.ix.2001, E. Deulufeut col, Malaise (LACM); **Magdalena**: PNN Tayrona, Gairaca, 11.33°N, 74.03°W, 5m, 3f#, 22.ii–5.iii.2001, R. Henriquez col, CAP-1350, Malaise trap (LACM), 1f#, 5–21.iii.2001, R. Henriquez col, CAP-1479, Malaise trap (LACM), PNN Tayrona, Neguanje, 11.33°N, 74.03°W, 10m, 1f#, 21.ii–5.iii.2001, R. Henriquez col, CAP-1351, Malaise trap (LACM), PNN Tayrona, Palangana, 11.33°N, 74.03°W, 30m, 5f#, 21.ii–5.iii.2001, R. Henriquez col, CAP-1352, Malaise trap (LACM); **Valle de Cauca**: PNN Farallones de Cali, Alto Anchicaya, 3.43°N, 76.8°W, 650m, 1f#, 24.iv–8.v.2001, S.Sarria, CAP-1900, Malaise trap (LACM).

***Neodohrniphora pseudoacromyrmecis* sp. nov.** (as sp. nov.7 in chapter 1)

(Figs 8, 19, 31, 36)

Neodohrniphora acromyrmecis nec Borgmeier, 1925*:* Prado, 1976: 590, figs. 66–67 (misindetification).

Diagnosis. Movable lateral plate with two processes, one ventral short ventrally directed, and the other dorsal long with setae on anterior and posterior half. Lobe arm longer than globular lobe, with a long sclerotized part and a hook–shaped fold at the apex facing inwards.

Description. Female. Body length 1.7 mm**. Head**. Frons dark brown, with 4–4–4 setae, without supra antennal setae, position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto–orbital setae, and presence of setulae on frons. Antenna. Flagellomere 1 with arista subapical. Palpus yellow with distinct apical setae, 2 shorter setae and two setulae rows. **Thorax**. Yellow, scutum with one postpronotal seta, two notopleural setae, one intra–alar seta, one postalar seta and one pre–scutellar dorsocentral seta. Scutellum with an anterior pair of setulae (subequal to acrostichal hair) and a posterior pair of long setae. **Wing.** 1.9 mm long, 0.69 mm wide. Costal vein 0.79 mm. Costal ratios : 6.4:2.4:1. Around 60 costal cilia. Sc not reaching vein 1. Axillary ridge: alula with 4 setae, upper calyptra with 5 setae. Basicosta with 2 and tegula with 5 setae. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, with dorsal setula and each side of the segment: anteroventral part with 8–9 long feathered setae of different sizes in a transverse row and with distinctly sclerotized insertion points; ventral part with setae; and three different and filamentous setae on posteroventral part. Tg 2–5 dark brown with sides darker than the center. **Oviscape**. Heavily sclerotized, dark brown. Tg7 with two parallel dorsal rows of 4 small macrosetae on each side, in the posterior apex two different setae ventrally directed. S7 with movable lateral plate with two processes, one ventrally directed and another long with setae (9–12) presenting before and after presenting before and after the half way point. Dorsal base with 10 thick setulae. Globular lobe with two rounded lobes, lobe arm longer then globular lobe with two short setae and with filamentous setulaeon unsclerotized part and long sclerotized with a fold in the apex facing inwards. Hook shorter than movable lateral plate Tg8 with rounded apex.

Distribution: Missiones, Argentina.

Etymology: This new species is named since it was considered as *N. acromyrmecis* for the last 40 years.

Remarks: After dissecting the paratype of *N. acromyrmecis* and compare it to Prado's (1976) drawing, we concluded that he did not examined and drawed *N. acromyrmecis*, but a new species, which is described herein. As *N. cognata*, the examined material of Prado 1976 was not found.

Material examined: Holotype. f#. ARGENTINA: Missiones: Reserva Vida Silvestre Urugua–í, 25.97°S, 54.11°W, 400m, 7–9.xiii.2003, B. Brown, G. Kung, Malaise #1, (LACM) [LACM ENT 186000].

***Neodohrniphora* queirozi sp. nov.** (as sp. nov. 6 in chaper one)

(Figs 9, 20, 32, 36)

Diagnosis. Movable lateral plate with only one elongate slightly sclerotized rounded process, parallel to Tg7. Lobe arm shorter than globular lobe and sclerotized part ventrally directed. Hook with dorsal process and tip flattened dorsoventrally

Description. Female. Body length 1.9–2.1 mm . **Head.** Frons dark brown, with 4–4–4 setae, without supra antennal setae, Position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae and presence of setulae on frons. Antenna. Flagellomere 1 with arista subapical. Palpus yellow with distinct apical setae, 2 shorter setae and two setulae rows .**Thorax.** Yellow. Thoracic scutum with one postpronotal seta, two notopleural setae, one intra–alar seta, one postalar seta and one pre–scutellar dorsocentral seta. Scutellum with an anterior pair of setulae (subequal to acrostichal hair) and a posterior pair of long setae. **Wing.** 2.1 mm long, 0.8 mm wide. Costal vein 0.8. Costal ratios: 9.8: 3.5:1. Around 60 costal cilia. Sc not reaching vein 1. Axillary ridge: alula with 4 setae, upper calyptra with 6. Basicosta with 3 setae and tegula with 4. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, without dorsal setula and each side of the segment:

anteroventral part with 7–8 long feathered setae of different sizes in a transverse row and with distinctly sclerotized insertion points; ventral part without setae; and two different and filamentous setae on posteroventral part. **Oviscape**. Heavily sclerotized, dark brown. Tg7 with one parallel dorsal row of 4 small macrosetae on each side, in the posterior apex two different setae ventrally directed. S7 with movable lateral plate with only one elongate rounded process posteriorly facing with 4–5 setae. Dorsal base with 4 thick setulae. Globular lobe without pointy posterior apex. Lobe arm shorter than globular lobe with three filamentous setae on unsclerotized part and sclerotized part ventrally directed. Hook shorter than movable lateral plate, flattened dorsoventrally and with a dorsal structure. Tg8 thick with rounded apex.

Distribution: Rio de Janeiro – Brazil.

Etymology: Named for Dr. Jarbas Queiroz, a Brazilian ant researcher who coordinated the projects from which the type material were collected.

Material examined: Holotype. f#. **BRAZIL**: **Rio de Janeiro**: Cachoeiras de Macacu, Regua, 22.416°S, 42.733°W, ii.2012, L. Elizalde, Over *Acromyrmex niger* A1T8, (MZSP) [MZSP EDP 00112].

Paratypes. **BRAZIL**: **Rio de Janeiro**: Cachoeiras de Macacu, Regua, 22.416°S, 42.733°W, 1f#, 26.01.2015, Barrera, C, Over *Acromyrmex niger* MC2I1–3 (MZSP), 2f#, ii.2012, L. Elizalde, Over *Acromyrmex niger* A1T8 (MZSP), 1f#, 26.01.2016, Barrera, C, Over *Acromyrmex niger* MC1I5 (MZSP), Vassouras, 22.216°S, 43.633°W, 1f#, ii.2012, L. Elizalde (MZSP).

***Neodohrniphora rapunzel* sp. nov.** (as sp. nov. 2 in chapter one)

(Figs10, 21, 33, 35)

Diagnosis. Tg7 with a parallel dorsal row of very long feathered macrosetae, some the same length of the Tg7 Movable lateral plate with two long and thin processes, one process facing down and the other long backward Dorsal base keel shaped dorsal part (best seen in lateral view) with 2–3 small and thin setulae. Globular lobe sclerotized rounded. Lobe arm bigger than globular lobe with sclerotized apex part facing down.

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Description. Female. Body length 2.0–2.1 mm. **Head.** . Frons brown, with 4–4–4 setae, without supra antennal setae, position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae, and presence of setulae on frons. Antenna flattened, flagellomere 1 conical with arista subapical. Palpus yellow with one distinct apical setae, 2 shorter setae and two setulae rows. **Thorax.** Yellow, being darkest on top. Thoracic scutum with one postpronotal seta, two notopleural setae, one intra–alar seta, one postalar seta and one pre–scutellar dorsocentral seta. Scutellum with an anterior pair of setulae (subequal to acrostichal setae) and a posterior pair of long setae. **Wing.** 2.3–2.8 mm long, 1.0 mm wide. Costal vein 1.0–1.2 mm. Costal ratios : 6.5:3.1:1. Around 50 costal cilia. Sc not reaching vein 1. Axillary ridge: alula with 5 setae, upper calyptra with 8 setae. Basicosta with 3 setae and tegula with 4 setae. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, with few and sparse dorsal seta and each side of the segment: anteroventral part with 5–6 long feathered setae in a transverse row and with distinctly sclerotized insertion points; ventral part with few or no setae; and posteroventral with three different setae shorter and thinner than anteroventral. Tg 2–5 dark brown with sides darker than the center. **Oviscape.** Heavily sclerotized, dark brown. Tg7 with a parallel dorsal row of 8–10 very long feathered macrosetae on each side, some the same length as the Tg7, in the posterior apex two different setae ventrally directed. S7 with movable lateral plate with two long and thin processes, one process facing down and another long backward, with four thick setae. Dorsal base keel shaped dorsal part (best seen in lateral view) with 2–3 small and thin setulae. Globular lobe sclerotized rounded. Lobe arm bigger than globular lobe with one short setae and sclerotized apex part facing down like a cat nail. Hook shorter than movable lateral plate Tg8 with Globular apex.

Distribution: Colombia: Huila. Ecuador: Napo.

Etymology: This species has long setae on segment 7, like the hair of *Rapunzel* (Brothers Grimm).

Material examined: Holotype. f#. **COLOMBIA**: **Huila**: PNN Cueva de Los Guácharos, Mirador, 1.62°S, 76.11°W, 1980m, 18.ii–07.iii.2002, F. Quevedo, Malaise–CAP-3039, (LACM) [LACM ENT 232503].

Paratype(s). **COLOMBIA**: **Huila**: PNN Cueva de Los Guácharos, Mirador, 1.62°S, 76.11°W, 1980m, 1f#, 18.ii–07.iii.2002, F. Quevedo, Malaise-CAP-3039 (LACM). **ECUADOR**: **Napo**: 2km S. Baeza, 0.488°S, 77.889°W, 2000m, 1f#, 21.ii.1979, H., A. Howden, Dung (LACM).

Remarks: Only collected around 2,000 m above sea level.

Neodohrniphora truncata **sp. nov.** (as sp. nov. 3 on chapter one)

(Figs 11–13,34)

Diagnosis. Movable lateral plate with two processes, one short and wide facing down and the other long and truncate. Lobe arm bigger than globular lobe, sclerotized part with a fold in the apex truncate, fold facing inwards.

Description. Female. Body length 2.3–2.7 mm . **Head**. . Frons dark brown, with 4–4–4 setae, without supra antennal setae. Position of fronto-dorsal row of setae with interfrontal setae more posterior than fronto-orbital setae and presence of setulae on frons. Antenna flattened, flagellomere 1 with arista subapical (Fig. 1). Palpus yellow with distinct apical setae, 2 shorter setae and two setulae rows. **Thorax.** Yellow. Thoracic scutum with one postpronotal seta, two notopleural setae, one intra–alar seta, one postalar seta and one pre–scutellar dorsocentral seta. Scutellum with an anterior pair of setulae (subequal to acrostichal hair) and a posterior pair of long setae. **Wing.** 2.3–

2.9 mm long, 1.0–1.2 mm wide. Costal vein 1.0–1.2 mm. Costal ratios: 4.5:3.1:1. Around 50 costal cilia. Sc not reaching vein R1. Axillary ridge: alula with 6 setae, upper calyptra with 6, basicosta 2, tegula with 5. Haltere knob brown. **Abdomen**. First abdominal segment shorter than the others, second one elongated, tergite 3–5 with approximately equal lengths. Sternite 1–5 unsclerotized. Segment 6 ring shape, with dorsal seta and each side of the segment: anteroventral part with 3 long feathered setae in a transverse row and with distinctly sclerotized insertion points; ventral part with around 40 setae; and posteroventral with three different setae shorter and thinner than anteroventral. Tg 2–5 dark brown with sides darker than the center. **Oviscape.** Heavily sclerotized, dark brown. Tg7 with a parallel dorsal row of 4–5 feathered macrosetae on each side, in the posterior apex two different setae ventrally directed. S7 with movable lateral plate with two processes, one short and wide process facing down and another long truncate, with 11 thick setae. Dorsal base with 4 thick setulae. Globular structure bilobed, the anterior with pointy apex. Lobe arm bigger then globular lobe with three setae and two filamentous setulae, the posterior much longer than anterior on unsclerotized part and long sclerotized part with a fold in the apex truncate facing inwards. Hook the same size as movable lateral plate. Tg8 with rounded apex. .

Distribution: Costa Rica.

Etymology: The name *truncata* (latin) refers to the truncate apex of the movable lateral plate and globular lobe arm.

Material examined: Holotype f#. **COSTA RICA**: **Guanacaste** : 14km S Cañas, 10.3°N, 85.09°W, 16–19.xi.1990, F. D. Parker (LACM) [LACM ENT 349987].

Paratypes. **COSTA RICA**: **Guanacaste**: 14km S Cañas, 10.3°N, 85.09°W, 1f#, 23–31.i.1990, F. D. Parker (LACM); **Limon**: 7 mil N Guácimo, 10.31°N, 83.68°W, 1f#, 22.ii–3.iii.1988, F. D. Parker (LACM); **San José**: Escazú, 9.91°N, 84.15°W, 1f#, 11–18.iv.1988, F. D. Parker (LACM), 1f#, 2–13.v.1988, F. D. Parker (LACM), 1f#, 19–24.iv.1988, F. D. Parker (LACM).

Key to species of *Neodohrniphora* (females)

In this work we found only 3% of all *Neodohrniphora* specimens with the ovipositors protracted (*e.g.,* Figs. 6, 7, 22 and 23), thus to visualize the necessary structures for an adequate identification dissection of the females is probably necessary (see Material and methods for details).

1 – Tg7 with a tooth posteriorly, close to apex; mov lat pl with two processes, the dorsal shorter than the ventral; mov lat pl chela crab–like (Fig. 18). . . . .***N. canina* sp.nov.**

– Tg7 without a tooth posteriorly; mov lat pl with one or two processes, but the dorsal never shorter than ventral; mov lat pl not like chela crab, (Figs 13–17, 19–23). 2

2 (1) –Mov. lat. pl. with one process (Figs 14, 16, 20);. 3

–Mov. lat. pl. with two processes (Figs. 13, 15, 17, 19, 21–23). 5

3 (2) – Mov. lat. pl. knife shape; lob. arm. parallel to the dorsal part of Tg7 (Fig. 16). . . . . ***N. cognata* Prado**

– Mov lat. pl. rounded; lob. arm. not–parallel to the dorsal part of Tg7 (Figs. 14,20). 4

4 (3) – Mov. lat. pl. short and compact, less than half the length of Tg7; hook without dorsal process and acuminate (Fig. 14) . . . .***N. acromyrmecis* Borgmeier**

– Mov. lat. pl. elongate, about half the length of Tg7; hook with dorsal process, and apex flattened dorsoventrally. (Fig. 20) . . . . ***N. queirozi* sp.nov.**

5 (2) – Lobe arm with only a sclerotized part; Mov. lat. pl. with the two processes dorsal and ventral long and thin; Tg7 with a dorsal parallel row of long setae, some of these setae as long as Tg7 (Fig.21). . . . .***N. rapunzel* sp. nov.**

–. Lobe arm clearly divided into an unsclerotized part and another sclerotized one; Mov. lat. pl with the dorsal and ventral not as above; Tg7 with a dorsal parallel row of short setae, shorter than length of Tg7 (Figs 13, 15, 17, 19, 22, 23). 6

6 (5) – Mov. lat. pl. with the two processes both in the posterior part (after the middle), one short ventral and the other dorsal divided at the posterior part; Tg7 posterior apex with two enlarged conical setae (Fig.15). . . . .***N. calverti* Malloch**

– Mov. lat. pl with one process in the anterior part; Posterior part and Tg7 not as above (Figs.13, 17, 19, 22, 23). 7

7 (6) – Mov. lat. pl with triangular and acute apex processes (Figs 22, 23). 8

– Mov. lat. pl without triangular processes and rounded apex (Figs 13, 17, 19) 9

8 (7) – Lob. arm parallel to the ventral part of Tg7; Tg7 with one parallel dorsal para row of macrosetae; Mov lat plate with the dorsal process apex facing inwards. (Figs 22). . . . .***N. gigantea* sp. nov.**

– Lob. arm not –parallel to the ventral part of Tg7; Two parallel dorsal row of macrosetae on Tg7; Mov lat plate with the dorsal process apex straight. (Figs 23). . . . . ***N. mokana* sp. nov.**

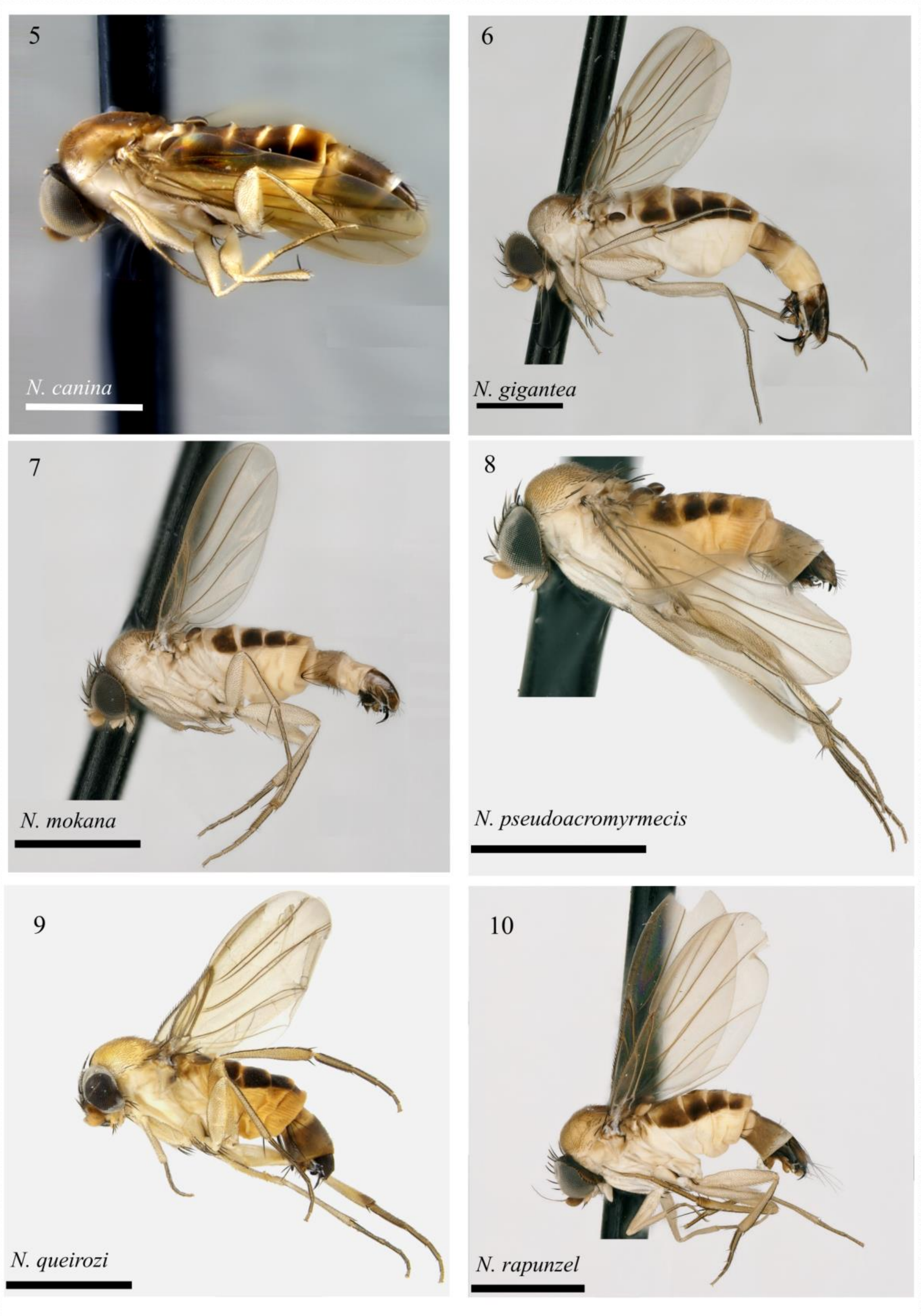
9 (7) – Mov. lat. pl. with the dorsal process with setae on anterior and posterior half; Lob. arm with the sclerotized part hook–shaped (Fig. 19). . . . . **N. *pseudoacromyrmecis* sp. nov.**

– Mov. lat. pl. with setae restricted to the anterior half; Lob. arm with the sclerotized part pointed or truncated (Figs. 13, 17). 10

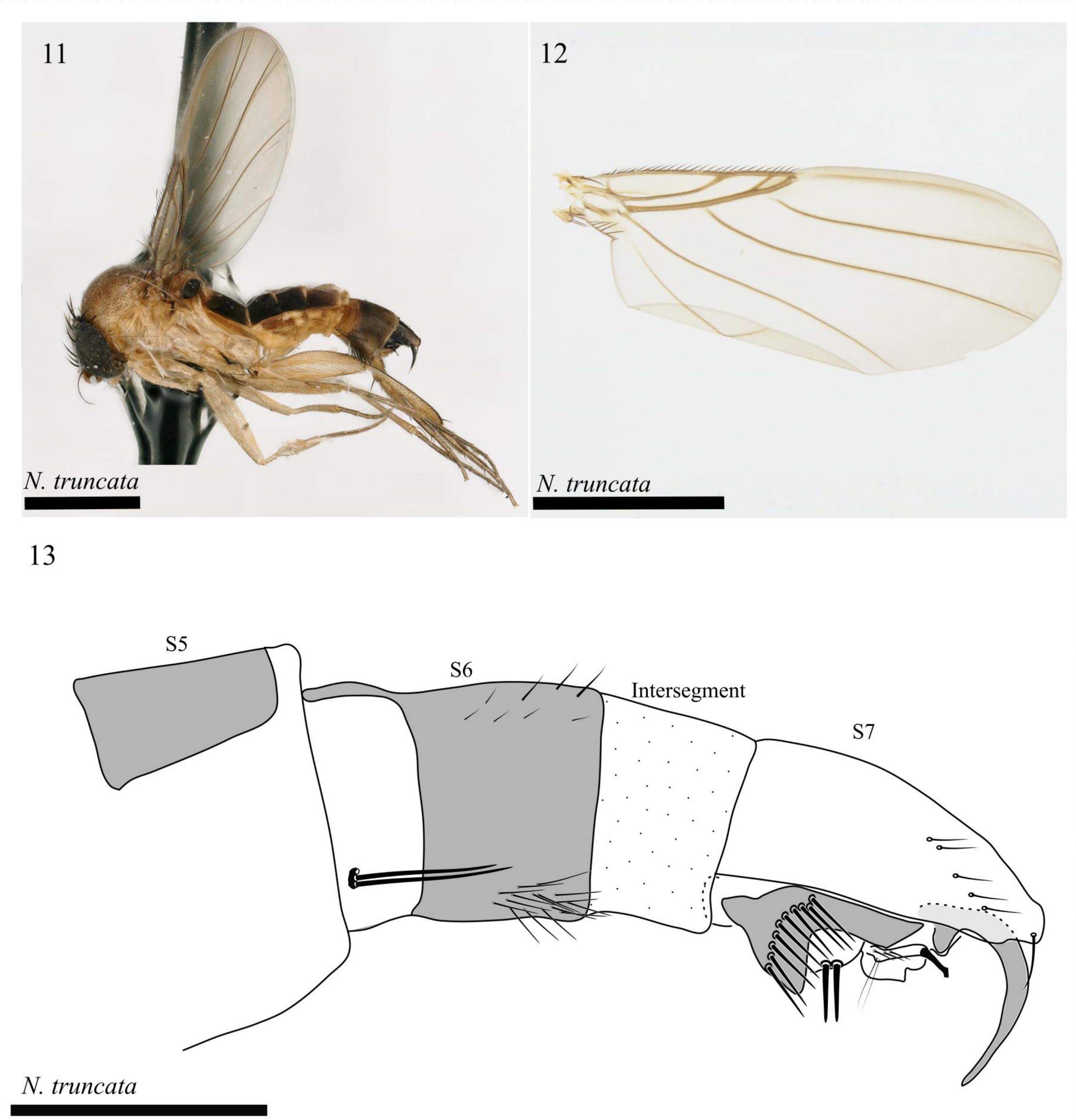
10 (9) – Mov. lat. pl. with the apex of dorsal process truncated. Lob. arm with the apex truncated (Fig 13). . . . . **N. *truncata* sp. nov**

– Mov. lat. pl with the apex of dorsal process rounded. Lob. arm and apex of sclerotized part of pointed (Figs 17) . . . .**N. *wasmanni*** Borgmeier

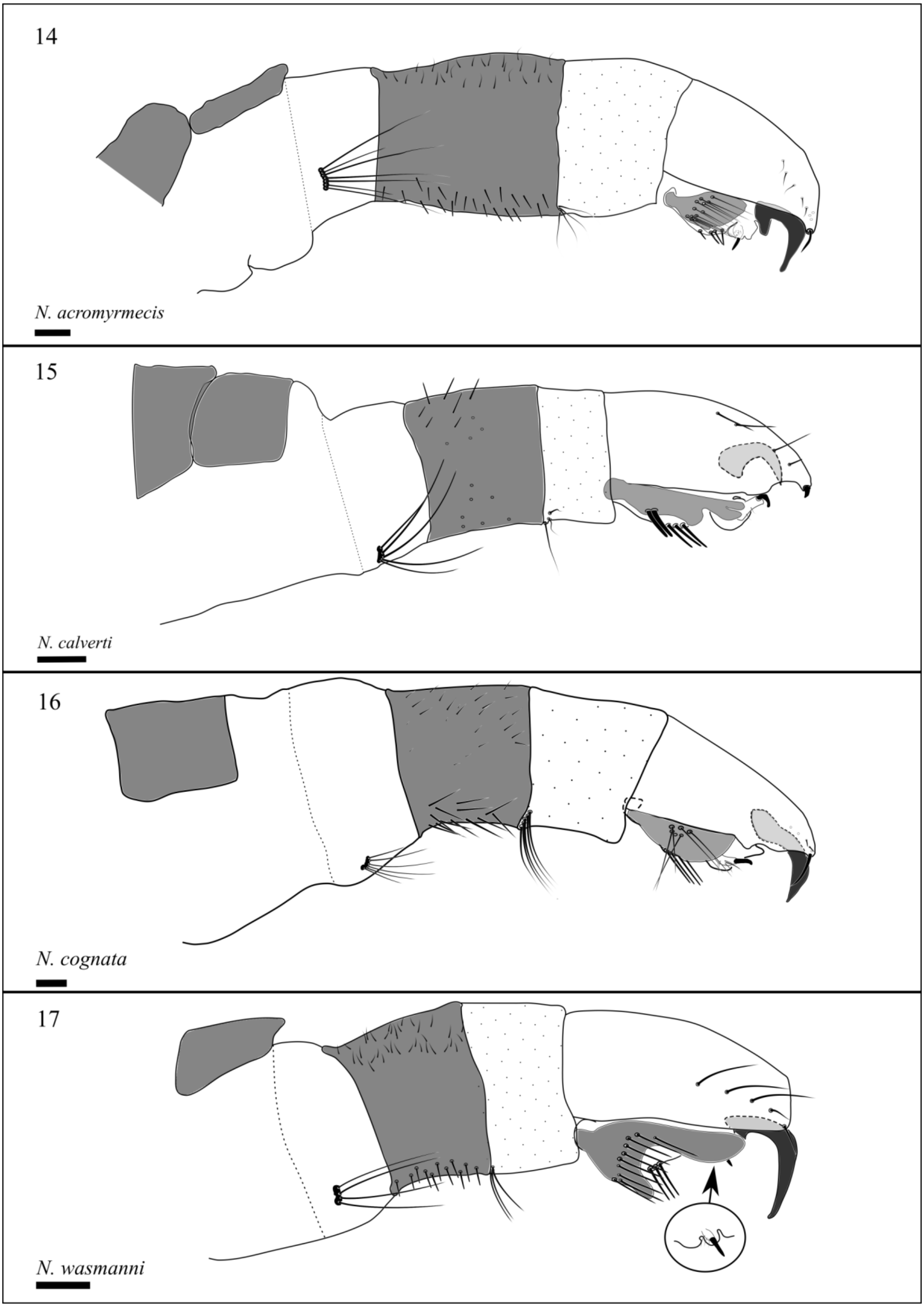
FIGURES 1–4. Habitus images (left lateral) of female *Neodohrniphora* spp. Scale bar = 0.50 mm.



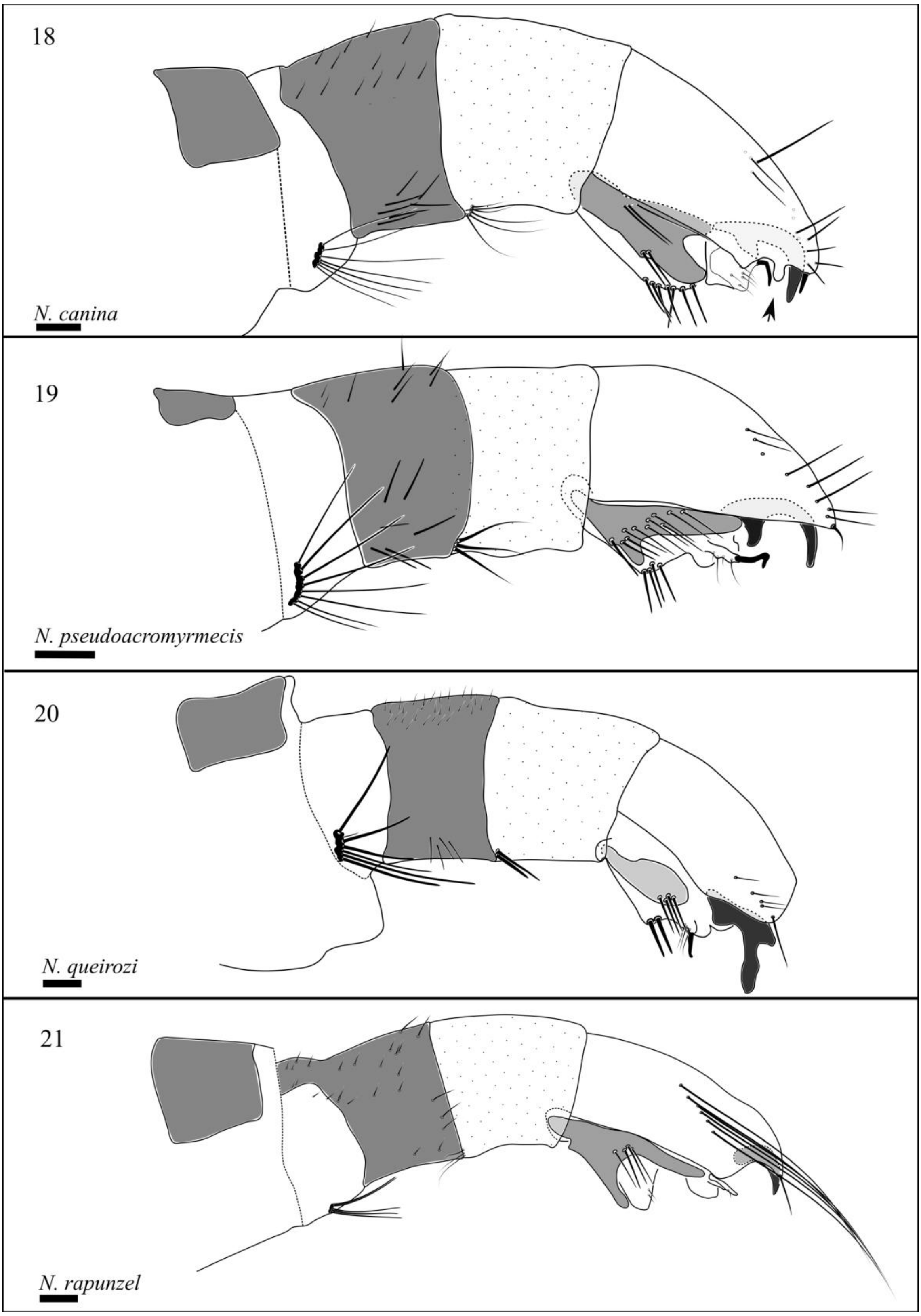
FIGURES 5–10. Habitus images (left lateral) of female *Neodohrniphora* **spp nov.**. Scale bar = 1.0 mm.



FIGURES 11–13 *Neodohrniphora truncata* **sp. nov***:* 11. Habitus image (left lateral). 12.Wing (dorsal). 13. Oviscape (left lateral). Scale bar = 1.0 mm.

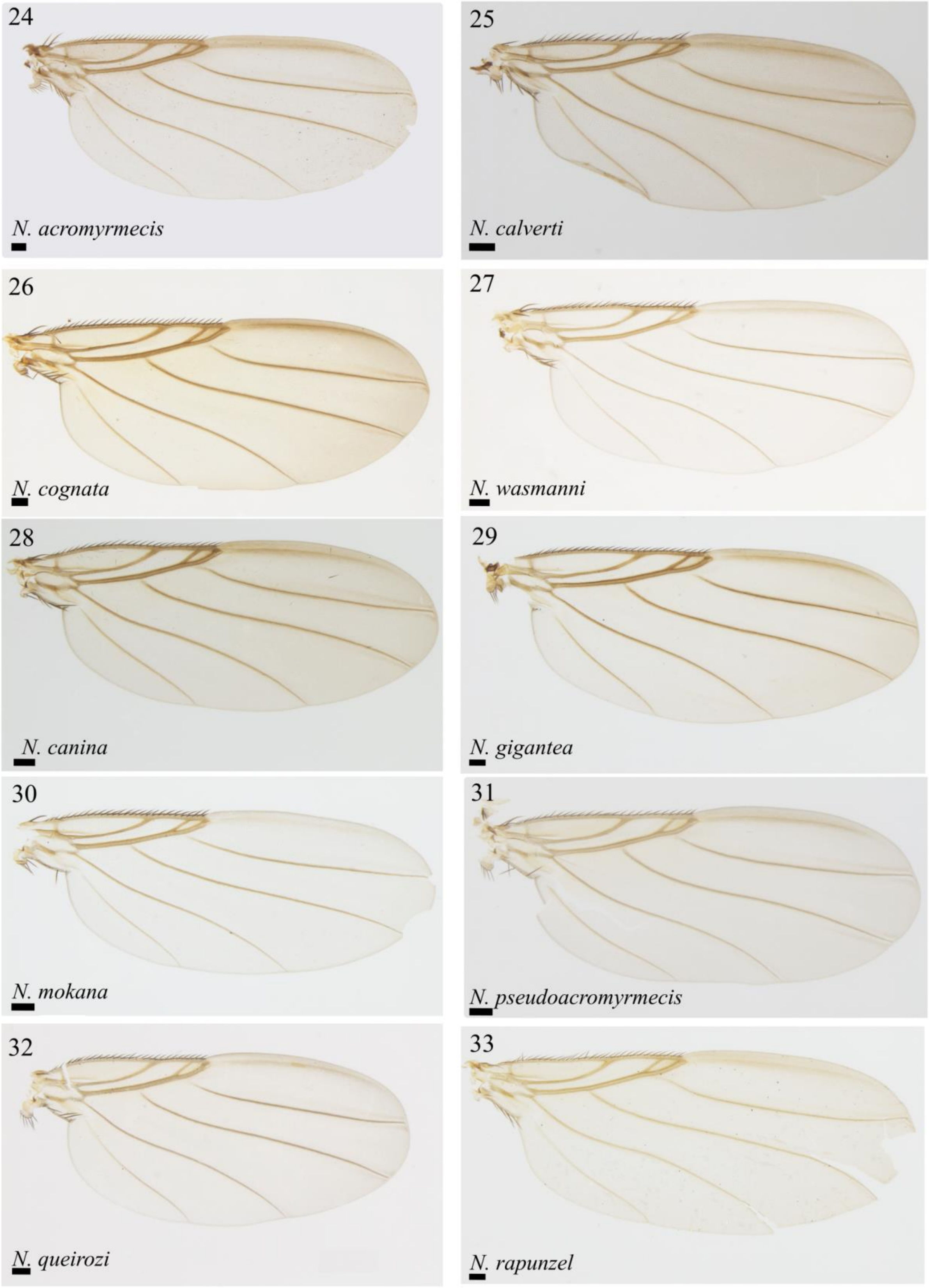


FIGURES 14–17. Oviscape (left lateral) images of female *Neodohrniphora* spp. Scale bar = 0.10 mm.



FIGURES 18–21. Oviscape (left lateral) images of female *Neodohrniphora* **spp. nov.** Scale bar = 0.10 mm.

FIGURES 22–23. Oviscape (left lateral) images of female *Neodohrniphora* spp. Scale bar = 0.10 mm.



FIGURES 24–27. Wings (dorsal) of female *Neodohrniphora* spp. 28–33. Wings (dorsal) of female *Neodohrniphora* **spp. nov.** Scale bar = 0.10 mm.

FIGURE 34 *Neodohrniphora* species distribution map. Triangles represent holotype and square paratypes and additional material. Blue represent *N. calverti* and red represent *N. truncata* **sp. nov**.

FIGURE 35 *Neodohrniphora* species distribution map. Yellow triangles represent *N. rapunzel* **sp. nov**. White squares represent *N. gigantea* **sp. nov**. Orange hexagon represent *N. mokana*. **sp. nov** Blue circle represent *N. cognata* **sp. nov**. Red rhombus represents *N. canina* **sp. nov**.

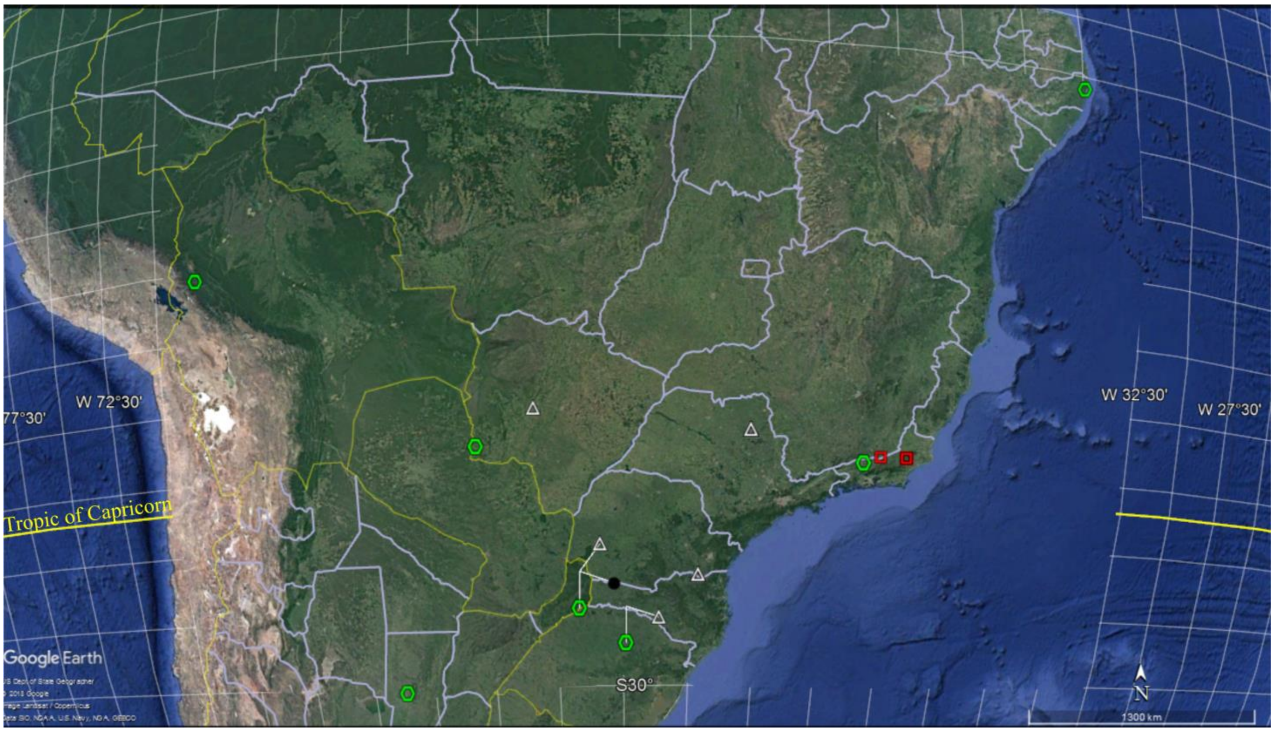


FIGURE 36 *Neodohrniphora* species distribution map. White triangles represent *N. acromyrmecis*. Red squares represent *N. queirozi* **sp. nov**. Green hexagons represent *N. wasmanni*. Black circle represent *N. pseudoacromyrmecis* **sp. nov**.

TABLE 2. *Neodohrniphora species* and their records on host ant species.

Phorid species	Host species	*References
***N. acromyrmecis* Borgmeier**	*Acromyrmex*	1
***N. calverti* Malloch**	Unknown	2
***N. canina* sp. nov.**	Unknown	New reference
***N. cognata* Prado**	*Acromyrmex octospinosus*	New reference
***N. gigantea* sp. nov**.	Unknown	New reference
***N. mokana* sp. nov.**	Unknown	New reference
N. pseudoacromyrmecis	Unknown	New reference

***N. queirozi* sp. nov.**	*Acromyrmex niger*	New reference
***N. rapunzel* sp. nov.**	Unknown	New reference
***N. truncata* sp. nov.**	Unknown	New reference
***N. wasmanni* Borgmeier**	*Acromyrmex crassispinus*	3
	Acromyrmex heyeri	
	Acromyrmex hispidus	

*Refs:1.Borgmeier (1925); 2. Prado (1976); 3. Disney *et al*. (2009).

Some references were not considered due to synonyms and possible divergences in the identifications made by the authors.

References

Ament, D.C & Pereira, T.P.L. 2019. Phoridae *In: Catálogo Taxonômico da Fauna do Brasil*. PNUD. Available in: <http://fauna.jbrj.gov.br/fauna/faunadobrasil/183530>. Accessed in: January/2019

Brues, C.T. 1915. A synonymic catalogue of the dipterous family Phoridae. *Bulletin of the Wisconsin Natural History Society,* 12, 85–152.

Borgmeier, T. 1925. Novos subsidios para o conhecimento da familia Phoridae. *Archivos do Museu Nacional do Rio de Janeiro,* 25, 85–281, pls. I–X4I.

Borgmeier, T. 1928. Investigacoes sobre Phorideos Myrmecophilos (Diptera-Phoridae). *Archivos do Instituto Biologico de Defesa Agricola e Animal São Paulo,* 1, 159–192.

Borgmeier, T. 1929. Ueber attophile Phoriden. *Zoologischer Anzeiger*. vol. 80 (Wasmann Festband) pp. 493–517, 24 figs.

Borgmeier, T. 1961. Weitere Beitraege zur Kenntnis der neotropischen Phoriden, nebst Beschreibung einiger *Dohrniphora*–Arten aus der indo–australischen Region (Diptera, Phoridae). *Studia Entomologica,* 4, 1–112.

Borgmeier, T. 1963. Revision of the North American Phorid Flies. Part 1. (Dipt. Phoridae). *Studia Entomologica,* 6, 1–256.

Borgmeier, T. 1966. Revision of the North American phorid flies. Part III. The species of the genus *Megaselia,* subgenus *Megaselia*. *Studia Entomologica,* 8(1965), 1–160.

Borgmeier, T. 1968. A catalogue of the Phoridae of the World (Diptera, Phoridae). *Studia Entomologica,* 11, 1–367

Borgmeier, T. 1971. Further studies on phorid flies, mainly of the Neotropical Region (Diptera, Phoridae). *Studia Entomologica,* 14, 1–172.

Brown, B.V. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea). *Memoirs of the Entomological Society of Canada*, 164, 1–144.

Brown, B.V. 2001. Taxonomic revision of *Neodohrniphora*, subgenus *Eibesfeldtphora* (Diptera: Phoridae). *Insect Systematics Evolution*, 32 (4), 393–409. http://dx.doi.org/10.1163/187631201x00272

Brown, B.V. 2004. Revision of the subgenus *Udamochiras* of *Melaloncha* bee–killing flies (Diptera: Phoridae: Metopininae). *Zoological Journal of the Linnean Society, 140*(1), 1–42.

Brown, B.V. 2010. Phoridae. 725–761. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M. & Zumbado, M.A. (Eds.): *Manual of Central American Diptera, Volume 1,* NRC Research Press, Ottawa, Canada, 729 pp.

Cumming, J.M & Wood, D.M. (2017) 3. Adult Morphology and Terminology. *In*: Kirk–Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families*. Suricata 4. SANBI Graphics & Editing, Pretoria, pp. 69–88.

Curran, C.H. 1934. The Diptera of Kartabo, Bartica District, British Guiana, with descriptions of new species from other British Guiana localities. *Bulletin of the American Museum of Natural History,* 66, 287–532.

Disney, R.H.L. 1994. *Scuttle flies: the Phoridae*. Chapman and Hall, London, xii + 467 pp.

Disney, R.H.L. 1996. A key to *Neodohrniphora* (Diptera: Phoridae), parasites of leaf–cutter ants (Hymenoptera: Formicidae). *Journal of Natural History*, 30(9), 1377–1389.

Disney, R.H.L. 2007. New species and revisionary notes on scuttle flies (Diptera: Phoridae) associated with Neotropical army ants (Hymenoptera: Formicidae). *Sociobiology,* 49 (3), 1–58.

Disney, R.H.L., Elizalde, L. & Folgarait, P.J. 2009. New species and new records of scuttle flies (Diptera: Phoridae) that parasitize leaf–cutter and army ants (Hymenoptera: Formicidae). *Sociobiology*, 5 (2), 601–632.

Guénard, B., Weiser, M., Gomez, K., Narula, N. & Economo, E.P. (2017) The Global Ant Biodiversity Informatics (GABI) database: a synthesis of ant species geographic distributions. *Myrmecological News,* 24, 83–89

Malloch, J.R. 1914. Costa Rican Diptera collected by Philip P. Calvert, Paper I. A partial report on the Borboridae, Phoridae and Agromyzidae, by J. R. Malloch. *Transactions of the American Entomological Society*, 40, 8–36, 1 plate. [1914.03.23].

Prado, A.P. do. 1976. Records and descriptions of phorid flies, mainly of the Neotropical Region (Diptera; Phoridae). *Studia Entomologica*, Petropolis, 19, 561–609."

PCAT – Phorid Catalog – Online data for phorid flies. Available in: < http://www.phorid.net/pcat/> Accessed in: January/2019

Schmitz, H. 1914. Die myremecophilen Phoriden der Wasmann'schen Sammlung. Mit Beschreibung neuer Gattungen und Arten und einem Verzichnis aller bis Anfang bekannten myrmecophilen und termitophilen Phoriden. *Zoologische Jahrbücher* (Syst.), 37, 509–566.

Schmitz, H. 1927. Revision der Phoridengattungen, mit Beschreibung neuer Gattungen und Arten. *Natuurhistorisch maandblad*. 16: 30–40., 45–50, 59–65, 72–79, 92–100, 110–116, 128–132, 142–148, 164, 176, figs.

Schmitz, H. 1929. Revision der phoriden nach forschungsgeschichtlichen und nomenklatorischen, systematischen und anatomischen biologischen und faunisischen gesichtspunkten. *Berlin und Bonn. F. Duemmler*, 211 p., 49 figs., 2 pis.

Schuh, R.T. 2000. *Biological Systematics: Principles and Applications*. Cornell University Press, New York. 236 pp,

Scotland, R.E. & Pennington, R.T. 2000. *Homology and Systematics: Coding Characters for Phylogenetic Analysis*. The Systematics Association Special Volume, Taylor & Francis, London & New York. 217 pp.

Schultz, T.R. & Meier, R. 1995. A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. *Systematic Entomology*, 20, 337–370.

Smith, P.T. & Brown, B.V. 2008. Utility of DNA sequences for inferring phylogenetic relationships and associating morphologically dissimilar males and females of the bee-killing flies, genus Melaloncha (Diptera: Phoridae). *Annals of the Entomological Society of America*, *101*(4), 713–721.

Thompson, F.C. 2008. *The Diptera site*. *The biosystematics database of world Diptera*. Nomenclator status statistics. Version 1 0.5. <http://www.sel.barc.usda.gov/diptera/ names/Statuslbdwdstat.htm >. Acessed on: January/2019.

Uribe, S., Brown, B.V., Braganca, M.A., Queiroz, J.M. & Nogueira, C.A. 2014. New species of *Eibesfeldtphora* Disney (Diptera: Phoridae) and a new key to the genus. *Zootaxa*, 3814(3), 443–450.

Zuha, R.M. & Disney, R.H.L. (2018). A new genus of scuttle fly (Diptera: Phoridae) from malaysia. *Serangga*, *23*(2), 92–98.

Discussão Geral e Conclusões

Análises cladísticas freqüentemente resultam em árvores com bom suporte de caracteres sinapomórficos e homoplásticos, permitindo que hipóteses mais sofisticadas sejam propostas com base nesses resultados. Quando comparado com inferências feitas por análises empíricas, mas com agrupamentos intuitivos sem uma metodologia objetiva e robusta, este estudo gerou uma base sólida para decisões taxonômicas e classificação dos gêneros estudados.

Os gêneros *Neodohrniphora, Cremersia e Eibesfeldtphora* foram recuperados como monofiléticos e válidos, rejeitando a proposta anterior de Disney *et al.* (2009), quando sinonimizou *Cremersia* com *Neodohrniphora.* Uma nova classificação para os gêmeros é proposta aqui e reconhecida.

Este trabalho foi importante para a compreensão comparativa e análise detalhada das estruturas genitais femininas dos parasitoides. Além também da descoberta de várias espécies novas do gênero *Neodohrniphora,* e da resolução de vários problemas encontrados na taxonomia do gênero.

Significativos progressos foram feitos também para o entendimento e propostas de homologias em terminálias femininas de Phoridae com base no exame cuidadoso de *Neodohrniphora, Cremersia* e *Eibesfeldtphora* e do grupo externo.

Pretendo nos meus estudos futuros ampliar os gêneros estudados adicionando mais espécies de *Pseudacteon* e *Apocephalus,* além de outros gêneros de parasitóides (Brown, 1992), com isso poderiam também ser esclarecidas as relações entre os gêneros do Grupo *Apocephalus*.

Outra barreira a ser superada no futuro é com relação aos machos dos parasitoides, um estudo detalhado integrando morfologia, molecular e morfometria provavelmente iluminará as incertezas que existem sobre o pareamento de casais. Depois disso, novos passos poderão ser dados no estudo e uso caracteres de machos para análises filogenéticas.

Referências Bibliográficas

Ament, D.C. & Amorim, D.S. 2010. Five new species of *Coniceromyia* Borgmeier (Diptera: Phoridae) from the Atlantic Forest, Brazil. Zootaxa, 2421, 35–48.

Ament, D.C. & Pereira T.P.L. Phoridae. Catálogo Taxonômico da Fauna do Brasil. Em preparação.

Bacci Jr, M., Solomon, S. E., Mueller, U. G., Martins, V. G., Carvalho, A. O., Vieira, L. G., & Silva-Pinhati, A. C. O. (2009). Phylogeny of leafcutter ants in the genus< i> Atta</i> Fabricius (Formicidae: Attini) based on mitochondrial and nuclear DNA sequences. Molecular phylogenetics and evolution, 51(3), 427-437.

Beyer, E. M. 1966. Neue und wenig bekannte Phoriden, zumeist aus dem Bishop Museum, Honolulu. Pac. Insects 8: 165-217.

Boehme, P., Amendt, J., Disney, R. H. L., & Zehner, R. 2010. Molecular identification of carrion-breeding scuttle flies (Diptera: Phoridae) using COI barcodes. International Journal of Legal Medicine, 124(6), 577-581.

Borgmeier, T. 1925. Novos subsidios para o conhecimento da familia Phoridae. Arch. Mus. Nac. Rio de Janeiro 25: 85-281, pls. I-XVII.

Borgmeier, T. 1926. Phorideos Myrmecophilos da Argentina (Dipt.). Bol. Mus. Nac. Rio de J.2: 1-16.

Borgmeier, T. 1928. Investigacoes sobre Phorideos Myrmecophilos (Diptera - Phoridae). Arch. Inst. Biol. Def. Agric. Amin. S. Paulo. 1: 159-192.

Borgmeier, T. 1961. Weitere Beitraege zur Kenntnis der neotropischen Phoriden, nebst Beschreibung einiger *Dohrniphora*-Arten aus der indo-australischen Region (Diptera, Phoridae). Stud. Ent. n. ser., 4: 1-112.

Borgmeier, T. 1963. Revision of the North American Phorid Flies. Part 1. (Dipt. Phoridae). Studia Ent.6: 1-256.

Borgmeier, T. 1971. Further studies on phorid flies, mainly of the Neotropical Region (Diptera, Phoridae). Studia Ent. 14: 1-172.

Bremer, K. 1994. Branch support and tree stability. Cladistics, 10: 295–304.

Brown, B.V. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridea). Memoirs of the Entomological Society of Canada 164: 1–144.

Brown, B.V. 2001. Taxonomic revision of *Neodohrniphora*, subgenus *Eibesfeldtphora* (Diptera: Phoridae). Insect Systematics Evolution, 32 (4), 393–409. http://dx.doi.org/10.1163/187631201x00272

Brown, B. V. 2009. Phoridae. 725-761. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M. & Zumbado, M.A. (Eds.): Manual of Central American Diptera, Volume 1, NRC Research Press, Ottawa, Canada, 729 pp.

Brown, B. V., & Smith, P. T. .2010. The bee-killing flies, genus Melaloncha Brues (Diptera: Phoridae): a combined molecular and morphological phylogeny. Systematic Entomology, 35(4), 649-657.

Brown, B.V., Braganca, M.A.L., Gomes, D.S., Queiroz, J.M. & Teixeira, M.C. 2012. Parasitoid phorid flies (Diptera: Phoridae) from the threatened leafcutter ant Atta robusta Borgmeier (Hymenoptera: Formicidae). Zootaxa, 3385, 33–38.

Brown, B. V., Souza Amorim, D., & Kung, G. A. 2015. New morphological characters for classifying Phoridae (Diptera) from the structure of the thorax. Zoological Journal of the Linnean Society, 173(2), 424-485.

Brues, C. T. 1915. Some new Phoridae from Java. J.N.Y. Ent. Soc. 23: 184-192.

Buck, M. 1997 A new genus and species of Phoridae (Diptera) from Central Europe with remarkably primitive male genitalia. Insect Systematics & Evolution. Vol. 28, Nº.3, pp. 351-359(9).

Cook, C. E., & Mostovski, M. B. 2002. 16S mitochondrial sequences associate morphologically dissimilar males and females of the family Phoridae (Diptera). *Biological Journal of the Linnean Society*, *77*(2), 267-273.

Cook, C. E., Austin, J. J., & Disney, R. H. L. 2004. A mitochondrial 12S and 16S rRNA phylogeny of critical genera of Phoridae (Diptera) and related families of Aschiza. *Zootaxa*, *593*, 1-11.

Coquillett, D. W. 1907. A new phorid genus with horny ovipositor. Can. Entomol. 39: 207-208.

Cristiano, M. P., Cardoso, D. C., & Fernandes-Salomão, T. M. (2013). Cytogenetic and molecular analyses reveal a divergence between *Acromyrmex striatus* (Roger, 1863) and other congeneric species: taxonomic implications. PloS one, 8(3), e59784.

Cumming, J.M. & Wood, D.M. 2009.Adult morphology and terminology. In: Brown, B.V. et al. (head ed.), Manual of Central

Disney, R.H.L. 1994. Scuttle flies: the Phoridae. Chapman and Hall, London, xii + 467 pp.

Disney, R. H. L. 1996 . A key to Neodohrniphora (Diptera: Phoridae), parasites of leaf-cutter ants (Hymenoptera: Formicidae). Journal of Natural History, 30(9), 1377-1389.

Disney, R. H. L. 2007. New species and revisionary notes on scuttle flies (Diptera: Phoridae) associated with Neotropical army ants (Hymenoptera: Formicidae). Sociobiology 49 (3): 1-58. [2007.??.??

Disney, R.H.L., Elizalde, L. & Folgarait, P.J. 2009. New species and new records of scuttle flies (Diptera: Phoridae) that parasitize leaf-cutter and army ants (Hymenoptera: Formicidae). Sociobiology, 5 (2), 601–632.

Disney, R. H. L. & Franquinho Aguiar, A. M. 2008. Scuttle flies (Diptera: Phoridae) of Madeira. Fragm. Faun. Warsaw. 51: 23-62.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution, 783-791.

Goloboff, P., Farris, S.; Nixon, K. 2000. TNT (Tree analysis using New Technology) (BETA) Published by the authors, Tucumán, Argentina.

Grimaldi, D. & Engel, M.S. 2005. Evolution of the Insects. xv + 755 pp. Cambridge, New York, Melbourne: Cambridge University Press

Hash, J. M., Brown, B. V., & Smith, P. T. 2011. Preliminary use of DNA sequences for Dohrniphora (Diptera: Phoridae) phylogeny and taxonomy.*Zootaxa*, *2991*, 13-20.

Hash, J. M., Brown, B. V., Smith, P. T., & Kanao, T. 2013. A molecular phylogenetic analysis of the genus *Dohrniphora* (Diptera: Phoridae). *Annals of the Entomological Society of America*, *106*(4), 401-409.

Kitching I.J,. Forey P.LHumphries, C.J.,. Williams D.M. 1998. Cladistics. (Second Edition), Oxford University Press, Oxford, p. xiii + 228

Plataforma Lattes-CNPq,< http://lattes.cnpq.br>, acesso em 05/08 de 2015.

Malloch, J. R. 1912. The insects of the Dipterous family Phoridae in the United States National Museum. Proceedings of the United States National Museum 43: 411-529."

Malloch, J. R. 1914. Costa Rican Diptera collected by Philip P. Calvert, Paper I. A partial report on the Borboridae, Phoridae and Agromyzidae, by J. R. Malloch. Trans. Am. Ent. Soc. 40: 8-36, 1 plate. [1914.03.23].

Marques, A. C., & Lamas, C. J. E. 2006. Taxonomia zoológica no Brasil: estado da arte, expectativas e sugestões de ações futuras. *Papéis Avulsos de Zoologia (São Paulo)*, *46*(13), 139-174.

Nickele, M. A., Pie, M. R., Reis Filho, W., & Penteado, S. D. R. C. 2013. Formigas cultivadoras de fungos: estado da arte e direcionamento para pesquisas futuras. *Pesquisa Florestal Brasileira*, *33*(73), 53-72.

Nixon, K. C. Winclada. 2002. Program and documentation distributed by the author.

Orr, M. (1992) Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology, 30 (6), 395–402. http://dx.doi.org/10.1007/bf00176174

Prado, A. P. do. 1976. Records and descriptions of phorid flies, mainly of the Neotropical Region (Diptera; Phoridae). Studia Entomologica, Petropolis 19: 561-609."

Schmitz, H. 1914. Die myremecophilen Phoriden der Wasmann'schen Sammlung. Mit Beschreibung neuer Gattungen und Arten und einem Verzichnis aller bis Anfang bekannten myrmecophilen und termitophilen Phoriden. Zool. Jb. (Syst.) 37: 509-566.

Schmitz, H. 1924. Een nieuwe phoride, Cremersia zikani n. g. n. sp. Natuurhist. Maandbl. 13: 32-34.

Schmitz, H. 1927. Revision der Phoridengattungen, mit Beschreibung neuer Gattungen und Arten. Nat. Maandbl. 16: 30-40., 45-50, 59-65, 72-79, 92-100, 110-116, 128-132, 142-148, 164, 176, figs.

Schuh, R.T. 2000. Biological Systematics: Principles and Applications. Cornell University Press, New York. 236 pp,

Scotland, R. E.; Pennington, R. T. 2000. Homology and Systematics: Coding Characters for Phylogenetic Analysis. Taylor e Francis London and New York. 217 pp. (The Systematics Association Special Volume).

Schultz, T.R. & Meier, R. 1995. A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. Systematic Entomology 20, 337-370.

Smith, P. T., & Brown, B. V. 2008. Utility of DNA sequences for inferring phylogenetic relationships and associating morphologically dissimilar males and females of the bee-killing flies, genus Melaloncha (Diptera: Phoridae).*Annals of the Entomological Society of America*, *101*(4), 713-721.

Smith, P. T., & Brown, B. V. 2010. A molecular phylogenetic analysis of genus *Anevrina* (Diptera: Phoridae), with the description of a new species and updated world key. *Zootaxa*, *2397*, 29-40.

Smith, P. T., & Brown, B. V. 2010. A molecular phylogenetic analysis of genus Anevrina(Diptera: Phoridae), with the description of a new species and updated world key. Zootaxa, 2397, 29-40.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular biology and evolution, 28(10), 2731-2739.

Thompson, F.C. 2008. The Diptera site. The biosystematics database of world Diptera. Nomenclator status statistics. Version 1 0.5. <http://www.sel.barc.usda.gov/diptera/ names/Statuslbdwdstat.htm >. Acesso: out/2013.

Uribe, S., Brown, B. V., Braganca, M. A., Queiroz, J. M., & Nogueira, C. A. 2014. New species of *Eibesfeldtphora* Disney (Diptera: Phoridae) and a new key to the genus. Zootaxa, 3814(3), 443-450.

Ward, P. S. 2010 “Taxonomy, phylogenetics, and evolution,” in Ant Ecology, L. Lach, C. L. Parr, K. L. Abbott *et al.*, Eds., pp. 3–17, Oxford University Press, New York, NY, USA.

Wetterer, J. K., Schultz, T. R., & Meier, R. 1998. Phylogeny of fungus-growing ants (Tribe Attini) based on mtDNA sequence and morphology. Molecular phylogenetics and evolution, 9(1), 42-47.

Wheeler, Q.D.; Raven, P.H. & Wilson, E.O. 2004. Taxonomy: impediment or expedient? Science, 303(5656):285.

Wiley, E. O., & Lieberman, B. S. 2011. Phylogenetics: theory and practice of phylogenetic systematics. John Wiley & Sons.