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ANA VALENTINA CASTRO HUERTAS

PHYLOGENETIC ANALYSIS WITH MORPHOLOGICAL CHARACTERS OF THE TRIBE METAPTERINI STÅL, 1859 AND TAXONOMIC REVISION OF THE GENUS *Ghilianella* SPINOLA, 1850 (HEMIPTERA: REDUVIIDAE: EMESINAE).

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

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Orientadora: Prof. Dra. Jocelia Grazia
Coorientador: Prof. Dr. Dimitri Forero

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Aprovada em ____ de ____________ de _____.

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Dedicado a mis abuelitos: *Helda Maria Castro Moreno*
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Éste doctorado es nuestro!

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SUMÁRIO

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CAPÍTULO IV. Revision and phylogenetic analysis of the genus *Ghilianella* Spinola, 1850 (Hemiptera: Reduviidae: Emesinae).

RESUMO

Metapterini Stål, 1859 pertence à Emesinae (Hemiptera: Reduviidae), apresenta ampla distribuição, e morfologicamente se caracteriza pelo conspícuo processo basal da série póstero-ventral do profemur e pela presença de polimorfismo alar. Na tribo há alta proporção de gêneros com espécies micropteras e ápteras. A única hipótese filogenética disponível para a subfamília assumiu Metapterini como monofilético, embora nunca tenha sido formalmente testado com metodos cladísticos. Além disso, conjuntos de dados moleculares não publicados sugerem parafilia do grupo. *Ghilianella* Spinola, 1850 é o gênero mais diversificado dentro de Metapterini, exclusivamente Neotropical, e com 72 espécies válidas. Morfologicamente se caracteriza pela série anteroventral do profemur composta por processos espiniformes misturas com setas simples, e genitália do macho simétrica, entre outros caracteres. Os objetivos desta tese são: 1) Testar o monofiletismo de Metapterini usando caracteres morfológicos numa análise cladística; 2) explorar a informatividade filogenética de caracteres morfológicos aqui propostos; 3) avaliar as relações filogenéticas entre os gêneros de Metapterini; 4) hipotetizar as relações filogenéticas entre os gêneros *Ghilianella*, *Ghinallelia* e *Liaghinella*, taxonomicamente problemáticos, para ajudar as suas delimitações e parentesco; e 5) apresentar a revisão taxonômica de *Ghilianella* explorando novos caracteres morfológicos para ajudar a delimitar as espécies.

Palavras Chave: Filogenia, Reduviidae, Emesinae, Metapterini, *Ghilianella*, caracteres morfológicos, revisão taxonômica

ABSTRACT

The assassin bug tribe Metapterini belongs to the subfamily Emesinae (Hemiptera: Reduviidae). Morphologically, it is characterized by the conspicuous basal process of the postero ventral series in the foreleg and the presence of the wing polymorphism, with high proportion of genera with micropterous and apterous species. The only available phylogenetic hypothesis for the subfamily assumed that Metapterini is monophyletic, although it has never been formally tested. In addition, unpublished molecular data sets suggest that this group might be paraphyletic. The genus *Ghilianella* Spinola, 1850 is the most diversified genus of the Metapterini, exclusively Neotropical with approximately 72 species. Morphologically, it is characterized by having the anteroventral and posteroventral setal series on the two distal thirds of the fore femur, the anteroventral series composed by spines and setae and not interrupted in the base, conspicuous posteroventral process located far from the base of the article, both process of the fore femur to the apical extreme end with acute dentiform process, symmetric phallus, among other characters. The goals of this study are to: 1) evaluate the monophyly of the tribe Metapterini with morphological characters; 2) explore novel morphological characters that may be informative for the phylogenetic analysis; 3) assess the phylogenetic relationships among the genera of Metapterini; 4) resolve the phylogenetic relationships among taxonomically problematic genera *Ghilianella, Ghinallelia,* and *Liaghinella*; and 5) undertake the taxonomic revision of the large genus *Ghilianella* exploring novel morphological characters to help delimit the species.

Keywords: Phylogeny, Reduviidae, Emesinae, Metapterini, *Ghilianella*, morphological characters, taxonomic revision.

INTRODUÇÃO GERAL

Os percevejos assassinos (Hemiptera: Reduviidae) correspondem a uma das maiores e morfologicamente mais diversas famílias de Hemiptera (Schuh and Slater 1995; Forero 2004; Weirauch 2008). Eles são considerados um grupo economicamente importante, por algumas espécies serem usadas como agentes de controle biológico, e algumas espécies de Triatominae são vetores da doença de Chagas (Lent and Wygodzinsky 1979). Análises filogenéticas no nível de subfamília estão disponíveis para Reduviidae, com caracteres morfológicos (Weirauch 2008) e moleculares (Weirauch and Munro 2009; Hwang and Weirauch 2012) Apesar disto, as relações entre gêneros dentro da subfamília e tribos ainda são pobremente conhecidas. Weirauch (2008) recupera Reduviidae como grupo monofilético tendo como sinapomorfias a presença de um sulco estridulatório e a presença de três glândulas abdominais dorsais em ambos os estágios imaturo e adulto. O sulco estridulatório tem sido amplamente utilizado como um caráter diagnóstico para a família, e também corrobora a inclusão de Elasmodeminae e Phymatinae em Reduviidae (Weirauch 2008).

Emesinae Amyot and Serville 1843, com aproximadamente 90 gêneros e mais de 900 espécies descritas (Rédei 2007; Rédei and Tsai 2010), é um grupo peculiar devido a três características morfológicas: o estreitamento progressivo do corpo com o alongamento dos apêndices, a frequente ocorrência de dimorfismo sexual (às vezes polimorfismo de asas) e a presença de genitália masculina assimétrica em alguns gêneros (Wygodzinsky 1966). Outros caracteres que definem o grupo são: a ausência de ocelos - exceto no gênero australiano *Armstrongocoris* Wygodzinsky, 1949-, as pernas anteriores raptoriais, alongamento da coxa anterior e a ausência de fóssula spongiosa em todas as pernas (Wygodzinsky 1966).

A primeira hipótese filogenética de Emesinae e suas tribos foi proposta por Wygodzinsky (1966), designando como caracteres que definem a subfamília: a abertura do acetábulo anteriormente, o alongamento das coxas anteriores, a posição do pterostigma e as sensillas laterais campaniformes da prótibia; porém esta hipótese não usa métodos cladísticos. Weirauch (2008) recupera Emesinea como um grupo monofilético baseado na abertura do acetábulo anteriormente e a presença de sensillas campaniformes na prótibia. No entanto, o monofiletismo do grupo não é suportado com caracteres moleculares (Weirauch and Munro 2009; Hwang and Weirauch 2012).

Metapterini Stål, 1859 é uma tribo de Emesinae com 28 gêneros e aproximadamente 280 espécies descritas (Maldonado Capriles 1990; Ishikawa 2002). Morfologicamente caracteriza-se pelo conspícuo processo basal da série póstero-ventral do prófemur e a presença de polimorfismo nas asas, com grande proporção de gêneros com indivíduos micrópteros e ápteros. Dentro da tribo, 17 gêneros são completamente ápteros. Sete deles são restritos à ilhas, e outros sete têm espécies insulares e continentais. Wydgonzinsky (1966) propôs que Metapterini é grupo irmão de Deliastini baseado no processo basal da serie póstero-ventral maior que os outros processos espiniformes da região ventral do prófemur. O autor define como caracteres que agrupam a Metapterini: o tamanho reduzido dos olhos e na perda da veia cruzada m-cu na asa posterior.

Ghilianella Spinola, 1850 é o gênero mais diversificado de Metapterini, exclusivamente Neotropical e contém 72 espécies válidas (Maldonado Capriles 1960; Wygodzinsky 1966; Maldonado Capriles 1990). Morfologicamente está caracterizado pelas séries antero-ventral e póstero-ventral ocupando os dois terços distais do profemur, a série anteroventral do profemur composta de processos espiniformes misturados com setas, a presença de indivíduos ápteros e com asas (e.g. *Ghilianella borgmeieri* Wygodzinsky, 1966) e a genitália simétrica do macho (McAtee and Malloch 1925; Maldonado Capriles 1960; Wygodzinsky 1966). Wygodzinsky (1966) separou *Ghilianella* em *Ghilianella* sensu stricto e um novo gênero, *Ghinallelia*, baseado na estrutura simplificada da série anteroventral do profemur e no falo assimétrico altamente modificado deste último. Além disso, ele descreveu *Liaghinella* e sugeriu afinidade com *Ghinallelia* baseado na estrutura da série antero-ventral do profemur muito semelhante. No entanto, a relação entre *Ghilianella*, *Ghinallelia* e *Liaghinella* não foi avaliada com métodos cladísticos, e os limites desses gêneros não são claros.

A incongruência entre a hipótese filogenética com caracteres morfológicos e moleculares, a ausência de uma avaliação crítica do monofiletismo desta tribo com a aplicação de métodos recentes de análise, e a exclusão de caracteres morfológicos da genitália feminina e masculina em estudos anteriores, justificam uma análise filogenética morfológica para Metapterini. Além disso, tal análise também pode esclarecer a relação entre *Ghilianella*, *Ghinallelia* e *Liaghinella*. A revisão taxonômica de *Ghilianella* irá explorar caracteres morfológicos adicionais para ajudar a delimitar as espécies, fornecer informações sobre sua distribuição e, certamente, descrever várias novas espécies.

Estrutura da tese

Esta tese esta estruturada em formato de artigos, composta por quatro capítulos:

Capítulo I. As estruturas genitais ectodérmicas masculinas e femininas são documentadas para dez gêneros e 23 espécies de Metapterini, incluindo oito espécies de *Ghilianella*. Descrições e macrofotografias digitais são fornecidas para o segmento abdominal 8 do macho, pigóforo, parâmero e falo; e para a fêmea os tergito 8 e 9, gonocoxas 8 e 9, gonapofisses 8 e 9, gonoplaca e bursa copulatrix. A genitália masculina assimétrica dentro de Emesinae é discutida. A partir desta documentação morfológica, 66 caracteres filogenéticos são codificados, apresentados como uma matriz de dados e analisados com método cladístico.

Capítulo II. Estruturas da perna anterior são documentadas para 13 gêneros de Metapterini, usando estereomicroscopio e microscopia eletrônica de varredura (MEV). Descrições detalhadas e macrofotografias digitais são fornecidas para a maioria dos gêneros pela primeira vez, e a partir desta documentação morfológica 38 caracteres filogenéticos são codificados, apresentados como uma matriz de dados, e analisados com método cladístico.

Capítulo III. Um conjunto de dados morfológicos de Metapterini inclui caracteres morfológicos externos, características detalhadas das pernas anteriores e genitália de ambos os sexos foi analisado com método cladístico pela primeira vez. Somando 138 caracteres e 55 terminais, que compreendem 43 espécies de Metapterini, pertendentes a 24 gêneros, e 12 outgroups, foram examinados e incluídos na análise. Além disso, reconstrução do estado ancestral do polimorfismo das asas e a assimetria da genitália do macho foram analisadas usando a filogenia resultante.

Capítulo IV. Apresenta-se a revisão taxônomica de *Ghilianella.* Setenta e oito espécies são reconhecidas, 21 descritas como novas e dois novos sinônimos são propostos. Nós exploramos caracteres morfológicos adicionais para ajudar a delimitar as espécies, fornecer informações sobre sua distribuição, uma chave de nível de espécie, macrofotografias digitais da morfologia externa e estruturas genitais para cada espécie. Além disso, oferecemos a primeira hipótese de relacionamento dentro de *Ghilianella*, e teste dos subgêneros *Ghilianella* e *Ploeodonyx* usando métodos cladísticos.

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CAPÍTULO I*

Comparative genitalic morphology in ten genera of thread-legged bugs of the tribe Metapterini, and its phylogenetic importance (Hemiptera: Heteroptera: Reduviidae)

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Abstract. The assassin bug tribe Metapterini belongs to the subfamily Emesinae (Hemiptera: Heteroptera: Reduviidae). Morphologically, it is characterized by the conspicuous basal process of the posteroventral series in the foreleg and the presence of wing polymorphism, with a high proportion of the genera with micropterous or apterous species. Here, the male and female ectodermal genitalic structures are documented for ten genera and twenty-three species of Metapterini, including eight species of the speciose genus *Ghilianella* Spinola, 1850. Descriptions and digital macrophotographs are provided for abdominal segment 8, pygophore, parameres, and phallus of the male, and for tergite 8, tergite 9, gonocoxae, gonapophyses, gonoplac, and bursa copulatrix of the female. The asymmetric male genitalia within Emesinae are discussed. From this morphological documentation sixty six phylogenetic characters are coded, presented as a data matrix and analyzed cladistically, and their potential usefulness for resolving relationships among Metapterini is discussed.

Key words. Hemiptera, Heteroptera, Reduviidae, *Ghilianella*, *Ghinallelia*, *Liaghinella*, morphological characters, male and female genitalia, phylogeny

Introduction

Metapterini Stål, 1859 is a worldwide tribe of Emesinae, with 28 genera and approximately 280 described species (ISHIKAWA 2002, MALDONADO CAPRILES 1990, WYGODZINSKY 1966). Morphologically, this tribe is characterized by the conspicuous basal process of the posteroventral series on the foreleg and presence of wing polymorphism, with a large proportion of the genera having micropterous or apterous individuals. Some genera are associated with spider webs as *Emesaya* Mcatee and Malloch, 1925 have on the protibia setae very similar to the calamistrum found on the metatarsus of the hind legs of cribellate spiders (WYGODZINSKY 1966). The first available phylogenetic hypothesis for the subfamily (WYGODZINSKY 1966) assumed that Metapterini is monophyletic, although it has never been formally tested. In addition, molecular data sets are contradictory about the monophyly of Emesinae (HWANG & WEIRAUCH 2012, WEIRAUCH & MUNRO 2009).

The male genitalia offer ideal characters for phylogenetic analyses, providing information for resolving relationships at various taxonomic levels, besides being one of the most important and useful species-diagnostic characters in insect systematics (SONG & BUCHELI 2010). The study of female genitalic morphology has focused on external structures, but both internal and external features have taxonomic and phylogenetic importance, at least in Reduviidae (FORERO & WEIRAUCH 2012, WEIRAUCH 2008). Despite this, in Reduviidae there still are few studies documenting in detail genitalic structures, and even less employing such character system in phylogenetic analyses (FORERO & WEIRAUCH 2012; WEIRAUCH 2004, 2008).

In Metapterini both males and females are known for most genera, except in *Anandromesa* Wygodzinsky, 1966 and *Nandariva* Wygodzinsky, 1966, which are known only from females, and *Emesella* Dohrn, 1859, *Hornylia* Wygodzinsky, 1966 and *Taitaia* Wygodzinsky, 1966, which are known only from males. MALDONADO (1960) provided illustrations of the external morphological configuration of the pygophore and parameres for the males, and tergites 8 and 9 for females in species of *Ghilianella* Spinola, 1850 and *Ghinallelia* Wygodzinsky, 1966 (as *Ghilianella* sensu lato). WYGODZINSKY (1966) studied the internal and external genital structures of the male, and the external female genitalia across the entire subfamily, and provided detailed descriptions for all Metapterini genera except *Roslania* Distant, 1913, and illustrations of at least one genitalic structure for 93 species (pygophore, parameres and phallus – usually extended – for the male; and the undissected gonocoxae, gonapophyses, and the gonoplac), but without a consistent documentation pattern among species. COBBEN & WYGODZINSKY (1975) examined specimens of *Barce* Stål, 1866 and *Ghinallelia* from Netherlands Antilles, and they indicated the presence of two pseudospermathecae, the vermiform gland, the ring gland in *Ghinallelia*, besides other characteristics of the internal female genitalia. Despite this, proper documentation has not been adequately achieved in Metapterini taxa so far. For instance, the bursa in the female has not been consistently studied or documented, as well as the processes on the extended endosoma and the asymmetry of the phallus in the males are scarcely documented and consequently poorly understood.

This study documents the male and female genitalia for about 36% of the known genera of Metapterini, including species of *Ghilianella*, and explores novel morphological genitalic characters that may be informative within a phylogenetic analysis. We propose a phylogenetic hypothesis for Metapterini that explores the potential phylogenetic usefulness of the genitalic characters and help elucidate the relationships and limits among taxonomically problematic genera (such as *Ghilianella*, *Ghinallelia*, and *Liaghinella*), focusing on *Ghilianella*.

Materials and methods

Taxon sampling. We examined ten genera and 23 species of Metapterini, two species of other tribes, Deliastini: *Bergemesa brachmanni* (Berg, 1884); Emesini: *Gardena faustina* McAtee and Malloch, 1925, and one species of Saicinae, *Tagalis seminigra* Champion, 1898. We believe that the taxa selected are a good representation of the variation found in Metapterini. Specimens are deposited in the following institutions:

BMNH	British Museum of Natural History, London, England;
CELM	Colección Taxonómica Nacional “Luis María Murillo”, Corpoica, Mosquera, Colombia;
FIOC	Coleção Entomologica Instituto Oswaldo Cruz, Rio de Janeiro, Brazil;
IAVH	Instituto Alexander von Humboldt, Villa de Leyva, Colombia;
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia;
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil;
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;

MLPA	Colección de entomología de la Facultad de Ciencias Naturales y Museo Universidad de La Plata, La Plata, Argentina;
MCNZ	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil;
MPUJ	Colección de Entomología, Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia;
TUA	Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Tokyo, Japan;
UCR	Entomology collection, University of California Riverside, Riverside, USA;
UNAB	Museo Entomológico Facultad de Agronomía, Universidad Nacional de Colombia, Bogotá, Colombia.

Material examined. See Table 1.

Terminology. For male and female genitalia, we follow mostly the terminology provided by Forero & Weirauch (2012). Cobben & Wygodzinsky (1975) and Wygodzinsky (1966), which have been standardized here to improve character interpretation within Reduviidae. For the lateral and posterolateral process of genital opening of the pygophore, we follow Varela & Melo (2017).

The names of structures are identified by following abbreviations:

aed	aedeagus	*mpm8*	medial posterior margin of the tergite 8
amg8	anterior margin of the gonocoxa 8	*mpm9*	medial posterior margin of the tergite 9
ao	anterior opening of the pygophore	*mpo*	lateral margin of posterior opening of the pygophore
app	apical projection of the paramere	*mpp*	medial posterior process of the

			pygophore
apt	articulatory apparatus	*pa*	paramere
bc	bursa copulatrix	*pex*	basal plate extension
bp	basal plate	*pha*	phallosoma
br	transverse bridge of the pygophore	*pmg8*	posterior margin of the gonocoxa 8
dlb	dorsolateral basal portion of the endosoma	*pgo*	posterolateral process of the posterior genital opening
dlm	dorsolateral median portion of the endosoma	*po*	posterior opening of the pygophore
dld	dorsolateral distal portion of the endosoma	*ppe*	posteroventral projections of the endosoma
dps	dorsal phallothecal sclerite	*pro*	proctiger
duc	ductifer	*ps*	paramere socket
end	endosoma	*rg*	ring gland of the bursa copulatrix
gap8	gonapophysis 8	*S8*	abdominal segment 8
gap9	gonapophysis 9	*S9*	abdominal segment 9 = pygophore
gcx8	gonocoxa 8	*sdg*	subapical dorsal margin of the gonoplac
gcx9	gonocoxa 9	*svg*	subapical ventral margin of the gonoplac
gpl	gonoplac	*T8*	tergite 8
lap	lateral anterior prolongation of the gonocoxa 8	*T9*	tergite 9
lpg	lateral process of the posterior genital opening	*vg*	vermiform gland

mm	medial margin of the gonocoxa 8	*vpp*	ventral protruding of the pygophore
mov	median oviduct	*vps*	ventral phallothecal sclerite

Dissections of male and female genitalia. We mostly follow Forero & Weirauch (2012) for dissections. The specimens studied were pinned dry or preserved in ethanol. Dry specimens were relaxed with a Barber solution or humid chamber for 24 hours. The whole abdomen in the females and the genital capsule in the males were removed and digested with 10% KOH solution at room temperature for 48 to 60 hours, continually checking the structure, until no traces of fat body or muscles remained. The structures were rinsed in distilled water and transferred to 90% ethanol. Dissections were carried out in glycerol under a Nikon SMZ1500 dissecting scope. The structures were not stained, the coloration of the structures has been maintained.

Male. Segments 8 and 9 were removed from the abdomen. Segment 8 and the right paramere were removed from the pygophore. When both parameres were removed, the right one was documented separately. The ligaments of the articulatory apparatus were severed and the phallus removed from the pygophore through the anterior opening. The endosoma was extended using forceps.

Female. If the specimen was carrying eggs, these were removed before dissections. Tergites 8 and 9 were separated from the connecting gonocoxa 9. Each gonocoxa 8 was then separated from sternite 7, thus freeing the bursa copulatrix from the abdomen. The right gonocoxae 8, and in some cases, the gonapophysis 8 were removed.

Imaging. Genitalic structures were documented using a Nikon AZ100M, equipped with a NIS-Elements AR software. Structures were placed in a small glass dish on top of a drop of KY jelly and the dish was then filled with 70% ethanol; this setup allows for re-positioning of structures during imaging. All structures are oriented with anterior (cephalad) parts towards the top of the page. *Bargylia longinota* Wygodzinsky, 1956 was documented from the holotype specimen (already dissected specimen, with phallus lost) in which the male genitalia were embedded in resin; therefore for this specimen photographs were taken directly from this montage. For image editing we used Adobe Photoshop CS6 v13.1.2.

Cladistic analysis. Sixty six genital characters were coded for 26 taxa: 23 species of Metapterini as the ingroup (*Barce fraterna* (Say, 1832), *Bargylia longinota*, *Emesaya brevipennis* (Say, 1828), *Emesaya pollex* McAtee & Malloch, 1925, *Emesella* sp., *Ghilianella approximata* McAtee & Malloch, 1925, *Ghilianella aracataca* McAtee & Malloch, 1925, *Ghilianella atriclava* Bergroth, 1911, *Ghilianella fenestrata* Maldonado, 1960, *Ghilianella gladiator* McAtee & Malloch, 1925, *Ghilianella globulata* McAtee & Malloch, 1925, *Ghilianella mirabilis* McAtee & Malloch, 1925, *Ghilianella* sp., *Ghinallelia globifera* (Bergroth, 1906), *Ghinallelia minimula* McAtee & Malloch, 1925, *Ghinallelia* sp., *Liaghinella andina* Forero, 2007, *Liaghinella tuberculata* Forero & Castro-Huertas, 2017, *Onychomesa gokani* Ishikawa, 2000, *Pseudometapterus argentinus* (Berg, 1900), *Pseudometapterus* sp., *Schidium marcidum* (Uhler, 1896), and *Schidium plumarium* Ishikawa, 2002); and one species of Saicinae (*Tagalis seminigra*), and two other non-Metapterini (*Bergemesa brachmanni* and *Gardena faustina)* as outgroups. All characters and character states are indicated in the figures with arrows as “23-1” (i.e., character 23, character state 1).

The characters were organized and coded using MESQUITE version 2.75 (MADDISON & MADDISON 2011). The description of each character and its states follow SERENO (2007). We used 46 binary and 20 non-additive multistate characters. The analyses were conducted in TNT v. 1.5 (GOLOBOFF & CATALANO 2016), using parsimony as optimality criterion. Uninformative characters (autapomorphies) were included during the analysis. A heuristic search was carried out holding a maximum of 10001 trees in memory, with a 1000 random addition replications, and 10 trees to hold per replication. The search strategy considered Tree Bisection and Reconnection (TBR). Consistency index (CI) and retention index (RI) were calculated for each character, the resultant trees, and for the strict consensus tree. The output was visualized using WinClada (NIXON 2002) and characters were mapped using unambiguous optimization. Bremer support was calculated using a script (dobrem.run) and GC frequencies were calculated using symmetric resampling with 1000 replicates, and expressed as GC values (groups present/contradicted) (GOLOBOFF et al. 2003). Negative values of GC frequencies (groups with low support) are within square brackets. All trees were rooted with *Tagalis seminigra* (Saicinae). The strict consensus tree with all characters supported in the unambiguous optimization was used for the discussion. *Pseudometapterus* species were coded just from males. Characters of the male genitalia of *Bargylia longinota* (10 characters) and *Emesella* sp. (15 characters) were coded from the literature (WYGODZINSKY 1966) given the unavailability of male specimens.

Results

Male genitalia

We include in the description the segment 8, part of the pregenital abdomen The male genitalia is composed of the pygophore (*S9*) that carries the paired parameres, and the phallus. The latter is composed of the articulatory apparatus (*apt*) and the aedeagus (*aed*). Two main elements can be distinguished in the aedeagus, the phallosoma (*pha*) and the endosoma (*end*) (DAVIS 1965, FORERO & WEIRAUCH 2012, WYGODZINSKY 1966).

Segment 8 (S8) (Figs 1–44)

Structure. Its dorsum is membranous, whilst its ventral part is composed of a large sclerite which is greatly but probably not fully of sternal origin. This sclerite is nearly rectangular with the lateral margins curved dorsally. The posteromedial margin is straight, emarginated (Figs 16, 17, 21), or produced (Fig. 1). The posterior margin in lateral view can be entire (Figs 29–34) with the spiracles parallel to the dorsal margin, or produced (Figs 40–44). The anteromedial margin is usually concave, with differences in the depth; or straight (Figs 1, 2). The lateral margins are usually entire, concave or slightly produced. In lateral view, the spiracles are usually located on the posterolateral margin, on a projection of the surrounding sclerite, but can be located subapically and not projected (Figs 24, 43).

In *Ghilianella*, in lateral view, the spiracles can be situated on a projection of the surrounding sclerite or not (Fig. 27) and the posterior margin is straight or slightly concave near the spiracle (Figs 28, 30).

Comments. This structure is usually poorly described and documented for the subfamily. In *Ghilianella* and *Schidium* it is a variable structure.

Pygophore (Figs 45–110)

Structure. The pygophore (*S9*) shape is variable from elongate ovoid to globular, in some species it can be ventrally produced (*vpp*) (Figs 82, 83, 85, 86) as a keel (Figs 82, 83) or a blunt projection (Figs 85, 86). A transverse bridge (*br*) (= anterior dorsal sclerotization, Wygodzinsky, 1966) separates the genital posterior opening (*po*) and the anterior opening (*ao*) in all taxa. The transverse bridge is sclerotized and can be medially narrow (Figs 45, 48) or wide (Figs 57, 58). The margins of the posterior genital opening are usually entire, but in some species of *Ghilianella* the lateral margin can be produced (*lpg*, Figs 72, 76, 78), or both lateral (*lpg*) and posterolateral (*pgo*) margins are produced (*lpg*, *pgo*, Fig. 74). Both processes of the lateral margins of the posterior genital opening have usually a tuft of long setae on the structure. The proctiger (*pro*) is membranous or with lateral sclerotizations and setae (Figs 62, 63, 66). The margin between the insertion of the parameres and the genital bridge (*mpo*) can be entire or produced (Fig. 50). The lateral margins of the paramere socket (*ps*) are usually entire, and in some species of *Ghilianella* can be produced into blunt (Fig. 50) or rounded (Fig. 56) processes.

The posterior margin of the pygophore has usually a conspicuous medial process (*mpp*), the shape of which is species specific. In Reduviidae the *mpp* might be formed either from the posterior wall of its posterior margin, or from its anterior wall as an outgrowth of the cup-like sclerite (H.R. Gil-Santana, D. Rédei, G. Zhang, pers. comm.). In the examined taxa all *mpp* are originating from the posterior wall, thus making all these structures homologous. The *mpp* is usually projected in Metapterini, except in *Emesaya pollex* (Fig. 92). The apical portion of *mpp* can be produced, truncate, rounded, or emarginated. Frequently, the median process is placed at about 45 degrees (Figs 72, 76, 80), but it can also be nearly vertical (Figs 73, 74, 81, 88).

The paramere insertion (*pa*) is on the apical third of the pygophore. The socket (*ps*) of this insertion is formed by anterior and posterior component, both encircling the base of the paramere.

Comments. The particular structure of the median process of the pygophore is species specific in the examined species of *Ghilianella*, *Ghinallelia*, *Liaghinella* and *Pseudometapterus*. The high structural variation found in the median process of the pygophore suggests that this character is probably of little value for the delimitation of supraspecific taxa.

Parameres

Structure. The parameres (*pa*) range from narrowly elongate (Figs 62, 63) to apically expanded (Figs 59, 87). The body of the paramere is uniform in diameter, widening towards the middle (Figs 59, 65, 66), or with a medial notch (Fig. 52). The apex of the paramere is clubbed, acute or otherwise irregularly shaped. The parameres have a single subapical projection (*app*), which can be as a blunt (Figs 97, 98, 103), pointed (Fig. 96) or rectangular process (Fig. 48).

The paramere setae distribution is usually uniform with both short and large setae, or ventrally with a row of long setae (Figs 52, 66). Some of the setae of the apical portion of the paramere are replaced by microchaetae (= spinulets, WYGODZINSKY 1966) (e.g., *Onychomesa* and *Schidium*. Figs 62, 66).

Comments. The number and arrangement of the setae and microchaetae on the parameres are of taxonomic value, at least on the species level in *Onychomesa* and *Schidium* (ISHIKAWA 2000, 2002; WYGODZINSKY 1966).

A subapical projection of the paramere was described for *Ghinallelia minimula* (McAtee & Malloch, 1925) and other, not specified species, belonging to the "*minimula* group" by WYGODZINSKY (1966), as a unique character within Emesinae. Probably this projection is homologous with the *app*, present in all genera of Metapterini examined, except *Onychomesa*.

Phallus (Figs 111–171)

Articulatory apparatus

Structure. The articulatory apparatus (*apt*) is composed of the basal plate (*bp*) and the basal plate extension (*pex*) (DAVIS 1965, FORERO & WEIRAUCH 2012, WYGODZINSKY 1966). The shape of the basal plate, in anterior view, is rectangular with the arms converging towards the ductifer (*duc*) (Fig. 125). The arms are usually short, slightly projected laterally or not (*Schidium*, Figs 150, 151) and with the capitate process rounded. The basal plate extension is usually narrow, but wide in *Schidium* (Figs 150, 151).

Phallosoma

Structure. The phallosoma is elongate and cylindrical, totally (Figs 149, 151) or partially sclerotized, dorsally usually sclerotized (Figs 122–125) or membranous (Fig. 127); and membranous (Figs 134, 164, 165) or sclerotized (Figs 152, 157, 167) ventrally. The dorsal phallothecal sclerite (*dps*) is usually present, except in *Onychomesa* (Fig. 127); and it is elongate, and can be variously shaped apically, ranging from rounded to emarginated. The disc is symmetrical in all genera, but asymmetrical in *Ghinallelia* (Figs 122–124). In lateral view, the *dps* is flat (Figs 132–147). The ventral phallothecal sclerite (*vps*) is glabrous (Figs 157, 163). The ductus seminis, which runs through the phallosoma and endosoma, is not discernible in the taxa examined; similarly, the secondary gonopore that opens on the endosoma was not located.

Comments. The dorsal phallothecal sclerite is species specific in at least *Ghilianella*, *Ghinallelia* and *Liaghinella*. The asymmetrical dorsal phallothecal sclerite in *Ghinallelia* has a high shape variability and sclerotization degree that might be taxonomically useful (WYGODZINSKY 1966).

The slightly sclerotized processes of the ventral region of the phallosoma are not easily visible because of the endosomal strong sclerotizations, and might be visible only in some cases in which the endosoma is everted.

Endosoma

Structure. The endosoma varies in shape from irregular to subcylindrical, from completely membranous (*Onychomesa* and *Pseudometapterus*, Fig. 148) to having frequently paired sclerotizations (Figs 120, 121, 130, 131) or asymmetrically arranged (*Emesaya* and *Ghinallelia,* Figs 112, 113, 122–124). The endosoma can be divided dorsolaterally into three regions, basal, median, and distal portions (Fig. 121). The dorsolateral basal portion (*dlb*) is frequently membranous, but it can have microtrichia (Figs 116, 119) or sclerotizations usually oriented longitudinally (Figs 111, 140). The dorsolateral median portion (*dlm*) is membranous, with microtrichia or with semicircular (Fig. 121) or elongate sclerites (Fig. 135). The dorsolateral distal portion (*dld*) is the most structurally variable, at least in *Ghilianella* and *Ghinallelia*, it can be membranous, with microtrichia, with denticulate sclerites, serrated, or with paddle-shaped or acuminated projections.

Ventrally, the endosoma is membranous or with sclerotizations, microchaetae or one elongate sclerite (Figs 158, 163), two rectangular sclerites (Fig. 166) or a longitudinal saw-like sclerite with accessory lateral rows of microtrichia (*Liaghinella,* Figs 146, 147, 168). The posteroventral margin of the endosomal membrane is usually entire, but *Barce* and *Schidium* have two membranous or slightly sclerotized projections (*ppe*) (Figs 132, 152).

Comments. Despite detailed descriptions by WYGODZINSKY (1966), the structure and process variation of the endosoma are poorly documented in Metapterini. The eversion of the endosoma is a process with high probability of damage for the structure; therefore the phallus is usually documented with the endosoma not everted.

The endosomal sclerites are variable in shape, number and position, and therefore can be an important character at the species (*Ghilianella*, *Ghinallelia*) and supraspecific level (*Liaghinella*, *Barce*).

The ventral process of the endosoma in *Liaghinella* was documented previously by FORERO (2007) and CASTRO-HUERTAS & FORERO (2017) as "saw-like process of the endosoma" and "tubercle-shaped sclerites or tss", respectively.

Female genitalia

The female genitalia are composed by: the tergites 8 (*T8*) and 9 (*T9*), two sets of gonocoxae (*gcx8*, *gcx9*), the gonapophyses (*gap8*, *gap9*), the gonoplac (= syngonapophysis) (*gpl*), and the bursa copulatrix (*bc*) (DAVIS 1965, FORERO & WEIRAUCH 2012, WYGODZINSKY 1966).

Tergite 8 (Figs 174–193)

Structure. Tergite 8 (*T8*) usually has a vertical orientation, but in a few genera it is directed nearly horizontally (*Emesaya)*. Tergite 8 is usually smaller than the tergite 9 (*T9)*, but the latter can be covered partially or completely by the tergite 8 as in *Schidium* (Figs 192, 193). The shape of tergite 8 can be semicircular, oval, or nearly rectangular. The posterior margin (*mpm8*) is usually entire, but it can be medially produced (Figs 191–193), and with the lateral margins projected ventrally (Figs 192, 193).

Sparse setae covering entire surface dorsally, or restricted to the lateral and distal margins and medially forming a longitudinal stripe. The pigmentation can be brownish, or unpigmented medially.

Tergite 9 (Figs 174–193)

Structure. As in T8, tergite 9 (*T9*) has usually a vertical orientation, but can be directed nearly horizontally; usually it is exposed, or covered by tergite 8. Tergite 9 is usually oval, or nearly rectangular, with the anterior margin concave (the union with the tergite 8). The posterior margin (*mpm9*) can be medially entire (Figs 179, 182, 183, 186–188), produced (Fig. 176), or emarginated (Figs 174, 177, 190). The subapical region is usually flat, but in some species of *Ghilianella* can be posterolaterally projected (Figs 180, 185). The dorsal surface is very similar with the tergite 8.

Comments. Tergite 8 and tergite 9 were previously illustrated or described for 22 genera and several species within Metapterini (e.g. MALDONADO (1960): *Ghilianella* and *Ghinallelia*; WYGODZINSKY (1966): 20 genera; MALDONADO (1993): *Ghinallelia claviventris*; ISHIKAWA (2002): *Schidium*; FORERO (2007): *Liaghinella andina*; GIL-SANTANA (2009) and GIL-SANTANA et al. (2009): *Ghilianella beckeri* and *Ghinallelia talitae*; etc.). In general, T8 and T9 have been used for species delimitation because of their variability in shape and vestiture (MALDONADO 1960, WYGODZINSKY 1966).

Gonocoxa 8 (Figs 194–213)

Structure. The gonocoxa 8 (*gcx8*) can be from L-shaped to nearly rectangular. The anterior margin (*amg8*) can be straight, rounded (Figs 202, 203, 205, 207, 208), or produced nearly parallel to the longitudinal axis of the body (Fig. 212). The posterior margin (*pmg8*) is nearly straight or convex. The medial margin (*mm*) is straight or produced (Figs 200–207, 211, 213). The lateral anterior area is always produced into a prolongation (*lap*) straight or sinuous apically; long and narrow (Figs 194, 211–213) or short and wide (Figs 198–210).

The ventral surface vestiture varies from having rather sparse to densely set setae (Fig. 196), usually on the distal region of the structure. The ventral cuticular surface is flat. The pigmentation can be homogeneous brownish or with several patches unpigmented.

Comments. The *gcx8* was previously illustrated and described for 20 genera of the tribe by WYGODZINSKY (1966). In the species examined the *gcx8* is variable at the species level.

Gonapophysis 8

Structure. The gonapophysis 8 (*gap8*) is a triangular and small sclerite. The surface is smooth and usually set with setae varying from sparse to dense. Gonapophysis 8 acute apically.

Gonocoxa 9

Structure. Gonocoxa 9 (*gcx9*) is a small sclerite, placed between the gonoplac and the gonapophysis 8 (*gap8*). This is an elongated and thin sclerite with a narrow base.

Comments. We did not detect variation of this structure in the genera examined.

Gonapophysis 9

Structure. The gonapophysis 9 (*gap9*) is usually a small, elongate and thin sclerite; weakly sclerotized, and about as long as the gonocoxa 9. This structure can be sclerotized at the internal margin, forming a denticle-like sclerite, as in *Barce*, *Onychomesa* and *Schidium* (Figs 232, 233).

Gonoplac

Structure. The gonoplac (*gpl*) is a trapezoidal sclerite, strongly sclerotized in all Metapterini (WYGODZINSKY 1966). The posterior margin can be rounded (Figs 258–265) or with a medial emargination (Figs 254–256), usually with long setae. In ventral view, the subapical region (*svg*) is produced as a longitudinal projection (Figs 258–269) or not. In dorsal view, the subapical margin (*sdg*) can be entire (Figs 218–223) or medially emarginated (Figs 216, 217, 231–233).

Bursa copulatrix (Figs 214–273)

Structure. The bursa copulatrix is a membranous sac that can be elongate-ovoid (Figs 223, 225, 229, 230), or elongate-rectangular (Figs 226, 227), and with the pseudospermathecae projected anteriorly (*Onychomesa*, *Schidium*, Figs 271–273) or not. In lateral view, the subapical region of the membranous sac can be entire (Figs 234, 251–253), with a dorsal folding (*Emesaya*, Figs 215, 216, 235, 236) or with several small foldings (Figs 237–250). In ventral view, the medial region of the sac is usually membranous, or with sclerites (Figs 255, 256, 261, 263).

The vermiform gland (vg) (= spermatheca of other Heteroptera, see SCHUH & SLATER 1995) is present in all Emesinae examined, confirming the previous observation by

WEIRAUCH (2008) (Figs 214, 228, 232, 234, 245, 252). Given that it is not always possible to keep the bursa inflated, the exact shape of this structure and its foldings are difficult to discern (e.g., *Barce*, Figs 214, 234).

On the cuticular lining of the bursa copulatrix there is a ring gland (*rg*) (COBBEN & WYGODZINSKY 1975), a narrow band usually rather sinuous (Figs 220, 223, 226) or nearly straight in some regions (Figs 219, 221), which is located transversely around the dorsal region of the bursa copulatrix; it is present in *Emesella*, *Ghilianella*, *Ghinallelia*, and *Liaghinella* (Figs 217–230).

The median oviduct is inserted (*mov*, Figs 236, 241) into the dorsal, proximal (anteriad) portion of the bursa copulatrix or anteriorly (Fig. 252). This area is totally membranous in the examined specimens.

Comments. The ring gland was first described by COBBEN & WYGODZINSKY (1975) for an unidentified species of *Ghinallelia* from Netherland Antilles. It is not clear if this structure has really a glandular function, and the reasons to be called a "ring gland" were not mentioned by COBBEN & WYGODZINSKY (1975). Similar sclerotizations with a probable glandular function have been described for Miridae on the dorsal surface of the seminal depository, but there is no strong evidence about the functionality of these structures (DAVIS 1955). This is the first documentation of this transversal sclerotization in other genera of Metapterini.

Phylogenetic characters

From the documentation of the genitalic structures above, we coded the variation found, as shown below:

Male genitalia:

1. S8, anteromedial margin, structure: (0) straight (Fig. 1); (1) concave (Fig. 4); (2) emarginated (Fig. 8). CI = 28/RI = 37.
2. S8, posteromedial margin, structure: (0) emarginated (Fig. 17); (1) straight (Fig. 13); (2) produced posteriorly (Fig. 1). CI = 40/RI = 40.
3. S8, spiracles, position: (0) on posterolateral margin (Fig. 25); (1) on subapical lateral margin (Fig. 24). CI = 50/RI = 0.
4. S8, spiracles, structure: (0) not projected (Fig. 40); (1) projected (Fig. 39). CI = 20/RI = 33.
5. Pygophore, ventral region, structure: (0) entire (Fig. 79); (1) protruding (*vpp*) (Fig. 83). CI = 50/RI = 66.
6. Pygophore, ventral protruding of the pygophore, shape: (0) blunt (Fig. 85); (1) keeled (Fig. 83). CI = 100/RI = 100.
7. Pygophore, transverse bridge, width: (0) narrow (Fig. 47), (1) wide (Fig. 56). CI = 20/RI = 33
8. Pygophore, anterolateral margin of the posterior opening, structure: (0) produced (*pgo*) (Figs 74, 285); (1) entire (Fig. 73). CI = 50/RI = 0.
9. Pygophore, posterolateral margin of the posterior opening, structure: (0) produced (*lpg*) (Fig. 74); (1) entire (Fig. 73). CI = 33/RI = 50.
10. Pygophore, paramere socket, lateral margin, structure: (0) entire (Fig. 49); (1) produced (Fig. 50). CI = 25/RI = 40.
11. Pygophore, posteromedial margin, structure: (0) with a protruding process (Fig. 94); (1) flat (Fig. 92). CI = 50/RI = 0.
12. Pygophore, posteromedial process, position: (0) nearly horizontal (Fig. 285); (1) nearly 45° to the base (Fig. 76); (2) nearly vertical (Fig. 88). CI = 66/RI = 0.

13. Pygophore, apex of posteromedial process, shape: (0) produced (Fig. 94); (1) truncate (Fig. 89); (2) rounded (Fig. 108); (3) emarginated (Fig. 93). CI = 30/RI = 46.
14. Pygophore, anterolateral angles of posteromedial process, structure: (0) entire (Fig. 94); (1) produced (Fig. 95). CI = 50/RI = 80.
15. Pygophore, posteromedial process, length related to width: (0) longer (Fig. 96); (1) equal (Fig. 97); (2) shorter (Fig. 106). CI = 33/RI = 60.
16. Paramere, body shape: (0) curved (Fig 47); (1) nearly straight (Fig. 65). CI = 33/RI = 66.
17. Paramere, shape: (0) uniform (Fig. 58), (1) broader in the base (Fig. 281); (2) broader in the medial and apical regions (Fig. 59). CI = 40/RI = 25.
18. Paramere, medial margin, structure: (0) entire (Fig. 56); (1) with a notch (Fig. 52). Uninformative character because the medial notch of the paramere is present only in *Ghilianella fenestrata*.
19. Paramere, apex, shape: (0) acute (Fig. 281); (1) rounded (Fig. 65). CI = 33/RI = 33.
20. Paramere, apical structure: (0) entire (Fig. 62); (1) with an apical process (*app*) (Fig. 54). CI = 50/RI = 0.
21. Paramere, apical process, shape: (0) blunt (Fig. 47); (1) rectangular (Fig. 48). CI = 33/RI = 0.
22. Paramere, vestiture: (0) setae; (1) microchaetae. CI = 100/RI = 100.
23. Articulatory apparatus, arms of the basal plate, structure: (0) narrow (Fig. 148); (1) wide (Fig. 152) CI = 100/RI = 100.
24. Articulatory apparatus, arms of the basal plate, length related to dorsal process of the basal plate: (0) as long as (Fig. 294); (1) longer (Fig. 115). Uninformative character because the arms of the basal plate are as long as the process of the basal plate only in *Tagalis seminigra*.

25. Articulatory apparatus, arms of the basal plate, structure: (0) fused in all its length (Fig. 115); (1) basally fused and apically divergent (Fig. 116); (2) divergent in all its length (Fig. 289). CI = 66/RI = 66.
26. Articulatory apparatus, basal plate bridge, width related to the arms of basal plate: (0) as wide as (Fig. 124); (1) wider than (Fig. 127). CI = 50/RI = 0.
27. Articulatory apparatus, basal plate extension, structure: (0) narrow (Fig. 148); (1) wide (Fig. 151). CI = 100/RI = 100.
28. Articulatory apparatus, basal plate extension, length related to basal plate: (0) shorter (Fig. 294); (1) as long as (Fig. 134); (2) longer (Fig. 132). Uninformative character because the basal plate extension is shorter than the basal plate only in *Tagalis seminigra* and the basal plate is longer than the basal plate only in *Barce fraterna*.
29. Dorsal phallothecal region, sclerotization: (0) sclerotized (*dps*) (Fig. 147); (1) not sclerotized (Fig. 148). Uninformative character because the dorsal phallothecal region is unsclerotized only in *Onychomesa gokani*.
30. Dorsal phallothecal sclerite, symmetry: (0) symmetrical (Fig. 125); (1) asymmetrical (Fig. 123). CI = 100/RI = 100.
31. Dorsal phallothecal sclerite, apical margin, structure: (0) produced (Fig. 291); (1) emarginated (Fig. 115); (2) entire (Fig. 122). CI = 50/RI = 60.
32. Dorsal phallothecal sclerite, structure in lateral view: (0) dorsally curved (Fig. 294); (1) only the apex dorsally curved (Fig. 292); (2) flat (Fig. 134). CI = 66/RI = 50.
33. Phallosoma, ventral region, structure: (0) membranous (Fig. 155); (1) with microtrichia (Fig. 156); (2) with ventral phallothecal sclerite (*vps*) (Fig. 153). CI = 66/RI = 75.
34. Phallosoma, ventral phallothecal sclerite, structure: (0) one medial sclerite (Fig. 167); (1) two lateral sclerites (Fig. 157). CI = 50/RI = 87.

35. Endosoma, dorsolateral basal region, structure: (0) membranous (Fig. 291); (1) with microtrichia (Fig. 118); (2) with lateral sclerites (Fig. 111). CI = 33/RI = 69.
36. Endosoma, dorsolateral distal portion, structure: (0) with sclerites (Fig. 117); (1) membranous (Fig. 111); (2) with microtrichia (Fig. 115). CI = 50/RI = 80.
37. Endosoma, sclerites of the dorsolateral distal portion, shape: (0) elongate oval (Fig. 117); (1) triangular (Fig. 292); (2) rectangular (Fig. 123). CI = 50/RI = 75.
38. Endosoma, sclerites on the medial and distal dorsolateral region, symmetry along medial axis of the endosoma: (0) symmetric (Fig. 120); (1) asymmetric (Fig. 122). CI = 50/RI = 0.
39. Endosoma, distal dorsolateral elongate sclerites, symmetric arrangement: (0) several in a transversal row (Fig. 291); (1) two side to side (Fig. 121); (2) several in a longitudinal row (Fig. 141). CI = 66/RI = 0.
40. Endosoma, basal portion of the ventral region, structure: (0) with a medial sclerite (Fig. 158); (1) with microtrichia (Fig. 161); (2) membranous (Fig. 165); (3) with a longitudinal saw-like sclerite (Fig. 168); (4) with two longitudinal sclerites (Fig. 296). CI = 50/RI = 69.
41. Endosoma, posteroventral margin, structure: (0) with elongate sclerites (Fig. 297); (1) entire (Fig. 155); (2) with projections (*ppe*) (Fig. 153). CI = 66/RI = 50.
42. Endosoma, distal entire sclerites on posteroventral margin, structure of surface: (0) smooth (Fig. 166); (1) with denticles (Fig. 164). CI = 50/RI = 0.

Female genitalia:

43. T8, position: (0) adjacent to T9 (Fig. 178); (1) overlapping T9 (Fig. 192). CI = 100/RI = 100.

44. T8, posteromedial margin, structure: (0) entire (Fig. 187); (1) produced (Fig. 192). CI = 100/RI = 100.
45. T8, posterolateral margin, structure: (0) entire (Fig. 187); (1) produced (Fig. 191). CI = 100/RI = 100.
46. T8, surface: (0) flat (Fig. 188); (1) transversely striated (Fig. 189). CI = 50/RI = 66.
47. T9, posteromedial margin, structure: (0) entire (Fig 175); (1) emarginated (Fig. 177); (2) produced (Fig. 176). CI = 50/RI = 60.
48. T9, subapical dorsal region, structure: (0) flat (Fig. 179); (1) elevated (Fig. 183). CI = 33/RI = 0.
49. T9, dorsal surface, structure: (0) flat (Fig. 191); (1) with a longitudinal carina (Fig. 190). CI = 100/RI = 100.
50. Gonocoxa 8, shape: (0) near oval (Fig 197); (1) rectangular (Fig. 196). CI = 100/RI = 100.
51. Gonocoxa 8, lateral posterior angle, structure: (0) short and wide (Fig. 210); (1) long and narrow (Fig. 212). CI = 100/RI = 100.
52. Gonocoxa 8, anterior margin, sublateral region, structure: (0) produced (Fig. 303); (1) entire (Fig. 196). CI = 20/RI = 20.
53. Gonocoxa 8, anterior margin, submedial region, structure: (0) entire (Fig. 199); (1) produced (Fig. 198). CI = 33/RI = 0.
54. Gonocoxa 8, medial margin, structure: (0) entire (Fig. 194); (1) produced (Fig. 200). CI = 20/RI = 50.
55. Gonocoxa 8, setae, arrangement: (0) on the posterior margin (Fig. 303); (1) at least covering the subapical region. Uninformative character because the setae of the gcx8, restricted at the posterior margin is present only in *Tagalis seminigra*.

56. Gonoplac, posteromedial margin, structure: (0) entire (Fig. 257); (1) emarginated (Fig. 256). CI = 25/RI = 25.

57. Gonoplac, subapical margin in dorsal view, structure: (0) entire (Fig. 218); (1) emarginated (Fig. 216). CI = 33/RI = 60.

58. Gonoplac, subapical margin in ventral view, structure: (0) entire (Fig. 254); (1) produced (Fig. 259). CI = 50/RI = 85.

59. Gonoplac, posterolateral margin, structure: (0) produced (Fig. 312); (1) entire (Fig. 311). Uninformative character because the produced posterolateral margin of the gonoplac is present only in *Tagalis seminigra*.

60. Gonapophysis 9, medial margin, structure: (0) membranous (Fig. 227); (1) sclerotized (Fig. 233). CI = 100/RI = 100.

61. Bursa copulatrix, anterior region, structure: (0) entire (Fig. 270); (1) with pseudospermathecae (Fig. 271). CI = 100/RI = 100.

62. Bursa copulatrix, median oviduct, insertion on the bursa copulatrix: (0) anteriorly (Fig. 252); (1) dorsally (Fig. 249). CI = 50/RI = 66.

63. Bursa copulatrix, dorsal region of the bursa copulatrix, structure: (0) entire (Fig. 240), (1) with a dorsal folding (Fig. 236). CI = 100/RI = 100.

64. Bursa copulatrix, dorsomedial region, structure: (0) membranous (Fig. 214); (1) with ring gland (Fig. 217). CI = 100/RI = 100.

65. Bursa copulatrix, ring gland on dorsal region, structure: (0) a transversal band (Fig. 217); (1) two medial rings (Fig. 304). Uninformative character because the dorsal region of the bursa copulatrix has two medial rings only in *Bergemesa brachmanni*.

66. Bursa copulatrix, ventral region, structure: (0) membranous (Fig. 262); (1) with wide sclerites (Fig. 263); (2) with narrow sclerites (Fig. 255). CI = 100/RI = 100.

Cladistic analysis

The phylogenetic analysis inferred two equally most parsimonious trees of 180 steps (CI = 48, RI = 59), differing in the position of *Barce fraterna* and *Bargylia longinota*. In the strict consensus tree (182 steps, CI = 48, RI = 58), two nodes collapse (*Barce fraterna* and *Bargylia longinota*) (Fig. 313). The genitalic structures do not support Metapterini as monophyletic, but offer some characters that help delimit some genera.

Gardena faustina was inferred as the sister-group of the other Emesinae genera, the latter are grouped in a clade with weak support (Bremer support and GC frequencies). Within this clade we found three main clades: *Barce* group, *Emesaya,* and *Ghilianella* clade.

– ***Barce* group** is composed of *Barce*, *Bargylia*, *Pseudometapterus*, *Onychomesa* and *Schidium*. This group is supported by two female genitalic non-homoplasious characters, the posterior angle of the gonocoxa 8 long and narrow (#51, Figs 194, 212) and the internal margins of the gonapophysis 9 sclerotized (#60, Figs 214, 231); and two homoplasious characters from the male genitalia, the nearly straight paramere (#16, Figs 45, 62) and the distal portion of the endosoma membranous (#36, Figs 132, 148). Both female characters were not examined in *Bargylia* and the species of *Pseudometapterus*. Bremer support and GC frequencies offer low support.

– ***Pseudometapterus*.** The monophyly of this genus is supported by three homoplasious characters of the male genitalia, sternite 8 with the anteromedial margin emarginated (#1, Figs 19, 20); pygophore ventrally with a protruding process (*vpp*) (#5, Figs 85, 86); and apical margin of the dorsal phallothecal sclerite entire (#31, Figs 128, 129). Clade with high support values.

– ***Onychomesa* group** is composed of *Onychomesa* and *Schidium*. The clade is supported by three non-homoplasious synapomorphies, the paramere vestiture composed by microchaetae (#22, Figs 62, 66); the posteromedial margin of tergite 8 produced in the female (#44, Figs 191–193), and the anterior region of the bursa copulatrix with membranous projections (#61, Figs 231–233). In addition, three homoplasious characters supports the clade, the concave anteromedial margin of sternite 8 in the male (#1, Fig. 21); gonoplac of the female with the subapical margin in dorsal view emarginated (#57, Figs 231–233); and the median oviduct inserted anteriorly to the bursa copulatrix (#62, Figs 251, 252). Contradicted support values (Bremer support with low value, GC values with high support).

– ***Schidium*.** The monophyly of this genus is supported by four synapomorphies: two characters of the articulatory apparatus, the wide arms of the basal plate (#23, Figs 130, 131) and the wide basal plate extension (#27, Figs 151, 152); and two characters from the female genitalia: the tergite 8 overlapping with tergite 9, and the posterolateral margin of the tergite 8 produced (#43, #45, Figs 192, 193). Besides, three homoplasious characters supports the clade: paramere broader in the medial and apical regions (#17, Fig. 87); dorsolateral basal region of the endosoma with lateral sclerites (#35, Figs 130, 131), and posteroventral margin of the endosoma with projections (#41, Figs 151, 152). Clade with high support values.

– ***Ghilianella* group** is composed by *Emesaya* and *Ghilianella* clade, and supported by three characters: tergite 8 of the male with anteromedial margin concave; phallosoma with two ventral sclerites (#34, Figs 157, 161); and gonoplac with produced subapical margin in ventral view (#58, Figs 258, 260). Clade weakly supported.

– ***Emesaya*.** The genus is considered monophyletic, it is supported by four synapomorphies, three non-homoplasious and one homoplasious, from the female genitalia: gonocoxa 8 rectangular (#50, Figs 195, 196); bursa copulatrix with a dorsal folding (#63, Figs 235, 236); ventral region of the bursa copulatrix with narrow sclerites (#66, Figs 255, 256) and gonoplac with the subapical margin emarginated in dorsal view (#57, Figs 215, 216). Clade with high support values.

– ***Ghilianella* clade** is composed of *Ghinallelia* and *Ghilianella* complex, supported by two characters from the female genitalia: medial margin of the gonocoxa 8 produced (#54, Figs 206–208), and the dorsomedial region of the bursa copulatrix with ring gland (#64, Figs 226–229). Clade weakly supported.

– ***Ghinallelia*.** This genus is monophyletic in the analysis, and it is supported by the asymmetrical dorsal phallothecal sclerite (#30, Figs 122–124) and four homoplasious characters, produced lateral margin of the paramere socket (#10, Figs 57–59); posteromedial process of the pygophore produced (#13, Figs 101–103); apical margin entire of the dorsal phallothecal sclerite (#31, Figs 122–124) and ventral region of the phallosoma membranous (#33, Figs 164–166). Clade strongly supported.

– ***Ghilianella* complex** is composed of species of *Ghilianella*, *Liaghinella*, *Emesella*, and *Bergemesa brachmanni* (Deliastini). This clade is supported by characters from the male genitalia, the dorsolateral basal region of the endosoma with microtrichia (#35, Figs 117, 118) and the posterolateral margin of the posterior opening of the pygophore produced (#9, Fig. 74). The genitalic characters analyzed do not support the monophyly of *Ghilianella*. Clade weakly supported.

– ***Liaghinella.*** This genus is monophyletic in the analysis, and it is supported by the basal portion of the ventral region of the endosoma with a longitudinal saw-like sclerite (#40, Figs146, 147) and the tergite 9 of the female with a longitudinal carina dorsally (#49, Figs 189, 190). Besides of four homoplasious characters, pygophore with ventral protruding process (#5, Figs 82, 83); wide transverse bridge of the pygophore (#7, Figs 60, 61); phallosoma with a medial sclerite ventrally (#34, Fig. 167) and transversal striated surface of the tergite 8 in the female (#46, Fig. 189). Clade strongly supported.

Discussion

The genitalia in Metapterini are informative at multiple taxonomic levels: they are valuable for diagnoses of species and species groups, as well as for genera and groups of genera, but they also provide information that can be used to elucidate phylogenetic relationships among genus-level taxa.

Genitalia at the tribal level. We confirmed the previous statement of WYGODZINSKY (1966) about the high morphological variation of the genitalic structures among Metapterini species and the importance of this character complex for the diagnoses of their taxa. The flat dorsal phallothecal sclerite in lateral view is the only genitalic feature common to all the examined genera of Metapterini, but the interpretation is problematic given the unavailability of male specimens of *Bargylia* and *Emesella*. In the redescription of the Metapterini offered by WYGODZINSKY (1966) he documented the morphological variation of several genitalic structures among various taxa: phallus varying from symmetrical to highly asymmetrical; phallosoma from membranous to extensively sclerotized, from irregularly bladder-shaped to elongate-cylindrical, although the latter was the most frequently found; endosoma from irregularly shaped to subcylindrical, its processes frequently paired or asymmetrically arranged, membranous or more or less sclerotized, smooth, denticulate or serrated; and the genital region of female being strongly sclerotized, often conspicuously sculptured.

In our analyses, Metapterini is resolved as paraphyletic because of the inclusion within the *Ghilianella* complex of *Bergemesa brachmanni*, which has been treated as a Deliastini by previous authors. *Bergemesa* was placed in Deliastini by WYGODZINSKY (1966), and this tribe was considered by him as the sister group of Metapterini based on the loss of the mesonotal and metanotal spines, and the presence of large basal process on the posteroventral series of the profemur; whereas Metapterini was considered monophyletic by the reduction in size of the eyes and the loss of m-cu cross vein in the hind wing (WYGODZINSKY 1966). The monophyly of the tribes have not been tested before with modern cladistic approaches, being this the first exploratory study using genitalic characters. Because WYGODZINSKY (1966) based his hypothesis on the higher groupings within Emesinae using other characters complexes from the ones used here, future analyses should test more rigorously his ideas incorporating the same set of characters.

Suprageneric groupings and genitalia. The close relationship of *Ghilianella*, *Ghinallelia*, *Emesella* and *Liaghinella* (MALDONADO 1960, WYGODZINSKY 1966) was confirmed in this study, but with the novel inclusion of *B. brachmanni* placed into Deliastini by previous authors. This generic grouping is supported by the presence of a ring gland in the female genitalia. This may suggest that the tribes, as presently delimited in Emesinae by WYGODZINSKY (1966), might not represent natural groups. This morphologically homogenous clade is exclusively Neotropical.

Another relationship recovered in our analyses, although weakly supported, is between *Emesella* and *Bergemesa*. This relationship was suggested by WYGODZINSKY (1950) without further elaboration. *Emesella* is a poorly known and scarcely collected genus (CASTRO-HUERTAS & FORERO 2017, WYGODZINSKY 1966). Hypotheses about the relationship of *Emesella* with other genera have been uncertain, given that this genus was synonymized with *Ghilianella* (WYGODZINSKY 1954), and then reinstated by WYGODZINSKY (1966) commenting on the similarity to *Ghinallelia* rather than to *Ghilianella*, by the structure of the anteroventral series of the profemur composed by setae only, but having a symmetrical phallus like *Ghilianella*. It is necessary to include male characters of *Emesella* and additional taxa of Deliastini in future analyses to fully assess the phylogenetic position of these genera.

Genitalia at the generic level. The generic delimitation in Metapterini had focused on the external morphology, particularly wing features and the arrangement and shape of the processes of the raptorial leg (WYGODZINSKY 1966). Despite the detailed description of the genitalic structures of Emesinae by WYGODZINSKY (1966), at least within Metapterini, very few genitalic characters were used to delimit genera, except in the strongly asymmetrical male genitalia of *Ghinallelia*. Besides, characters from both external and internal morphology have never been used for testing generic limits among Metapterini using cladistic methods. This comparative study and the analyses presented offer several genitalic characters useful for delimiting genera within Metapterini, particularly in taxonomically problematic groups (e.g. *Ghinallelia*, *Ghilianella* complex).

Ghinallelia, was segregated from *Ghilianella* based on the simplified structure of the anteroventral series of the profemur and the highly modified asymmetrical phallus, the latter state also shared with *Emesaya* (WYGODZINSKY 1966). However, with a detailed revision of the phallus, it is possible to recognize that the asymmetry occurs on different regions of the phallus and as discussed below, *Ghinallelia* has an asymmetric dorsal phallothecal sclerite, unique among the Metapterini genera examined.

The genitalic features support *Liaghinella* as monophyletic with the species included, and offer several diagnostic characters for the genus. *Liaghinella* comprises four described species: one from Jamaica – *Liaghinella farri* Wygodzinsky, 1966; and three from the Andean region – *Liaghinella heldamariae* Castro-Huertas & Forero, 2017, *L. andina* and *L. tuberculata*. In this study only two species from the Andes in Colombia were included. The male genitalic characters of *L. farri* (the female is unknown) as documented by WYGODZINSKY (1966) were compared to the examined Andean species, showing that they are not present in *L. farri*. It is probable that *L. farri* might not be congeneric with at least *L. andina* and *L. tuberculata* (CASTRO-HUERTAS & FORERO 2017), but this has to be tested with additional characters and taxa.

Ghilianella has been traditionally separated from other genera using characters from the structure and arrangement of the anteroventral and posteroventral processes of the profemur (MALDONADO 1960, MCATEE & MALLOCH 1925, WYGODZINSKY 1966). Diagnostic genitalic characters were offered by WYGODZINSKY (1966), mostly expressed as a range of variation of these structures. In our analyses, the genitalic characters do not support the monophyly of *Ghilianella* as currently defined, being polyphyletic. Future analyses with additional taxa and external morphological characters could help to better understand the limits of this complex genus.

Asymmetric male genitalia. Asymmetric genitalia in Heteroptera have evolved multiple times convergently (at least eight times) (HUBER et al. 2007), and may occur in several structures, including the phallus, the parameres and even pregenital segments in the male but rarely in the female genitalia (HUBER et al. 2007, HUBER 2010). Several hypotheses try to explain the evolution of asymmetrical structures in the genitalia (HUBER 2010, SCHILTHUIZEN 2013), although it still is a not well understood phenomenon, at least within true bugs. In Reduviidae the male genitalia are mostly symmetric, except in Peiratinae and some genera of Emesinae (HUBER et al. 2007, WEIRAUCH 2008, WYGODZINSKY 1966). The asymmetry in the male genitalia of Peiratinae occurs in the pygophore, parameres, and phallus (WEIRAUCH 2008). The male genitalia are symmetrical in most Emesinae, but certain genera of Leistarchini (*Bagauda*, *Ploiaria*), Emesini (*Phasmatocoris*) and Metapterini (*Emesaya*, *Ghinallelia*), show one or several portions of the phallus conspicuously asymmetrical (WYGODZINSKY 1966). Within Metapterini, the asymmetry in the phallus occurs in two structures: in the dorsal phallothecal sclerite at its apex or at the lateral regions, and on the endosoma, in which the endosomal sclerites are arranged in an asymmetrical pattern.

Ghinallelia has the apical region of the dorsal phallothecal sclerite asymmetric, and the sclerotizations on the endosoma not paired. In *Emesaya*, the asymmetry is present only in the endosomal processes. The observation of the endosomal sclerotizations depends of the eversion of the endosoma, and this procedure carry on a high risk of damage of the structure that probably have been the cause of the poor documentation of the endosomal processes in the tribe. For this reason, the interpretation of the symmetric and asymmetric genitalia is still a problematic topic (e.g., *Ghilianella beckeri* Gil-Santana, 2009).

Future research studies should include other character systems (e.g. from external morphology) and additional taxa to test if Metapterini is monophyletic and to test the phylogenetic relationships among its genera. Furthermore, studies focusing on the association of copulatory behaviors with particular genitalic structures could help to better understand the evolution of genitalic asymmetry within Emesinae.

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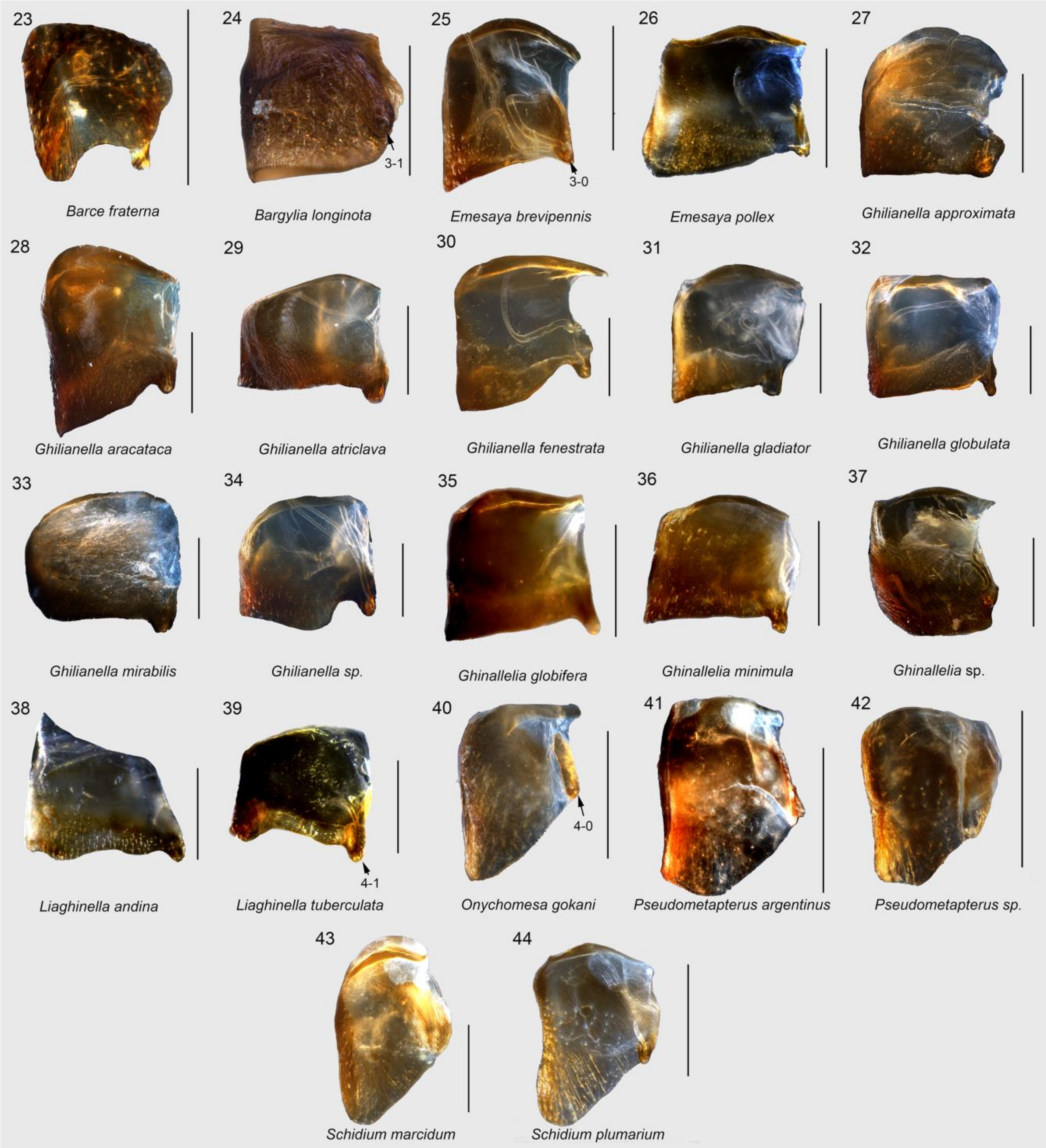
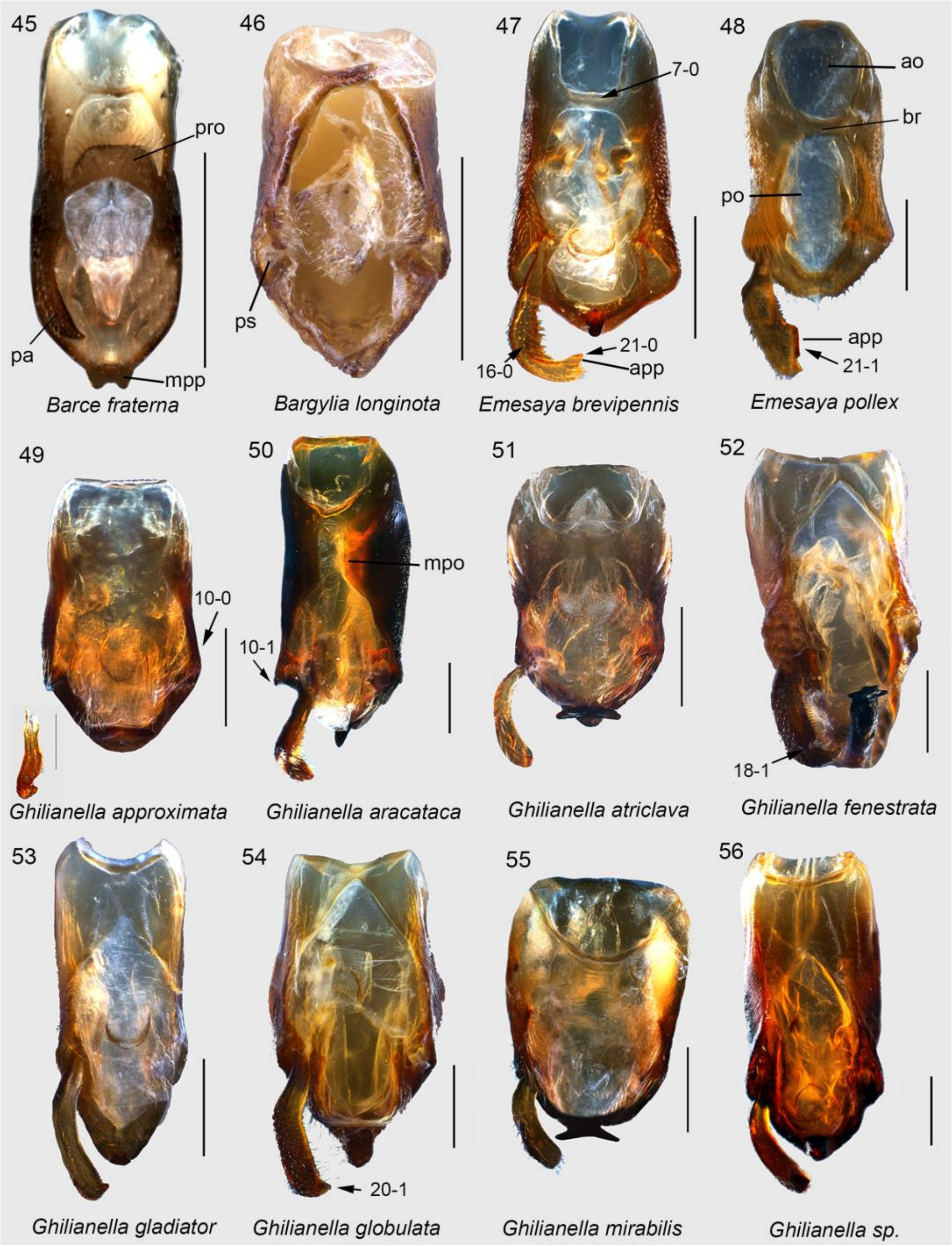
PLATES

Figs. 1–22. Segment 8 (*S8*) in ventral view. *Barce*, *Bargylia*, *Emesaya*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm.

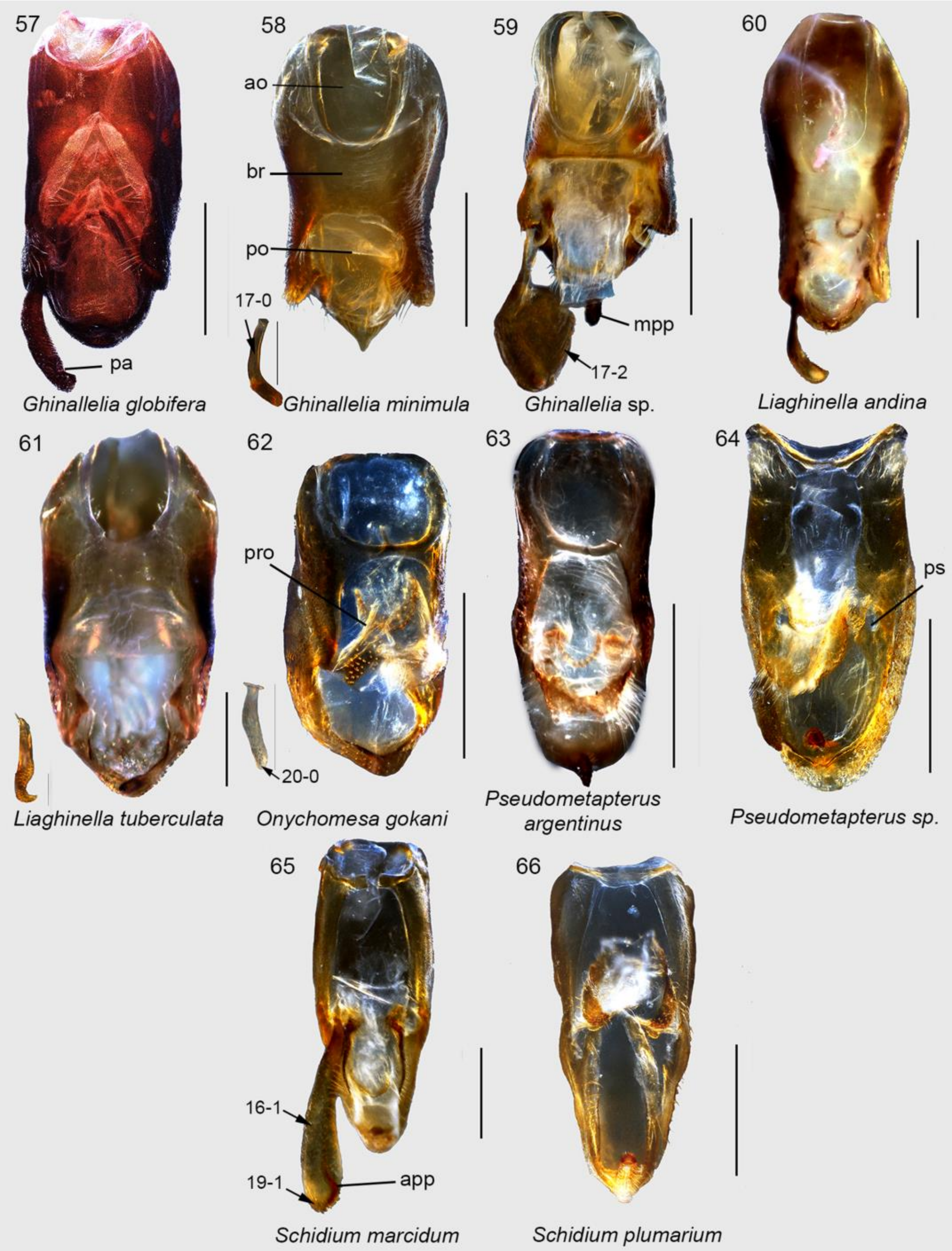


Figs. 23–44. Segment 8 (*S8*) in lateral view. *Barce*, *Bargylia*, *Emesaya*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm.

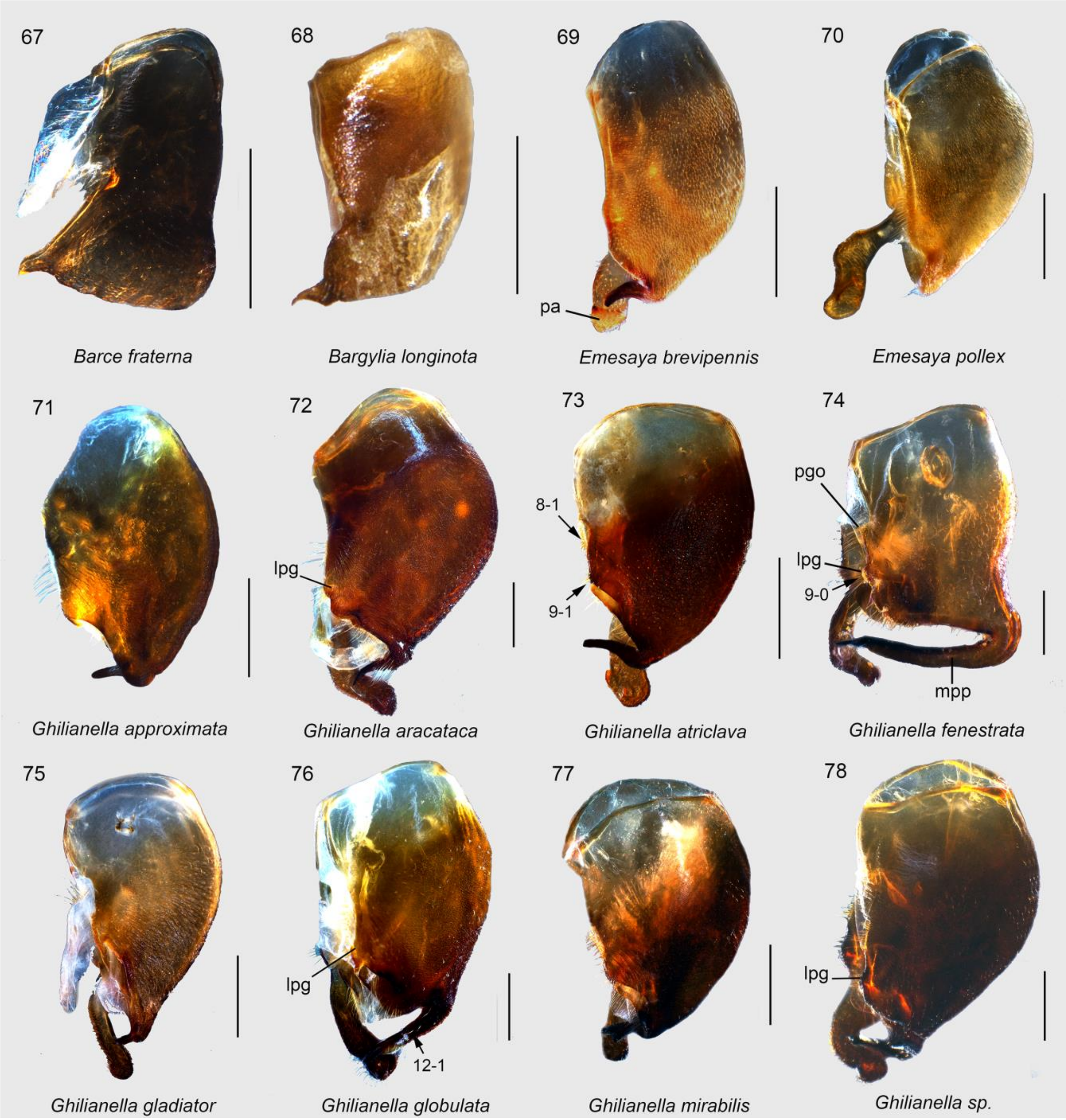


Barce fraterna
Bargylia longinota
Emesaya brevipennis
Emesaya pollex
Ghilianella approximata
Ghilianella aracataca
Ghilianella atriclava
Ghilianella fenestrata
Ghilianella gladiator
Ghilianella globulata
Ghilianella mirabilis
Ghilianella sp.

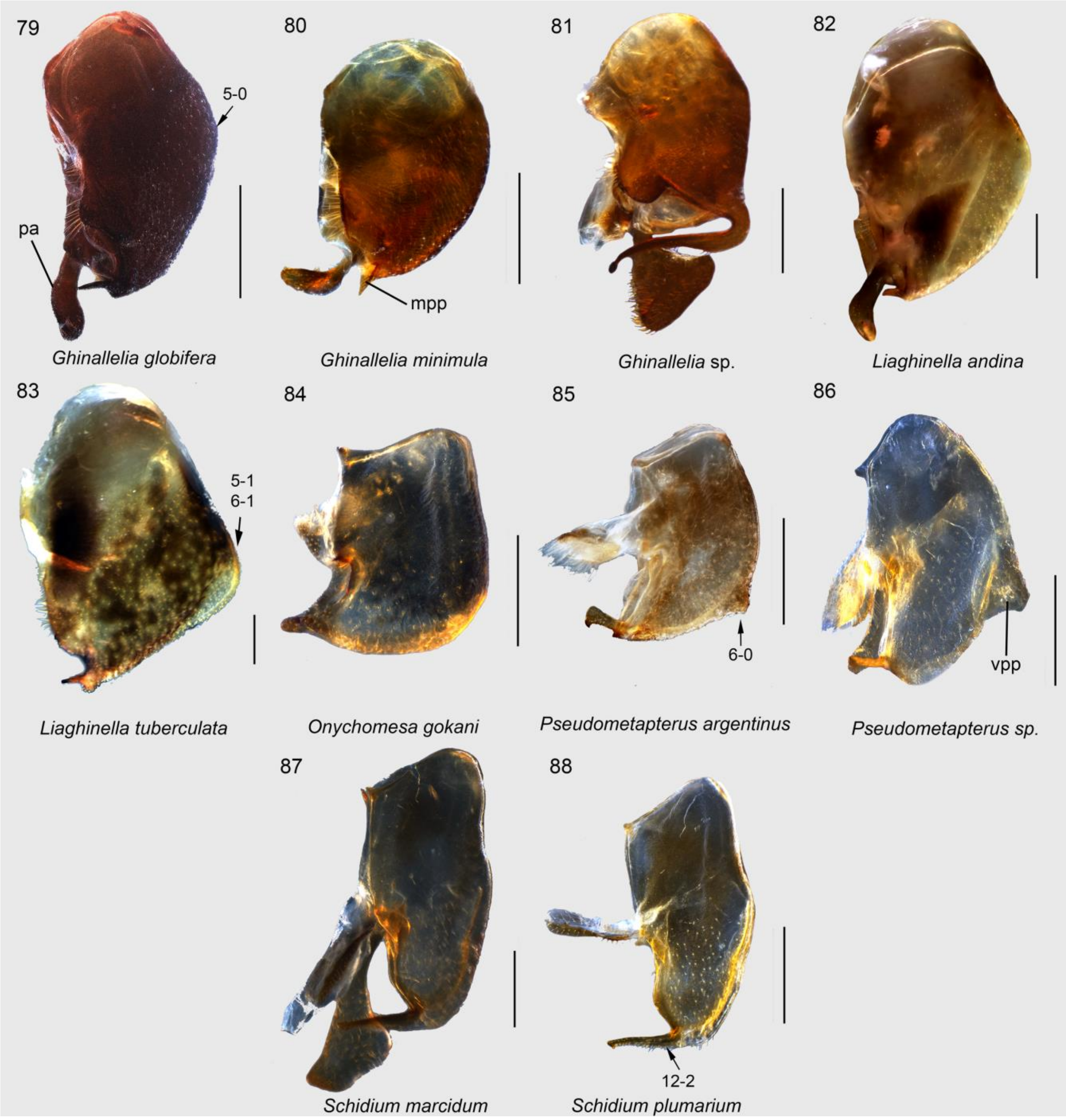
Figs. 45–56. Pygophore in dorsal view. *Barce*, *Bargylia*, *Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: ao – anterior opening of the pygophore; app – apical projection of the paramere; br – transverse bridge of the pygophore; mpo – lateral margin of posterior opening of pygophore; mpp – medial posterior process of pygophore; pa – paramere; po – posterior opening of the pygophore; ps – paramere socket; pro – proctiger.



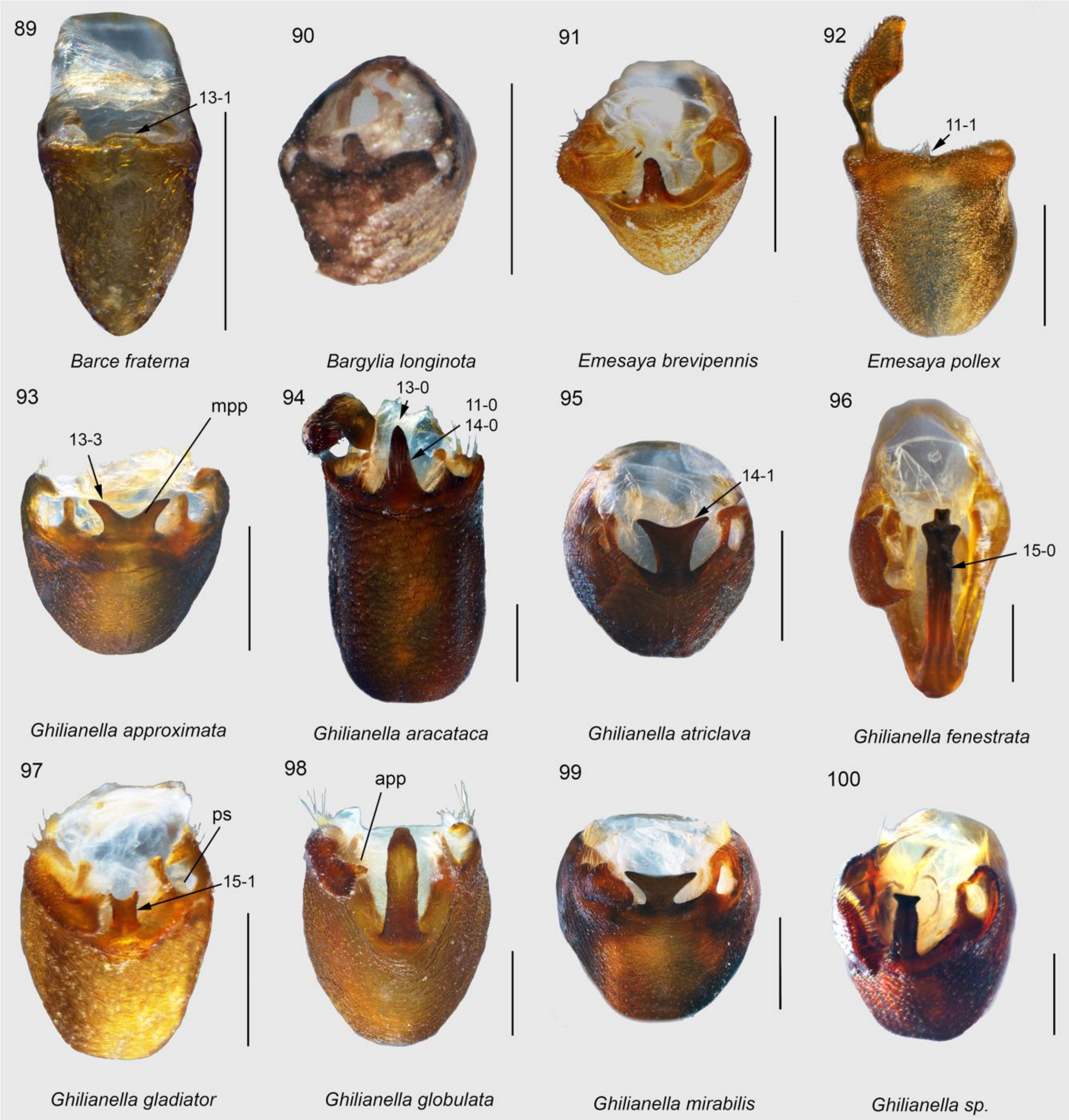
Figs. 57–66. Pygophore in dorsal view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: ao – anterior opening of the pygophore; app – apical projection of the paramere; br – transverse bridge of the pygophore; mpp – medial posterior process of pygophore; pa – paramere; po – posterior opening of the pygophore; ps – paramere socket; pro – proctiger.



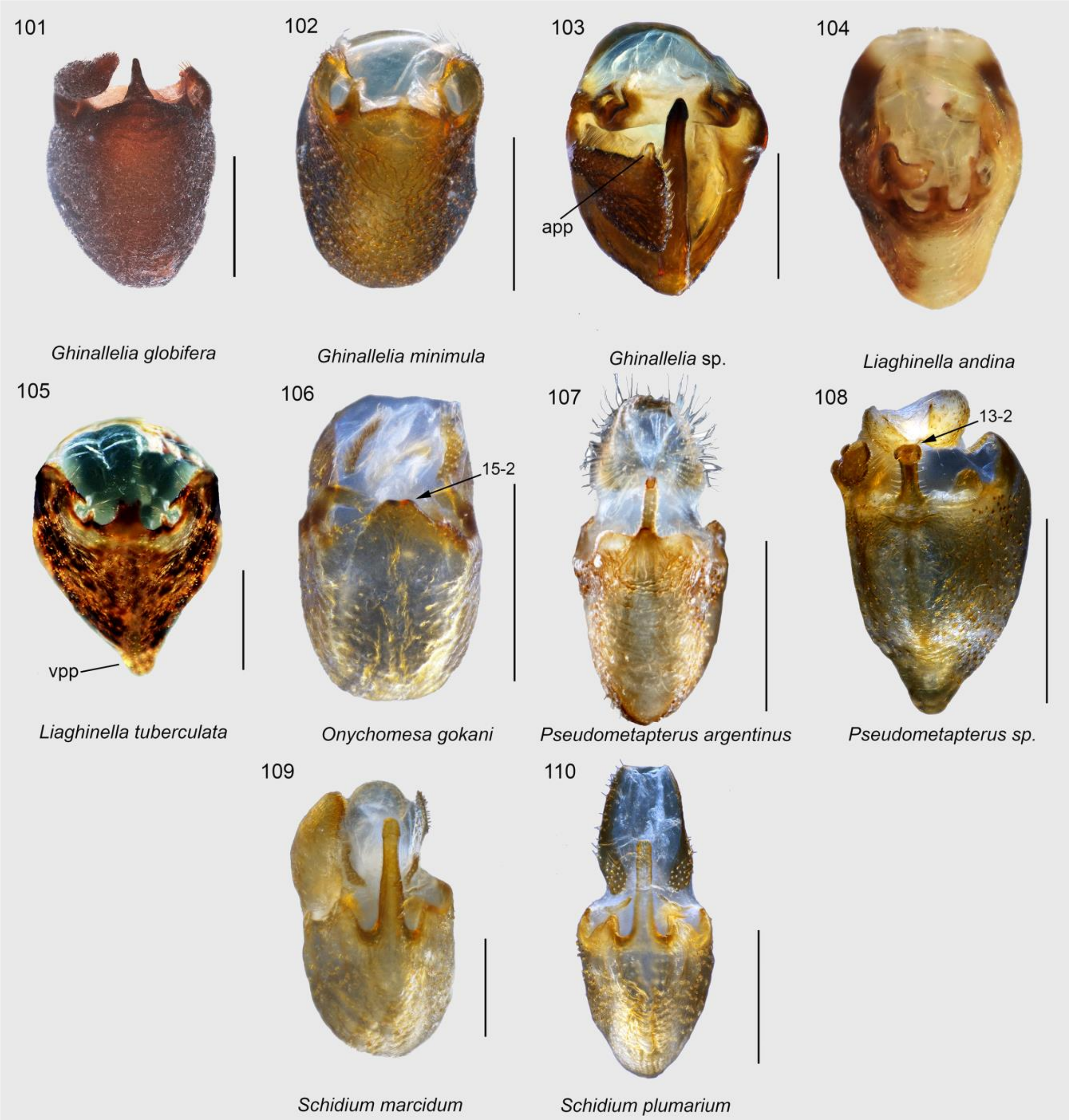
Figs. 67–78. Pygophore in lateral view. *Barce*, *Bargylia*, *Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: lpg – lateral process of genital opening; mpp – medial posterior process of pygophore; pa – paramere; pgo – process of the genital opening.



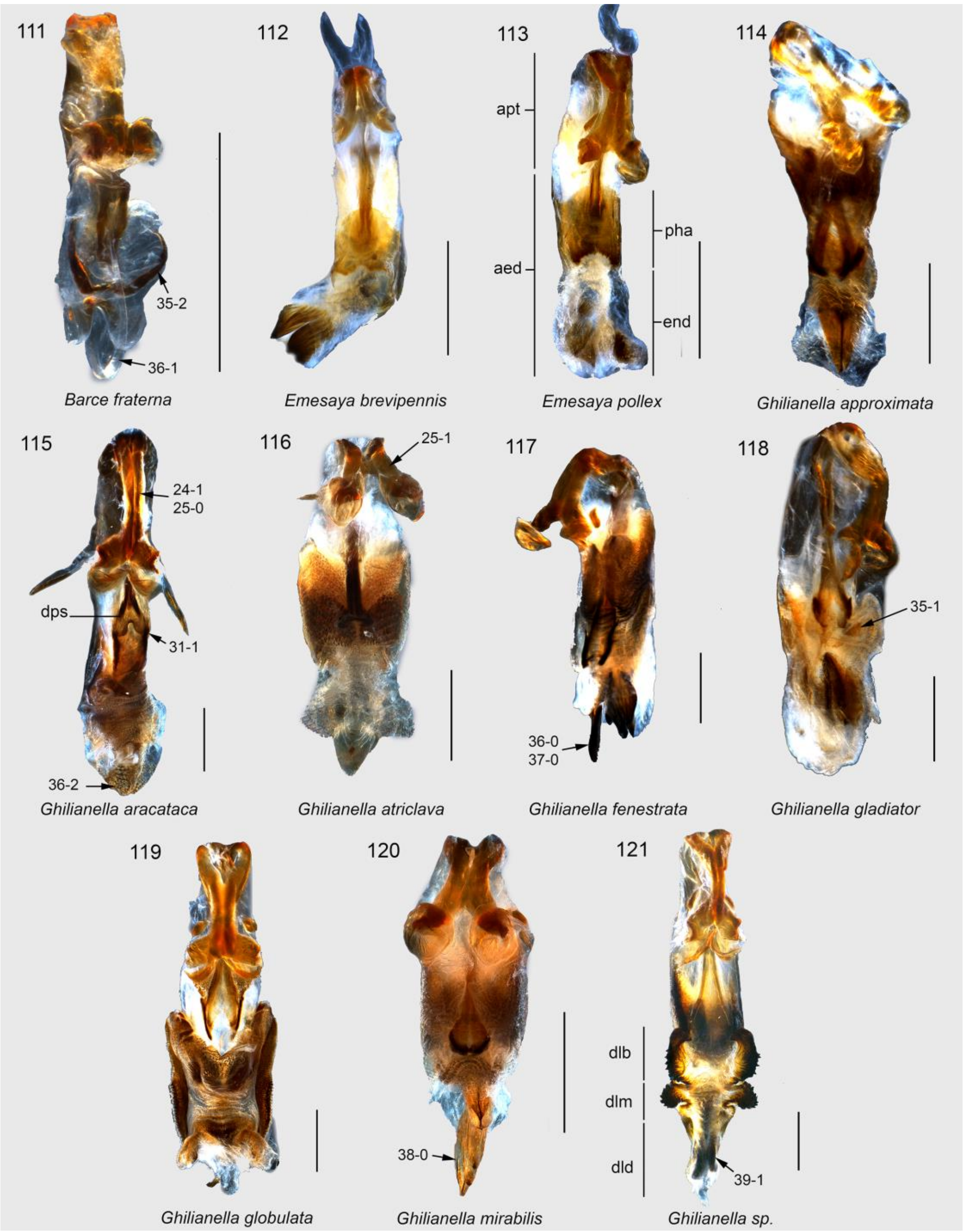
Figs. 79–88. Pygophore in lateral view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: mpp – medial posterior process of pygophore; pa – paramere; vpp – ventral protruding of the pygophore.



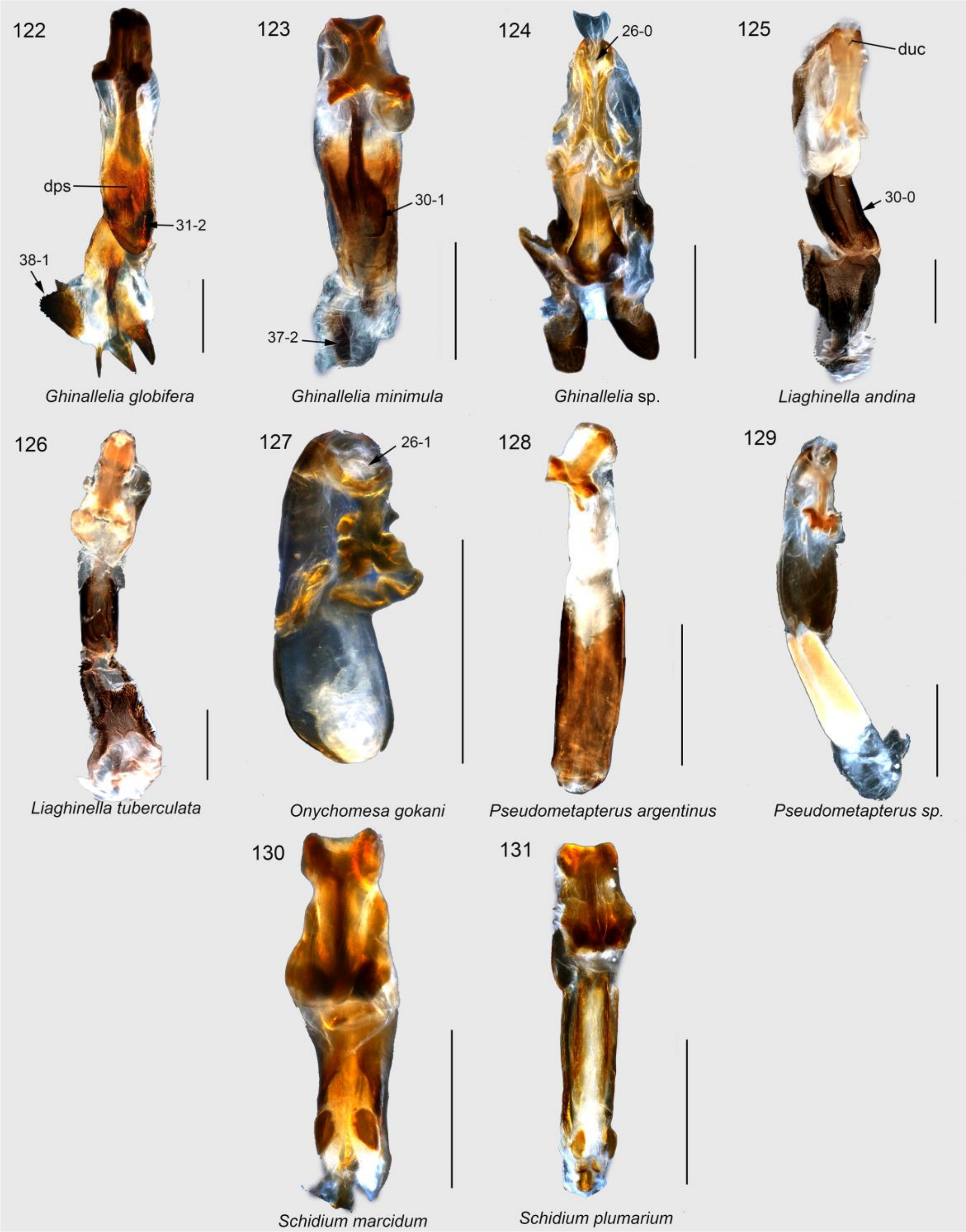
Figs. 89–100. Pygophore in caudal view. *Barce*, *Bargylia*, *Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: app – apical projection of the paramere; mpp – medial posterior process of pygophore; ps – paramere socket.



Figs. 101–110. Pygophore in caudal view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: app – apical projection of the paramere; vpp – ventral protruding of the pygophore.

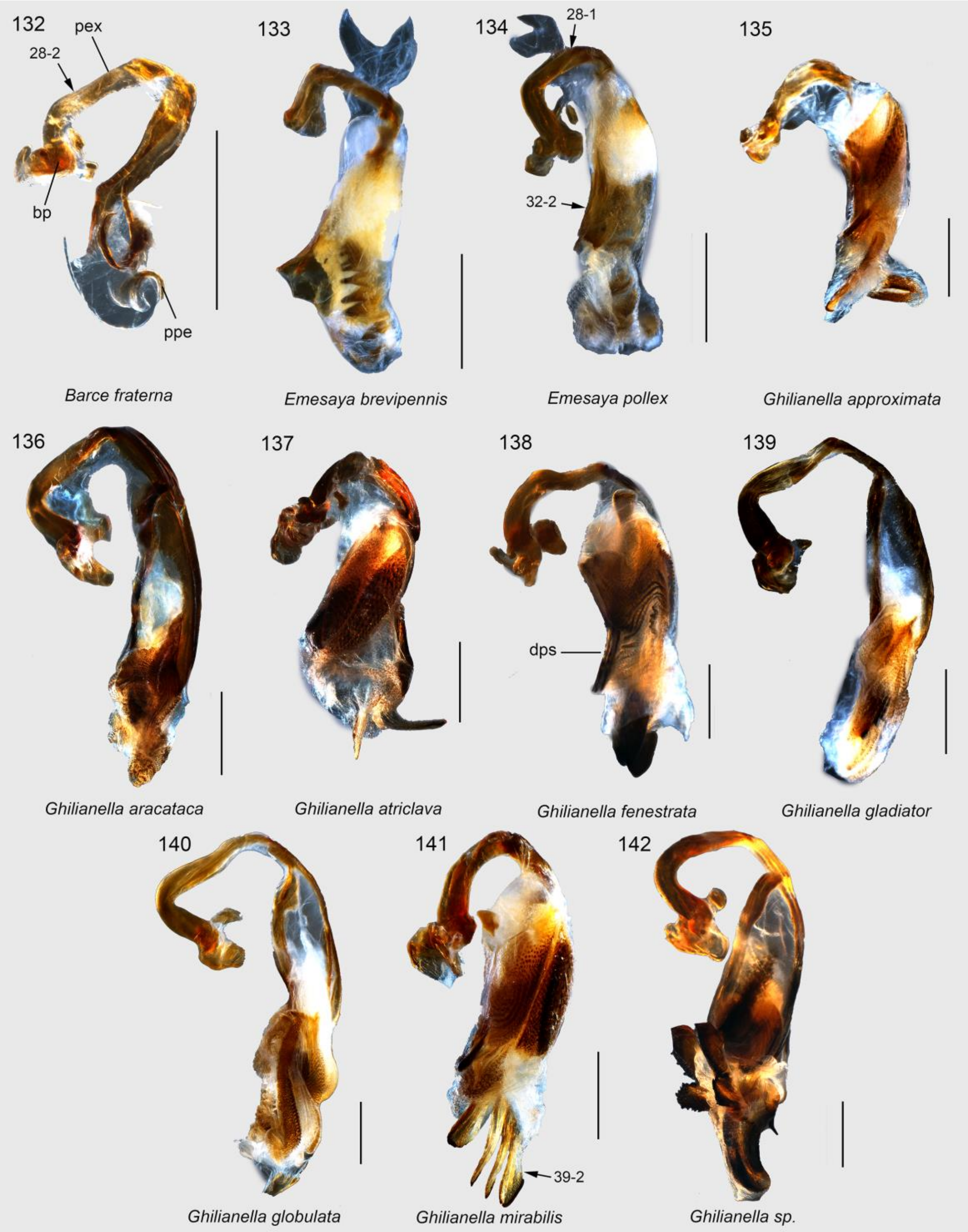


Figs. 111–121. Phallus in dorsal view. *Barce*, *Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: aed – aedeagus; apt – articulatory apparatus; dlb – dorsolateral basal portion of the endosoma; dlm – dorsolateral medial portion of the endosoma; dld – dorsolateral distal portion of the endosoma; dps – dorsal phallothecal sclerite; end – endosoma; pha – phallosoma

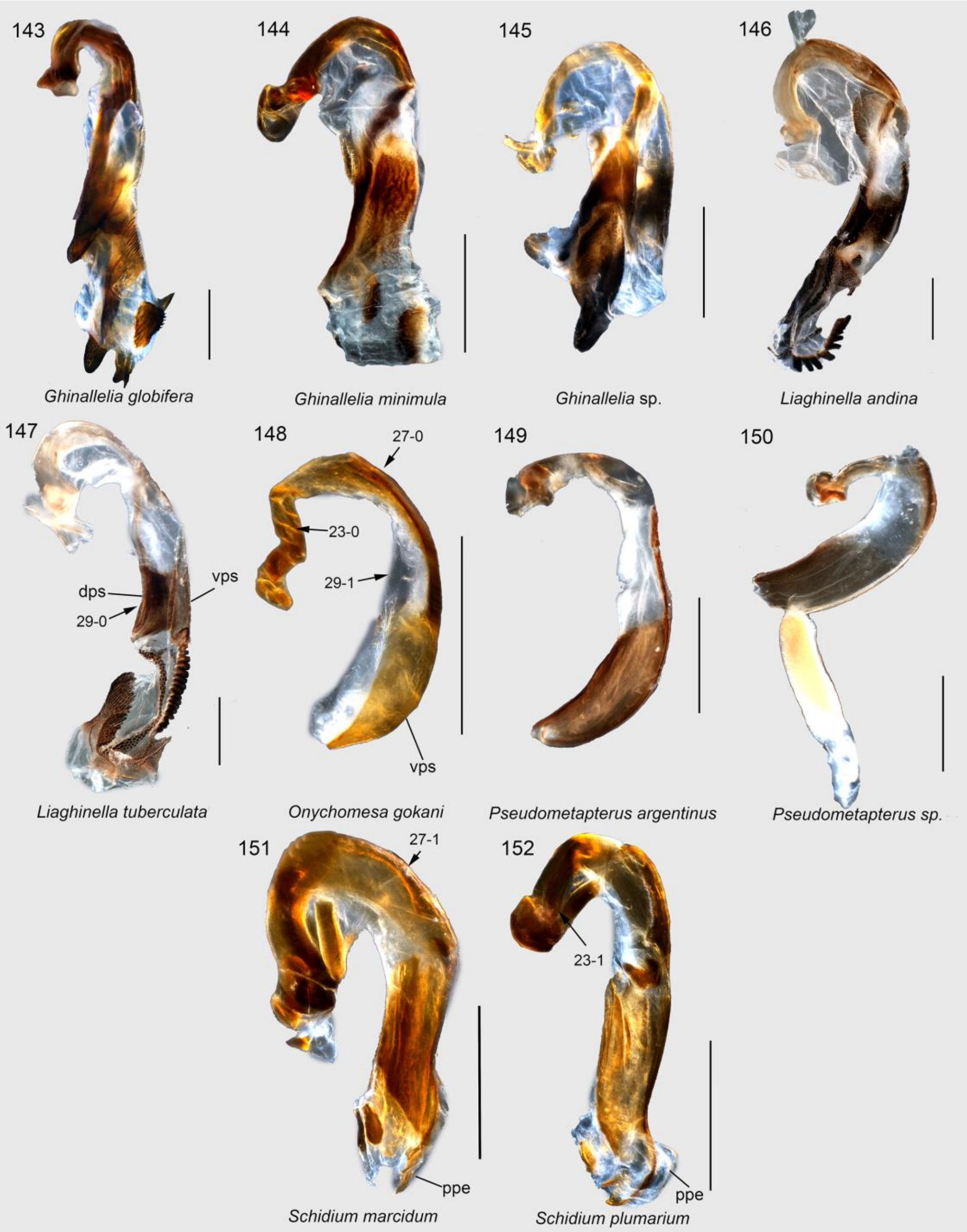


Ghinallelia globifera
Ghinallelia minimula
Ghinallelia sp.
Liaghinella andina
Liaghinella tuberculata
Onychomesa gokani
Pseudometapterus argentinus
Pseudometapterus sp.
Schidium marcidum
Schidium plumarium

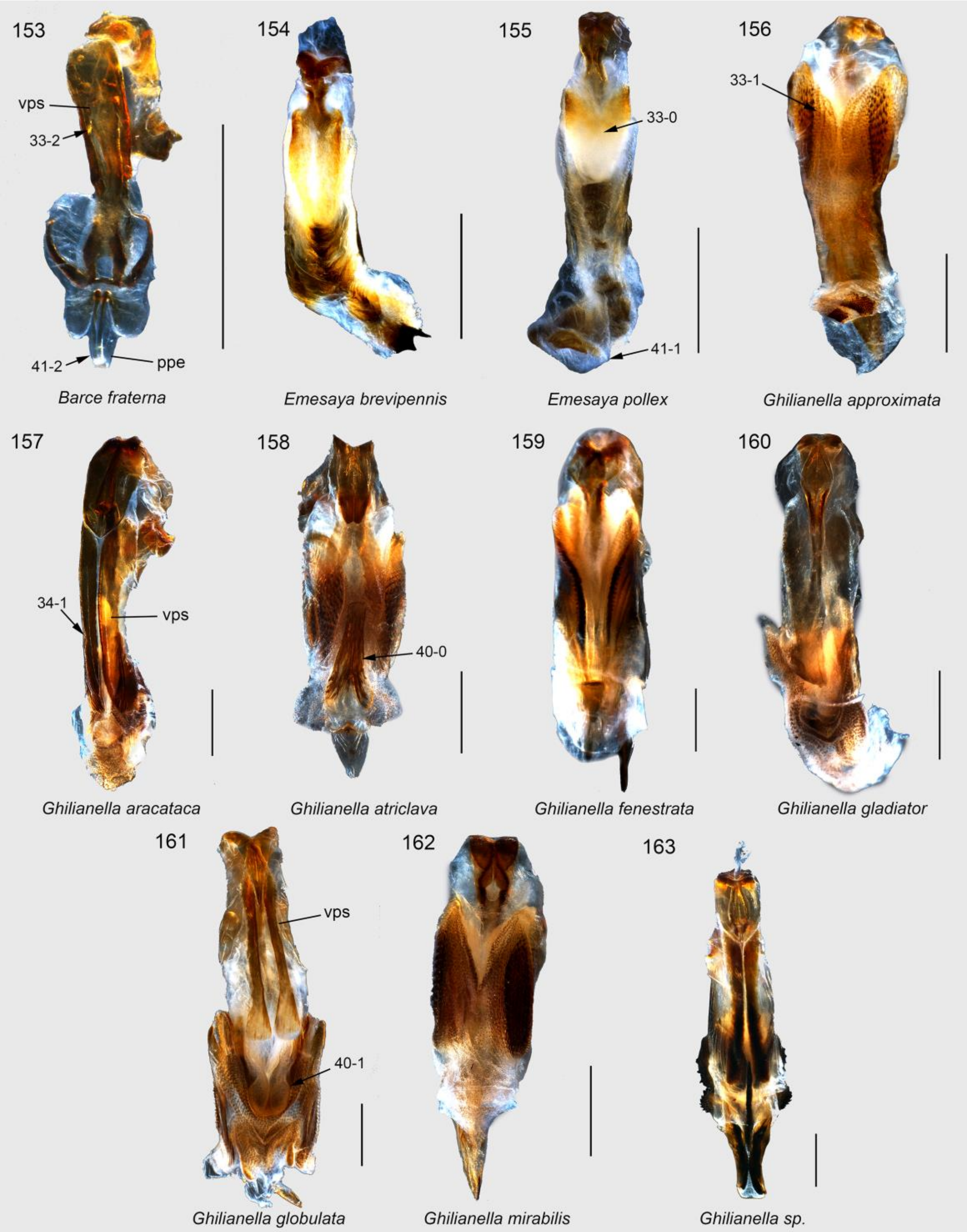
Figs. 122–131. Phallus in dorsal view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: dps – dorsal phallothecal sclerite; duc – ductifer.



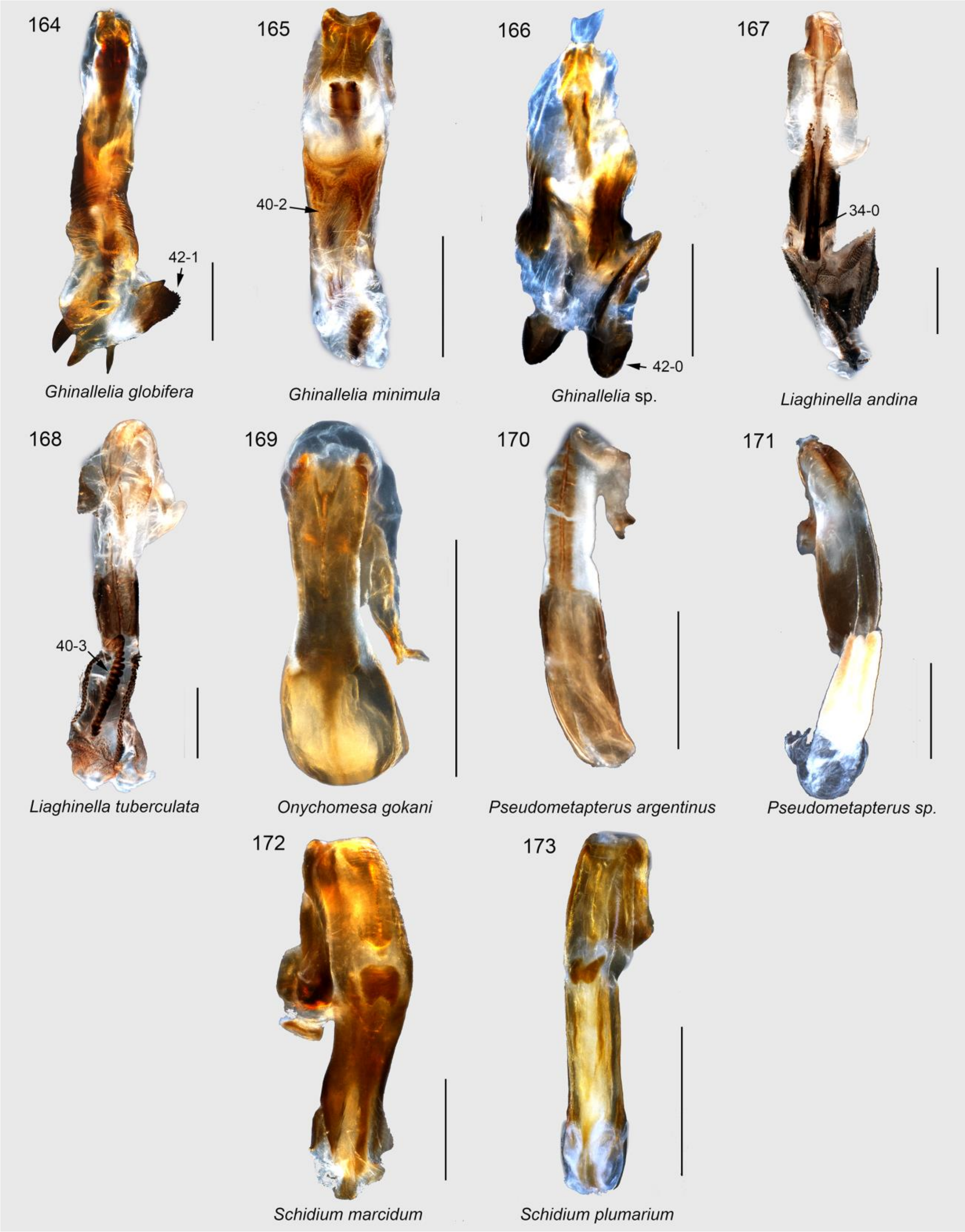
Figs. 132–142. Phallus in lateral view. *Barce*, *Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: bp – basal plate; dps – dorsal phallothecal sclerite; pex – basal plate extension; ppe – posteroventral projections of the endosoma.



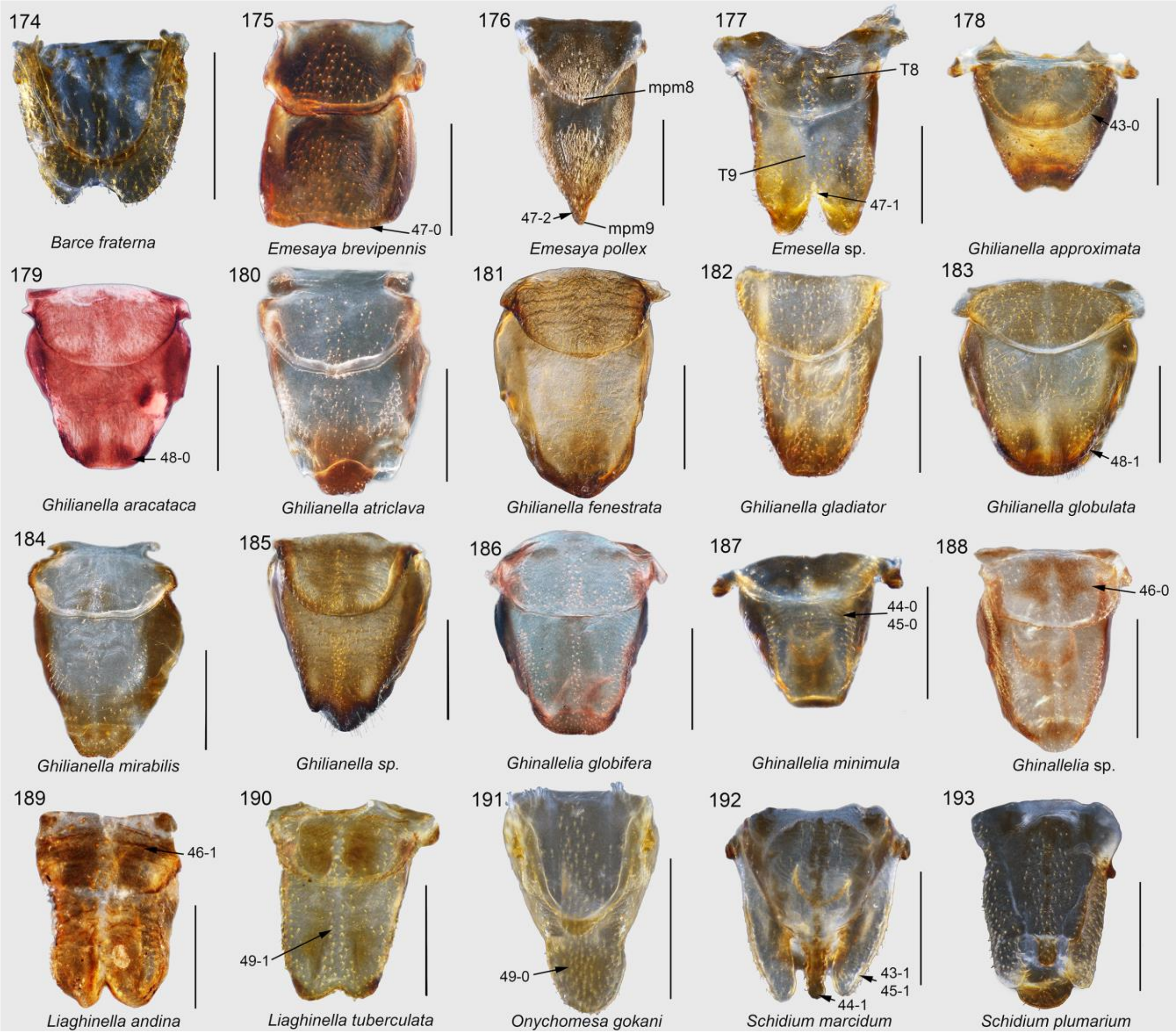
Figs. 143–152. Phallus in lateral view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: dps – dorsal phallothecal sclerite; ppe – posteroventral projections of the endosoma; vps – ventral phallothecal sclerite.



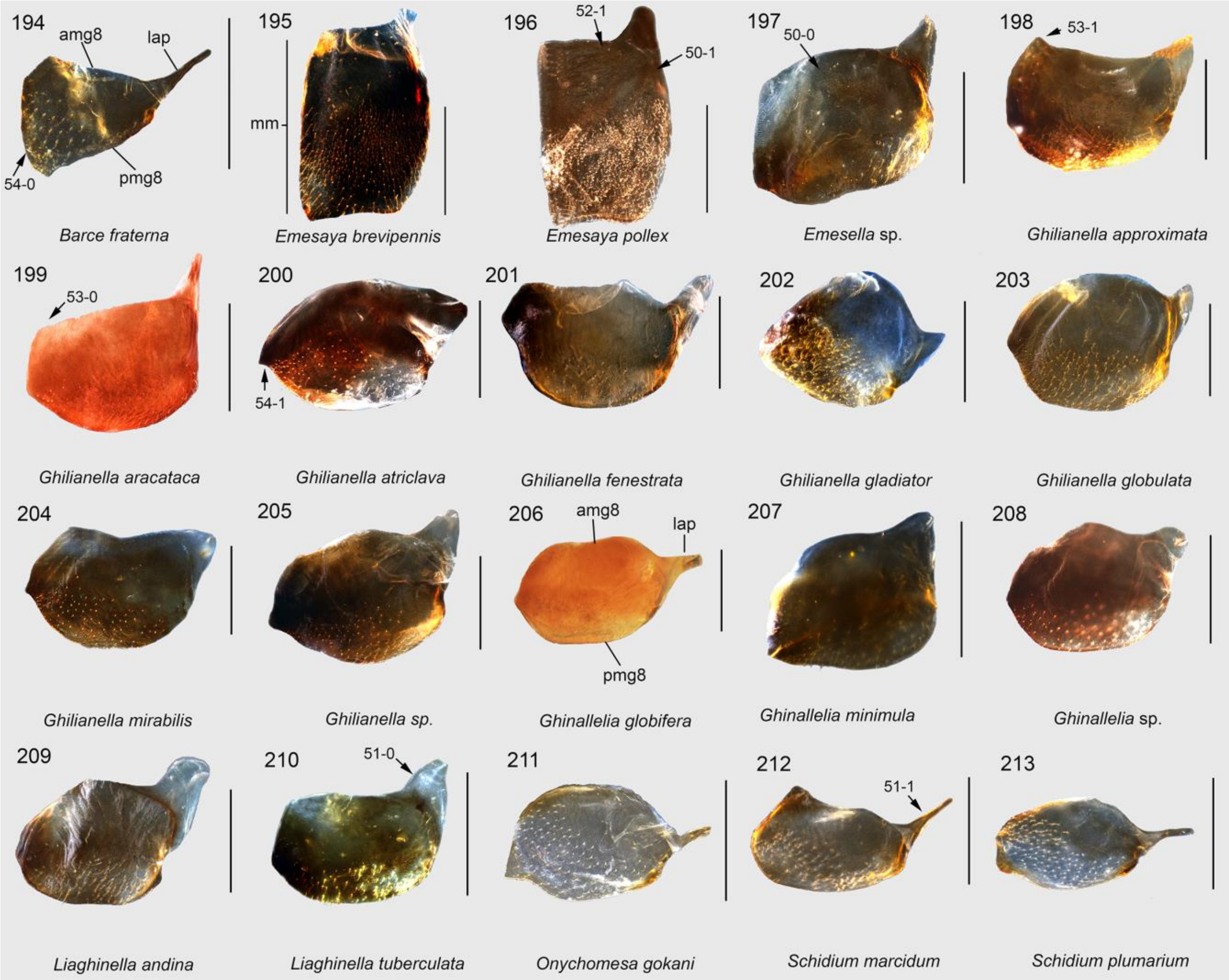
Figs. 153–163. Phallus in ventral view. *Barce, Emesaya* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: ppe – posteroventral projections of the endosoma; vps – ventral phallothecal sclerite.



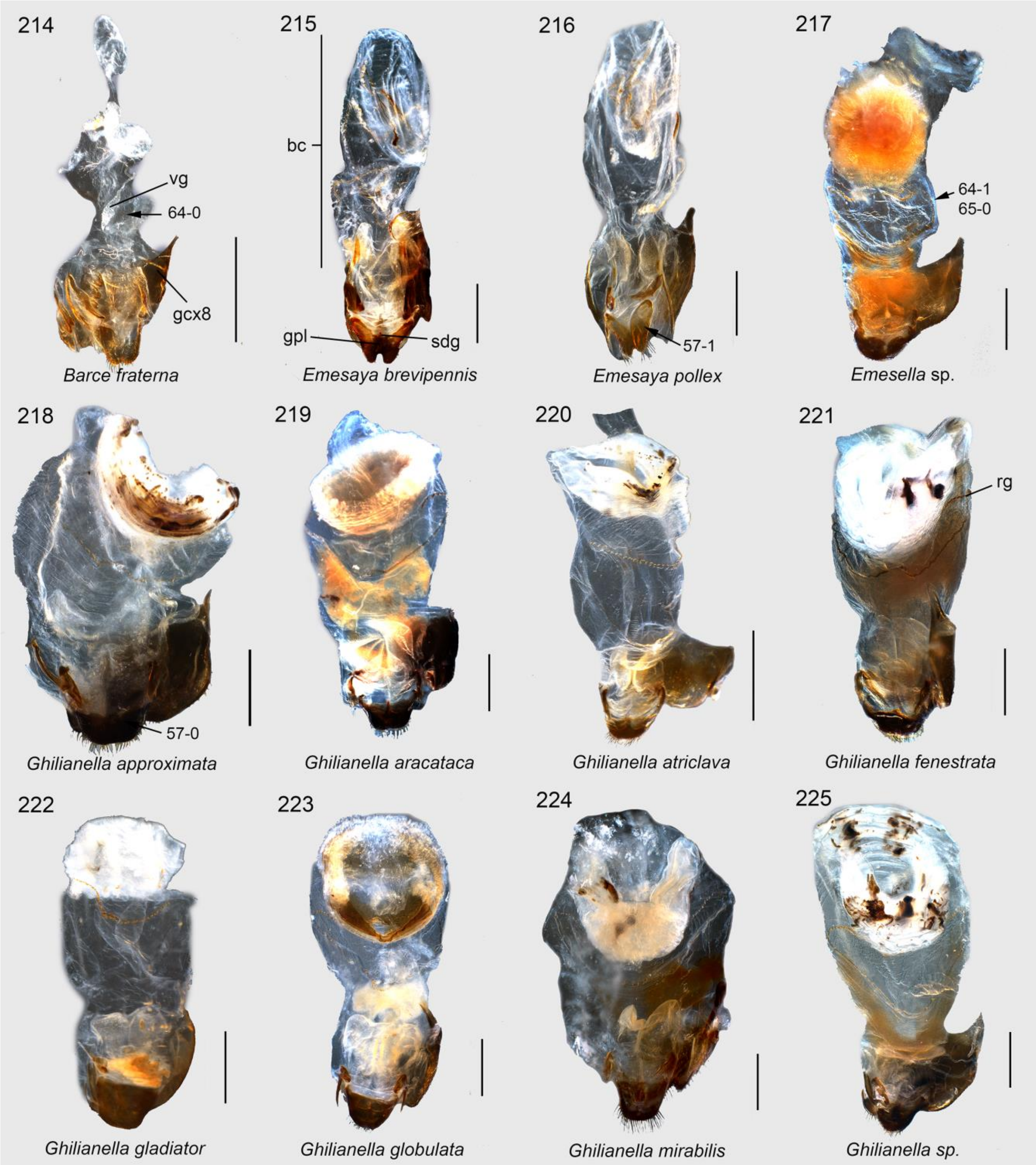
Figs. 164–173. Phallus in ventral view. *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus* and *Schidium*. Scale bar: 0.5 mm.



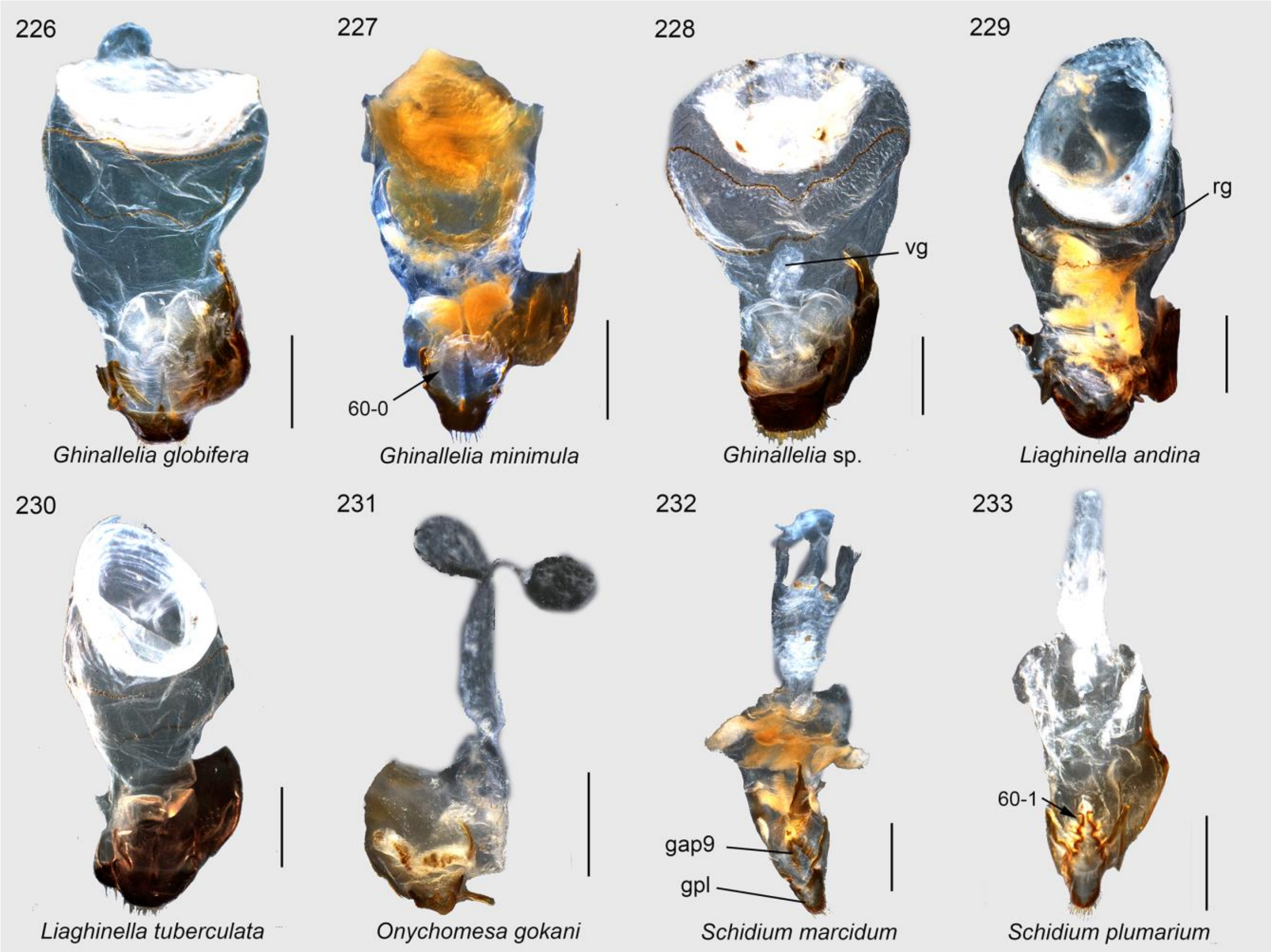
Figs. 174–193. Tergite 8 and tergite 9 in caudal view. *Barce*, *Emesaya*, *Emesella*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa* and *Schidium*. Scale 0.5 mm. Abbreviations: mpm8 – medial posterior margin of tergite 8; mpm9 – medial posterior margin of tergite 9; T8 – abdominal segment 8; T9 – abdominal segment 9.



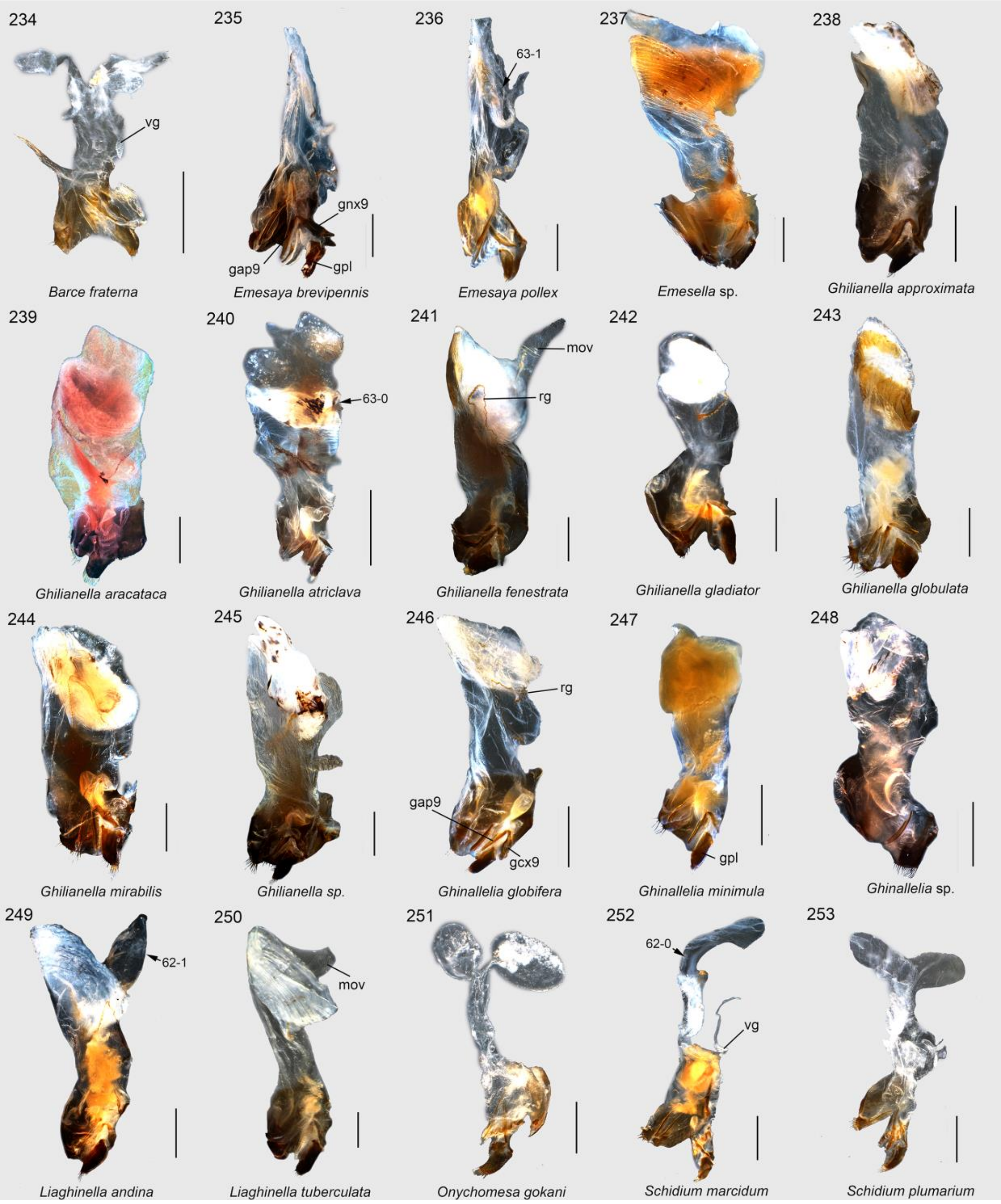
Figs. 194–213. Gonocoxa 8 in ventral view. *Barce*, *Emesaya*, *Emesella*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: amg8 – anterior margin of the gonocoxa 8; lap – lateral anterior prolongation of gonocoxa 8; mm – medial margin of gonocoxa 8; pmg8 – posterior margin of the gonocoxa 8.



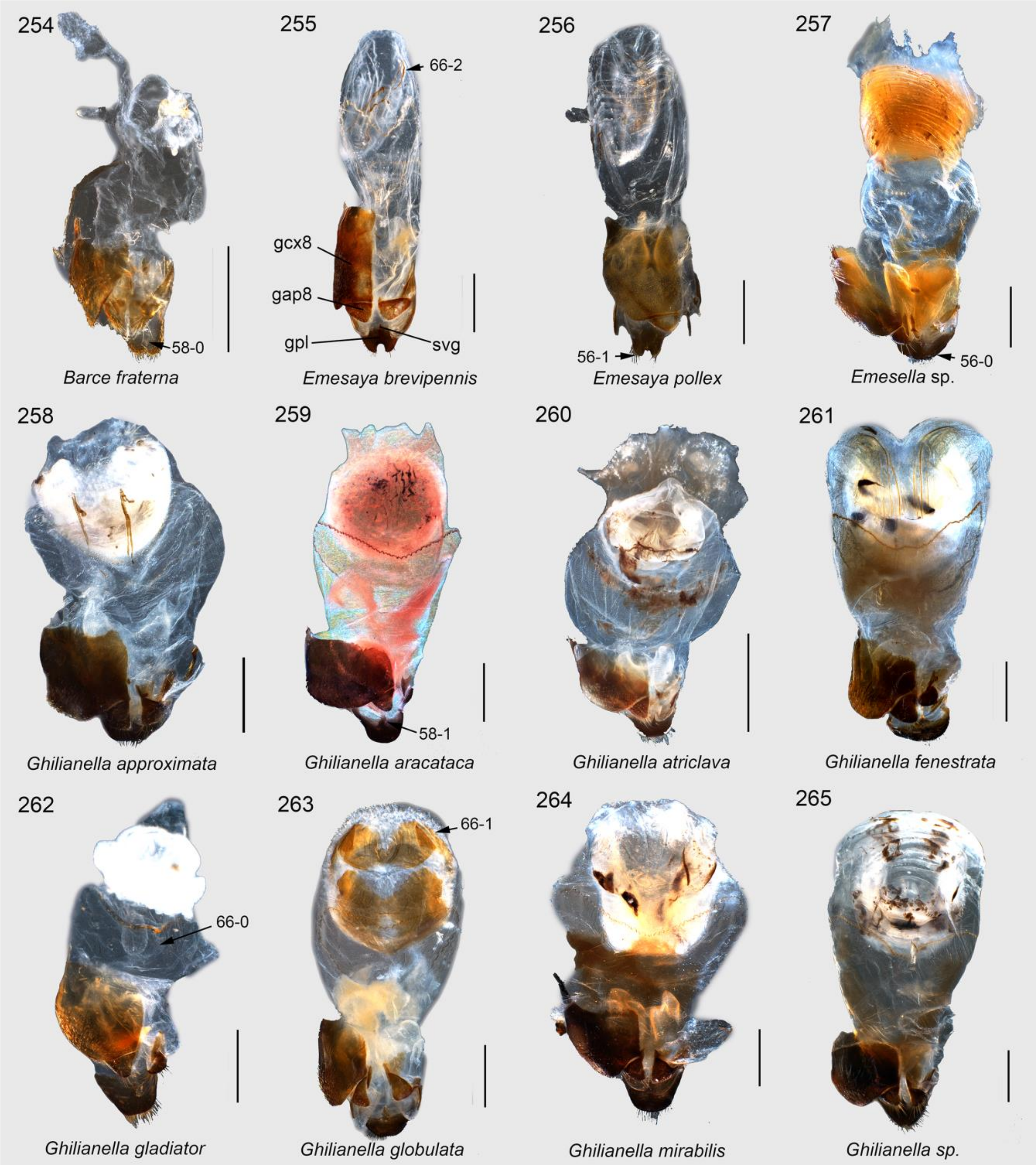
Figs. 214–225. Bursa copulatrix in dorsal view. *Barce*, *Emesaya*, *Emesella* and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: bc – bursa copulatrix; gcx8 – gonocoxa 8; gpl – gonoplac; rg – ring gland; sdg – subapical dorsal margin of the gonoplac; vg – vermiform gland.



Figs. 226–233. Bursa copulatrix in dorsal view. *Ghinallelia*, *Liaghinella*, *Onychomesa* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: gap9 – gonapophysis 9; gpl – gonoplac; rg – ring gland; vg – vermiform gland.



Figs. 234–253. Bursa copulatrix in lateral view. *Barce*, *Emesaya*, *Emesella*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: gap9 – gonapophysis 9; gcx9 – gonocoxa 9; gpl – gonoplac; mov – median oviduct; rg – ring gland of the bursa copulatrix; vg – vermiform gland.



Figs. 254–265. Bursa copulatrix in ventral view. *Barce*, *Emesaya*, *Emesella*, and *Ghilianella*. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gcx8 – gonocoxa 8; gpl – gonoplac; svg – subapical ventral margin of the gonoplac.

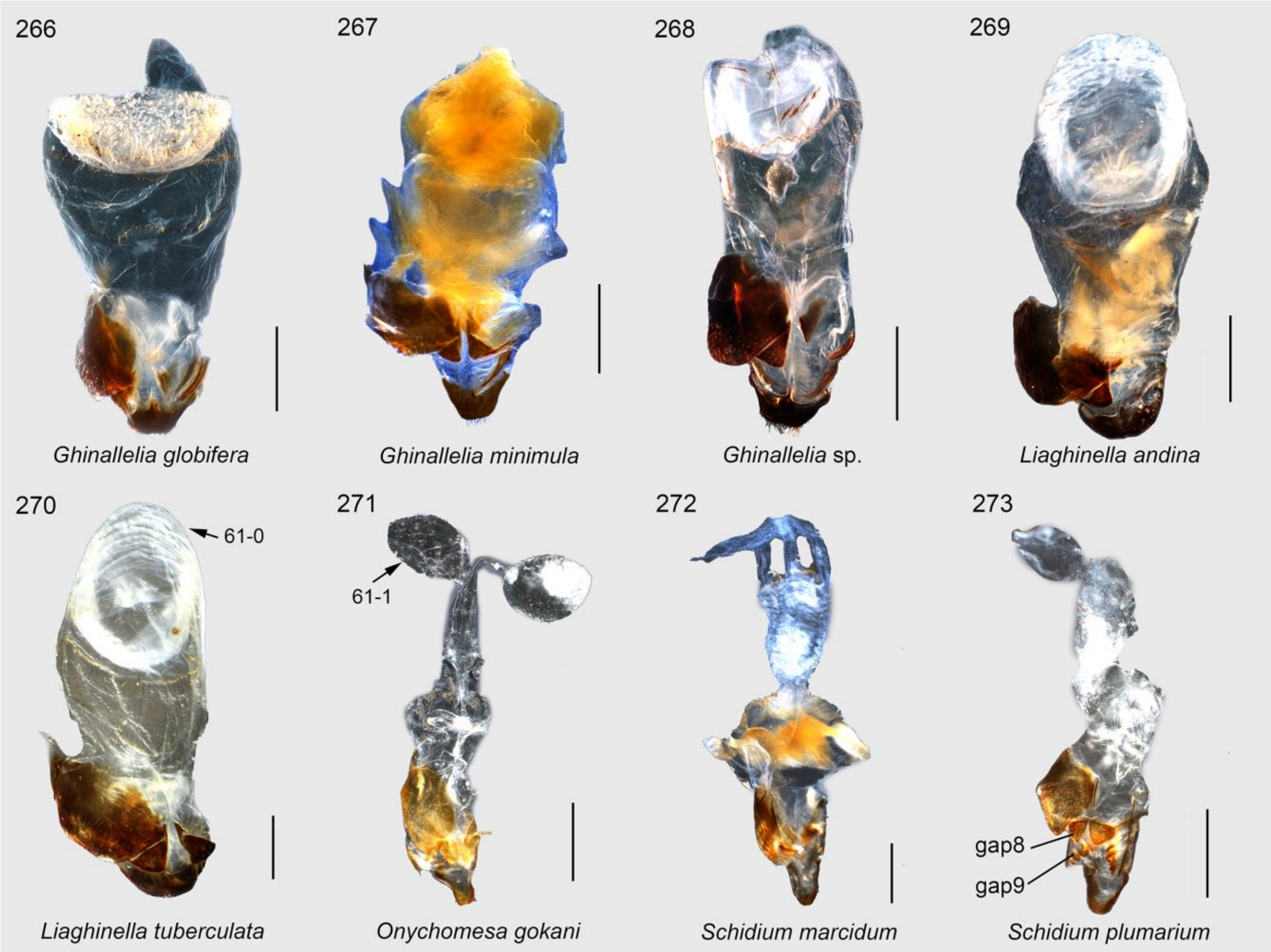
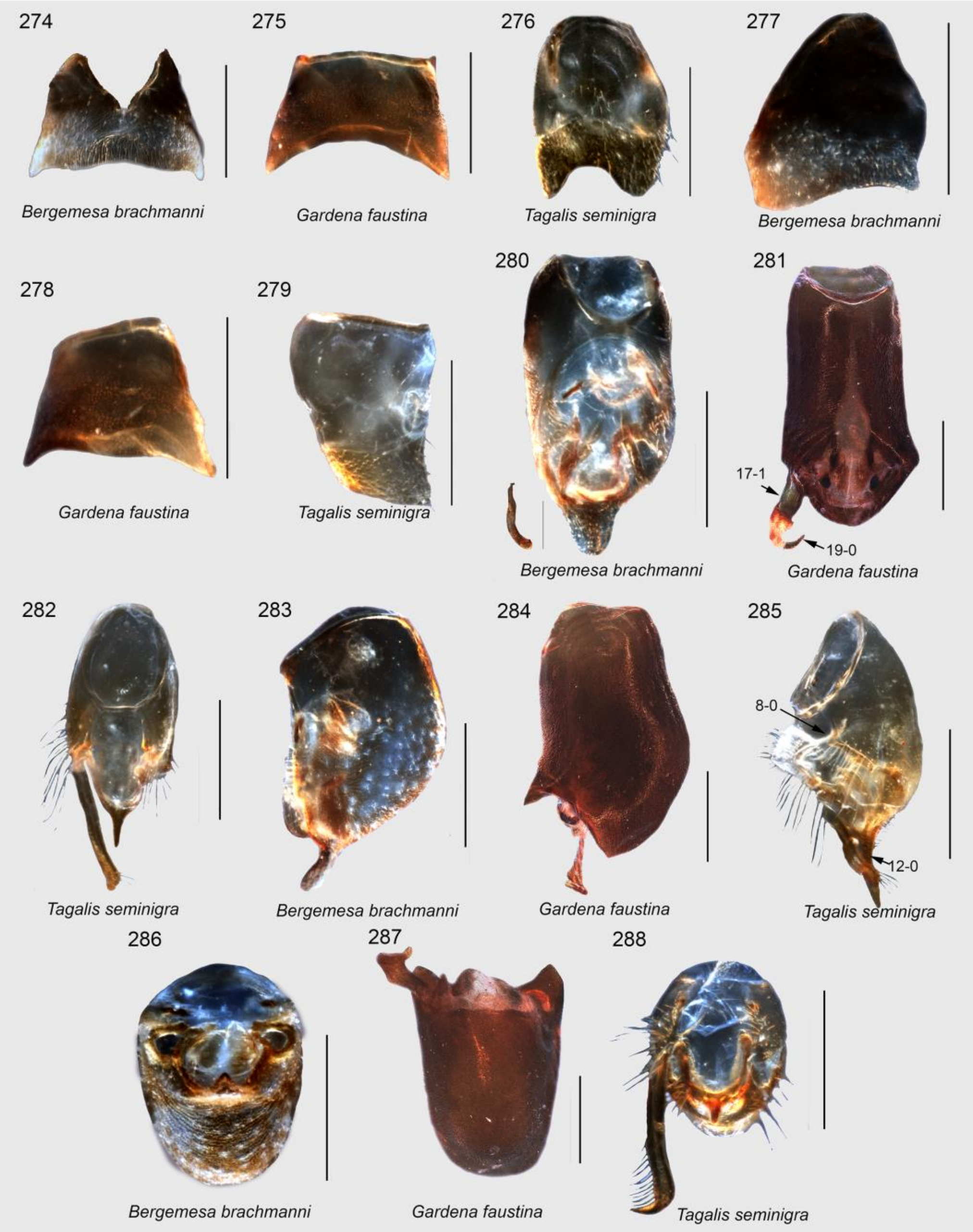
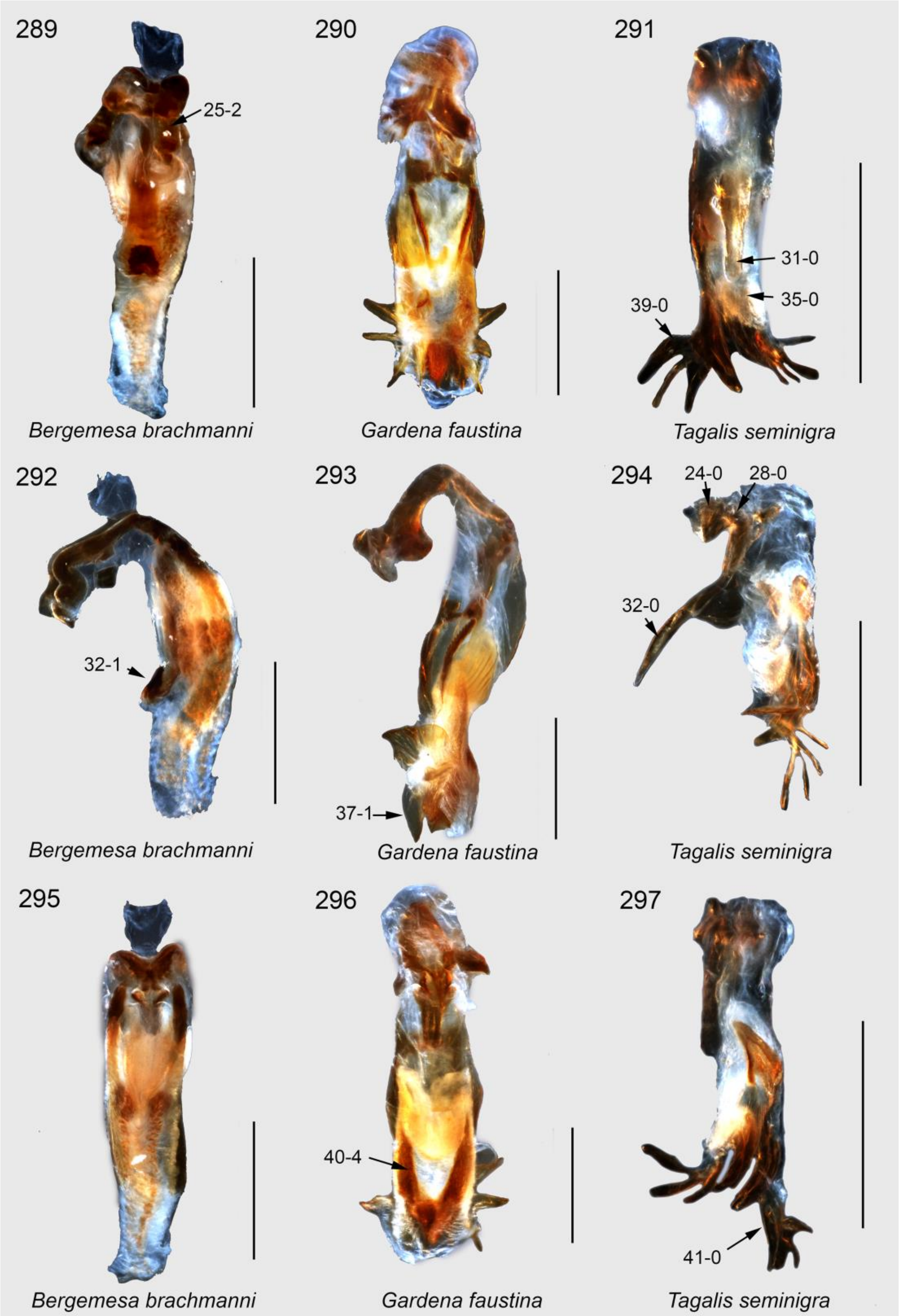


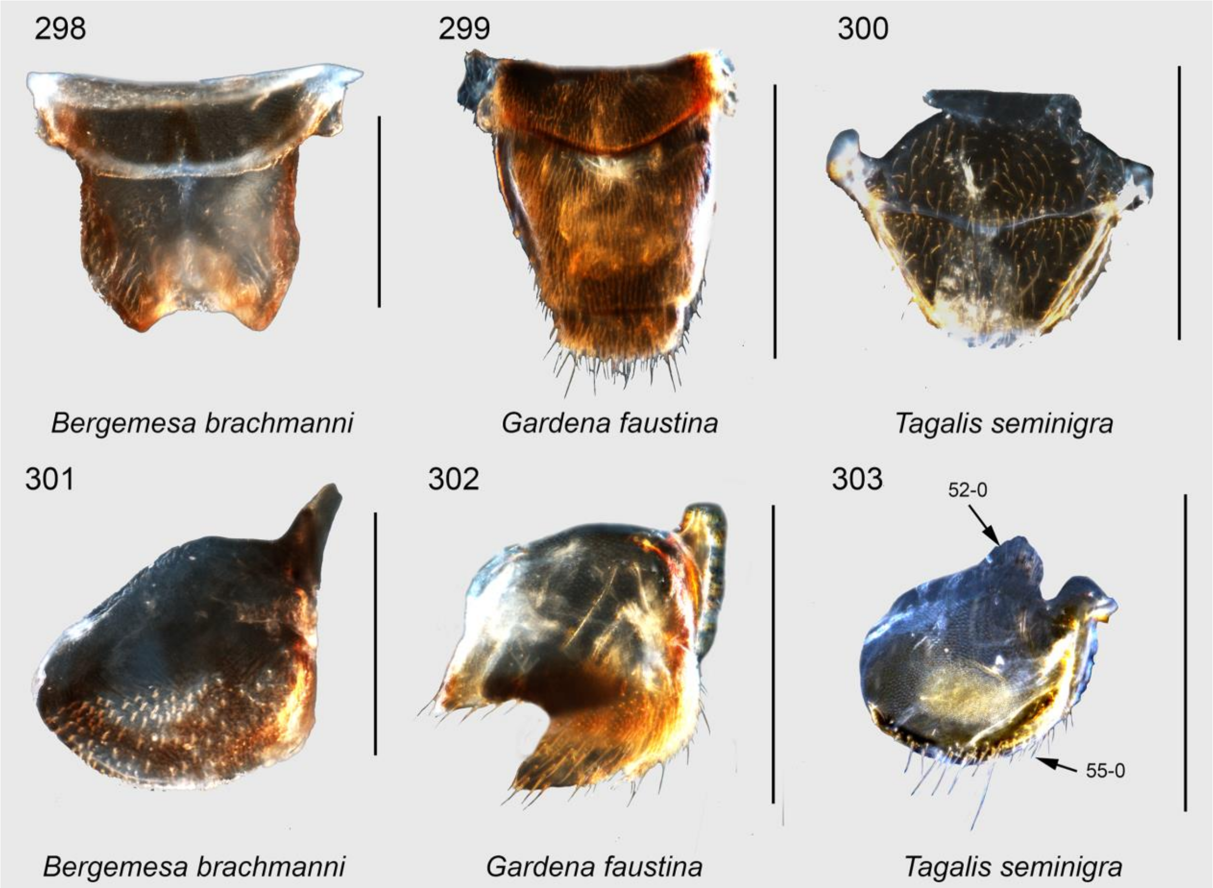
Fig. 266–273. Bursa copulatrix in ventral view. *Ghinallelia*, *Liaghinella*, *Onychomesa* and *Schidium*. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gap9 – gonapophysis 9.



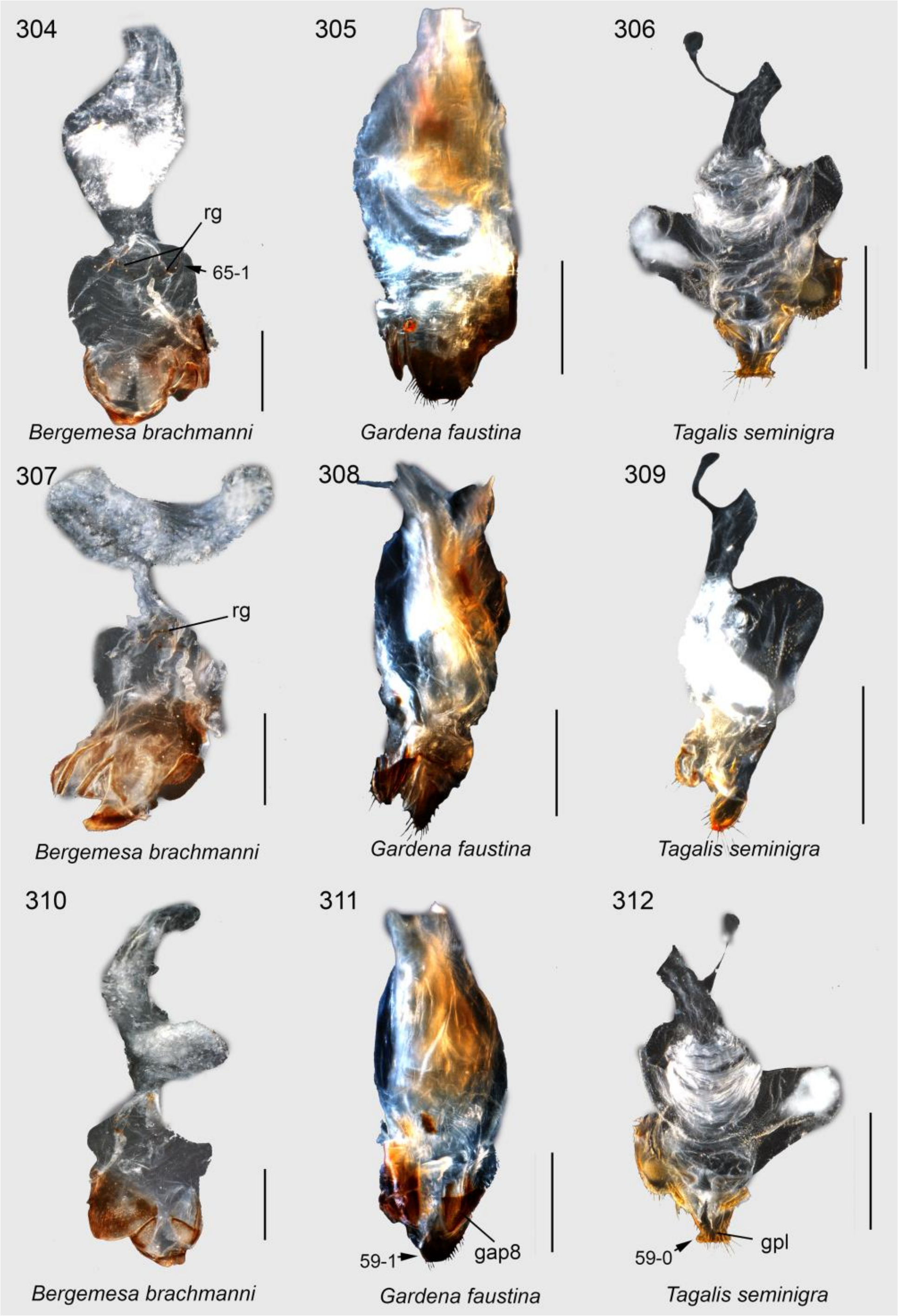
Figs. 274–276. Sternite 8 (S8) in ventral view. 277–279. Lateral view. 280–282. Pygophore in dorsal view. 283–285. Lateral view. 186–288. Ventral view. *Bergemesa brachmanni* (Berg, 1884), *Gardena faustina* McAtee & Malloch, 1925 and *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm.



Figs. 289–297. Phallus. Above in dorsal view. Mid in lateral view. Under in caudal view. *Bergemesa brachmanni* (Berg, 1884), *Gardena faustina* McAtee & Malloch, 1925 and *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm.



Figs. 298–303. Tergite 8, tergite 9 and gonocoxa 8. Above T8 and T9 in caudal view. Under gcx8 in ventral view. *Bergemesa brachmanni* (Berg, 1884), *Gardena faustina* McAtee & Malloch, 1925 and *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm.



Figs. 304–312. Bursa copulatrix. Above in dorsal view. Mid in lateral view. Under in ventral view. *Bergemesa brachmanni* (Berg, 1884), *Gardena faustina* McAtee & Malloch, 1925 and *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gpl – gonoplac; rg – ring gland of the bursa copulatrix.

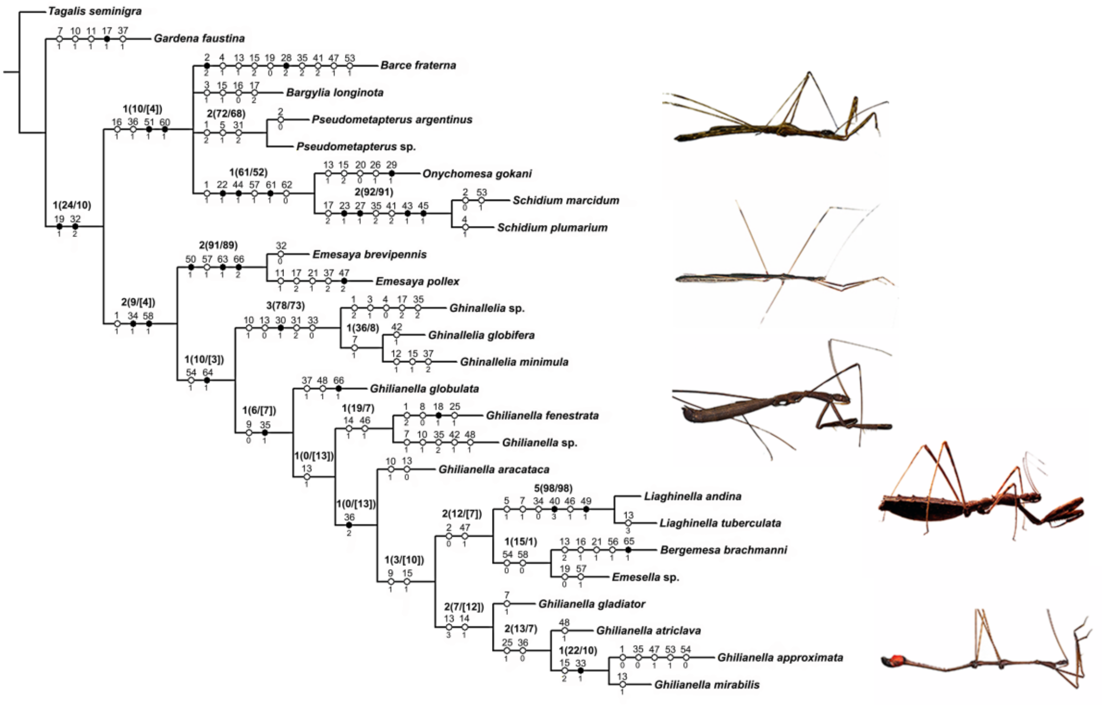


Fig. 313. Strict consensus tree of the male and female genitalic characters. Apomorphies mapped on the tree, non-homoplasious changes as full circles, homoplasious changes as empty circles. Support values in the branches (Bremer support, first value; GC frequencies, inside brackets, square brackets represent negative values of GC).

Table 1. Examined material.

Species	Locality	Sex, USI, and collection
Barce fraterna (Say, 1832)	COLOMBIA: Tolima, Espinal, 28 iv 1960, M. Revelo, light trap.	1 m* 1 f* (CELM)
Bargylia longinota Wygodzinsky, 1956	AUSTRALIA: Port Darwin, NW Australia, J.J. Walker.	1 m* holotype (BMNH)
Bergemesa brachmanni (Berg, 1884)	ARGENTINA: Sgo. Estero, Ojo de Agua, at light, iii. 1969, coll. Martínez	1 m* (MACN)
	ARGENTINA: La Paz (Dep. San Javier), Córdoba, 15.–31.xii.1928, C. Bruch	1 f***** (No 24113, MACN)
Emesaya brevipennis (Say, 1828)	COLOMBIA: Nariño, Tumaco, Dimar, 1°48′N 78°45′W, (0) a 30 mts, 4–14 marzo 2015, Estudiantes taxonomía animal ICN.	1 m* (ICN)
	COLOMBIA: Putumayo, Villa Garzón, Vda. San Rafael, Fca. El Escondite, N1°7′0,6″ W76°37′58,7″, 584 m alt., sweep net, 19.ix.2015, E. Gómez.	1 f* (UNAB)
Emesaya pollex Mcatee & Malloch, 1925	BRAZIL: RS, Palmares do Sul, Ilha grande, 10.iv.2003, equipe Probio.	1 m* (MCNZ)
	BRAZIL: RS, Novo Hamburgo, 20.viii.1982, C. J. Becker leg.	1 f* (MCNZ 47287) (MCNZ)
Emesella sp.	COLOMBIA: Subparamo de Guasca, 3000 m alt, in fallen leaves of *Espeletia corymbosa*, 23.vii.1968, Sturm leg.	1f* (ICN 091391) (ICN)
Gardena faustina McAtee & Malloch, 1925	COLOMBIA: Guaviare, San José del Guaviare Vda. Playa Güio, Isla Laguna Negra, 2°39′54.9″N 72°45′54″W, 197 m alt., 23.x.2012, C. Alvarez.	1 m* (ICN)
	BRAZIL: Amazonas, Manaus. 25.v.1982, F.U.A., Latorre L.R.	1 f* (INPA)
Ghilianella approximata Mcatee & Malloch, 1925	PERU: Satipo, Huancayo, viii.1944, Paprzycki, Zikan coll.	1 m* (FIOC)
	BRAZIL: AM, Ipixuna, rio Liberdade, Estirão da preta (07°21′46.7″S, 71°52′07.1″W).	1 f* (INPA)
Ghilianella aracataca Mcatee & Malloch, 1925	COLOMBIA: Magdalena, PNN Tayrona. Cañaveral, Arrecifes, 11°20′N 74°2′W, 50 m, Red, 18. –.20.vii. 2002, M. Sharkey, D. Arias & F. Torres.leg. M4172.	1 m* (IAvH-E-126058) 1 f* (IAvH-E-126063) (IAvH)
Ghilianella atriclava Bergroth, 1911	COLOMBIA: Meta, Villavicencio, Vda. La Argentina, Piedemonte llanero, Sistemática Animal leg.	1 m*1 f* (ICN)
Ghilianella fenestrata Maldonado, 1960	COSTA RICA: Heredia, La Selva Biological Sation, nr Puerto Viejo, 10.430862°N, 84.006467°W, 52 m, 9–15.viii.2010, OTS	1 m* (UCR_ENT 00003767) 1 f* (UCR_ENT

	Heteroptera course, hand collecting.	00003779) (UCR)
Ghilianella gladiator Mcatee & Malloch, 1925	TRINIDAD: 21.ii.1929, J.G. Myers, T299.	1 m* 1 f* (BMNH)
Ghilianella globulata Mcatee & Malloch, 1925	GUATEMALA: Chacoj, R. Polochic, Champion.	1 m* (BMNH)
	GUATEMALA: Panima, Champion.	1 f* (BMNH)
Ghilianella mirabilis Mcatee & Malloch, 1925	BRAZIL: Amazonas, Manaus, 20.v.1977, APA Luna Dias.	1 m* (INPA)
	BRAZIL: AM, Manaus, Faz NAF, 6-Br 174 – km 31, data: 27.v.1977, col. E. Rufino.	1f* (INPA)
Ghilianella sp.	COLOMBIA: Chocó, Acandí, Capurgana, borde del camino, 27.iii.2009, N. Novoa, manual	1 m* (MPUJ_ENT 0000428) (MPUJ)
	COLOMBIA: Chocó, Acandí, Capurganá, Jardín Botánico del Darien, 8°37′42.72″N 77°21′21.58″W, 40 m, 31.iii.2009, A. Bernal, manual.	1 f* (MPUJ_ENT 0041138) (MPUJ)
Ghinallelia globifera Bergroth, 1906	COLOMBIA: Meta, Acacias, Vda. Esmeralda, abr 2004, 514 m alt, E. Flórez y estud. Sistemática.	1 m* (ICN)
	COLOMBIA: Boyacá, Santa María, Camino La Almenara, 13.x.2005, G. Andrade-C.leg, 880 m alt, GAC10138.	1 f* (ICN)
Ghinallelia minimula	BRASIL. RS, Cidreira, (Mata Restinga), 29.xi.2003, J. Alvenir.leg, pitfall	1 m* (MCNZ 180179) (MCZN)
	BRASIL. RS, Cidreira, (Mata Restinga), 20.xi.2003, J. Alvenir.leg, pitfall	1 f* (MCN 180180) (MCZN)
Ghinallelia sp.	BRASIL. Amazonas, Río Nhamunda, Ig. Areias, 01°35′11″S 57°37′32″W, 25 m. 16.v.2008, J.A. Rafael, manual. INPA	1m*1f* (INPA)
Liaghinella andina Forero 2007	COLOMBIA: Cundinamarca, Cundinamarca, Reserva Chicaque, robledal, 04,6172500°N 74,3139500°W, 2.250 m, 23.xii.2015, E. Tulande	1 m* (MPUJ_ENT 0047555) (MPUJ)
	COLOMBIA: Cundinamarca, Bogotá D.C., EAAB, Quebrada La Vieja (04°38′N 74°02′W), 26.viii.2001, 2850 m alt, D. Forero	1 f* paratype (MPUJ_ENT 0010690) (MPUJ)
Liaghinella tuberculata Forero & Castro-Huertas, 2017	COLOMBIA: Cundinamarca, Reserva Chicaque, refugio, 4º36.892′N 74º18.677′W, 2,221 m, 8.–12.iv.2013, D. Forero leg / near to refuge, under Ficus, in forest litter, at night]	1 m* (MPUJ_ENT 0010584) 1f* (MPUJ_ENT 0010771) (MPUJ)
Onychomesa gokani Ishikawa, 2000	JAPAN: Komi, Iriomote-jima Is., The Ryukyus, 9.x.2004, T. Ishikawa.	1 m* 1 f* (TUA)

Pseudometapterus argentinus (Berg, 1900)	ARGENTINA: Sierra Córdoba. 14.i.1980, Williner S.J.	1 m* (MACN)
Pseudometapterus sp.	BRAZIL: RJ, Vassouras, E. do Rio, 1940, D. Machado.	1 m* (524 Inst. Oswaldo Cruz) (FIOC)
Schidium marcidum (Uhler, 1896)	JAPAN: Ibusuki, Kagoshima pref., 19.iv.2007, A. Ishizuka.leg.	1 m* (TUA)
	JAPAN: Machida, Tosayamada’cho, Kochi pref., 13.iv.2002, T. Ishikawa leg.	1 f* (TUA)
Schidium plumarium Ishikawa, 2002	JAPAN: Komi, Iriomote-jima Is., The Ryukyus, 7.–9.x.2004, H. Mizushima	1 m* (TUA)
	JAPAN: Toyohara, Iriomote Is., The Ryukyus, 7.iv.2003, M. Takai	1 f* (TUA)
Tagalis seminigra Champion, 1899	PERU: Ucayali, Kirigueti (luz), vii 2004, J. Williams, 73°07′08″W, 11°38′13″S	1 m*(MLPA)
	PERU: Cuzco, Pagoreni (luz), vii.2004 Williams, 72°54′07″W 11°42′22″S	1 f* (MLPA)

CAPÍTULO II*

Comparative morphology of the raptorial leg in thread-legged bugs of the tribe Metapterini Stål, 1859 (Hemiptera, Heteroptera, Reduviidae, Emesinae)

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ABSTRACT

Assassin bugs (Hemiptera, Heteroptera, Reduviidae) have diverse and complex morphological and behavioral adaptations for prey capture. Several of these morphological adaptations occur on the proleg. The prolegs of Emesinae are typically raptorial and they are used for grooming, grasping and hunting prey. Several morphological characters that define Emesinae as a group are found on the proleg, such as the anterior opening of the acetabula, the elongation of the procoxa, and the lateral (campaniform) sensilla on the protibia. Metapterini comprises 28 genera and approximately 280 described species, and are characterized by a conspicuous basal process of the anteroventral series of the profemur, and highly modified pretarsal structures. In this study, structures of the proleg are documented for 13 genera of Metapterini, using stereomicroscopy and scanning electron microscopy (SEM). Detailed descriptions and digital

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macrophotographs are provided for most of the genera for the first time, and from this morphological documentation 38 phylogenetic characters are coded, presented as a data matrix, and analyzed cladistically, and their potential usefulness for resolving relationships among Metapterini is discussed.

Keywords: cuticular processes, proleg, phylogenetic analysis

INTRODUCTION

Assassin bugs (Hemiptera, Heteroptera, Reduviidae) are the largest family of predatory terrestrial Heteroptera (Gil-Santana et al. 2015) having evolved diverse and complex morphological and behavioral adaptations for prey capture. Several of these morphological adaptations occur on the proleg, such as hairy attachment structures, chelate or subchelate prolegs, conspicuous spiniform processes and even structures that allow the development of "sticky traps" (Weirauch 2007; Forero et al. 2011; Weirauch et al. 2011; Zhang et al. 2016a, b). Legs with morphological modifications for seizing prey are referred to as raptorial legs (Torre-Bueno 1989; Zhang et al. 2016a) and have evolved multiple times convergently within Hexapoda (Beutel et al. 2014); however their evolution, at least within Reduviidae, is a process not yet fully understood (Weirauch 2007; Zhang et al. 2016a).

One of the Reduviidae groups with modified front legs are the Emesinae Amyot and Serville, 1843, with approximately 90 genera and more than 900 described species (Rédei 2007a; Rédei and Tsai 2010). This is a peculiar group because of two morphological characteristics: the progressive narrowing of the body with lengthening of the appendages, and the frequent occurrence of sexual dimorphism (sometimes wing polymorphism) (Wygodzinsky 1966). The prolegs of Emesinae are typically raptorial, different to its cursorial meso- and metalegs, and they are used for grasping, cleaning and hunting, with less functionality in locomotion (Wygodzinsky 1966). Several morphological characters that define Emesinae as a group are found on the proleg and could be associated to a raptorial function, such as the anterior acetabula opening which probably have influence in the coxal displacement on the parallel-front plane (Gorb 1995), the elongation of the procoxae which apparently increases their striking range (Weirauch et al. 2011), and the lateral (campaniform) sensilla on the protibia with a likely sensorial function (Wygodzinsky 1966). In addition, ventral spiniform conspicuous processes on the profemur and the protibia have taxonomic importance, at least to the tribal and generic level (Wygodzinsky 1966; Weirauch 2008).

Emesinae are classified in six tribes, one of which are the Metapterini Stål, 1859 which include 28 genera and approximately 280 described species (Maldonado Capriles 1990, 1993, Ishikawa 2000, 2002, Gil-Santana et al. 2005, 2009; Forero 2007; Rédei 2007b; Gil-Santana 2009). Two of the characters describing this tribe are a conspicuous basal process of the posteroventral series on the proleg, a shared feature with Deliastini Villiers, 1949, and having wing polymorphism, in which a large proportion of the genera have micropterous and apterous individuals. Wygodzinsky (1966) described and illustrated the structures of the proleg for most genera of Metapterini using stereomicroscopy and light microscopy, but without documenting consistently the same structures across taxa. Weirauch (2005) described pretarsal structures using SEM and light microscopy in Reduviidae, including two Metapterini, *Barce* sp. and *Ghilianella filiventris* Spinola, 1850, highlighting the modified pretarsal structures in emesines and the importance of detailed studies about these characters set with additional taxa.

Despite the conspicuousness of emesines, due to their modified morphology for prey capture, no modern phylogenetic hypothesis is available for the group. The first available phylogenetic hypothesis was proposed by Wygodzinsky (1966) and it proposed Deliastini as the sister group of Metapterini. Wygodzinsky (1966) also considered Metapterini as monophyletic based on the reduction of the eye size and the loss of the M-Cu cross vein in the hind wing, but this hypothesis has never been tested with quantitative cladistic approaches. A recent study analyzed characters of the male and female genitalia (Castro-Huertas et al. 2018), and suggest that this group might be paraphyletic. This study aims on providing a detailed documentation of the morphology of the procoxa, femur, tibia, tarsus and pretarsal structures of 13 genera of Metapterini. We offer a descriptive groundwork of morphological characters of the proleg with emphasis on its cuticular processes from we coded and tested 38 characters with cladistic methodology.

MATERIALS AND METHODS

Taxon sampling. 13 genus-level taxa comprising 20 species of Metapterini and eight outgroups were examined and included in the analysis (see table 1, material examined). Specimens are deposited in the following institutions, abbreviations for institutions follow Evenhuis (2017): (ANIC) Australian National Insect Collection, Division of Entomology, CSIRO, Camberra, Australia; (BMNH) The Natural History Museum, London, England; (CELM) Colección Entomologica "Luis Maria Murillo", Corpoica, Bogotá, Colombia; (IAVH) Instituto Alexander von Humboldt, Villa de Leyva, Colombia; (ICN) Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; (INPA) Instituto Nacional de Pesquisas da Amazonia, Colecão Sistemática da Entomologia, Manaus, Amazonas, Brazil; (MACN) Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; (MCNZ) Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; (MLPA) Universidad Nacional de La Plata, Museo de la Plata, La Plata, Argentina; (MNRJ) Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; (MPUJ) Colección Entomológica, Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia; (TUA) Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Tokyo, Japan; (UFRG) Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Rio Grande do Sul, Porto Alegre, Brazil; (UFVB) Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil; and (USNM) National Museum of Natural History, Washington D.C., USA.

Material examined. See Table 1.

Specimen preparation and dissection. The specimens studied were pinned dry or preserved in ethanol. Dry specimens were relaxed with Barber’s fluid modified from Stuben and Linsenmair (2009), and the left proleg was removed, cleaned manually with forceps and a fine brush with isopropyl alcohol, kept submerged in contact lens solution Renu® for 24 hours, and then agitated in an ultrasonic bath (5.400 kHz) with warm water and detergent solution for three minutes or less for small structures. Subsequently, the profemur, protibia and protarsus were separated with fine forceps and dehydrated at 50 °C for 24 hours, sputter coated with gold and observed by scanning electron microscopy (SEM).

Imaging. Proleg structures were documented using a stereoscope Nikon AZ100M, equipped with a NIS-Elements AR software. The tegumentary fine structure was studied using scanning electron microscopy (SEM) on a JEOL JSM6060 at the Centro de Microscopia e Microanálise of the Universidade Federal do Rio Grande do Sul (CMM-UFRGS). *Bargylia longinota* Wygodzinsky, 1956 was documented from the holotype specimen only using a stereomicroscope. Following Forero et al. (2011), anterior, posterior, dorsal and ventral surfaces were identified on the profemur, protibia and protarsus as if extended and perpendicular to the longitudinal body axis. For image editing, Adobe Photoshop CS6 v13.1.2 was used.

Terminology. The terminology of Wygodzinsky (1966), Cobben (1978), Schuh and Slater (1995), and Weirauch (2005) was adopted. In Metapterini, the proleg armature occurs as two distinct types: 1) simple setae, on a flat base and with thin or slightly stout apex (Figs. 23, 24), and 2) strongly stout spiniform setae on cuticular projections (Fig. 22, 24), the length of the base and the apex are variable. Here, we use “simple setae” and “spiniform process” for each type of process.

Within Emesinae the claws of the proleg are usually parallel with respect to longitudinal axis of tarsus, and the terms “outer claw” and “inner claw” are used for the posterior and anterior claws respectively (Wygodzinsky 1966; Weirauch 2005). Here, we use posterior claw and anterior claw, respectively, to be consistent with topological relationships.

We use the following abbreviations for the structures identified: *ac*, anterior claw; *asp*, accessory setae of the profemur; *avs*, anteroventral series of the profemur; *bl*, basal lamella; *bp*, basal protuberance of claw; *bas*, basal process of the anteroventral series of the profemur; *bps*, basal process of the posteroventral series of the profemur*; bta*, basal process of the protarsus; *cx*, coxa; *dl*, distal lamella; *dsc*, dorsal surface of the procoxae; *dta*, distal process of the protarsus; *dts*, dorsal tibial surface; *fem*, femur; *fts*, first tarsal segment; *i*, incision between basal and distal lamella; *ls*, lateral seta; *pc*, posterior claw; *ps*, parempodial seta; *ptc*, protibial comb; *pvs*, posteroventral series of the profemur; *sts*, second tarsal segment; *tar*, tarsus; *tb*, tibia; *tts*, third tarsal segment; *tr*, trochanter; *ts*, tricoid sensillum; *utr*, unguitractor plate; *vs*, ventrolateral seta, *vtp*, ventral tibial process.

Cladistic analysis. Characters were organized and coded using MESQUITE version 3.5 (Maddison and Maddison 2018). The description of each character and its states follow Sereno (2007). We used 30 binary and eight non-additive multistate characters. The analysis was conducted in TNT v. 1.5 (Goloboff and Catalano 2016), using implied weighting (Goloboff 1993) which uses a concave function that weights characters against homoplasy (Goloboff 1993). To calculate the value of the constant k for the implied weighting we followed Mirande (2009) in which 11 k-values were calculated with a fit range of 50–90% of a perfectly hierarchical character. A similarity matrix of subtree pruning regrafting (SPR) distances was constructed to compare the 11 strict consensus calculated from the trees resulting from each k-value; based in these values, the trees with higher sums of similarity of SPR distances, indicating more stable k-values. The highest value of the SPR distances sum of the consensus trees was obtained for six k-value that corresponds to K= 1.391453. Sectorial searches were performed using a New Technology Search, with settings as follow, *ratchet*: stop perturbation phase when 20 substitutions made, or 99% swapping complete, perturbation phase 4 up-weighting and prob., 4 down weighting prob., and 200 iterations; *tree-drifting*: stop perturbation phase when 20 substitutions made, or 99% swapping complete, accept suboptimal rearrangements with 1 maximum fit difference, 20 maximum relative fit difference, 30 rejection factor, and 200 cycles. Consistency index (CI) and retention index (RI) were calculated for each character and for the strict consensus tree. The output was visualized using WinClada (Nixon 2002) and characters were mapped using unambiguous optimization. Support was calculated as relative Bremer values using a script (dobrem.run) and GC frequencies, the latter using symmetric resampling with 1000 replicates expressed as groups present/contradicted (Goloboff et al. 2003). All trees were rooted with *Tagalis seminigra*. The strict consensus tree with all characters supported in the unambiguous optimization was used for the discussion. All characters and character states are indicated in the figures with arrows as “20-1” (i.e., character 20, character state 1).

RESULTS

Comparative morphology

The description of the proleg of Metapterinae is organized from basal to apical structures (coxa, trochanter, femur, tibia, tarsus and pretarsal structure), and from dorsal to ventral cuticular processes.

Procoxa (Figs. 1–6)

Structure. The procoxa within Metapterini can be strongly elongate and narrow (Fig. 1), or elongate and wider (Fig. 2). Usually with a dorsal longitudinal row of short curved setae (Fig. 5) or with a medial row of strong and short setae and two rows of narrow lateral setae (*Jamesella*, *dsc*, Fig. 6). In the examined genera, the procoxa length ranges from 0.5 to 0.75 times the profemur length.

Comments. The cuticular surface in Metapterini genera is usually glabrous, in contrast to *Bergemesa* (Deliastini) with rugose cuticle, although both tribes have a similar dorsal longitudinal row of short curved setae.

Protrochanter (Fig. 7)

Structure. Rhomboid sclerite, short and not particularly modified within Metapterini, with sparse short setae and campaniform sensilla located ventrally at the base of segment (Fig 7).

Comments. Campaniform sensilla located in similar areas were found in all examined specimens (Emesinae and Saicinae). These structures have been described previously for others groups of Heteroptera in a similar position on the protrochanter (Gerridae and Veliidae, Andersen 1982; Enicocephalidae, Baňař and Štys 2006; Štys and Baňař 2007; Corixidae, Melo and Scheibler 2011). Comparative morphological studies, including a wider taxon sampling could clarify the phylogenetic significance of these structures.

Profemur (Figs. 10–18)

Structure. The profemur is elongated, usually longer and narrower than the procoxa (Figs. 11, 13), except in *Emesella* (Fig. 12) and *Liaghinella* (Fig. 14) in which the profemur is wider. Dorsally with a longitudinal row of short and curved setae (Fig. 17), or with long and sparse setae (e.g. *Emesaya*, Fig. 18). Ventrally with an anterior (*avs*) and posterior (*pvs*) series (Fig. 12).

The posteroventral series has a basal spiniform process (*bps*) which is conspicuously longer than other processes of the series, it is directed at about 45 degrees or nearly vertical with respect to the longitudinal axis of the femur, and it is located between the basal fourth (Figs. 12, 14) to about the mid length (Figs. 11, 13, 15) of the profemur. The posteroventral series is composed of spiniform processes and setae, in a row parallel to the longitudinal axis of femur, or with some spiniform processes in a slightly irregularly arrangement, as *Taitaia* (Fig. 25).

The anteroventral series can be composed exclusively of spiniform processes (Fig. 22), setae (Fig. 23), or mixed spiniform processes and simple setae (*Ghilianella*, Fig. 24); and can be arranged parallel to the longitudinal axis of the profemur (Fig. 13) or with the basal spiniform process or setae of the row, arranged more dorsally than the rest (Fig. 14). In addition to the anteroventral series there can be accessory setae arranged to the side of the process (*asp*, Fig. 22). The basal spiniform process of the anteroventral series (*bas*) can be located basal (Fig. 10), at the same level (Fig. 15) or distal (Fig. 14) to the basal spiniform process of the posteroventral series. The anteroventral processes can be placed continuous to the basal process (Figs. 12, 14) or be separated from it by a space (Figs. 10, 15).

Comments. In Deliastini and Metapterini, the basal process of the posteroventral series is conspicuously enlarged and this character was used by Wygodzinsky (1966) to consider them as sister groups. However, the relationships among tribes and genera of Emesinae have not been tested in a modern cladistic context, and thus the significance of this character has never been appropriately evaluated.

The arrangement and extension of the anterior and posterior ventral setal series, composed by simple setae or/and spiniform processes, are the taxonomic characters frequently used to separate genera in Metapterini (Wygodzinsky 1966; Forero 2004).

Protibia (Figs. 26–76)

Structure. The protibia is elongated, being about half or less than half the total length of the profemur; it is basally slightly curved, uniformly narrow (Fig. 27) or slightly wider at the basal and distal regions (Fig. 28). Dorsally with a single row of short and thin (Fig. 31) or short and thick simple setae (Fig. 32), or with a dense area of long simple setae on the dorsal region (*dts, Emesaya*, Figs. 27, 33, 34). The dorsal dense area of long simple setae in *Emesaya brevipennis* is medially located, occupying nearly 60% of the dorsal margin of the protibia, with longer setae on the subbasal portion of the surface. Ventrally with a series of spiniform processes (*vtp*), arranged in a continuous row (Fig. 27) or interleaved (Fig. 26), each process with the apex rounded (Figs. 37, 43) or with an acute apex strongly curved distally (Figs. 38–42).

On the ventral region, basal to the series of spiniform processes (*vtp*), there are campaniform sensilla (Figs. 47–59), which are rounded and variable in number (3 to 5). On the anterior surface, on the basal or sub basal region, there is one rounded or oval process, probably corresponding to the anterior campaniform sensillum documented by Wygodzinsky (as lateral campaniform sensillum, 1966), observed only in a few of the examined genera (Figs. 60–63).

Area of the protibial comb (*ptc*) located on the anteroventral apical margin and composed by dense long setae and protibial comb, which is located medially on the area (Figs. 64–76). The setae of the protibial comb are apically straight (Fig. 76) or slightly capitated (Fig. 72). Distal to the protibial comb the setal arrangement can be continuous (Fig. 68) or with an interruption of a glabrous area (Fig. 75).

Comments. The dorsal tibial surface with dense long setae (*dts*) (*calamistrum-like*, Wygodzisnky 1966) is a bristle area, resembling the calamistrum on the metatarsus of the hind legs in cribellate spiders, and this structure is present only in *Emesaya* (Figs. 33, 34).

Each of the ventral protibial processes of the examined genera, showed two general shapes: apically rounded or acute and strongly bent. Wygodzinsky (1966) described the ventral protibial processes of *Emesella, Ghilianella, Ghinallelia* and *Liaghinella* as “hooklike denticles” and in *Emesaya* as “knifelike denticles”. The SEM images showed relative similar shapes of each of the ventral protibial processes among these genera.

We observed two sets of sensilla on the protibia: the ventral sensilla of the protibia are very conspicuous structures, present in all genera examined including *Tagalis*, for which there was no previous documentation, and one anterolateral sensillum. The anterior campaniform sensilla on the protibia were described by Wygodzinsky (1966) as a unique character in Emesinae, and the documentation provided by him shows that can be single or paired structures located on the anterior surface of the protibia, but not in the same position for each examined taxon, and only in one case it can be unambiguously identified as a campaniform sensillum. The approximate position of the anterior campaniform sensillum was described only for *Ploiaria brincki* Wygodzinsky, 1958 (Leistarchini) and *Ischnonyctes barbarus* (Lucas, 1849) (Metapterini) by Wygodzinsky (1966). Weirauch (2008) found this structure in a comparable position in the three Emesinae species included in her phylogenetic analysis (*Ghilianella filiventris* Spinola, 1850; *Metapterus linearis* Costa, 1863 and *Empicoris xambeui* (Montandon, 1885)), and treated this character as synapomorphy for the subfamily. The anterior sub-basal structure of the protibia documented here as the anterior campaniform sensillum probably correspond to the “lateral campaniform sensilla” observed by Wygodzinsky (1966) and Weirauch (2008). The presence of this structure might still be considered a synapomorphy for Emesinae, but the variable position and number (De Pinna 1991) of these sensilla on the anterior surface of the tibia makes difficult to postulate homology statements among these structures, besides the difficulty to recognize those structures as sensilla in some of the examined genera.

Protarsus (Figs. 77–85)

Structure. The protarsus is usually quite elongated, at least half or more than half of the total length of the protibia, but can be slightly shorter (e.g. *Emesaya*). Protarsus usually with segments fused (Fig. 78), sometimes with two (*fts, sts*) (e.g. *Ischnobaenella, Jamesella*; Fig. 80) or three (*fts, sts, tts*) (*Emesaya*, Fig. 79) not articulated segments (Wygodzinsky 1966). Dorsal cuticular surface with a row of very short setae. Ventrally with spiniform processes usually differentiated into a basal and apical region (Fig. 78). Basally, the structure of the ventral region (*bta*) can be composed by a row of strong forward directed setae (Fig. 82), or by a row with decumbent spiniform processes (Fig. 83). Apically the ventral region processes (*dta*), are composed by long setae conspicuously forward inclined arranged in a single row (Fig. 85) or two rows (Figs. 128, 132), or by decumbent spiniform processes (Fig. 84).

Comments. Wygodzinsky (1966) mentioned the taxonomic importance of the ventral processes of the protarsus to separate *Hornylia*, *Leaylia* and other genera within Metapterini, but without discriminating between a basal and an apical ventral region, likely leaving aside some characters that could have taxonomic importance. Genera of the *Ghilianella* complex have a set of setae basolaterad to the ventral medial row processes.

Pretarsal structures (Figs. 86–109)

The pretarsal structures comprises structures distal to the last tarsomere, but can include structures of the last tarsomer, which are functionally correlated with the protarsus (Weirauch 2005). The sclerotized structures of the pretarsal structures comprise the unguitractor plate (*utr*), a median sclerite with a dorsomedian sensillum, and claws.

Structure. The unguitractor plate (*utr*) is short with horizontal ridges (Fig. 91). The lateral setae (*ls*), ventral setae (*vs*) and the trichoid sensilla (*ts*) of the pretarsal structures can be present (Fig. 89) or not (Figs. 91). The paired parempodia (*ps*) are setiform and usually short and symmetric (Fig. 88).

The claws of the proleg are always in a parallel arrangement, usually asymmetric, with the posterior claw (*pc*) quite reduced (Figs. 88, 90–97), or nearly symmetric (Fig. 89). The anterior claw (*ac*) is clearly separate from the posterior claw (Fig. 88) or fused at the base (Figs. 90–92). The anterior claw has a distal lamella (*dl*), basal lamella (*bl*), an incision (*i*) between basal and distal lamella, and a basal protuberance of the claw (*bp*) (Fig. 91) (Weirauch 2005).

Comments. Weirauch (2005) observed the parallel position of the claws and the fusion of the anterior and posterior claws through its base (stub-like region) in *Ghilianella filiventris*. We observed this same condition as well in *Ghilianella, Ghinallelia, Emesella* and *Liaghinella.*

In asymmetric claws, the length of the posterior claw is quite variable: very reduced (i.e. *Pseudometapterus*, Fig. 96), moderately (i.e. *Barce*, Fig. 88) or slightly reduced (i.e. *Onychomesa*, Fig. 95). In addition, the posterior claw is usually more curved than anterior claw.

Primary homologies for the proleg of Metapterini

From the description of the variation of the proleg structures above, we propose 38 characters, following Sereno (2007), described below:

VESTITURE.

1. Procoxa, dorsolateral surface: (0) with long spiniform processes (Fig. 3), (2) with simple setae (Fig. 4). (CI=100/RI=100).

2. Procoxa, dorsal simple setae, structure: (0) elongate (Fig. 4); (1) short (Fig. 5). (CI=100/RI=100).

3. Procoxa, dorsal cuticular processes, arrangement: (0) uniformly distributed (Fig. 4), (1) in a longitudinal row (Fig. 5). (CI=100/RI=100).

4. Protrochanter, cuticular surface: (0) with spiniform processes (Fig. 8), (1) with sparse long setae (Fig. 9); (2) with sparse short setae (Fig. 7). (CI=66/RI=75).

5. Profemur, laterodorsal surface: (0) with spiniform processes (Fig. 19), (1) with simple setae (Fig. 18). (CI=100/RI=100).

6. Profemur, dorsal cuticular processes, arrangement: (0) uniform (Fig. 18); (1) in a londitudinal row (Fig. 17). (CI=100/RI=100).

7. Profemur, spiniform processes of the posteroventral series, structure: (0) with short bases (Fig. 20), (1) long bases (Fig. 25). (CI=50/RI=66).

8. Profemur, spiniform processes with short bases of the posteroventral series, apex shape: (0) rounded (Fig. 20), (1) acute (Fig. 21). (CI=100/RI=100).

9. Profemur, spiniform process of the posteroventral series, arrangement: (0) in a row (Fig. 24), (1) with some processes slightly separated nearly in a second row (Fig. 25). (CI=100/RI=100).

10. Profemur, basal spiniform process of the posteroventral series, length: (0) same length as others processes (Fig. 21); (1) conspicuously longer (Fig. 11). (CI=100/RI=100). (Wygodzinsky 1966).

11. Profemur, basal spiniform process of posteroventral series, relative position with respect to the length of femur: (0) on basal fourth or less (Fig. 14), (1) on mid length or further apically (Fig. 11). (CI=25/RI=76). (Wygodzinsky 1966).

12. Profemur, anteroventral series, structure: (0) composed by simple setae (Fig. 23); (1) composed by spiniform processes and simple setae (Fig. 24); (2) composed only by spiniform processes (Fig. 22). (CI=66/RI=83). (Maldonado Capriles 1960; Wygodzinsky 1966; Forero 2004).

13. Profemur, anteroventral series, relative position in relation to the longitudinal axis of the profemur: (0) parallel (Fig. 15), (1) basally divergent (Fig. 14). (CI=100/RI=100).

14. Profemur, anteroventral series, relative distribution in relation to the basal process: (0) entire, not separated from it by a space (Fig. 14), (1) separated from it by a space (Fig. 10). (CI=50/RI=90). (Wygodzinsky 1966).

15. Profemur, basal process of the anteroventral series, relative position to basal process of posteroventral series: (0) at same level of posteroventral process (Fig. 15), (1) basal to posteroventral process (Fig. 10), (2) distal to posteroventral process (Fig. 12). (CI=50/RI=77). (Wygodzinsky 1966).

16. Protibia, dorsal cuticular process, structure: (0) spiniform processes and simple setae (Fig. 29); (1) only simple setae (Fig. 30). (CI=100/RI=100).

17. Protibia, dorsal setae, arrangement: (0) in a longitudinal, dense area (Fig. 34), (1) in a longitudinal row (Fig. 31). (CI=50/RI=83).

18. Protibia, dorsal row of setae, structure of each setae: (0) thin, simple setae (Fig. 31); (1) thick setae (Fig. 32). (CI=50/RI=75).

19. Protibia, ventral surface, structure: (0) simple setae (Fig. 35), (1) stout setae (Fig. 36), (2) spiniform processes (Fig. 37). (CI=50/RI=60). (Wygodzinsky 1966).

20. Protibia, ventral cuticular processes, arrangement: (0) in an uniform area (Fig. 35), (1) in a row (Fig. 39). (CI=50/RI=50).

21. Protibia, apex of each spiniform processes on ventral surface, shape: (0) rounded (Fig. 37), (1) decumbent (Fig. 39), (2) acute (*Stenolemus*). (CI=100/RI=100).

22. Protibial comb area, relative position of protibial comb with respect to the apical setae on protibial comb area: (0) reaching or very close to (Fig. 68), (1) far, with a conspicuous glabrous area (Fig. 75). (CI=33/RI=77).

23. Protarsus, preapical region, structure: (0) with scopula (Fig. 77), (1) without scopula (Fig. 78). (CI=100/RI=100). (Wygodzinsky 1966).

24. Protarsus, anteroventral region, basal structure: (0) with a set of simple setae (Fig. 83), (1) glabrous (Fig. 82). (CI=100/RI=100).

25. Protarsus, ventral processes, structure: (0) simple, erect setae (Fig. 77), (1) stout, decumbent setae (Fig. 81), (2) decumbent spiniform processes (Fig. 83). (CI=100/RI=100).

26. Protarsus, distal margin of the last tarsomere in posterior view, surface: (0) with lateral setae (Fig. 89), (1) glabrous (Fig. 91). (CI=100/RI=100).

27. Pretarsal structures, parempodial setae, length: (0) at least half the length of the claw (Fig. 98); (1) less than half the length of the claw (Fig. 88). (CI=100/RI=100). (Weirauch 2005).

STRUCTURE.

28. Procoxa, relative length to the profemur: (0) half as long or shorter, (1) 0.75 times as long or longer. (CI=100/RI=100).

29. Profemur, medial region in anterior view, relative width with respect to basal region: (0) about as wide (Fig. 13); (1) 1.5 times as wide or wider (Fig. 14). (CI=100/RI=100).

30. Protibia, relative length to profemur: (0) about as long, (1) half as long or shorter. (CI=100/RI=100).

31. Protarsus, relative length to protibia: (0) half as long or shorter, (1) about as long. (CI=50/RI=83).

32. Protarsus, segmentation: (0) three tarsomeres (Fig. 79); (1) two tarsomeres (Fig. 80); (2) not segmented (Fig. 78). (CI=50/RI=80). (Wygodzinsky 1966).

33. Protarsus, tarsomeres, structure: (0) freely movable between segments (Fig. 77), (1) immovable (Fig. 79). (CI=100/RI=100). (Wygodzinsky 1966).

34. Claws, structure: (0) both (anterior and posterior) claws developed (Fig. 89), (1) with a single claw (Fig. 87). (CI=100/RI=100). (Weirauch 2005).

35. Claws, relative position with respect to longitudinal axis of tarsus: (0) orthogonal (Fig. 86), (1) parallel (Fig. 88). (CI=100/RI=100). (Weirauch 2005).

36. Claws, posterior claw, basal structure: (0) flat (Fig. 104), (1) with denticles (Fig. 98). (CI=100/RI=100). (Weirauch 2005).

37. Claws, posterior claw, relative length in relation to the anterior claw: (0) nearly equal (Fig. 89); (1) shorter (Fig. 88). (CI=50/RI=85). (Wygodzinsky 1966; Weirauch 2005).

38. Claws, dorsal surface of the base of the posterior claw, structure in relation with the anterior claw: (0) separated (Fig. 95); (1) fused (Fig. 94). (CI=100/RI=100). (Weirauch 2005).

Cladistic analysis

The phylogenetic analysis resulted in three equally most parsimonious trees with a length of 68 steps (CI = 67, RI = 87). In the strict consensus tree (72 steps, CI = 63, RI = 85), 15 nodes collapse (Fig. 110). *Empicoris armatus* (Ploiariolini) was inferred as the sister-group of the other Emesinae genera. Emesini (i.e., *Stenolemus* and *Gardena*) were found not to be monophyletic. The characters of the proleg support the hypothesis of Metapterini as a paraphyletic group due to the inclusion of Deliastini taxa. The clade *Ploiaria*+*Leistarches* (Leistarchini) was inferred as the sister-group of Metapterini+Deliastini clade, the latter supported by the large basal process of the posteroventral series of the femur (#10) located at mid length or farther from the base of the article, with a reversal of the condition in *Liaghinella* + *Emesella* and in Deliastini, in which the basal process of the posteroventral series is located on the basal fourth or less (#11). The clade (*Ghilianella* group + (Deliastini + *Barce* group)) is supported by the presence of a dorsal row of simple and short setae on the procoxa (#2, 3), a longitudinal row of setae on profemur (#6), having the protarsus not segmented (#32), and having the posterior claw shorter than anterior claw (#37).

Within the Metapterini+Deliastini clade, we found three main clades: *Emesaya*, *Ghilianella* group, and *Barce* group+Deliastini.

– ***Emesaya***: this genus was not recovered as monophyletic, and either of the two included species is recovered as the sister-group of the clade (*Ghilianella* group + (*Barce* group+Deliastini)).

– ***Ghilianella* group**: this clade is composed of *Ghinallelia, Ghilianella, Liaghinella* and *Emesella*. This clade is supported by four non-homoplastic synapomorphies: the position of the anteroventral series in relation to the posteroventral series is basally divergent (#13), the protarsus has decumbent spiniform processes ventrally (#25), the distal margin of the last tarsomere in posterior view is glabrous (#26), and the dorsal surface of the base of the posterior claw is fused with the anterior claw (#38). The clade *Liaghinella*+*Emesella* is supported by one non-homoplastic synapomorphy: the medial region of the profemur is 1.5 times as wide or wider than the basal region (#29).

– ***Barce* group+Deliastini clade**: this group is supported by one non-homoplastic synapomorphy: the protarsus has a set of simple setae on the lateroventral basal region (#24). The clade *Bergemesa*+*Stalemesa* (Deliastini) clade was recovered as the sister-group of the *Barce* group and it is supported by several homoplasious characters (#11, #18, #19, #32). The *Barce* group is composed by *Barce, Bargylia, Ischnobaenella,* *Jamesella, Onychomesa, Pseudometapterus, Schidium,* and *Taitaia,* and it is supported by the basal process of the anteroventral series of the femur located basally to the basal process of the posteroventral process (#15), but with low support values.

DISCUSSION

The proleg bears a set of characters commonly used in Emesinae taxonomy at the tribal, generic and specific levels (Wygodzinsky 1966), but the lack of adequate documentation among several taxa has prevented their use in phylogenetic analyses (Weirauch 2008). In this study we documented the variation of proleg structures in about half of Metapterini genera, from which a phylogenetic hypothesis is advanced. Based on the exploration of this set of proleg characters, interesting relationships were recovered, such as the sister group relationship of *Empicoris* (Ploiariolini) with the remaining tribes of Emesinae, contrary to the hypothesis proposed by Wygodzinsky (1966) in which Ploiariolini was probably the sister group of Metapterini+Deliastini. Similarly, we recovered an unexpected relationship in which Leistarchini is regarded the sister group of the clade Deliastini+Metapterini, and not as the sister group of Emesini, Ploiariolini, Metapterini and Deliastini, as proposed by Wygodzinsky (1966). Thus, we are certain that there is valuable phylogenetic signal in this character system to be further explored within Emesinae. We discuss the significance of the proleg character system on the evolution of the Metapterini.

Paraphyletic Metapterini

In our analyses, Metapterini are resolved as paraphyletic because of the inclusion of *Bergemesa* and *Stalemesa,* both assigned to Deliastini, as a derived clade sister to the *Barce* group. The hypothesis of having a derived Deliastini within Metapterini was proposed previously with genitalic characters (Castro-Huertas et al. 2018). The relationship of Deliastini and Metapterini as sister-groups was proposed by Wygodzinsky (1966) based on the loss of the mesonotal and metanotal spines, and the presence of a large basal process on the posteroventral series of the profemur, the latter character in fact supporting the clade Metapterini + Deliastini in our analysis. Nonetheless, Deliastini is recovered as a sister group of only part of Metapterini by two characters previously discussed by Wygodzinsky (1966) as characters shared by both Deliastini and Metapterini, the non-segmented protarsus and the posterior claw shorter than anterior claw. Additional characters on the length and arrangement of dorsal setae on the procoxa and the protibia support the relationship of Deliastini being more related to only part of Metapterini.

The position of the basal process of the posteroventral series of the femur located on the basal fourth or closer to the base of the article was considered by Wygodzinsky (1966) as a plesiomorphic character present in all tribes except Metapterini. Nonetheless, most but not all Metapterini genera included in the analysis exhibit the derived condition of having the basal process of the posteroventral series located at about the middle or farther apically from the base of the profemur, except in *Barce*, *Emesella*, *Liaghinella*, *Taitaia* and the two included Deliastini genera, in which the process is located close to the base of profemur. This shows that the interpretation of the character distribution and its evolution is more complex than Wygodzinsky (1966) envisioned.

The present phylogenetic analysis is congruent with the results of Castro-Huertas et al. (2018), in that Deliastini are not the sister-group of Metapterini as proposed by Wygodzinsky (1966), but make Metapterini paraphyletic as being a derived clade within Metapterini. Even when these analyses are limited by using restricted characters sets and not including characters used by Wygodzinsky (1966) to support the hypothesis of Deliastini being the sister group of Metapterini, such as the eye length or the structure of the wings, the results show that Metapterini, as it is currently defined, is probably not a natural group (Castro-Huertas et al. 2018), and suggest that Deliastini and Metapterini comprise a single clade.

Considering the limitations of using a single character system and that these characters from the proleg were not tested in concert with characters proposed by Wygodzinsky (1966) to separate the tribes (eye length and wing structure), additional combined analyses should be carried out including the present character system as well as others, in order to elucidate the systematic position of these tribes.

Generic groupings and prolegs

The proleg of *Emesaya* is rather different compared to other genera within Metapterini. It has a 3-segmented protarsus, a plesiomorphic condition shared with Emesini and Leistarchini, whereas in most of the remaining Metapterini the protarsus is not segmented, except in *Ischnobaenella* and *Jamesella* which present a two segmented tarsus, similar to the condition present in *Stalemesa* and *Bergemesa* (Deliastini). *Emesaya* has also a conspicuous area with dense long setae on the dorsal region of the protibia, which is a shared character state with Ploiariolini and Emesini. Thus there are no unambiguous proleg characters that support *Emesaya* as monophyletic.

The close relationship of the exclusively Neotropical genera *Ghilianella, Ghinallelia, Emesella* and *Liaghinella* (Maldonado Capriles 1960; Wygodzinsky 1966), was first suggested based on genitalic characters (Castro-Huertas et al. 2018) and confirmed in this study by the particular structure of the pretarsal structures. Of the internal relationships among genera, only the relationship between *Emesella* and *Liaghinella* was supported by proleg characters.

Proleg structures have been used heavily as diagnostic characters to delimit tribal and generic taxa (Wygodzinsky 1966), but in our analyses they behave poorly as phylogenetically informative characters at the generic level. For instance, the anteroventral process of the profemur composed by both spiniform processes and setae (#12) is used to define *Ghilianella* (Wygodzinsky 1966), but in our analyses this character state is considered homoplastic.

Evolution of selected characters of the proleg

The proleg of Emesinae exhibits particular modifications for prey capture. Several characters on the proleg are thus probably being strongly selected from a functional perspective. Our phylogenetic analyses show several transitions probably associated with functional traits. In general, the ventral processes on the profemur, protibia and protarsus change from simple setae present in most of the outgroups, to heavily sclerotized spiniform processes within Metapterini. One exception is found in the structure of the processes of the anteroventral series of the profemur, which in most genera are composed by spiniform processes, whereas in *Emesella*, *Ghinallelia* and *Liaghinella* they are composed by simple setae, and only *Ghilianella* has both, simple setae and spiniform processes.

Similarly, the protarsus show an increase in length and a reduction in the number of segments in Metapterini, except for *Emesaya* as discussed above. Both changes in the structure and in the relative length of segments are probably related to changes in predatory behavior. On the pretarsal structures we observed a reduction of the paired parempodia and a conspicuous asymmetry between the claws in Metapterini, except for *Emesaya*. The interaction of the pretarsal structures with others traits associate with different kinds of prey is unknown.

What these transformations suggest is that the evolution of the proleg armature that help in prey capture is more complex than previously thought and it is probably related to functional constrains, likely to prey specialization. Also, they imply that in Metapterini larger prey might be preferred in comparison to other more delicate prey as has been documented for other Emesinae groups (Usinger 1941; Wygodzinsky 1943; Gillet 1957; Hagerty et al. 2001).

Some functional aspects of the raptorial legs

The modifications of the raptorial proleg of Reduviidae can be present on different regions of the leg or as specific adaptive types. Zhang et al. (2016) defined six categories of modifications on the raptorial leg of Reduviidae: with fossula spongiosa on tibia; chelate or subchelated model (Phymatinae); with processes (spiniform processes, tubercles, etc.) on trochanter, femur and/or tibia; and sticky substances on prolegs (endogenous or exogenous). Emesinae proleg follows a typical raptorial leg model, without hairy attachment structures or production of sticky substances, but with spiniform processes on the trochanter (Collartidini), and more conspicuously, on the profemur and protibia.

The procoxa of Emesinae is usually at least four times as long as wide, attaining the maximum length in some genera of Metapterini (Wygodzinsky 1966). The elongation of the procoxa is an usual phenomenon in insects with raptorial legs and apparently increases their striking range (Weirauch et al. 2011; Brannoch et al. 2017). The armature of the profemur and protibia is very conspicuous within Metapterini, and presumably allows for efficient capture of prey (Weirauch et al. 2011). Besides the presence of conspicuous processes on the proleg, the diversity on the structure and arrangement of the cuticular processes within Metapterini suggests that some unknown variable, for instance prey specificity, could be playing an important evolutionary role shaping proleg structure.

The dorsal tibial surface with dense long setae (*dts*) is present in several araneophagic genera of Emesini, Leistarchini, Ploiariolini and *Emesaya* within Metapterini (Wygodzinsky 1966). The presence of this structure in groups associated with spiders, has been suggested as an aid for locomotion on spider webs (Wygodzinsky 1966; Resende et al. 2016), although without observational data. However, studies with *Stenolemus* (Emesini), an araneophagic genus with dense long setae on the dorsal tibial surface, showed that the protarsus and pretarsal structures probably have a more important role in prey predation, because with these structures the silk threads of spider webs can be manipulated, apparently reducing the amplitude of the vibrations produced when breaking threads in webs (Soley 2016) or to deceive spiders with patterns of vibrations that mimic prey falling in the web (Wignall and Taylor 2011). Given the little modified structure of the proleg in *Emesaya* as described above, it might be assumed that from a biological and functional perspective it should exhibit rather generic predatory behaviors. This is in part congruent with observations in which *E. brevipennis* and *E. brevicoxa* are reported as generalist species feeding on insects; nonetheless, *E. brevicoxa* has also been reported as having araneophagic habits (Usinger 1941; Hagerty et al. 2001). If *Emesaya* species are more araneophagic than generalists, it is then likely that they might rely more on behavioral strategies for araneophagy than having particular morphological modifications for such preying strategies, as have been reported for other Emesinae (Wignall and Taylor 2010; Soley 2016). In other Metapterini species that also exhibit araneophagic behaviors, such as *Liaghinella andina* it is unknown if the shorter femur and associated modified structures are also related to preying upon spiders. In *L. andina*, the preys are likely ground dwelling spiders (Forero 2007). If that is the case, a different strategy is needed in order to subdue more mobile prey, and thus, large processes might be needed on the prolegs.

The protibial comb is present in all Heteroptera, and apparently it has a cleaning function against dust or soil particles accumulated in structures such as the antennae or labium (Lis and Schaefer 2005; Weirauch 2008). Within Reduviidae, this structure apparently has not significant variation. In Emesinae, the protibial comb has been neglected by comparative morphological studies, probably because the observation requires SEM methods. Our observations show variation on the setal arrangement of the medial protibial comb in relation to the setal area within Metapterini, with a glabrous area present in the genera of the *Ghilianella* group, for which its biological meaning is currently unknown.

Tarsal and pretarsal structures in Emesinae show remarkable morphologic modifications within Reduviidae. The claws in parallel position with respect to the longitudinal axis of the tarsus is present in all Emesinae tribes, and the asymmetry of the posterior claw is commonly found, except within Collartidini and Leistarchini (Wygodzinsky 1966), even to the point of not having a claw, probably the posterior claw (e.g. *Leistarches*), or having both claws completely missing (e.g. *Tubuataita*). The biological significance of the extreme modified claws within Emesinae is unknown, although they apparently have an important role in shaping the evolution of very complex hunting behaviors (e.g. aggressive mimicry, bypassing the sensory systems of spiders), as have been documented for some species of *Stenolemus* (Wignall and Taylor 2010, 2011; Soley 2016).

Comparative studies on proleg morphology in other genera, combined with natural history observations on predatory behaviors, and robust phylogenetic hypotheses, will help to better understand the evolution of proleg structures and their relationship with different kinds of prey and predatory strategies.

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Table 1. Examined material. USI numbers correspond to catalog numbers provided by each of the collections, if provided.

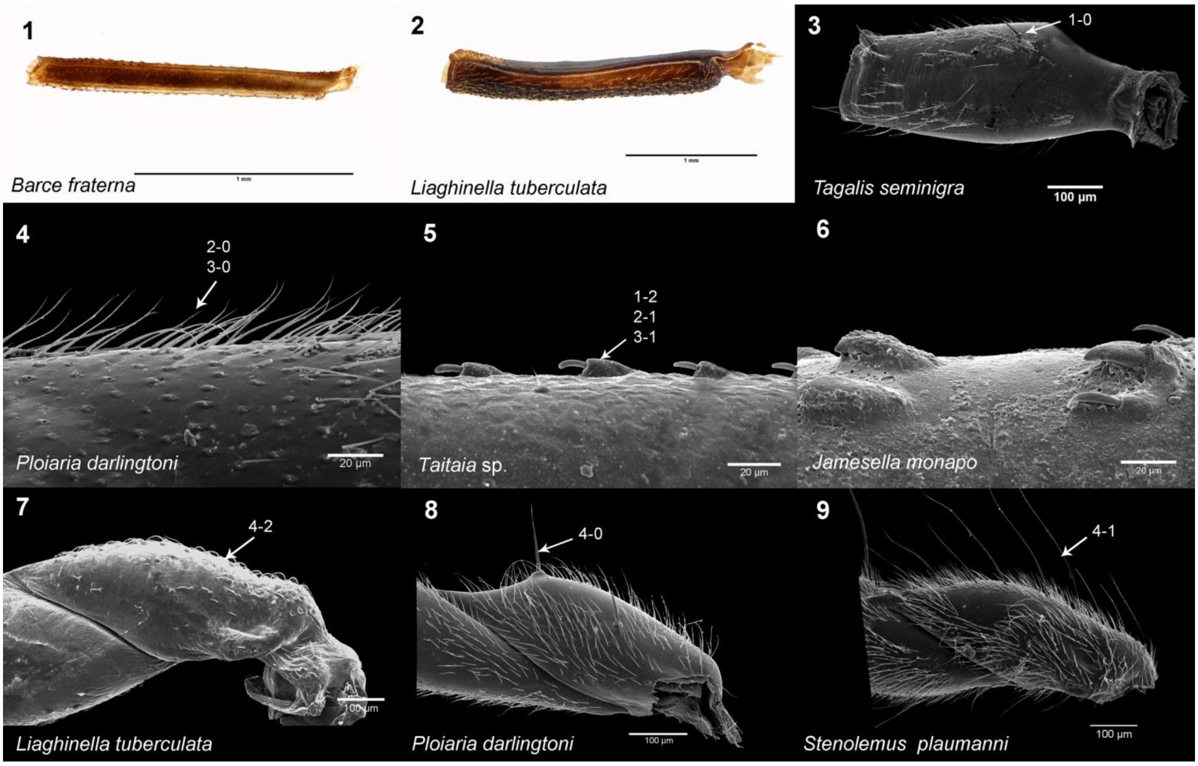
Species	**Locality**	**Sex, USI, and collection**
SAICINAE		
Tagalis seminigra Champion, 1898	PERU: Ucayali, Kirigueti (luz), vii 2004, J. Williams, 73˚07’08’’ ´W, 11˚ 38’ 13’’ S	1♂ (MLPA)
EMESINAE: Deliastini		
Bergemesa brachmanni (Berg, 1884)	ARGENTINA: Neuquen (ciudad), leg. Q. de Ferrariis, viii 1985.	1♀ (MACN)
Stalemesa carvalhoi Wygodzinsky, 1966	BRAZIL: Est. do Rio, Paraiba do Sul. JCM Carvalho col.	1♂ Holotype (MNRJ)
Emesini		
Gardena faustina McAtee and Malloch, 1925	BRAZIL: Acre, 11 km NE de Rio Branco, 5-10 v 1981, Penny E. Bindá.	1♀ (INPA)
Stenolemus plaumanni Wygodzinsky, 1943	BRAZIL: RS, Palmares do Sul, Faz. Rincão do Anastacio, 12 xi 2003, Equipe Probio col / 30˚22’34.6’’ S, 50˚41’42.0’’ W, guarda-chuva ent.	1♂ (MCN 175303) (MCNZ)
Leistarchini		
Leistarches serripes Dohrn, 1860	AUSTRALIA: 15.47S, 145.14E, Shiptons Flat, 17 may 1981, QLD, D.H. Colless (Malaise trap).	1♂ (ANIC)

Ploiaria darlingtoni (Wygodzinsky, 1954)	BRAZIL: SC, Palhoça, Serro do Tabuleiro, Mano de Pipa, 27˚48’4.5’’ S, 48˚37’51.8’’ W, 26 iii 2017, Brugnera et al. leg	1♂ (UFRG)
Ploiariolini		
Empicoris armatus (Champion, 1898)	BRAZIL: RS, Riozinho, 29˚38’28’’ S, 50˚27’0.9’’ W, 2–4 vi 2017, LES-UFRGS.leg	1♂ (UFRG)
Metapterini		
Barce fraterna (Say, 1832)	COLOMBIA: Nariño, Tumaco, Pinar, Morro. 1˚48’ N, 78˚45’ W, alt. 0-30m, 4-14 marzo 2015, Est. Taxonomia Animal.	1♂ (CELM)
Barce uhleri Banks, 1909	USA: NJ, Lakehurst, 2.v.08 / H. G. Barber colln 1950.	1♂ NMNH
Bargylia longinota Wygodzinsky, 1956	AUSTRALIA: Port Darwin, NW Australia, J.J. Walker.	1♂ Holotype (BMNH)
Emesaya brevipennis (Say, 1828)	COLOMBIA: Magdalena, Tigrera, la Curva, Camino Jamonacal, jameo, 18 ix 2013, V. Castro.leg	1♂ (ICN)
Emesaya pollex McAtee and Malloch, 1925	BRAZIL: RS, Palmares do Sul, Ilha Grande, 10 iv 2003, equipe Probio.	1♂ (MCNZ)
Emesella sp.	COLOMBIA: Subparamo de Guasca, 3000 m, hojas muertas de *Espeletia corymbosa*, 23 vii 1968, Sturm.leg.	1♀ (ICN 091391) (ICN)
Ghilianella approximata McAtee	BRAZIL: AM, Ipixuna, rio Liberdade, Estirão da Preta (07˚21’46.7’’ S, 71˚52’07.1’’ W).	1♀ (INPA)

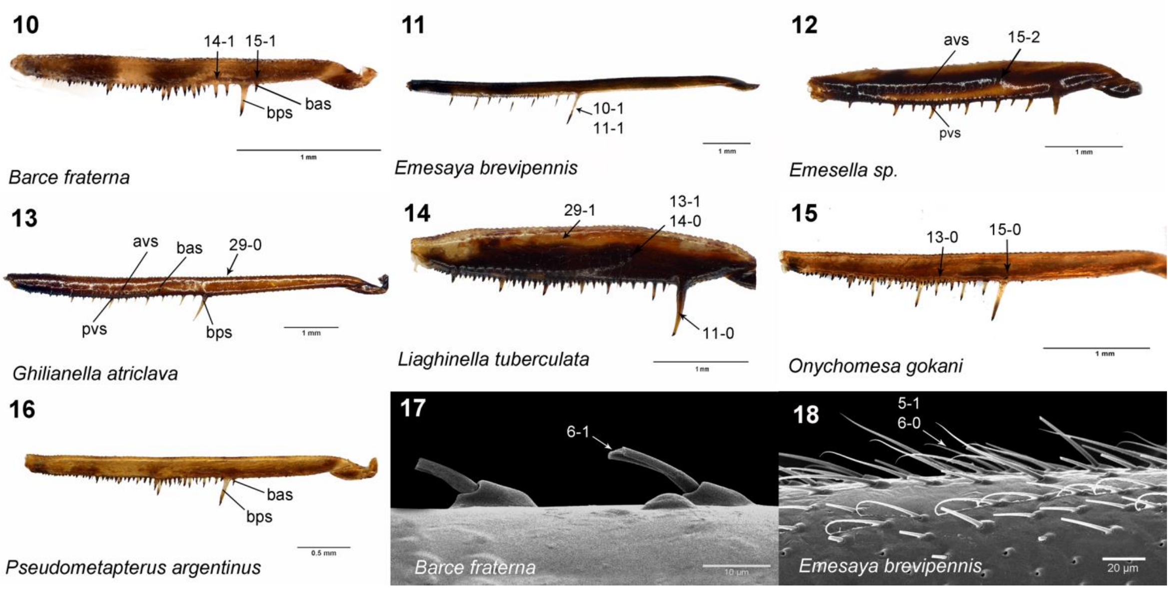
and Malloch, 1925		
Ghilianella aracataca McAtee and Malloch, 1925	COLOMBIA: Magdalena, PNN Tayrona. Cañaveral, Arrecifes, 11˚20’ N, 74˚2’ W, 50m, Red, 18-20 jul 2002, M. Sharkey, D. Arias & F. Torres.leg. M4172.	1♂ (IAvH-E-126058) (IAVH)
Ghinallelia globifera (Bergroth, 1906)	COLOMBIA: Without locality data	1♂ (ICN)
Ghinallelia minimula McAtee and Malloch, 1925	BRASIL. RS, Cidreira, (Mata Restinga), 29 xi 2003, J. Alvenir.leg, pitfall	1♂ (MCNZ 180179) (MCZN)
Ichnobaenella pollymela (Kirkaldy, 1901)	SINGAPORE: H.N. Ridley, 95–176.	1♀ (BMNH)
Jamesella monapo (Wygodzinsky, 1966)	MOZAMBIQUE: Port. E. Africa, Africa, Monapo, 15 ix 1918, G.D.H. Carpenter, 1919–36.	1♀ (BMNH)
Liaghinella andina Forero, 2007	COLOMBIA: Cundinamarca, Cundinamarca, Reserva Chicaque, robledal, 04,6172500˚ N, 74,3139500˚ W, 2.250m, 23 ene 2015, E. Tulande	1♂ (MPUJ_ENT 0047555) (MPUJ)
Liaghinella tuberculata Forero and Castro-Huertas, 2017	COLOMBIA: Cundinamarca, Reserva Chicaque, refugio, Feb 2014.	1♀ (MPUJ_ENT 0046844) (MPUJ)
Onychomesa gokani	JAPAN: Komi, Iriomote-jima Is., The Ryukyus,	1♂ 1♀ (TUA)

Ishikawa, 2000	9 x 2004, T. Ishikawa.	
Pseudometapterus argentinus (Berg, 1900)	ARGENTINA: Sierra Córdoba. 14 i 1980,Williner S.J.	1♂ (MACN)
Pseudometapterus carioca (Wygodzinsky, 1945)	BRAZIL: MG, Coimbra, 27 i 1999, C. Shetino.	1♂ (UFVB)
Schidium marcidum (Uhler, 1896)	JAPAN: Sachigaoka, Yotsukaidô-shi, Chiba-ken, 8 viii 2009, Y. Kodo.	1♀ (TUA)
Schidium plumarium Ishikawa, 2002	JAPAN: Komi, Iriomote-jima Is., The Ryukyus, 7-9 x 2004, H. Mizushima	1♂ (TUA)
Taitaia sp.	AUSTRALIA: 28.40˚ S, 114.36˚ E, W.A.: Geraldton Drmmond Cove, 25 oct 1972, D.&N. McFarland, U.V. light.	1♀ (ANIC)

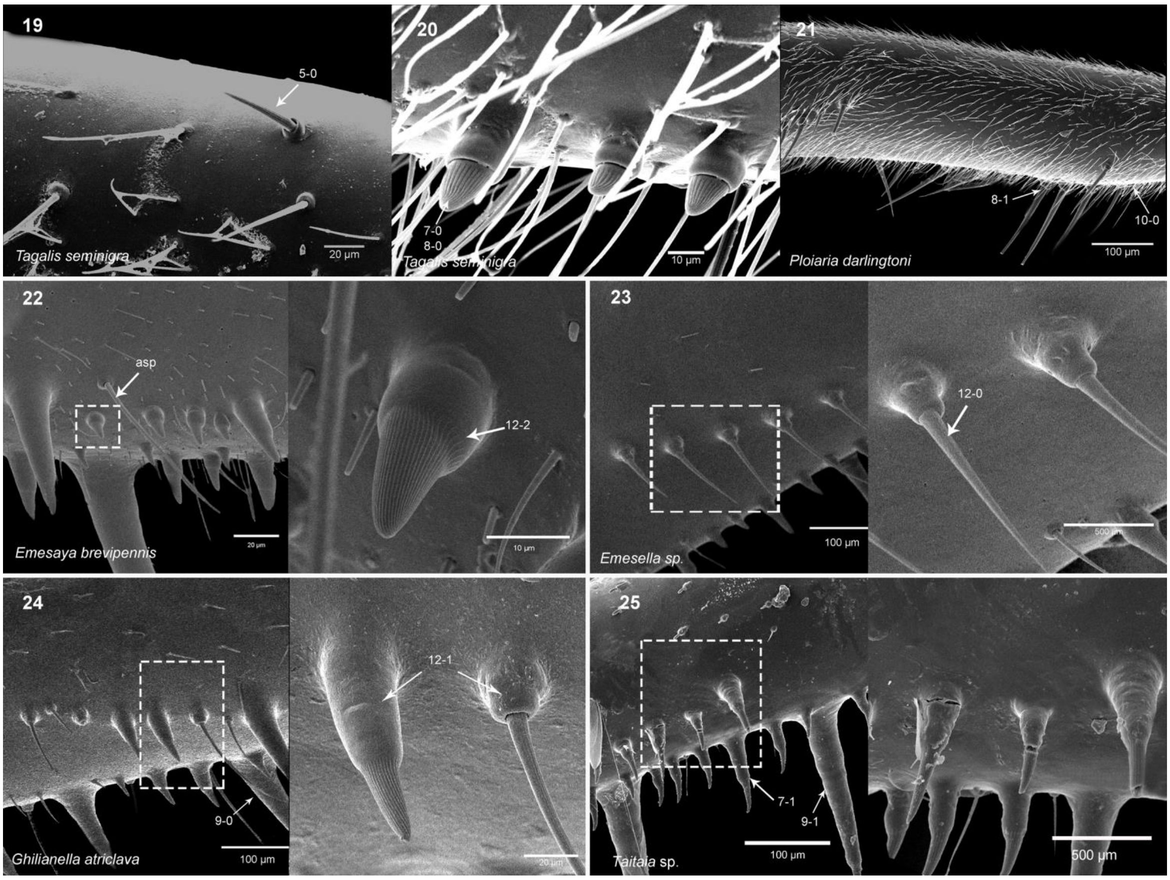
PLATE LEGENDS



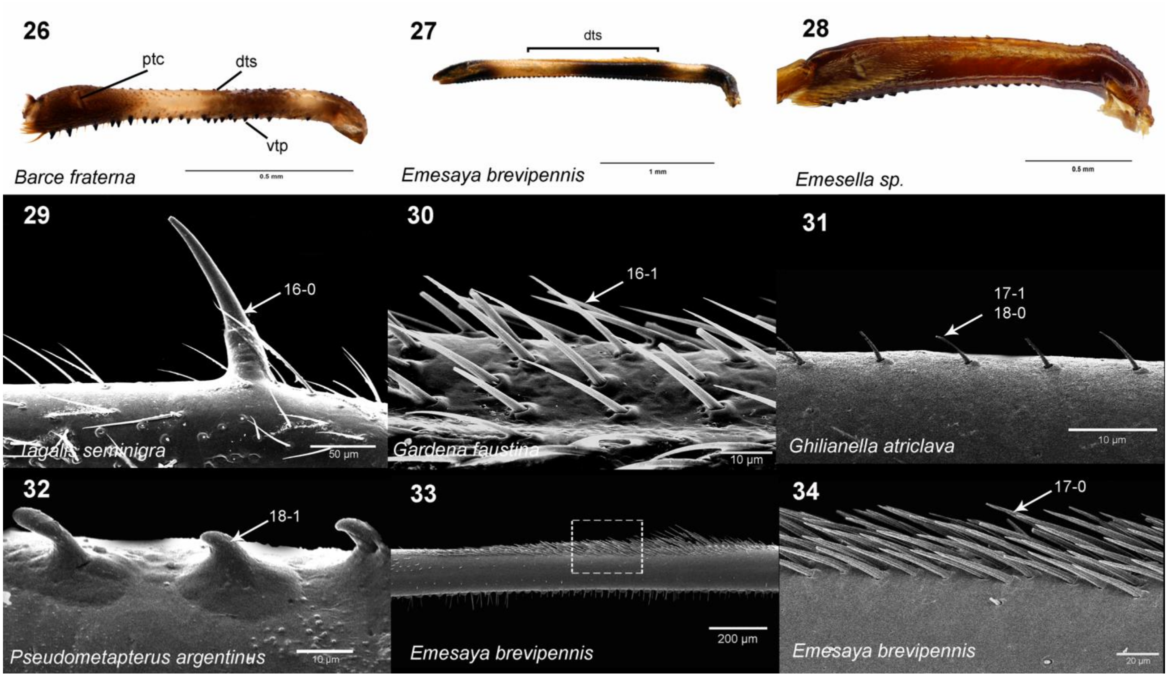
Figures 1–9. Procoxa and protrochanter. Figs. 1–3. Procoxa in lateral view. Figs. 4–6. Scanning electron micrographs of the procoxal dorsal surface. Figs. 7–9. Scanning electron micrographs of the trochanter in lateral view.



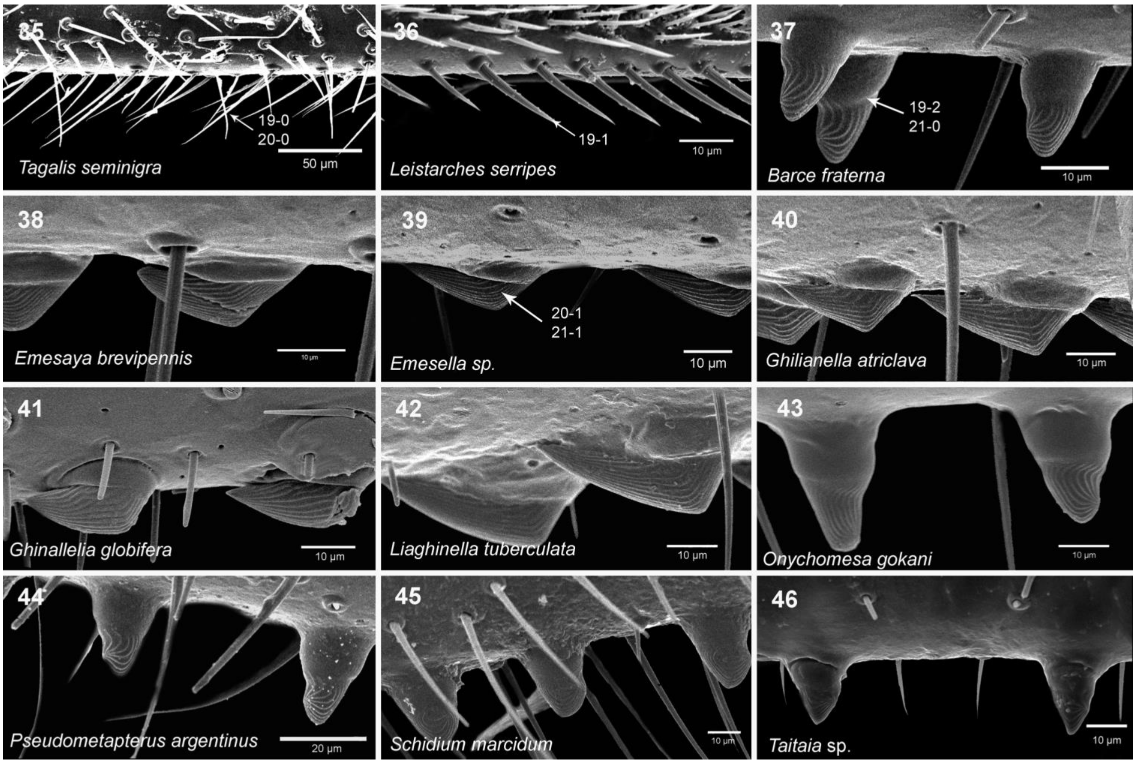
Figures 10–18. Profemur Metapterini. Figs. 10–16. Profemur in lateral view. Figs. 17–18. Scanning electron micrographs of the dorsal surface of the profemur. Abbreviations: avs, anteroventral series of the profemur; bas, basal process of the anteroventral series of the profemur; bps, basal process of the posteroventral series of the profemur; pvs, posteroventral series of the profemur.



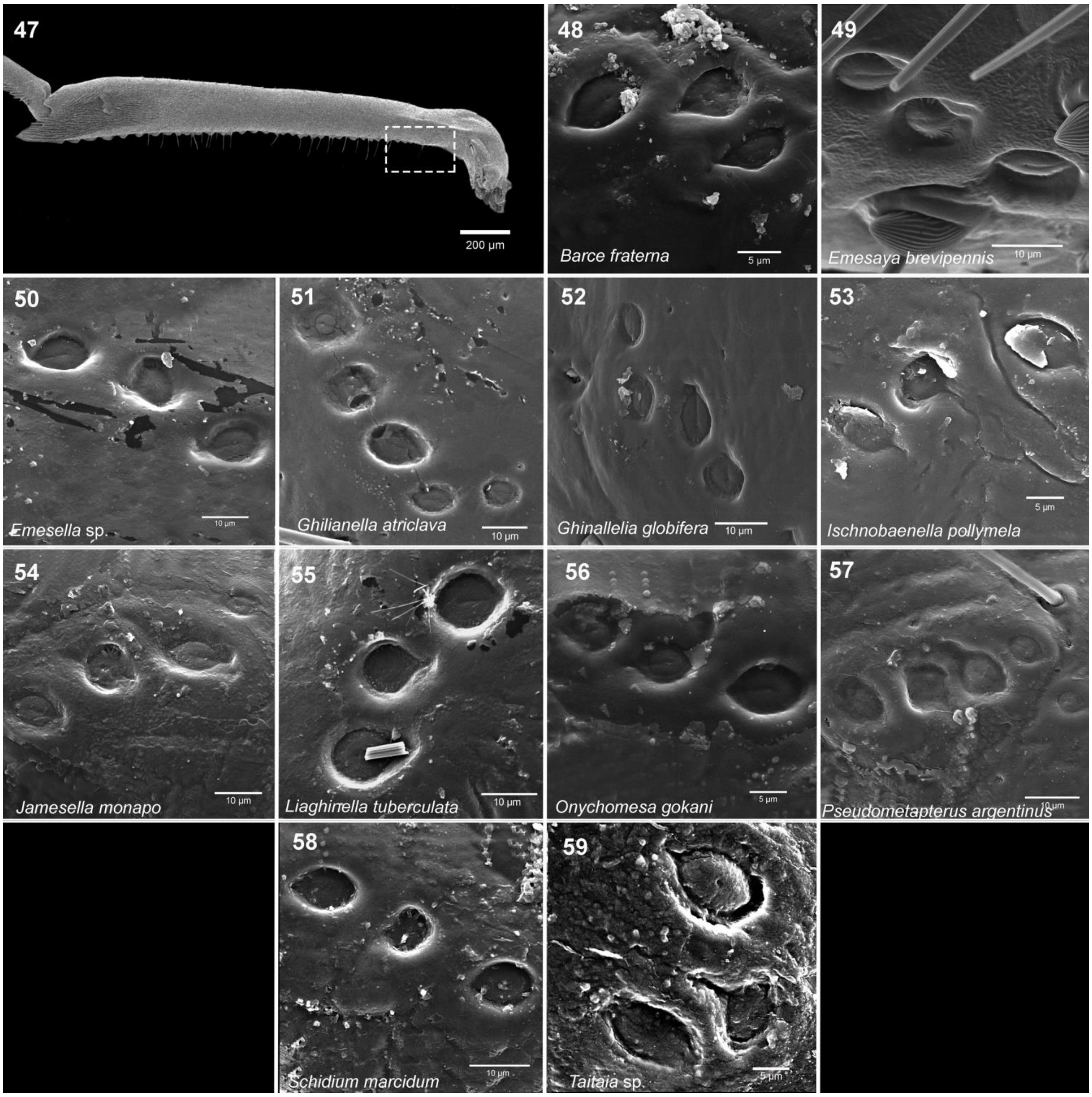
Figures 19–25. Scanning electron micrographs of the cuticular processes of the profemur. Fig. 19. Dorsal surface in *Tagalis* (Saicinae). Fig. 20–21. Ventral surface in *Tagalis* and *Ploiaria* (Leistarchini). Figs. 22–25. Anteroventral process of the profemur in *Emesaya, Emesella, Ghilianella,* and *Taitaia*. Square indicates the detail of the right side. Abbreviations: asp, accessory setae of the profemur.



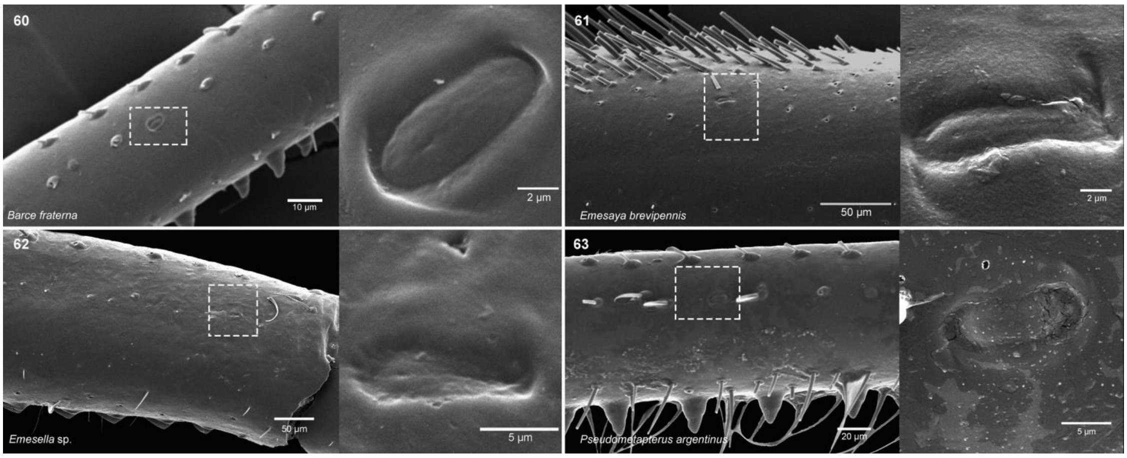
Figures 26–34. Protibia. Figs. 26–28. Protibia in lateral view in *Barce*, *Emesaya* and *Emesella*. Figs. 29–34. Scanning electron micrographs of the dorsal surface of the protibia in *Tagalis* (Saicinae), *Gardena* (Emesini), *Ghilianella*, *Pseudometapterus* and *Emesaya*. Abbreviations: dts, dorsal tibial surface; ptc, protibial comb; vtp, ventral tibial process. Square indicates the detail of the right side



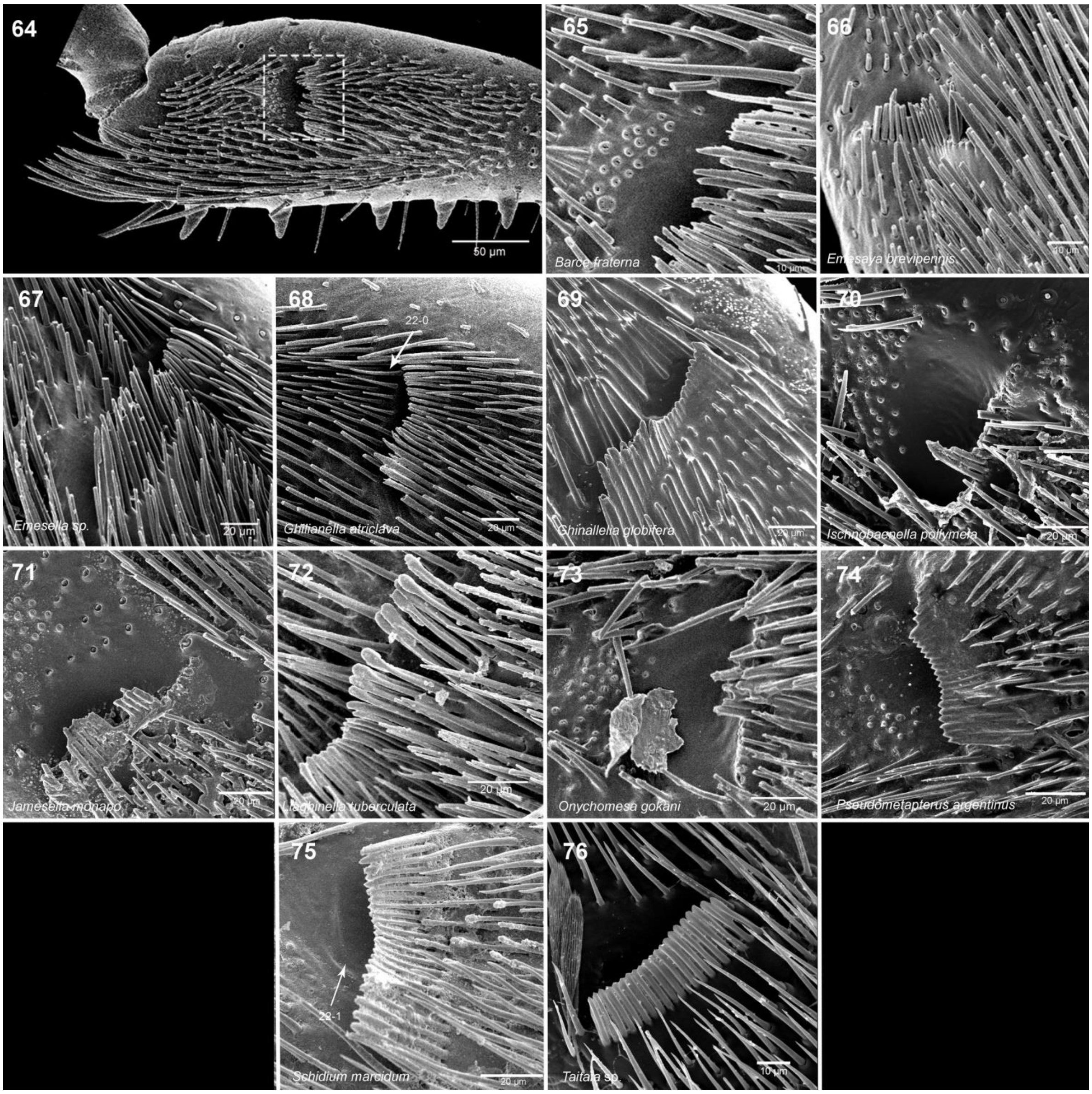
Figures 35–46. Scanning electron micrographs of the protibial ventral processes. Figs. 35–36. Protibial ventral processes in *Tagalis* (Saicinae) and *Leistarches* (Leistarchini). Figs. 37–46. Protibial ventral processes in *Barce*, *Emesaya*, *Emesella*, *Ghilianella*, *Ghinallelia*, *Liaghinella*, *Onychomesa*, *Pseudometapterus*, *Schidium* and *Taitaia*.



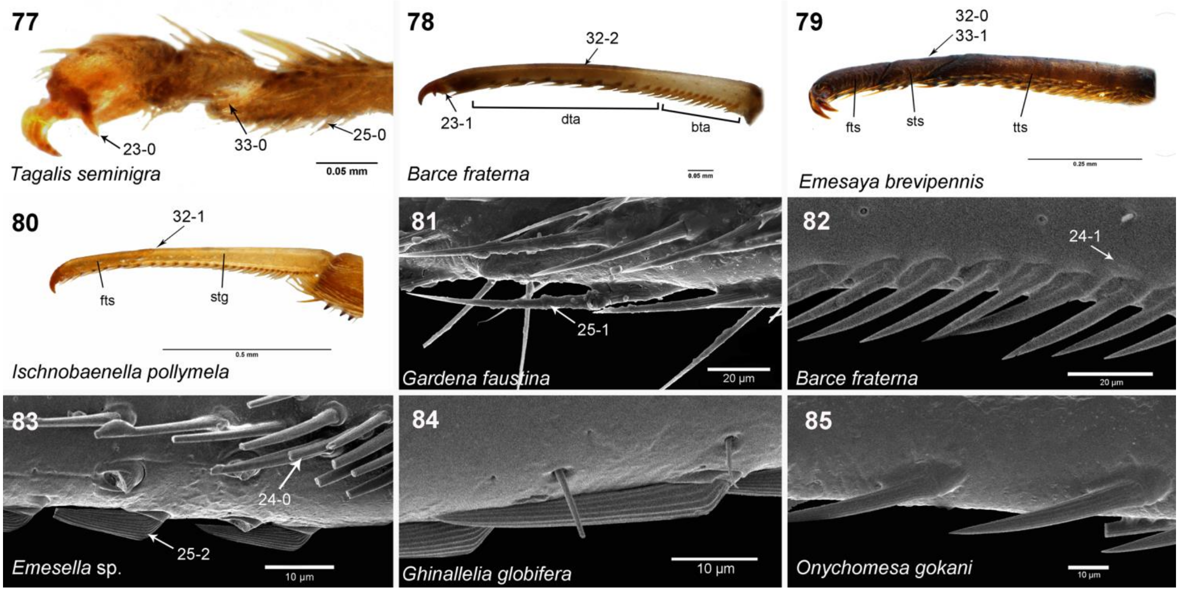
Figures 47–59. Scanning electron micrographs of the ventral campaniform sensillum of the protibia of Metapterini genera. Square indicates the position on the protibia.



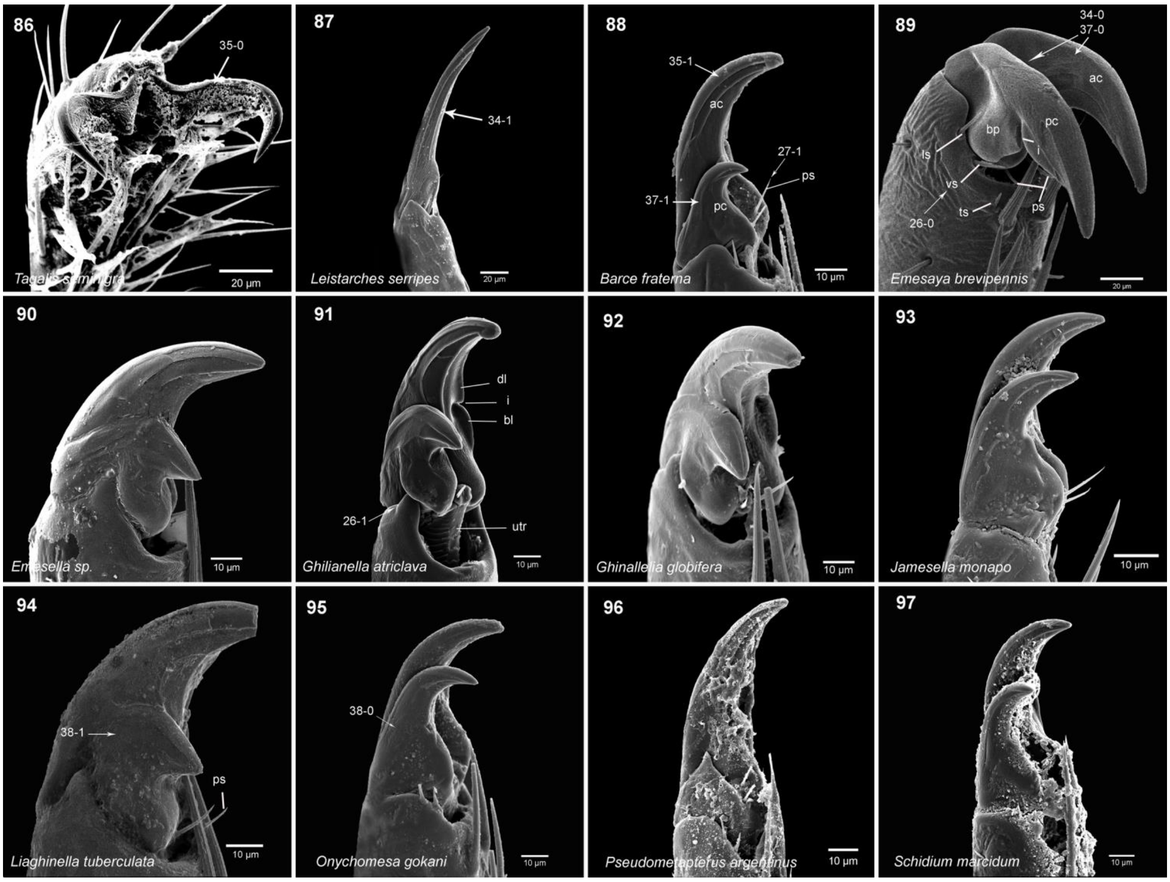
Figures 60–63. Scanning electron micrographs of the lateral sensilla of the protibia in *Barce*, *Emesaya*, *Emesella* and *Pseudometapterus*. Square indicates the detail of the right side.



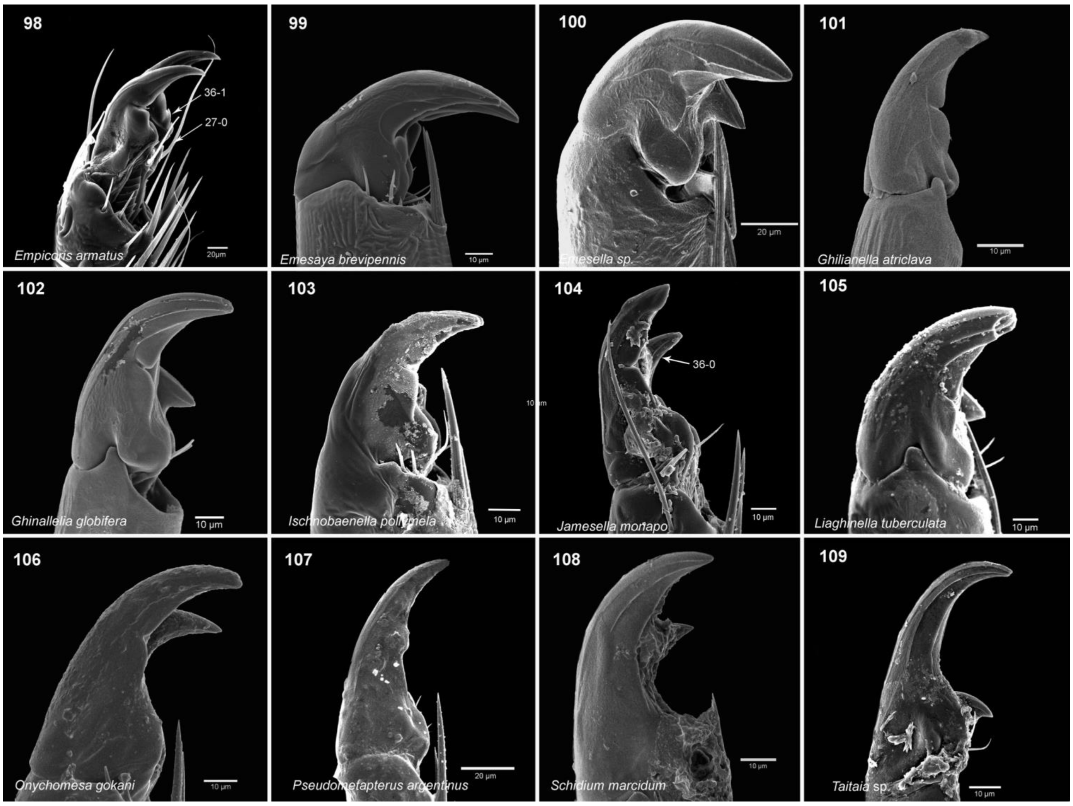
Figures 64–76. Scanning electron micrographs of the protibial comb of Metapterini genera. Square indicates the position.



Figures 77–85. Protarsus. Figs. 77–80. Protarsus in lateral view in *Tagalis* (Saicinae), *Barce*, *Emesaya* and *Ischnobaenella*. Fig. 81. Scanning electron micrographs of the ventral process of the protarsus in *Gardena* (Emesini). Figs. 82–83. Scanning electron micrographs of the basal ventral process (bta) of the protarsus processes in *Barce* and *Emesella*. Figs. 84–85. Scanning electron micrographs of the distal process of the protarsus (dta) in *Ghinallelia* and *Onychomesa*. Abbreviations: bta, basal ventral process of the protarsus; fts, first tarsal segment; dta, posteroventral process of the protarsus; sts, second tarsal segment; tts, third tarsal segment.



Figures 86–97. Scanning electron micrographs of the claws in external view. Figs. 86–87. Claw in *Tagalis* (Saicinae) and *Leistarches* (Leistarchini). Figs. 88–97; Claw in *Barce, Emesaya, Emesella, Ghilianella, Ghinallelia, Jamesella, Liaghinella, Onychomesa*, *Pseudometapterus* and *Schidium*. Abbreviations: ac, anterior claw; bp, basal protuberance of claw; ts, tricoid sensillum; dl, distal lamella; i, incision between basal and distal lamella; ls, lateral seta; pc,posterior claw; bl, basal lamella; ps, parempodial setae.



Figures 98–109. Scanning electron micrographs of the claws in internal view. Fig. 98. Claw in *Empicoris* (Ploiariolini). Figs. 99–109. Claw in *Emesaya*, *Emesella*, *Ghilianella*, *Ghinallelia*, *Jamesella*, *Liaghinella*, *Onychomesa*, *Pseudometapterus*, *Schidium* and *Taitaia*.

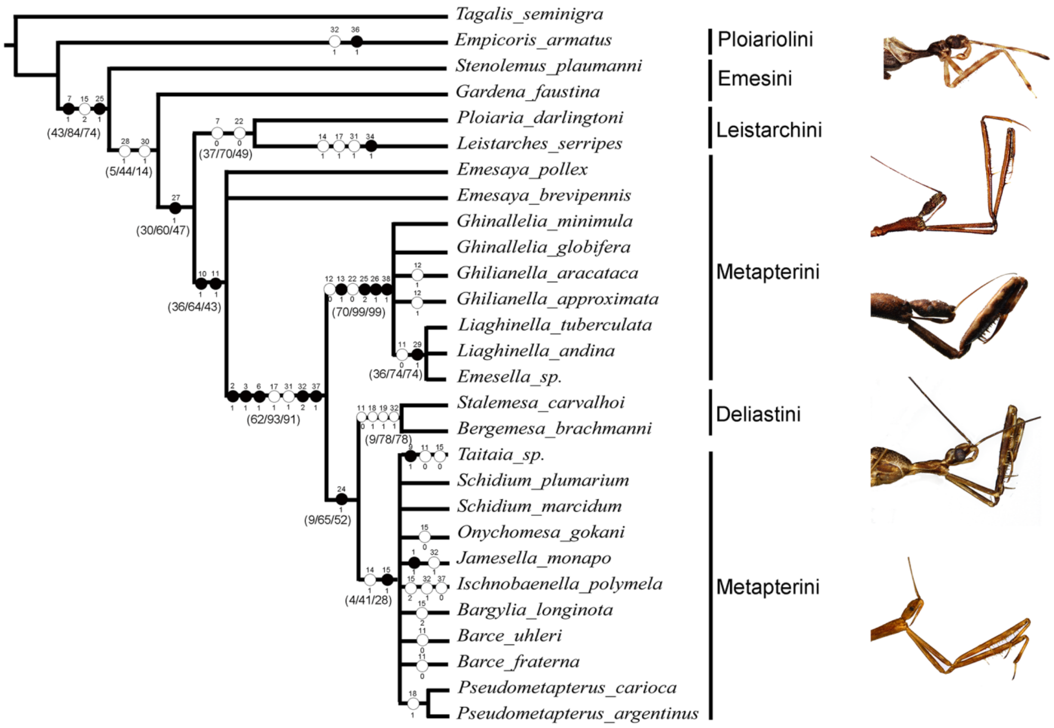


Figure 110. Strict consensus tree of the proleg characters. Apomorphies mapped on the tree, non-homoplasious changes as full circles, homoplasious changes as empty circles. Support values in the branches (Relative Bremer support, first value; GC frequencies, second and third value).