

RESEARCH PAPER

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

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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 associated with spider webs as *Emesaya* Mcatee & 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 CAPRILES (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 the 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, Deliastrini: *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 Natural History Museum, 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
 amg8 anterior margin of the gonocoxa 8
 ao anterior opening of the pygophore
 app apical projection of the paramere
 apt articulatory apparatus
 bc bursa copulatrix
 bp basal plate
 br transverse bridge of the pygophore
 dlb dorsolateral basal portion of the endosoma
 dlm dorsolateral median portion of the endosoma
 dld dorsolateral distal portion of the endosoma
 dps dorsal phallosomal sclerite
 duc ductifer
 end endosoma
 gap8 gonapophysis 8
 gap9 gonapophysis 9
 gcx8 gonocoxa 8
 gcx9 gonocoxa 9
 gpl gonoplac
 lap lateral anterior prolongation of the gonocoxa 8
 lpg lateral process of the posterior genital opening
 mm medial margin of the gonocoxa 8
 mov median oviduct
 mpm8 medial posterior margin of the tergite 8
 mpm9 medial posterior margin of the tergite 9
 mpo lateral margin of posterior opening of the pygophore
 mpp medial posterior process of the pygophore
 pa paramere
 pex basal plate extension
 pha phallosoma
 pmg8 posterior margin of the gonocoxa 8
 pgo posterolateral process of the posterior genital opening
 po posterior opening of the pygophore
 ppe posteroventral projections of the endosoma
 pro proctiger
 ps paramere socket
 rg ring gland of the bursa copulatrix
 S8 abdominal segment 8
 S9 abdominal segment 9 = pygophore
 sdg subapical dorsal margin of the gonoplac
 svg subapical ventral margin of the gonoplac
 T8 tergite 8
 T9 tergite 9
 vg vermiform gland
 vpp ventral protruding of the pygophore
 vps ventral phallosomal sclerite

Table 1. List of material examined, its label data and depositories.

Species	Label data	Sex, USI, and collection
<i>Barce fraterna</i> (Say, 1832)	Colombia: Tolima, Espinal, 28 iv 1960, M. Revelo, light trap	1♂ 1♀ (CELM)
<i>Bargylia longinota</i> Wygodzinsky, 1956	Australia: Port Darwin, NW Australia, J.J. Walker	1♂ holotype (BMNH)
<i>Bergemesa brachmanni</i> (Berg, 1884)	Argentina: Sgo. Estero, Ojo de Agua, at light, iii. 1969, coll. Martínez	1♂ (MACN)
	Argentina: La Paz (Dep. San Javier), Córdoba, 15.–31.xii.1928, C. Bruch	1♀ (No 24113, MACN)
<i>Emesaya brevipennis</i> (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♂ (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♀ (UNAB)
<i>Emesaya pollex</i> Mcatee & Malloch, 1925	Brazil: RS, Palmares do Sul, Ilha grande, 10.iv.2003, equipe Probio	1♂ (MCNZ)
	Brazil: RS, Novo Hamburgo, 20.viii.1982, C. J. Becker leg.	1♀ (MCNZ 47287)
<i>Emesella</i> sp.	Colombia: Subparamo de Guasca, 3000 m alt, in fallen leaves of <i>Espeletia corymbosa</i> , 23.vii.1968, Sturm leg.	1♀ (ICN 091391)
<i>Gardena faustina</i> 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♂ (ICN)
	Brazil: Amazonas, Manaus, 25.v.1982, F.U.A., Latorre L.R.	1♀ (INPA)
<i>Ghilianella approximata</i> McAtee & Malloch, 1925	Peru: Satipo, Huancayo, viii.1944, Paprzycki, Zikan coll.	1♂ (FIOC)
	Brazil: AM, Ipixuna, rio Liberdade, Estirão da preta (07°21'46.7"S, 71°52'07.1"W)	1♀ (INPA)
<i>Ghilianella aracataca</i> 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♂ (IAvH-E-126058) 1♀ (IAvH-E-126063)
	Colombia: Meta, Villavicencio, Vda. La Argentina, Piedemonte llanero, Sistemática Animal leg.	1♂ 1♀ (ICN)
<i>Ghilianella atriclava</i> Bergroth, 1911	Colombia: Meta, Villavicencio, Vda. La Argentina, Piedemonte llanero, Sistemática Animal leg.	1♂ 1♀ (ICN)
<i>Ghilianella fenestrata</i> Maldonado Capriles, 1960	Costa Rica: Heredia, La Selva Biological Station, nr Puerto Viejo, 10.430862°N, 84.006467°W, 52 m, 9–15.viii.2010, OTS Heteroptera course, hand collecting	1♂ (UCR_ENT 00003767) 1♀ (UCR_ENT 00003779)
<i>Ghilianella gladiator</i> McAtee & Malloch, 1925	Trinidad: 21.ii.1929, J.G. Myers, T299	1♂ 1♀ (BMNH)
<i>Ghilianella globulata</i> McAtee & Malloch, 1925	Guatemala: Chacoj, R. Polochic, Champion	1♂ (BMNH)
	Guatemala: Panima, Champion	1♀ (BMNH)
<i>Ghilianella mirabilis</i> McAtee & Malloch, 1925	Brazil: Amazonas, Manaus, 20.v.1977, APA Luna Dias	1♂ (INPA)
	Brazil: AM, Manaus, Faz NAF, 6-Br 174 – km 31, data: 27.v.1977, col. E. Rufino	1♀ (INPA)
<i>Ghilianella</i> sp.	Colombia: Chocó, Acandí, Capurgana, borde del camino, 27.iii.2009, N. Novoa, manual	1♂ (MPUJ_ENT 0000428)
	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♀ (MPUJ_ENT 0041138)
<i>Ghinallielia globifera</i> Bergroth, 1906	Colombia: Meta, Acacias, Vda. Esmeralda, abr 2004, 514 m alt, E. Flórez y estud. Sistemática	1♂ (ICN)
	Colombia: Boyacá, Santa María, Camino La Almenara, 13.x.2005, G. Andrade-C.leg, 880 m alt, GAC10138	1♀ (ICN)
<i>Ghinallielia minimula</i> McAtee & Malloch, 1925	Brazil: RS, Cidreira, (Mata Restinga), 29.xi.2003, J. Alvenir.leg, pitfall	1♂ (MCNZ 180179)
	Brazil: RS, Cidreira, (Mata Restinga), 20.xi.2003, J. Alvenir.leg, pitfall	1♀ (MCN 180180)
<i>Ghinallielia</i> sp.	Brazil: Amazonas, Río Nhamunda, Ig. Areías, 01°35'11"S 57°37'32"W, 25 m. 16.v.2008, J.A. Rafael, manual. INPA	1♂ 1♀ (INPA)
<i>Liaghinella andina</i> Forero, 2007	Colombia: Cundinamarca, Cundinamarca, Reserva Chicaque, roble dal, 04,6172500°N 74,3139500°W, 2.250 m, 23.xii.2015, E. Tulande	1♂ (MPUJ_ENT 0047555)
	Colombia: Cundinamarca, Bogotá D.C., EAAB, Quebrada La Vieja (04°38'N 74°02'W), 26.viii.2001, 2850 m alt, D. Forero	1♀ paratype (MPUJ_ENT 0010690)
<i>Liaghinella tuberculata</i> Forero & Castro-Huertas, 2017	Colombia: Cundinamarca, Reserva Chicaque, refugio, 4°36.892'N 74°18.677'W, 2,221 m, 8–12.iv.2013, D. Forero leg / near to refuge, under Ficus, in forest litter, at night]	1♂ (MPUJ_ENT 0010584) 1♀ (MPUJ_ENT 0010771)
<i>Onychomesa gokani</i> Ishikawa, 2000	Japan: Komi, Iriomote-jima Is., The Ryukyus, 9.x.2004, T. Ishikawa	1♂ 1♀ (TUA)
<i>Pseudometapterus argentinus</i> (Berg, 1900)	Argentina: Sierra Córdoba. 14.i.1980, Williner S.J.	1♂ (MACN)
<i>Pseudometapterus</i> sp.	Brazil: RJ, Vassouras, E. do Rio, 1940, D. Machado	1♂ (524 Inst. Oswaldo Cruz)
<i>Schidium marcidum</i> (Uhler, 1896)	Japan: Ibusuki, Kagoshima pref., 19.iv.2007, A. Ishizuka leg.	1♂ (TUA)
	Japan: Machida, Tosayamada'cho, Kochi pref., 13.iv.2002, T. Ishikawa leg.	1♀ (TUA)
<i>Schidium plumarium</i> Ishikawa, 2002	Japan: Komi, Iriomote-jima Is., The Ryukyus, 7.–9.x.2004, H. Mizushima	1♂ (TUA)
	Japan: Toyohara, Iriomote Is., The Ryukyus, 7.iv.2003, M. Takai	1♀ (TUA)
<i>Tagalis seminigra</i> Champion, 1899	Peru: Ucayali, Kiriguetti (luz), vii 2004, J. Williams, 73°07'08"W, 11°38'13"S	1♂ (MLPA)
	Peru: Cuzco, Pagoreni (luz), vii.2004 Williams, 72°54'07"W 11°42'22"S	1♀ (MLPA)

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 Capriles, 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 Emesinae (*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

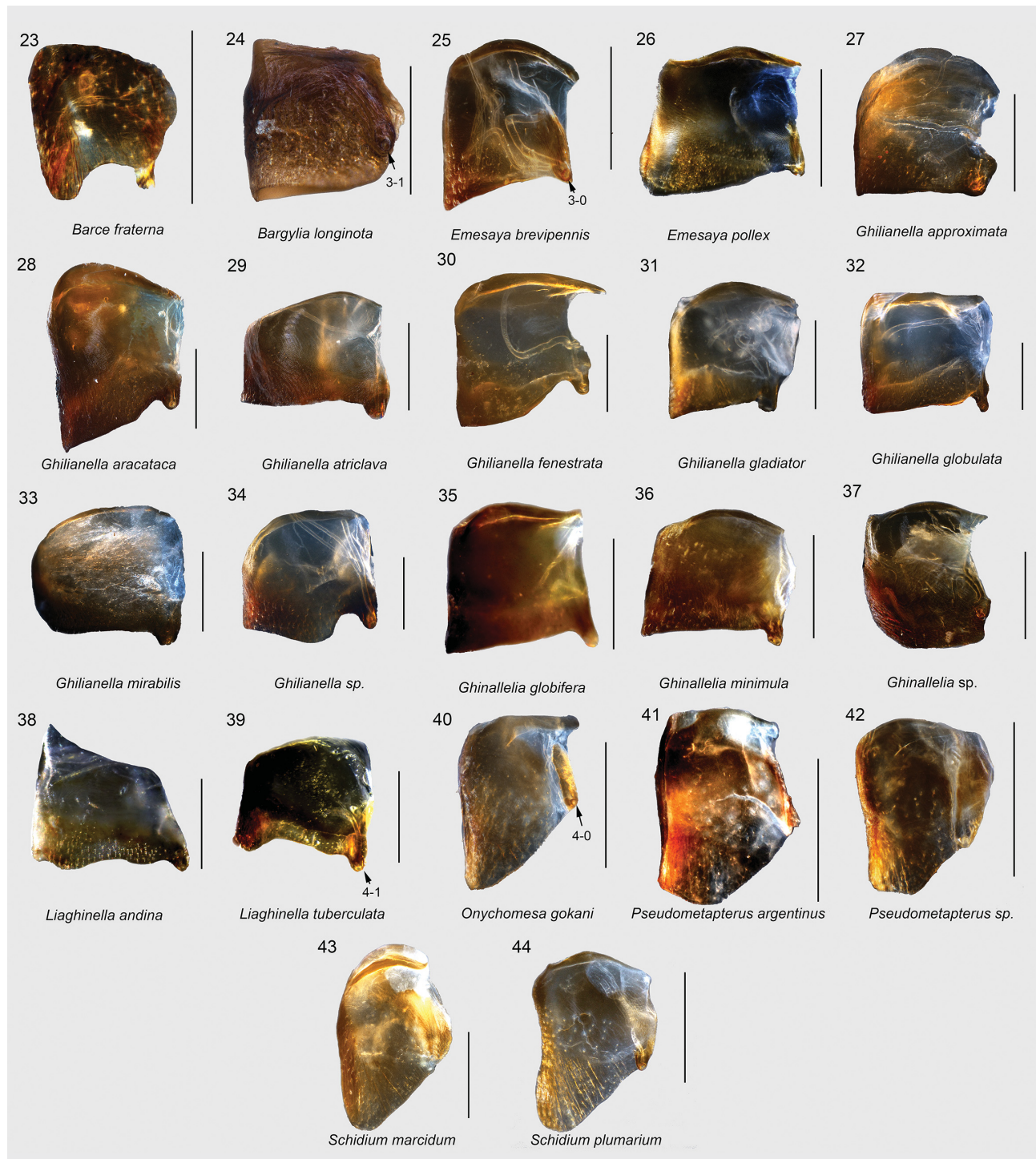


Figs 1–22. Male segment 8 (*S8*) in ventral view. 1 – *Barce* Stål, 1865; 2 – *Bargylia* Stål, 1865; 3–4 – *Emesaya* McAtee & Malloch, 1925; 5–12 – *Ghilianella* Spinola, 1850; 13–15 – *Ghinallelia* Wygodzinsky, 1966, 16–17 – *Liaghinella* Wygodzinsky, 1966, 18 – *Onychomesa* Wygodzinsky, 1966, 19–20 – *Pseudometapterus* Wygodzinsky, 1966, 21–22 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm.

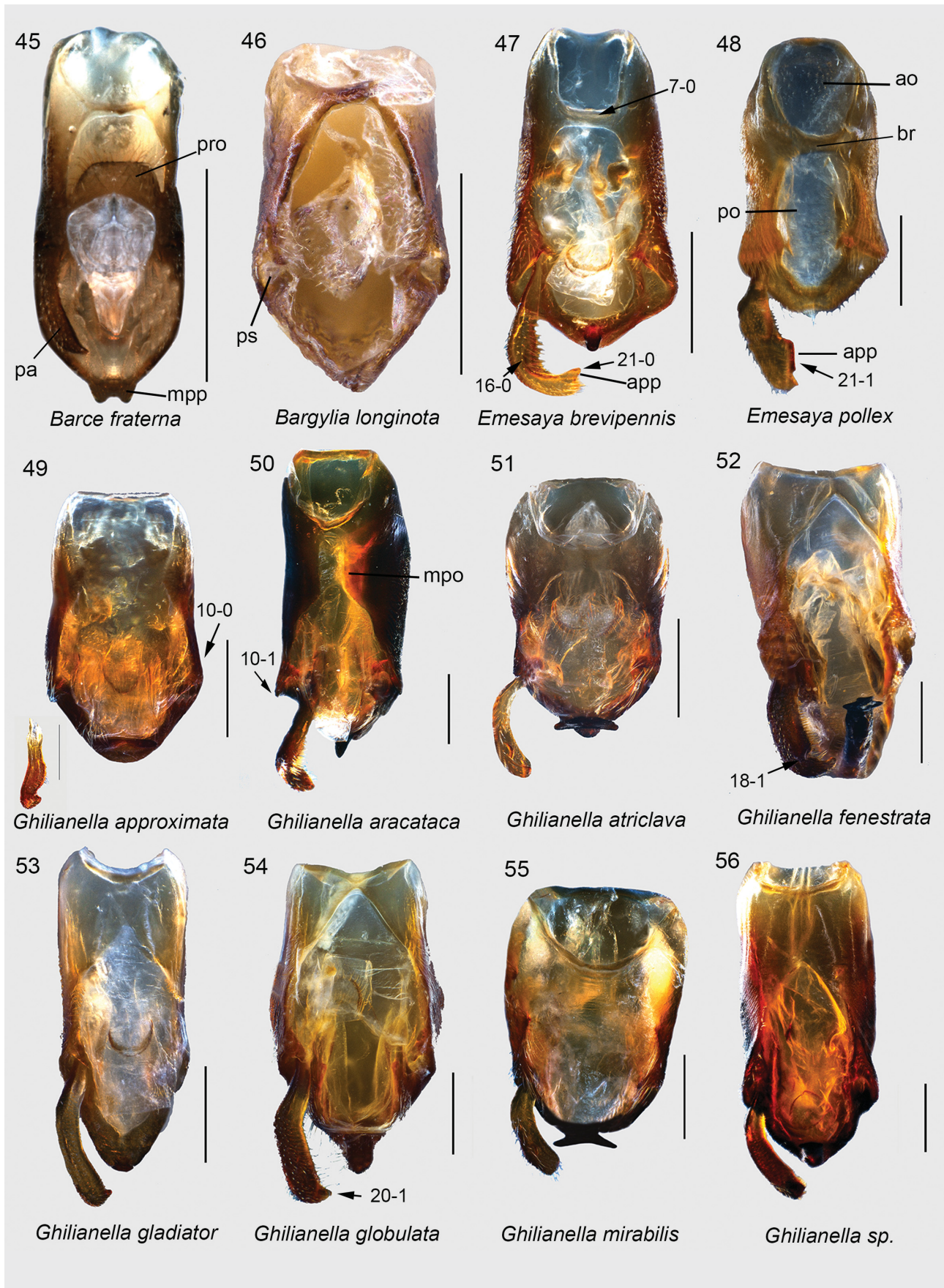
(*pro*) is membranous or with lateral sclerotizations and setae (Figs 62, 63, 66). The margin between the insertion of the parameres and the genital bridge (*mpp*) can be entire or produced (Fig. 50). The lateral margins of the paramere socket (*ps*) are usually entire, and in some species of *Ghilianella* 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

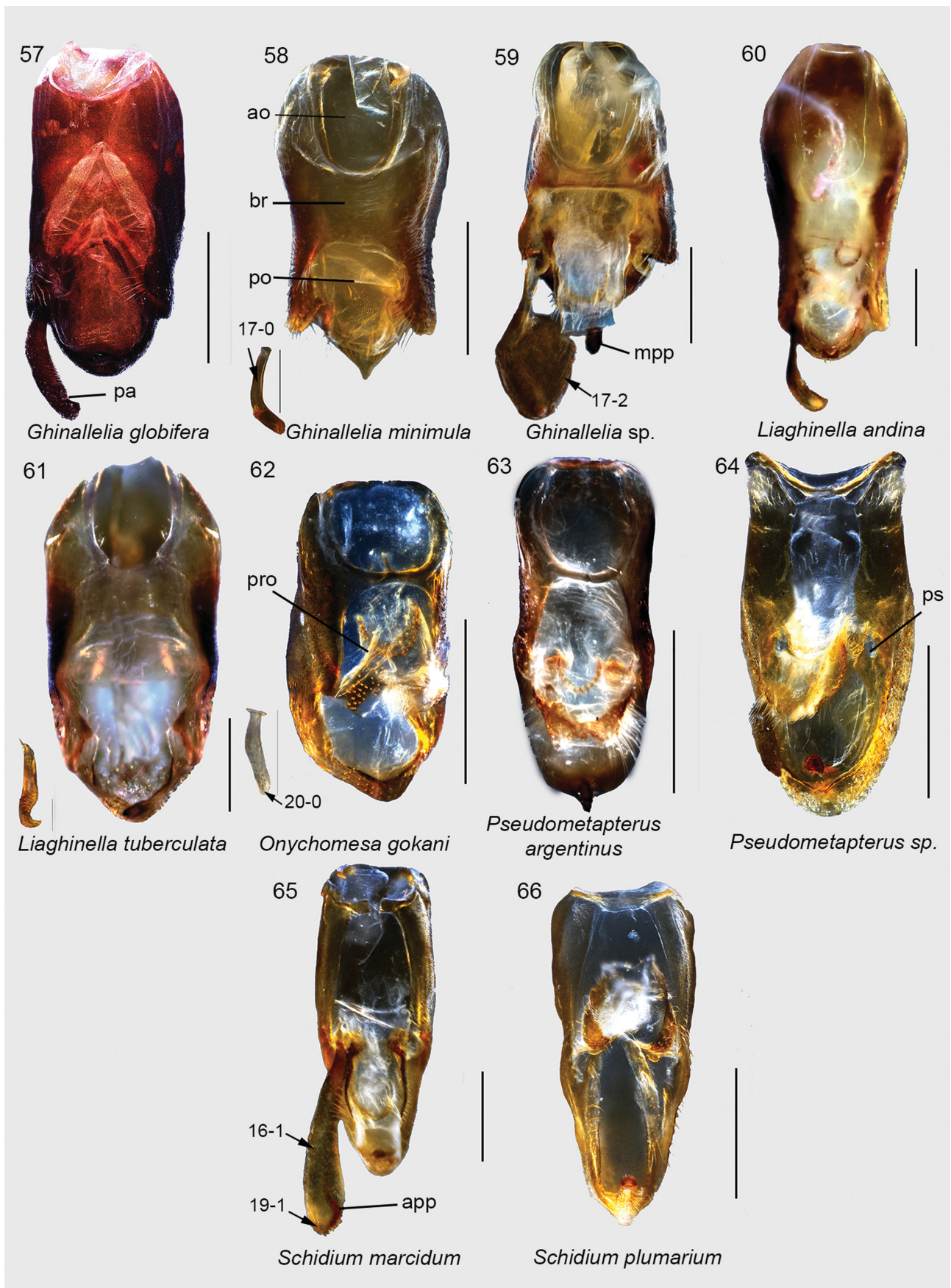
either from the posterior wall of its posterior margin, or from its anterior wall as an outgrowth of the cup-like sclerite (H.R. Gil-Santana, D. Rédei, G. Zhang, pers. comm.). In the examined taxa all *mpp* are originating from the posterior wall, thus making all these structures homologous. The *mpp* 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).



Figs 23–44. Male segment 8 (S8) in lateral view. 23 – *Barce* Stål, 1865; 24 – *Bargylia* Stål, 1865; 25–26 – *Emesaya* McAtee & Malloch, 1925; 27–34 – *Ghilianella* Spinola, 1850; 35–37 – *Ghinallelia* Wygodzinsky, 1966, 38–39 – *Liaghinella* Wygodzinsky, 1966, 40 – *Onychomesa* Wygodzinsky, 1966, 41–42 – *Pseudometapterus* Wygodzinsky, 1966, 43–44 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm.



Figs 45–56. Pygophore in dorsal view. 45 – *Barce* Stål, 1865; 46 – *Bargylia* Stål, 1865; 47–48 – *Emesaya* McAtee & Malloch, 1925; 49–56 – *Ghilianella* Spinola, 1850. 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. 57–59 – *Ghinallelia* Wygodzinsky, 1966; 60–61 – *Liaghinella* Wygodzinsky, 1966; 62 – *Onychomesa* Wygodzinsky, 1966; 63–64 – *Pseudometapterus* Wygodzinsky, 1966; 65–66 – *Schidium* Bergroth, 1916. 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.

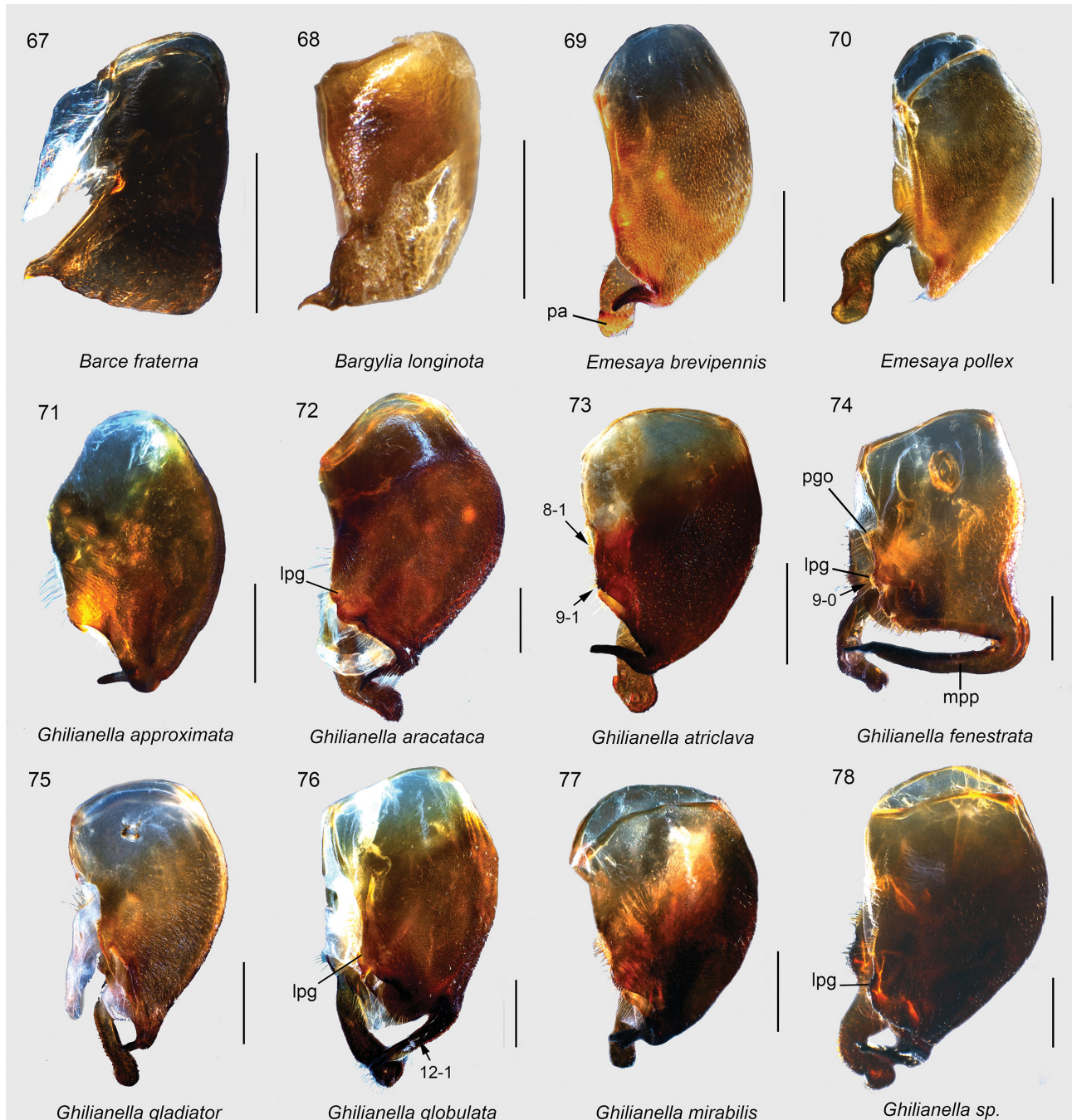
The paramere insertion (*pa*) is on the apical third of the pygophore. The socket (*ps*) of this insertion is formed by anterior and posterior component, both encircling the base of the paramere.

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



Figs 67–78. Pygophore in lateral view. 67 – *Barce* Stål, 1865; 68 – *Bargylia* Stål, 1865; 69–70 – *Emesaya* McAtee & Malloch, 1925; 71–78 – *Ghilianella* Spinola, 1850. 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.

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).

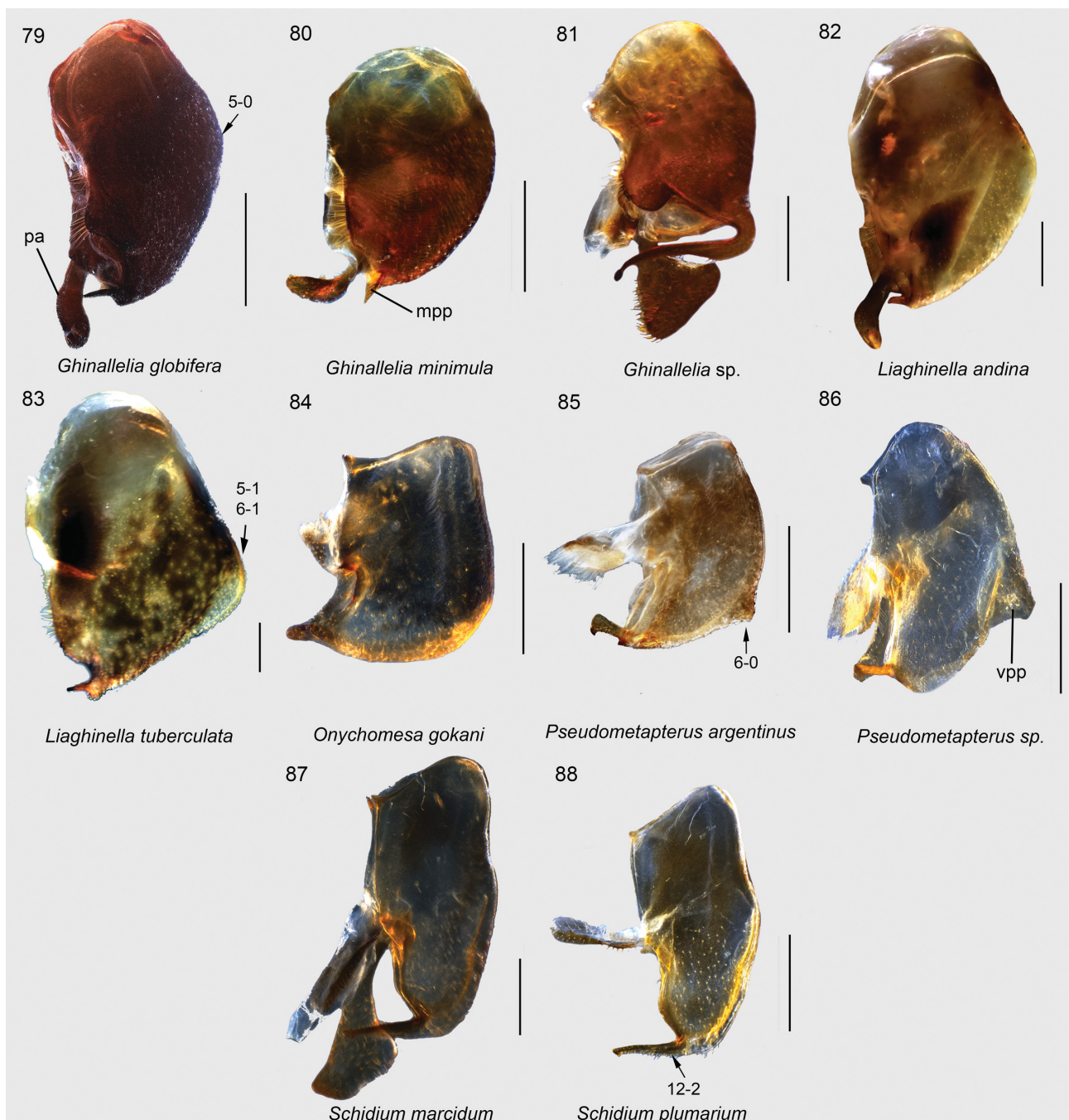
A subapical projection of the paramere was described for *Ghinallelia minimula* (McAtee & Malloch, 1925) and other, not specified species, belonging to the “*minimula* group” by WYGODZINSKY (1966), as a unique character

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,



Figs 79–88. Pygophore in lateral view. 79–81 – *Ghinallelia* Wygodzinsky, 1966; 82–83 – *Liaghinella* Wygodzinsky, 1966; 84 – *Onychomesa* Wygodzinsky, 1966; 85–86 – *Pseudometapterus* Wygodzinsky, 1966; 87–88 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm. Abbreviations: mpp – medial posterior process of pygophore; pa – paramere; vpp – ventral protruding of the pygophore.

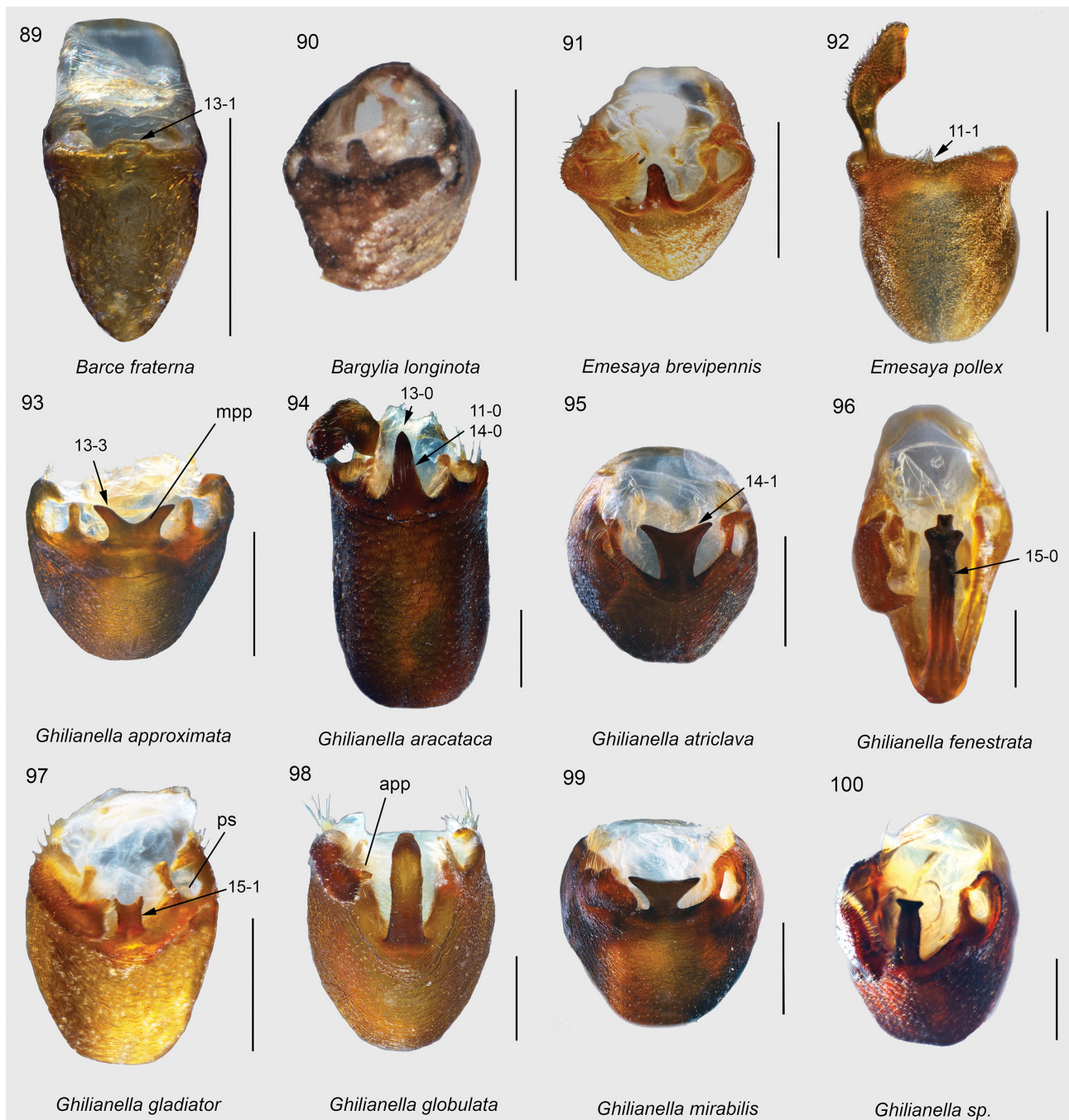
slightly projected laterally or not (*Schidium*, Figs 150, 151) and with the capitate process rounded. The basal plate extension is usually narrow, but wide in *Schidium* (Figs 150, 151).

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 *Ghinalle-*



Figs 89–100. Pygophore in caudal view. 89 – *Barce* Stål, 1865; 90 – *Bargylia* Stål, 1865; 91–92 – *Emesaya* McAtee & Malloch, 1925; 93–100 – *Ghilianella* Spinola, 1850. Scale bar: 0.5 mm. Abbreviations: app – apical projection of the paramere; mpp – medial posterior process of pygophore; ps – paramere socket.

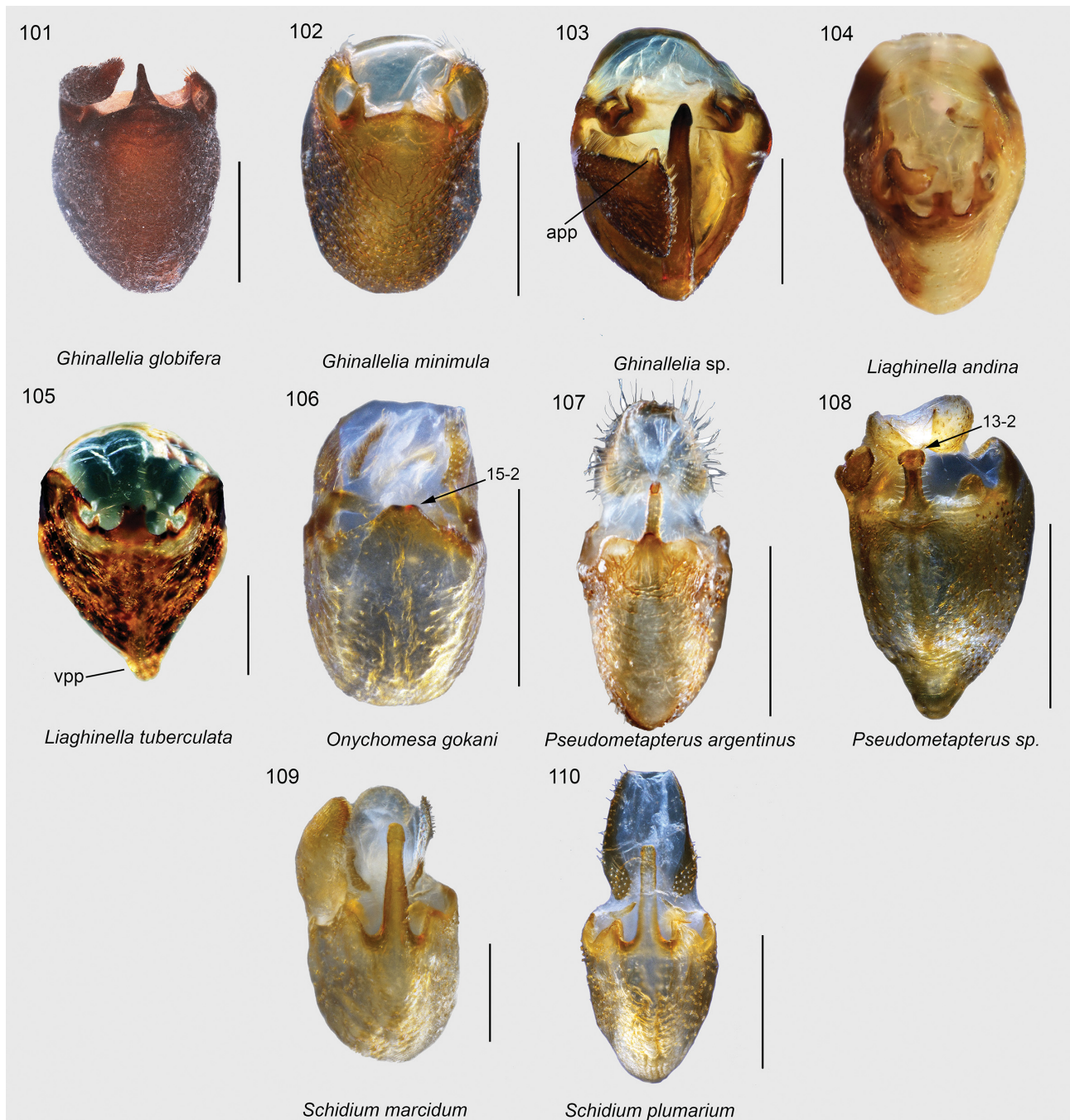
lia has a high shape variability and sclerotization degree that might be taxonomically useful (WYGODZINSKY 1966).

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.

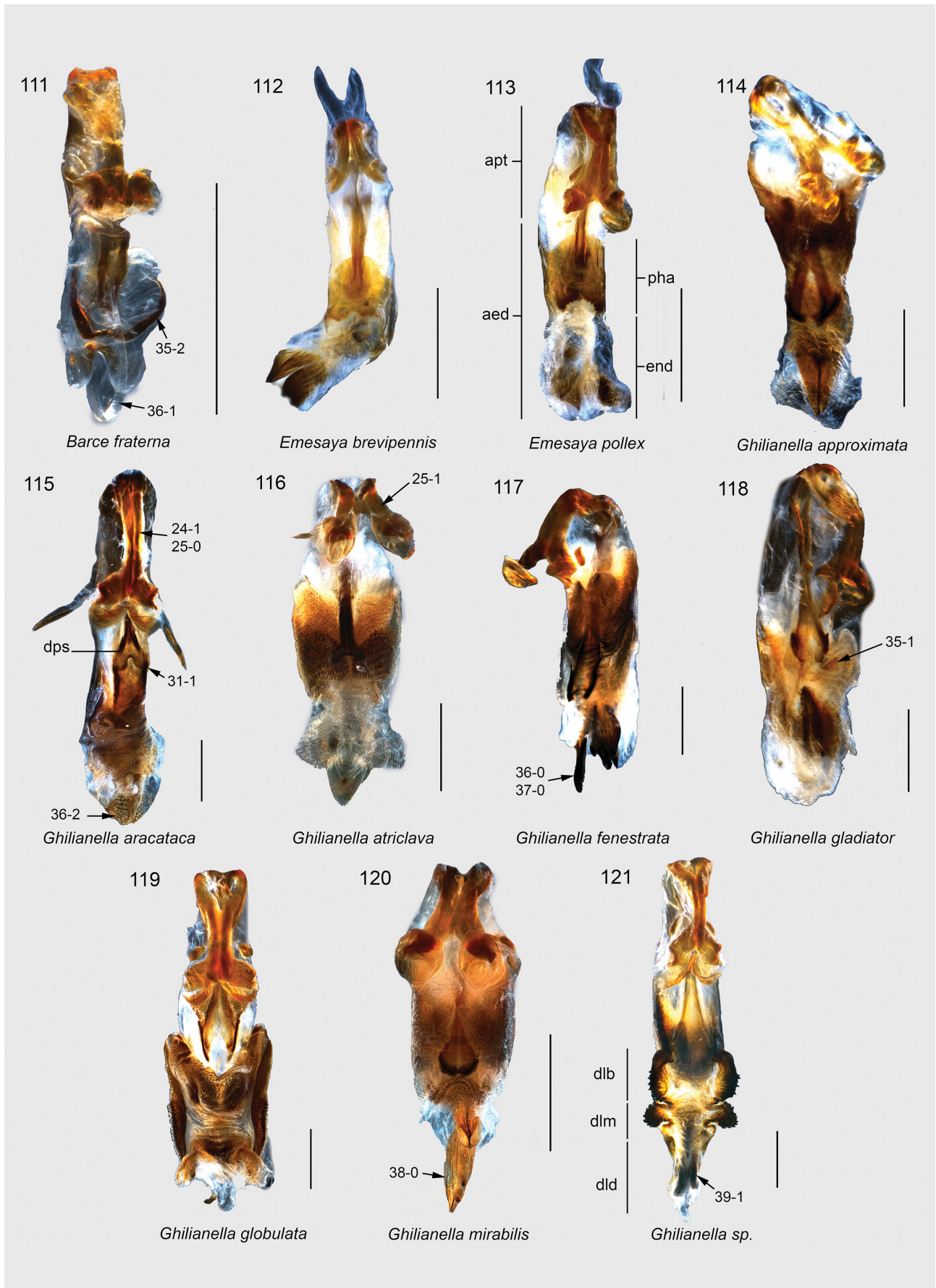
Endosoma

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)

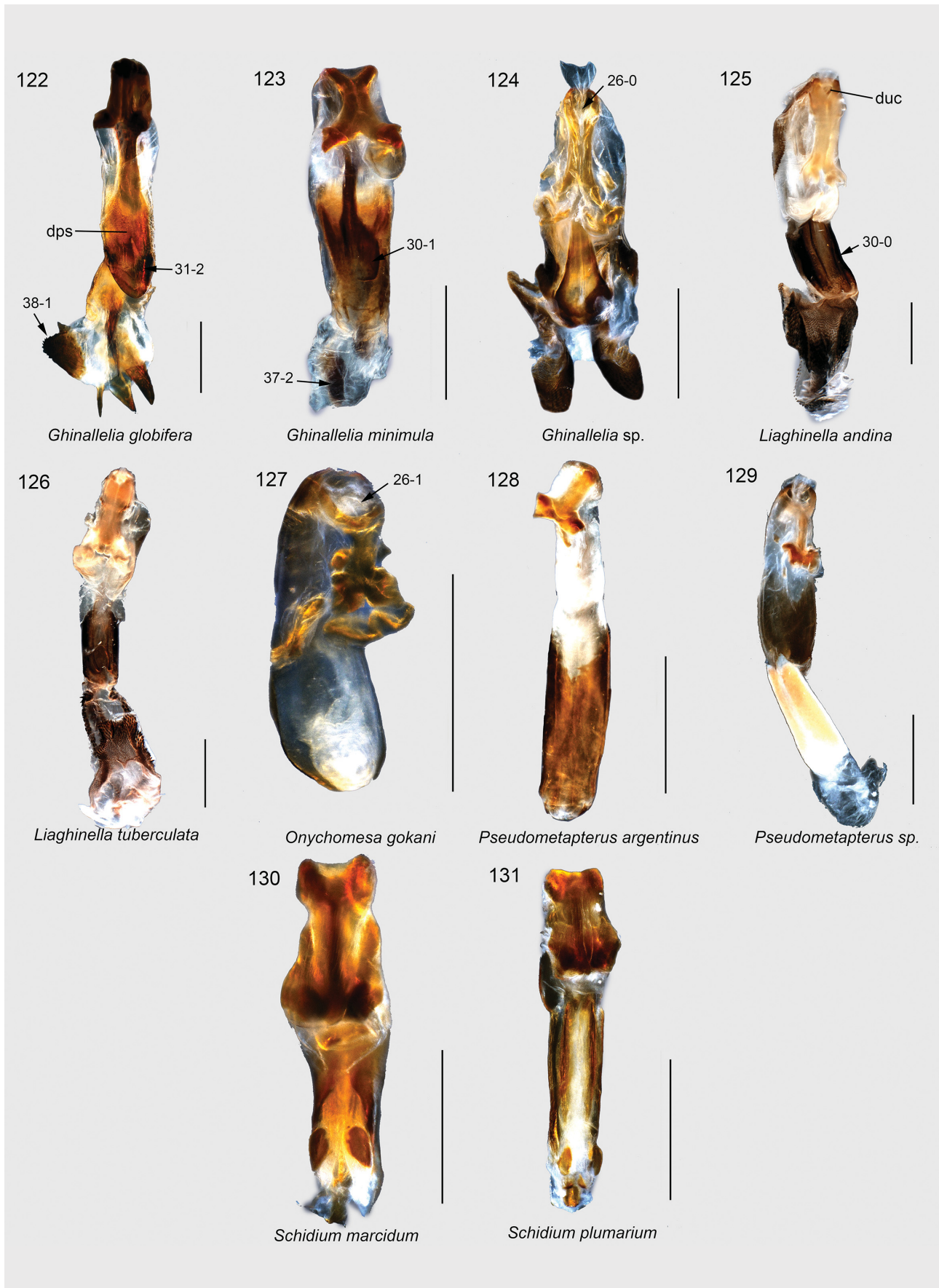
or asymmetrically arranged (*Emesaya* and *Ghinallelia*, Figs 112, 113, 122–124). The endosoma can be divided dorsolaterally into three regions, basal, median, and distal portions (Fig. 121). The dorsolateral basal portion (*dlb*) is frequently membranous, but it can have microtrichia (Figs 116, 119) or sclerotizations usually oriented longitudinally (Figs 111, 140). The dorsolateral median portion (*dml*) 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



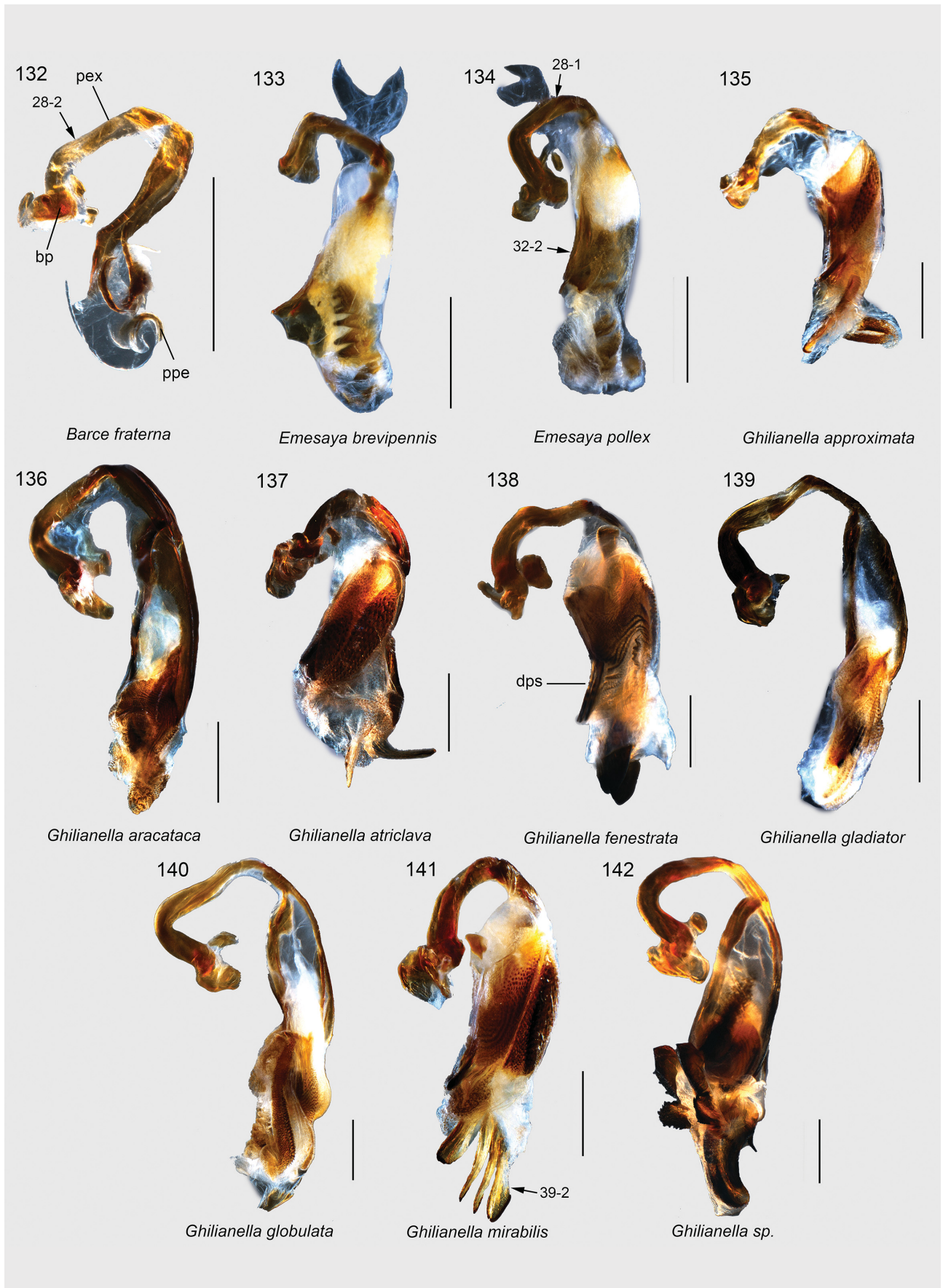
Figs 101–110. Pygophore in caudal view. 101–103 – *Ghinallelia* Wygodzinsky, 1966; 104–105 – *Liaghinella* Wygodzinsky, 1966; 106 – *Onychomesa* Wygodzinsky, 1966; 107–108 – *Pseudometapterus* Wygodzinsky, 1966; 109–110 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm. Abbreviations: app – apical projection of the paramere; vpp – ventral protruding of the pygophore.



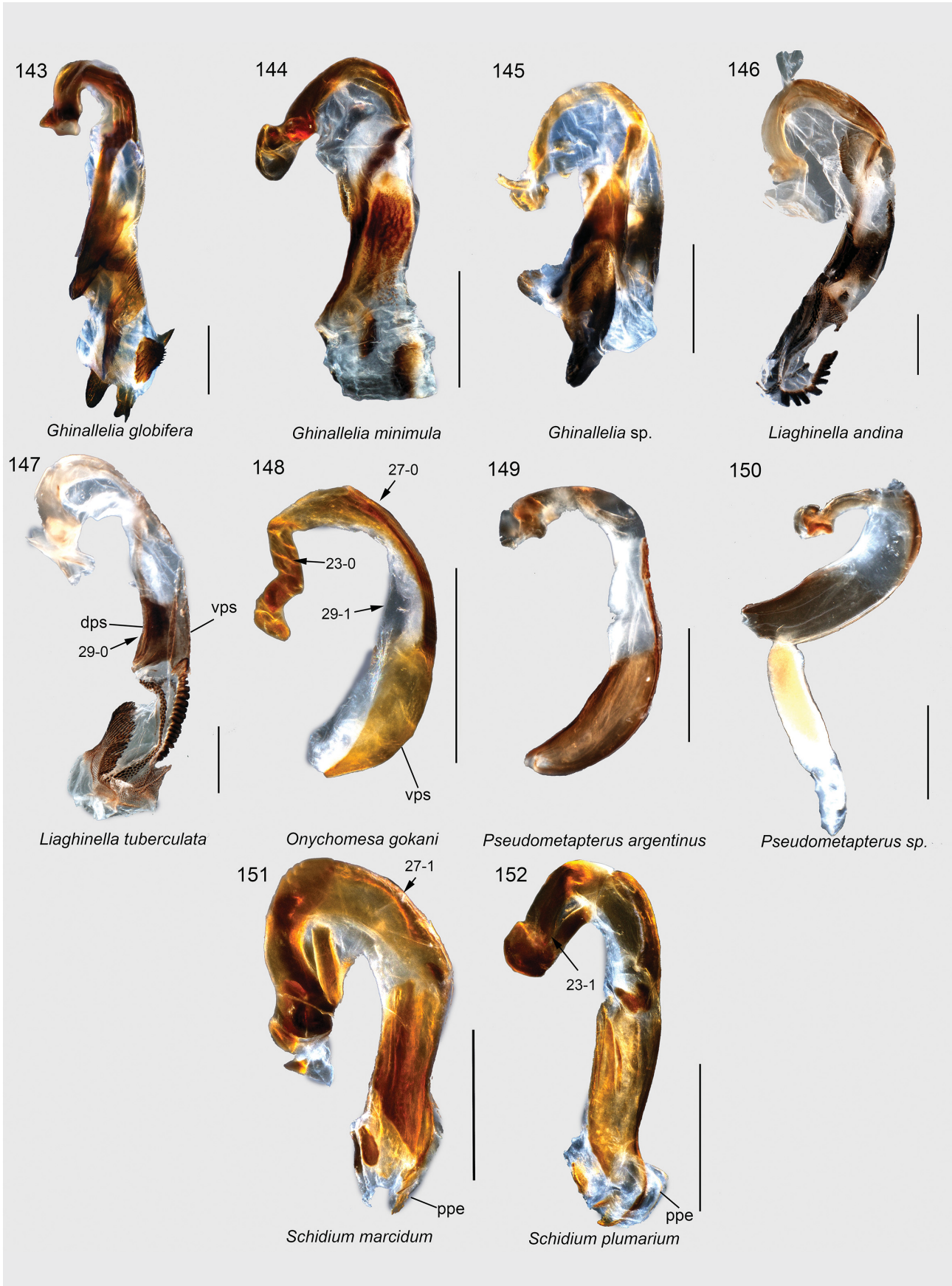
Figs 111–121. Phallus in dorsal view. 111 – *Barce* Stål, 1865; 112–113 – *Emesaya* McAtee & Malloch, 1925; 114–121 – *Ghilianella* Spinola, 1850. Scale bar: 0.5 mm. Abbreviations: aed – aedeagus; apt – articular apparatus; dlb – dorsolateral basal portion of the endosoma; dlm – dorsolateral medial portion of the endosoma; dld – dorsolateral distal portion of the endosoma; dps – dorsal phallosomal sclerite; end – endosoma; pha – phallosoma.



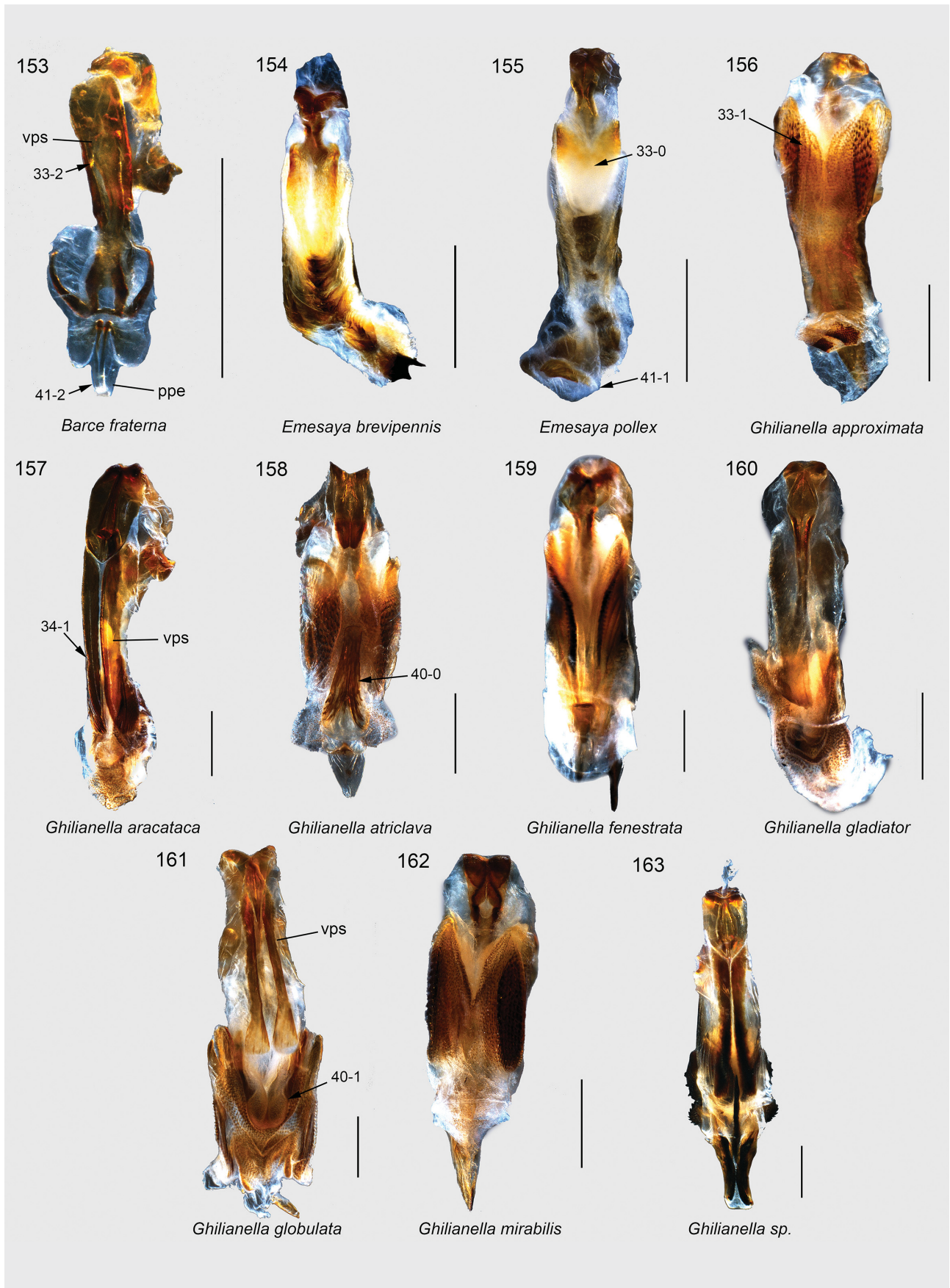
Figs 122–131. Phallus in dorsal view. 122–124 – *Ghinallelia* Wygodzinsky, 1966; 125–126 – *Liaghinella* Wygodzinsky, 1966; 127 – *Onychomesa* Wygodzinsky, 1966; 128–129 – *Pseudometapterus* Wygodzinsky, 1966; 130–131 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm. Abbreviations: dps – dorsal phallosclerite; duc – ductifer.



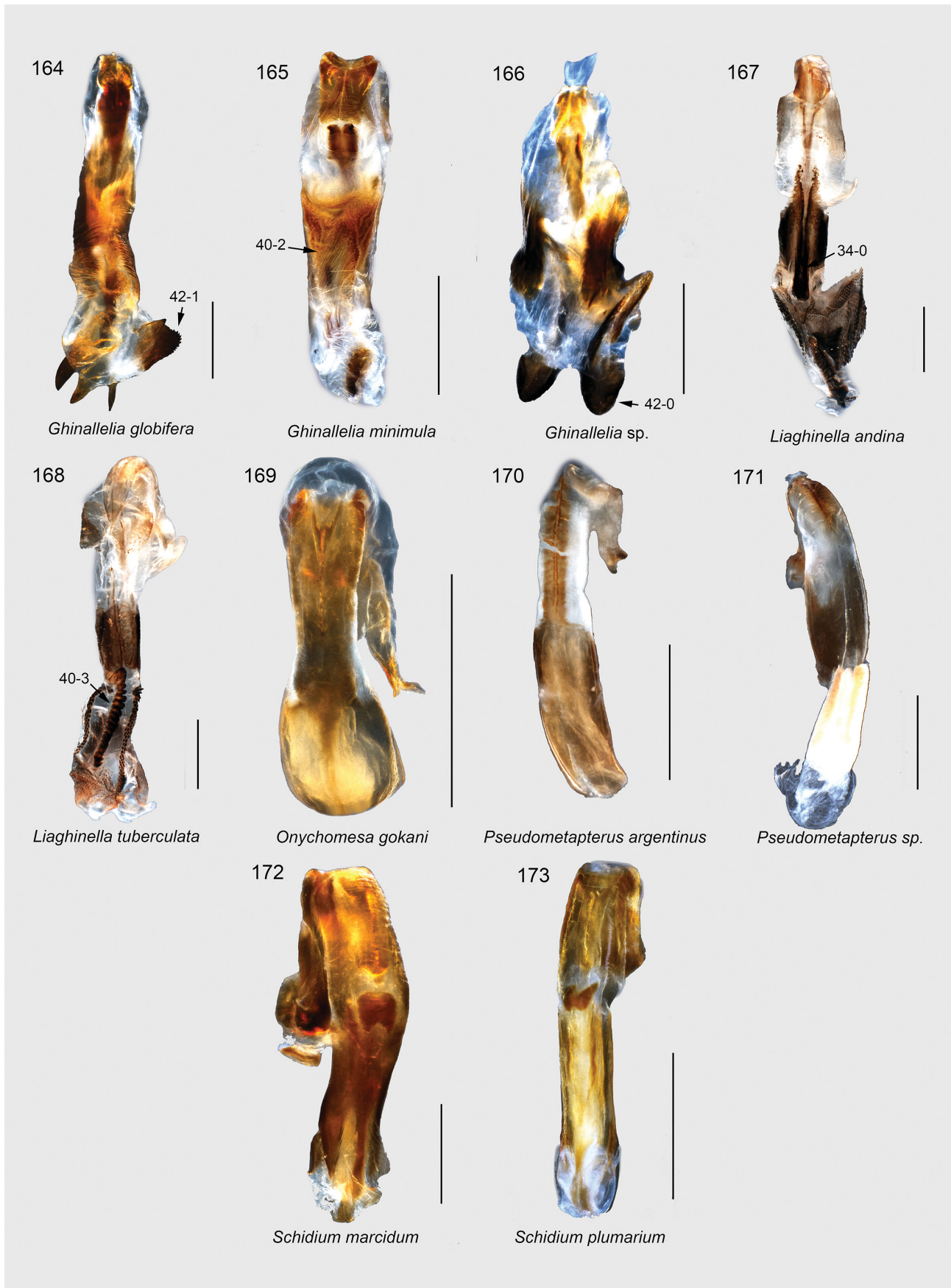
Figs 132–142. Phallus in lateral view. 132 – *Barce* Stål, 1865; 133–134 – *Emesaya* McAtee & Malloch, 1925; 135–142 – *Ghilianella* Spinola, 1850. Scale bar: 0.5 mm. Abbreviations: bp – basal plate; dps – dorsal phallothecal sclerite; pex – basal plate extension; ppe – posteroventral projections of the endosoma.



Figs 143–152. Phallus in lateral view. 143–145 – *Ghinallelia* Wygodzinsky, 1966; 146–147 – *Liaghinella* Wygodzinsky, 1966; 148 – *Onychomesa* Wygodzinsky, 1966; 149–150 – *Pseudometapterus* Wygodzinsky, 1966; 151–152 – *Schidium* Bergroth, 1916. 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. 153 – *Barce* Stål, 1865; 154–155 – *Emesaya* McAtee & Malloch, 1925; 156–163 – *Ghilianella* Spinola, 1850. Scale bar: 0.5 mm. Abbreviations: ppe – posteroventral projections of the endosoma; vps – ventral phallothecal sclerite.



Figs 164–173. Phallus in ventral view. 164–166 – *Ghinallelia* Wygodzinsky, 1966; 167–168 – *Liaghinella* Wygodzinsky, 1966; 169 – *Onychomesa* Wygodzinsky, 1966; 170–171 – *Pseudometapterus* Wygodzinsky, 1966; 172–173 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm.

sclerites, serrated, or with paddle-shaped or acuminate 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*).

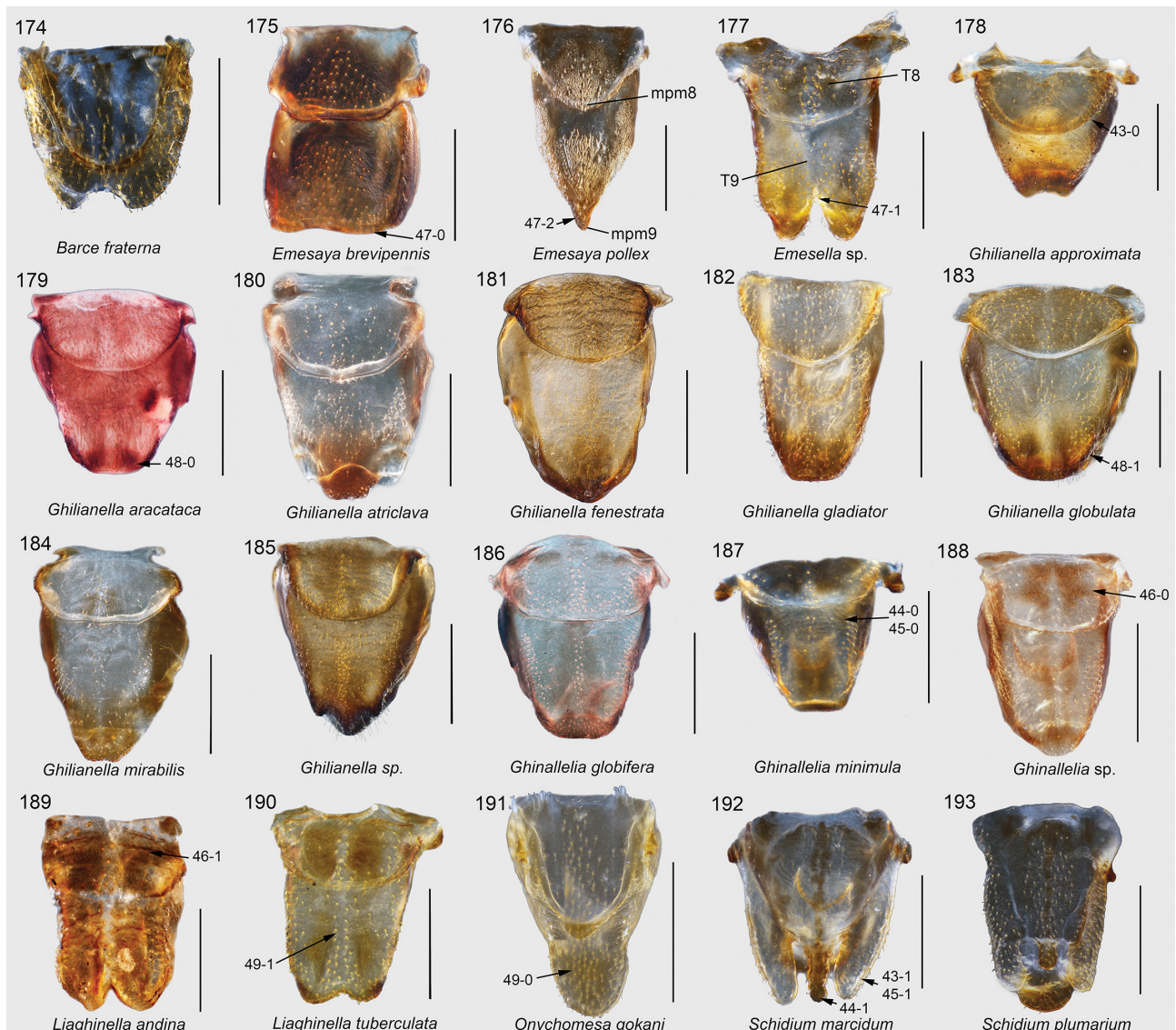
The ventral process of the endosoma in *Liaghinella* was documented previously by FORERO (2007) and CASTRO-HUERTAS & FORERO (2017) as “saw-like process of the endosoma” and “tubercle-shaped sclerites or tss”, respectively.

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



Figs 174–193. Female tergites 8 and 9 in caudal view. 174 – *Barce* Stål, 1865; 175–176 – *Emesaya* McAtee & Malloch, 1925; 177 – *Emesella* Dohrn, 1859; 178–185 – *Ghilianella* Spinola, 1850; 186–188 – *Ghinallelia* Wygodzinsky, 1966; 189–190 – *Liaghinella* Wygodzinsky, 1966; 191 – *Onychomesa* Wygodzinsky, 1966; 192–193 – *Schidium* Bergroth, 1916. 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.

(*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)

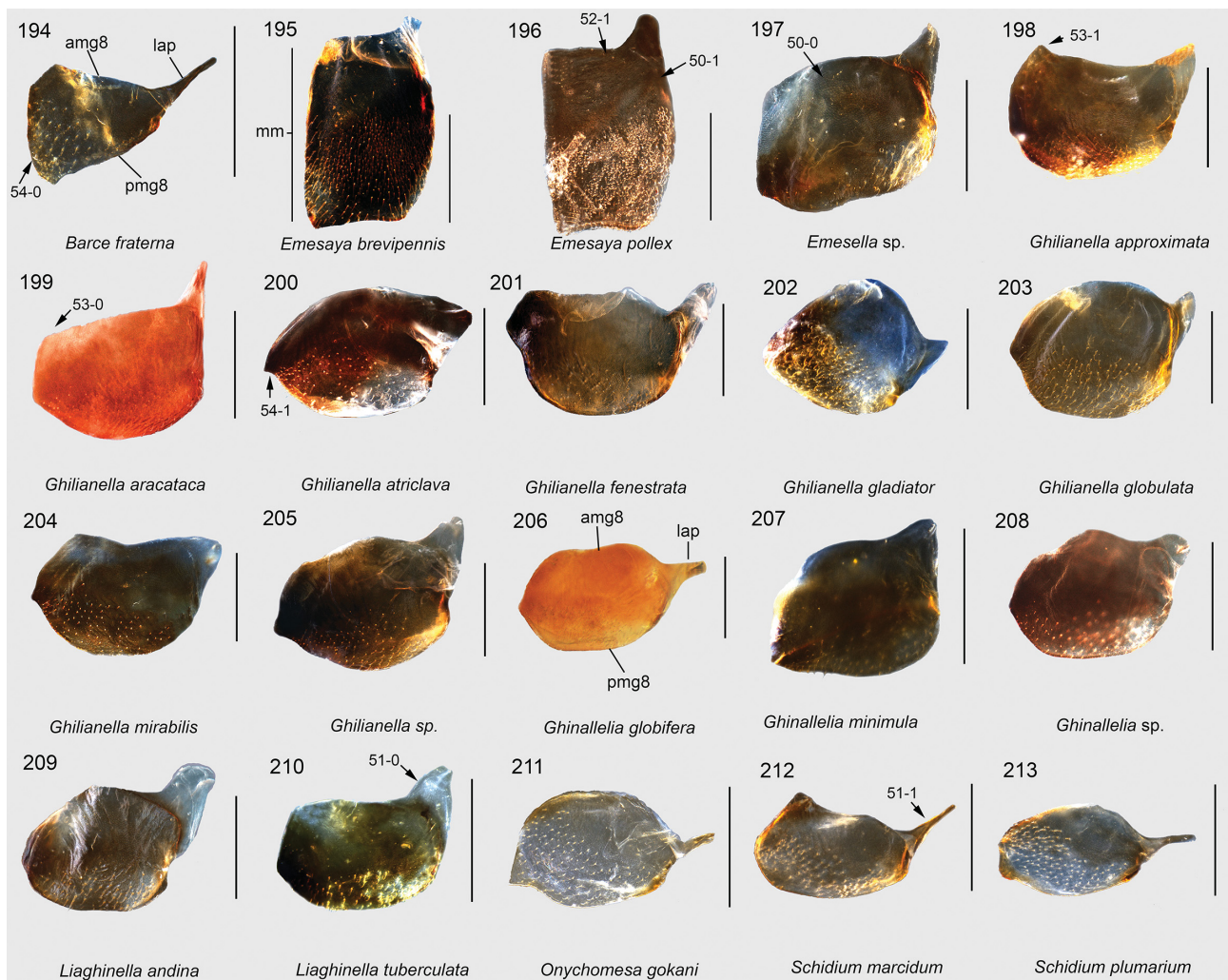
Structure. As in *T8*, tergite 9 (*T9*) has usually a vertical orientation, but can be directed nearly horizontally; usually it is exposed, or covered by tergite 8. Tergite 9 is usually oval, or nearly rectangular, with the anterior margin concave (the union with the tergite 8). The posterior margin (*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 CAPRILES (1960): *Ghilianella* and *Ghinallelia*; WYGODZINSKY (1966): 20 genera; MALDONADO CAPRILES (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 CAPRILES 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



Figs 194–213. Gonocoxa 8 in ventral view. 194 – *Barce* Stål, 1865; 195–196 – *Emesaya* McAtee & Malloch, 1925; 197 – *Emesella* Dohrn, 1859; 198–205 – *Ghilianella* Spinola, 1850; 206–208 – *Ghinallelia* Wygodzinsky, 1966; 209–210 – *Liaghinella* Wygodzinsky, 1966; 211 – *Onychomesa* Wygodzinsky, 1966; 212–213 – *Schidium* Bergroth, 1916. 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.

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 is 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.



Figs 214–225. Bursa copulatrix in dorsal view. 214 – *Barce* Stål, 1865; 215–216 – *Emesaya* McAtee & Malloch, 1925; 217 – *Emesella* Dohrn, 1859; 218–225 – *Ghilianella* Spinola, 1850. 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.

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),

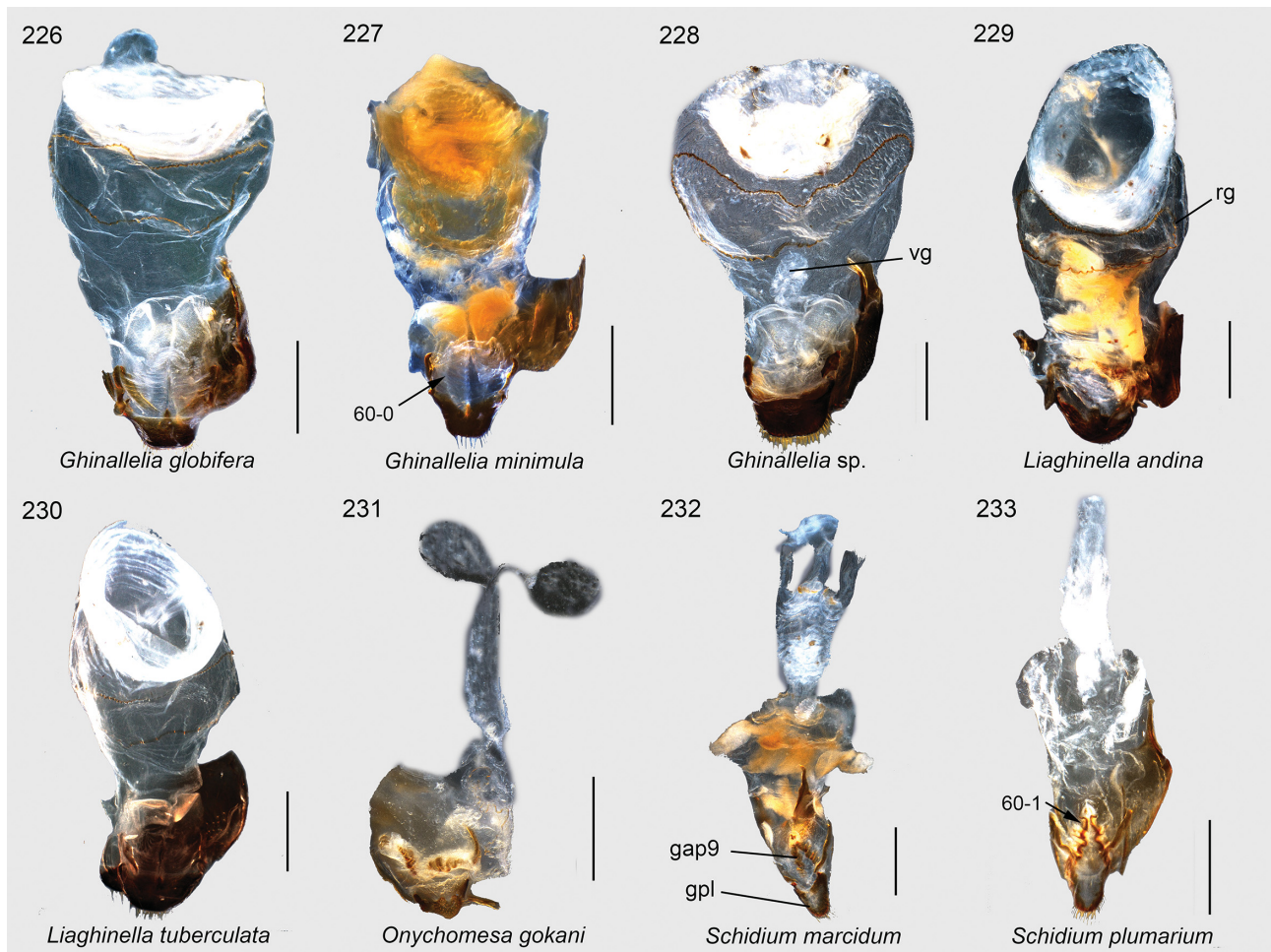
with a dorsal folding (*Emesaya*, Figs 215, 216, 235, 236) or with several small foldings (Figs 237–250). In ventral view, the medial region of the sac is usually membranous, or with sclerites (Figs 255, 256, 261, 263).

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).

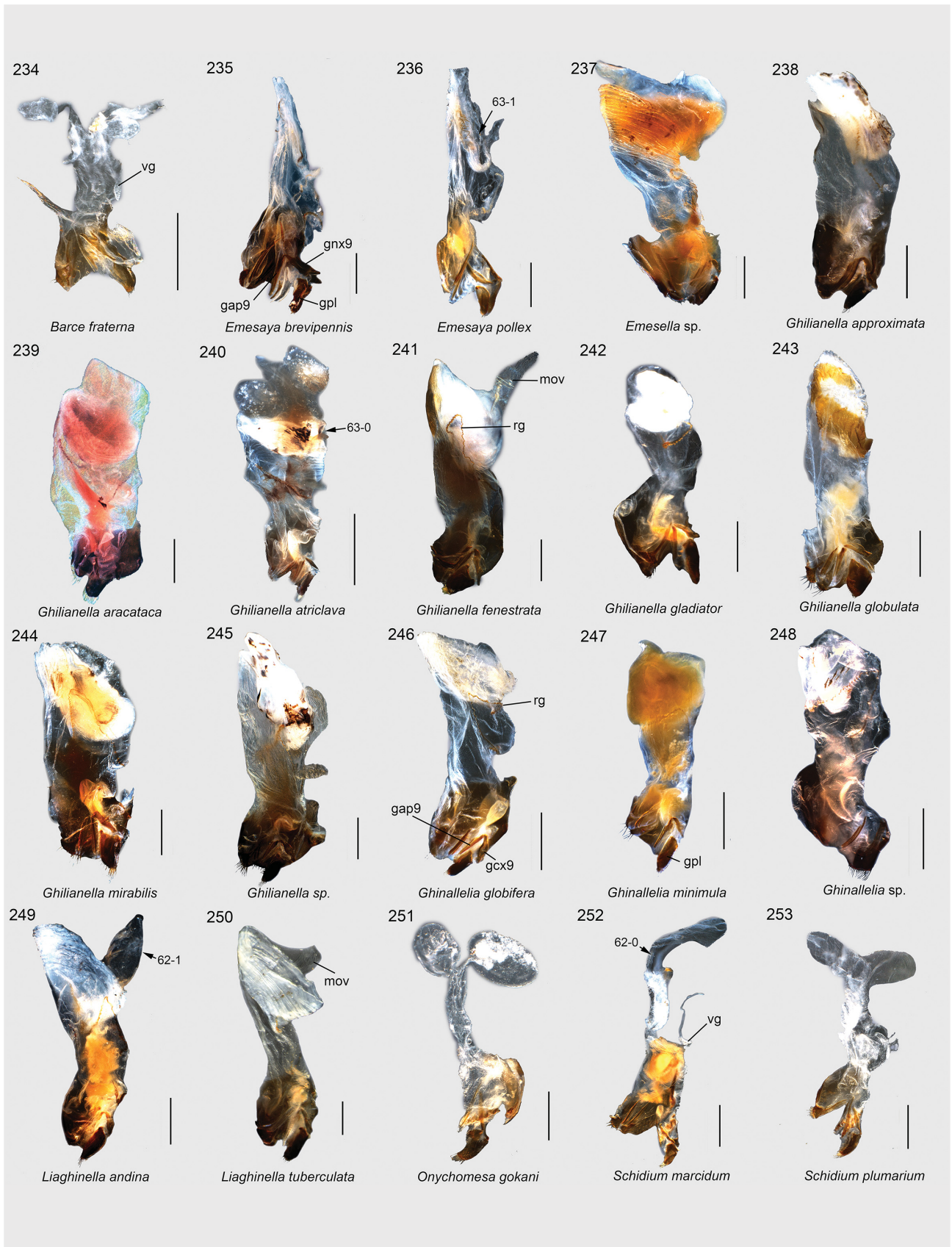
On the cuticular lining of the bursa copulatrix there is a ring gland (*rg*) (COBBEN & WYGODZINSKY 1975), a narrow band usually rather sinuous (Figs 220, 223, 226) or nearly straight in some regions (Figs 219, 221), which is located transversely around the dorsal region of the bursa copulatrix; it is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



Figs 226–233. Bursa copulatrix in dorsal view. 226–228 – *Ghinallelia* Wygodzinsky, 1966; 229–230 – *Liaghinella* Wygodzinsky, 1966; 231 – *Onychomesa* Wygodzinsky, 1966; 232–233 – *Schidium* Bergroth, 1916. 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. 234 – *Barce* Stål, 1865; 235–236 – *Emesaya* McAtee & Malloch, 1925; 237 – *Emesella* Dohrn, 1859; 238–245 – *Ghilianella* Spinola, 1850; 246–248 – *Ghinallelia* Wygodzinsky, 1966; 249–250 – *Liaghinella* Wygodzinsky, 1966; 251 – *Onychomesa* Wygodzinsky, 1966; 252–253 – *Schidium* Bergroth, 1916. 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.

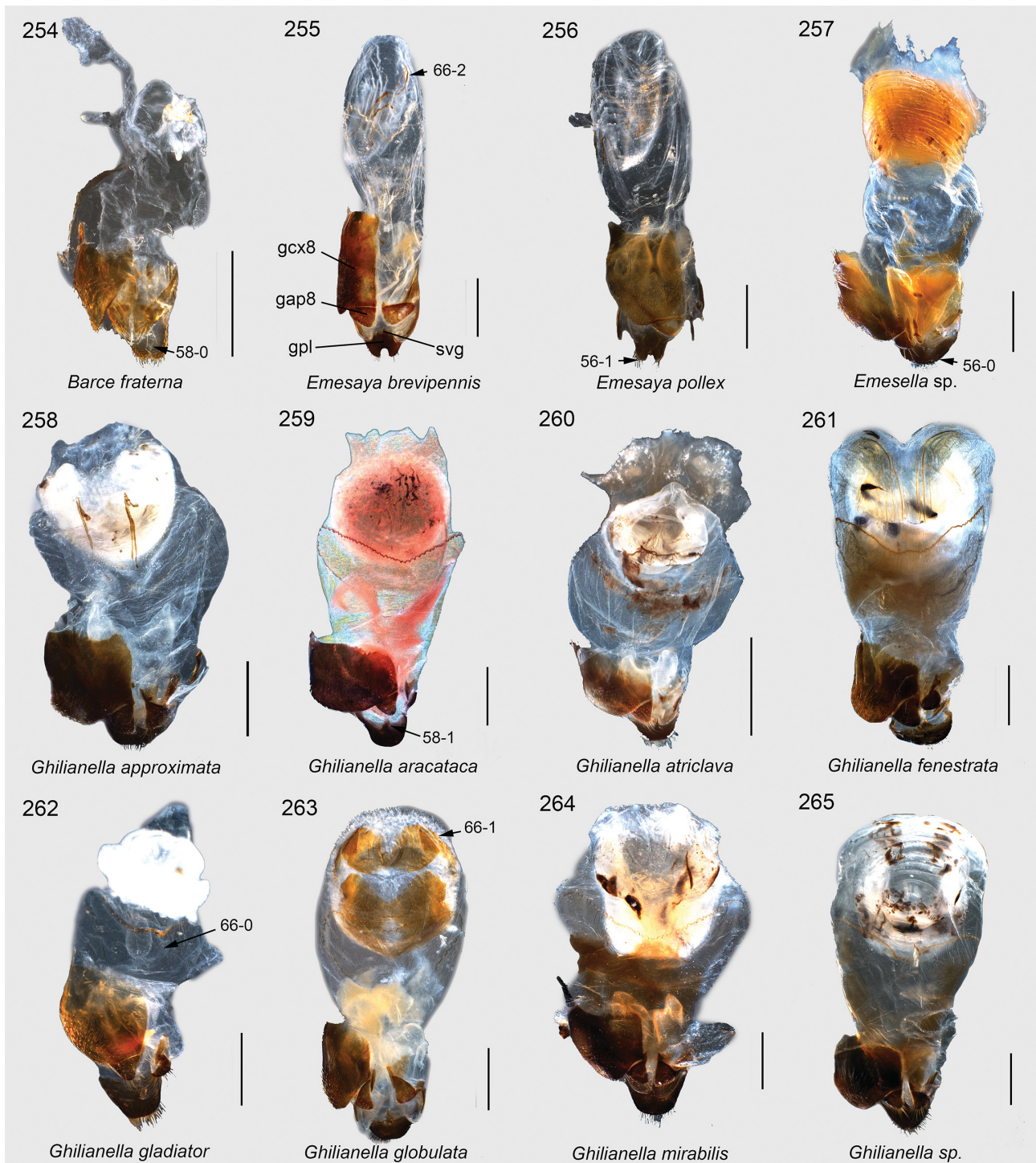
structure has really a glandular function, and the reasons to be called a “ring gland” were not mentioned by COBBEN & WYGODZINSKY (1975). Similar sclerotizations with a probable glandular function have been described for Miridae on the dorsal surface of the seminal depository, but there is no strong 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.



Figs 254–265. Bursa copulatrix in ventral view. 254 – *Barce* Stål, 1865; 255–256 – *Emesaya* McAtee & Malloch, 1925; 257 – *Emesella* Dohrn, 1859; 258–265 – *Ghilianella* Spinola, 1850. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gcx8 – gonocoxa 8; gpl – gonoplac; svg – subapical ventral margin of the gonoplac.

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.

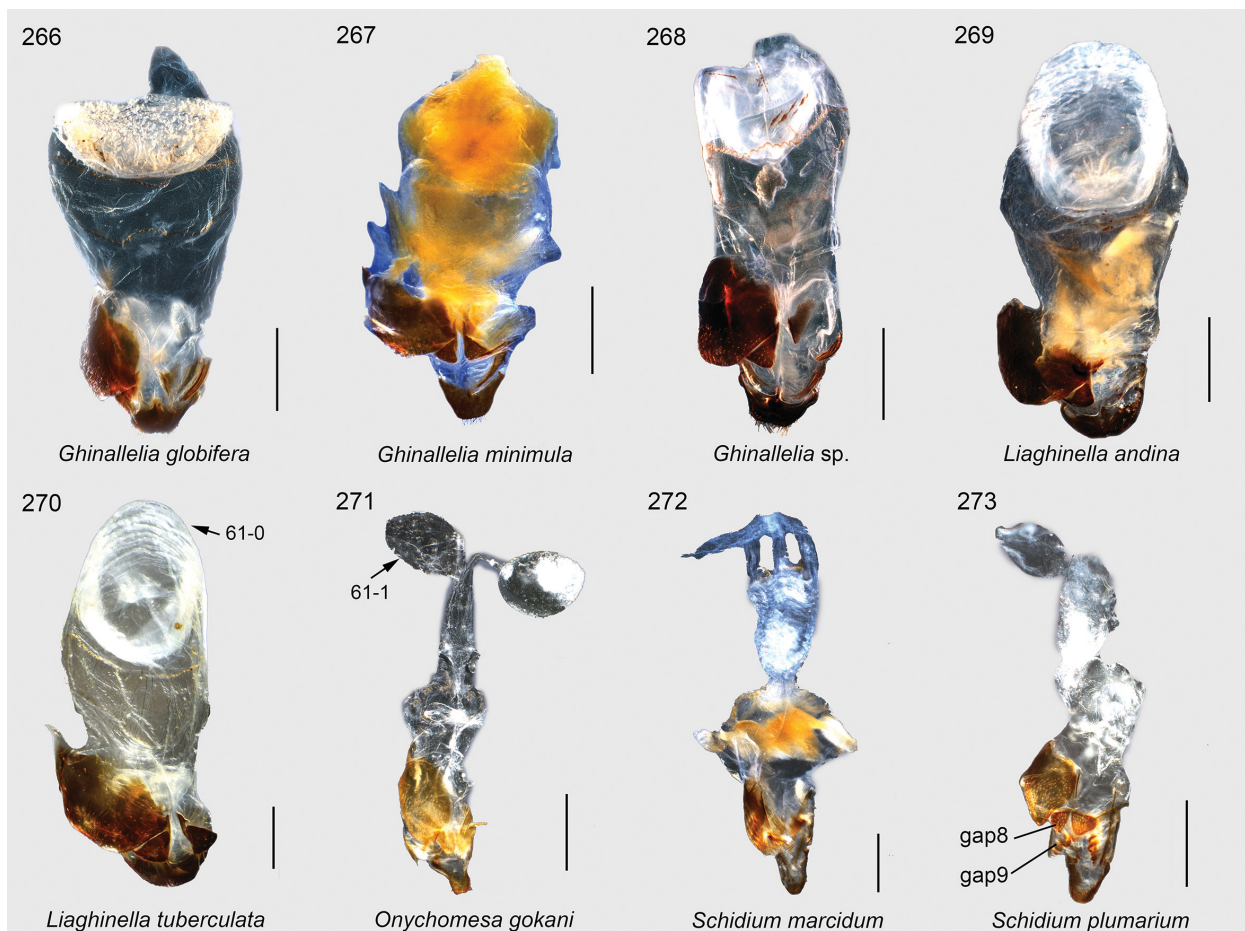
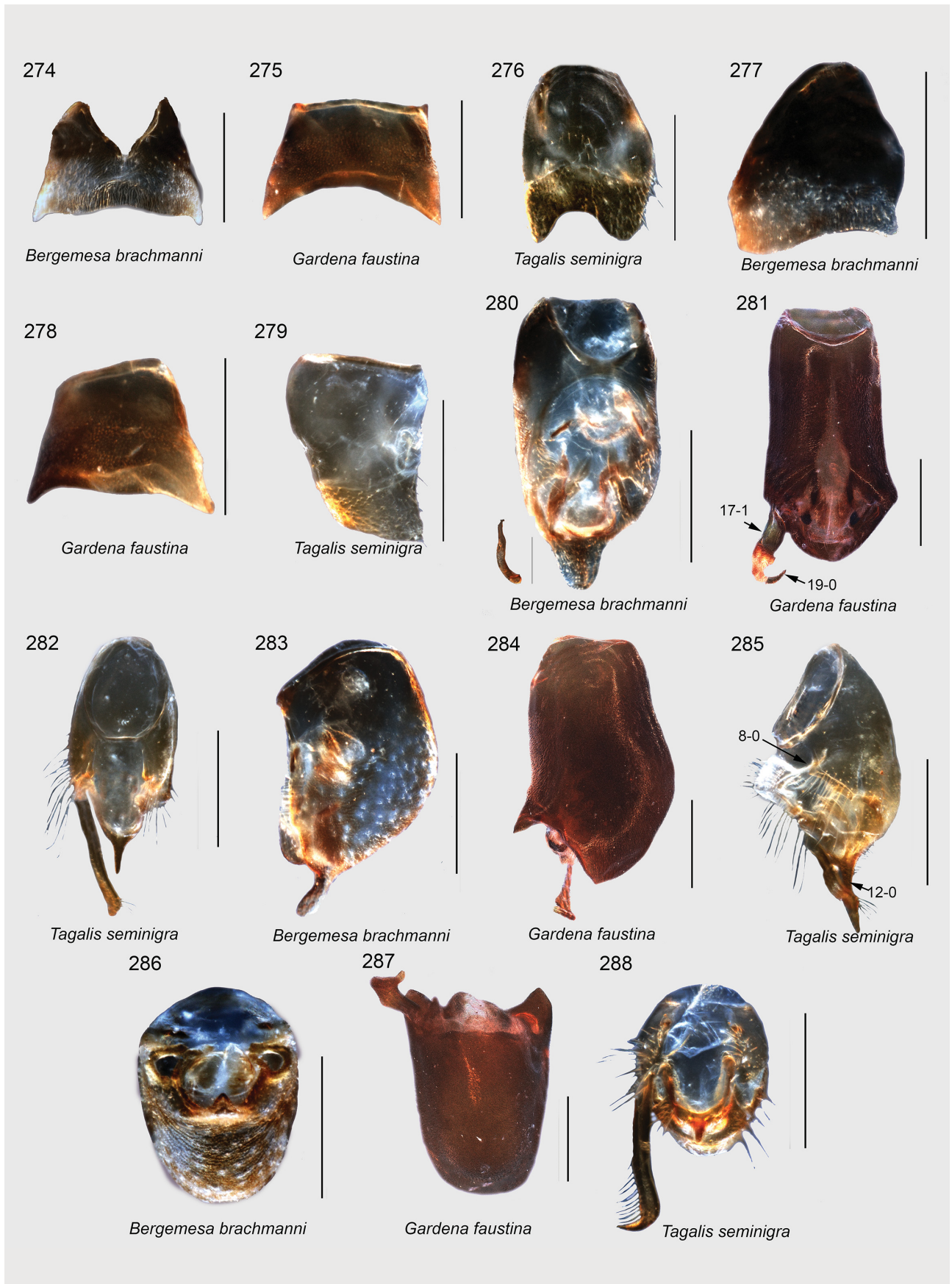


Fig. 266–273. Bursa copulatrix in ventral view. 266–268 – *Ghinallelia* Wygodzinsky, 1966; 269–270 – *Liaghinella* Wygodzinsky, 1966; 271 – *Onychomesa* Wygodzinsky, 1966; 272–273 – *Schidium* Bergroth, 1916. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gap9 – gonapophysis 9.

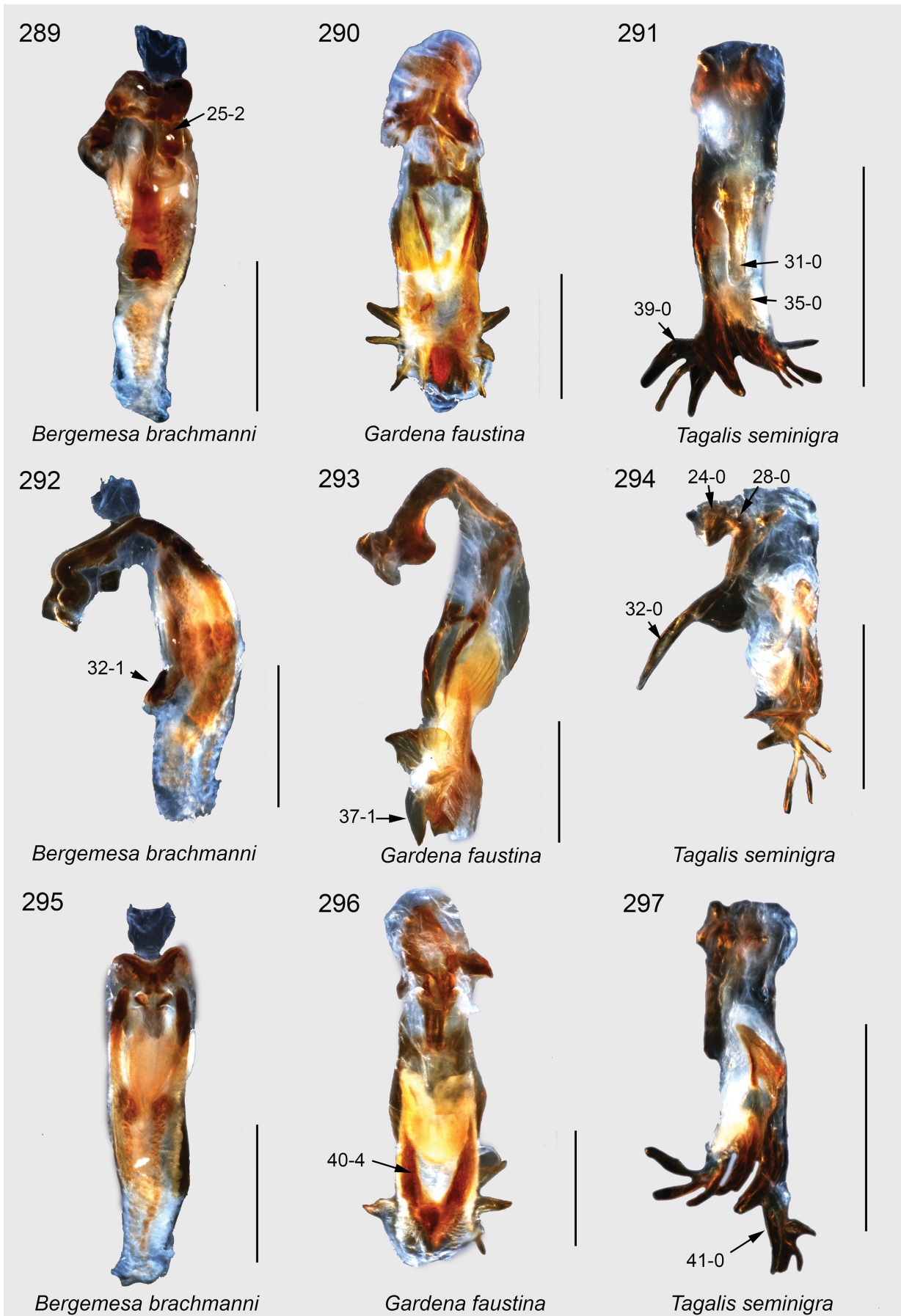
22. Paramere, vestiture: (0) setae; (1) microchaetae. CI = 100/RI = 100.
23. Articulatory apparatus, arms of the basal plate, structure: (0) narrow (Fig. 148); (1) wide (Fig. 152) CI = 100/RI = 100.
24. Articulatory apparatus, arms of the basal plate, length related to dorsal process of the basal plate: (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 phallosomal region, sclerotization: (0) sclerotized (*dps*) (Fig. 147); (1) not sclerotized (Fig. 148). Uninformative character because the dorsal phallosomal region is unsclerotized only in *Onychomesa gokani*.
30. Dorsal phallosomal sclerite, symmetry: (0) symmetrical (Fig. 125); (1) asymmetrical (Fig. 123). CI = 100/RI = 100.
31. Dorsal phallosomal sclerite, apical margin, structure: (0) produced (Fig. 291); (1) emarginated (Fig. 115); (2) entire (Fig. 122). CI = 50/RI = 60.
32. Dorsal phallosomal 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 phallosomal sclerite (*vps*) (Fig. 153). CI = 66/RI = 75.
34. Phallosoma, ventral phallosomal 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

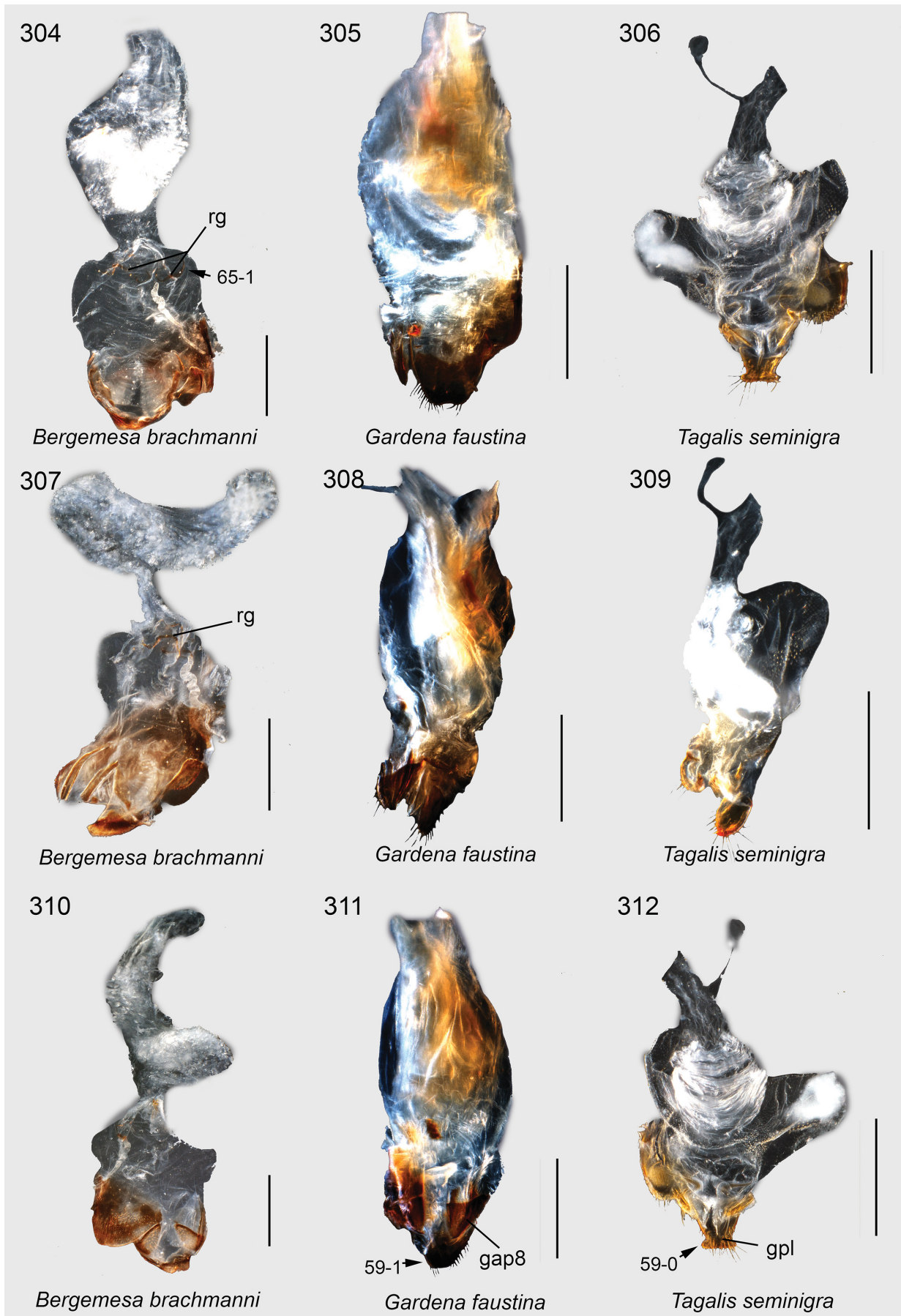
43. T8, position: (0) adjacent to T9 (Fig. 178); (1) overlapping T9 (Fig. 192). CI = 100/RI = 100.
44. T8, posteromedial margin, structure: (0) entire (Fig. 187); (1) produced (Fig. 192). CI = 100/RI = 100.
45. T8, posterolateral margin, structure: (0) entire (Fig. 187); (1) produced (Fig. 191). CI = 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.



Figs 274–288. 274–279 – male sternite 8 (S8): 274–276 – ventral view, 277–279 – lateral view; 280–288 – pygophore: 280–282 – dorsal view, 283–285 – lateral view, 286–288 – ventral view. 274, 277, 280, 283, 286 – *Bergemesa brachmanni* (Berg, 1884); 275, 278, 281, 284, 287 – *Gardena faustina* McAtee & Malloch, 1925; 276, 279, 282, 285, 288 – *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm.



Figs 289–297. Phallus: 289–291 – dorsal view; 292–294 – lateral view; 295–297 – caudal view. 289, 292, 295 – *Bergemesa brachmanni* (Berg, 1884); 290, 293, 296 – *Gardena faustina* McAtee & Malloch, 1925; 291, 294, 297 – *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm.



Figs 304–312. Bursa copulatrix in dorsal (304–306), lateral (307–309), and ventral (310–312) view. 304, 307, 310 – *Bergemesa brachmanni* (Berg, 1884); 305, 308, 311 – *Gardena faustina* McAtee & Malloch, 1925; 305, 308, 311 – *Tagalis seminigra* Champion, 1899. Scale bar: 0.5 mm. Abbreviations: gap8 – gonapophysis 8; gpl – gonoplac; rg – ring gland of the bursa copulatrix.

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

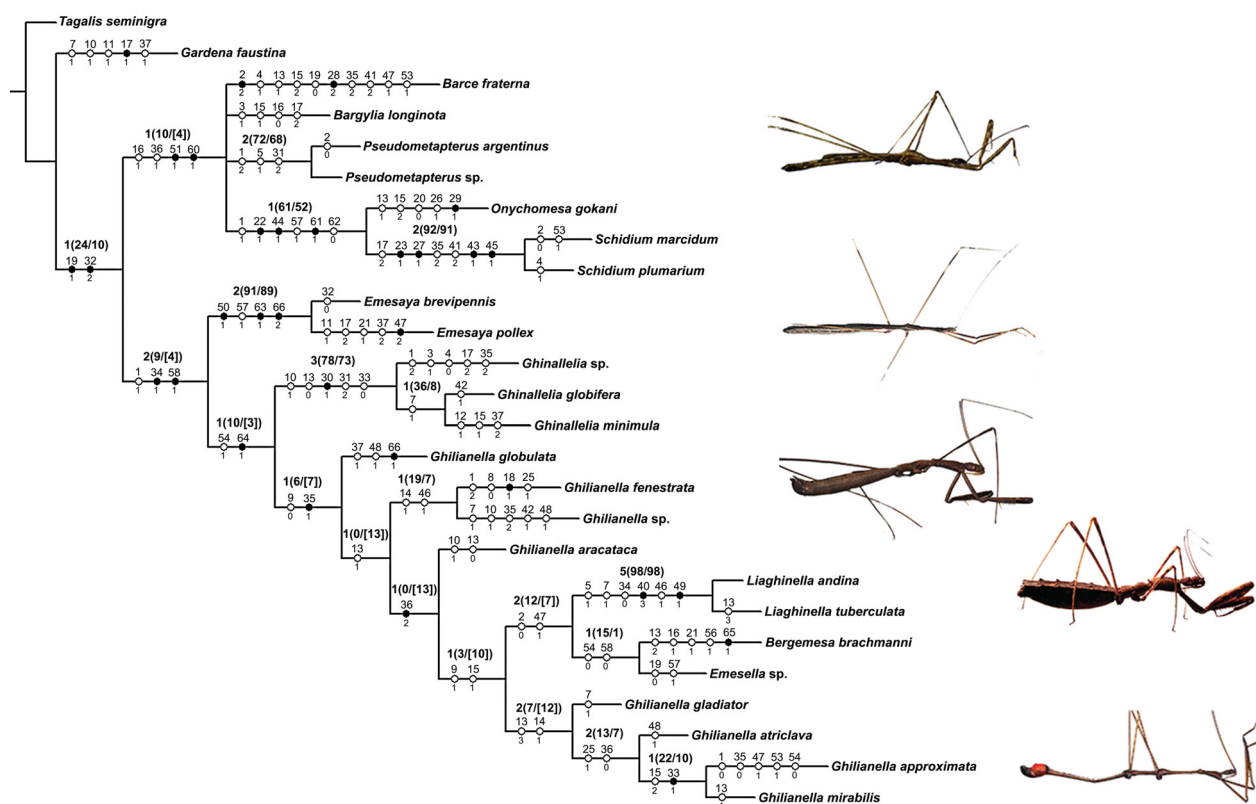


Fig. 313. Strict consensus tree of the male and female genitalic characters. Apomorphies mapped on the tree, non-homoplasious changes as full circles, homoplasious changes as empty circles. Support values in the branches (Bremer support, first value; GC frequencies, inside brackets, square brackets represent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

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, Figs 146, 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 CAPRILES 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 phallosclerite, 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 CAPRILES 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 Leis-tarchini (*Bagauda* BERGROTH, 1903, *Ploiaria* SCOPOLI, 1786), Emesini (*Phasmatocoris* BREDDIN, 1904) 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 phallosclerite 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 phallosclerite 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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References

- BERG C. 1884: Addenda et emendanda ad Hemiptera Argentina. *Anales de la Sociedad Científica Argentina* **17**: 97–118.
- BERG C. 1900: Tres Reduviidae novae argentinae. *Comunicaciones del Museo Nacional de Buenos Aires* **1**(6): 187–190.
- BERGROTH E. 1906: Zur Kenntnis der Ploeariinen. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **56**: 305–321.
- BERGROTH E. 1911: New Neotropical Ploeariinae. *Psyche* **18**: 15–20.
- CASTRO-HUERTAS V. & FORERO D. 2017: Small range distributions in the high Andes: two new species of Liaghinella (Hemiptera: Heteroptera: Reduviidae: Emesinae) from Colombia. *Zootaxa* **4277**(3): 399–412.
- CHAMPION G. 1898: Rhynchota. Hemiptera-Heteroptera. Vol. II. In: GODMAN F. & SALVIN O. (eds.): *Biología Centrali-Americana*. Taylor & Francis, London, 416 pp.
- COBBEN R. & WYGODZINSKY P. W. 1975: The Heteroptera of the Netherlands Antilles – IX Reduviidae (Assassin bugs). *Studies on the Fauna of Curaçao and other Caribbean Islands* **48**(158): 1–62.
- DAVIS N. T. 1955: Morphology of the female organs of reproduction in the Miridae (Hemiptera). *Annals of the Entomological Society of America* **48**: 132–150.
- DAVIS N. T. 1965: Contributions to the morphology and phylogeny of the Reduvidae (Hemiptera: Heteroptera), Part III, The male and female genitalia. *Annals of the Entomological Society of America* **59**: 911–924.
- DISTANT W. 1913: Reports on the Percy Sladen Trust Expeditions to the Indian Ocean in 1905. Part 5, Rhynchota: Suborder Heteroptera. *Transactions of the Linnean Society of London* **16**: 139–191.
- DOHRN A. 1859: Catalogus hemipterorum. Herrcke & Lebeling, Stettin, vii + 112 pp.
- FORERO D. 2007: Description of a new species of Liaghinella (Hemiptera: Heteroptera: Reduviidae: Emesinae) from the Colombian Andes, with notes on its feeding habits and conservation status. *Zootaxa* **68**: 55–68.
- FORERO D. & WEIRAUCH C. 2012: Comparative genitalic morphology in the New World resin bugs Apiomerini (Hemiptera, Heteroptera, Reduviidae, Harpactorinae). *Mitteilungen aus dem Museum für Naturkunde in Berlin – Deutsche Entomologische Zeitschrift* **59**: 5–41.
- GIL-SANTANA H. R. 2009: Ghilianella beckeri sp. nov. of Emesinae from Brazil (Hemiptera, Reduviidae). *Revista Brasileira de Entomologia* **53**: 7–10.
- GIL-SANTANA H. R., COSTA L. A. & SILVA H. 2009: Nova espécie de Ghinallia Wygodzinsky, 1966 do estado do Espírito Santo, Brasil (Hemiptera, Heteroptera, Reduviidae, Emesinae). *Arquivos do Museu Nacional* **67**: 27–34.
- GOLOBOFF P. A. & CATALANO S. A. 2016: TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**: 221–238.
- GOLOBOFF P. A., FARRIS J. S., KÄLLERSJÖ M., OXELMAN B., RAMÍREZ M. J. & SZUMIK C. A. 2003: Improvements to resampling measures of group support. *Cladistics* **19**: 324–332.
- HUBER B. A. 2010: Mating positions and the evolution of asymmetric insect genitalia. *Genetica* **138**: 19–25.
- HUBER B. A., SINCLAIR B. J. & SCHMITT M. 2007: The evolution of asymmetric genitalia in spiders and insects. *Biological Reviews* **82**: 647–698.
- HWANG W. S. & WEIRAUCH C. 2012: Evolutionary history of assassin bugs (Insecta: Hemiptera: Reduviidae): insights from divergence dating and ancestral state reconstruction. *Plos One* **7**(9) (e45523): 1–12.
- ISHIKAWA T. 2000: Onychomesa gokani, a new emesine assassin bug (Insecta: Heteroptera: Reduviidae) from Japan. *Species Diversity* **5**: 375–379.
- ISHIKAWA T. 2002: A new species of the genus Schidium, with notes on the tribe Metapterini of Japan (Heteroptera, Reduviidae, Emesinae). *Japanese Journal of Systematic Entomology* **8**: 287–292.
- MADDISON W. & MADDISON D. 2011: *Mesquite: A modular system for evolutionary analysis, version 2.75*.
- MALDONADO CAPRILES J. 1960: Assassin bugs of the genus Ghilianella in the Americas (Hemiptera: Reduviidae: Emesinae). *Proceedings of the United States National Museum* **112**: 393–450.
- MALDONADO CAPRILES J. 1990: Systematic catalogue of the Reduviidae of the world (Insecta: Heteroptera). *Caribbean Journal of Science Special Edition*. University of Puerto Rico, Mayagüez, 694 pp.
- MALDONADO CAPRILES J. 1993: A new species of Ghilianella and the female of Ghinallia claviventris (Bergroth) (Heteroptera: Reduviidae: Emesinae). *Proceedings of the Entomological Society of Washington* **95**: 558–561.
- McATEE W. & MALLOCH J. 1925: Revision of the American bugs of the reduviid subfamily Ploiariinae. *Proceedings of the United States National Museum* **67**: 1–135.
- NIXON K. 2002: *WinClada ver. 1.00.08*.
- SAY T. 1828: *American entomology or Descriptions of the insects of North America. Illustrated by coloured figures from original drawings executed from nature. Part 3*. Philadelphia, Pennsylvania, plates 37–54.
- SAY T. 1832: *Descriptions of new species of heteropterous Hemiptera of North America*. New Harmony, Indiana, 39 pp.
- SCHILTHUIZEN M. 2013: Something gone awry: unsolved mysteries in the evolution of asymmetric animal genitalia. *Animal Biology* **63**: 1–20.
- SCHUHR T. & SLATER J. A. 1995: *True Bugs of the World (Hemiptera: Heteroptera). Classification and natural history*. Cornell University Press, Ithaca, London, 336 pp.

- SERENO P. 2007: Logical basis for morphological characters in phylogenetics. *Cladistics* **23**: 565–587.
- SONG H. & BUCHELI S. R. 2010: Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. *Cladistics* **26**: 23–35.
- SPINOLA M. 1850: *Tavola sinottica dei generi spettanti alla classe degli insetti artroidignati, Hemiptera, Linn. Latr. - Rhynchota, Fab.-Rhynchota.*, *Burm.* Camera, Modena, 138 pp. [Also published in *Memorie di Matematica e di Fisica delle Società Italiana delle Scienze* **25** [1852]: 43–178.]
- STÅLA. 1859: Till k annedomen om Reduvini. [To the knowledge about Reduvini]. * fversigt af Kongliga Vetenskaps-Akademiens F rhandlingar* **16**: 175–204 (in Swedish and Latin).
- ST L A. 1866: *Hemiptera Africana. Vol. III.* Norstedtiana, Holmiae, [1865], 200 pp.
- UHLER P. 1896: Summary of the Hemiptera of Japan, presented to the United States National Museum by Professor Mitzukuri. *Proceedings of the United States National Museum* **19**: 255–297.
- VARELA P. S. & MELO M. C. 2017: A new species of *Tagalis* St l, 1860 (Hemiptera, Reduviidae, Saicinae) from Argentina. *Proceedings of the Entomological Society of Washington* **119**: 122–129.
- WEIRAUCH C. 2004: Distribution of a sternal glandular area among female Reduviidae (Heteroptera) with a discussion of a possible pheromonal function. *Mitteilungen aus dem Museum fur Naturkunde in Berlin – Deutsche Entomologische Zeitschrift* **51**: 3–6.
- WEIRAUCH C. 2008: Cladistic analysis of Reduviidae (Heteroptera : Cimicomorpha) based on morphological characters. *Systematic Entomology* **33**: 229–274.
- WEIRAUCH C. & MUNRO J. B. 2009: Molecular phylogeny of the assassin bugs (Hemiptera: Reduviidae), based on mitochondrial and nuclear ribosomal genes. *Molecular Phylogenetics and Evolution* **53**: 287–299.
- WYGODZINSKY P. W. 1950: Sobre el g nero *Bergemesa* nov. (Emesinae, Reduviidae, Hemiptera). *Anales de la Sociedad Cientifica Argentina* **150**: 28–45.
- WYGODZINSKY P. W. 1954: Apuntes sobre Emesinae americanas (Reduviidae, Hemiptera). *Acta Zoologica Lilloana* **14**[1953]: 281–315.
- WYGODZINSKY P. W. 1956: Synopsis of the Australian Emesinae (Hemiptera: Reduviidae). *University of California Publications in Entomology* **11**(4): 193–246.
- WYGODZINSKY P. W. 1966: A monograph of the Emesinae (Reduviidae, Hemiptera). *Bulletin of the American Museum of Natural History* **133**: 1–614.

