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Phylogeny, evolution and male terminalia functionality of Sarcophaginae (Diptera: Sarcophagidae)

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The first comprehensive genus-level phylogeny of the subfamily Sarcophaginae is presented. A morphology-based phylogenetic analysis using parsimony is performed with 141 terminal taxa representing all 50 nominal genera of Sarcophaginae. In total, 222 morphological characters are coded, 150 of which are from the male terminalia. The homology of relevant male terminalia structures is assessed for the first time across the entire subfamily. Of 38 polyspecific genera represented by more than one species, the monophyly of 33 genera was recovered. This cladistic study found the genera *Lepidodexia*, *Retrocitomyia*, *Sarcodexiopsis* and *Titanogrypa* to be non-monophyletic as currently defined. Of nine monospecific genera, *Mecynocorpus* changes its status from monospecific to polyspecific with the discovery of a new species, *Promayoa* also becomes polyspecific with the transfer of one *Titanogrypa* species, and the remaining seven monospecific genera remain as such. Support was obtained for treating *Sarcodexia* as a subgenus of *Peckia*, and for treating *Helicobia* and *Lipoptilocnema* as valid genera rather than subgenera of *Sarcophaga*, and *Halliosca* as a valid genus rather than a subgenus of *Lepidodexia*. Morphological synapomorphies are discussed for all genera, including reviewed character interpretations of previous authors. We are here presenting a much more unifying interpretation of the Sarcophaginae acrophallus. New insights into the functional aspects of the sarcophagine phallus are presented. Our phylogeny shows the early lineages in Sarcophaginae as being mostly dung breeding, while lineages emerging later have more diverse life habits, including necrophagy and parasitism. Based on our phylogeny, 46 genera are recognized. The following nominal genus-group taxa are synonymized, with the junior synonym receiving a new status as subgenus under its respective senior synonym: under genus *Dexosarcophaga* Townsend, 1917 is subgenus *Cistudinomyia* Townsend, 1917, **syn. nov.** & **stat. nov.**; under *Lepidodexia* Brauer & Bergenstamm, 1891 is subgenus *Archimimus* Reinhard, 1952, **syn. nov.** & **stat. nov.**; under *Malacophagomyia* Lopes, 1966 is subgenus *Dodgeisca* Rohdendorf, 1971, **syn. nov.** & **stat. nov.**; under *Sarcofahrtiopsis* Hall, 1933 is subgenus *Pacatuba* Lopes, 1975, **syn. nov.** & **stat. nov.**; and under *Udamopyga* Hall, 1938 is subgenus *Carinoclypeus* Dodge, 1965, **syn. nov.** & **stat. nov.** One nominal taxon is raised from subgenus to valid genus: *Halliosca* Lopes, 1975, **stat. nov.** (from *Lepidodexia* Brauer & Bergenstamm, 1891). A morphological circumscription is provided for all the genera of Sarcophaginae.

ADDITIONAL KEYWORDS: flesh flies – homology – parsimony – phylogenetic analysis – morphology – acrophallus – male genitalia.

INTRODUCTION

The spectacular diversity of male terminalia of insects is as extravagant as that of more traditionally discussed sexually selected traits such as bird plumage or frog calls (Eberhard, 1993), and also plants can show exaggerated floral traits that may have evolved at least in part through sexual selection (Moore & Pannell, 2011). Insect male terminalia are complex in shape, and conspicuously divergent even among closely related species (Eberhard, 1985), and are for this reason often recognized as more useful for a precise species delimitation than any other source of morphological characters (Tuxen, 1970; Song & Bucheli, 2009). This is particularly true for flesh flies of the subfamily Sarcophaginae, where taxonomy, species recognition and delimitation of species have been largely

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based on character states of the male terminalia ever since these were discovered to be an exceptional source of highly diagnostic features by the French dipterist Louis Pandellé (1895, 1896) (Böttcher, 1912, 1913a, b, c, d; Aldrich, 1916; Rohdendorf, 1937, 1965; Dodge, 1965a, b; Lopes, 1984; Nandi, 1990; Lopes & Leite, 1991; Pape, 1994; Blackith, Blackith & Pape, 1998; Mello-Patiu, 2002; Whitmore, 2009; Carvalho-Filho & Esposito, 2012; Buenaventura & Pape, 2013; Mulieri & Mello-Patiu, 2013). As a consequence, the current classification of these dipterans finds most of the supportive character states in the male terminalia (Pape, 1996; Giroux, Pape & Wheeler, 2010; Whitmore, Pape & Cerretti, 2013; Buenaventura & Pape, 2015).

There is a widespread notion that male terminalia evolve faster than other body parts because character states under sexual selection pressures tend to show high evolutionary rates (Eberhard, 1985; Arnqvist, 1997; Hosken & Stockley, 2004; Ingram *et al.*, 2008; Puniamoorthy, Kotrba & Meier, 2010). Traits that evolve rapidly are said to have less phylogenetic inertia than slowly evolving traits (Morales, 2000). This has led to claims, such as sexually selected traits having a low phylogenetic inertia (Losos, 1999; Arnqvist & Rowe, 2002a, b); i.e. that a high amount of phenotypic dissimilarity may not be explained by the phylogeny, with a consequent decrease in the utility of these traits in systematics and comparative studies. This assertion, however, has been challenged by the remarkable number of studies that have found character states of insect male terminalia to contain significant phylogenetic signal (Couri & Pont, 2000; Skevington & Yeates, 2001; Soulier-Perkins, 2001; Winterton *et al.*, 2001; Daugeron & Grootaert, 2003; Savage, Wheeler & Wiegmann, 2004; Solodovnikov & Newton, 2005; Willmott & Lamas, 2006; Yoshizawa & Johnson, 2006). In studies on Sarcophaginae, the male terminalia usually provide the bulk of phylogenetic information (Roback, 1954; Lopes, 1984; Pape, 1992; Blackith *et al.*, 1998; Giroux *et al.*, 2010; Whitmore *et al.*, 2013; Buenaventura & Pape, 2015).

The male terminalia of Diptera are composed of six main elements, the homologues of which can be traced across most of the Insecta (Snodgrass, 1935; Sharov, 1966; Tuxen, 1970; Matsuda, 1976; McAlpine, 1981; Wood, 1991; Cumming & Wood, 2009). According to Wood (1991) and in agreement with the definitions of the revised epandrial hypothesis (Cumming & Wood, 2009), these elements are: (1) epandrium (tergite 9, which bears a pair of articulated lobes or surstyli in the Cyclorrhapha); (2) hypandrium (ST9); (3) pre- and postgonites (structures of uncertain homology found only in the Eremoneura); (4) aedeagus, generally bearing a basal sperm pump and a single external opening (phallotrema), and in most 'higher' Diptera indistinguishably fused to the parameral sheath (see element 5) to form the phallus; (5) paired, unsegmented parameres, flanking the aedeagus as posteriorly directed processes that in the Muscomorpha are fused over the aedeagus in a parameral sheath to form a modified composite intromittent organ or phallus (which in Cyclorrhapha is subdivided into a basi-, epi-, disti- and acrophallus); and (6) the proctiger or anal segment that bears the cerci flanking or surrounding the anus (Cumming & Wood, 2009; Sinclair, Brooks & Cumming, 2013). The morphological variation of these elements is used in diagnostic definitions of subfamilies and genera presented in the Catalogue of the Sarcophagidae of the World (Pape, 1996), which contains the most recent classification of the family, and which has been accepted and used by a large part of the community (Mello-Patiu & Pape, 2000; Mello-Patiu, 2002; Szpila & Pape, 2005; Pape & Mello-Patiu, 2006; Silva & Mello-Patiu, 2008; Giroux & Wheeler, 2009; Mello-Patiu, Soares & Silva, 2009; Mulieri, Mariluis & Patitucci, 2010; Richet, Blackith & Pape, 2011; Whitmore, 2011; Carvalho-Filho & Esposito, 2012; Buenaventura & Pape, 2013; Mulieri & Mello-Patiu, 2013; Whitmore *et al.*, 2013; Buenaventura, Whitmore & Pape, 2016). In Pape's (1996) diagnoses, the articulation of the surstyli to the epandrium seems to vary only at the subfamily level (surstyli fused to epandrium as one of the diagnostic character states for Paramacronychiinae). Within the Sarcophaginae, the variation in the shape and apical setosity of the surstyli, the hypandrium and the pregonites is used for defining at least one genus, the shape of the postgonites (parameres in Pape, 1996) takes part in the definition of three genera, while the form of the cerci is used for the definition of more than 10 genera. In addition, differences in the shape of the pregonites are used to define subgenera of *Blaesoxipha* Loew. With few exceptions (i.e. *Carinoclypeus* Dodge, *Helicobia* Coquillett, *Malacophagula* Bequaert and *Rafaelia* Townsend), all generic diagnoses contain at least one character state of the male terminalia, usually of the phallus. While the variation of the surstyli, epandrium, hypandrium, pregonites, postgonites and cerci is useful for the recognition of genera, the configuration of elements of the phallus provides diagnostic character states at both the generic and specific levels. The more simple structures of the male terminalia consisting in general of only one component, such as the surstyli, epandrium, hypandrium, pregonites, postgonites, seem to be diagnostic at higher hierarchical levels of classification in Sarcophaginae (i.e. subfamily, genus). In contrast, more complex structures of composite nature like the distiphallus, delimit genera and species due to their highly variable components. Variation of phallic configuration is species-specific, as shown by almost every thorough taxonomic work (e.g. Pandellé, 1896; Aldrich, 1916; Hall, 1933; Curran, 1934; Pape, 1994; Blackith *et al.*, 1998; Mello-Patiu, 2000; Pape & Mello-Patiu, 2006; Silva & Mello-Patiu, 2008; Whitmore, 2011; Carvalho-Filho & Esposito, 2012; Buenaventura & Pape, 2013; Mulieri & Mello-Patiu, 2013). Accordingly, in Sarcophaginae, as in other insects, male terminalia consist of different components evolving independently and at different rates, which make them an ideal source of characters for phylogenetic analyses, providing information for resolving different levels of the phylogenetic hierarchy (Song & Bucheli, 2009). Although the male terminalia in Sarcophaginae, by their complexity and structural detail, would appear to be very suitable for phylogenetic studies, there are few published trees, and the phylogenetic relationships within this insect radiation are still poorly understood.

Roback (1954) made an admirably ambitious (pre-Hennigian) attempt to disentangle the evolutionary relationships of the Sarcophaginae at the generic level. In spite of its methodological constraints, Roback's work has been extensively cited, but surprisingly few studies have challenged his evolutionary scenarios. Only eight phylogenetic studies include several genera of Sarcophaginae (Lopes, 1984; Sugiyama & Kano, 1984; Pape, 1994; Giroux *et al.*, 2010; Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura & Pape, 2015), five of which include morphological data. Other phylogenetic studies that include sarcophagines are focused on relationships at the infra-generic level, mainly in the mega-diverse genus *Sarcophaga* Meigen (Kurahashi & Kano, 1984; Blackith *et al.*, 1998; Song, Wang & Liang, 2008; Giroux & Wheeler, 2009, 2010; Meiklejohn *et al.*, 2013b; Whitmore *et al.*, 2013; Zhang *et al.*, 2013; Buenaventura & Pape, 2017) and the mainly New World genus *Ravinia* Robineau-Desvoidy (Wong *et al.*, 2015). A third group of studies that include a large sample of sarcophagine species, and where a tree is presented, are studies with a forensic approach that aim to provide a tool to reliably identify specimens by their fit in molecular phylogenies (Wells, Pape & Sperling, 2001; Tan *et al.*, 2010; Meiklejohn, Wallman & Dowton, 2011; Meiklejohn *et al.*, 2012; Meiklejohn, Wallman & Dowton, 2013a; Jordaens *et al.*, 2013; Zhang & Zhang, 2013), but which cannot be considered as rigorous phylogenetic hypotheses in their own right.

With almost 90% of the phylogenetic studies still fresh since their publication, the large number of markers (mostly molecular) and the use of modern algorithms for assessing their phylogenetic signal, it may appear that modern Sarcophaginae systematics is experiencing rapid progress. However, most of the relationships presented in these phylogenies are not comparable to each other due to differences in taxon sampling. The available topologies either are focused on a single (sub)genus (Pape, 1994; Giroux & Wheeler, 2009; Meiklejohn *et al.*, 2013b; Whitmore *et al.*, 2013; Buenaventura & Pape, 2017), or include sets of genera not particularly compatible for comparisons (Giroux *et al.*, 2010; Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014). In addition, published hypotheses are weakly supported in their deep nodes and therefore highly unstable, and newer topologies are often radically different despite sharing some taxa, and even when using similar molecular markers. One example of the various conflicting results of these trees is the controversial monophyly and phylogenetic position of the genus *Tricharaea* Thomson. One molecular-based analysis indicates this genus to be monophyletic (Piwczyński *et al.*, 2014), while another study recovers *Tricharaea* as polyphyletic (Kutty *et al.*, 2010). Two analyses, one using morphology (Giroux *et al.*, 2010) and another using molecules (Piwczyński *et al.*, 2014), recover this genus in a basal position within the Sarcophaginae, while another two molecular-based analyses reject this hypothesis by recovering species of *Tricharaea* either as two separate non-basal clades (Kutty *et al.*, 2010) or as sister to the clade composed of *Boettcheria* Parker and *Tripanurga* Brauer & Bergenstamm (Stamper *et al.*, 2012), but not as part of a basal divergence within the subfamily. Another example is the generally accepted and morphologically well-supported sister-group relationship of the genera *Oxysarcodexia* Townsend and *Ravinia* (Lopes, 1983; Pape, 1994), which is confirmed by Giroux *et al.* (2010) and Stamper *et al.* (2012) but contradicted by Kutty *et al.* (2010) and Piwczyński *et al.* (2014). The list of conflicting relationships among these phylogenies can be extended with the unresolved position of the genera *Blaesoxipha*, *Helicobia* and *Titanogrypa* Townsend, among others. Despite the mentioned conflicts, the phylogenetic position and monophyly of some other genera have been consistently supported in these studies. For example, the monophyly of the genera *Oxysarcodexia*, *Ravinia*, *Helicobia* and *Sarcophaga* is supported in at least three of the five Sarcophaginae topologies published (Pape, 1994; Giroux *et al.*, 2010; Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura *et al.*, 2016; Buenaventura & Pape, 2017). Also, in the large majority of molecular analyses, the monophyletic (Stamper *et al.*, 2012) or paraphyletic (Kutty *et al.*, 2010; Piwczyński *et al.*, 2014) genus *Peckia* Robineau-Desvoidy is found to be the sister group of the large genus *Sarcophaga* or closely related to it (Buenaventura & Pape, 2015, 2017). The sampling of Sarcophaginae species for phylogenetic analyses has encompassed fewer than half of the genera of this subfamily so far, and any of the currently hypothesized phylogenetic relationships could be compromised with the inclusion of any or all of the remaining recognized genera. Thus, very few of these recent studies actually provide rigorous tests of the more than 60-year-old pre-Hennigian system of Roback (1954), nor do they broadly corroborate, improve or refute the most recent classification of Pape (1996), which has become the dominant foundation for taxonomic revisions, regional catalogues and checklists (Mello-Patiu, 2002; Mello-Patiu *et al.*, 2009; Whitmore, 2009; Richet *et al.*, 2011; Ramírez-Mora *et al.*, 2012; Buenaventura & Pape, 2013; Mulieri & Mello-Patiu, 2013). Either the pre-Hennigian hypothesis of Roback (1954) and the classification of Pape (1996) are robust, stable and well supported, or the new hypotheses are not decisive enough to firmly support or reject the current classification of Sarcophaginae.

Although there has been an important increase in the amount of available morphological data to be analysed with modern methods, such data become characters only from being 'interpreted', i.e. put into a conceptual context of homology (Mooi & Gill, 2010). Thus, to improve the phylogeny of the Sarcophaginae, an alternative solution is to go back to the data and re-examine homology hypotheses of the already well-known informative characters of the male terminalia, analyse the revised character states using modern phylogenetic methods and use the resulting synapomorphies to reassess and re-diagnose all the genera.

This study explores the evolution and diversification of flesh flies of the largest subfamily, the Sarcophaginae, which includes about 2000 species. The subfamily appears to have its early evolution in the Neotropical Region (Pape, 1994, 1996; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura *et al.*, 2016), with species of a few genera (*Boettcheria*, *Emblemasoma* Aldrich, *Fletcherimyia* Townsend, *Helicobia*, *Microcerella* Macquart, *Oxysarcodexia*, *Spirobolomyia* Townsend, *Titanogrypa* and *Tripanurga*) spreading to the warmer southern parts of the boreal latitudes of the northern Nearctic Region, and with *Blaesoxipha*, *Ravinia* and *Sarcophaga* as the major sarcophagine lineages reaching the cooler northern boreal latitudes. These three lineages are probably also the only non-introduced sarcophagine lineages occurring in the Old World, whose dispersal into the Palaearctic Region is hypothesized to have occurred via a Beringian land bridge (Pape, 1996; Buenaventura & Pape, 2017). In today's scenario of the diversity of sarcophagines, the relatively older and morphologically more diverse lineages are found in the Neotropics, while the relatively younger and morphologically more homogenous lineages are found in the Old World. Sarcophagidae flies of New and Old World lineages were catalogued by Pape (1996), who proposed a generic classification of the Sarcophaginae. As outlined above, however, the monophyly and phylogenetic relationships of Pape's (1996) generic concepts have not been properly tested and understood. Consequently, the present study aims at analysing the phylogenetic relationships within the entire Sarcophaginae using morphological features, especially those of the male terminalia. By reassessing especially the complex structures of the distiphallus, this analysis will provide new insight into the evolution of terminalia structures in one of the largest radiations of calyptrate flies, as well as provide more rigorous morphological definitions for all genera in this subfamily.

MATERIAL AND METHODS

Specimen repositories

The studied specimens are housed in the following institutions (see details in Supporting Information, Table S1): Entomology Department, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA; Instituto Alexander von Humboldt, Villa de Leyva, Colombia; Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogota, Colombia; Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; Museo Entomologico Francisco Luis Gallego, Universidad Nacional de Colombia, Medellin, Colombia; Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; National Museum of Natural History, Washington, DC, USA; Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden; Tecnologico de Antioquia, Institucion Universitaria, Medellin, Colombia; and Instituto de Biologia, Universidad de Antioquia, Medellin, Colombia.

Specimen preparation and documentation

When male terminalia were found to be already dissected and glued to a small piece of card below the pinned specimen, the whole piece of card was placed in distilled water to separate the terminalia. Non-dissected males with their terminalia pulled out but still attached to the abdomen had the terminalia cut-off with a pair of iridectomy scissors, whereas non-dissected males with their terminalia still retracted within the abdomen had their entire abdomen carefully broken off by means of a gentle push from below with fine forceps. Soft tissues of the terminalia (with or without the remaining abdomen) were digested with hot 10% lactic acid for about 5 min, after which the terminalia were transferred to glycerine, where the phallus, pregonites and postgonites were separated from the remaining terminalia. All structures were rinsed twice in distilled water, once in 70% ethanol, once in 96% ethanol, placed in 20% acetic acid for 5–8 min and washed again in 70% ethanol. Once dried, the male abdomen without the terminalia was glued to a piece of card below the pinned specimen. The terminalia were examined using a Leica M205C stereomicroscope and subsequently stored in glycerine in a plastic microvial pinned below the source specimen.

Digital images were taken using a Leica MZ16A stereomicroscope equipped with a Leica DFC450C system camera. Photos were generated using the Automontage Leica Application Suite software and stacked in Zerene Stacker 1.04 (Zerene Systems LLC, 2014). Procedures for preparation and production of SEM (scanning electronic microscopy) images follow Buenaventura & Pape (2013), where the male terminalia structures were dehydrated in 96% ethanol, air-dried, mounted on adhesive electrical tape attached to aluminium stubs, coated with platinum/palladium and studied in a JEOL JSM-6335 F scanning electron microscope housed in the Natural History Museum of Denmark. Part of the SEM images were kindly provided by M. Giroux as indicated in the relevant captions, and produced as given by Giroux *et al.* (2010). All illustrations were edited using Adobe Photoshop CS6 and assembled in plates with Indesign CS6 and Adobe Illustrator CS6. Illustrations of the hind trochanter in posterior view and phallus in lateral view were prepared by tracing and vectorizing relevant structures on photographs using Adobe Illustrator CS6.

Nomenclature and terminology

Classification, names and authorship for species and genera/subgenera follow Pape (1996). The terminology of structures, except the male terminalia, follows McAlpine (1981). For male terminalia structures, we follow the revised epandrial hypothesis of Cumming & Wood (2009) with the updated interpretations of homology and definitions of Giroux *et al.* (2010) and Sinclair *et al.* (2013). We also use some specific terms proposed and/or redefined by Whitmore *et al.* (2013) (i.e. membrane, hypophallus, paraphallus and paraphallic window), Buenaventura & Pape (2015) (capitis, median process here as median stylus) and Mulieri (2017) (median juxtal sclerite, juxtal lobe). We revise and provide new and updated interpretations of homology for the acrophallus (i.e. lateral styli, median stylus, capitis and hillae), harpes, juxta, phallotrema, stylar lateral plates, stylar membranous lobes and vesica, and we propose definitions for the acrophallic levers, paraphallic proximal expansions, paraphallic blinkers, paraphallic lateral expansions, paraphallic apical expansions, vesical lateral arms, distal section of the vesica and vesical arm-shaped lever; these are outlined in the Results. The revised homologies of phallic structures are presented in a sequence from base to apex of the phallus. For simplicity, the term 'expansion' is used to refer to extensions of the ventral margin of the paraphallus lacking a desclerotized strip or a hinge separating them from the paraphallus. Plates, lobes and blinkers possess a desclerotized strip separating them from the paraphallus or the structure from which they arise.

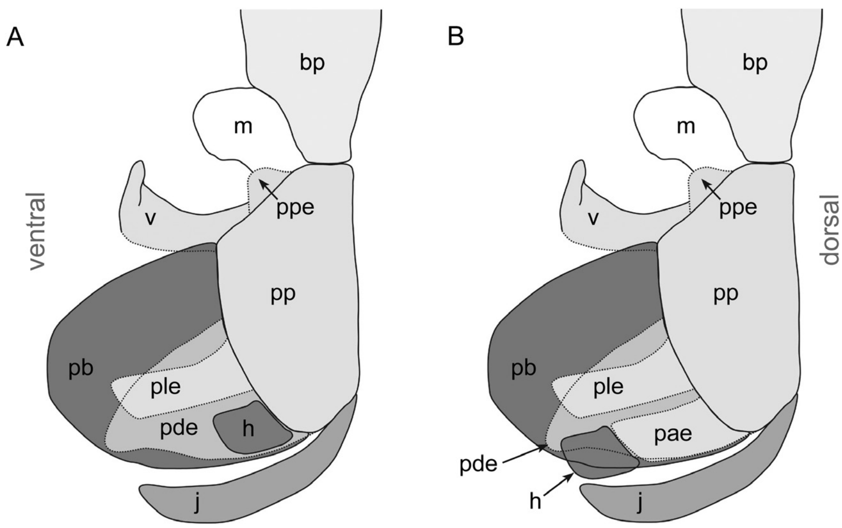

Figure 1. Paraphallic homologies. A, paraphallus without paraphallic apical expansion (pae). B, paraphallus modified, bearing paraphallic apical expansion (pae), harpes slightly displaced ventrally. Dashed lines for expansions and continuous lines for structures separated from the paraphallic wall by a desclerotized strip. Abbreviations as in Table 1.

The ventral and dorsal directions are labelled in the figure of paraphallic homologies (Fig. 1). For clarity, the dorsal side of the phallus is a continuation of the dorsal side of the body, corresponding to the tergites, while the ventral side of the phallus is opposite to this.

The abbreviations used for morphological structures in the text and figures are given in Table 1.

Taxa

The ingroup consisted of 138 sarcophagine species (Supporting Information, Table S1) representing all 51 genera assigned to this subfamily by Pape (1996), except that we treat *Lipoptilocnema* Townsend as a valid genus rather than a subgenus of *Sarcophaga* following Mulieri, Mello-Patiu & Aballay (2016) and Zhang *et al.* (2016); *Sarcodexia* Townsend as a subgenus of *Peckia* as proposed by Buenaventura & Pape (2013); and *Wulpisca* Lopes as a junior synonym of *Panava* Dodge as proposed by Carvalho-Filho & Esposito (2011). This gives a total of 50 nominal genera included here. Of these, 10 – *Austrophyto* Lopes, *Carinoclypeus*, *Cistudinomyia* Townsend, *Dodgeisca* Rohdendorf, *Duckemyia* Kano & Lopes, *Mecynocorpus* Roback, *Pacatuba* Lopes, *Promayoa* Dodge, *Rettenmeyerina* Dodge and *Sarothromyiops* Townsend – were monospecific taxa according to Pape (1996). However, since two new species were described for *Austrophyto* by Mulieri (2017), one new species is discovered for *Mecynocorpus* and one *Titanogrypa* species is transferred to *Promayoa* during the present study, these three genera are no longer monospecific.

Representative species of each genus were selected using the following three criteria: (1) maximum possible coverage of the range of distribution, (2) inclusion of as many infra-generic groupings, like subgenera or species groups, as possible, and (3) any a priori suspicion of misplacement with regard to the current classification.

As the monophyly of Sarcophaginae appears to be exceedingly well corroborated and the Paramacronychiinae have been hypothesized as their sister group (Pape, 1992, 1998a; Giroux *et al.*, 2010; Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014), testing and corroborating this was not

Table 1. Abbreviations for morphological structures

ah	apical process of distal part of harpes	**nt**	notopleural setae
al	acrophallic lever	**pae**	paraphallic apical expansion
as	anepimeral setosity	**pb**	paraphallic blinker
bjh	basal juxal horn	**pc**	proclinate fronto-orbital setae
bp	basiphallus	**pde**	paraphallic distal expansion
ca	capitis	**pg**	pregonite
dh	distal part of harpes	**ph**	proximal part of harpes
djh	distal juxtal horn	**ple**	paraphallic lateral expansion
dp	distiphallus	**pp**	paraphallus
ed	ejaculatory duct	**ppe**	paraphallic proximal expansion
ep	epiphallus	**pte**	paraphallic triangular expansion
epd	epandrium	**pw**	paraphallic window
h	harpes	**rh**	point of rotation of distal part of harpes
hh	hinge between proximal and distal part of harpes	**sa**	sclerotized area of paraphallic blinker
hi	hillae	**slp**	stylar lateral plate
hib	hillae with membranous bladder	**sml**	stylar membranous lobe
hig	hillae with groove	**sr**	surstylus
hn	hinge between basiphallus and distiphallus	**ST**	abdominal sternite
ho	hinge between paraphallic wall and harpes	**syn**	syntergosternite 7 + 8
hp	hypophallus	**T**	abdominal tergite
j	juxta	**ts**	tube-shaped structure of paraphallic blinker
jce	juxtal convex membranous expansion	**v**	vesica
jd	juxtal demarcation	**vb**	ventro-medial bridge
jl	juxtal lobe	**vbs**	vesical proximal, bilobed and microserrated section
jlp	juxtal lateral plate	**vd**	distal section of the vesica
ls	lateral stylus	**vdl**	vesical denticulated lobe
m	membrane	**vdp**	vesical denticulated process
mjs	medial juxtal sclerite	**vl**	vesical arm-shaped lever
ms	median stylus	**vla**	vesical lateral arm

an aim of this study. The outgroup was therefore composed of only three species representing the two other subfamilies of Sarcophagidae: *Macronychia aurata* Coquillett, 1902 from the Miltogramminae, and *Brachicoma devia* (Fallén, 1820) and *Wohlfahrtia indigens* Villeneuve, 1928 from the Paramacronychiinae. Trees were rooted at *M. aurata*.

Character matrix

Species of Sarcophaginae have for the large majority been described based only on males, since the male terminalia traits are those most commonly used for identification and species delimitation (Pape & Mello-Patiu, 2006; Giroux & Wheeler, 2009; Mulieri & Mariluis, 2011; Buenaventura & Pape, 2013; Mulieri, 2017), and for the study of phylogenetic relationships (Roback, 1954; Pape, 1994, 1998a; Blackith *et al.*, 1998; Giroux *et al.*, 2010; Whitmore *et al.*, 2013). Females and larvae are mostly unknown, although at least the former are identifiable at the genus level based on scattered morphological data in various papers (Pape & Dahlem, 2010 in particular), and with a noteworthy exception in the genus *Blaesoxipha*, where females have a highly species-specific ovi-larvipositor (Léonide & Léonide, 1986; Pape, 1994). There are revisionary works including illustrations and descriptions that provide information on females (Lopes, 1941a, 1975a; Dodge, 1961, 1965b, 1966, 1967; Tibana & Mello-Patiu, 1985a, b; Mello-Patiu & dos Santos, 2001; Dahlem & Naczi, 2006; Giroux & Wheeler, 2009; Whitmore, 2009; Richet *et al.*, 2011; Carvalho-Filho & Esposito, 2012; Mulieri *et al.*, 2015) and larvae (Lopes, 1943, 1958, 1968, 1983; Kano & Shinonaga, 1969; Ferrar, 1979; Jirón & Bolaños, 1986; Léonide & Léonide, 1986; Lopes & Leite, 1986; Leite & Lopes, 1987; Szpila & Pape, 2005; Pérez-Moreno, Marcos-García & Rojo, 2006; Augul, 2008; Buenaventura, 2013; Mendonça *et al.*, 2013; Szpila, Richet & Pape, 2015). Some of the available information on female and larvae is restricted to species of particular regions (Aspoas, 1991; Richet *et al.*, 2011; Szpila *et al.*, 2015). The large gaps in our knowledge of females and larvae are due partly to the unknown breeding substrates of many sarcophagine flies that would be needed to collect the immature stages, partly to the more subtle characters and more elaborate processing involved in studying both females and larvae; but certainly also to the immensity of the task of studying the morphologically and biologically diverse Neotropical fauna.

In order to test the monophyly, validity and circumscription of the genera of the subfamily Sarcophaginae, and to infer their phylogenetic relationships, we built a matrix (Supporting Information, Table S2) of 222 morphological characters using the software Mesquite ver. 2.75 (Maddison & Maddison, 2011). The characters were drawn exclusively from the adult male morphology because of the sparse morphological information available on females and larvae across the sarcophagine genera. Of the total characters, 168 are binary, 54 multistate. Characters were chosen from the different regions of the adult male as follows: 23 characters were selected from the head, 43 from the thorax (including legs and wings), 6 from the abdomen (excluding the terminalia) and 150 from the terminalia (Supporting Information, File S1).

Phylogenetic analysis

Parsimony analyses were carried out in the computer program TNT ver. 1.1 (Goloboff, Farris & Nixon, 2008) using equal weights. Tree searches were conducted with the New Technology search option (level 50, initial addseqs = 9, find minimum tree length 20 times, default values for Drift, Ratchet, Sectorial search and Tree fusing), saving the most parsimonious trees (MPTs), and performing an additional run with the tree-bisection reconnection (TBR) swapping algorithm based on the trees found in the previous step, and extending this search until the maximum number of shortest trees was reached, using maximum length = 0 as the collapsing rule (collapsing rule 3 in TNT) during and after the tree search with a maximum of 10 000 trees in memory. The 52 multistate characters were treated as non-additive (Fitch, 1971). MPTs were summarized in a strict consensus tree. Absolute Bremer support (aBS), jackknife (JK) values, retention index (RI) and consistency index (CI) were calculated with TNT. For aBS values (Bremer, 1994), a rough precedent search was made setting suboptimal length to 20 extra steps to find the upper limit of supports based on 30 000 suboptimal trees. JK values were calculated from 1000 JK replicates (same search options as above) with 36.8% character deletion as recommended by Farris *et al.* (1996).

Nodes are numbered from the root to the tips in the consensus tree (Fig. 2). JK values for branches are presented as 'strong' for values > 80, 'moderate' for values 70–79 and 'weak' for values 50–69. Clades with JK values < 50 or with no aBS are considered as not supported.

Some groups of genera are named as 'grades' when they form paraphyletic assemblages on the phylogenetic tree, and 'clades' when they form monophyletic groups (Fig. 2A, B). Only character states shared by genera belonging to monophyletic groups or 'clades' are explicitly presented as synapomorphies or autapomorphies, depending on each case. The use of 'grades' and 'clades' eases the description and discussion of our results, but these groupings do not constitute a new classification. Nomenclatural changes supported by our phylogenetic analysis are highlighted and explicitly presented as such.

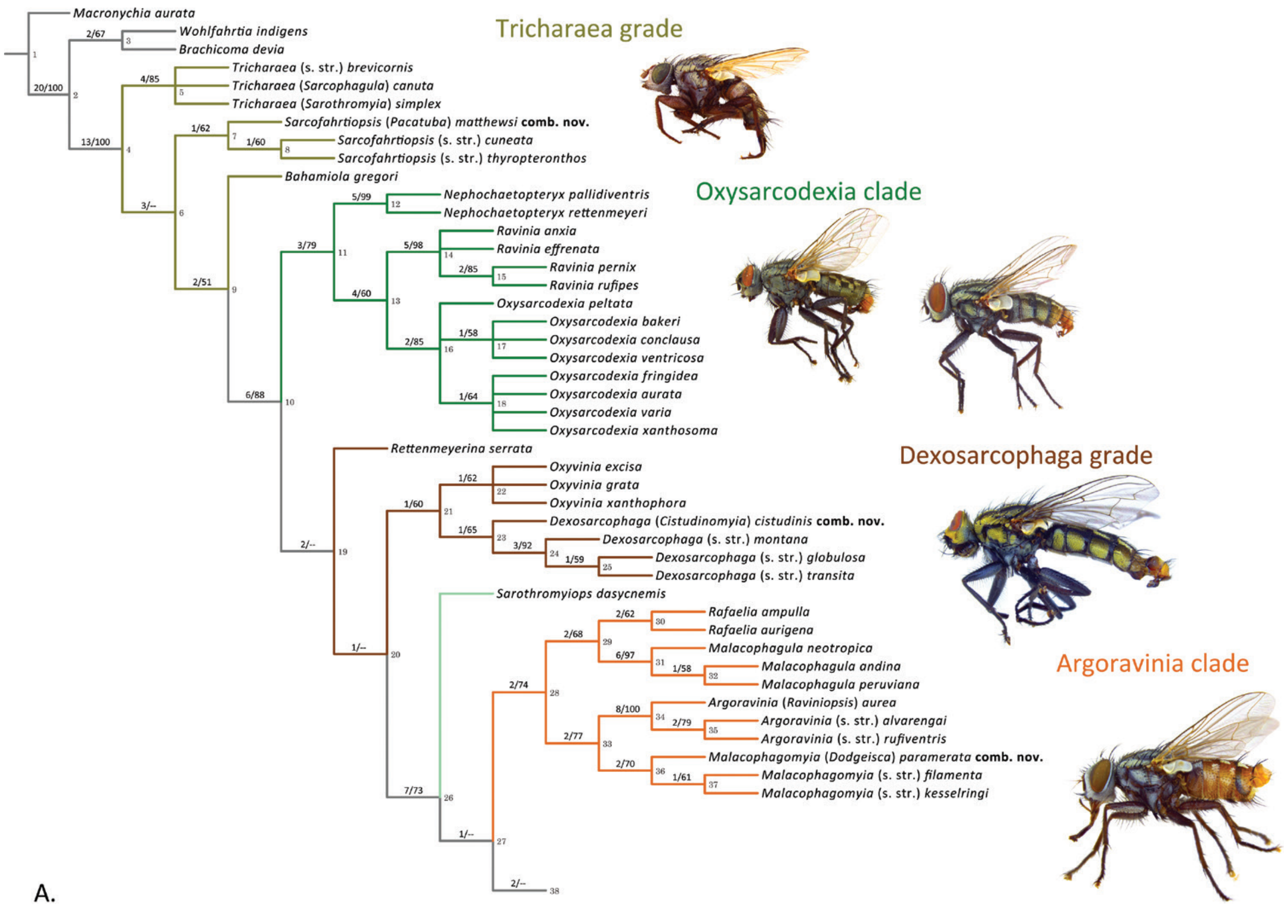

Figure 2. Strict consensus tree of 64 most parsimonious trees (L = 524, CI = 0.59, RI = 0.90); values in front of nodes are clade numbers and values on branches are left = absolute Bremer support, and right = jackknife support. A, Branches 1–38; B, Branches 38–113.

Character state history reconstruction

The parsimony package in Mesquite was used to calculate the most parsimonious states at the nodes of the tree assuming one step per state change, all characters unordered (Fitch parsimony), and polytomies treated as 'soft polytomies'. Character states were optimized on the strict consensus tree.

Generic circumscriptions

New and updated generic diagnoses are presented for all genera of Sarcophaginae, which are partially based on synapomorphies and autapomorphies reconstructed from our favoured phylogenetic tree. These new generic circumscriptions also include a new interpretation of some of the character states used by other authors for generic definitions, and particularly by Pape (1996). Character states given in Pape's (1996) and other authors' generic diagnoses that are generally present in genera of Sarcophaginae and therefore carry no diagnostic information in the present context were not included. Larval and female character states listed by Pape (1996) are included. Character states found to be autapomorphic in our study are highlighted with an asterisk (*).

RESULTS

Phylogeny

A hypothesis suggesting the phylogenetic relationships for all currently recognized genera in the Sarcophaginae is presented for the first time (Fig. 2). Of 38 polyspecific genera represented by more than one species, monophyly is recovered for 33 genera. The remaining genera are *Lepidodexia* Brauer & Bergenstamm, *Retrocitomyia* Lopes, *Sarcodexiopsis* Townsend and *Titanogrypa*, which emerge as paraphyletic in our analysis, and the possibly non-monophyletic *Blaesoxipha*, depending on the resolution of *Mecynocorpus* in the basal trichotomy. The polyspecific genera *Austrophyto*, *Bahamiola* Dodge and *Tulaeopoda* Townsend are represented by only one

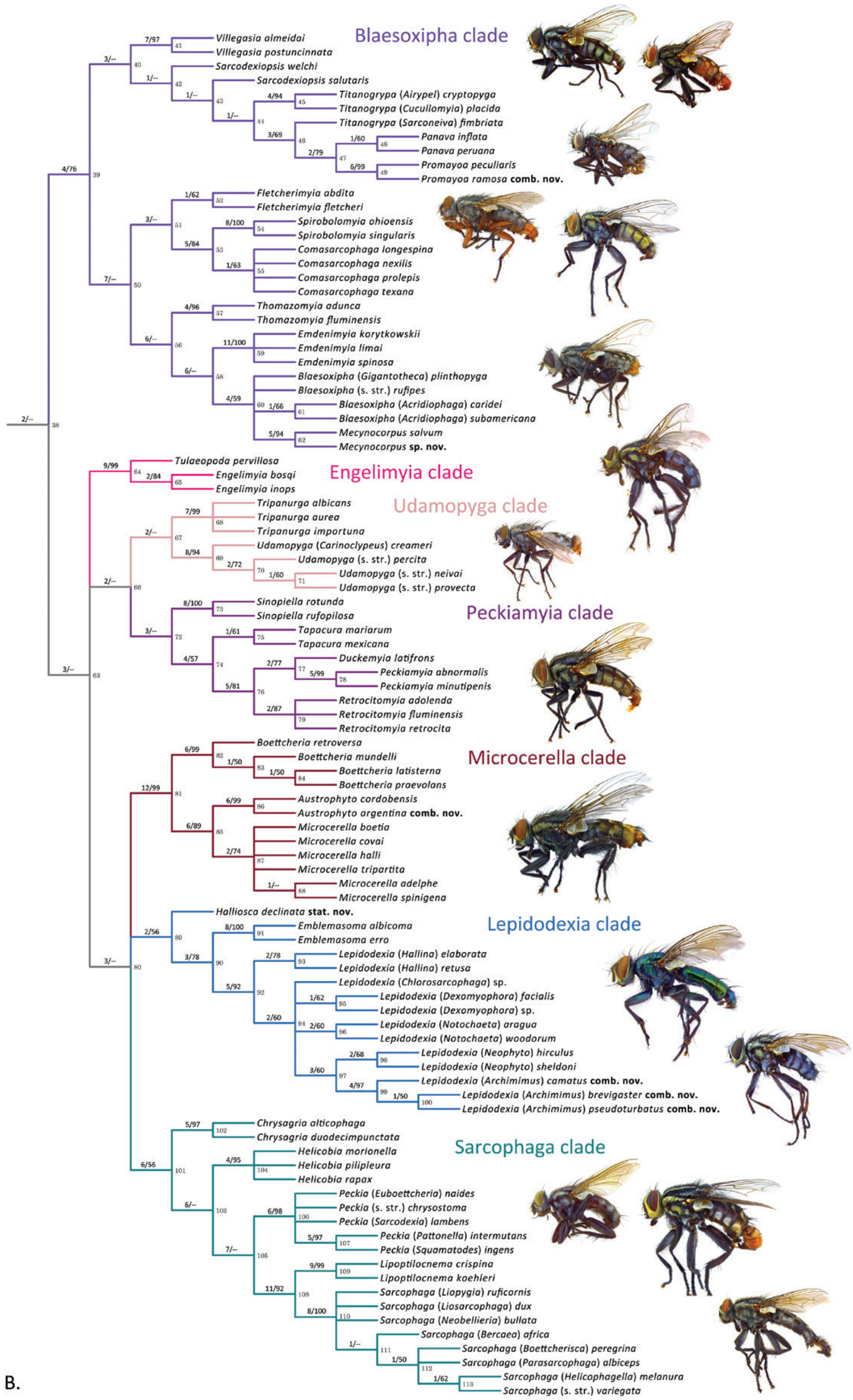

Figure 2. *Continued*

species each, but while the phylogenetic position of *Bahamiola* and *Tulaeopoda* does not compromise the monophyly of any other genus, the species of *Austrophyto* emerges as sister to a species of *Retrocitomyia*. Some polyspecific genera emerging as monophyletic are nested inside other genera, these are: *Archimimus* Reinhard nested inside *Lepidodexia*, and *Panava* nested inside *Titanogrypa*. Of the nine monospecific genera, the discovery in this study of a new species of *Mecynocorpus* changes the status of this genus from monospecific to polyspecific; the type species of *Promayoa* emerges as sister to *Promayoa ramosa* (Méndez, Mello-Patiu & Pape, 2008) [listed as subgenerically unplaced within *Titanogrypa* by Méndez *et al.* (2008)] inside the paraphyletic genus *Titanogrypa*. Each of the remaining seven monospecific genera emerge as sister taxon of another genus in our analysis, meaning that their phylogenetic position does not cause any other genus to become paraphyletic. Based on branch supports as well as availability of synapomorphies, we here recognize 46 out of the 51 sarcophagine genera of Pape's (1996) classification and, consequently, six generic synonyms are proposed as new [the seventh already proposed by Buenaventura & Pape (2013)], with six of the taxa given new status as subgenus. As a consequence of these generic synonymies, we propose 12 new combinations. One taxon is raised from subgenus to valid genus, and a single species-group taxon is synonymized. These nomenclatural acts are all properly argued for in the relevant phylogenetic context, and a summary is given in Supporting Information (File S2).

New Technology searches in TNT generated 57 trees (length = 524, CI = 0.60, RI = 0.91). A broadening of the search using TBR as swapping algorithm on the trees saved in RAM in the previous step increased the number of MPTs to 64. The results of this search are presented in a consensus tree (length = 528, CI = 0.59, RI = 0.90; see Fig. 2). An examination of the set of MPTs in order to identify conflicting nodes revealed the following: the Microcerella clade (clade 81, clade numbering as in Fig. 2) emerging either as sister to the Lepidodexia clade (clade 89) or to the Sarcophaga clade (clade 101); the Engelimyia clade (clade 64) emerging either as sister to clade 66 or to clade 80; the subgenus *Lepidodexia* (*Chlorosarcophaga*) Townsend in two alternative topologies within clade 94; and the species of *Blaesoxipha*, *Comasarcophaga* Hall, *Microcerella*, *Peckia* and *Sarcophaga* arranged into two or three alternative topologies within their respective genera.

The support values are given on the strict consensus tree (Fig. 2). All polyspecific genera represented by more than one species that were recovered as monophyletic received JK support above 50, and most of them showed moderate to strong JK values.

Revised terminalia homologies and evolution of male terminalia structures in the Sarcophaginae

Among the recent achievements in the study of terminalia homologies of flesh flies, it is worth mentioning the phylogenetic study by Giroux *et al.* (2010), which corroborated several genus-level relationships that had been proposed in the literature but not tested in a cladistic context before. A very important contribution of this study is the revision of the terminological framework used by previous researchers for the male terminalia, which produced a set of updated definitions and new interpretations of the homology of several acrophallic structures. Based on examination and homologization of structures from 19 genera, corresponding to almost 40% of the genera currently assigned to the subfamily Sarcophaginae in Pape's (1996) classification, Giroux *et al.* (2010) redefined the juxta, vesica, harpes, phallic tube, median stylus (i.e. median stylus + capitis) and hillae. Recently, Buenaventura & Pape (2015) also proposed redefinitions for the capitis, median process (= median stylus), harpes and juxta, and described the paraphallic lateral plates, stylar lateral plates and stylar membranous lobes based on a phylogenetic study that included 11 genera, i.e. 23% of the genera of Sarcophaginae, some of which were not included in Giroux *et al.*'s (2010) study. In the present study, the examination and comparison of the male terminalia structures from 100% of the genera currently recognized in this subfamily allowed for additional precision regarding some of the definitions by Giroux *et al.* (2010), and to some extent also Buenaventura & Pape (2015). In the following paragraphs, we present detailed definitions of the acrophallus (lateral styli, median stylus, capitis and hillae), harpes, juxta, phallotrema, stylar lateral plates, stylar membranous lobes and vesica, and for the first time we define and describe structures here termed acrophallic levers, paraphallic proximal expansions, paraphallic blinkers, paraphallic lateral expansions, paraphallic apical expansions and the vesical sections including arm-shaped lever, distal section and vesical lateral arms.

Phallotrema and acrophallus

The phallotrema is the secondary gonopore at the apex of the phallus, as opposed to the primary gonopore at the end of the ejaculatory duct from the sperm pump (Hennig, 1973; Ulrich, 1974; Sinclair, 2000). The phallotrema is a single opening in the Diptera groundplan (Wood, 1991), but a division into three openings has evolved independently several times, e.g. in Cylindrotomidae, Blephariceridae, Tanyderidae, Asilinae, some Rhinophoridae, some Tachinidae (Andersen, 1988; Wood, 1991; Dikow, 2009; Cerretti, Lo Giudice & Pape, 2014) and in the subfamily Sarcophaginae (Pape, 1989a). In calyptrates, the phallotrema is the opening of the acrophallus, which particularly in the Oestroidea is often clothed in small denticles (Sinclair, 2000). Thus, the three openings and the microserrations or small denticles are useful for recognizing the phallotrema in the Sarcophaginae (Giroux *et al.*, 2010). The tripartite condition of the phallotrema in this subfamily has originated by a folding of the acrophallic rim (red line in Fig. 3A–D) (Buenaventura & Pape, 2015). This folding results in three exits at the end of semi-tubular structures referred to as styli, which together constitute the acrophallus. The present updated definition considers the acrophallus as subdivided into two lateral styli, a median stylus ('ms' in Figs 3–8, 9A–D) arising from the postero-medial edge of the acrophallic rim (the styli are probably exits for sperm and/or accessory secretion), a paired capitis ('ca' Figs 3–8, 9A–D, 10A, E) deriving from latero-medial expansions of the dorsal acrophallic rim, which therefore are flanking the median stylus when this is present (Buenaventura & Pape, 2015), and a pair of hillae arising from the lateral expansions of the dorsal acrophallic rim, each of which therefore are flanking the lateral part of each lateral stylus ('hi' in Figs 4D, H, 5C, D, F). The main consequence of the present updated definition is that the acrophallic structures, i.e. the lateral styli, median stylus, capitis and hillae, are defined as fully independent of each other. Usually, the folding of the acrophallic rim gives origin to both the median stylus and the lateral styli, which may be semi-tubular or almost completely closed tubular structures (e.g. Fig. 3A–C), but in some groups (some *Chrysagria* Townsend, *Lipoptilocnema* and *Peckia*) the acrophallic rim is only slightly folded postero-medially, and it therefore does not form a conducting semi-tubular median structure. It should be noticed that we have reconsidered our interpretation of the juxta and median stylus for species of *Lipoptilocnema* as presented in a recent study (Buenaventura & Pape, 2015) and we have converged with the homologies as presented for these structures by Mulieri *et al.* (2016) in their taxonomic revision of this genus. Thus, the acrophallic rim as slightly folded postero-medially and not forming a conducting median structure is best interpreted as a reduction of the median stylus (Fig. 3D) in light of the present analysis. However, a reduction of the median stylus does not imply a reduction of the capitis (see Figs 3D, E, 11C), as this pair of processes can be present without a median stylus in some groups (*Helicobia* and *Sarcophaga*). The hillae, however, have only been observed when the lateral styli are present. The lateral styli are extremely variable, from straight to coiled, from short and stubby to long and filiform, and from narrow-tipped to trumpet-like flaring ('ls' in Figs 3A–F, 11B, 12H, 13A, B), and they may even be asymmetrical and deviate markedly from the ancestral semi-tubular shape.

Roback (1954) defined the hillae as 'well-sclerotized dorsal [latero-proximal] projections of the lateral arms [styli]', and as being present only in the genus *Ravinia*. This term was revised and redefined by Giroux *et al.* (2010), although the hillae *sensu* Roback (1954) had been accepted and used by other authors (Povolný & Verves, 1997; Pape, 1998b; Verves, 2000; Guimarães, 2004; Carvalho & Mello-Patiu, 2008). In the definition of Giroux *et al.* (2010), the hillae are 'paired, tube-like (sometimes hatchet-like) structures protruding outwards from the anterior [ventral] surface of the distiphallus proximally to the lateral and median styli and distally to the vesica'. The main consequence of Giroux *et al.*'s (2010) proposal is that the hillae are not developed from the lateral styli as originally described by Roback (1954) but novel attributes evolved from the ventral wall of the distiphallic tube. According to Giroux *et al.*'s (2010) observations, 'the hillae do not take part in the formation of the acrophallus proper, i.e. the lateral plus median styli [median stylus]' and, as evidence of this, they mentioned species of *Ravinia* with hillae but apparently with no lateral styli. However, as defined by Roback (1954) and supported by other authors (Povolný & Verves, 1997; Pape, 1998b; Verves, 2000), the hillae are derived from the lateral styli, and not separate structures to these, as Giroux *et al.* (2010) implied. We found that all species of *Ravinia* have lateral styli, in which the distal part is always flattened (or nearly so) and does not form a tubular or semi-tubular structure. Here, we accept the term hillae *sensu* Roback (1954) and provide a more precise definition as paired, ventrally directed, tube-like, hatchet-like, flat or bulbose expansions of the latero-proximal part of the lateral styli that may or may not have a groove. The groove ('hig' in Fig. 10B), if present, is essentially a proximal continuation of the seam or groove of the lateral stylus, which has expanded into a membranous bladder ('hib' in Figs 10C, D, 14G, H) in some species of *Ravinia*. The hillae are fully or partially sclerotized, and they protrude ventrally latero-distad to the vesica, and are often visible in a lateral view of the distiphallus. According to our definition, hillae are found in *Argoravinia* Townsend (Figs 5C, 15A–F), *Dexosarcophaga* Townsend (including *Cistudinomyia*), *Duckemyia* (Fig. 16F, G), *Malacophagomyia* Lopes (including *Dodgeisca*) (Figs 5D, F, 16C–E, 17A, B), *Malacophagula* (Fig. 17G), *Nephochaetopteryx* Townsend (Figs 4D, 18B, C), *Oxysarcodexia*, *Oxyvinia* Dodge (Figs 4H, 19D), *Peckiamyia* Dodge, *Rafaelia* (Figs 14A, 20H), *Ravinia* (Figs 10B–D, 14D–H), *Retrocitomyia*, *Rettenmeyerina*, *Sarothromyiops* (Fig. 21B) and *Tapacura* Tibana & Lopes. The genera of clade 21 [i.e. *Oxyvinia* and *Dexosarcophaga* (including *Cistudinomyia*)] and genus *Rettenmeyerina* possess hillae that are usually not visible in a lateral view of the distiphallus; instead, these extensions of the lateral styli remain hidden from lateral view by the lateral wall

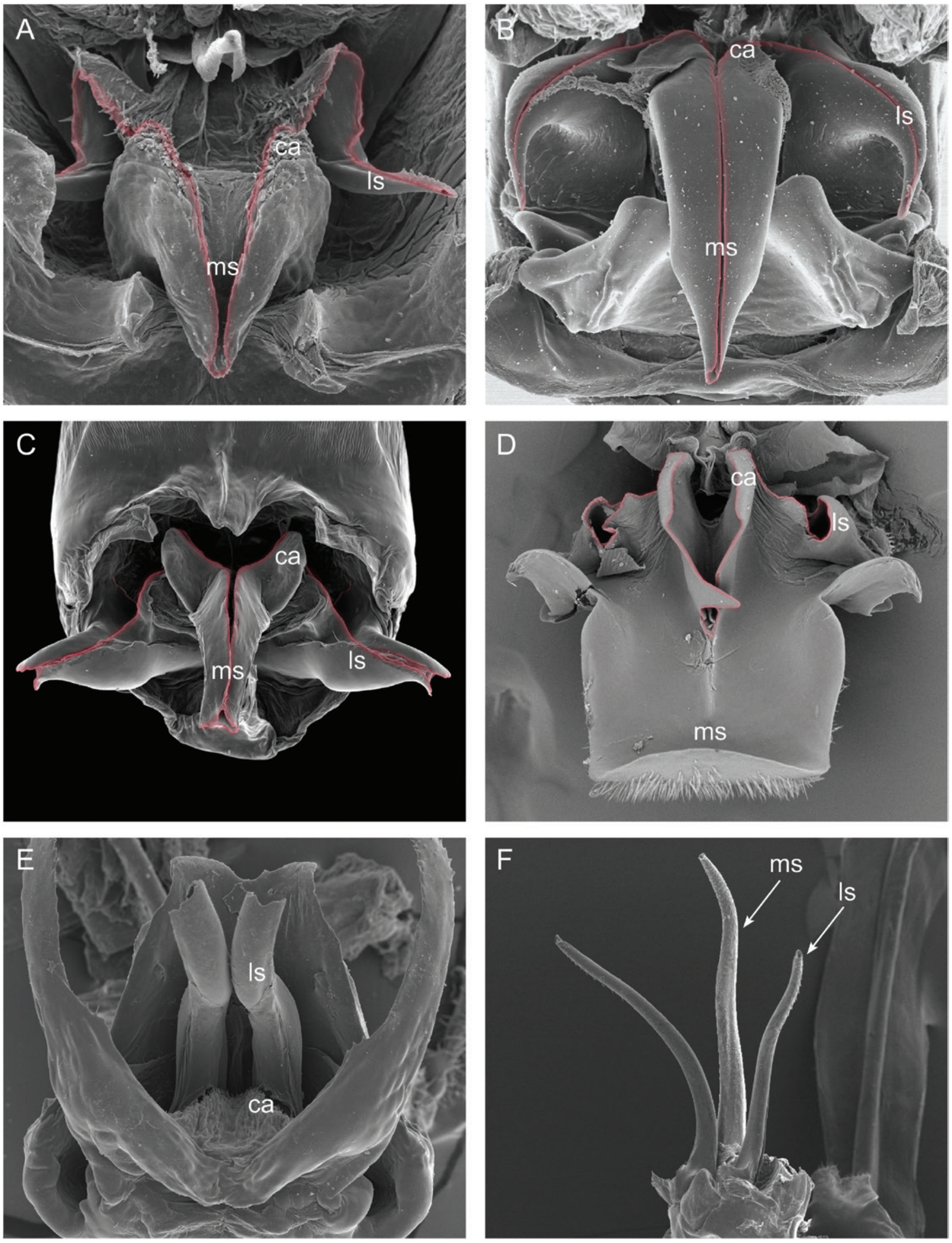

Figure 3. Acrophallus in Sarcophaginae, ventral view (red line indicates margin of acrophallic rim): A, *Microcerella spinigena*; B, *Tripanurga albicans*; C, *Rafaelia ampulla*; D, *Lipoptilocnema crispina*; E, *Chrysagria alticophaga*; F, *Titanogrypa* (*Cucullomyia*) *placida*. [F, courtesy M. Giroux; A, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

of the paraphallus. Thus, in these genera the hillae are directed proximally, towards the vesica (Figs 4H, 19D), making a curve along the inner paraphallic wall, and ending at the ventral paraphallic margin. The hillae are directed distally, towards the juxta in members of clade 74 (i.e. *Duckemyia*, *Peckiamyia*, *Retrocitomyia* and *Tapacura*) (Fig. 16F) and latero-ventrally in clade 28 [i.e. *Argoravinia*, *Malacophagomyia* (including *Dodgeisca*), *Malacophagula* and *Rafaelia*] and genus *Sarothromyiops* (Figs 5C, D, F, 14A, 15A–F, 16C–E, 17A, B, G, 20H). The hillae in the genus *Ravinia* may be equipped with a membranous bladder-like structure set proximally to a fully sclerotized distal part (Figs 10C, D, 14G, H), which in at least some species has a groove (Fig. 10B). An entirely membranous texture of the hillae is only found in *Malacophagomyia* (including *Dodgeisca*). The hillae are long and spoon-shaped in *Nephochaetopteryx*, *Oxysarcodexia*, *Rettenmeyerina* and members of clade

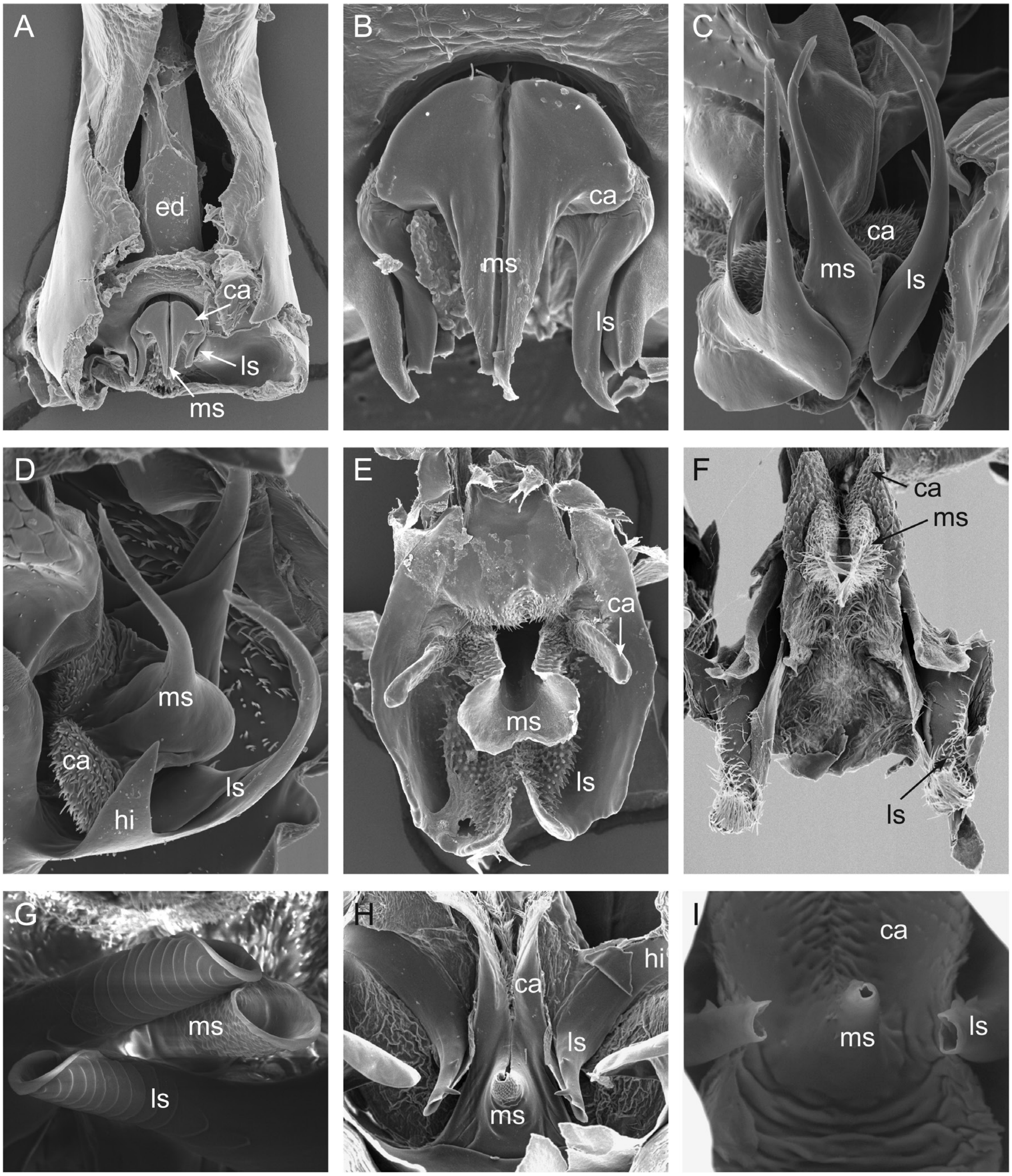

Figure 4. A, acrophallus and ejaculatory duct, ventral view: *Tricharaea* (*Sarothromyia*) *simplex*. B, acrophallus, ventral view: *Tricharaea* (*Sarothromyia*) *simplex*. C, acrophallus, postero-apical view: *Nephochaetopteryx* sp. D, acrophallus, latero-apical view: *Nephochaetopteryx* sp. E–I, acrophallus, ventral view: E, *Ravinia pernix*, hillae removed; F, *Oxysarcodexia timida*; G, *Rettenmeyerina serrata*; H, *Oxyvinia xanthophora*; I, *Dexosarcophaga* (*Cistudinomyia*) *cistudinis*. [A, courtesy M. Giroux; B, E, F, H, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

21. The hillae vary in shape, being noticeably developed in species of *Argoravinia*, where they are large and of a convoluted shape (Figs 5C, 15A–F), having undulations that expand laterally to cover the lateral styli (Fig. 15E). The hillae of *Argoravinia* were previously interpreted as two separate structures by Carvalho-Filho & Esposito (2012), one described as 'a large tube-like projection from the base' of the lateral stylus and the other as 'lateral projection of the distiphallus' also called 'lateral plate' in the same publication. These structures are

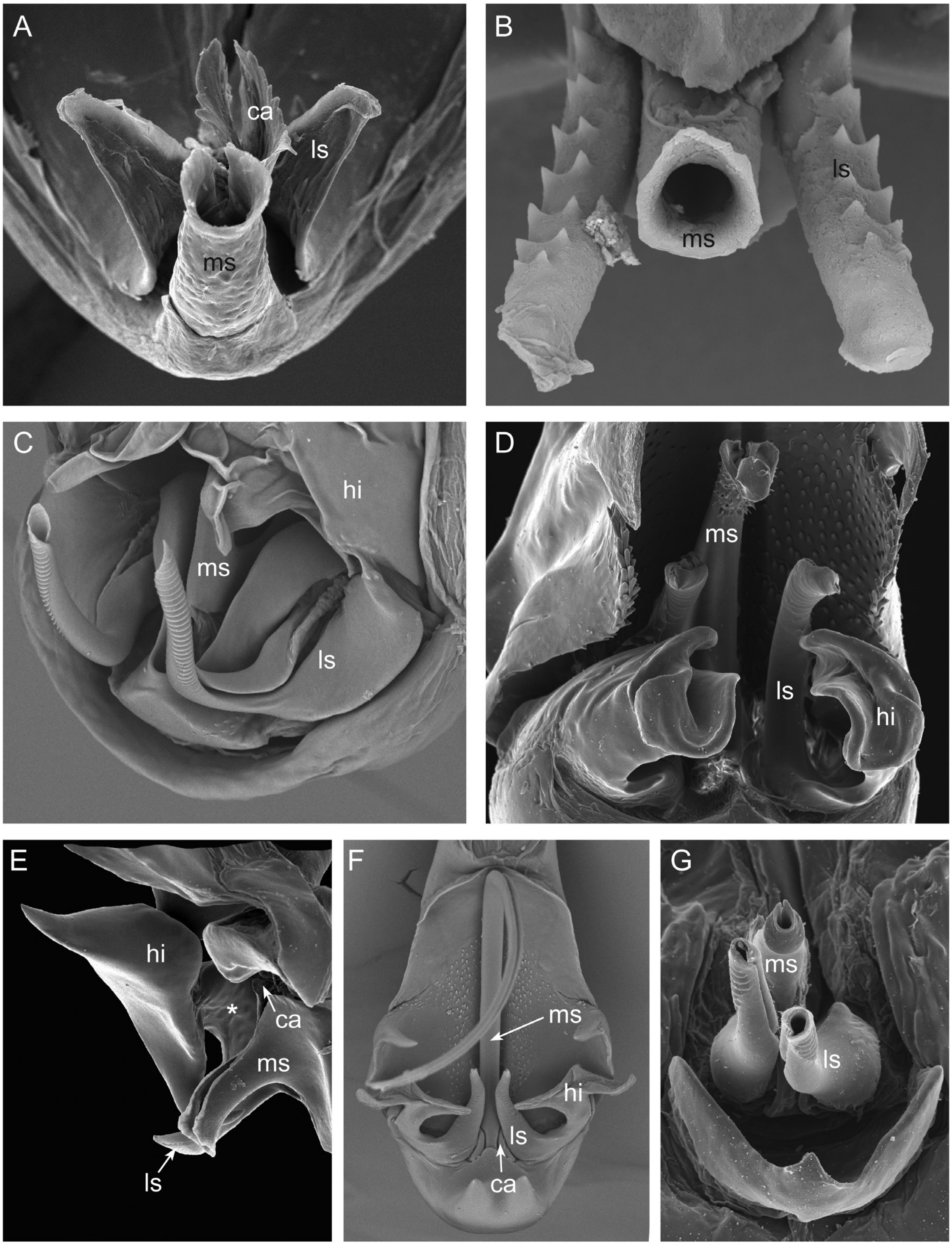

Figure 5. A–B, acrophallus, ventral view: A, *Dexosarcophaga* (*s.s.*) *transita*; B, *Malacophagula* (*s.s.*) *neotropica*. C–D, acrophallus, antero-lateral view: C, *Argoravinia aurea*; D, *Malacophagomyia* (*Dodgeisca*) *paramerata*. E, median stylus, and asterisk showing the connection between lateral stylus and hillae, antero-lateral view: *Ravinia derelicta*. F–G, acrophallus, ventral view: F, *Malacophagomyia* (*s.s.*) *kesselringi*; G, *Sinopiella rotunda*. [E, courtesy M. Giroux; A, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

proximally contiguous with the base of the lateral styli and are here interpreted as constituting the convoluted hillae of this genus. In some taxa, the hillae have a bifid apex (Fig. 15C), and they may be entirely or partially sclerotized. In *Argoravinia*, the hillae are convoluted, while they are filiform in the genera *Malacophagomyia* (*s.s.*), *Malacophagula*, *Rafaelia* and *Sarothromyiops*, and tube-like in *Malacophagomyia* (*Dodgeisca*). We are aware that hillae as defined here may not be homologous in all their manifestations, but we defer a thorough assessment of this until morphological and molecular data start converging upon a strongly supported phylogeny.

Buenaventura & Pape (2015) described the stylar lateral plates and stylar membranous lobes in species of *Engelimyia* Lopes (Fig. 22A), which are hillae-like extensions of the lateral styli. According to these authors, the stylar lateral plate emerges proximo-dorsally and the stylar membranous lobe emerges proximo-ventrally on each lateral stylus. Thus, due to differences in position, these structures are not homologous with the hillae, because the latter are proximo-lateral expansions of the lateral styli.

In the Sarcophaginae, the tripartite condition of the phallotrema is invariably optimized as a ground-plan feature, which means that observed absences and modifications in the components of the acrophallus are best interpreted as secondary. The lateral styli, median stylus, capitis and hillae that compose the acrophallus are generally present in the 'lower' sarcophagines, clade 28 and genus *Sarothromyiops* (Fig. 2A). Only a few genera of the 'lower' sarcophagines [i.e. *Bahamiola*, *Sarcofahrtiopsis* Hall (including *Pacatuba*) and *Tricharaea*] present an absence of the hillae. In the 'lower' sarcophagines, clade 28 and genus *Sarothromyiops*, the lateral styli and median stylus are generally short, and often broad proximally (Figs 4A–F, 5A, 10A, E), the capitis is broad and rounded or elongated distally (Figs 4A–F, H, I, 5A), while the hillae exhibit more variation in shape and texture.

The elements of the acrophallus vary in length and width across the sarcophagine genera, but in general the styli are tube-shaped or semi-tubular structures, the capitis is generally developed (Fig. 7D, G, H) while the hillae are mostly reduced. The stronger modifications related to the components of the acrophallus are found in clades 33, and certain groups within clades 39 and 63 (Fig. 2).

Some modifications of the lateral styli occur in members of clade 33 (Fig. 2A), where they are longer, with the median stylus particularly elongated in *Malacophagomyia* (including *Dodgeisca*) (Fig. 5F). Stronger modifications of the acrophallus are observed in clades 38 and 39 (Fig. 2B). For example, the hillae become reduced in the ancestor of clade 38. While in most Sarcophaginae the acrophallus is surrounded by the paraphallus and apically protected by the juxta, in clade 39 the acrophallic structures are generally exposed (Figs 6, 7A, B). The most dramatic modifications occur in the genus *Villegasia* Dodge and the genera forming clade 56 where, for example, the lateral styli are collapsed or form apparently non-conducting structures, whereas the median stylus is a short and broad semi-tubular structure (Figs 6, 7A, B). The apparently non-conducting lateral styli in these genera vary in shape and size. The lateral styli are small and finger-like in *Thomazomyia* Lopes (Fig. 6C), large and plate-like, with digitate margins in *Emdenimyia* Lopes (Fig. 23F) and *Mecynocorpus* (Fig. 6E), finger-like and collapsed in many *Blaesoxipha* (Fig. 6F) or very small, plate-like and collapsed structures with digitate margins in *Villegasia* (Fig. 6G). The styli seem to be semi-tubular conducting structures in the genera *Panava* (Fig. 7A) and *Promayoa* (Figs 7B, 20C, D), and they form tube-like structures in *Titanogrypa* (*Cucullomyia*) *placida* (Aldrich, 1925) (Fig. 3F). In the species of *Panava*, the lateral styli and median stylus are long and broad, while in the genus *Promayoa* (i.e., the clade *Promayoa peculiaris* Dodge, 1966 + *Promayoa ramosa* in Fig. 2B) only the lateral styli seem to be semi-tubular conducting structures. In these groups, the capitis is larger than in other Sarcophaginae, in *Panava* it is keel-shaped, and in *Promayoa* is rounded and expanded ventrally.

The large clade 63 (Fig. 2B) is composed mostly of genera that possess acrophallic modifications of the size of the styli, like in some species of *Boettcheria* that exhibit elongated styli (Fig. 8G), while in *Austrophyto* and *Microcerella* (Fig. 3A) these tube-shaped structures are shorter. Similarly, examples of genera bearing short styli are *Lepidodexia* (*Archimimus*) (Fig. 9C), *Emblemasoma* (Fig. 9A), *Tripanurga* (Fig. 3B) and *Udamopyga* Hall (including *Carinoclypeus*) (Fig. 9D). The median stylus is modified in *L.* (*Archimimus*) (clade 99 in Fig. 2B), where it does not form a conducting structure (Fig. 9C).

In the clade containing (*Engelimyia* + *Tulaeopoda*), the most remarkable modification of the acrophallus occurs in the species of *Engelimyia*. As described by Buenaventura & Pape (2015), the median stylus in *Engelimyia* is modified into a membranous, denticulated and bulbous structure. This modification was found to be autapomorphic for this genus (Buenaventura & Pape, 2015), which is confirmed in the present study. Other modifications in the acrophallus of species of *Engelimyia* are the stylar lateral plate ('slp' in Fig. 22A) and stylar membranous lobe ('sml' in Fig. 22A), which both constitute proximal expansions of the lateral styli, as defined by Buenaventura & Pape (2015), and whose autapomorphic condition for *Engelimyia*

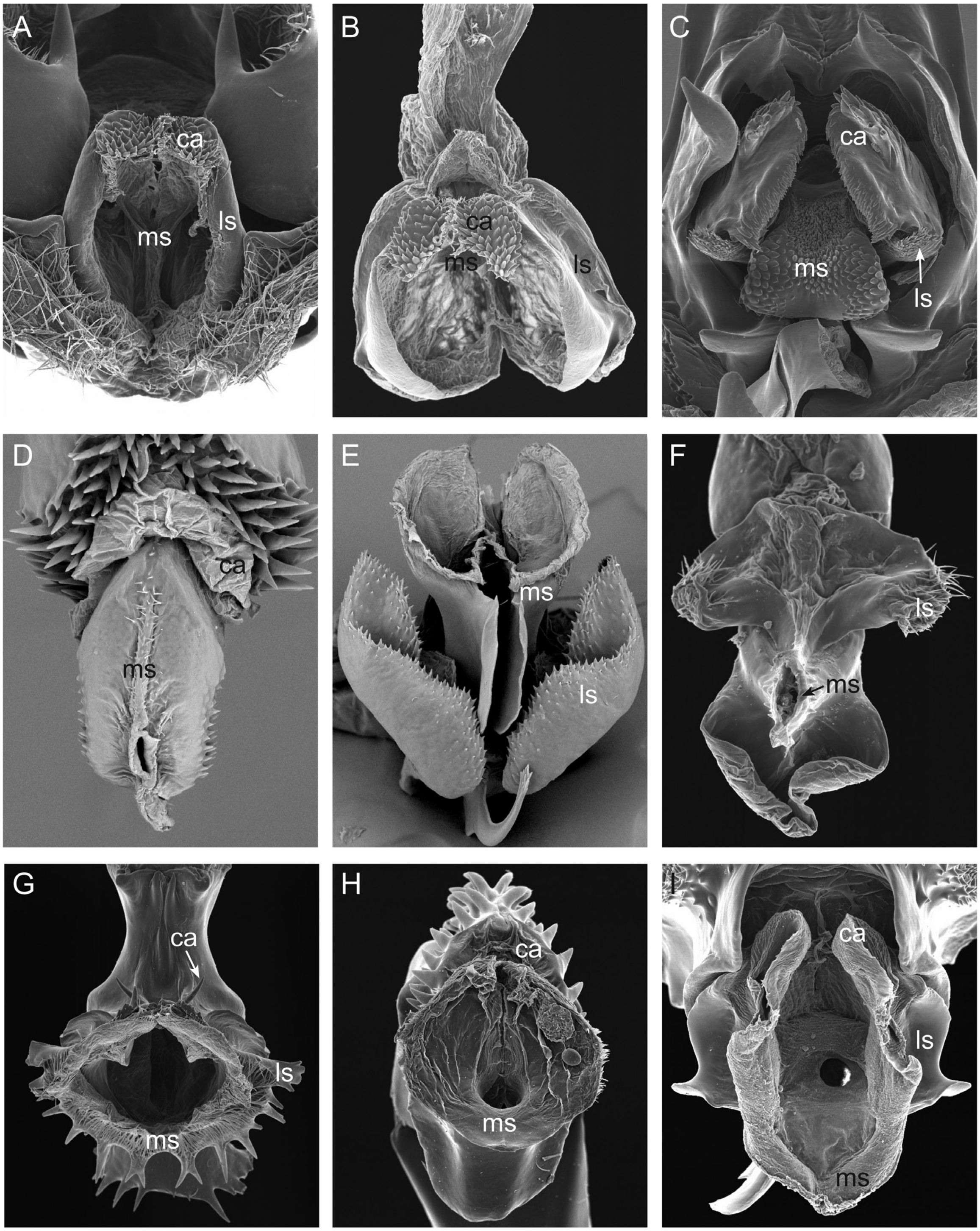

Figure 6. A, acrophallus and juxta, ventral view: *Fletcherimyia fletcheri*. B, acrophallus, ventral view: *Fletcherimyia fletcheri*. C–I, acrophallus, ventral view: C, *Thomazomyia adunca*; D, *Emdenimyia korytkowskii*; E, *Mecynocorpus salvum*; F, *Blaesoxipha* (*s.s.*) *rufipes*; G, *Villegasia postuncinnata*; H, *Sarcodexiopsis welchi*; I, *Titanogrypa* (*s.s.*) *melampyga*. [A, I, courtesy M. Giroux; B, F, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

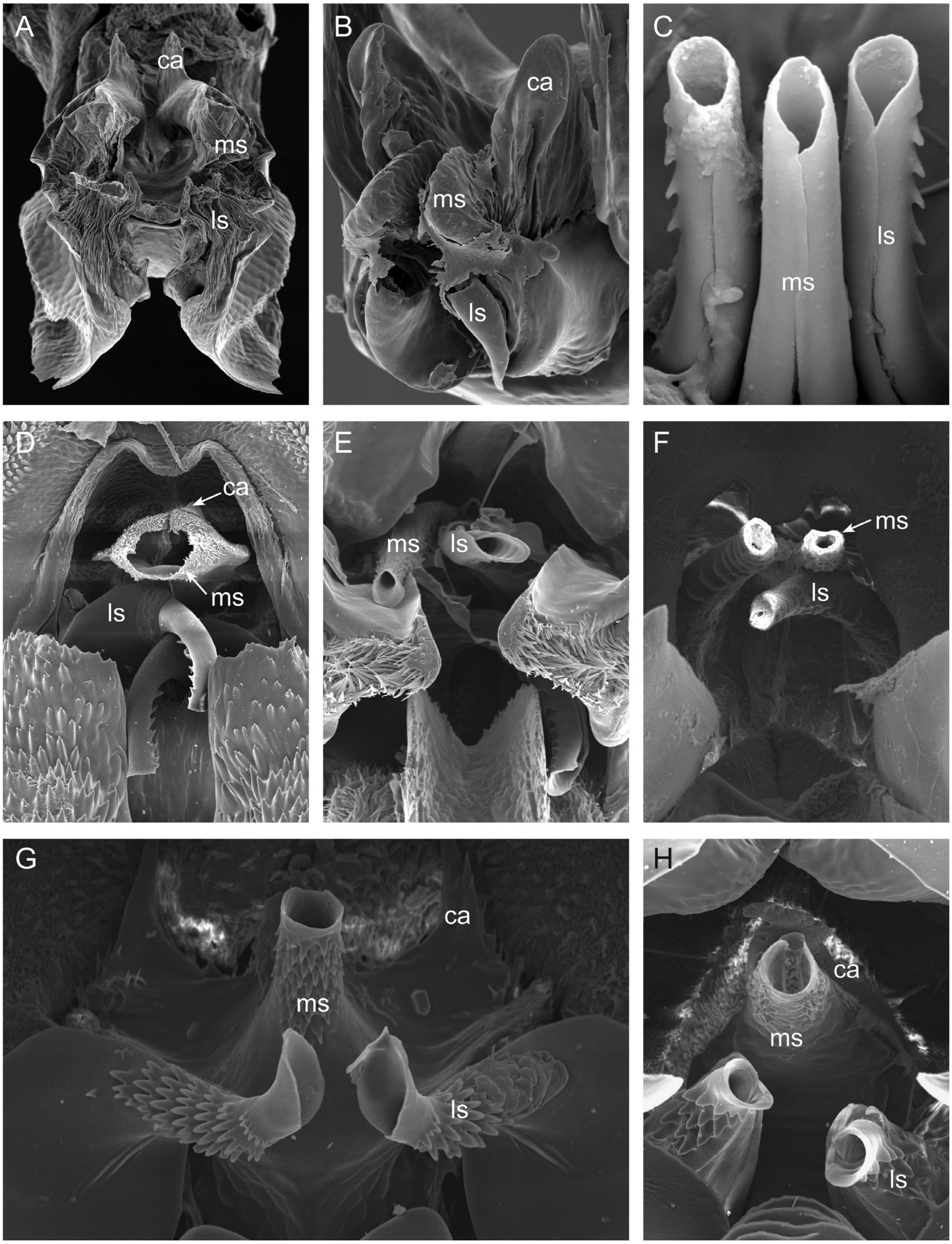

Figure 7. A, acrophallus, ventral view: *Panava inflata*. B, acrophallus, antero-apical view: *Promayoa ramosa*. C–H, acrophallus, ventral view: C, *Sarothromyiops dasycnemis*; D, *Tulaeopoda pervillosa*; E, *Peckiamyia abnormis*; F, *Retrocitomyia retrocita*; G, *Halliosca declinata*; H, *Lepidodexia* (*Dexomyophora*) *fascialis*. Abbreviations as in Table 1.

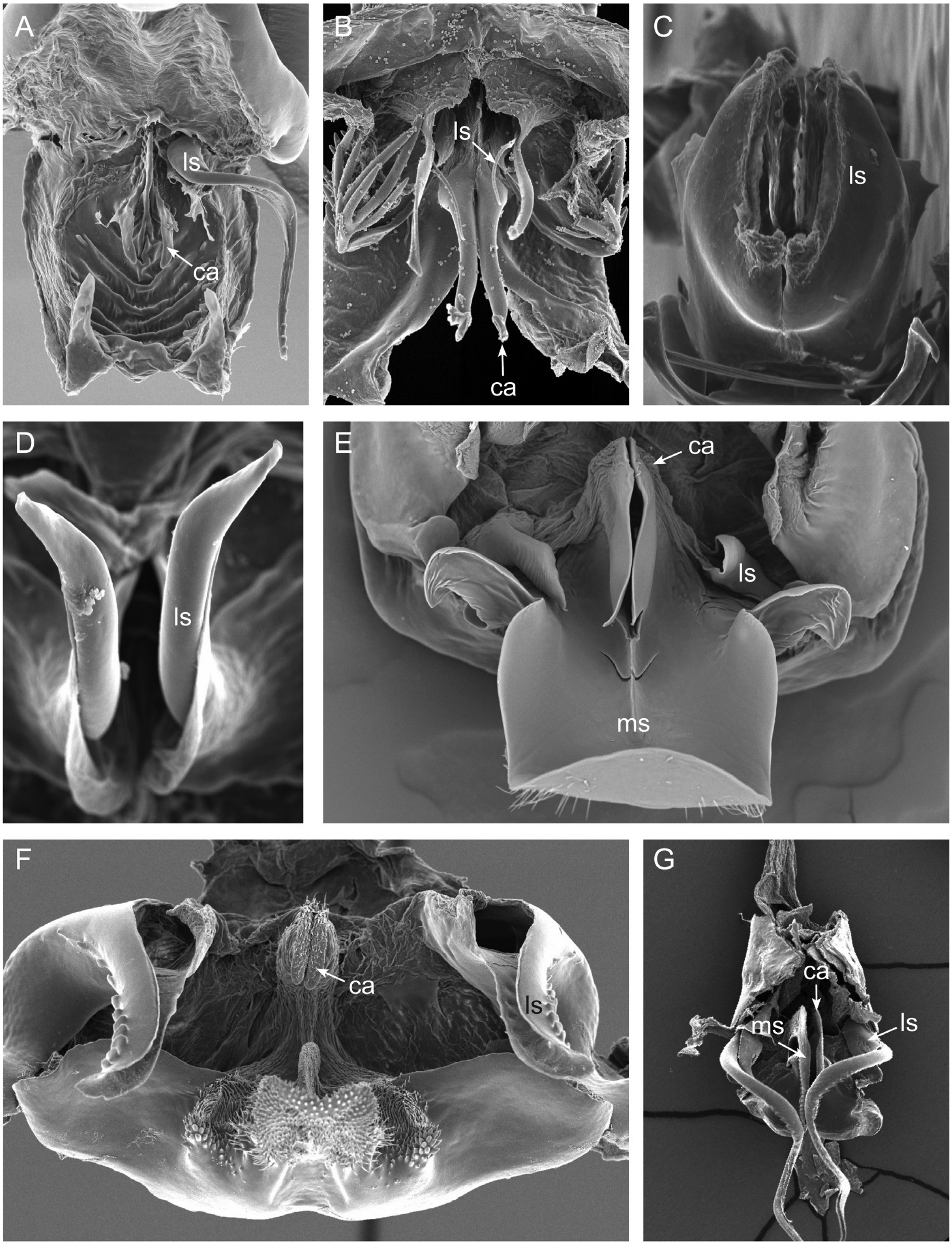

Figure 8. Acrophallus, ventral view: A, *Helicobia morionella*; B, *Helicobia surrubea*; C, *Peckia* (*Squamatodes*) *ingens*; D, *Peckia* (*s.s.*) *rubella*; E, *Lipoptilocnema koehleri*; F, *Sarcophaga* (*Neobellieria*) *bullata*; G, *Boettcheria latisterna*. [A, F, G, courtesy M. Giroux; B, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

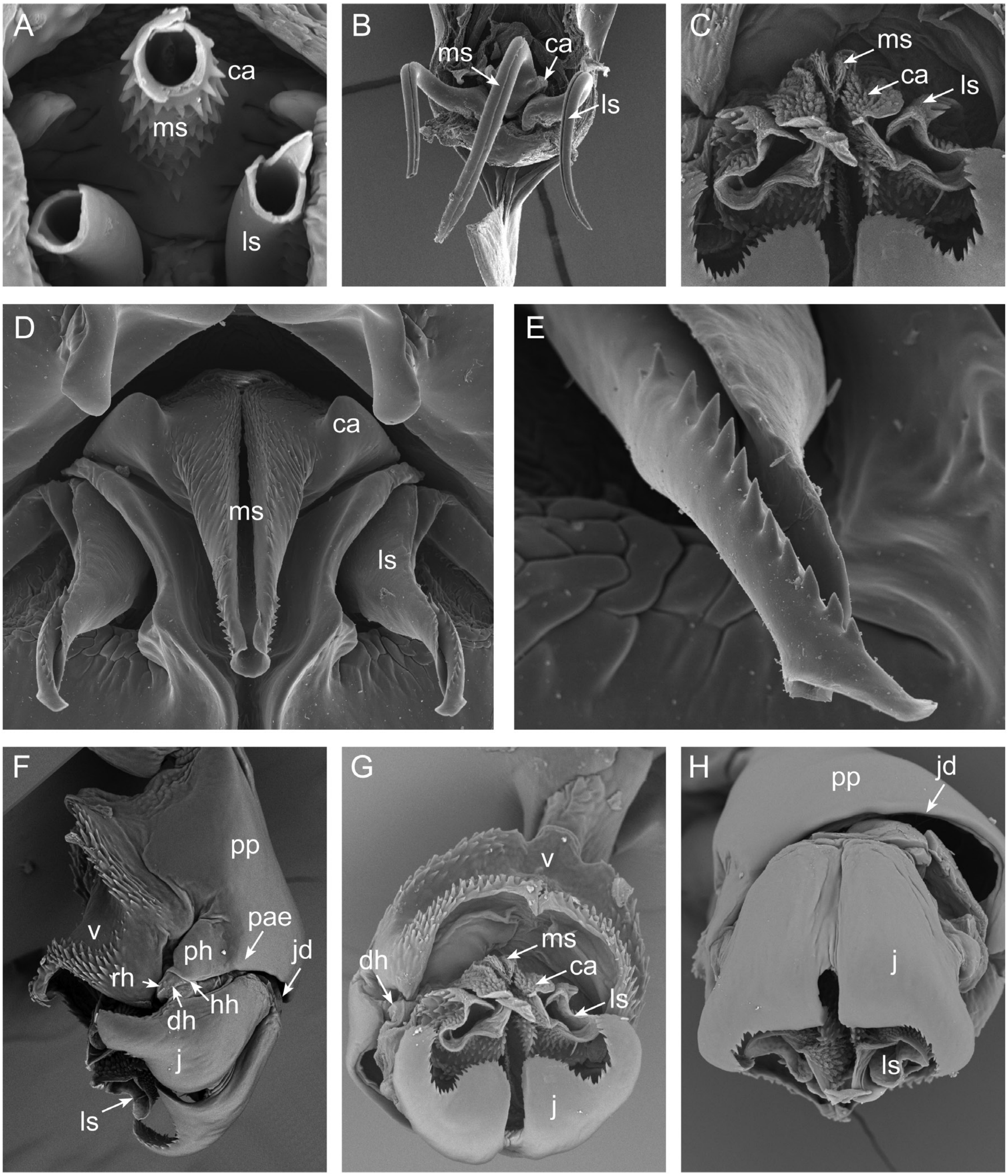

Figure 9. A–C, acrophallus, ventral view: A, *Emblemasoma albicoma*; B, *Spirobolomyia singularis*; C, *Lepidodexia* (*Archimimus*) *camatus*. D, acrophallus, ventral view: *Udamopyga* (*s.s.*) *neivai*. E, lateral stylus, ventral view: *Udamopyga* (*s.s.*) *neivai*. F, distiphallus, left lateral view: *Lepidodexia* (*Archimimus*) *camatus*. G, distiphallus, ventral view: *Lepidodexia* (*Archimimus*) *camatus*. H, distiphallus, postero-apical view: *Lepidodexia* (*Archimimus*) *camatus*. (B, courtesy M. Giroux). Abbreviations as in Table 1.

is also supported in the present study. Although *Tulaeopoda*, as the sister group of *Engelimyia*, does not possess these proximal expansions of the lateral styli, it has a thickening and a change in the texture (Fig. 7D) in the same area as the stylar lateral plate and stylar membranous lobe in *Engelimyia*.

A relevant modification appeared in the ancestor of clade 74 (Fig. 2B), which includes *Duckemyia*, *Peckiamyia*, *Retrocitomyia* and *Tapacura*, where the hillae are present and paddle-like (Fig. 16F, G).

In clade 101, major modifications and losses are observed. All species of this clade share a reduction of the median stylus (Figs 3E, 8A–F). In *Lipoptilocnema* (Fig. 8E), the acrophallic rim is folded postero-medially where the median stylus is supposed to originate, and it does not form a conducting semi-tubular structure. Instead, in this genus, the acrophallic rim is folded to form a strongly broadened extension ['medial projection of median stylus' in Mulieri *et al.* (2016)] equipped with paired lateral projections ['lateral projections of median stylus' in Mulieri *et al.* (2016)], and covered with dorsal microtrichiae in some species (Fig. 24E, H). However, in this genus, as in *Chrysagria* (Fig. 3E), *Helicobia* (Fig. 8A, B) and *Sarcophaga* (Fig. 8F), the capitis is developed and may even be elongated in some species of the latter two genera (Fig. 8A, B, F), while it is completely lost in species of *Peckia* (Fig. 8C, D). Conversely, the lateral styli are well developed, filiform or broad, and elongated in species of *Chrysagria*, *Helicobia*, *Peckia* and many *Sarcophaga*.

As outlined above, one of the conducting structures of the acrophallus (lateral styli or median stylus) is lost or strongly modified in two clades within the Sarcophaginae: (1) in members of clade 39 [except for *Comasarcophaga*, *Spirobolomyia* and *T*. (*Cucullomyia*) *placida*, see Fig. 3F], the lateral styli are collapsed or form apparently non-conducting structures (Fig. 2B); (2) in clade 101 all members lack the median stylus or this does not form a conducting structure. In the above-mentioned two clades, the tripartite condition of the phallotrema is either lost or strongly modified, which is optimized as a derived feature, thereby supporting the hypothesis of the tripartite condition having evolved only twice in the family, once in the miltogrammine *Senotainia trifida* Pape, 1989 and once in the ancestor of the subfamily Sarcophaginae (Pape, 1989a, 1992, 1996). Our phylogenetic hypothesis is in partial agreement with Giroux *et al.*'s (2010) phylogenetic hypothesis for Sarcophaginae, since we found the lateral styli to have lost their function as conducting structures multiple times: once in *Titanogrypa*, once in *Ravinia* and once in the ancestor of *Mecynocorpus* + *Blaesoxipha*. We found the lateral styli to be developed, although rarely semi-tubular, in all species of *Ravinia*, instead of reduced or collapsed as described by Giroux *et al.* (2010). This is not only through our definition of the hillae being latero-proximal expansions from the lateral styli, as also the distal part of these can be recognized (Fig. 5E). (It should be noted that the function of the acrophallus is still almost purely conjectural, and the hillae of some species of *Ravinia* may have acquired a secondary function through the evolution of a membranous, bladder-like part, which may conduct either sperm or accessory gland secretions.) Finally, Giroux *et al.* (2010) mentioned the reduction of the 'median stylus' (median stylus + capitis) in species of *Peckia* and in *Sarcodexia lambens* [= *Peckia* (*Sarcodexia*) *lambens* (Wiedemann, 1830)], but they did not mention these taxa as examples of the multiple ocurrences of loss of the tripartite condition of the phallotrema in the Sarcophaginae. *Peckia*, together with *Chrysagria*, *Helicobia*, *Lipoptilocnema* and *Sarcophaga*, form clade 101, which represents the second type of loss of the tripartite condition of the phallotrema in our phylogeny.

Vesical arm-shaped lever, distal section of the vesica, acrophallic levers and vesical lateral arms

We found support for considering the presence of a vesica as an autapomorphic groundplan character state for the subfamily Sarcophaginae as proposed by Pape (1996). By following Giroux *et al.*'s (2010) definition, we found a vesica to be present in most genera, and the absence of a vesica in clade 58 (Fig. 2B), in the genus *Villegasia* and in the species *Peckia* (*Squamatodes*) *ingens* (Walker, 1849) (Fig. 13C) is considered as three independent losses.

The vesica is divided into a proximal vesical arm-shaped lever and a distal section in the 'lower' sarcophagines [the tribes Sarcophagulini and Raviniini of Lopes (1969a), i.e. *Bahamiola*, *Dexosarcophaga* (including *Cistudinomyia*), *Nephochaetopteryx*, *Oxysarcodexia*, *Oxyvinia*, *Ravinia*, *Rettenmeyerina*, *Sarcofahrtiopsis* (including *Pacatuba*) and *Tricharaea*]. We define the vesical arm-shaped lever (green structure in Figs 25, 26) as the proximal sclerotized section of the vesica, which proximally is articulated to the ventral surface of the hypophallus and distally carrying the ornamented and less sclerotized distal section of the vesica. The vesical arm-shaped lever is attached to the hypophallus, and it is a groundplan feature of the vesica. The vesical arm-shaped lever is strongly sclerotized and usually angled in *Bahamiola* (Fig. 25D), *Nephochaetopteryx* (Fig. 25E), *Oxysarcodexia* (Fig. 25G), *Sarcofahrtiopsis* (including *Pacatuba*) (Fig. 25B, C) and *Tricharaea* (Fig. 25A). It is less sclerotized and gently angled in *Dexosarcophaga* (including *Cistudinomyia*) (Fig. 26B, C), *Oxyvinia* (Fig. 25H) and *Rettenmeyerina* (Fig. 26A), and it is straight and has a membranous appearance in *Ravinia* (Fig. 25F). The length of the vesical arm-shaped lever varies among these genera, from very short in *Ravinia* (Fig. 25F) through medium length in *Bahamiola*, *Dexosarcophaga* (including *Cistudinomyia*), *Nephochaetopteryx*, *Oxysarcodexia*, *Oxyvinia* and *Rettenmeyerina* (Figs 25D–H, 26), to elongated in *Tricharaea* (Fig. 25A), and very elongated in *Sarcofahrtiopsis* (including *Pacatuba*) (Fig. 25B, C). The apex of the vesical arm-shaped lever is hammer-shaped in *Sarcofahrtiopsis* (including *Pacatuba*) and *Tricharaea* ('vl' in Figs 19H, 27A), and bilobed or oval in *Bahamiola*, *Dexosarcophaga* (including *Cistudinomyia*), *Nephochaetopteryx*, *Oxysarcodexia*, *Oxyvinia*, *Ravinia* and *Rettenmeyerina* (Figs 10D, 11E, F, 14F, 16B, 18A, D, H, 28C). Most of the body of the vesical arm-shaped lever is generally visible in ventral and lateral views of the phallus, but its base is usually hidden by being partly recessed into the paraphallic tube, where it is touching or fused to the acrophallic levers. These are defined here as paired sclerotized bars, which run from the ventral base of the acrophallus to the base of the vesical arm-shaped lever, thus linking the vesica with the acrophallus ('al' in Fig. 18B, C). The acrophallic levers may be slender bars visible in lateral and ventral view of the distiphallus (Fig. 14D–F, H), or they may be complex, broad and strongly sclerotized bars (Fig. 18B, C). The acrophallic levers are generally hidden from lateral view by being recessed into the paraphallic tube, being visible in lateral and ventral views only in *Ravinia* (Fig. 14D–F, H). They correspond to the 'dorsal rods' and 'acrophallic bars' described by Roback (1954) and the 'hastes dorsais [dorsal bars]' mentioned by Guimarães (2004). Thus, the vesica seems to be part of an articulation system with a vesical arm-shaped lever able to move (or be moved) up and down, which was also suggested by Roback (1954). The distal section of the vesica (yellow structure in Figs 25, 26) consists of a less sclerotized part that varies in shape and ornamentation, being globose with small denticles in *Sarcofahrtiopsis* (including *Pacatuba*) (Fig. 25B, C) and *Tricharaea* (Fig. 25A), strongly ornamented with a complex shape in *Bahamiola* ('vd' in Figs 15G–I, 25D), *Nephochaetopteryx* (Figs 18A–C, 25E, 29H) and *Oxysarcodexia* (Figs 18D, F–H, 19A, 25G), bifid and not particularly ornamented in *Dexosarcophaga* (including *Cistudinomyia*) (Figs 11D–F, I, 16A, B, 26B, C), *Oxyvinia* (Figs 19B, 25H) and *Rettenmeyerina* (Figs 26A, 28B–D), and flat to reduced in *Ravinia* (Figs 10C, D, 14G, H, 25F).

The morphological complexity of the vesica is remarkable as can be observed throughout all sarcophagine genera. Two of the sections of this structure, i.e. vesical arm-shaped lever and distal section, are only distinguishable in the 'lower' sarcophagines (Figs 25, 26), whereas the vesica is undivided in the ancestor of clade 26 (Fig. 2A). However, the vesica is divided in the median plane ('v' in Fig. 20A, B) in the genera *Panava* and *Promayoa*. The vesica is complex in the genus *Boettcheria* (Fig. 30F), as in *Lepidodexia* (including *Archimimus*) (Fig. 2B), in which the vesica also has a proximal spinous lobe (see no. 1 in Figs 31D, 32C, F; red structure in Fig. 33), a C-shaped medial section with hook-shaped ends (see no. 3 in Figs 31D, 32C, F) and a distal convex sclerotized section (see no. 2 in Figs 31D, 32C, F). Conversely, the vesica is flat, broad and smooth in the genus *Sarothromyiops* (Fig. 21A–C) and in clade 28 (Fig. 2A) containing the genera *Argoravinia* (Fig. 15A, F), *Malacophagomyia* (including *Dodgeisca*) (Figs 16D, 17A, B), *Malacophagula* (Fig. 17F) and *Rafaelia* (Fig. 20F, H), and it is composed of two petal-shaped lateral plates each with a vesical denticulated lobe in *Udamopyga* (including *Carinoclypeus*) ('vdl' in Fig. 34C). The shape of the vesica of genera *Malacophagula* and *Rafaelia* might be described in a more complex form than our 'broad and flat', as this structure is equipped with various flat plates, some of which might be ventrally projected into lobes or even into filiform extensions. The presence of these projections varies across species of both genera. Thus, due to lack of evidence for supporting the homology of only one of these plates with the vesica, we chose to homologize all plates combined as the vesica, as they occupy the area where this structure is usually found in other sarcophagines.

Buenaventura & Pape (2015) described structures called paraphallic lateral plates in species of *Peckiamyia* and *Retrocitomyia* as 'paired, anteriorly [= ventrally] directed, flat, sclerotized expansions of the antero-medial margin of the paraphallus, situated proximal to the harpes but distal to the vesica, and whose sagittal plane runs parallel to paraphallic wall, and whose proximal margin may be partially or totally overlapping the vesica in lateral view'. Further observations made during the present study showed that these structures arise from the lateral parts of the vesica as vesical lateral arms, and, in some genera, are demarcated by a hinge or desclerotized strip ('vla' in Figs 10F, 16G, 35C), which can be used as a landmark for their recognition. These vesical lateral arms are ribbon-like in *Duckemyia* (Fig. 16F–H), trapezoid in *Peckiamyia* (Fig. 35C–F), elongated with undulated margin in *Sinopiella* Lopes & Tibana (Fig. 21F), paddle-like in *Retrocitomyia* (Fig. 10F–H), disc-like in *Tapacura* (Fig. 36A–C, E), and bulbous and with an inner denticulated process in *Tripanurga* ('vdp' in Fig. 27B–E).

Paraphallic proximal expansions

Whitmore *et al.* (2013) studied the phylogenetic relationships within the subgenus *Heteronychia* Brauer & Bergenstamm of the genus *Sarcophaga*, and described the ventral plates as 'ventrally directed lateral expansions of the paraphallus, partly or completely covering the membrane (from which they are free) in lateral view'. The membrane in their study was defined as

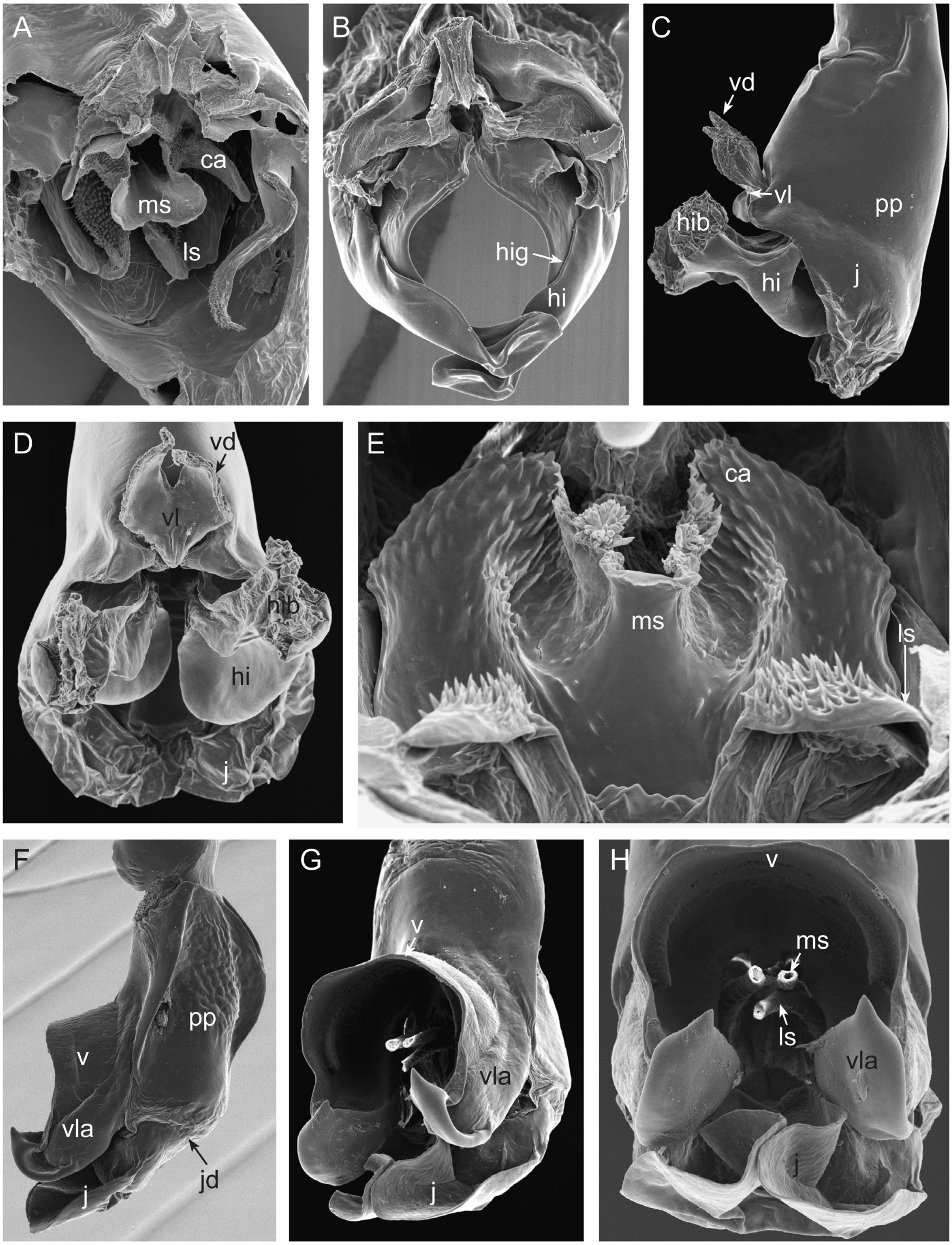

Figure 10. A, acrophallus, ventral view; hillae removed: *Ravinia pernix*. B, hillae with groove, inner surface: *Ravinia pernix*. C, distiphallus, left lateral view: *Ravinia rufipes*. D, distiphallus, ventral view: *Ravinia rufipes*. E, acrophallus, apical view: *Ravinia rufipes*. F, distiphallus, left lateral view: *Retrocitomyia retrocita*. G, distiphallus, antero-lateral view: *Retrocitomyia retrocita*. H, distiphallus, ventral view: *Retrocitomyia retrocita*. [A, B, D, E, courtesy M. Giroux; C, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

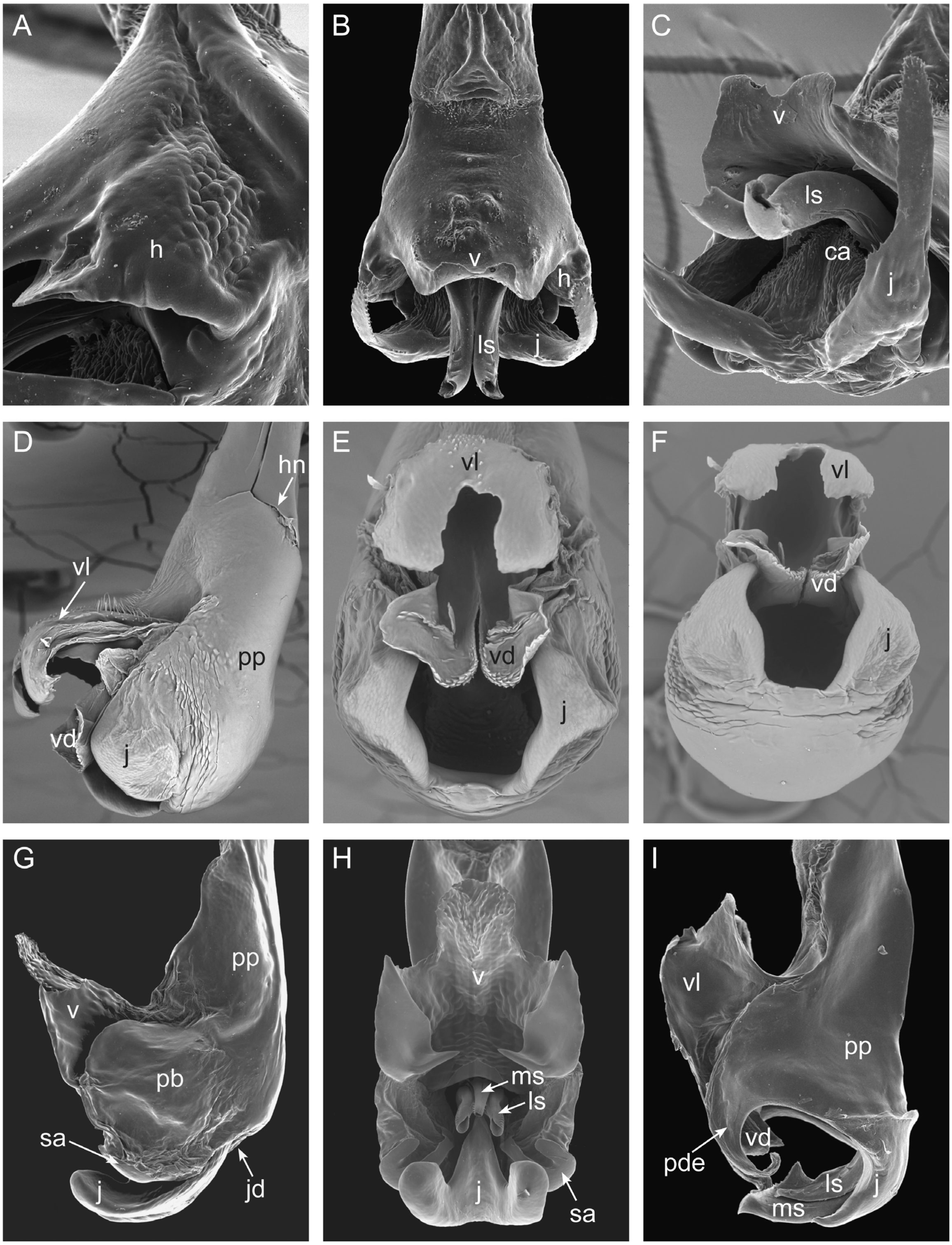

Figure 11. A, harpes, left lateral view: *Chrysagria alticophaga*. B, distiphallus, ventral view: *Chrysagria alticophaga*; C, acrophallus, latero-apical view: *Chrysagria alticophaga*. D, distiphallus, left lateral view: *Dexosarcophaga* (*Cistudinomyia*) *cistudinis.* E, distiphallus, ventral view: *Dexosarcophaga* (*Cistudinomyia*) *cistudinis.* F, distiphallus, apical view: *Dexosarcophaga* (*Cistudinomyia*) *cistudinis.* G, distiphallus, left lateral view: *Comasarcophaga texana*. H, distiphallus, ventral view: *Comasarcophaga texana*. I, distiphallus, left lateral view: *Dexosarcophaga* (*s.s.*) *transita*. [I, courtesy M. Giroux; G, H, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

'the most proximal section of the hypophallus', and the hypophallus was defined as 'the less sclerotized, ventral part of the phallic tube' or the antero-basal section of the distiphallic tube, and it corresponds to the 'membranocorpus' of (Roback, 1954). For precision and consistency with names for other structures proposed in the present study as well as with terminology previously proposed by other authors, Whitmore *et al.*'s (2013) ventral plates are here given the term paraphallic proximal expansions. We expand Whitmore *et al.*'s (2013) definition for ventral plates and define the paraphallic proximal expansions as a pair of sclerotized, ventrally directed, lateral expansions of the latero-ventral margin of the paraphallic wall, entirely fused to it, whose proximal margin is partly or completely overlapping the less sclerotized hypophallus (from which it is free) in lateral view, and whose distal margin is partly or completely overlapping the proximal margin of the vesica; in lateral view, the paraphallic proximal expansions take a proximal position with regard to the vesica, vesical lateral arms and harpes. According to our analysis, the paraphallic proximal expansions ('ppe' in Fig. 1) evolved only once: in the clade (*Lipoptilocnema* + *Sarcophaga*) ('ppe' in Figs 24C, D, 37E, I, J).

Paraphallic blinker

We define paraphallic blinkers ('pb' in Fig. 1) as paired, ventrally directed, bulbous or flat, semi-sclerotized expansions of the ventral margin of the paraphallus, and with a sagittal plane parallel to paraphallus. They are situated proximal to the juxta and distal to the vesica, and their proximal margin may be partially or totally overlapping the vesica in lateral view, while the distal margin may have either a tube-shaped structure or a sclerotized segment. We consider the desclerotized strip between the ventral margin of the paraphallus and the paraphallic blinkers as a landmark for delimiting these blinkers, which are found in the genera *Comasarcophaga* ('pb' in Fig. 11G) and *Spirobolomyia* (Fig. 21H). Plate-like structures found in the genus *Tapacura* have a similar position as the paraphallic blinkers. However, they are entirely fused to the ventral margin of the paraphallic wall without any sign of a desclerotized strip and their proximal margins overlap the vesica in lateral view. Also, the paraphallic blinkers are semi-sclerotized, while the plate-like structures of *Tapacura* are completely sclerotized.

Paraphallic lateral expansions

Paired, sclerotized, ventrally directed expansions of the lateral margin of the paraphallus, with no discontinuity between them and the paraphallus, situated distad to the vesica and proximad to the juxta, and whose proximal and distal margins never overlap the vesica and juxta in lateral view, respectively ('ple' in Fig. 1). According to our analysis, the paraphallic lateral expansions evolved only once and are found in the members of clade 33 (Fig. 2A), i.e. the genera *Argoravinia* ('ple' in Fig. 15A–C) and *Malacophagomyia* (including *Dodgeisca*) (Figs 16C, 17A).

Paraphallic distal expansions

In species of *Dexosarcophaga* (including *Cistudinomyia*), we observed sclerotized lateral expansions arising from the distal half of the ventral paraphallic margin ('pde' in Figs 11I, 16A, B). We name these paraphallic distal expansions ('pde' in Fig. 1) and define them as paired, sclerotized, ventrally directed lateral expansions arising from the distal half of the ventral margin of the paraphallus, entirely fused to the paraphallic wall, situated distad to the vesica and vesical lateral arms, and proximad to the juxta. Our phylogenetic analysis showed the paraphallic distal expansions to have evolved only once, i.e. in clade 23 (Fig. 2A).

Paraphallic apical expansions

Paired, often elongated, sclerotized, ventrally directed lateral extensions of the ventro-distal margin of the paraphallus, with no discontinuity with the latter, situated distad to the paraphallic lateral expansions, vesica and vesical lateral arms, and proximad to the juxta. Their position is slightly displaced ventrally with respect to the harpes, from which they are separated by a hinge ('pae' in Fig. 1B). Based on our definition, the paraphallic apical expansions are found in the genera *Emblemasoma* ('pae' in Fig. 23A, D), *Halliosca* Lopes (Fig. 31E) and *Lepidodexia* (including *Archimimus*) (Figs 9F, 31C, 32A, F), and they evolved only once, as an autapomorphy of clade 89 (Fig. 2B) of our phylogeny of Sarcophaginae.

Harpes and paraphallic window

The harpes were described by Roback (1954), and later studied by Giroux *et al.* (2010) and Whitmore *et al.* (2013). The most recent formal definition of harpes was provided by Giroux *et al.* (2010), who defined the harpes as 'paired, sclerotized processes arising from the anterior [= ventral] margin of the phallic tube [= paraphallus or sclerotized dorsal part of phallic tube *sensu* Whitmore *et al.* 2013] distal to the vesica and spreading ventro-medially over the base of the lateral styli'. This concept clearly defines the position of the harpes with regard to the vesica and the base of the lateral styli. However, it is not sufficiently clear whether the position of these structures along the ventral margin of the paraphallus is either (1) close to the vesica, and as such distal to it, or (2) close to the hinge between the paraphallus and the juxta, and as such inserted proximal to it. Whitmore *et al.* (2013) followed Giroux *et al.*'s (2010) definition, and they added information about the position of harpes with regard to other paraphallic structures found in the subgenus *Sarcophaga* (*Heteronychia*).

When defining the paraphallic (or phallic) window in *Sarcophaga* (*Heteronychia*) as 'a translucent area visible in lateral view dorsad to the harpes', Whitmore *et al.* (2013) stated that the harpes are not the most apical structure along the ventral paraphallic margin, but at least in *Sarcophaga* (*Heteronychia*), the paraphallic window (Whitmore *et al.*, 2013: fig. 4A) (Fig. 37A) is distal to the harpes. Through observations of species of other subgenera of *Sarcophaga*, we found the paraphallic window usually situated laterally or ventro-laterally on the paraphallus proximad to the juxta. Similar translucent areas of the paraphallus are found in the genus *Lepidodexia* (Fig. 32F), but they are not as clearly identifiable as in *Sarcophaga* ('pw' in Fig. 37A). Consequently, we coded the paraphallic window as present only in the latter genus. In genera with no paraphallic window, the ventro-lateral surface of the paraphallus is usually sclerotized, and the corner closest to the juxta is rounded, with the harpes emerging from a position slightly proximad to this.

With the variations in the configuration of the harpes described by Whitmore *et al.* (2013) and Buenaventura & Pape (2015), there is a need for a more detailed definition of this structure. Whitmore *et al.* (2013) proposed a division of the harpes into a proximal part and a distal part. Later, Buenaventura & Pape (2015) confirmed the presence of harpes, as defined by Giroux *et al.* (2010) and as further elaborated by Whitmore *et al.* (2013), in the genera *Helicobia*, *Lipoptilocnema* and *Sarcophaga*. Buenaventura & Pape (2015) confirmed Whitmore *et al.*'s (2013) finding of a desclerotized strip ('hh' in Figs 9F, 23A, D, 24B–D, 31B, E, 32F, 37A, B, E) in the area between the proximal and distal parts of the harpes, which can be used as a landmark indicating the origin of the distal part. In Giroux *et al.*'s (2010) definition, the harpes spread ventro-medially over the base of the lateral styli, but according to Buenaventura & Pape (2015), the paraphallic wall and proximal part of the harpes have the same orientation, thus the proximal part of the harpes is a continuation of the paraphallic wall (Fig. 37A, F). The distal part of the harpes is often twisted or rotated ('rh' in Figs 23A, D, 24G, 32C, 37A, B, F) to become perpendicular to the proximal part, and sometimes spreads ventro-medially over the base of the lateral styli (Figs 23A, D, 24D, 32C, G, 37E, I), as described by Giroux *et al.* (2010). According to Buenaventura & Pape (2015), this twist or rotation occurs only in the genera *Lipoptilocnema* ('rh' in Fig. 24B, G) and *Sarcophaga* ('rh' in Fig. 37A, B, E, F), but here we also found it in the genera *Emblemasoma* ('rh' in Fig. 23A, D) and *Lepidodexia* (including *Archimimus*) ('rh' in Figs 9F, 32A, C, F). According to our observations, the distal part of the harpes is spreading ventro-medially over the base of the lateral styli only in *Lepidodexia*, *Lipoptilocnema* and *Sarcophaga*. Other genera bearing harpes have a slightly different configuration without a hinge or desclerotized demarcation dividing the proximal and distal parts, which means that the harpes are straight over their full length as found in the genera *Austrophyto* (Fig. 38F), *Boettcheria*, *Chrysagria* ('h' in Figs 11A, 30I), *Helicobia* (Fig. 22G, H) and *Microcerella* (Fig. 29F). The main consequence of these observations is that the 'small expansions of the anterior [= ventral] margin of the paraphallus' of *Engelimyia* (Buenaventura & Pape, 2015: figs 1g, 4) are considered here as simple expansions that do not need a special term and are not considered as homologous to the harpes nor as part of the vesica.

To summarize, we expand Giroux *et al.*'s (2010) definition of harpes, add precision to the observations by Whitmore *et al.* (2013) and Buenaventura & Pape (2015) and define these structures as paired, sclerotized processes arising from the apical half of the paraphallic ventral margin proximal to the juxtal hinge; their position is proximad to the paraphallic window and distad to the vesica and paraphallic lateral expansions, and their distal margin is always distal to the distal margin of the paraphallic blinkers, distal and apical expansions ('h' in Fig. 1). In ventral view, the proximal margin of the harpes is usually at the same level to the base of the lateral styli and median stylus, or slightly proximal to them (Fig. 1); in some genera the harpes may be subdivided into a proximal and distal part, but in most taxa they are not subdivided. In taxa where this subdivision is found, the sagittal plane of the proximal part is always in the same orientation as the paraphallic wall, while sometimes there is a 90° rotation of the distal part. The distal part of the harpes always spreads parallel to the lateral styli and median stylus, either in a distal position with regard to the base of the lateral styli or in a lateral position with regard to the base of the lateral styli and median stylus; the shape of the distal part of the harpes is very variable and can be elongated, rounded, with or without spinous processes, flat or bulbous, translucent or strongly sclerotized. The harpes may or may not be connected to the (remaining) paraphallus by a hinge or a desclerotized strip that can be used as landmark to identify their origin ('ho' in Figs 23A, 24B, 32A, F, 37F).

Based on our definition of the harpes, these structures are found only in genera belonging to clade 80, which includes *Austrophyto*, *Boettcheria*, *Chrysagria*, *Emblemasoma*, *Helicobia*, *Halliosca*, *Lepidodexia* (including *Archimimus*), *Lipoptilocnema*, *Microcerella* and *Sarcophaga*. Only *Emblemasoma* ('ph' and 'dh' in Fig. 23A, B, D), *Lepidodexia* (including *Archimimus*) (Figs 9F, 31B, E, 32A, F), *Lipoptilocnema* (Fig. 24B, G) and *Sarcophaga* (Fig. 37A, B, F) possess harpes with a clear separation into a proximal and a distal part. A 90° rotation of the distal part of the harpes is only found in the genera *Lepidodexia* (including *Archimimus*) ('rh' in Fig. 32A, C, F), *Lipoptilocnema* ('rh' in Fig. 24B, G) and *Sarcophaga* ('rh' in Fig. 37A, B, E, F). The harpes seem to have evolved only once in the Sarcophaginae, in the ancestor of clade 80 (Fig. 2B). Structures considered as harpes in *Peckiamyia* and *Retrocitomyia* by Buenaventura & Pape (2015) are here homologized with hillae and vesical lateral arms, respectively.

Although the subdivision of the harpes into proximal and distal parts as described by Whitmore *et al.* (2013) was proposed in the context of the subgenus *Sarcophaga* (*Heteronychia*), it may be applicable to most or all *Sarcophaga*. In their definition, the proximal part is 'protruding ventrally [i.e. with regard to the ventral margin of the paraphallic wall] in lateral view, either rounded, elbow-shaped, or somewhat squared-off distally'. This protruding part as described by Whitmore *et al.* (2013) is only present in the genus *Sarcophaga*. Whitmore *et al.* (2013) described a 'discontinuity being a desclerotized strip of variable extension corresponding with a bend in the harpes' or 'the distal part is separated from the proximal part by a crease or displaced medially, sometimes forming a horizontal, concave ledge', both of which are here interpreted as landmarks to indicate the origin of the distal part of the harpes in *Sarcophaga*. We agree with Whitmore *et al.* (2013) when they defined an 'apical process' of harpes as 'a prolongation of the distal part'. The apical process as described by Whitmore *et al.* (2013) seems to be present only in the genus *Sarcophaga* ('ah' in Fig. 37E, F), since it is difficult to distinguish from the remaining distal part of the harpes in *Lepidodexia* and *Lipoptilocnema*. The apical process is coded as present only in *Sarcophaga*.

Juxta

Following the definition for juxta provided by Buenaventura & Pape (2015), we found this structure to be present in all genera of Sarcophaginae. The presence of a juxta is considered as a groundplan character state for this subfamily, and it is shared with the subfamily Paramacronychiinae. In the early lineages of the Sarcophaginae (Fig. 2A), there is a 'non-demarcated juxta grade', where the juxta is not clearly delimited from the remaining paraphallic wall by a hinge or a desclerotized strip. However, the distal position of the juxta with respect to the paraphallus, its proximality to the acrophallus, as well as its ventral curvature over the styli, are features useful for identifying the juxta when there is no evident demarcation between it and the paraphallus, such as a hinge or a desclerotized strip.

The 'non-demarcated juxta grade' is paraphyletic with regard to the remaining (and 'juxtate') Sarcophaginae, and is composed of the genera *Argoravinia*, *Bahamiola*, *Dexosarcophaga* (including *Cistudinomyia*), *Malacophagomyia* (including *Dodgeisca*), *Malacophagula*, *Nephochaetopteryx*, *Oxysarcodexia*, *Oxyvinia*, *Rafaelia*, *Ravinia*, *Rettenmeyerina*, *Sarcofahrtiopsis* (including *Pacatuba*), *Sarothromyiops* and *Tricharaea* (Fig. 2A). Within this grade, the 'lower' sarcophagines [the tribes Sarcophagulini and Raviniini of Lopes (1969a)] all have a hood-shaped juxta, which is variously modified: *Tricharaea* has the ventral juxtal margin smooth laterally and wrinkled medially ('j' in Figs 27A, 39H), *Sarcofahrtiopsis* (including *Pacatuba*) has the ventral juxtal margin globose and denticulated (Figs 19E–G, 28H–J), *Bahamiola* (Figs 15G, H, 30B), *Nephochaetopteryx* (Figs 18A, 29H), *Oxysarcodexia* (Figs 18D, G, H, 19A) and *Ravinia* (Figs 10C, D, 14G, H) have the ventro-lateral juxta smooth proximally and wrinkled distally, *Dexosarcophaga* (including *Cistudinomyia*) (Figs 11D–F, I, 16A) and *Oxyvinia* (Fig. 19B) possess an even and smooth ventral juxtal margin, while in *Rettenmeyerina* (Fig. 28B, D) there is a desclerotized area between the paraphallus and the juxta. The antero-lateral, wrinkled juxtal margin of *Tricharaea* forms a funnel (Fig. 39H), while it is enlarged and shaped like a capsule in *Sarcofahrtiopsis* (including *Pacatuba*) (Figs 19E–G, 28H–J), denticulated and ornamented in *Bahamiola* (Fig. 15G, H), *Nephochaetopteryx* (Figs 18A, 29H) and *Oxysarcodexia* (Fig. 18D, H), and slightly swollen in *Ravinia* (Figs 10C, D, 14G, H). The remaining genera within the 'non-demarcated juxta grade' have a curved juxta not forming a hood-shaped structure; it is small to vestigial in *Argoravinia* (Fig. 15A, E), smooth and composed of two small acute processes at the apex in *Malacophagomyia* (including *Dodgeisca*) (Figs 16C, D, 17A, B), or composed of one or two medium-sized processes in *Malacophagula* (Fig. 17G), *Rafaelia* (Fig. 14A, B) and *Sarothromyiops* (Fig. 21A).

According to our phylogeny (Fig. 2B), a demarcation between the rest of the paraphallus and the juxta arose in the ancestor of clade 38 ('jd' in Figs 9F, 12C, 16G, 21F, I, 28E, 29F, 30C, F, I, 34A, 35G, 36E, 37D). The juxta is partially to completely fused to the acrophallic structures (except the capitis) in all genera of clade 39 (Fig. 2B), which comprises *Blaesoxipha*, *Comasarcophaga*, *Emdenimyia*, *Fletcherimyia*, *Mecynocorpus*, *Panava*, *Promayoa*, *Sarcodexiopsis*, *Spirobolomyia*, *Thomazomyia*, *Titanogrypa* and *Villegasia*. In lateral view, the sarcophagine distiphallus generally has an arching juxta, although in the genera of clade 39, this structure is usually straight and follows the acrophallus (Figs 12A, 28E, 35G, H), to whose structures it is attached, while in *Emblemasoma* (Fig. 23A, D), *Halliosca* and *Lepidodexia* (including *Archimimus*) (Figs 9F, 32A), the juxta is angled with regard to the remaining paraphallus, and probably also attached to the acrophallus. Usually, the juxtal demarcation is a simple desclerotization in the otherwise continuous paraphallic wall (Figs 10F, 12C, 16H, 28A, 39A). In the genera *Tripanurga* (Fig. 27E) and *Udamopyga* (including *Carinoclypeus*) (Figs 30G, 34B, 38A, B), the juxta is slightly recessed within the phallic tube, deeply so in the genus *Sinopiella* (Fig. 21D, F). The juxta is accordingly displaced to a position 'sunken' into the phallic tube (Figs 27E, 30G, 34B, 38A) in *Tripanurga* and *Udamopyga* (including *Carinoclypeus*), while it is displaced ventrally (Figs 31C, 32A, F) in *Emblemasoma*, *Halliosca* and *Lepidodexia* (including *Archimimus*).

Generic circumscriptions

Genus Argoravinia

Head squared in profile, with squared anterior and posterior genal corners in profile; gena and postgenal with at least some white setulae; postalar wall setulose; stem of wing vein $R_{2+3+4+5}$ with ventral setulae elongated*; wing vein R_1 with setulae dorsally on basal half; male mid-femur with or without a ctenidium of rounded spines (circular cross section); male abdominal ST5 with posterior margin very widely V-shaped; cercal prong straight or almost straight, slightly bent backwards in *Argoravinia* (*s.s.*); pregonite proximally narrow and distally wide*; ejaculatory apodeme large; phallus with a distinct hinge between basi- and distiphallus; paraphallus dorso-distally rounded; paraphallus with paraphallic lateral expansions; vesica broad and flat; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae tapering*; hillae directed latero-ventrally, not touching the inner paraphallic wall; median stylus greatly elongated; median stylus S-shaped*; capitis as a smooth, rounded lobe, proximally swollen and strongly sclerotized*.

Subgenus Argoravinia (*s.s.*): male with 5–6 fronto-orbital setulae; epandrium with a lateral apophysis*; vesica superficially bifid; female T6 entire; female epiproct with one seta.

Subgenus Raviniopsis *Townsend*: male with 7–12 fronto-orbital setulae; epandrium without a lateral apophysis; vesica deeply bifid; female T6 divided; female epiproct with two setae.

Genus Austrophyto

Arista plumose in at most basal half; male with rows of frontal setae diverging anteriorly; parafacial plate with strong setae; thorax with metallic grey/golden stripes (highly contrasting with the blackish background); anepimeron with four strong setae and sparse weak setae; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind trochanter with a pad of short setae covering almost the entire posterior surface; male abdominal T5 higher than other abdominal tergites; male abdominal ST5 with a widely V-shaped cleft, with a swelling and a fold along cleft margin, and with a rounded or pointed lobe on the anterior half; epandrium and syntergosternite 7 + 8 orangish or reddish; cercal prong acute or almost acute; surstylus two to three times longer than wide; postgonite with two long setae*; phallus with a distinct hinge between basi- and distiphallus; phallus with a sclerotized, rigid and tubular ventral area between basi- and distiphallus; phallus with a paler ventral area between disti- and basiphallus; paler ventral area between disti- and basiphallus swollen*; vesica with a proximal desclerotized, microserrated and bilobed section*; distiphallus with a hinge between paraphallus and harpes; harpes parallel to the acrophallic structures; harpes enlarged ventrally, with a distal fold and a roughened surface; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; distiphallus with a medial juxtal sclerite*; juxta as two apico-lateral membranous lobes*.

Genus Bahamiola

Male with two proclinate fronto-orbital setae; notopleuron with subprimary setae; two katepisternal setae; postalar wall bare; third costal sector of wing bare ventrally; wing vein R_1 bare dorsally; male hind coxa with posterior setulae reduced (usually bare, occasional specimens with one or a few setulae); male ST5 with posterior margin straight or with a shallow concavity; male ST5 with a central patch of setae; phallus with basi- and distiphallus connected by a desclerotized strip; vesical arm-shaped lever not elongated; vesical arm-shaped lever bilobed distally; vesica with distal section ornamented; acrophallus formed of a capitis, lateral styli and a median stylus; juxta hood-shaped, with a smooth surface and with ventral margin enlarged to form a capsule; spermathecae oval; female without an epiproct.

Genus Blaesoxipha

Postalar wall setulose; wing vein R_1 without dorsal setulae; male mid-femur with a ctenidium of rounded

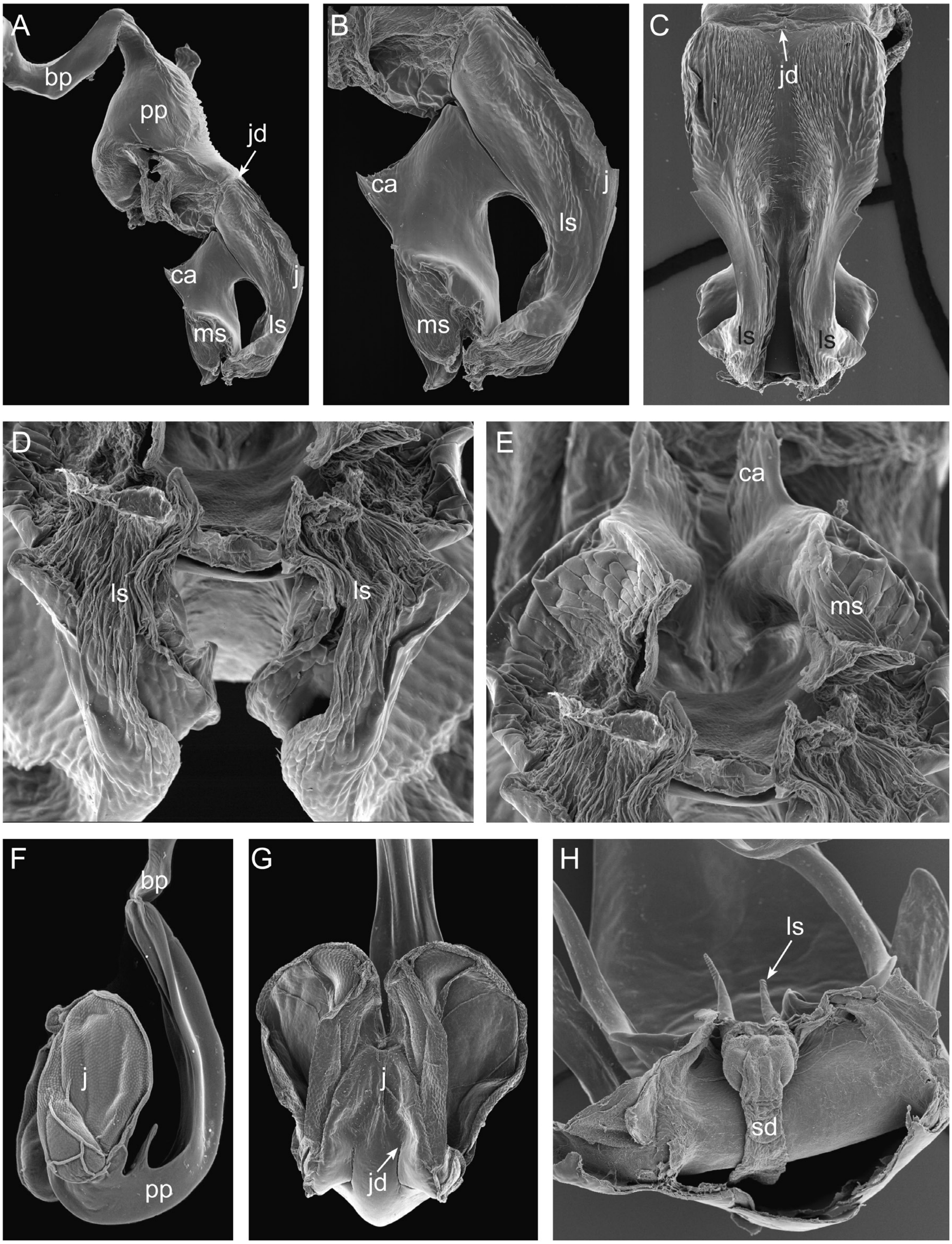

Figure 12. A, distiphallus, left lateral view: *Panava inflata*. B, acrophallus, left lateral view: *Panava inflata*. C, acrophallus, apical view: *Panava inflata*. D, lateral styli, ventral view: *Panava inflata*. E, median stylus and capitis, ventral view: *Panava inflata*. F, distiphallus, left lateral view: *Peckia* (*Pattonella*) *intermutans*. G, distiphallus, ventral view: *Peckia* (*Pattonella*) *intermutans*. H, lateral styli and sperm duct, postero-apical view: *Peckia* (*Pattonella*) *intermutans*. [F, courtesy M. Giroux; G, H, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

spines (circular cross section); male hind tibia with apical postero-ventral seta well differentiated; male hind trochanter with a postero-median row of spines; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in the proximal half; cercal prong with spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; phallus with a distinct hinge between basi- and distiphallus; vesica reduced or not developed; distiphallus not surrounding the acrophallus, styli entirely exposed; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli fused through a ventromedian bridge proximal to the median stylus; lateral styli collapsed and with no outlet; lateral styli plate-like, with digitate margins or finger-shaped processes; capitis flat and simple; median stylus with a distinct opening; median stylus straight; juxta partially or entirely fused to acrophallic structures; juxta straight; distal margin of juxta with spine-like processes.

Genus Boettcheria

Arista plumose in at most basal half; six or more frontal setae below dorsal limit of lunule*; male with rows of frontal setae diverging anteriorly; parafacial plate with strong setae; thorax with metallic grey/golden stripes (highly contrasting with the blackish background); anepimeron with four strong setae and sparse weak setae; postalar wall bare; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind trochanter with a postero-ventral brush-like clump of short, stubby setae distally*; male abdominal T5 higher than other abdominal tergites; male abdominal ST5 with a widely V-shaped cleft, with a swelling and fold along cleft margin, and with a rounded or pointed lobe on the anterior half; syntergosternite 7 + 8 blackish; cercal prong acute or almost acute; surstylus two to three times longer than wide; phallus with a distinct hinge between basi- and distiphallus; phallus with a sclerotized, rigid and tubular ventral area between basi- and distiphallus; vesica convoluted*; distiphallus with a hinge between paraphallus and harpes; harpes parallel to the acrophallic structures; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta squared with proximal corners slightly elongated*.

Genus Chrysagria

Two katepisternal setae; postalar wall setulose; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male abdominal ST5 with a widely V-shaped cleft, with a rounded or pointed process halfway between the angle and tip of the V; cercal prong acute or almost acute; cercus with a median tuft of long brown and yellow setae directed medially*; phallus with a distinct hinge between basi- and distiphallus; distiphallus with a hinge between paraphallus and harpes; proximal and distal parts of harpes fused; distal part of harpes entirely or partly desclerotized; harpes protruding parallel to lateral styli; acrophallus formed of the lateral styli and capitis; lateral styli tube-shaped and with an outlet; lateral styli long and curved, reaching beyond apex of distiphallus; capitis flat and simple; juxta composed of two elongated and smooth segments*; female abdominal ST9 in the shape of a plough-like larvipositor.

Genus Comasarcophaga

Pedicel length more than twice its width*; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in distal or subapical position; cercal prong with spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; phallus with a distinct hinge between basi- and distiphallus; paraphallic blinkers rounded with a ventral sclerotized area*; distiphallus partially surrounding the acrophallus, styli usually visible in lateral view; vesica bulbous; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped, with an outlet; lateral styli usually exposed in profile; capitis flat and simple; median stylus with a distinct opening; median stylus straight; juxta entirely separated from acrophallic structures; juxta straight to slightly arching; distal margin of juxta without spine-like processes.

Genus Dexosarcophaga

Male with rows of frontal setae almost parallel; occipital setulae above occipital foramen black; postalar wall setulose; wing vein R_1 bare dorsally; male mid-femur with a ctenidium of rounded spines (circular cross section); pregonite C-shaped*; phallus with a distinct hinge between basi- and distiphallus; vesical arm-shaped lever gently angled; vesica with distal section bifid and not particularly ornamented; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae long spoon-shaped with a squared apex; juxta hood-shaped with a smooth surface; female tergite 8 with broad and ventro-laterally truncated halves connected medially by a narrow strip.

Subgenus Cistudinomyia: posterior postgenal setulae white; epandrium reddish, usually the same colour as syntergosternite 7 + 8; distiphallus without paraphallic distal expansions.

Subgenus Dexosarcophaga: genal and postgenal setulae generally black; white setulae, when present, are very scarce and restricted to the posteriormost part of the postgena; epandrium blackish, usually the same colour as syntergosternite 7 + 8*; distiphallus with paraphallic distal expansions.

Genus Duckemyia

Male with one or two proclinate fronto-orbital setae; facial ridge with dense setosity on lower 0.85; postalar wall setulose; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft; cercal prong bilobed; cercal prong with a pointed tip; postgonite perpendicular to body axis; phallus almost as short or shorter than pregonite; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; vesica three-lobed composed of a proximal section not divided and two vesical lateral arms; vesical lateral arms ribbon-like*; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; hillae directed ventrally; hillae sclerotized; hillae paddle-like; hillae touching the inner paraphallic wall only at apex; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta squared, with distal margin even; juxta flat or slightly concave.

Genus Emblemasoma

Facial plate almost equibroad along its entire length*; parafacial plate widest at level of lunule*; palpus with long setae*; prosternum enlarged anteriorly*; three postsutural acrostichal setae; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male mid-femur with 1–4 setae at mid-length on antero-dorsal surface*; male abdominal ST5 with a wide V-shaped cleft and with a rounded to pointed process midway between the angle and tip of the V; cercal prong abruptly swollen and with a blunt apex*; phallus with a distinct hinge between basi- and distiphallus; vesica composed of two leaf-shaped lobes*; paraphallic apical expansions present; distiphallus with a hinge between paraphallus and harpes; proximal and distal parts of harpes separated by a hinge; distal part of harpes sclerotized; harpes parallel to lateral styli and median stylus; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta angled; juxta squared with an undulated distal margin; juxta slightly displaced anteriorly.

Genus Emdenimyia

Facial ridge with long dense setosity along its full length*; proepisternum setulose; postalar wall setulose; third costal sector of wing setulose ventrally; male hind trochanter with a postero-ventral brush-like clump of short, stubby setae medially*; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong without a bend; cercal prong without spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; phallus with a distinct hinge between basi- and distiphallus; basiphallus compressed laterally; basiphallus with a dorsal longitudinal keel; paraphallus tube-shaped and open dorsally*; distiphallus not surrounding the acrophallus, styli entirely exposed; vesica reduced or not developed; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli collapsed and with no outlet; lateral styli plate-like, with digitate margins; lateral styli directed dorsally*; median stylus with a distinct opening; median stylus straight; median stylus balloon-like*; juxta partially to entirely fused to acrophallic structures; juxta straight; distal margin of juxta with spine-like processes.

Genus Engelimyia

Postalar wall setulose; wing vein R_1 setulose dorsally; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind femur curved; male abdominal ST3 with one patch of dense, erect, black, setae*; male abdominal ST4 with two patches of dense, erect, black, setae; male abdominal ST5 with a widely V-shaped cleft; male ST5 with a small pad of strong short setae medially on inner margin of cleft; cercal prong gradually swollen with a knob-like apex; cercal prong with dorso-lateral keels; cercal prong with a lateral tuft of long setae; paraphallic tube as long as wide; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli with stylar lateral plates; lateral styli with stylar membranous lobes*; juxta globose, spiny and denticulated.

Genus Fletcherimyia

Postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in distal or subapical position; cercal prong without spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; phallus with a distinct hinge between basi- and distiphallus; distiphallus not surrounding the acrophallus, styli entirely exposed; vesica as a single, tongue-shaped structure; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped, with an outlet; median stylus with a distinct opening; median stylus straight; juxta entirely or partially fused to acrophallic structures; juxta straight to slightly arching; distal margin of juxta without spine-like processes; juxta with cuticular pubescence along its distal margin*; female abdominal T6 strongly convex; female abdominal ST6–7 fused.

Genus Halliosca

First flagellomere not elongated, two to three times the length of pedicel; facial ridge with scattered, not particularly dense setosity; distance between occiput and antennal base shorter than distance between occiput and vibrissal angle; proepisternum bare; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft, with two pointed black cuticular processes on the angle of the V; cerci with a proximal tuft of long black setae; cercal prong bent at mid-length; proximal margin of surstylus overlapping the hinge between epandrium and surstylus; margin of surstylus slightly folded or protruding outwards; phallus with a distinct hinge between basi- and distiphallus; paraphallic apical expansions present; distiphallus with a hinge between paraphallus and harpes; proximal and distal parts of harpes fused; distal part of harpes sclerotized; harpes parallel to lateral styli and median stylus; vesica bulbous; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta arching in lateral view; juxta squared with an undulated distal margin; juxta not displaced relative to longitudinal axis of phallic tube.

Genus Helicobia

Ocellar and vertical setae strong; parafacial plate with strong setae; postcranium concave or flat; three post-sutural dorso-central setae; postalar wall setulose; third costal sector of wing bare ventrally; wing vein R_1 setulose dorsally; male mid-femur without a ctenidium; male hind trochanter with a medial pad of short bristly setae, and with a strong seta at its posterior margin*; male hind tibia with apical postero-ventral seta well differentiated; male abdominal ST5 with a widely V-shaped cleft, with a rounded or pointed process halfway between the angle and tip of the V; cercal prong acute or almost acute; phallus with a distinct hinge between basi- and distiphallus; distiphallus with a hinge between paraphallus and harpes; proximal and distal parts of harpes fused; distal part of harpes entirely or partly desclerotized; harpes protruding parallel to lateral styli and median stylus; acrophallus formed of the lateral styli and capitis; lateral styli tube-shaped and with an outlet; capitis recurved; juxta dome-shaped with juxtal lateral plates; female T6 with a mid-dorsal desclerotized, fine strip or narrow membranous longitudinal cleft.

Genus Lepidodexia

Male abdominal ST5 with a widely V-shaped cleft, with a rounded expansion taking up the entire posterior half*; phallus with a distinct hinge between basi- and distiphallus; paraphallic apical expansions present; distiphallus with a hinge between paraphallus and harpes; proximal and distal parts of harpes separated by a hinge; vesica bipartite: with a C-shaped medial section and a convex, sclerotized distal section*; vesica with a proximal spinous lobe*; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; juxta angled relative to phallic tube; juxta squared with an undulated distal margin; juxta slightly displaced anteriorly relative to longitudinal axis of phallic tube*

Additional character states for internal classification of Lepidodexia: first flagellomere elongated, at least four times the length of pedicel (only in subgenera *Chlorosarcophaga*, *Dexomyophora* Townsend and *Notochaeta* Aldrich); facial ridge with dense setosity on lower 0.70 (only in subgenus *Dexomyophora*); male with proclinate fronto-orbital setae (only in subgenus *Neophyto* Townsend); postgenal setulae white or yellow (only in subgenus *Hallina* Lopes); distance between occiput and antennal base longer than distance between occiput and vibrissal angle (only in subgenera *Archimimus* and *Neophyto*); proepisternum setulose (only in subgenus *Notochaeta*); postalar wall setulose (only in subgenera *Chlorosarcophaga*, *Dexomyophora* and *Hallina*); third costal sector of wing setulose ventrally (except in subgenus *Hallina*); male mid-femur with a ctenidium of rounded spines (circular cross section) (only in subgenus *Archimimus*); male hind tibia with an apical postero-ventral seta differentiated (only in subgenera *Notochaeta* and *Neophyto*); male abdominal tergites metallic blue, purple or green (only in subgenus *Chlorosarcophaga* and some species of subgenus *Notochaeta*); pregonite distally spatulated (only in subgenus *Archimimus*); distal part of harpes sclerotized (except in subgenus *Hallina*); harpes dorso-medially over base of lateral styli (except in subgenus

Archimimus); median stylus tube-shaped and with an outlet (except in subgenus *Archimimus*).

Genus Lipoptilocnema

Male with rows of frontal setae divergent anteriorly; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft, with two pointed black cuticular processes on the angle of the V; cercal prong with a dorsal saddle-shaped excavation followed by a hump; cerci with a proximal tuft of long black setae; proximal margin of surstylus overlapping the hinge between epandrium and surstylus*; margin of surstylus slightly folded or protruding outwards; phallus with a distinct hinge between basi- and distiphallus; paraphalic dorsal wall with a shallow or deep desclerotized longitudinal strip; paraphallus with paraphallic proximal expansions; paraphallus with a spiny process arching over the juxta*; distiphallus with a hinge between paraphallus and harpes; harpes with a hinge between proximal and distal parts; distal part of harpes membranous*; harpes protruding dorso-medially over base of lateral styli; acrophallus formed of the lateral styli and capitis; lateral styli tube-shaped and with an outlet; capitis recurved; juxta recurved*; juxta triangular with longitudinal keel, laterally membranous, and apically bifid and spinose*.

Genus Malacophagomyia

Head squared in profile, with squared anterior and posterior genal corners in profile; postalar wall setulose; wing vein R_1 setulose dorsally; third costal sector of wing setulose ventrally; stem of wing vein $R_{2+3+4+5}$ with ventral setulae elongated; male abdominal ST4 with spine-like setae; male abdominal ST5 with posterior margin very widely V-shaped; cerci fused along their entire length*; phallus with a distinct hinge between basi- and distiphallus; paraphallus dorso-distally rounded; paraphallus with paraphallic lateral expansions; vesica broad and flat; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae directed latero-ventrally, not touching the inner paraphallic wall; hillae membranous distally*; median stylus greatly elongated; median stylus curved*; juxta arching over the lateral styli; juxtal apex with two pointed processes*.

Subgenus Dodgeisca: male mid-femur with a ctenidium of rounded spines (circular cross section); pregonite straight, sclerotized, as long as phallus; hillae tube-like distally*.

Subgenus Malacophagomyia: male mid-femur without a ctenidium; pregonite shorter than phallus, with a membranous area along the ventral margin and near the bent apical part (except in *Malacophagomyia rivadavia* Mulieri & Mello-Patiu, 2013); hillae filiform with a wide or bifid apex*.

Genus Malacophagula

Head rounded in profile*; first flagellomere shortened, at most two times the length of pedicel*; lunule widened*; parafacial plate with strong setae; postgena swollen in lateral view*; third costal sector of wing bare ventrally; postalar wall bare; lower calypter rounded*; male mid-femur with or without a ctenidium; male hind tibia with apical postero-ventral setae well differentiated; male abdominal ST5 with posterior margin very widely V-shaped, with an obtuse inner angle; paraphallus dorso-distally rounded; vesica broad and flat, with two small, rounded medial lobes; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae directed latero-ventrally, not touching the inner paraphallic wall; juxta demarcated.

Genus Mecynocorpus

Postalar wall setulose; wing vein R_1 setulose dorsally; male mid-femur with a ctenidium of flattened spines (oval or rectangular cross section); male hind tibia with apical postero-ventral seta well differentiated; male hind trochanter without a postero-median row of spines; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in the proximal half; cercal prong with spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; phallus with a distinct hinge between basi- and distiphallus; vesica reduced or not developed; distiphallus not surrounding the acrophallus, styli entirely exposed; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli fused through a ventro-median bridge proximal to the median stylus; lateral styli collapsed and with no outlet; lateral styli plate-like, with digitate margins or finger-shaped processes; capitis flat and simple; median stylus cone-shaped and noticeably widened*; median stylus with a distinct opening; median stylus straight; juxta partially fused to acrophallic structures; juxta straight; distal margin of juxta with spine-like processes.

Genus Microcerella

Eyes green*; arista plumose in at most basal half; male with rows of frontal setae diverging anteriorly; parafacial plate with strong setae; thorax with metallic grey/golden stripes (highly contrasting with the blackish background); anepimeron with four strong setae and sparse weak setae; postalar wall bare; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind trochanter with a pad of short setae covering almost the entire posterior surface; male abdominal T5 higher than other abdominal tergites; male abdominal ST5 with a widely V-shaped cleft, with a swelling and a fold along cleft margin, and with or without a rounded or pointed lobe on the anterior half; epandrium orangish or reddish, contrasting with the blackish colour of syntergosternite 7 + 8*; hypandrium swollen at level of pregonite*; cercal prong acute or almost acute; surstylus two to three times longer than wide; phallus with a distinct hinge between basi- and distiphallus; phallus with a sclerotized, rigid and tubular ventral area between basi- and distiphallus; phallus with a paler ventral area between disti- and basiphallus; paler ventral area between disti- and basiphallus flat; vesica bulbous; distiphallus with a hinge between paraphallus and harpes; harpes parallel to the acrophallic structures; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta campanulated to oval*.

Genus Nephochaetopteryx

Male with one or two proclinate fronto-orbital setae; notopleuron with subprimary setae; postalar wall setulose; metasternum setulose; hind coxa with strong setae posteriorly*; mid-tibia with neither antero-dorsal nor antero-ventral setae*; male mid-femur with a ctenidium of rounded spines (circular cross section); wing vein R_1 setulose dorsally; third costal sector of wing bare ventrally; wing fumose between apical part of veins R_{2+3} and C*; male terminalia red or black; male abdominal ST4 with a dense patch of erect black setae near posterior margin; phallus with basi- and distiphallus connected by a desclerotized strip; vesical arm-shaped lever not elongated, strongly angled in lateral view; vesica with distal section ornamented; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli with hillae directed proximally, sclerotized and long spoon-shaped; juxta hood-shaped, ornamented, smooth proximally and wrinkled distally; puparial spiracles in a shallow depression.

Genus Oxysarcodexia

Male with rows of frontal setae almost parallel; postalar wall setulose; tegula blackish and basicosta orange; male mid-femur with a ctenidium of flattened spines (oval or rectangular cross section); phallus with basi- and distiphallus connected by a desclerotized strip; paraphallus antero-proximally with a lateral triangular expansion proximal to the vesica*; vesical arm-shaped lever not elongated, strongly angled in lateral view; distal section of the vesica very ornamented; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli with hillae directed proximally, sclerotized and long spoon-shaped; juxta hood-shaped, ornamented, smooth proximally and wrinkled distally; juxta with a proximal convex membranous expansion*; larva I with convoluted, festoon-like oral ridges; larva I with rim of spiracular cavity microtrichose.

Genus Oxyvinia

Male with rows of frontal setae almost parallel; parafacial plate with setulae only; occipital setulae above occipital foramen black; anterior postgenal setulae black; postalar wall setulose; male mid-femur with a ctenidium of rounded spines (circular cross section); male terminalia red; phallus with a distinct hinge between basi- and distiphallus; paraphallus bent in its proximal third*; vesical arm-shaped lever gently angled; vesica with distal section bifid and not particularly ornamented; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae long spoon-shaped with a squared apex; juxta hood-shaped with a smooth surface; larva I with straight, festoon-like oral ridges; larva I with rim of spiracular cavity microtrichose.

Genus Panava

Male with one or two proclinate fronto-orbital setae; parafacial plate with setulae only; wing vein R_1 setulose dorsally; third costal sector of wing setulose ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia without an apical postero-ventral seta; surstylus with an apical patch of microsetulae; male abdominal ST5 cleft with subparallel sides; phallus with a distinct hinge between basi- and distiphallus; basiphallus with a dorsal hump at junction with distiphallus; basiphallus long and slender; vesica composed of two elongated bifid parts; distiphallus not surrounding the acrophallus, styli entirely exposed; acrophallus formed of a capitis, lateral styli and a median stylus; external walls of lateral styli fused medially*; lateral styli tube-shaped; median stylus with a distinct opening; median stylus straight; capitis wide and denticulated; juxta partially to entirely fused to acrophallic structures; juxta Y-shaped in frontal view.

Genus Peckia

Postalar wall setulose; third costal sector of wing bare ventrally; lower calypter with fringe of long, hair-like setulae along outer margin, extending to – or almost to – the posterior corner*; male mid-femur with or without a ctenidium; male abdominal ST5 with a widely

V-shaped cleft, with a rounded or pointed process halfway between the angle and tip of the V; cercal prong with a dorsal saddle-shaped excavation followed by a hump; phallus with a distinct hinge between basi- and distiphallus; paraphallic tube wider than long*; harpes reduced*; acrophallus formed of the lateral styli; lateral styli tube-shaped and with an outlet; lateral styli long and curved, reaching beyond apex of distiphallus; capitis reduced*; juxta dome-shaped, with juxtal lateral plates; female abdominal T6 divided into two lateral plates door-like closing the terminalia.

Genus Peckiamyia

Facial ridge with dense setosity on lower 0.85; postgenal setulae much longer than genal setulae*; postalar wall setulose; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male ST4 with two patches of dense erect black setae near posterior margin; male abdominal ST5 with a widely V-shaped cleft; cercal prong bilobed; cercal prong with a pointed tip; surstylus with a proximal lobe-shaped expansion*; surstylus with stubby setae on proximal half*; postgonite perpendicular to body axis; pregonite with strong proximal setae*; phallus almost as short or shorter than pregonite; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; vesica three-lobed, whose proximal section has a shallow proximal division giving two joined lobes*; vesical lateral arms trapezoid*; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; hillae directed ventrally; hillae sclerotized; hillae paddle-like; hillae touching the inner paraphallic wall only at apex; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta squared, with even distal margin; juxta flat or slightly concave.

Genus Promayoa

Postalar wall bare; wing vein R_1 setulose dorsally; third costal sector of wing setulose ventrally; dorsal setulae on wing vein R_{4+5} reaching crossvein r-m; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong rounded and narrow in posterior view; cercal prong straight or almost straight; surstylus equal to or longer than cercus; surstylus with an apical patch of microsetulae; phallus with a distinct hinge between basi- and distiphallus; basiphallus with a dorsal hump at junction with distiphallus; basiphallus long and slender; vesica composed of two elongated parts; distiphallus not surrounding the acrophallus, styli entirely exposed; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli not fused medially; lateral styli plate-like, with digitate margins or finger-shaped processes; median stylus with a distinct opening; median stylus straight; capitis wide and denticulated; juxta entirely fused to acrophallic structures; juxta straight.

Genus Rafaelia

Head squared in profile, with squared anterior and posterior genal corners in profile; parafacial plate with strong setae; gena and postgenal with at least some white setulae; postalar wall setulose; wing vein R_1 setulose dorsally (bare in *Rafaelia natiuscula* [Lopes, 1941]); third costal sector of wing bare ventrally; dorsal setulae on wing vein R_{4+5} not reaching crossvein r-m; male mid-femur without a ctenidium; male hind tibia with apical postero-ventral seta well differentiated; male abdominal ST5 with posterior margin very widely V-shaped; cercal prong straight or almost straight; phallus with a distinct hinge between basi- and distiphallus; paraphallus dorso-distally rounded; hypophallus globose, weakly sclerotized, with only the very apex of the vesica sclerotized*; vesica broad and flat, with two small, rounded to flattened medial lobes; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae directed latero-ventrally, not touching the inner paraphallic wall; juxta demarcated.

Genus Ravinia

Male with rows of frontal setae almost parallel; postalar wall setulose; tegula orange or yellowish, concolorous with basicosta; male mid-femur with a ctenidium of flattened spines (oval or rectangular cross section); phallus with basi- and distiphallus connected by a desclerotized strip; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli with blunt or distally pointed hillae*; hillae with a membranous bladder and/or a groove; vesica narrow and flake-shaped*; vesical arm-shaped lever straight proximally*; distal section of the vesica flat to reduced*; juxta hood-shaped, slightly swollen distally, partially wrinkled*; larva I with convoluted, festoon-like oral ridges; larva I with rim of spiracular cavity microtrichose.

Genus Retrocitomyia

Postalar wall setulose; tegula orange or yellowish; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft; cercal prong bilobed; cercal prong bilobed with a blunt tip*; cercal prong without dorso-medial setae*; postgonite perpendicular to body axis; phallus almost as short or shorter than pregonite; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; vesica three-lobed with a proximal section undivided and arch-shaped; vesical lateral arms paddle-like with a hook-shaped apex*; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; hillae directed ventrally; hillae sclerotized; hillae paddle-like; hillae touching the inner paraphallic wall only at apex; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta squared, with distal margin even; juxta undulated dorso-ventrally or with a median folding*.

Genus Rettenmeyerina

Male with one or two proclinate fronto-orbital setae; notopleuron with subprimary setae; postalar wall setulose; metasternum setulose; male mid-femur without a ctenidium; hind coxa setulose posteriorly; third costal sector of wing setulose ventrally; male terminalia red; male ST5 with a central patch of setae; phallus with a distinct hinge between basi- and distiphallus; vesical arm-shaped lever gently angled; vesica with distal section bifid and not particularly ornamented; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; desclerotized area between the paraphallus and the juxta; juxta hood-shaped with a smooth surface; spermathecae elliptical.

Genus Sarcodexiopsis *(possibly paraphyletic)*

Postalar wall setulose; wing vein R_1 setulose or bare dorsally; dorsal setulae on wing vein R_{4+5} not reaching crossvein r-m; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong straight or almost straight; apical half of surstylus with or without a patch of microsetae; phallus with a distinct hinge between basi- and distiphallus; basiphallus long and slender; basiphallus without a dorsal hump at junction with distiphallus; vesica bulbous; distiphallus not surrounding the acrophallus, styli entirely exposed; acrophallus formed of a capitis, lateral styli and a median stylus; median stylus with a distinct opening; median stylus straight; capitis wide and denticulated; lateral styli with or without a clear opening; lateral styli tube-shaped or plate-like, with digitate margins/finger-like processes; juxta entirely fused to acrophallic structures; juxta straight; distal margin of juxta smooth, with no spine-like processes.

Genus Sarcofahrtiopsis

Male with one or two proclinate fronto-orbital setae; notopleuron with subprimary setae reduced (usually entirely absent, occasional specimens with a single small subprimary seta); two katepisternal setae; postalar wall bare; third costal sector of wing bare ventrally; male hind coxa with posterior setulae reduced (usually bare, occasional specimens with one or a few setulae); male ST5 with posterior margin straight or with a shallow concavity; male ST5 with a central patch of setae; phallus with basi- and distiphallus connected by a desclerotized strip; vesical arm-shaped lever very elongated (twice its full length) ventrally; vesical arm-shaped lever with a hammer-shaped apex; distal section of the vesica globose, with small denticles; acrophallus formed of a capitis, lateral styli and a median stylus; juxta hood-shaped, with ventral margin enlarged to form a globose and denticulated hood; spermathecae oval; female without an epiproct.

Subgenus Pacatuba: male mid-femur with a ctenidium of rounded spines (circular cross section); wing vein R_1 bare dorsally; metasternum setulose.

Subgenus Sarcofahrtiopsis: male mid-femur without a ctenidium; wing vein R_1 setulose dorsally; metasternum with reduced setosity*.

Genus Sarcophaga

Male with rows of frontal setae divergent anteriorly; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur usually without a ctenidium; male hind trochanter with a postero-medial pad of short setae proximally*; male hind tibia with apical postero-ventral seta well differentiated; male abdominal ST5 with a widely V-shaped cleft; cercal prong with a dorsal saddle-shaped excavation followed by a hump; cerci with a proximal tuft of long, black setae; margin of surstylus slightly folded or protruding outwards; seta of postgonite slightly shortened*; seta of postgonite situated distal to middle*; phallus with a distinct hinge between basi- and distiphallus; paraphalic dorsal wall with a shallow or deep desclerotized longitudinal strip; paraphallus with proximal expansions; paraphallus with a window*; distiphallus with a hinge between paraphallus and harpes; harpes elbowed in proximal part*; harpes with a desclerotized strip between proximal and distal parts*; distal part of harpes entirely or partially desclerotized; distal part of harpes bearing an apical process*; harpes protruding dorso-medially over base of lateral styli; acrophallus formed of the lateral styli and capitis; lateral styli tube-shaped and with an outlet; lateral styli proximally coiled or spiraling*; capitis elongated, recurved and denticulated; juxta dome-shaped, with juxtal lateral plates.

Genus Sarothromyiops

Postalar wall bare; male mid-femur without a ctenidium; wing vein R_{4+5} with dorsal setulae reaching crossvein r-m; third costal sector of wing setulose ventrally; male terminalia black; cleft of abdominal ST5 of male without any special set of setae; male cercus dorso-laterally bare; cercal prong with subapical region swollen or curved; cerci with basal rounded expansions; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; basiphallus laterally compressed and with a longitudinal dorsal keel; vesica with no special mechanism of attachment to the hypophallus; vesica without divisions; vesica broad and flat; acrophallic levers absent; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; hillae filiform, latero-ventrally directed and touching the inner paraphallic wall only through the medial part; juxta without demarcation with respect to paraphallus; juxta with its lateral ends elongated ventrally.

Genus Sinopiella

Postalar wall setulose; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia without an apical postero-ventral seta; ST1–4 with white or yellow setae; male abdominal ST5 with a widely V-shaped cleft; cercal prong acute or almost acute; postgonite perpendicular to body axis; postgonite slightly swollen*; postgonite enlarged*; pregonite dorso-ventrally flattened and concave*; phallus almost as short or shorter than pregonite; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; paraphallus humped postero-distally*; vesica three-lobed with a proximal section undivided and lobe-shaped*; vesical lateral arms elongated with rounded apex*; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; lateral styli without hillae; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta deeply recessed within the phallic tube*; juxta squared, with anterior margin pointed*.

Genus Spirobolomyia

Tegula orange or yellowish; postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia with apical postero-ventral seta well differentiated; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in distal or subapical position; cercal prong with spine-like setae on dorsal surface; cercal prong with a proximal hump on dorsal surface; cercal prong with a sinuous lateral margin (dorsal view); postgonal apodeme elongated*; phallus with a distinct hinge between basi- and distiphallus; paraphallic blinkers rounded, with a membranous ventral tube-like process*; paraphallus with a strong keel on dorsal wall*; paraphallus with a beak-like projection arching over the juxta*; distiphallus surrounding the acrophallus, styli visible in lateral view; vesica bulbous; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped, with an outlet; lateral styli partially or entirely exposed in profile; lateral styli elongated; capitis flat and simple; median stylus with a distinct opening; median stylus greatly elongated; median stylus curved; juxta entirely separated from acrophallic structures; juxta straight; distal margin of juxta without spine-like processes; female abdominal ST6–8 fused; female abdominal T6 with the median part of the posterior margin devoid of setae, projecting and tongue-like.

Genus Tapacura

Postalar wall setulose; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft; cercal prong acute or almost acute; postgonite perpendicular to body axis; pregonite shorter than phallus; phallus short and compact; phallus with a distinct hinge between basi- and distiphallus; paraphallus with latero-ventral plate-like structures completely fused to the paraphallic wall and with a distal cleft; vesica three-lobed with a proximal section undivided and arch-shaped; vesical lateral arms disc-shaped; acrophallus formed of a capitis, hillae, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; hillae directed ventrally; hillae sclerotized; hillae paddle-like; hillae touching the inner paraphallic wall only at apex; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta squared, with anterior margin even and flat*.

Genus Thomazomyia

Postalar wall setulose; wing vein R_{4+5} with dorsal setulae reaching crossvein r-m; third costal sector of wing setulose ventrally; male mid-femur without a ctenidium; male hind trochanter with a postero-ventral brush-like clump of short, stubby setae proximally*; male hind tibia without an apical postero-ventral seta; male abdominal ST5 cleft with subparallel sides; cercal prong with a backwards bend in distal or subapical position; cercal prong with a proximal hump on dorsal surface; cercal prong without spine-like setae on dorsal surface; pregonite bifid distally; phallus with a distinct hinge between basi- and distiphallus; distiphallus not surrounding the acrophallus, styli entirely exposed; vesica bulbous; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli collapsed and with no outlet; lateral styli finger-like and small; capitis flat and simple; median stylus without distinct opening; median stylus straight; juxta partially to entirely fused to acrophallic structures; juxta straight; distal margin of juxta with spine-like processes.

Genus Titanogrypa

Postalar wall setulose; scutellum with a patch of whitish hair-like setulae on the lateral margins (except in subgenus *Sarconeiva* Lopes and the species *T*. (*Cucullomyia*) *luculenta* [Lopes, 1938], *Titanogrypa* (*Cucullomyia*) *larvicida* [Lopes, 1935] and *Titanogrypa* (*Cucullomyia*) *ecuatoriana* [Lopes, 1988]); wing vein R_1 setulose dorsally (only in subgenus *Sarconeiva*); wing vein R_{4+5} with dorsal setulae reaching crossvein r-m (only in subgenus *Sarconeiva*); third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal T5 with rounded margin ventrally (only in subgenera *Airypel* Dodge and *Cucullomyia* Roback); male abdominal ST5 cleft with subparallel sides; male ST5 with one or two rows of short and strong setae along posterior margin (only in subgenera *Airypel* and *Cucullomyia*); cercal prong with apex rounded and narrow in dorsal view; cercal prong straight or almost straight; surstylus equal to or longer than cercus (only in subgenus *Sarconeiva*); surstylus with an apical patch of microsetulae (only in subgenus *Sarconeiva*); phallus with a distinct hinge between basi- and distiphallus; basiphallus long and slender; basiphallus with a dorsal hump at junction with distiphallus (except in subgenus *Titanogrypa*); basiphallus laterally compressed (only in subgenera *Airypel* and *Cucullomyia*); basiphallus with a dorsal longitudinal keel (only in subgenera *Airypel* and *Cucullomyia*); vesica bulbous; distiphallus not surrounding the acrophallus, styli entirely exposed (except in subgenus *Cucullomyia*); acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli developed, with a sperm opening (except in subgenera *Sarconeiva* and *Titanogrypa*); capitis wide and denticulated; median stylus with a distinct opening; median stylus straight; median stylus short (greatly elongated in subgenus *Cucullomyia*); juxta Y-shaped in frontal view (only in subgenus *Airypel*); juxta partially fused to acrophallic structures (except in subgenus *Cucullomyia*); juxta straight.

Genus Tricharaea

Male with at least one proclinate fronto-orbital seta; postgena angled in lateral view*; anepimeral area with sparse, weak setulae*; two katepisternal setae; metasternum setulose; postalar wall bare; male ST5 with posterior margin straight or with a shallow concavity; male ST5 with a central patch of setae; epandrium brownish (not reddish); phallus with basi- and distiphallus connected by a desclerotized strip; vesical arm-shaped lever elongated; vesical arm-shaped lever with a hammer-shaped apex; distal section of the vesica globose, with small denticles; acrophallus formed of a capitis, lateral styli and a median stylus; juxta smooth laterally and wrinkled medially*; juxta funnel-shaped*; spermathecae spherical; female with an epiproct; puparial spiracles not in a recession.

Genus Tripanurga

Postalar wall bare; wing vein R_1 setulose dorsally; wing vein R_{4+5} with dorsal setulae reaching crossvein r-m; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal T5 with ventral margin pointed*; male abdominal ST5 with a widely V-shaped cleft; epandrium higher than wide in lateral view*; postgonal seta slightly compressed*; phallus with a distinct hinge between basi- and distiphallus; basiphallus proximally with a dorsal epiphallus-like process*; vesica three-lobed composed of a proximal section not divided and two vesical lateral arms; vesical lateral arms with an inner denticulated process*; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta slightly recessed within the phallic tube; juxta squared with a shallow notch medially.

Genus Tulaeopoda

Postalar wall setulose; wing vein R_1 setulose dorsally; third costal sector of wing bare ventrally; male mid-femur without a ctenidium; male hind posterior surface of the trochanter with a postero-median pad of short setae*; male hind femur curved; male abdominal ST3 with two patches of dense erect black setae*; male abdominal ST4 with two patches of dense erect black setae; male abdominal ST5 with a widely V-shaped cleft; male ST5 with a small pad of strong, short setae medially on inner margin of cleft; cercal prong gradually swollen, with a knob-like apex; cercal prong with dorso-lateral keels;

cercal prong with a lateral tuft of long setae; paraphallic tube as long as wide; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli with stylar lateral plates; juxta globose, spiny and denticulated.

Genus Udamopyga

Male with rows of frontal setae divergent anteriorly; postalar wall setulose; wing vein R_1 bare dorsally; wing vein R_{4+5} with dorsal setulae not reaching crossvein r-m; male mid-femur without a ctenidium; male hind tibia without an apical postero-ventral seta; male abdominal ST5 with a widely V-shaped cleft; posterior margin of the male abdominal ST5 with a slight undulation halfway between the angle and the tip of the V, and a rounded distal expansion*; cercal prongs fused at least halfway to tip*; phallus with a distinct hinge between basi- and distiphallus; basiphallus with a dorsal longitudinal keel; vesica composed of two petal-like lateral plates, each with a vesical denticulated lobe*; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli tube-shaped and with an outlet; capitis flat and simple; median stylus tube-shaped and with an outlet; juxta slightly recessed within the phallic tube; juxta squared, with a shallow notch medially.

Subgenus Carinoclypeus: facial carina parallel in full length to frontogenal suture*; cercal prong without a proximal tuft of long black setae.

Subgenus Udamopyga (*s.s.*): facial ridge with dense setosity on lower 0.50; cercal prong with a proximal tuft of long black setae.

Genus Villegasia

Postalar wall setulose; third costal sector of wing bare ventrally; male mid-femur with a ctenidium of rounded spines (circular cross section); male hind tibia without an apical postero-ventral seta; male abdominal T5 blackish*; male abdominal ST5 cleft with subparallel sides; male abdominal ST5 blackish; cercal prong straight or almost straight; phallus with a distinct hinge between basi- and distiphallus; distiphallus not surrounding the acrophallus, styli entirely exposed; basiphallus dorso-ventrally compressed*; basiphallus long and slender; vesica absent; acrophallus formed of a capitis, lateral styli and a median stylus; lateral styli collapsed and with no outlet; lateral styli very small and plate-like; capitis flat and simple; median stylus with a distinct opening; median stylus straight; juxta partially fused to acrophallic structures; juxta straight in lateral view; distal margin of juxta with spine-like processes.

DISCUSSION

Insights into functional aspects and mechanical relations between male terminalia elements

Whereas the non-demarcated juxta present within the first divergences in Sarcophaginae gives the appearance of immobility to this structure, a hinge or a desclerotized strip between the juxta and the remaining distiphallus implies a certain freedom of juxtal movement in the more derived clades. Thus, there seems to be an absolute immobility in genera with a non-demarcated juxta, like in genus *Malacophagomyia* (including *Dodgeisca*) (Fig. 17A), Dexosarcophaga clade (Fig. 11I), Oxysarcodexia clade (Figs 29H, 35G) and Tricharaea grade (Fig. 19E). A suture, narrow hinge or desclerotized strip between the juxta and the remaining distiphallus seems to allow restricted movements of the juxta, for example in *Boettcheria* (Fig. 9F), *Helicobia* (Fig. 23F), *Microcerella* (Fig. 29F), *Peckia* (Fig. 13F) and *Sarcophaga* (Fig. 10D). A greater mobility of the juxta is inferred from the large membranous hinge in clade 90, which includes the genera *Lepidodexia* (including *Archimimus*) (Fig. 22F) and *Emblemasoma* (Fig. 11D), and also in the genera *Chrysagria* (Fig. 9I) and *Comasarcophaga* (Fig. 11G).

Interestingly, groups with a non-demarcated juxta usually possess a certain degree of specialization in other structures, such as the vesica or the acrophallus. For example, the lower lineages of Sarcophaginae like *Bahamiola*, *Dexosarcophaga* (including *Cistudinomyia*), *Nephochaetopteryx*, *Oxysarcodexia*, *Oxyvinia*, *Ravinia*, *Rettenmeyerina*, *Sarcofahrtiopsis* (including *Pacatuba*) and *Tricharaea* are the only genera with acrophallic levers and a specialized vesica divided into a proximal arm-shaped lever, and a distal section. The vesical arm-shaped lever articulates the vesica to the hypophallus, and seems to be able to move up and down. In *Nephochaetopteryx*, the vesical arm-shaped lever is proximally joined to the proximal part of the acrophallus through the acrophallic levers, and all three components (vesical arm-shaped lever, acrophallus, acrophallic levers) form a single functional unit (Fig. 17B, C). In other words, the vesical arm-shaped lever runs along the proximal part of the distal section of the vesica, and it is proximally linked to the acrophallus through the acrophallic levers. The vesical arm-shaped lever ends either at the tip of the vesica, or it is elongated beyond the vesica and in some cases has a hammer-shaped apex. Since the vesical arm-shaped lever is usually elongated, it seems that when the distal part of the vesical arm-shaped lever is pushed downwards (i.e. towards the base of the phallus), the movement is transmitted to its proximal margin that in turn pushes the acrophallic structures

Figure 13. A, lateral styli and sperm duct, ventral view: *Peckia* (*Pattonella*) *intermutans*. B, lateral styli, sperm duct and vesica, ventral view: *Peckia* (*Pattonella*) *intermutans*. C, distiphallus, left lateral view: *Peckia* (*Squamatodes*) *ingens*. D, distiphallus, dorsal view: *Peckia* (*Squamatodes*) *ingens*. E, distiphallus, left lateral view: *Peckia* (*Euboettcheria*) *naides*. F, distiphallus, left lateral view: *Peckia* (*s.s.*) *chrysostoma*. G, distiphallus, ventral view: *Peckia* (*s.s.*) *chrysostoma*. H, distiphallus, apical view: *Peckia* (*s.s.*) *chrysostoma*. I, distiphallus, left lateral view: *Peckia* (*Sarcodexia*) *lambens*. J, distiphallus, ventral view: *Peckia* (*Sarcodexia*) *lambens*. [B, H–J, courtesy M. Giroux; A, G, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

upwards/outwards and probably make them emerge from within the juxtal hood. This vesica-acrophallus lever system is hypothesized to be functionally related to an extrusion of the styli during mating.

The length of the vesical arm-shaped lever seems to be inversely proportional to the length of the styli, since an elongated vesical arm-shaped lever is observed only in genera with short styli, i.e. *Bahamiola*, *Nephochaetopteryx*, *Sarcofahrtiopsis* (including *Pacatuba*) and *Tricharaea*, while the styli are longer in genera with a shorter vesical arm-shaped lever, such as *Dexosarcophaga* (including *Cistudinomyia*), *Oxysarcodexia*, *Oxyvinia* and *Rettenmeyerina*. A different functionality has probably evolved in species of *Ravinia*, which all have a partly desclerotized, narrow and flake-shaped vesica, and where a hillae-acrophallus lever system might be in place instead.

In the remaining groups with a non-demarcated juxta (i.e. in the Argoravinia clade), the vesica is not specialized and has no divisions. Except for the genera *Malacophagula* and *Rafaelia*, in which the vesica has two elongated processes on each side (Fig. 17E, F, 40D), all other genera with a non-demarcated juxta have a flat and broad vesica, which leads to the question on how these genera compensate for the absence of a vesica-acrophallus lever system. In *Argoravinia* and *Malacophagomyia* (including *Dodgeisca*), a mechanical solution to push the acrophallus outwards seems not to be needed, although the specific functional aspects are not clear. In these two genera, both the median stylus and the lateral styli are modified: (1) the median stylus is spectacularly elongated (Figs 5D, F, 15B, E), and (2) lateral styli possess hillae (Figs 5B, C, E, 16E, 17B). The evolution of an elongate median stylus may intuitively be explained as a measure to ensure sperm transfer during mating. On the other hand, the configuration of the lateral styli suggests a hillae-lateral styli lever system. Unlike the vesica-acrophallus lever system, where hypothetically the three styli are pushed upwards and outwards of the distiphallus to accomplish the sperm transfer, the mechanism for sperm transfer in the genera *Argoravinia* and *Malacophagomyia* (including *Dodgeisca*) seems to have evolved independent movements for the median stylus and the lateral styli.

Male terminalia and intersexual selection in Sarcophaginae

Divergence in male traits evolves more rapidly in characters under sexual selection, and this effect is more pronounced in male genitalia structures than in any other trait of animals with internal fertilization (Eberhard, 1985, 1996; Arnqvist, 1997, 1998).

Darwin (1871) was the first to argue that sexual selection acts on the elaborate (mainly male) characteristics that increase mating success, such as 'singing' in cicadas, colours in birds and Lepidoptera, and the horns of many beetles. Under Darwin's concept, such an exertion in investments for males to possess any or many of a variety of extravagant morphological 'weapons' and impressive colour patterns, complex behaviours and deployment of capabilities to catch and deliver a prey or build a nest, as well as potent glands to produce specific substances to stimulate and attract females, has evolved in order to increase the chances of being selected to copulate with a female. Males of the same species are thus under male–male competition or intrasexual selection (Darwin, 1871). Morphological, behavioural and chemical traits for male–male competition for females, however, are not known in species of the subfamily Sarcophaginae (apart from some territorial behaviour). Instead, sarcophagine flies, like several other arthropod groups, exhibit an impressive variety of complex structures in the male sperm-transmitting organs, which are rarely if ever used in male–male aggressive interactions. Thus, mating success in male sarcophagine flies must be an intersexual selection type, or female mate choice, that is driven by females rather than by competition directly between males.

Phylogenetic topology and life habits

Our phylogeny shows that the early lineages in the Sarcophaginae are mostly dung decomposers, while lineages emerging later have more diverse life habits, including saprophagy and parasitism. Species of the Tricharaea grade and those of the Oxysarcodexia clade generally breed in dung (D'Almeida, 1994; D'Almeida & Almeida, 1998; Buenaventura *et al.*, 2009; Pape & Dahlem, 2010; Carvalho *et al.*, 2012; Yepes-Gaurisas *et al.*, 2013). These groupings of dung-breeding flies appeared early in the phylogeny of Sarcophaginae, while all other genera, mainly saprophagous like those in the Sarcophaga clade and genera with parasitic life habits such as those in the Blaesoxipha clade, the Lepidodexia clade and the Udamopyga clade, or with mixed saprophagous-parasitic feeding modes such as those in the Microcerella clade, appear in more derived clades.

Historical biogeography

Our phylogeny supports the hypothesis according to which the Sarcophaginae originated in the Neotropical Region (Fig. 2), where most of the diversity of this subfamily is currently found (Pape, 1996). The tree also indicates a minimum of three colonization events of the Palaearctic Region, corresponding to dispersal events of the *Blaesoxipha*, *Ravinia* and *Sarcophaga* lineages. These dispersals were probably two-step processes, with originally Neotropical lineages of these three genera first dispersing into the Nearctic Region, and later reaching the Palaearctic. Thus, our results are in agreement with all available evidence (Roback, 1954; Pape, 1994; Giroux *et al.*, 2010; Stamper *et al.*, 2012; Buenaventura & Pape, 2017) supporting a New World origin and early diversification of the subfamily Sarcophaginae.

The hypothetical origin and early diversification of *Sarcophaga* in the New World, which has been indicated in previous studies (Kutty *et al.*, 2010; Stamper *et al.*, 2012; Buenaventura *et al.*, 2016; Buenaventura & Pape, 2017), can now be considerably elaborated. All species of *Peckia*, which is the sister taxon of (*Lipoptilocnema* + *Sarcophaga*), are currently distributed in the Neotropics (a few Neotropical species of *Peckia* reach the southern Nearctic). Also, the only species of *Sarcophaga* endemic to the Neotropics are the few species of the widely distributed and probably non-basal subgenus *Mehria* Townsend plus the sole representative of the genus-group taxon *Torgopampa* Lopes, for which the assignment to *Sarcophaga* is in need of further study (Pape, 1996; Buenaventura *et al.*, 2016). The common ancestor of (*Lipoptilocnema* + *Sarcophaga*) must therefore have originated in the Neotropics, and a subsequent expansion of its range by dispersal into the Nearctic, combined with a speciation by vicariance, may have given rise to an originally Neotropical *Lipoptilocnema* and an originally Nearctic *Sarcophaga*. The common ancestor of *Sarcophaga* and *Lipoptilocnema* probably dispersed from the Neotropics into the Nearctic (or more precisely from South America into North America) through the Isthmus of Panama, and it was in the latter biogeographic region – the Nearctic – that the first splits of *Sarcophaga* occurred (Buenaventura & Pape, 2017). The Nearctic lineages of *Sarcophaga*, as producing the early diversifications within this genus, support a Nearctic origin (Buenaventura & Pape, 2017). A combination of our results with those of Buenaventura *et al.* (2016) suggests that after the initial radiation in the Nearctic, a single lineage of *Sarcophaga* dispersed into the Old World, where the largest radiation of lineages within this genus occurred [note that we are here considering the sister-group relationship between the Australian species *S. torvida* and the Nearctic subgenus *Wohlfahrtiopsis* Townsend as given by Buenaventura *et al.* (2016) as an artefact]. A recent study by Buenaventura & Pape (2017) based on a larger data set found *Sarcophaga* to be split into a Nearctic clade and an Old World clade, which would imply that *Sarcophaga* dispersed into the Old World very soon after having originated in the Nearctic. Note that Buenaventura & Pape (2017) found (*Lipoptilocnema* + *Peckia*) as the sister group of *Sarcophaga*, which does not contradict the hypothesis with a Neotropical origin for the ancestor of (*Sarcophaga* + (*Lipoptilocnema* + *Peckia*)) given by Buenaventura & Pape (2017), or of (*Lipoptilocnema* + *Sarcophaga*) as given in the present study.

Two similar Neotropical-Nearctic dispersal-vicariance events are also indicated by our phylogeny. The common ancestor of (*Oxysarcodexia* + *Ravinia*) as well as that of ((*Blaesoxipha* + *Mecynocorpus*) + *Emdenimyia*) probably arose in the Neotropics, as their sister groups, *Nephochaetopteryx* and *Thomazomyia*, respectively, are confined to this region. However, due to the low phylogenetic resolution within the genera *Blaesoxipha* and *Ravinia*, our study cannot assess whether these genera originated in the Neotropics or the Nearctic. Although we did not include representatives of *Blaesoxipha* and *Ravinia* from all regions, these genera are widespread in the Neotropical, Nearctic and Palaearctic Regions. Thus, there are at least two biogeographic scenarios for the origin of the *Blaesoxipha* and *Ravinia* lineages. One is their origin and early diversification within the Neotropics with a subsequent dispersal into the Nearctic enabled by the rise of the Isthmus of Panama and the closure of the Central American Seaway. The other is the expansion of the distribution of the common ancestor of each of the clades ((*Blaesoxipha* + *Mecynocorpus*) + *Emdenimyia*) and (*Oxysarcodexia* + *Ravinia*) to colonize the Nearctic, with a subsequent diversification within this region followed by dispersal 'back' into the Neotropics. *Blaesoxipha* emerged as sister to the clade (*Comasarcophaga* + *Spirobolomyia*) in Pape (1994) and Giroux *et al.* (2010), and to (*Fletcherimyia* + *Mecynocorpus*) in Stamper *et al.* (2012), both of which are Nearctic clades. Thus, the morphology-based phylogenies of Pape (1994) and Giroux *et al.* (2010), as well as the molecular-based phylogeny of Stamper *et al.* (2012), support the scenario of a Nearctic origin of *Blaesoxipha*. Regarding the origin of *Ravinia*, molecular evidence from Piwczyński *et al.* (2014) supports an early diversification of this genus in the Nearctic, whereas the morphological evidence of Giroux *et al.* (2010) was inconclusive in this regard.

Suprageneric relationships, generic monophyly and discussion of generic circumscriptions

The intromittent organ or phallus is equipped with a diversity of structures that have been informative when used as characters in phylogenetic analyses (Pape, 1992; Blackith *et al.*, 1998; Giroux *et al.*, 2010; Whitmore *et al.*, 2013; Buenaventura & Pape, 2015). Giroux *et al.* (2010) used the acrophallic configuration as the primary source of characters to reconstruct the phylogenetic relationships of 19 of the 51 recognized genera (*sensu* Pape, 1996) in the Sarcophaginae, but low bootstrap values and low relative Bremer support for many nodes were an indication of a high amount of homoplasy (Nixon & Carpenter, 2012). Homoplasy among characters used in our analysis is considered low, with the favoured cladogram (Fig. 2) having an RI of 0.90. The cladogram shows generally high branch supports and is almost completely resolved, with most of the polytomies occurring at the species level. The relationships found here may be considered stable. From this perspective, our results appear to represent a solid basis for discussing character evolution across sarcophagine genera.

In the following sections, genera are arranged into grades or clades when they are part of paraphyletic assemblages or monophyletic groups on the cladogram, respectively (Fig. 2A, B). The genus *Sarothromyiops* is not assigned to any of these generic groups.

Tricharaea grade

This grade is composed of *Bahamiola*, *Sarcofahrtiopsis* (including *Pacatuba*) and *Tricharaea*, which correspond to the three first splits of the 'lower' Sarcophaginae (Fig. 2A). The monophyletic genus *Tricharaea* is positioned near the base of the subfamily, as sister to the remaining Sarcophaginae. The phylogenetic closeness between genera of the Tricharaea grade was inferred in a cladistic study by Lopes (1990), who included them in the tribe Sarothromyiini together with *Nephochaetopteryx* and *Rettenmeyerina*. Reduction in the number of setae on the meron was suggested as a synapomorphy for members of the tribe Sarothromyiini (Lopes, 1990), whose phylogenetic arrangement showed a monophyletic *Tricharaea* [in the wide sense of Pape (1996)] as sister taxon of the clade (((*Pacatuba* + *Sarcofahrtiopsis*) + *Bahamiola*) + (*Nephochetopteryx* + *Rettenmeyerina*)). This is the only published topology for all genera of the Tricharaea grade before the current study, and it is partially supported by our results in that we also found *Tricharaea* to be monophyletic, as well as a clade consisting of *Sarcofahrtiopsis* species (including *Pacatuba*). However, in the broader context of the present analysis, many of the similarities shared by these genera appear to be symplesiomorphic. A basal position of the genus *Tricharaea* was first inferred by Roback (1954) and Lopes (1983) in their non-cladistic studies. The first author implied this position based on male terminalia characters, while the second one used characters from the cephaloskeleton of the first-instar larvae. This assumption was later corroborated by Pape (1994) and Giroux *et al.* (2010), who also found *Tricharaea* to be the sister taxon of the remaining sarcophagine flies included in their morphology-based phylogenetic analyses. In Kutty *et al.*'s (2010) tree, *Sarcofahrtiopsis cuneata* (Townsend, 1935) was found as sister species of *Tricharaea occidua* (Fabricius, 1794), and these emerged together in the lower part of the Sarcophaginae, although not at the base and with no branch support. In their molecular studies, Kutty *et al.* (2010) recovered a polyphyletic genus *Tricharaea*, and Stamper *et al.* (2012) had their single included species of *Tricharaea* as the sister taxon of (*Tripanurga* + *Boettcheria*), and not as part of the 'lower' sarcophagines. Recently, the molecular study by Piwczyński *et al.* (2014) showed a clade consisting of *S. cuneata* and a monophyletic *Tricharaea* placed at the base of the Sarcophaginae, but with no branch support. A sister-group relationship between *Sarcofahrtiopsis* and *Tricharaea* is not supported here and its recovery in other studies can be interpreted as being due to incomplete sampling or to a different homology assessment. We found support for a basal position of *Tricharaea* and the lineages of *Bahamiola* and *Sarcofahrtiopsis* (including *Pacatuba*) (clades 4–9 in Fig. 2A) splitting off next from the remaining Sarcophaginae. With part of the molecular evidence from previous studies, and with the morphological data from both adults and larvae found here and in previous studies being in favour of a basal position of *Tricharaea*, we consider this as the better-supported placement for this genus.

It is noteworthy that the four genera of the Tricharaea grade share a fair number of features not found outside this group, yet they emerge as paraphyletic in our analysis. The following shared character states would appear particularly relevant in this context: proclinate fronto-orbital setae in males ('pc' in Fig. 41), notopleuron without subprimary setae ('nt' in Fig. 41B–D), two katepisternal setae, postalar wall bare, wing vein R_{4+5} with dorsal setulosity reaching crossvein r-m, ST5 with posterior margin straight or with a shallow concavity (Fig. 42A, B), ST5 with a central patch of setae (Fig. 42A), vesica divided into a proximal and a distal section (Fig. 25A–D), vesical arm-shaped lever elongated to very elongated ventrally (Fig. 25A–D), vesical arm-shaped lever with a hammer-shaped or bilobed to oval apex (Figs 19H, 27A, 28H, J) and distal section of the vesica globose, with small denticles (Figs 19E, 28G, H, 39H). The last five character states are found only in species of the Tricharaea grade. The genera *Bahamiola* and *Sarcofahrtiopsis* (including *Pacatuba*) do not form a monophyletic group, but they share a vesical arm-shaped lever very elongated ventrally (Figs 15H, 19E, 28H) and a hood-shaped juxta with a denticulated lateral margin that is enlarged ventrally to form a capsule-like structure (Figs 15G, 19E–G, 28H, J, 30A, B). Additional characters and a larger sample of outgroup taxa will be a proper test of this topology, and therefore of the polarity of the character transformation series involved in the evolution of the 'lower' sarcophagines.

The monophyly of *Tricharaea* was previously supported by molecular data (Piwczyński *et al.*, 2014), but here it is also supported by four autapomorphies: epandrium brownish (not reddish), vesical arm-shaped lever elongated (Figs 25A, 27A), juxta smooth laterally and wrinkled medially (Figs 27A, 39H), juxta funnel-shaped (Fig. 39H). Within the Sarcophaginae, two plesiomorphic character states are shared by the three taxa of *Tricharaea* and Paramacronychiinae: postgena angled in lateral view (Fig. 41D, E), and sparse, weak anepimeral setulae ('as' in Fig. 41D). In the handmade cladogram of the tribe Sarothromyiini, Lopes (1990) argued for the monophyly of *Tricharaea* based on its species sharing spherical spermathecae. Later, Pape (1996) used this character state plus five features of male terminalia structures, three of female terminalia and one of the puparium, to diagnose the genus *Tricharaea*. Pape's (1996) male character states were: (1) male with at least one strong proclinate orbital seta, (2) postalar wall bare, (3) metasternum setulose, (4) male ST5 with a central patch of setae, (5) terminalia brownish (not red), (6) spermathecae spherical, (7) female with an epiproct and (8) puparial spiracles not in a recession. Except for female and larval character states 6–8, all others were included here, and only character states 1 and 5 (slightly modified) were found to be autapomorphic for this genus. However, all of Pape's (1996) character states and the two plesiomorphic and one autapomorphy found in the present study are used to diagnose this genus.

With a single species, the genus *Sarcofahrtiopsis* was described by Hall (1933) based on ST5 not having a cleft. Dodge (1965b) added more character states to the diagnosis of this genus, such as the hind coxa bare posteriorly, wing vein R_1 setulose and proclinate orbital setae present in males. Later, Lopes (1990) suggested the setulose wing vein R_1 and the long and bristly pregonite as synapomorphies; however, the first character state is also shared with genera such as *Helicobia*, *Malacophagomyia* (including *Dodgeisca*), *Nephochaetopteryx*, *Panava*, *Promayoa*, *Rafaelia*, among others, and the second character state does not diagnose *Sarcofahrtiopsis*, as it is not present in all species of the genus. Pape's (1996) diagnosis included the mentioned character states plus the following: notopleuron with subprimary setae, postalar wall bare, metasternum bare, third costal sector of wing bare ventrally, male ST5 with a central patch of setae, terminalia usually black, spermathecae elliptical and female without an epiproct. Finally, Mello-Patiu & Pape (2000) discussed all these features and suggested a list of 16 character states as a generic diagnosis of *Sarcofahrtiopsis*, highlighting the reduced metasternal setosity and the slender and elongated parameral (=postgonal) apodeme as autapomorphies. From these, the slender parameral apodeme should probably be removed as an autapomorphy, since this structure is not elongated in *Sarcofahrtiopsis thyropteronthos* Pape, Dechmann & Vonhof, 2002 (Pape, Dechmann & Vonhof, 2002). Here, the 13 male character states of Mello-Patiu & Pape (2000) were analysed and only the reduction in the setosity of the metasternal area came out as autapomorphic for *Sarcofahrtiopsis*.

Neither the monospecific genus *Pacatuba* nor the polyspecific genus *Bahamiola* of the classification of Pape (1996), here represented by a single species only, were found to possess any autapomorphies. However, *Pacatuba* and *Sarcofahrtiopsis* share one autapomorphy, vesical arm-shaped lever very elongated (twice its full length). The clade of *Sarcofahrtiopsis* (including *Pacatuba*) received aBS and weak JK support; however, *Pacatuba* shares 10 out of the 13 male character states listed by Mello-Patiu & Pape (2000) to define *Sarcofahrtiopsis*. Therefore, we suggest *Pacatuba* as a **new synonym** of *Sarcofahrtiopsis*. Consequently, we present a new generic diagnosis for *Sarcofahrtiopsis*, which is divided into the two subgenera *Pacatuba*, **new status**, and *Sarcofahrtiopsis* (*s.s.*), for which we also include subgeneric diagnoses.

Oxysarcodexia clade

Nephochaetopteryx, *Oxysarcodexia* and *Ravinia* are included in the Oxysarcodexia clade. These genera showed only one topology with *Nephochaetopteryx* as the sister taxon of (*Oxysarcodexia* + *Ravinia*), which received aBS and is supported by moderate JK values (Fig. 2A). This clade is supported by three homoplasies and the following autapomorphy: juxta smooth proximally and wrinkled distally (Figs 10C, D, 14G, H, 18A, D, G, 29H).

Species of *Nephochaetopteryx* are here included for the first time in a phylogenetic study. The phylogenetic affinity between this genus and *Tricharaea*, and also the position of these two genera within the 'lower' Sarcophaginae, was suggested by Lopes (1983) on the basis of these genera sharing first-instar larval character states such as a vestigial labrum [= mandible in Lopes (1983)] and the dorsal bridge [= clypeal arch in Lopes (1983)] situated posterior to the parastomal bar [= paraclypeal phragma in Lopes (1983)]. Interestingly, in the same study, Lopes also considered the clade composed of *Oxysarcodexia* and *Ravinia* as sister group of *Nephochaetopteryx* due to these genera also sharing the first-instar larval character states mentioned above. Later, in his phylogenetic study of

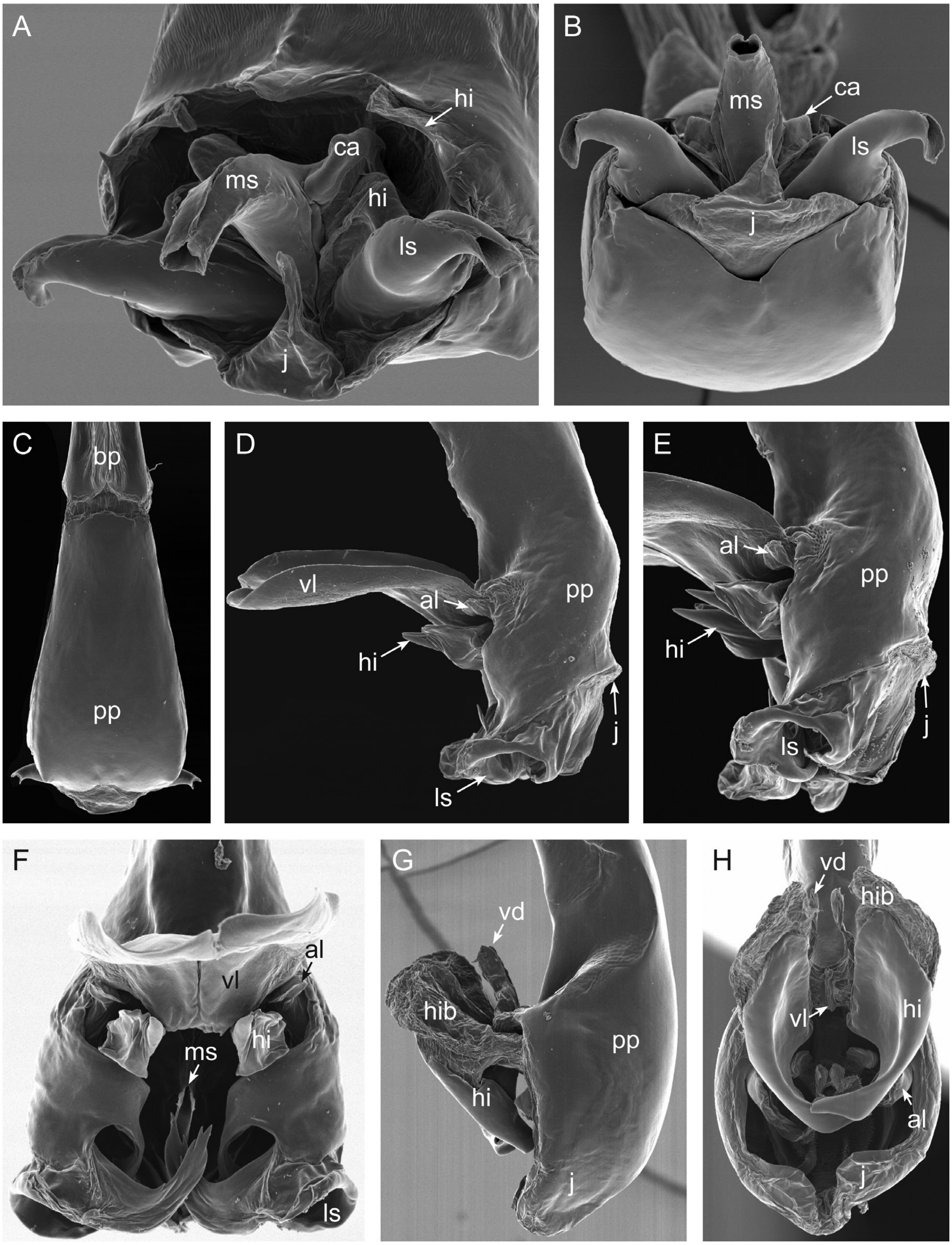

Figure 14. A, acrophallus, ventral view: *Rafaelia ampulla*. B, acrophallus and juxta, apical view: *Rafaelia ampulla*. C, phallus, dorsal view: *Rafaelia ampulla*. D, distiphallus, left lateral view: *Ravinia effrenata*. E, distiphallus, detail left lateral view: *Ravinia effrenata*. F, distiphallus, ventral view: *Ravinia effrenata*. G, distiphallus, left lateral view: *Ravinia pernix*. H, distiphallus, ventral view: *Ravinia pernix*. [E, F, H, courtesy M. Giroux; D, G, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

the Sarcophaginae males with proclinate orbital setae, Lopes (1990) placed *Nephochaetopteryx* as sister to *Rettenmeyerina* due to these two genera sharing the distiphallus articulated with the basiphallus. However, here we found that only *Rettenmeyerina* possesses a fully developed hinge between basi- and distiphallus (Fig. 28D), while *Nephochaetopteryx* generally has a desclerotized strip or a superficial hinge and only dorsally (Fig. 29H). *Nephochaetopteryx* was placed together with *Bahamiola*, *Sarcofahrtiopsis*, *Rettenmeyerina* and *Tricharaea* in the tribe Sarothromyiini by Lopes (1969a), due to all males of these genera having proclinate fronto-orbital setae. Males with proclinate fronto-orbital setae are largely confined to genera within the 'lower' Sarcophaginae, with few exceptions like in *Duckemyia*, two species of *Lepidodexia*, species of *Panava*, one species of *Tripanurga* and a few species of *Helicobia*. The sister-group relationship between *Oxysarcodexia* and *Ravinia* was highlighted already by Roback (1954), who pointed out similarities in phallic structures such as the lack of a juxta (i.e. the lack of juxtal hinge) and the presence of the acrophallic levers [= dorsal rods in Roback (1954)]. This was later followed by Downes (1955), who added larval and female traits in support of this relationship. Using Buenaventura & Pape's (2015) broader definition of the juxta, all genera of Sarcophaginae possess this structure. The hypothesis of a sister-group relationship between *Oxysarcodexia* and *Ravinia* was corroborated by Pape (1994) and Giroux *et al.* (2010) based on morphological data. One molecular-based phylogenetic analysis found strong support for this relationship (Stamper *et al.*, 2012), while two others (Kutty *et al.*, 2010; Piwczyński *et al.*, 2014) did not, although the last two analyses showed low branch supports. In our analysis, the clade (*Oxysarcodexia* + *Ravinia*) is supported by the homoplasious character state of a ctenidium of flattened spines (also found in *Mecynocorpus* and most Paramacronychiinae). This clade is also supported by the first-instar larval character state of festoon-like oral ridges (Downes, 1955; Lopes, 1983; Leite & Lopes, 1987; Lopes & Leite, 1987; Pape, 1996).

For the first time, the monophyly of *Nephochaetopteryx* is tested in a modern phylogenetic context, and its monophyly received strong JK support and has three male external autapomorphies: apical part of wing membrane between veins R_{2+3} and C fumose, mid-tibia without antero-dorsal setae and hind coxa with strong posterior setae. None of these character states were used in the original description of *Nephochaetopteryx* by Townsend (1934), but later Dodge (1968a) provided a first diagnosis for this genus, where he included the following character states: mid-tibia with neither antero-dorsal nor antero-ventral setae, wing vein R_1 setulose and arista plumose on basal three-fifths. Later, Lopes (1990), in his handmade cladogram, included the second character state of Dodge (1968a) plus the reduction of the female eighth tergite in his 'list of synapomorphies' of *Nephochaetopteryx*. Lastly, Pape (1996) provided a diagnosis including 14 character states, 13 of which were analysed here, and three of which were found to be autapomorphies for this genus. These three character states, in combination with some of Pape's (1996) other character states, are used here to diagnose *Nephochaetopteryx*.

The monophyly of *Oxysarcodexia* was already inferred in non-cladistic studies (Lopes, 1943, 1983; Roback, 1954), and later confirmed by phylogenetic analyses using both morphological (Giroux *et al.*, 2010) and molecular (Stamper *et al.*, 2012; Piwczyński *et al.*, 2014) characters. In our analysis, *Oxysarcodexia* is supported by two autapomorphies: (1) paraphallus antero-proximally with a paraphallic triangular expansion proximal to the vesica ('pte' in Fig. 18H) and (2) juxta with a proximal convex membranous expansion ('jce' in Fig. 18H). The first character state was recognized as diagnostic for this genus in previous studies (Lopes, 1946; Dodge, 1966; Giroux *et al.*, 2010). The second character state was first described by Lopes (1946) in his detailed revision of *Oxysarcodexia*, where the species descriptions used mostly male terminalia characters, such as the vesica, since this structure has a remarkable morphological diversity in this genus. In a subsequent work, Lopes (1975b) erected the subtribe Oxysarcodexiina, which he defined with a reduced list of diagnostic character states when compared to his earlier work. A selection of eight of Lopes's (1946, 1975b) character states was listed in a more recent diagnosis for this genus (Pape, 1996), which, however, did not include the character states found as autapomorphic here. Subsequent authors used these two character states in descriptions of new species (Soares & Mello-Patiu, 2010) and in morphological comparative studies (Silva & Mello-Patiu, 2008). Besides the two autapomorphies and some homoplasies found in our analysis, *Oxysarcodexia* is here diagnosed with three additional external male character states and two first-instar larval character states as suggested by previous studies.

The monophyly of *Ravinia* was suggested by Roback (1954) and Lopes (1983), and recently both morphology-based (Giroux *et al.*, 2010) and molecular-based (Stamper *et al.*, 2012; Piwczyński *et al.*, 2014) phylogenetic studies have corroborated this hypothesis. Here, five autapomorphies supported the monophyly of *Ravinia*: juxta hood-shaped, partially wrinkled and slightly swollen (Figs 10C, D, 14G, H), hillae distally blunt (Fig. 10C) or pointed (Fig. 14E), vesica narrow and flake-shaped (Figs 10C, D, 14G), vesical arm-shaped lever straight proximally (Fig. 35D) and distal section of the vesica flattened or reduced (Fig. 10D). Giroux *et al.* (2010) found the presence of hillae as the only autapomorphy for this genus, but in our definition this structure is also found in an additional 15 genera. However, the hillae in *Ravinia* are highly specialized in comparison to those found in other genera. Specifically, hillae with a membranous bladder (Figs 10C, D, 14G, H) and a groove (Fig. 10B), as described by Giroux *et al.* (2010), are only found in some species of this genus. The importance of the hillae in the definition of *Ravinia* was already mentioned by Roback (1954), who also inferred the origin of the acrophallic levers [= acrophallic bars in Roback (1954)] in other taxa [acrophallic levers originated in the ancestor of all Sarcophaginae (clade 4 in Fig. 2A) according to our analysis] before the emergence of the *Ravinia* lineage. Five autapomorphies supporting the monophyly of *Ravinia* are used to diagnose this genus in combination with other male structures and two larval character states.

Dexosarcophaga grade

This grade is composed of the genera *Dexosarcophaga* (including *Cistudinomyia*), *Oxyvinia* and *Rettenmeyerina* (clade 21 and *Rettenmeyerina* in Fig. 2A). These four genera share two character states: vesical arm-shaped lever gently angled (green in Fig. 26B), and distal section of the vesica bifid and not particularly ornamented (yellow structure in Figs 25H, 26). The clade (*Oxyvinia* + *Dexosarcophaga* [including *Cistudinomyia*]) (Fig. 2A) received a weak JK value. This clade is supported by the homoplasious character state 'ctenidium of rounded spines present' and two autapomorphies: occipital setulae above occipital foramen black, and hillae long and spoon-shaped, with a squared apex. The genera *Oxyvinia* and *Dexosarcophaga* (including *Cistudinomyia*), as well as the clade combining the two, all received weak branch support.

Roback (1954) considered *Cistudinomyia* as part of the subtribe Raviniina, Dodge (1968b) considered *Dexosarcophaga* as closely related to *Oxysarcodexia*, while Lopes (1969a, 1975b, 1983) did not include *Cistudinomyia* in his tribal array of the Sarcophaginae, but he placed *Dexosarcophaga* in the tribe Cuculomyiina, *Oxyvinia* in Raviniini and *Rettenmeyerina* in Sarothromyiini. Giroux *et al.* (2010) included *Cistudinomyia*, *Dexosarcophaga* and *Oxyvinia* in their taxon sample and found a weakly supported clade ((*Dexosarcophaga* + *Oxyvinia*) + (*Cistudinomyia* + other Sarcophaginae)) using morphological characters. The molecular studies of Kutty *et al.* (2010) and Piwczyński *et al.* (2014) included *Dexosarcophaga* and recovered the topologies (*Dexosarcophaga* + (*Argoravinia* + *Blaesoxipha*)) and (*Dexosarcophaga* + *Argoravinia*), respectively, both with low branch support.

Lopes (1969a) placed *Rettenmeyerina* together with *Bahamiola*, *Sarcofahrtiopsis* and *Tricharaea* in the tribe Sarothromyiini on the basis of these genera sharing proclinate fronto-orbital setae in the male. Here, *Rettenmeyerina* is diagnosed only by homoplasies, as we found no autapomorphies for this genus. The presence of a desclerotized area between the paraphallus and the juxta in *Rettenmeyerina* is relevant for defining this genus. *Rettenmeyerina* emerges as sister taxon to the remaining 'higher' Sarcophaginae, which has (*Oxyvinia* + *Dexosarcophaga* [including *Cistudinomyia*]) as sister clade of the remaining Sarcophaginae species (Fig. 2A). The presence of proclinate fronto-orbital setae in the male is a plesiomorphic feature in the Tricharaea grade, which means that the absence of male proclinate fronto-orbital setae in the ancestor of the 'higher' sarcophagines (excl. of *Rettenmeyerina*) has to be considered an apomorphic reversal. Male proclinate fronto-orbital setae, i.e. male and female with the same frontal chaetotaxy, are of very sporadic occurrence in the Calyptratae, and there is to our knowledge no other instance where the presence of male proclinate orbital setae has been hypothesized as a reversal.

Oxyvinia was monophyletic in our analysis, but its JK supports were low (Fig. 2A). One autapomorphy supports this genus: paraphallus bent ventrally in its proximal third (Fig. 19B). Different placements of *Oxyvinia* by different authors are due to the use of different character systems. For example, Lopes (1983) considered *Oxyvinia* as closely related to *Ravinia* and *Oxysarcodexia* because these three genera share the festoon-like larval oral ridges (Leite & Lopes, 1987), while Giroux *et al.* (2010) found a sister-group relationship between *Dexosarcophaga* and *Oxyvinia* supported by adult character states. Our diagnosis of *Oxyvinia* is in agreement with the one proposed by Pape (1996) for this genus, except that we define the juxta differently and therefore consider it as present.

The clade composed of *Dexosarcophaga* (including *Cistudinomyia*) showed weak branch support in our analysis (Fig. 2A). The branch support value for *Dexosarcophaga* (*s.s.*), i.e. excluding *Cistudinomyia*, was stronger than those supporting its sister-group relationship with the monospecific *Cistudinomyia*. One autapomorphy supported the clade of *Dexosarcophaga* (including *Cistudinomyia*): pregonite C-shaped (see figs in Mello-Patiu & Pape, 2000). Different interpretations of the connection between basiphallus and distiphallus of *Cistudinomyia* have led to different phylogenetic positions of this genus in available studies, as highlighted by Giroux *et al.* (2010). Roback (1954) included *Cistudinomyia*, *Ravinia* and *Oxysarcodexia* in the subtribe Raviniina based on these genera having no clear demarcation between basiphallus and distiphallus, as well as sharing other similarities in the shape of ST5. Pape (1994) recovered (*Tricharaea* (*Cistudinomyia* + remaining Sarcophaginae)) and considered *Cistudinomyia* as having a distinct desclerotized strip between basi- and distiphallus. Here, we scored *Cistudinomyia* as bearing a hinge between basi- and distiphallus (Fig. 11D), a condition shared with its sister group, *Dexosarcophaga* (*s.s.*). Except for one character state, *Cistudinomyia* possesses all features cited in the latest diagnosis of *Dexosarcophaga*, provided by Mello-Patiu & Pape (2000). The exception corresponds to the colour of the terminalia, red in *Cistudinomyia* and blackish in *Dexosarcophaga* (*s.s.*). Based on the autapomorphies of the clade of *Dexosarcophaga* (including *Cistudinomyia*), we suggest *Cistudinomyia* as a **new synonym** of *Dexosarcophaga*. We have chosen to maintain *Cistudinomyia* as a subgenus, and our new diagnosis for *Dexosarcophaga* accordingly also includes *Cistudinomyia* as a subgenus, **new status**.

Genus Sarothromyiops

The single known species of this genus is only found in the Galápagos Islands. The most noteworthy autapomorphic features of this genus are: basiphallus laterally compressed and with a longitudinal dorsal keel (arrow in Fig. 21A), the presence of rounded expansions at the base of the cerci (Fig. 42D, E) and cerci bare dorsolaterally (Fig. 42E). The last two character states were listed by Pape (1996) as part of the diagnosis of this genus. Lopes's (1969a) tribal classification places this species in the Microcerellini together with genera such as *Microcerella* and *Chrysagria*, but we did not find support for this relationship. Instead, the sister-group relationship of *Sarothromyiops dasycnemis* (Thomson, 1869) to clade 27 received moderate JK support (clade 26 in Fig. 2A). Clade 26 is supported by a cleft posterior margin of the male abdominal ST5 without any special set of setae (Fig. 42C), reduction of the divisions of the vesica, vesica broad and flat (Fig. 21A, C), vesica with no special mechanism of attachment to the hypophallus, reduction of the acrophallic levers, hillae directed latero-ventrally (Fig. 21B), hillae filiform and the hillae touching the inner paraphallic wall only through the medial part. Thus, our analysis does not support synonymizing *Sarothromyiops* under any other genus, and therefore it remains a valid genus.

Argoravinia clade

This clade is composed of four genera arranged in the topology (*Malacophagula* + *Rafaelia*) + (*Argoravinia* + *Malacophagomyia* [including *Dodgeisca*]). Most of these nodes received aBS and moderate to strong JK supports in our analysis (Fig. 2A). The Argoravinia clade is supported by five autapomorphies: (1) posterior margin of ST5 very widely V-shaped with an obtuse inner angle (Fig. 42G), (2) paraphallus dorsodistally rounded (Figs 14C, 15D, 17A, F), (3) vesica broad and flat (Figs 15F, 17A, B, D), (4) hillae directed latero-ventrally (Figs 15A, 16C, 17A) and (5) hillae not touching the inner paraphallic wall (Fig. 15E).

The clade (*Malacophagula* + *Rafaelia*) is supported by four homoplasies: parafacial plate with strong setae (Fig. 42F), male hind tibia with apical postero-ventral setae well differentiated, a median stylus moderately elongated and a demarcated juxta with a hinge or a desclerotized strip between the juxta and the remaining distiphallus (Figs 14B, 17G). Species of the genera *Malacophagula* and *Rafaelia* have never been studied with modern phylogenetic methods, but the tribal classification based on first-instar larval character states proposed by Lopes (1983) included these genera together with species of *Lepidodexia* and *Titanogrypa* in the tribe Johnsoniini. Mello-Patiu & Azevedo (1998) also highlighted similarities observed by Lopes (1983) in the median and lateral styli of genera *Malacophagula* and *Rafaelia* and differences in head morphology for which we found support here. The vesica in these genera requires deeper study, as it could carry informative characters for defining the two genera and reconstructing their species-level phylogenetic relationships.

The monophyly of *Malacophagula* is strongly supported by five autapomorphies: head rounded in profile (Fig. 42F), first flagellomere shortened (Fig. 42F), lunule widened, postgena swollen (Fig. 42F) and lower calypter rounded (Fig. 43A).

One autapomorphy and three homoplasies supported the monophyly of *Rafaelia*, which received moderate branch support (Fig. 2B). The only autapomorphy for this genus was hypophallus weakly sclerotized, with only the very apex of the vesica sclerotized. Species of *Rafaelia* have a hypophallus that is mostly membranous, globose and well developed, while the paraphallus consists of a thin, sclerotized dorsal plate (Figs 20F, 40C, D), which is a rare condition in Sarcophaginae.

Roback (1954) considered *Argoravinia* as part of the *Johnsonia* Coquillett group, which included species of *Lepidodexia*, *Emblemasoma* and *Helicobia*, although he explicitly affirmed this as a tentative placement since he did not find any resemblance of the phallic structures of this genus to those of any other Sarcophaginae. In his classification based on first-instar larval character states, Lopes (1983) included *Argoravinia* in the Sarcodexiina group together with species of *Peckia*, *Helicobia* and *Lipoptilocnema*. Molecular studies including only few Neotropical

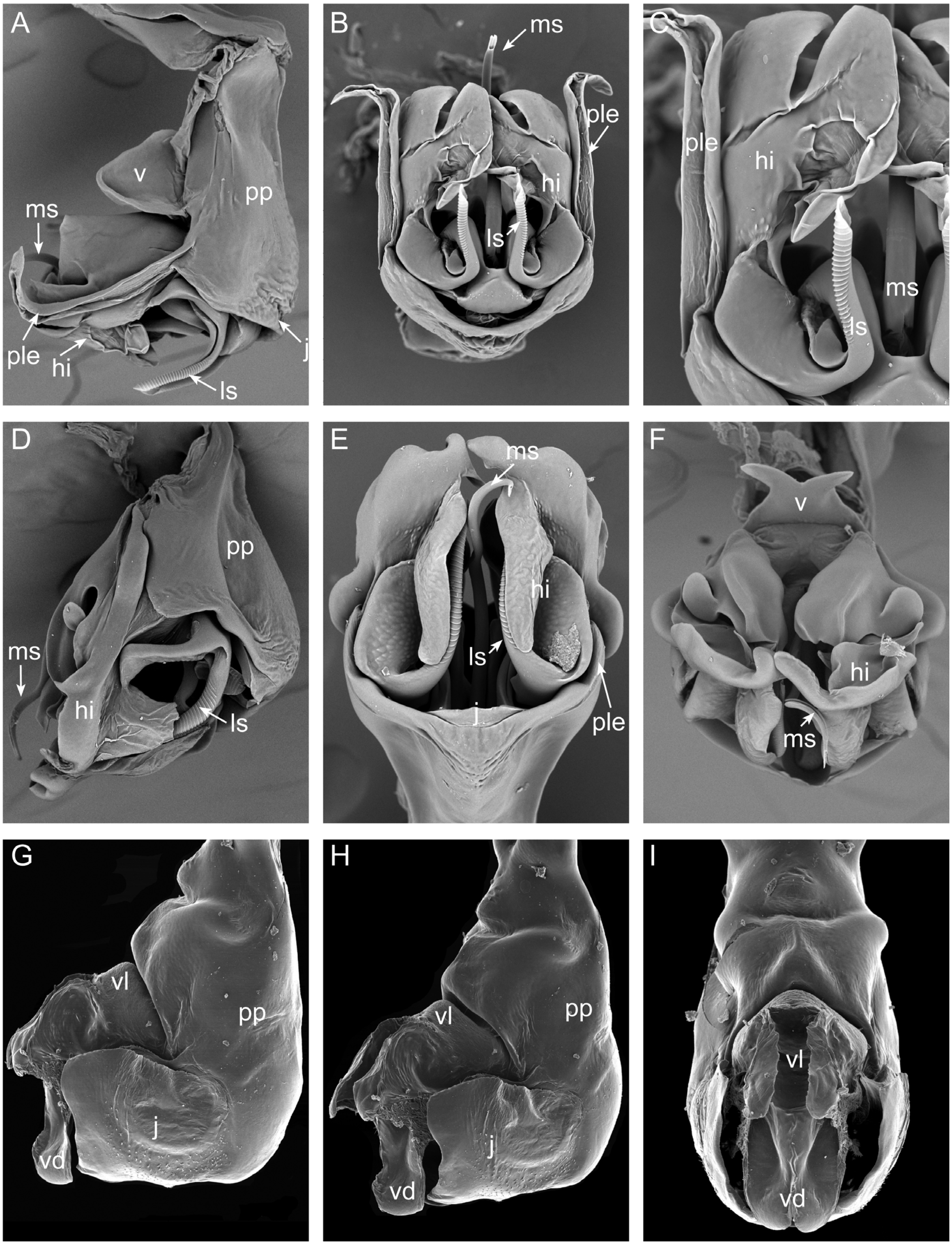

Figure 15. A, phallus, left lateral view: *Argoravinia aurea*. B, distiphallus, apical view: *Argoravinia aurea*. C, details of acrophallus, harpes and hillae, apical view: *Argoravinia aurea*. D, distiphallus, left lateral view: *Argoravinia rufiventris*. E, distiphallus, apical view: *Argoravinia rufiventris*. F, distiphallus, ventral view: *Argoravinia rufiventris*. G, phallus, left lateral view: *Bahamiola gregori.* H, phallus, antero-lateral view: *Bahamiola gregori.* I, phallus, ventral view: *Bahamiola gregori*. Abbreviations as in Table 1.

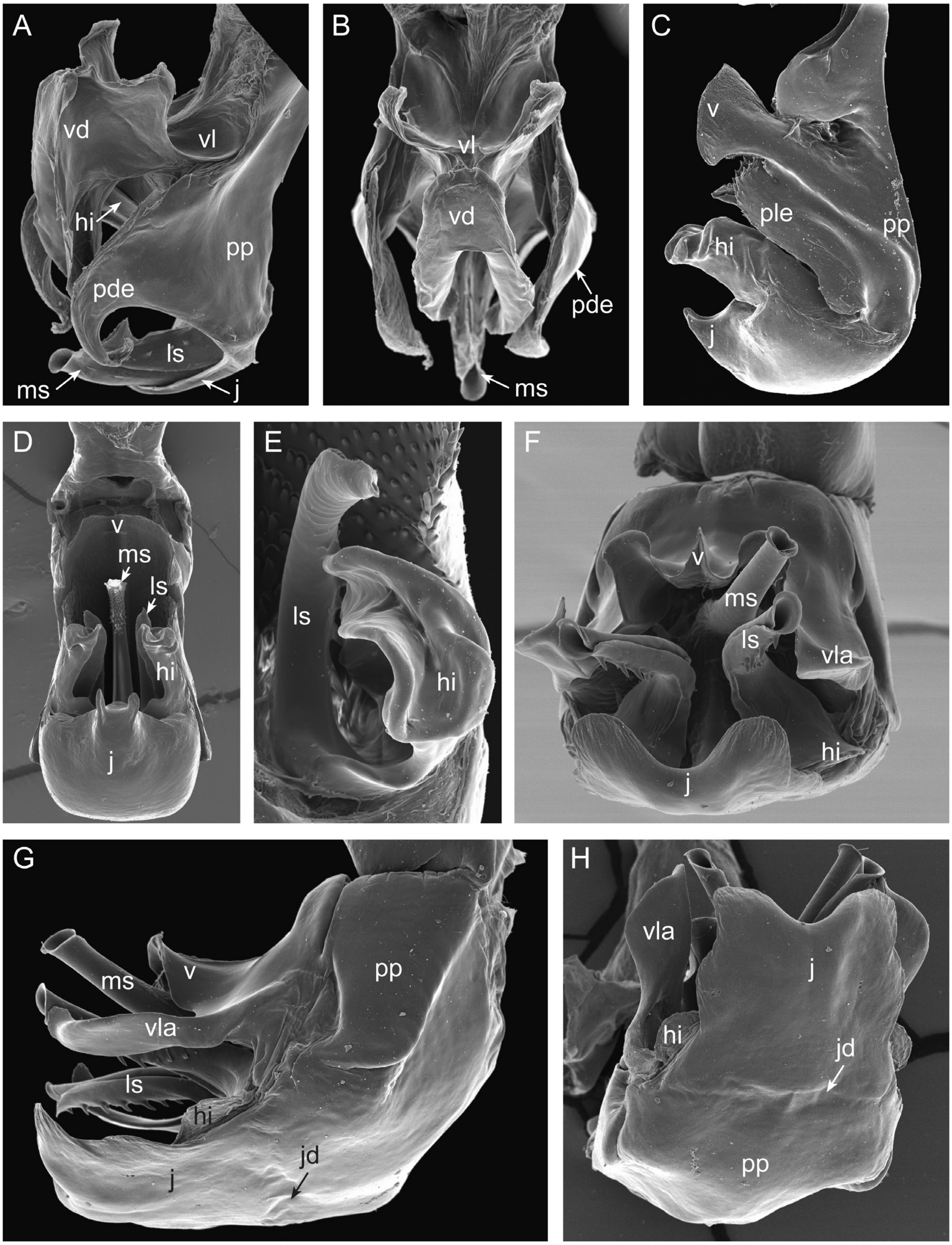

Figure 16. A, distiphallus, left lateral view: *Dexosarcophaga* (*s.s.*) *transita*. B, distiphallus, ventral view: *Dexosarcophaga* (*s.s.*) *transita*. C, distiphallus, left lateral view: *Malacophagomyia* (*Dodgeisca*) *paramerata*. D, distiphallus, ventral view: *Malacophagomyia* (*Dodgeisca*) *paramerata*. E, lateral stylus and hillae, ventral view: *Malacophagomyia* (*Dodgeisca*) *paramerata*. F, distiphallus, ventral view: *Duckemyia latifrons*. G, distiphallus, left lateral view: *Duckemyia latifrons*. H, distiphallus, apical view: *Duckemyia latifrons*. (A, B, courtesy M. Giroux). Abbreviations as in Table 1.

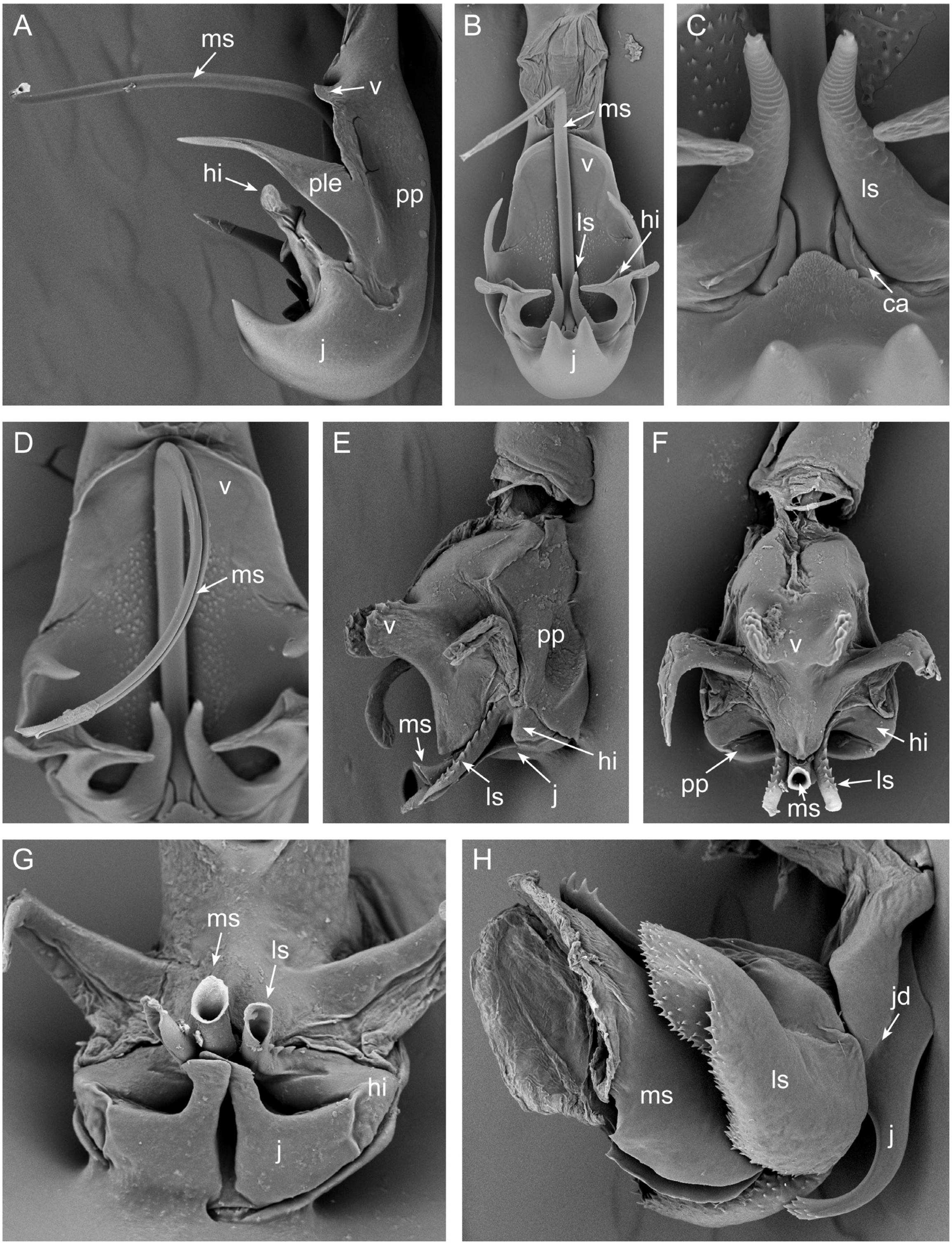

Figure 17. A, distiphallus, left lateral view: *Malacophagomyia* (*s.s.*) *kesselringi*. B, distiphallus, ventral view: *Malacophagomyia* (*s.s.*) *kesselringi*. C, lateral styli and capitis, ventral view: *Malacophagomyia* (*s.s.*) *kesselringi*. D, acrophallus, ventral view: *Malacophagomyia* (*s.s.*) *kesselringi*. E, distiphallus, left lateral view: *Malacophagula neotropica*. F, distiphallus, ventral view: *Malacophagula neotropica*. G, acrophallus, antero-apical view: *Malacophagula neotropica*. H, *Mecynocorpus salvum*, distiphallus, left lateral view. Abbreviations as in Table 1.

genera have marginally touched upon the phylogenetic position of *Argoravinia* with regard to other Sarcophaginae (Kutty *et al.*, 2010; Piwczyński *et al.*, 2014). These studies showed conflicting relationships for this genus, either as sister to *Blaesoxipha setosa* (Salem, 1938) with moderate to strong support (Kutty *et al.*, 2010), or to *Dexosarcophaga transita* Townsend, 1917 with no branch support (Piwczyński *et al.*, 2014). In our analysis, which includes a larger taxon sample than previous phylogenetic studies on Sarcophaginae, *Argoravinia* emerges as sister to *Malacophagomyia* (including *Dodgeisca*) due to these taxa sharing three autapomorphies: (1) head profile with squared anterior and posterior genal corners, (2) paraphallic lateral expansions (Figs 15A–C, 16C, 17A) and (3) median stylus greatly elongated (Figs 15B, E, 16D, 17A, B, D).

The delimitation and monophyly of *Argoravinia* was revised by Pape (1990) but is here explicitly tested for the first time, and it received aBS and strong JK support. This genus is supported by six autapomorphies: (1) stem of wing vein $R_{2+3+4+5}$ with ventral setulae elongated, (2) pregonite proximally narrow and distally wide, (3) hillae convoluted (Fig. 15B–F), (4) capitis as a smooth, rounded lobe, proximally swollen, (5) median stylus S-shaped (Fig. 15B, E) and (6) juxta very small to vestigial (Fig. 15E). Some of these character states were previously included in the generic diagnoses for *Argoravinia* (Lopes, 1976a; Pape, 1990, 1996; Carvalho-Filho & Esposito, 2012). For example, Lopes (1976a) mentioned the long styli with a conspicuous free base, and a 'median process of glans' with a long slender 'apophysis', which partially correspond to our character states of the hillae and capitis, respectively. Similarly, in the diagnosis of *Argoravinia*, Pape (1990, 1996) included stem of wing vein $R_{2+3+4+5}$ with ventral setulae elongated, and the median stylus S-shaped, both found here as autapomorphic for this genus. More recently, Carvalho-Filho & Esposito (2012) diagnosed this genus based on nine character states, but only the vestigial juxta emerged as autapomorphic, and all others as homoplastic in the present analysis. Due to their utility for sorting *Argoravinia* species from other genera, most of the character states proposed by the above-mentioned authors are included in our diagnosis. Finally, the monophyly of the subgenera proposed by Carvalho-Filho & Esposito (2012) is partially supported by our phylogeny, as we recovered a monophyletic *Argoravinia* (*s.s.*), but as only a single species of *Raviniopsis* was included, its possible monophyly remains untested (Fig. 2A). The subgeneric classification of the genus *Argoravinia* proposed by Carvalho-Filho & Esposito (2012) was supported by the following character states: (1) setulae colour on the gena as black for *Argoravinia* (*s.s.*) and white for *Raviniopsis*, but here scored as gena and postgena having at least some setulae white for all *Argoravinia* species; (2) number of fronto-orbital setulae, which was not included here; (3) bending of the cerci and presence/absence of a cluster of spines apically, which we considered as two separate characters and scored cerci as straight or almost straight for all *Argoravinia* species since the 'bent' condition is only observed in taxa of the Blaesoxipha clade, and the cercal spines as 'a cluster' were not included here; (4) male epandrium with a lateral apophysis for *Argoravinia* (*s.s.*) or without for *Raviniopsis*, which was included and supported the monophyly of *Argoravinia* (*s.s.*) in our phylogenetic analysis; (5) vesica bifid for *Argoravinia* (*s.s.*) or composed of two separated lobes for *Raviniopsis*, which is here scored as bifid for all *Argoravinia* species, since species that appear to have two separated vesical lobes, might actually have the lobes fused at the base; (6) shape of the female T6, which was not included here; and (7) female with one seta on the epiproct in *Argoravinia* (*s.s.*) or two seate in *Raviniopsis*, which was not included here. Thus, our results support the subgeneric classification by Carvalho-Filho & Esposito (2012), since the presence of an epandrial lateral apophysis in species of *Argoravinia* (*s.s.*) was found as autapomorphic for this subgenus.

Species of *Malacophagomyia* are here included for the first time in a phylogenetic study. Lopes (1969a, 1983) implied a phylogenetic affinity of this genus to genera such as *Titanogrypa*, *Panava*, *Dexosarcophaga* and *Udamopyga*, but this is not supported by our results. The three studies providing a diagnosis for this genus (Lopes, 1966; Pape, 1996; Mulieri & Mello-Patiu, 2013) highlighted the remarkably elongated median stylus and the conspicuous juxta, which are characteristic for all species of *Malacophagomyia*. In at least two (i.e. Pape, 1996; Mulieri & Mello-Patiu, 2013) of these studies, the authors agree on the following consensus list of diagnostic character states: (1) postalar wall setulose, (2) male mid-femur without a ctenidium, (3) wing vein R_1 setulose dorsally, (4) third costal sector of wing setulose ventrally, (5) pregonite with membranous area along the ventral margin and near the bent apical part, (6) acrophallus with median stylus greatly elongated and curved (Fig. 17A, B, D) and (7) juxta arching over the lateral styli (Fig. 17A, B, D). Interestingly, the most remarkable character states (6 and 7) are shared with the species *Dodgeisca paramerata* Rohdendorf, 1971 (Fig. 16C, D), the only known species of *Dodgeisca*, which also shares with *Malacophagomyia* character states 1, 3, 4 of this consensus list. In addition, according to the most recent revision of *Malacophagomyia* (Mulieri & Mello-Patiu, 2013), not all species of this genus possess character

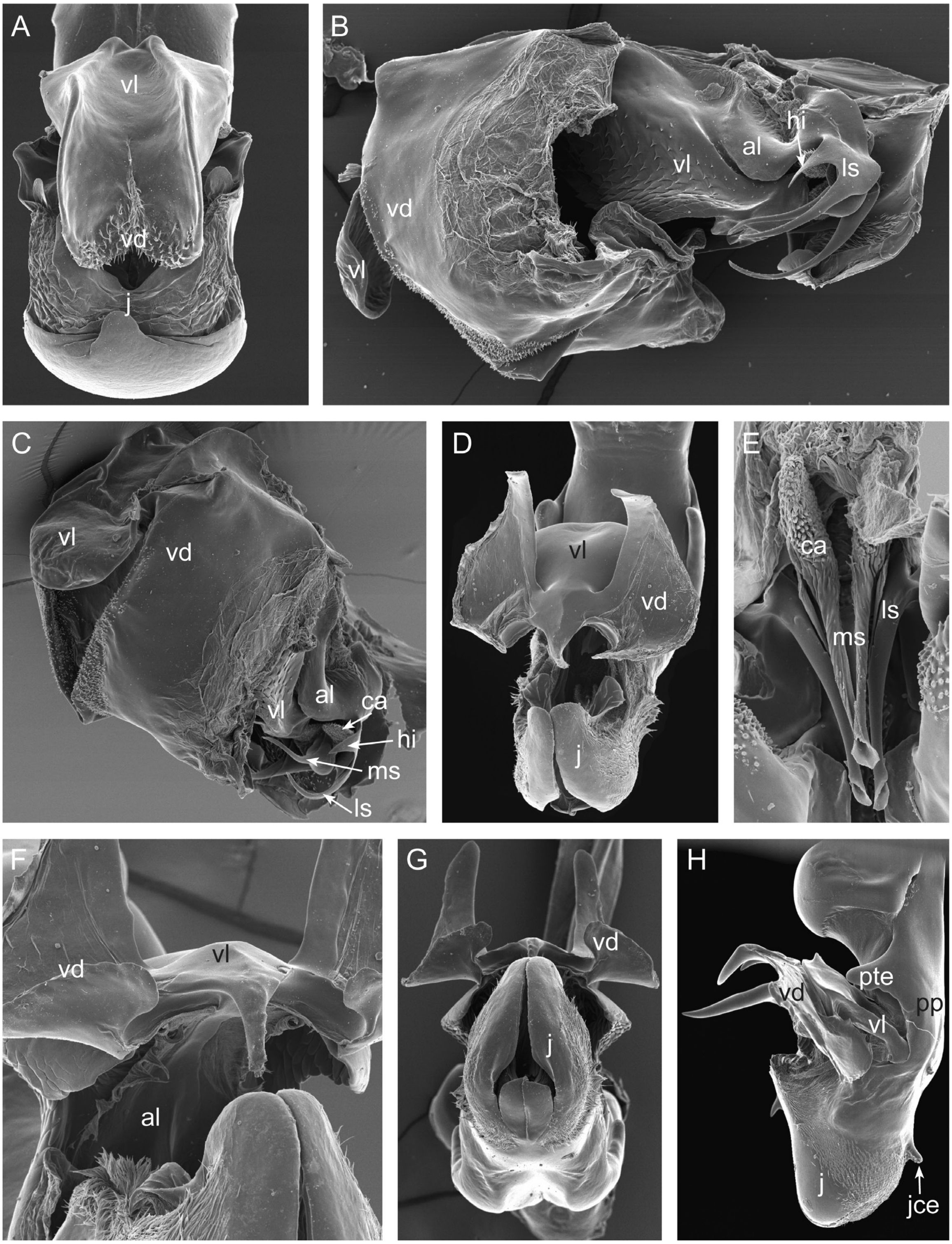

Figure 18. A, distiphallus, ventral view: *Nephochaetopteryx rettenmeyeri*. B, acrophallus and vesica, left lateral view: *Nephochaetopteryx* sp. C, acrophallus and vesica, antero-lateral view: *Nephochaetopteryx* sp. D, distiphallus, ventral view: *Oxysarcodexia angrensis*. E, acrophallus, ventral view: *Oxysarcodexia angrensis*. F, acrophallic levers and vesica, apical view: *Oxysarcodexia angrensis*. G, distiphallus, apical view: *Oxysarcodexia angrensis*. H, distiphallus, left lateral view: *Oxysarcodexia timida*. (D–H, courtesy M. Giroux). Abbreviations as in Table 1.

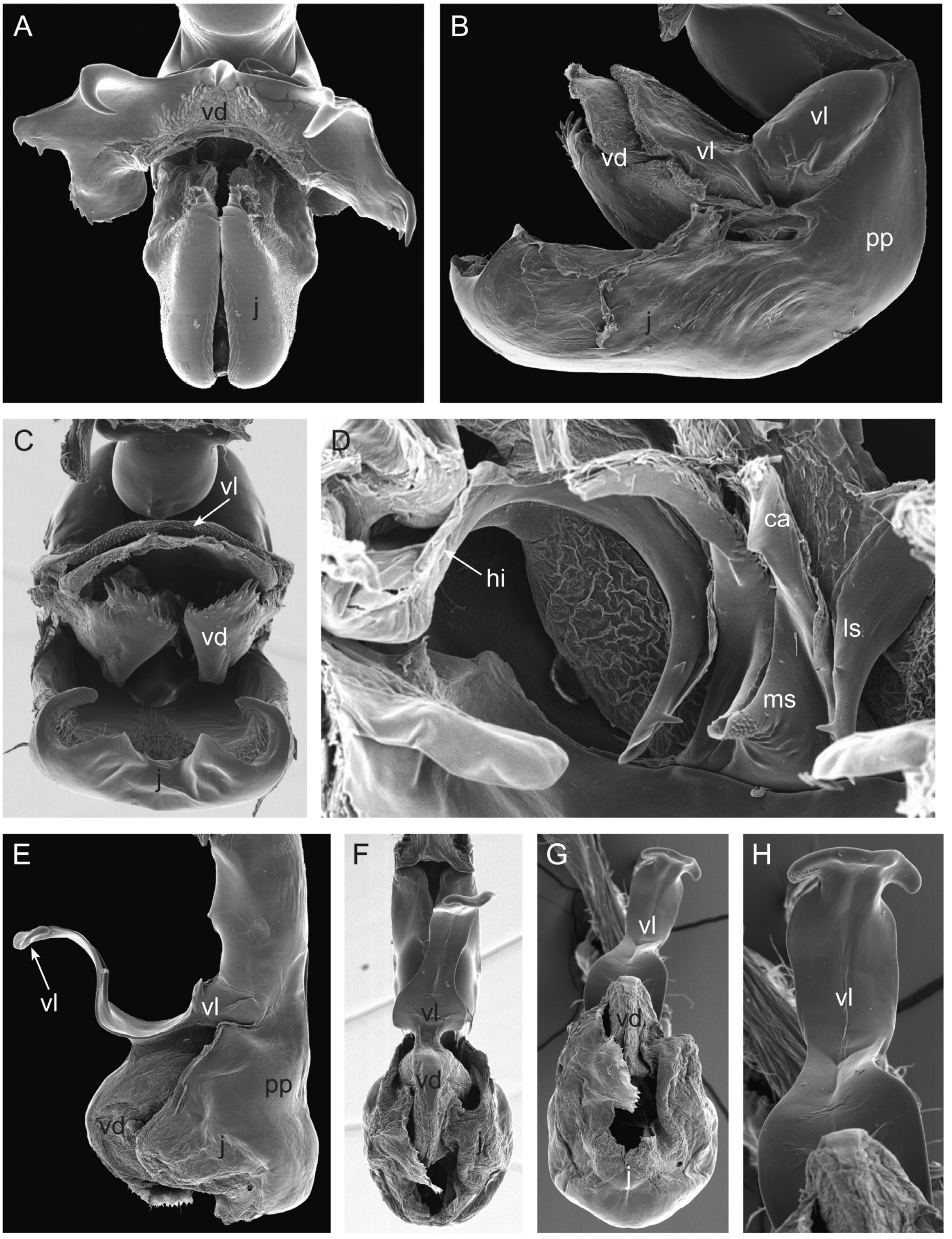

Figure 19. A, distiphallus, ventral view: *Oxysarcodexia timida*. B, distiphallus, left lateral view: *Oxyvinia xanthophora*. C, distiphallus, ventral view: *Oxyvinia xanthophora*. D, acrophallus and hillae, antero-lateral view: *Oxyvinia xanthophora*. E, distiphallus, left lateral view: *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. F, distiphallus, ventral view: *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. G, distiphallus, apical view: *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. H, vesical arm-shaped lever, apical view: *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. [A–D, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

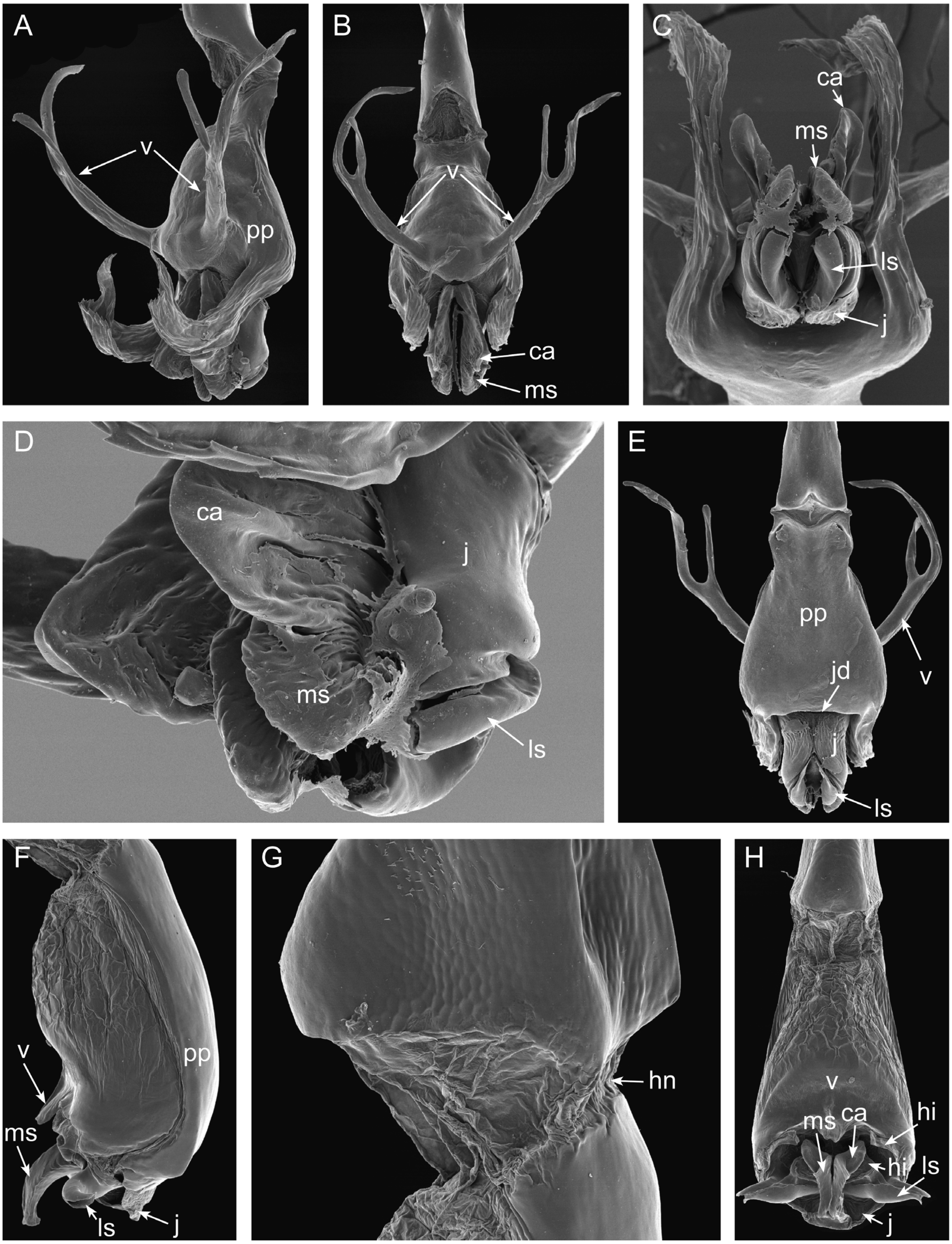

Figure 20. A, phallus, antero-lateral view: *Promayoa ramosa*. B, phallus, ventral view: *Promayoa ramosa*. C, distiphallus, apical view: *Promayoa ramosa*. D, acrophallus, antero-lateral view: *Promayoa ramosa*. E, phallus, dorsal view: *Promayoa ramosa*. F, distiphallus, left lateral view: *Rafaelia ampulla*. G, hinge between basi- and distiphallus, left lateral view: *Rafaelia ampulla*. H, phallus, ventral view: *Rafaelia ampulla*. Abbreviations as in Table 1.

Figure 21. A, distiphallus, left lateral view: *Sarothromyiops dasycnemis*. B, distiphallus, apical view: *Sarothromyiops dasycnemis*. C, distiphallus, antero-apical view: *Sarothromyiops dasycnemis*. D, phallus, left lateral view: *Sinopiella rufopilosa*. E, acrophallus and juxta, left lateral view: *Sinopiella rufopilosa*. F, phallus, ventral view: *Sinopiella rufopilosa*. G, phallus, dorsal view: *Sinopiella rufopilosa*. H, phallus, left lateral view: *Spirobolomyia singularis*. I, phallus (paraphallic blinkers removed), ventral view: *Spirobolomyia singularis*. J, phallus, dorsal view: *Spirobolomyia singularis*. [I, courtesy M. Giroux; H, J, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

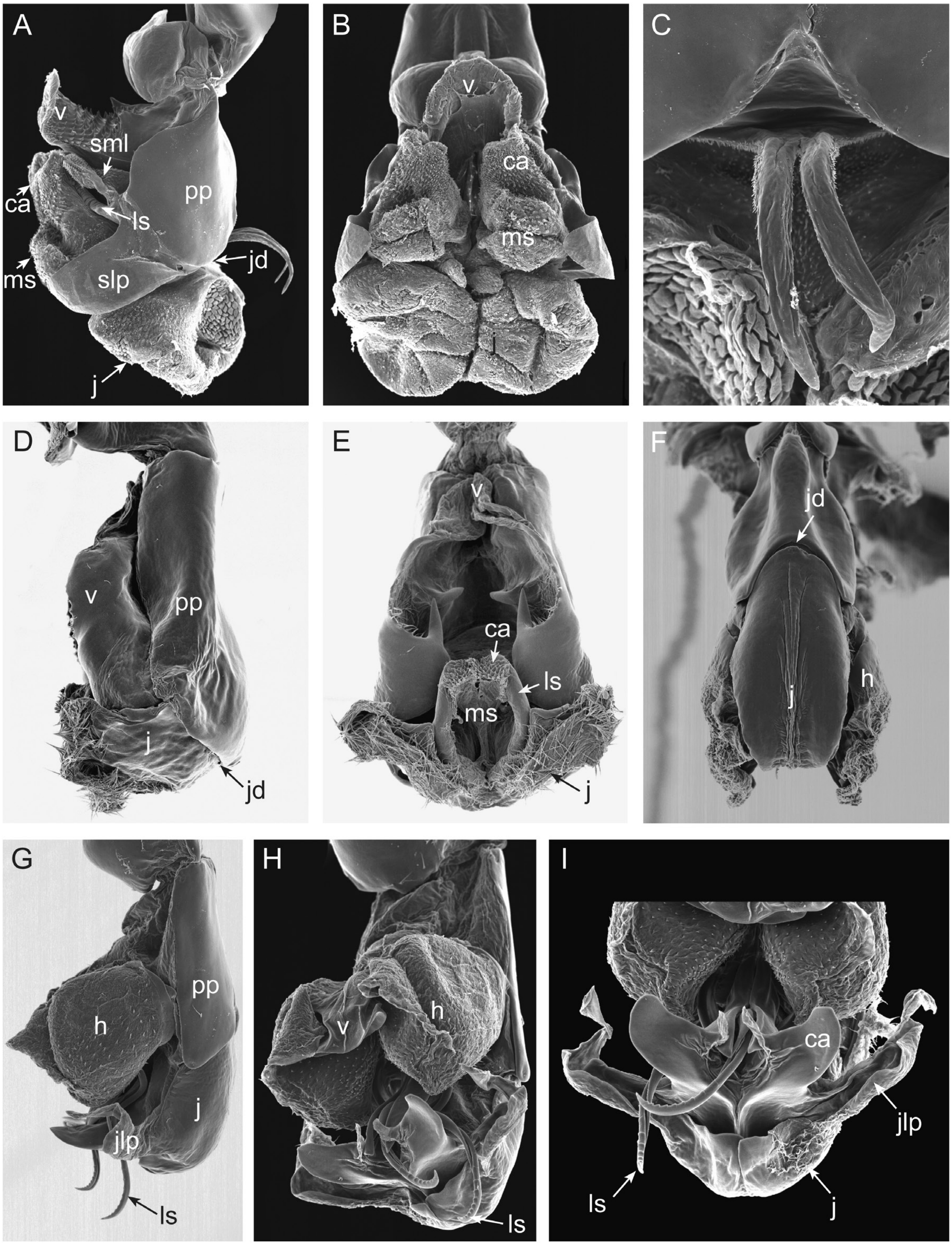

Figure 22. A, distiphallus, left lateral view: *Engelimyia inops*. B, distiphallus, ventral view: *Engelimyia inops*. C, distiphallus, apical view: *Engelimyia inops*. D, distiphallus, left lateral view: *Fletcherimyia fletcheri*. E, distiphallus, ventral view: *Fletcherimyia fletcheri*. F, phallus, dorsal view: *Helicobia morionella*. G, distiphallus, left lateral view: *Helicobia rapax*. H, distiphallus, antero-lateral view: *Helicobia rapax*. I, acrophallus and juxta, antero-apical view: *Helicobia rapax*. [C–I, courtesy M. Giroux; A, B, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

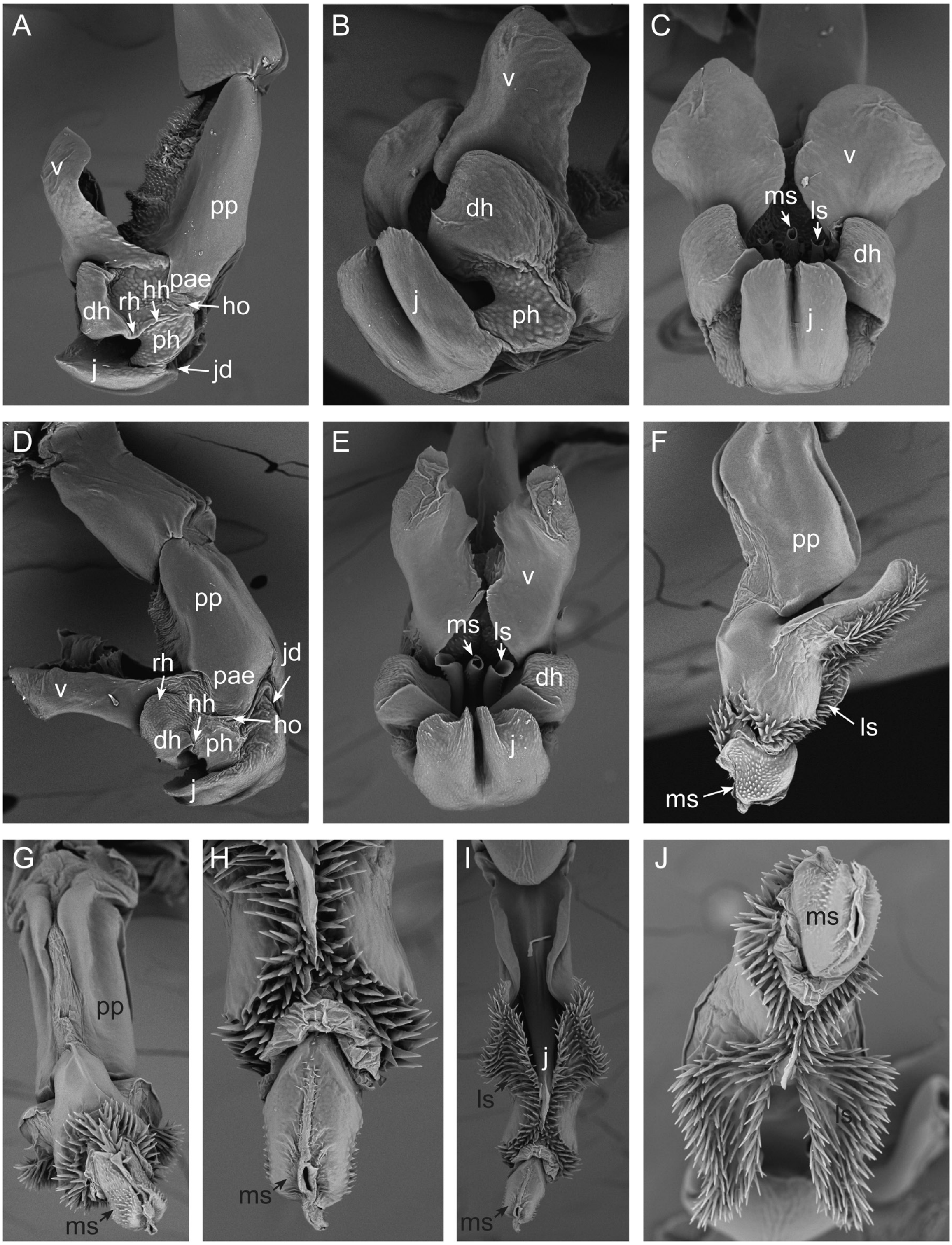

Figure 23. A, distiphallus, left lateral view: *Emblemasoma albicoma*. B, distiphallus, latero-apical view: *Emblemasoma albicoma*. C, distiphallus, ventral view: *Emblemasoma albicoma*. D, distiphallus, left lateral view: *Emblemasoma erro*. E, distiphallus, ventral view: *Emblemasoma erro*. F, distiphallus, left lateral view: *Emdenimyia korytkowskii*. G, distiphallus, ventral view: *Emdenimyia korytkowskii*. H, median stylus, ventral view: *Emdenimyia korytkowskii*. I, distiphallus, dorsal view: *Emdenimyia korytkowskii*. J, acrophallus, apical view: *Emdenimyia korytkowskii*. Abbreviations as in Table 1.

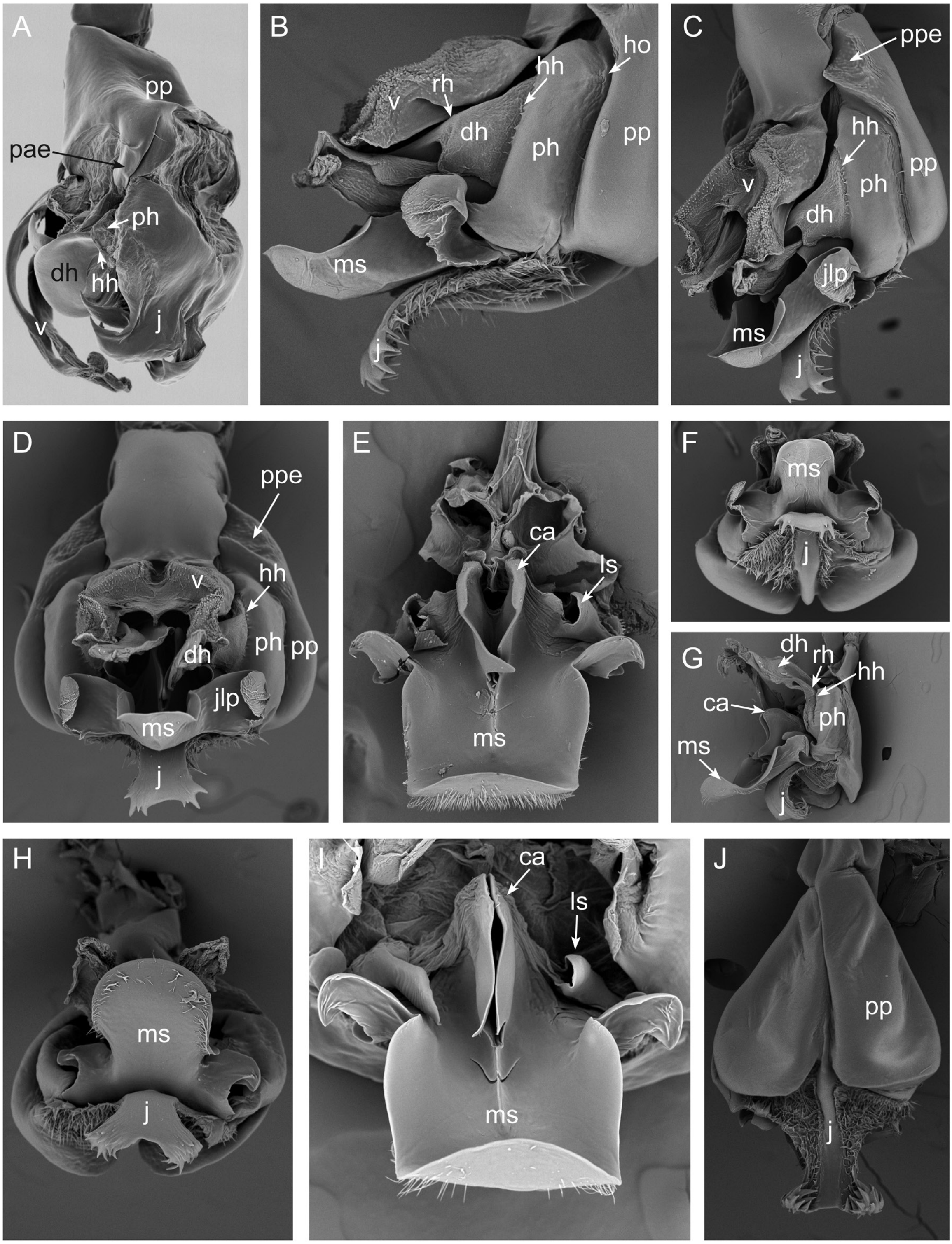

Figure 24. A, distiphallus, postero-lateral view: *Lepidodexia* (*Notochaeta*) *woodi*. B, distiphallus, left lateral view: *Lipoptilocnema crispina*. C, distiphallus, antero-lateral view: *Lipoptilocnema crispina*. D, distiphallus, ventral view: *Lipoptilocnema crispina*. E, acrophallus and sperm duct, ventral view: *Lipoptilocnema crispina*. F, distiphallus, apical view: *Lipoptilocnema crispina*. G, distiphallus, antero-lateral view: *Lipoptilocnema koehleri*. H, distiphallus, apical view: *Lipoptilocnema koehleri*. I, acrophallus, ventral view: *Lipoptilocnema koehleri*. J, distiphallus, dorsal view: *Lipoptilocnema koehleri*. (A, courtesy M. Giroux). Abbreviations as in Table 1.

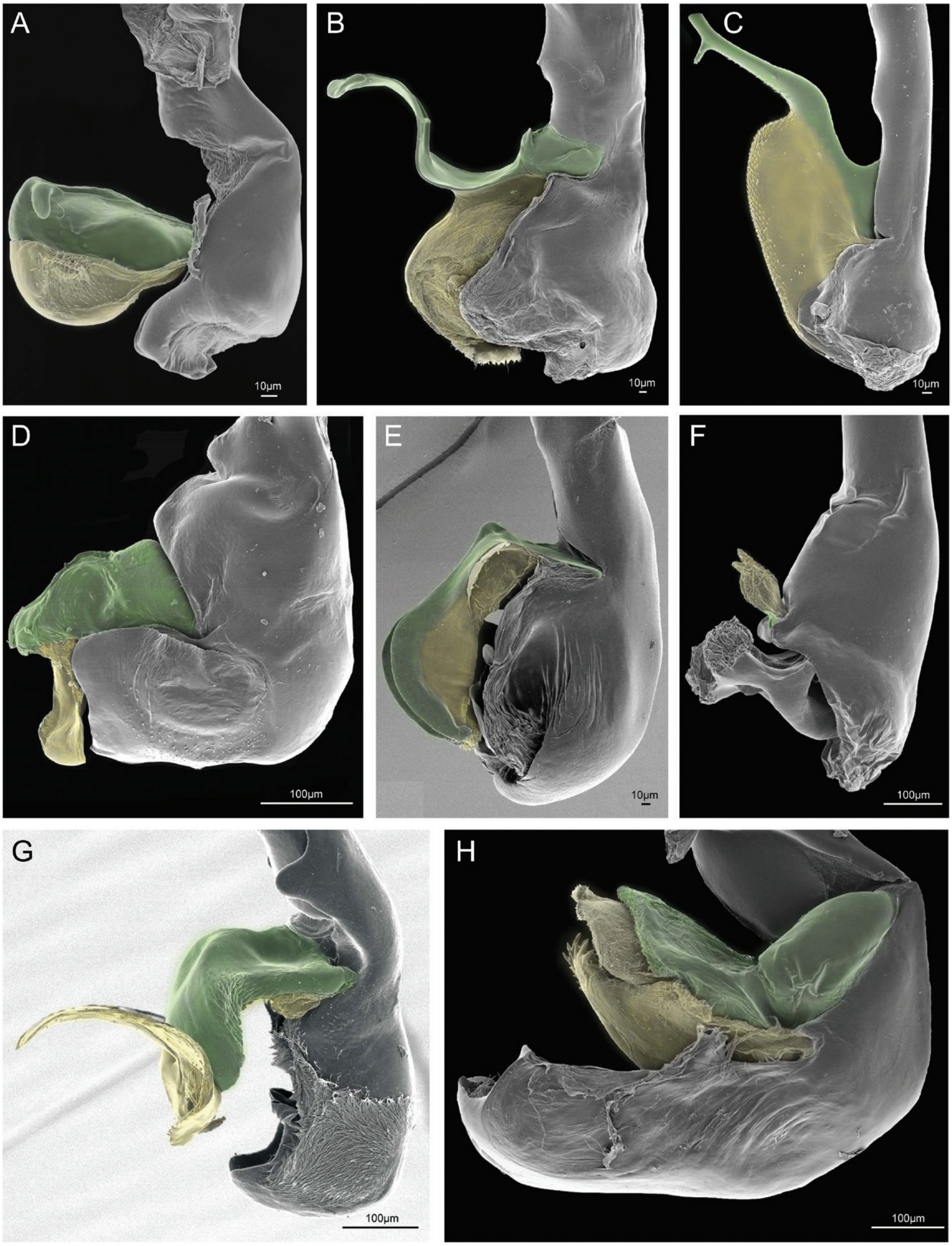

Figure 25. Phallus in the 'lower' Sarcophaginae, left lateral view showing vesica divided into vesical arm-shaped lever (highlighted in green) and distal section of the vesica (highlighted in yellow): A, *Tricharaea* (*Sarothromyia*) *simplex*; B, *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*; C, *Sarcofahrtiopsis* (*s.s.*) *cuneata*; D, *Bahamiola gregori*; E, *Nephochaetopteryx rettenmeyeri*; F, *Ravinia rufipes*; G, *Oxysarcodexia angrensis*; H, *Oxyvinia xanthophora*. [A, G, courtesy M. Giroux; F, H, from Giroux *et al.* (2010)].

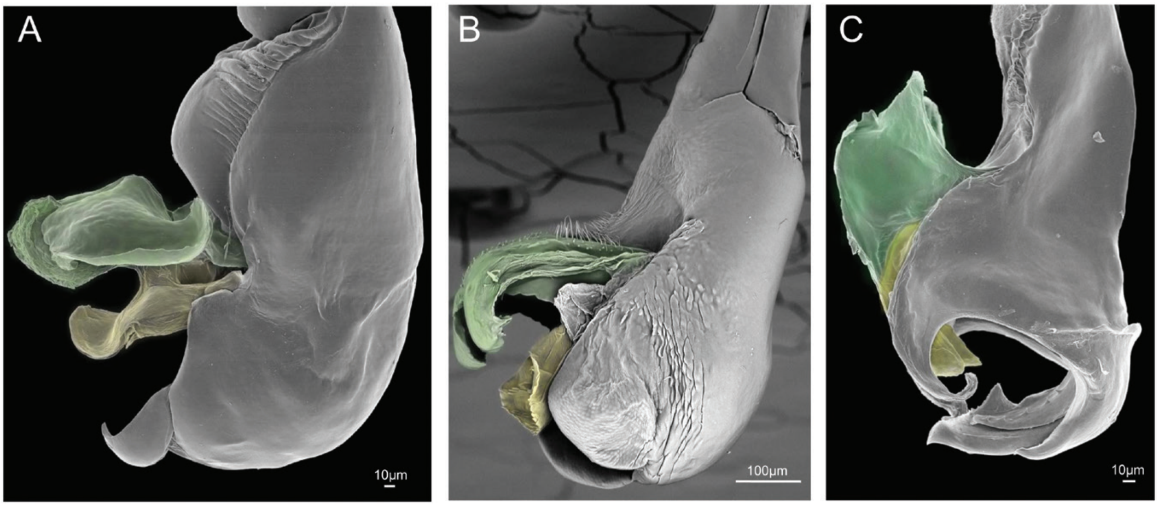

Figure 26. Phallus in the 'lower' Sarcophaginae, left lateral view showing vesica divided into vesical arm-shaped lever (highlighted in green) and distal section of the vesica (highlighted in yellow): A, *Rettenmeyerina serrata*; B, *Dexosarcophaga* (*Cistudinomyia*) *cistudinis*; C, *Dexosarcophaga* (*s.s.*) *transita*. (C, courtesy M. Giroux).

state 5, which leaves only character state 2 (male mid-femur without a ctenidium) as a difference between *Dodgeisca* and *Malacophagomyia*. Besides that, in their revision of the latter genus, Mulieri & Mello-Patiu (2013) highlighted the cerci fused along their entire length and the spine-like setae on ST4 as possible autapomorphies of *Malacophagomyia*. Both of these character states are also present in *D. paramerata*. Mulieri & Mello-Patiu (2013) also included the absence of a vesica, the presence of harpes and arms of the lateral styli as part of their diagnosis of *Malacophagomyia*. According to our observations, both *Malacophagomyia* and *Dodgeisca* possess a broad and flat vesica (Figs 16C, D, 17A, B, D), which, however, is not as prominent as in other sarcophagines. Also, the 'arms of the lateral styli' described by Mulieri & Mello-Patiu (2013) are consistent with our definition of hillae, while the structures considered as harpes by these authors do not follow our definition for that structure. Consequently, the 'arms of the lateral styli' (Mulieri & Mello-Patiu, 2013) are homologized with the hillae (Figs 16C–E, 17A, B), and their 'harpes' with the paraphallic lateral expansions (Figs 16C, 17A). In addition to the synapomorphies mentioned above, we found *Malacophagomyia* and *Dodgeisca* to share the presence of two pointed processes on the juxtal apex (Figs 16D, 17B), and distal part of hillae membranous. Based on all the above, we suggest *Dodgeisca* as a **new junior synonym** of *Malacophagomyia*, and we maintain it and give it a **new status** as a subgenus of the latter genus.

Blaesoxipha clade

This clade received strong support and it is composed of the genera *Blaesoxipha*, *Comasarcophaga*, *Emdenimyia*, *Fletcherimyia*, *Mecynocorpus*, *Panava*, *Promayoa*, *Sarcodexiopsis*, *Spirobolomyia*, *Thomazomyia*, *Titanogrypa* and *Villegasia*, which are arranged into the two clades: 40 and 50 (Fig. 2B).

The genera of the Blaesoxipha clade share four apomorphic character states: (1) male with abdominal ST5 cleft with subparallel sides (Fig. 43B, C), (2) distiphallus not surrounding the acrophallus, styli entirely exposed (except in *Comasarcophaga* and *Spirobolomyia*) (Figs 12A, 23F, 28E, 29D, 30D, 34D, 36G), (3) juxta partially to entirely fused to acrophallic structures (Figs 12B, 22E, 30C, 35H, 39E) and (4) juxta straight (Figs 35H, 39E). Three additional autapomorphies that evolved in the ancestor of this clade, but which have subsequently become reduced or modified in some of these genera, are: distal margin of juxta with spine-like processes (Figs 30D, 34D–F), which evolved into distal margin smooth in clades 42 and 51 (Figs 11H, 28E, 35H, 39E); lateral styli collapsed with no outlet (Figs 23J, 28F, 29B, 30E, 34E, 36H, 39F), which is reversed in clades 43 and 51 where a sperm outlet is found (Figs 11H, 20D, 21I, 39B–D); and lateral styli plate-like, with digitate margins or finger-shaped processes (Figs 23F, 29E, 30C, 34E, 36G), which are reversed in clades 45, 48 and 51 where the lateral styli are tube-shaped (Figs 11H, 12B, 21I, 22E, 39C).

Some branches within the Blaesoxipha clade had low supports, and alternative topologies were retrieved differing in the position of the paraphyletic

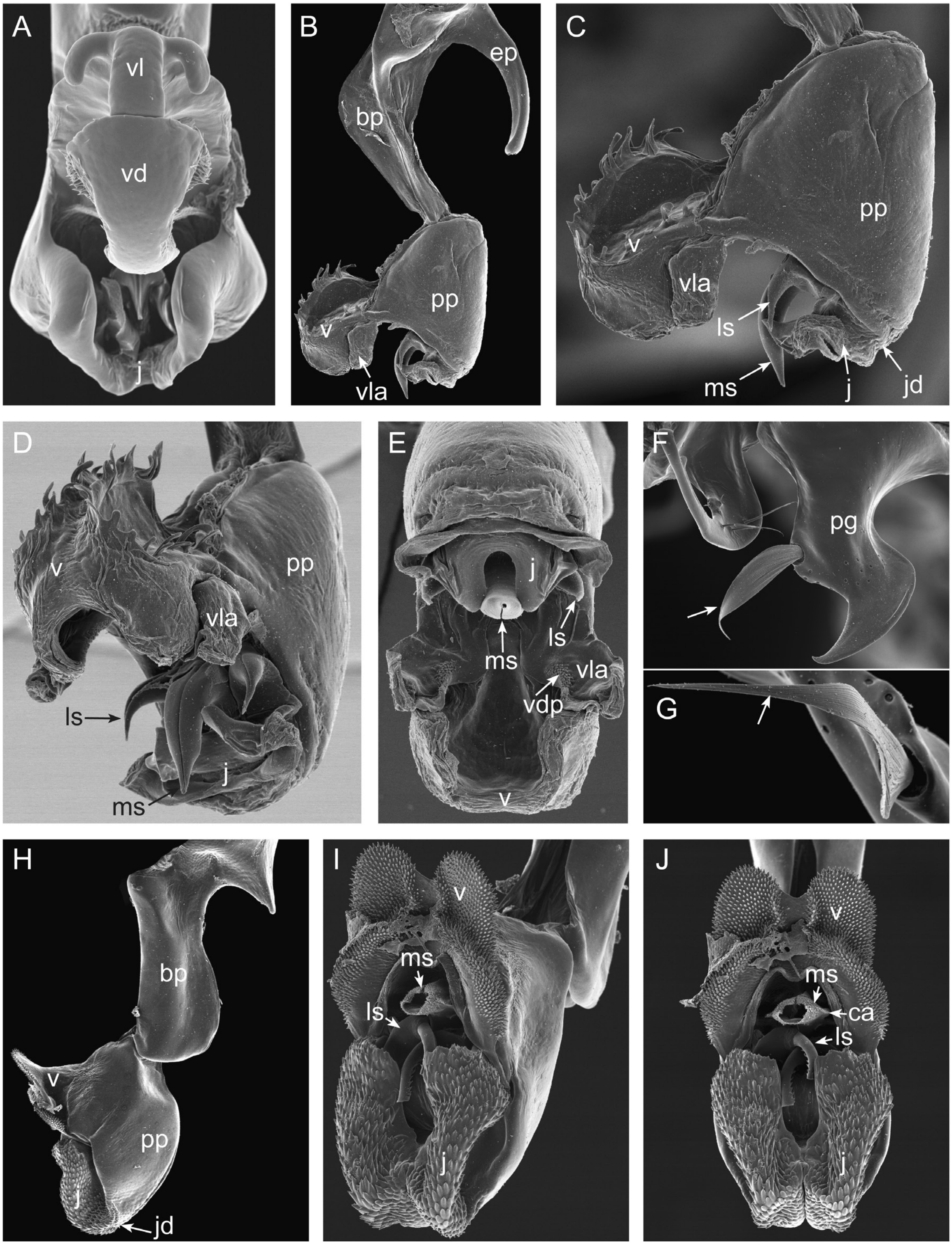

Figure 27. A, distiphallus, ventral view: *Tricharaea* (*Sarothromyia*) *simplex*. B, phallus, left lateral view: *Tripanurga albicans*. C, distiphallus, lateral view: *Tripanurga albicans*. D, distiphallus, antero-lateral view: *Tripanurga albicans*. E, distiphallus, apical view: *Tripanurga albicans*. F, postgonite, left lateral view (arrow showing seta): *Tripanurga albicans*. G, seta (arrow) of postgonite, apical view: *Tripanurga albicans*. H, phallus, left lateral view: *Tulaeopoda pervillosa*. I, distiphallus, antero-lateral view: *Tulaeopoda pervillosa*. J, distiphallus, ventral view: *Tulaeopoda pervillosa*. (A, courtesy M. Giroux). Abbreviations as in Table 1.

Figure 28. A, distiphallus, dorsal view: *Retrocitomyia retrocita*. B, distiphallus, left lateral view: *Rettenmeyerina serrata*. C, distiphallus, ventral view: *Rettenmeyerina serrata*. D, distiphallus, antero-lateral view: *Rettenmeyerina serrata*. E, distiphallus, left lateral view: *Sarcodexiopsis welchi*. F, distiphallus, ventral view: *Sarcodexiopsis welchi*. G, distiphallus, ventral view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. H, distiphallus, left lateral view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. I, distiphallus, ventral view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. J, distiphallus, latero-apical view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. Abbreviations as in Table 1.

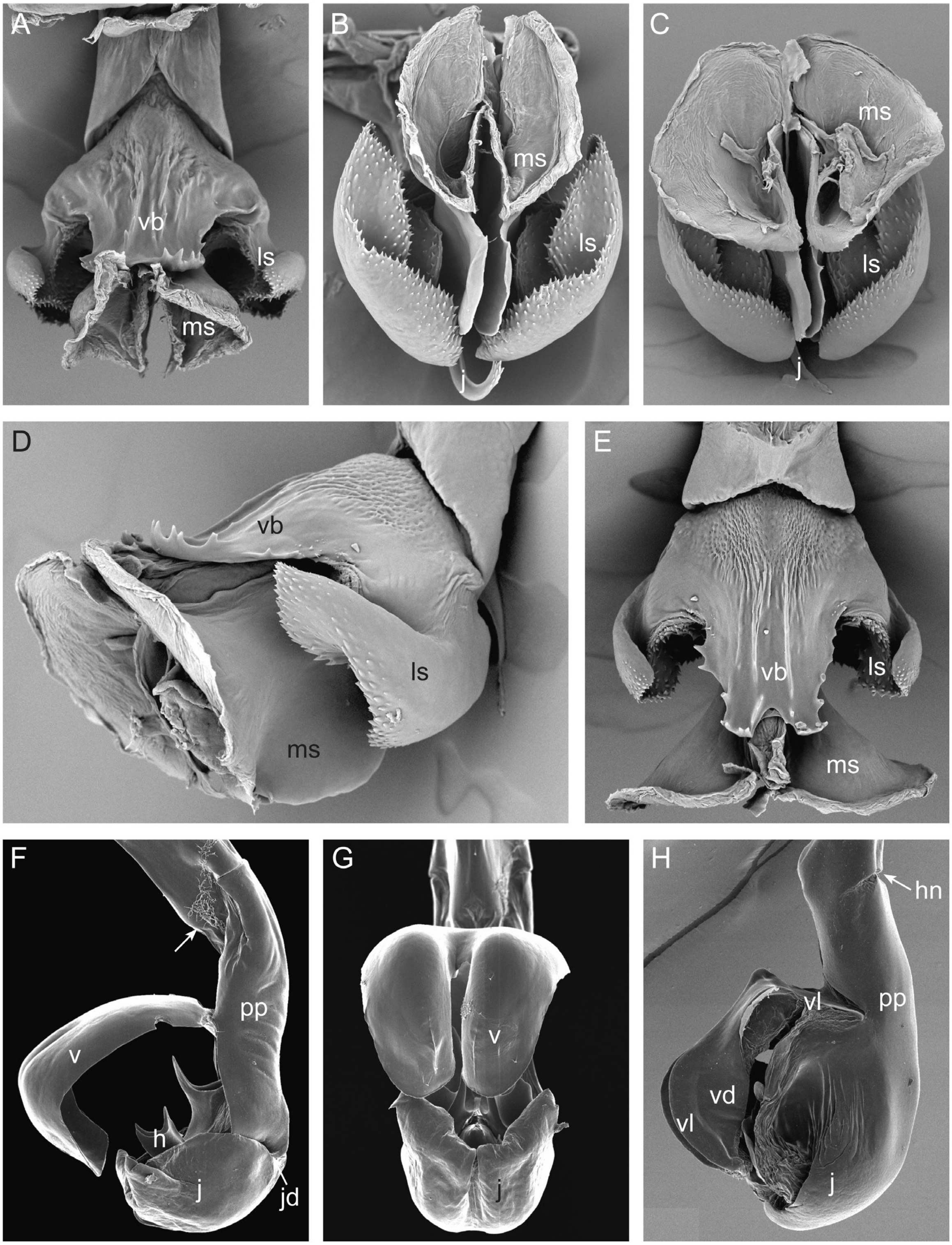

Figure 29. A, distiphallus, ventral view: *Mecynocorpus salvum*. B, distiphallus, apical view: *Mecynocorpus salvum*. C, distiphallus, apical view: *Mecynocorpus* sp. nov. D, distiphallus, left lateral view: *Mecynocorpus* sp. nov. E, distiphallus, ventral view: *Mecynocorpus* sp. nov. F, distiphallus, left lateral view (arrow indicates tubular ventral area between basi- and distiphallus): *Microcerella spinigena*. G, distiphallus, ventral view: *Microcerella spinigena*. H, distiphallus, left lateral view: *Nephochaetopteryx rettenmeyeri*. [G, courtesy M. Giroux; F, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

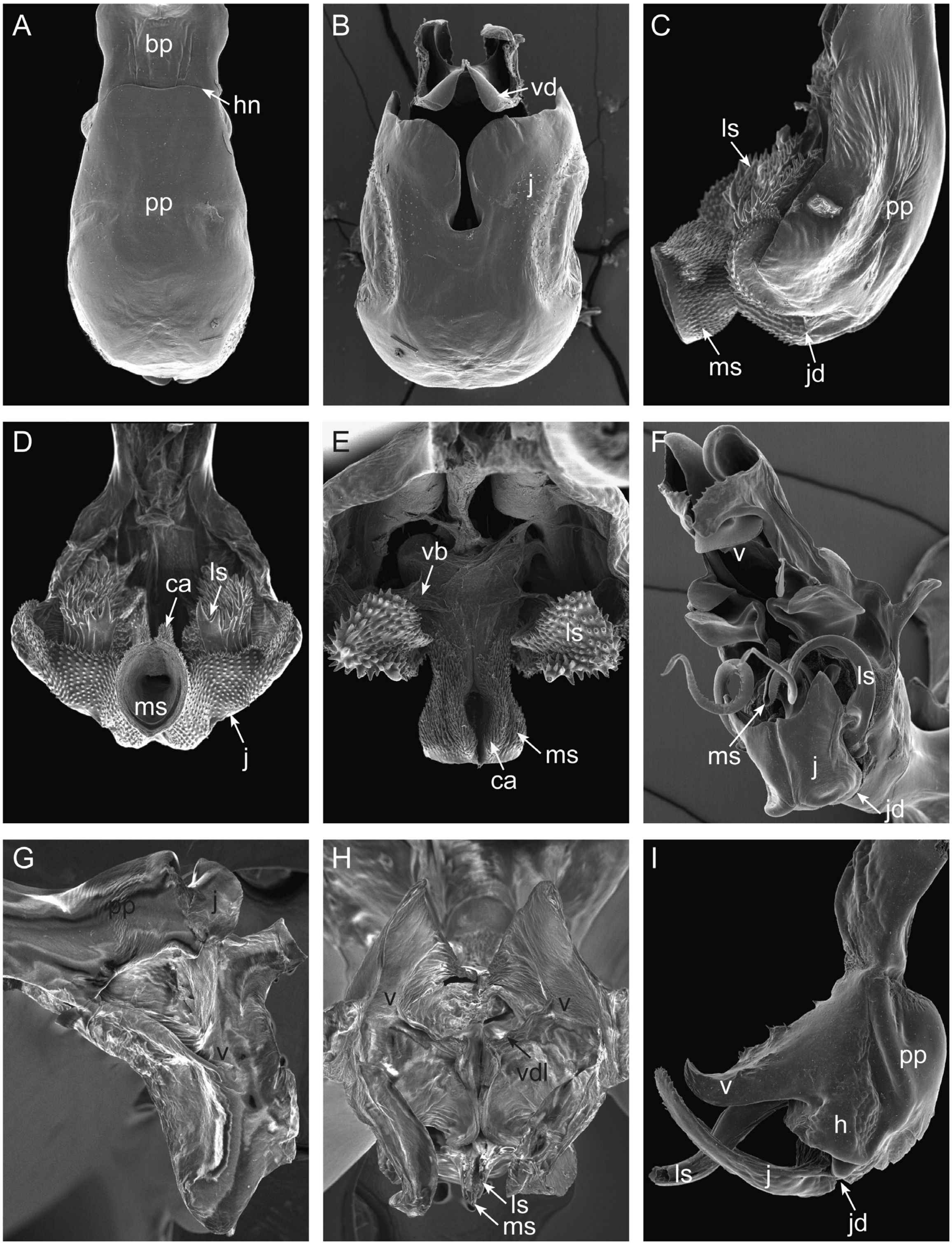

Figure 30. A, phallus, dorsal view: *Bahamiola gregori.* B, phallus, apical view: *Bahamiola gregori*. C, distiphallus, left lateral view: *Blaesoxipha* (*Gigantotheca*) *plinthopyga*. D, distiphallus, ventral view: *Blaesoxipha* (*Gigantotheca*) *plinthopyga*. E, acrophallus, proximo-ventral view: *Blaesoxipha* (*Gigantotheca*) *plinthopyga*. F, distiphallus, latero-apical view: *Boettcheria latisterna*. G, distiphallus, left lateral view: *Udamopyga* (*Carinoclypeus*) *creameri*. H, distiphallus, apical view: *Udamopyga* (*Carinoclypeus*) *creameri*. I, phallus, left lateral view: *Chrysagria alticophaga*. [E, F, courtesy M. Giroux; C, D, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

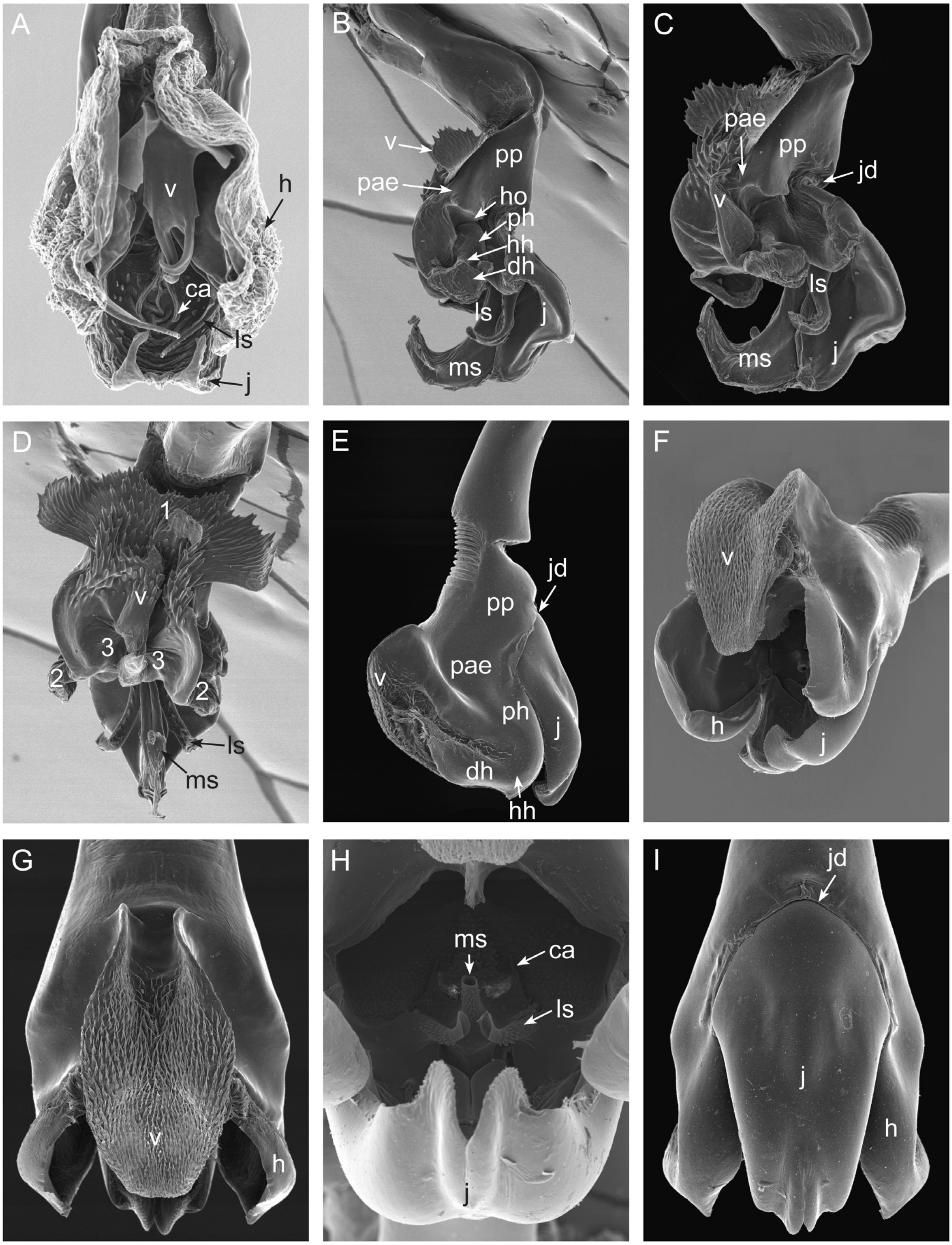

Figure 31. A, distiphallus, ventral view: *Helicobia morionella*. B, distiphallus, left lateral view: *Lepidodexia* (*Hallina*) *retusa*. C, distiphallus, left ventro-lateral view: *Lepidodexia* (*Hallina*) *retusa*. D, distiphallus, ventral view showing a vesica with a spinous lobe proximal to it (no. 1), a convex sclerotized distal section (no. 2) and a C-shaped medial section (no. 3): *Lepidodexia* (*Hallina*) *retusa*. E, phallus, left lateral view: *Halliosca declinata*. F, distiphallus, latero-apical view: *Halliosca declinata*. G, distiphallus, ventral view: *Halliosca declinata*. H, acrophallus, apical view: *Halliosca declinata*. I, distiphallus, dorsal view: *Halliosca declinata*. (A, courtesy M. Giroux). Abbreviations as in Table 1.

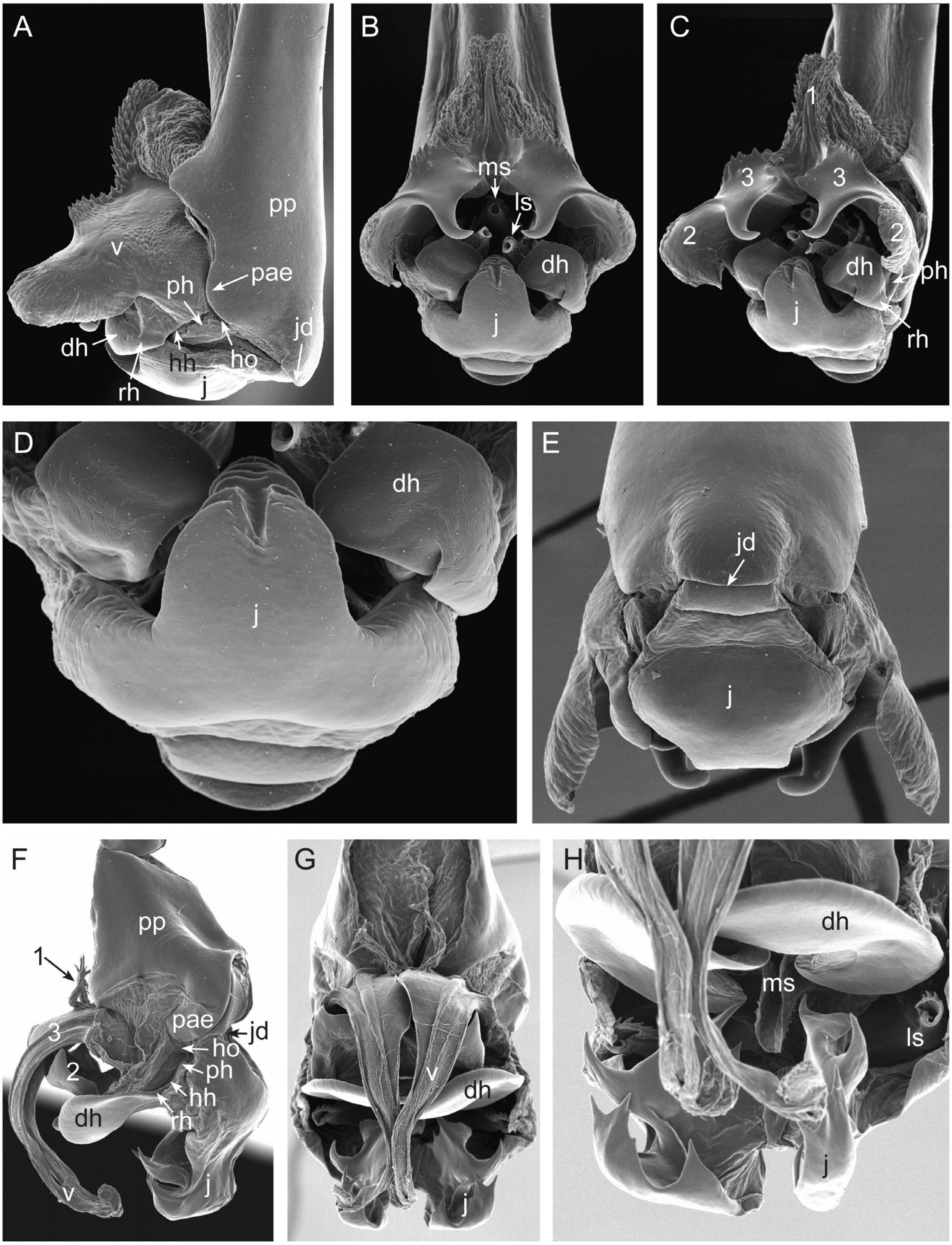

Figure 32. A, distiphallus, left lateral view: *Lepidodexia* (*Dexomyophora*) *fascialis*. B, distiphallus, ventral view: *Lepidodexia* (*Dexomyophora*) *fascialis*. C, distiphallus, antero-lateral view showing a vesica with a spinous lobe proximal to it (no. 1), a convex sclerotized distal section (no. 2) and a C-shaped medial section (no. 3): *Lepidodexia* (*Dexomyophora*) *fascialis*. D, juxta, apical view: *Lepidodexia* (*Dexomyophora*) *fascialis*. E, distiphallus, apical view: *Lepidodexia* (*Dexomyophora*) *fascialis*. F, distiphallus, left lateral view showing a vesica with a spinous lobe proximal to it (no. 1), a convex sclerotized distal section (no. 2) and a C-shaped medial section (no. 3): *Lepidodexia* (*Notochaeta*) *woodi*. G, distiphallus, ventral view: *Lepidodexia* (*Notochaeta*) *woodi*. H, distiphallus, detail ventral view: *Lepidodexia* (*Notochaeta*) *woodi*. [F, G, courtesy M. Giroux; H, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

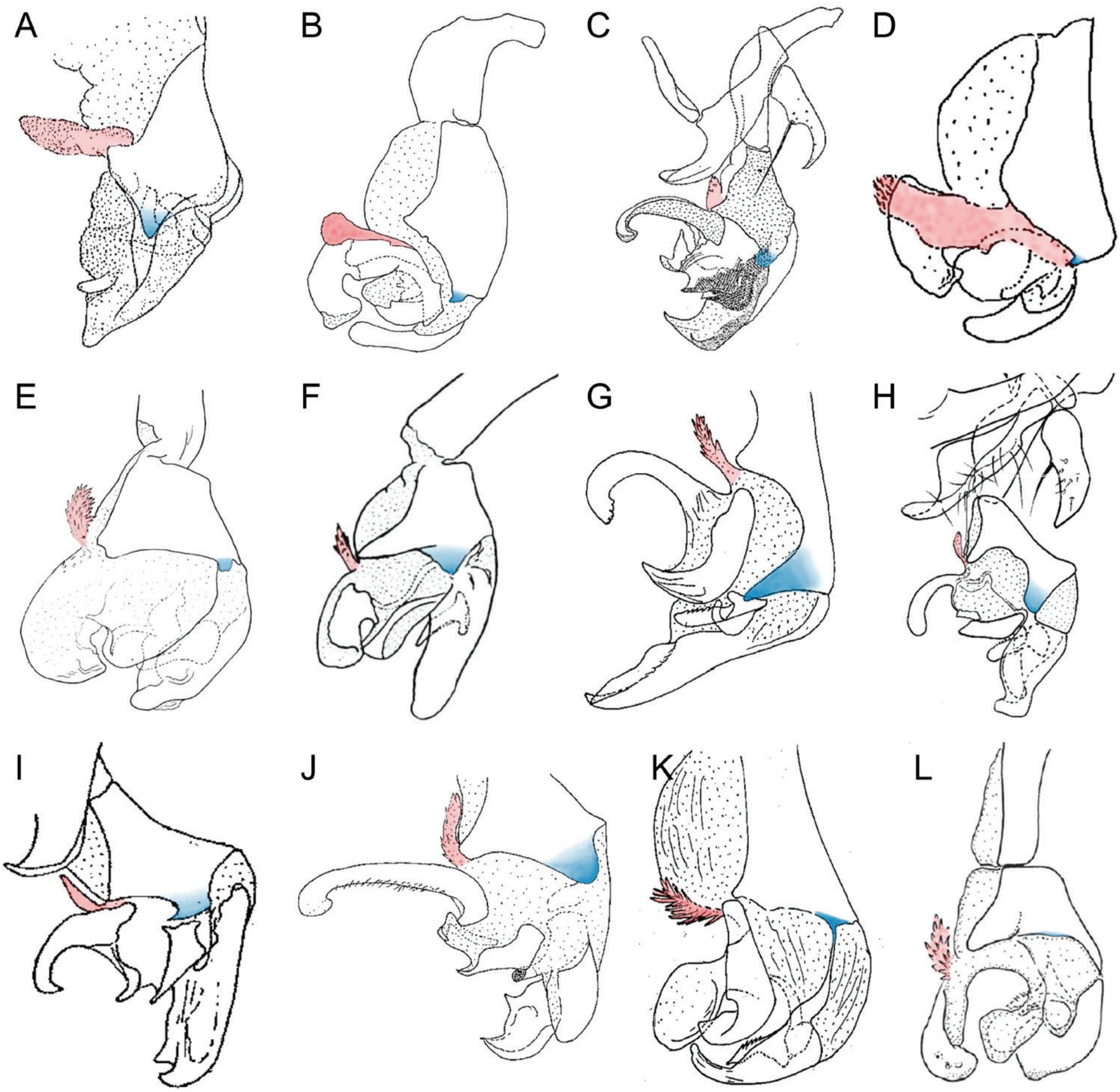

Figure 33. Phallus (and distiphallus) in *Lepidodexia*, with the vesica bearing a proximal spinous lobe (highlighted in red) and ventro-distal paraphallic apical expansion (highlighted in blue): A, *Lepidodexia* (*Chamayamyia*) *pilosa* (Lopes, 1969); B, *Lepidodexia* (*Eufletcherimyia*) *downsi* (Lopes, 1984); C, *Lepidodexia* (*Geijskesia*) *brevigaster* (Lopes, 1945); D, *Lepidodexia* (*Johnsonia*) *pomaschi* (Lopes, 1991); E, *Lepidodexia* (*s.s.*) *apolinari* (Lopes, 1951); F, *Lepidodexia* (*s.s.*) *sarcophagina* (Townsend, 1927); G, *Lepidodexia* (*Neophyto*) *sheldoni* (Coquillett, 1898); H, *Lepidodexia* (*Notochaeta*) *centenaria* (Mello-Patiu & Luna-Dias, 2010); I, *Lepidodexia* (*Notochaeta*) *diversinervis* (Wulp, 1895); J, *Lepidodexia* (*Orodexia*) *opima* (Wiedemann, 1830); K, *Lepidodexia* (*Pachygraphia*) *bocainensis* (Lopes, 1979); L, *Lepidodexia* (*Xylocamptopsis*) *teffeensis* (Silva & Mello-Patiu, 2012). [A, from Lopes (1969b), B, D, from Lopes (1991), C, from Lopes (1945), E, F, from Lopes (1951), G, K, from Lopes (1979), H, from Mello-Patiu & Luna-Dias (2010), I, from Lopes & Tibana (1988), J, from Lopes (1979), L, from Silva & Mello-Patiu (2012)].

assemblage of species of *Sarcodexiopsis*, subordinate either to clade 44 or 46, and the position of the genus *Villegasia*, emerging as sister to either *Emdenimyia* or clade 42. Examples of character states giving these conflicting and weakly supported topologies are: the third costal sector of wing setulose ventrally, found only in *Emdenimyia*, *Panava*, *Promayoa* and *Thomazomayia*; male mid-femur with

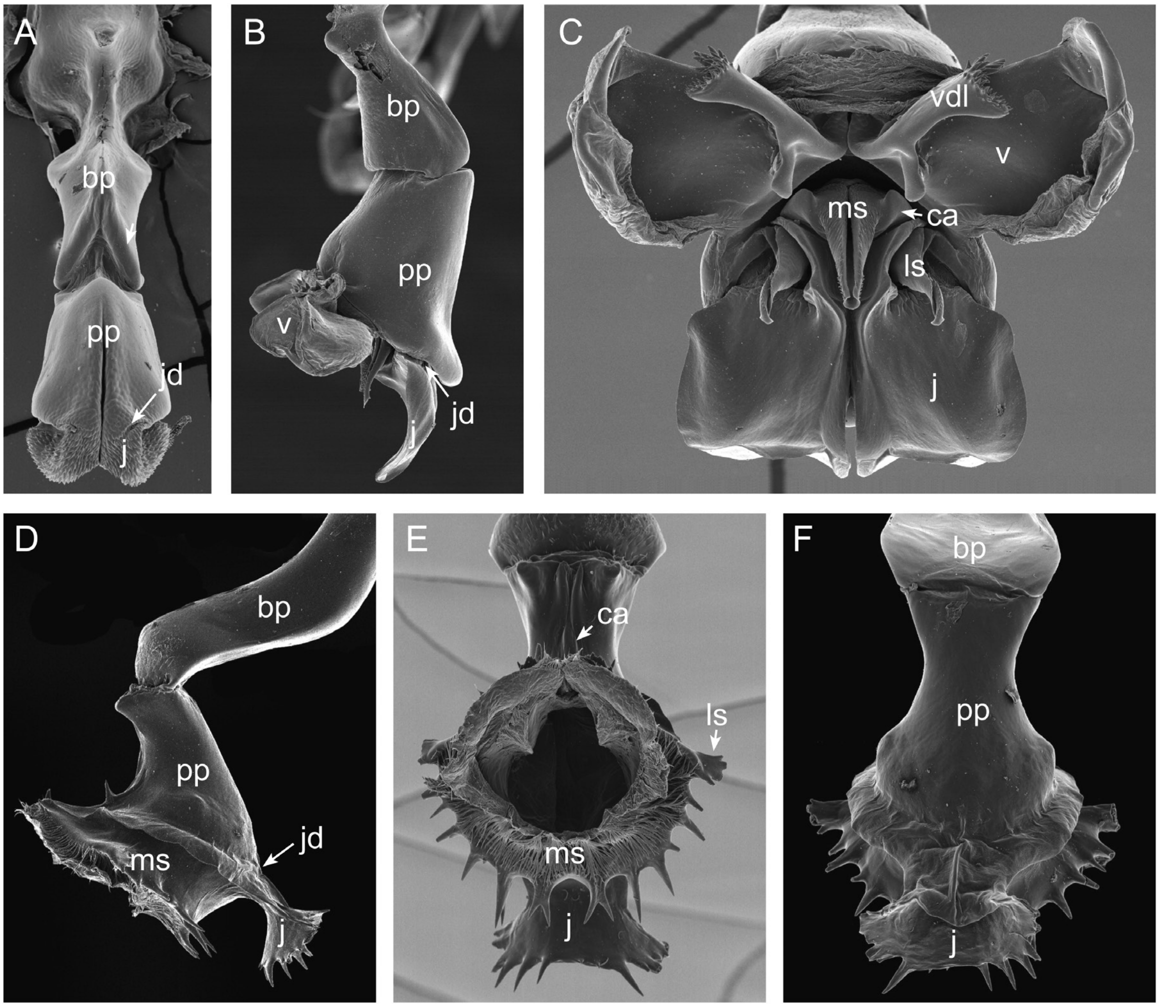

Figure 34. A, phallus, dorsal view: *Tulaeopoda pervillosa*. B, phallus, left lateral view: *Udamopyga* (*s.s.*) *neivai*. C, distiphallus, apical view: *Udamopyga* (*s.s.*) *neivai*. D, phallus, left lateral view: *Villegasia postuncinnata*. E, distiphallus, ventral view: *Villegasia postuncinnata*. F, distiphallus, dorsal view: *Villegasia postuncinnata*. Abbreviations as in Table 1.

a ctenidium, found only in the genera of clades 51, 60 and in *Villegasia*; male hind tibia with apical posteroventral seta well differentiated only in the genus *Spirobolomyia*, and in some species of *Blaesoxipha*, while in all other genera of the Blaesoxipha clade this seta is not differentiated; cercal prong with spine-like setae on dorsal surface, which evolved, in parallel, in *Comasarcophaga* and *Spirobolomyia* (clade 53 in Fig. 2B), and in species of *Blaesoxipha* and *Mecynocorpus* (clade 60 in Fig. 2B); pregonite proximally wide and distally bifid; two presutural dorso-central setae, present only in *Fletcherimyia* and *Thomazomyia*; the reduction of the vesica occurring in clade 58, which includes *Emdenimyia* and *Blaesoxipha*, and *Mecynocorpus*, and in parallel in *Villegasia*; and lateral styli collapsed, with no outlet, in these four genera and *Thomazomyia*.

Our results are in partial agreement with Roback's (1954) arrangement of the subtribe Servaisiina, since we find the genera *Blaesoxipha*, *Fletcherimyia*, *Mecynocorpus*, *Thomazomyia* and *Titanogrypa* to form a moderately to strongly supported clade. Within the Servaisiina, Roback (1954) had (*Blaesoxipha* + *Mecynocorpus*), which is a close match to the present results. Differences are due to his narrow concept of *Blaesoxipha*, based on which he assigned species to several genera under the Impariina, Servaisiina and Hystricocnemina.

Lopes (1983) described the acrophallic structures of the tribes Impariini and Protodexiini (i.e. *Blaesoxipha sensu* Pape [1994]) as: 'glans of penis shows a special structure, without tubular styli, presenting a large opening'. This finds support in our study, where the lateral styli are seen as collapsed or at least appearing

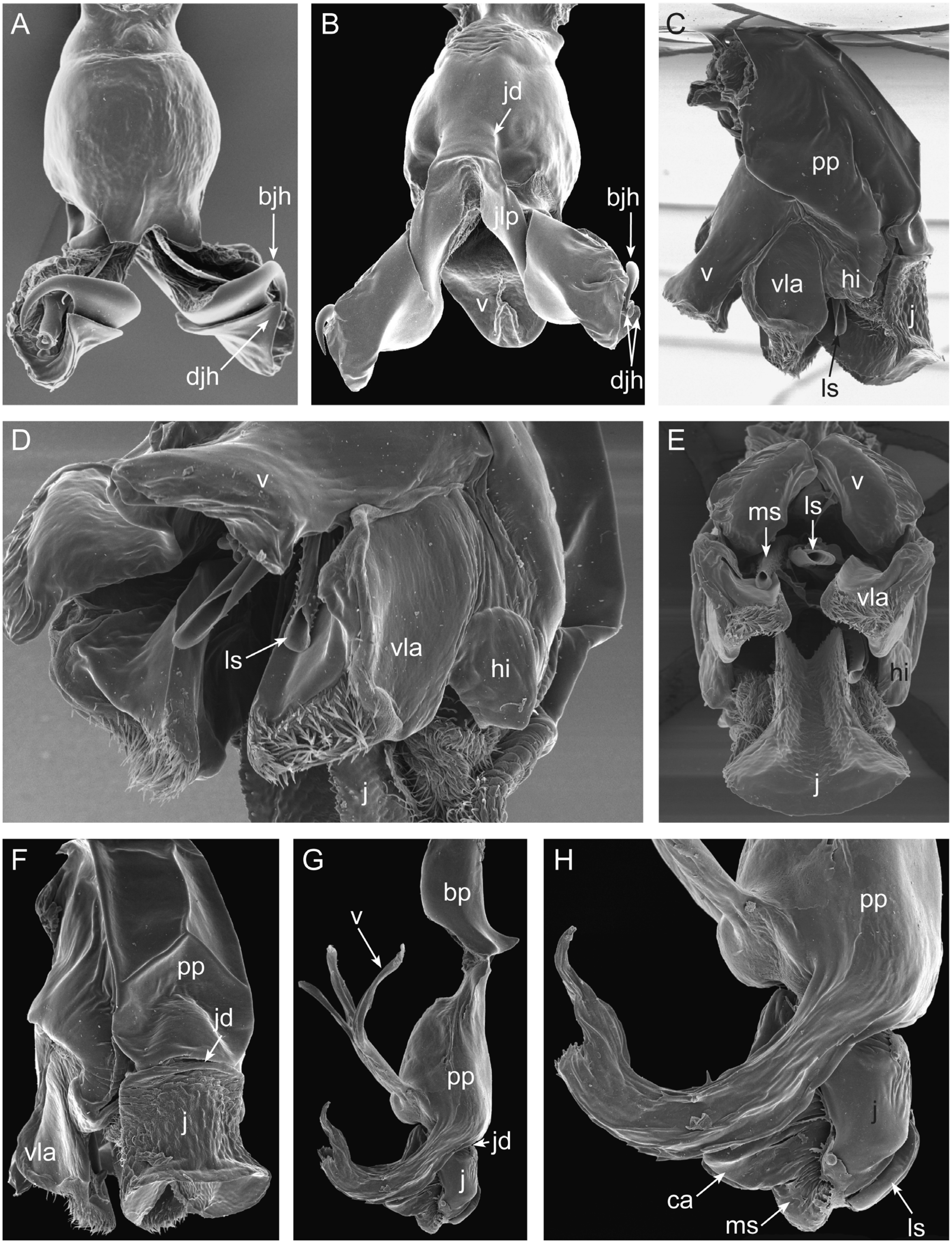

Figure 35. A, distiphallus, ventral view: *Peckia* (*Sarcodexia*) *lambens*. B, distiphallus, dorsal view: *Peckia* (*Sarcodexia*) *lambens*. C, distiphallus, left lateral view: *Peckiamyia abnormis*. D, distiphallus, antero-lateral view: *Peckiamyia abnormis*. E, distiphallus, ventral view: *Peckiamyia abnormis*. F, distiphallus, postero-lateral view: *Peckiamyia abnormis*. G, phallus, left lateral view: *Promayoa ramosa*. H, acrophallus, left lateral view: *Promayoa ramosa*. (A, B, courtesy M. Giroux). Abbreviations as in Table 1.

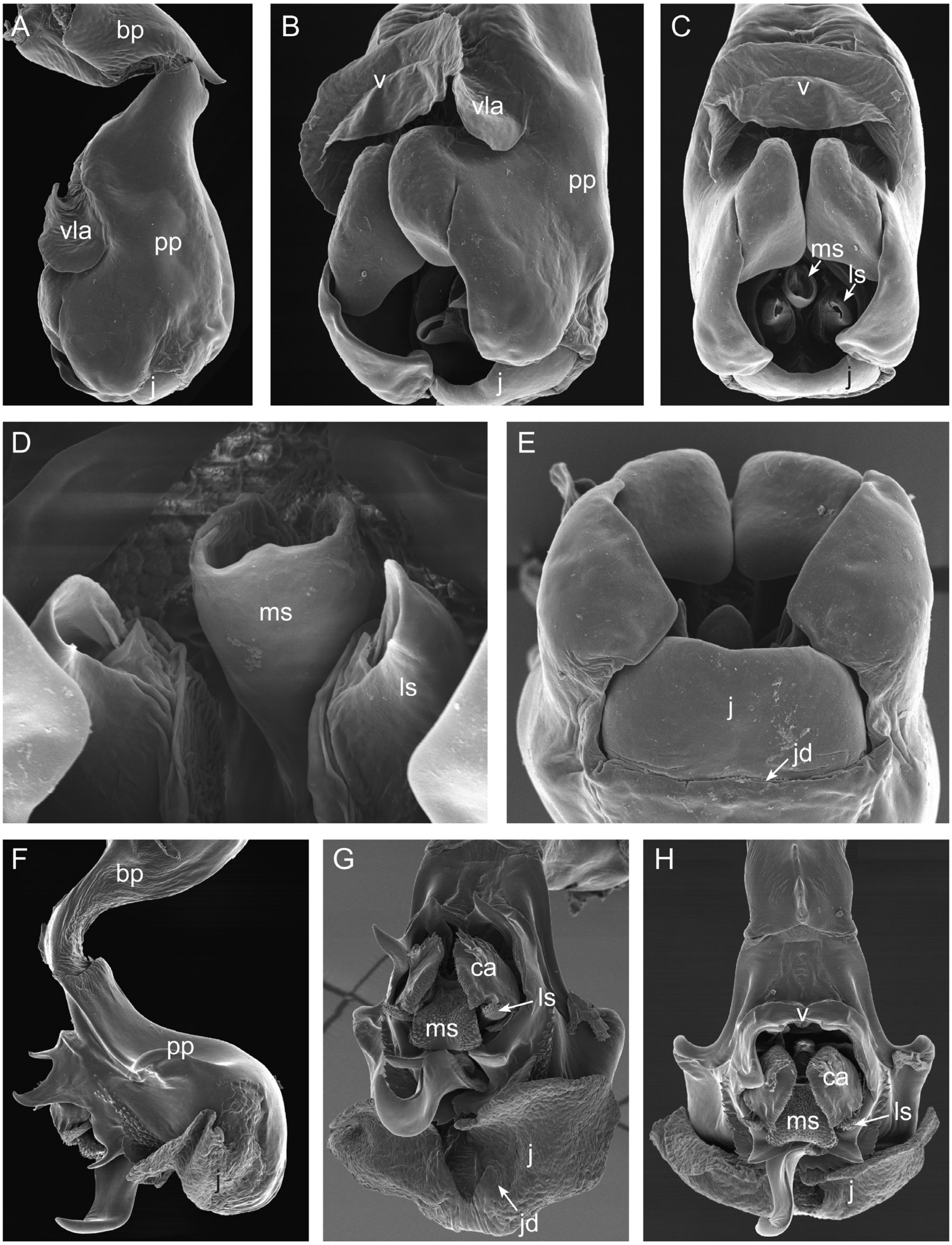

Figure 36. A, distiphallus, left lateral view: *Tapacura mariarum*. B, distiphallus, antero-lateral view: *Tapacura mariarum*. C, distiphallus, ventral view: *Tapacura mariarum*. D, acrophallus, ventral view: *Tapacura mariarum*. E, distiphallus, apical view: *Tapacura mariarum*. F, phallus, left lateral view: *Thomazomyia adunca*. G, distiphallus, latero-ventral view: *Thomazomyia adunca*. H, phallus, ventral view: *Thomazomyia adunca*. Abbreviations as in Table 1.

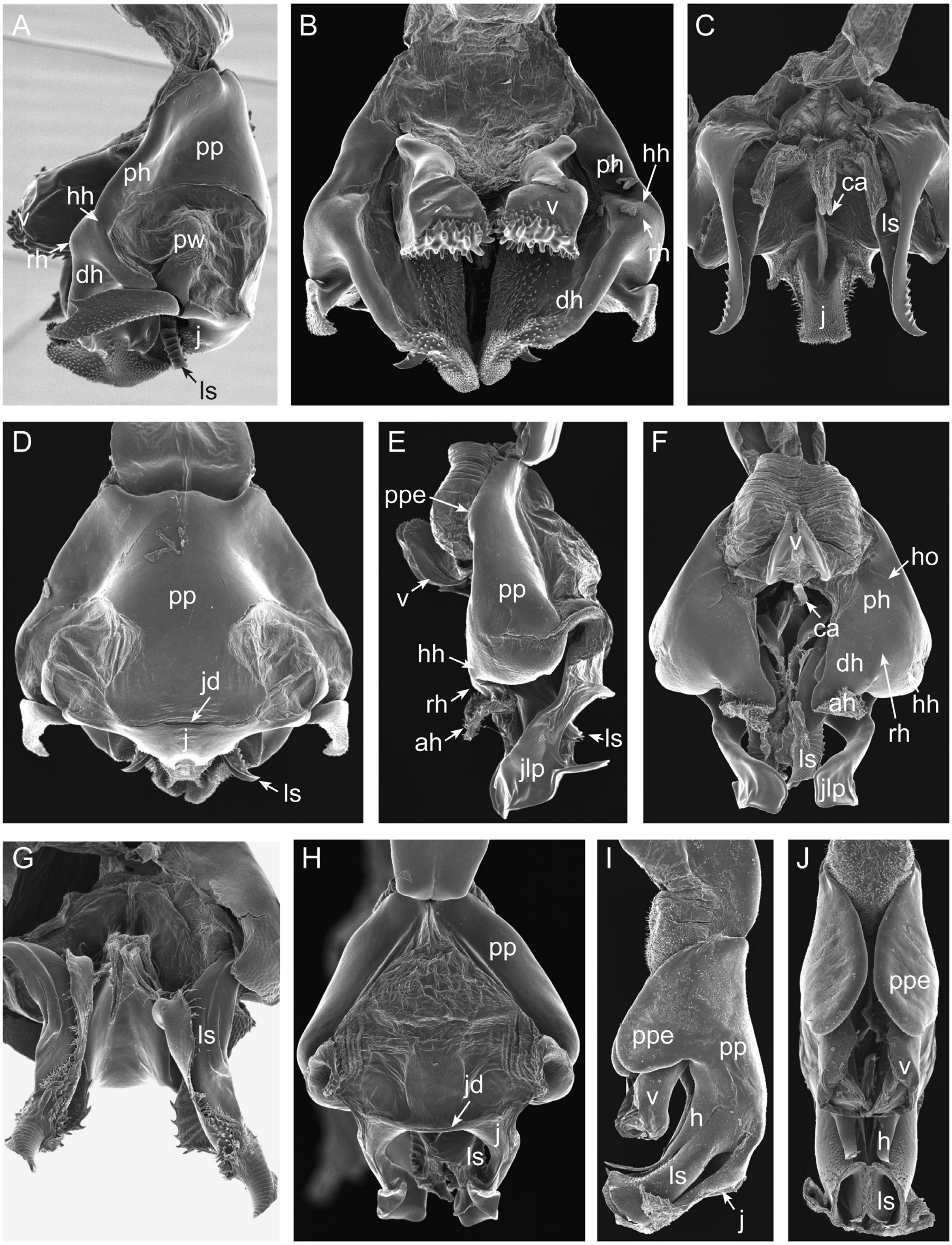

Figure 37. A, distiphallus, left lateral view: *Sarcophaga* (*Neobellieria*) *bullata*. B, distiphallus, ventral view: *Sarcophaga* (*Neobellieria*) *bullata*. C, acrophallus, ventral view: *Sarcophaga* (*Neobellieria*) *bullata*. D, distiphallus, dorsal view: *Sarcophaga* (*Neobellieria*) *bullata*. E, distiphallus, left lateral view: *Sarcophaga* (*Liopygia*) *ruficornis*. F, distiphallus, ventral view: *Sarcophaga* (*Liopygia*) *ruficornis*. G, acrophallus, ventral view: *Sarcophaga* (*Liopygia*) *ruficornis*. H, distiphallus, dorsal view: *Sarcophaga* (*Liopygia*) *ruficornis*. I, distiphallus, left lateral view: *Sarcophaga* (*s.s.*) *variegata*. J, distiphallus, ventral view: *Sarcophaga* (*s.s.*) *variegata*. [A–D, G, I, J, courtesy M. Giroux; E, F, H, from Giroux *et al.* (2010)]. Abbreviations as inTable 1.

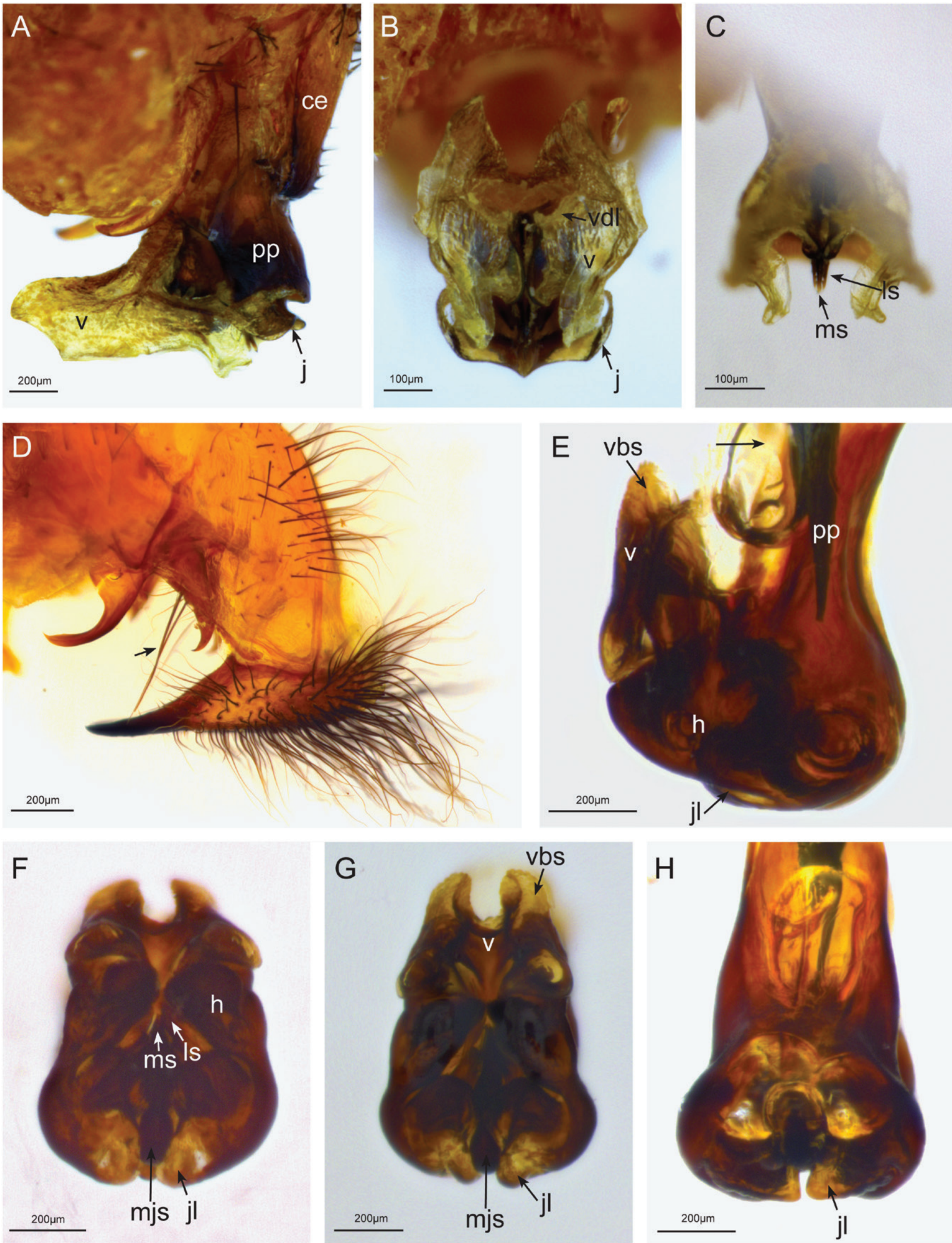

Figure 38. A, male terminalia, left lateral view: *Udamopyga* (*Carinoclypeus*) *creameri*. B, phallus, ventral view: *Udamopyga* (*Carinoclypeus*) *creameri*. C, median and lateral styli, ventral view: *Udamopyga* (*Carinoclypeus*) *creameri*. D, male terminalia, left lateral view (arrow indicates the two long setae on postgonite): *Austrophyto argentina*. E, distiphallus, left lateral view: *Austrophyto argentina*. F, distiphallus, apical view: *Austrophyto argentina*. G, distiphallus, ventro-apical view: *Austrophyto argentina*. H, distiphallus, dorsal view: *Austrophyto argentina*. Abbreviations as in Table 1.

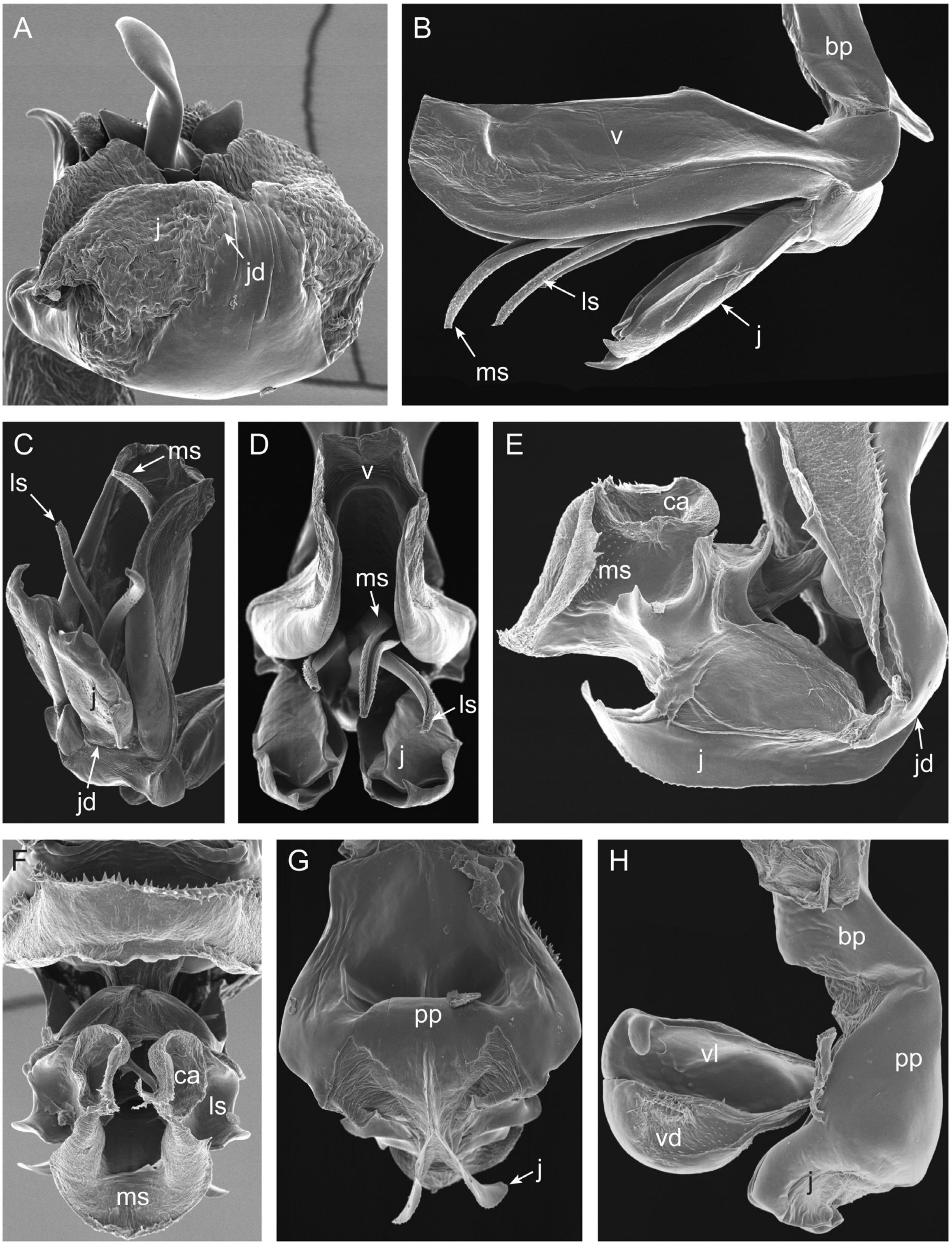

Figure 39. A, distiphallus, apical view: *Thomazomyia adunca*. B, distiphallus, left lateral view: *Titanogrypa* (*Cucullomyia*) *placida*. C, distiphallus, latero-apical view: *Titanogrypa* (*Cucullomyia*) *placida*. D, distiphallus, ventral view: *Titanogrypa* (*Cucullomyia*) *placida*. E, distiphallus, left lateral view: *Titanogrypa* (*s.s.*) *alata*. F, distiphallus, ventral view: *Titanogrypa* (*s.s.*) *alata*. G, distiphallus, dorsal view: *Titanogrypa* (*s.s.*) *melampyga*. H, distiphallus, left lateral view: *Tricharaea* (*Sarothromyia*) *simplex*. [C, E–H, courtesy M. Giroux; B, D, from Giroux *et al.* (2010)]. Abbreviations as in Table 1.

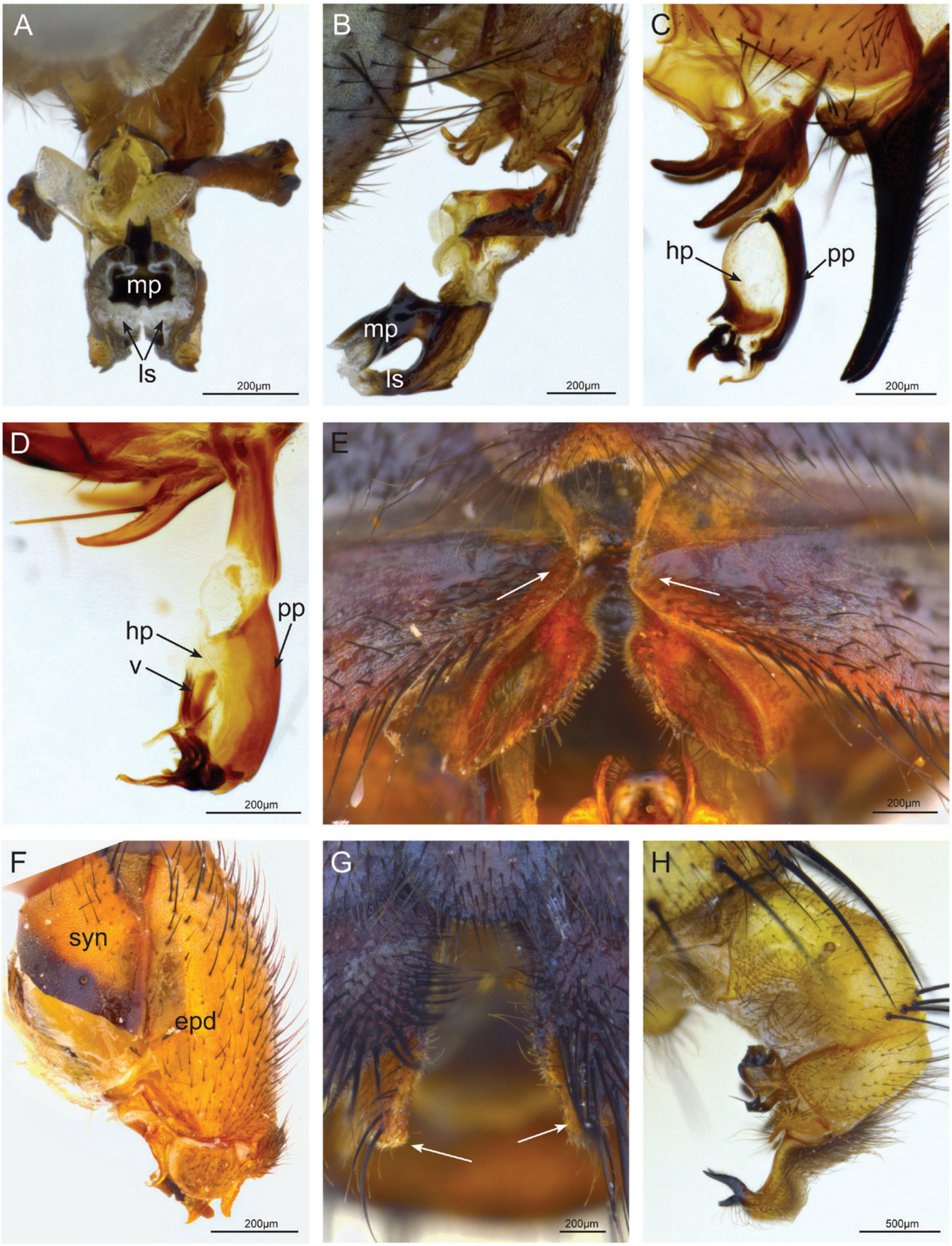

Figure 40. A, distiphallus, ventral view: *Panava inflata*. B, male terminalia, left lateral view: *Panava inflata*. C, male terminalia, left lateral view: *Rafaelia ampulla*. D, male terminalia, left lateral view: *Rafaelia aurigena*. E, male abdominal ST5, ventral view (arrow at pointed ventral margin): *Tripanurga importuna*. F, epandrium, left lateral view: *Tripanurga aurea*. G, male abdominal ST5, ventral view (arrow at undulation): *Udamopyga* (*s.s.*) *neivai*. H, male terminalia, left lateral view: *Peckiamyia minutipenis*. Abbreviations as in Table 1.

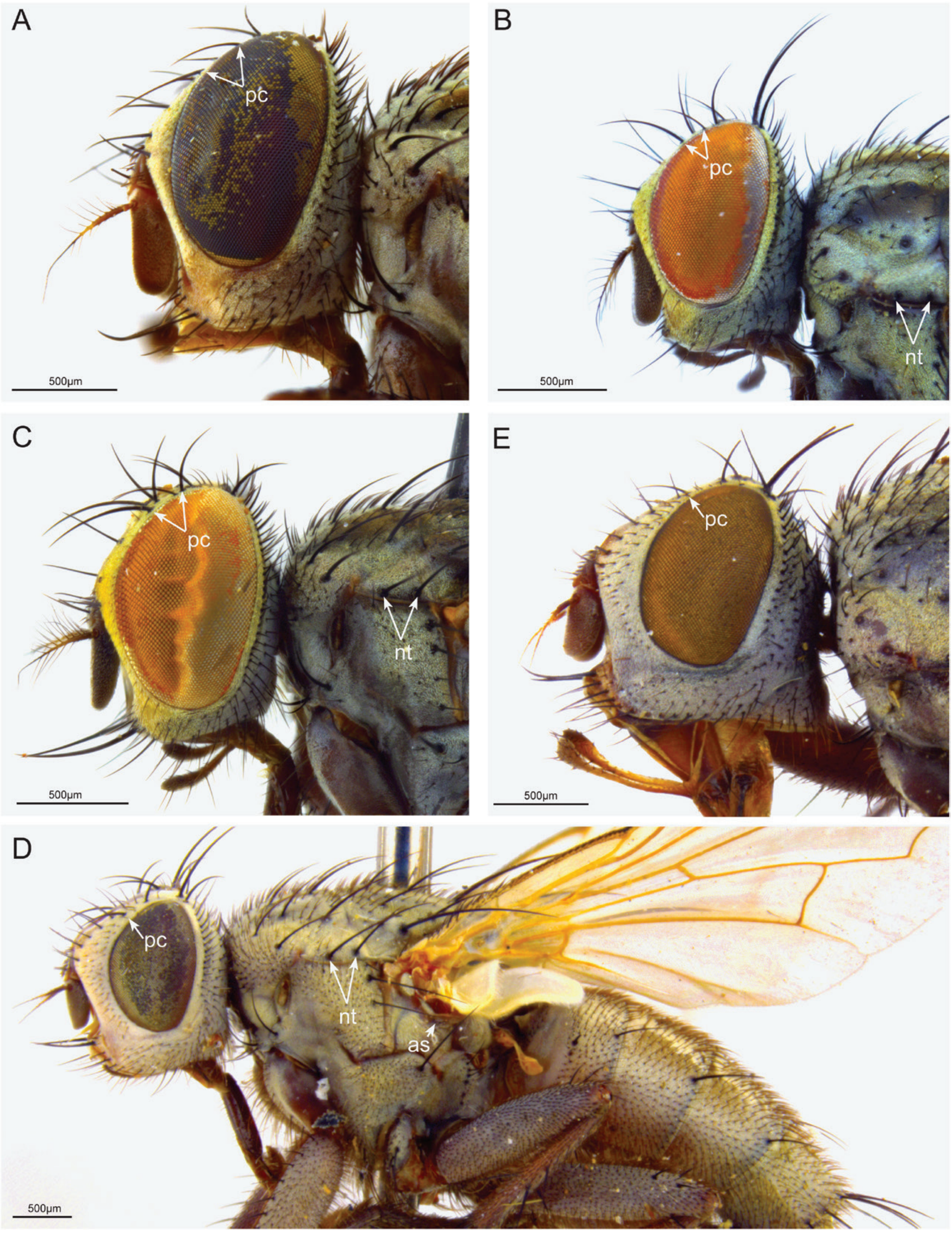

Figure 41. A, head with rounded postgena, left lateral view: *Bahamiola gregori*. B, head with rounded postgena, left lateral view: *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. C, head with rounded postgena, left lateral view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. D, head with angled postgena, left lateral view: *Tricharaea* (*Sarothromyia*) *femoralis*. E, habitus and head with angled postgena, left lateral view: *Tricharaea* (*s.s.*) *brevicornis*. Abbreviations as in Table 1.

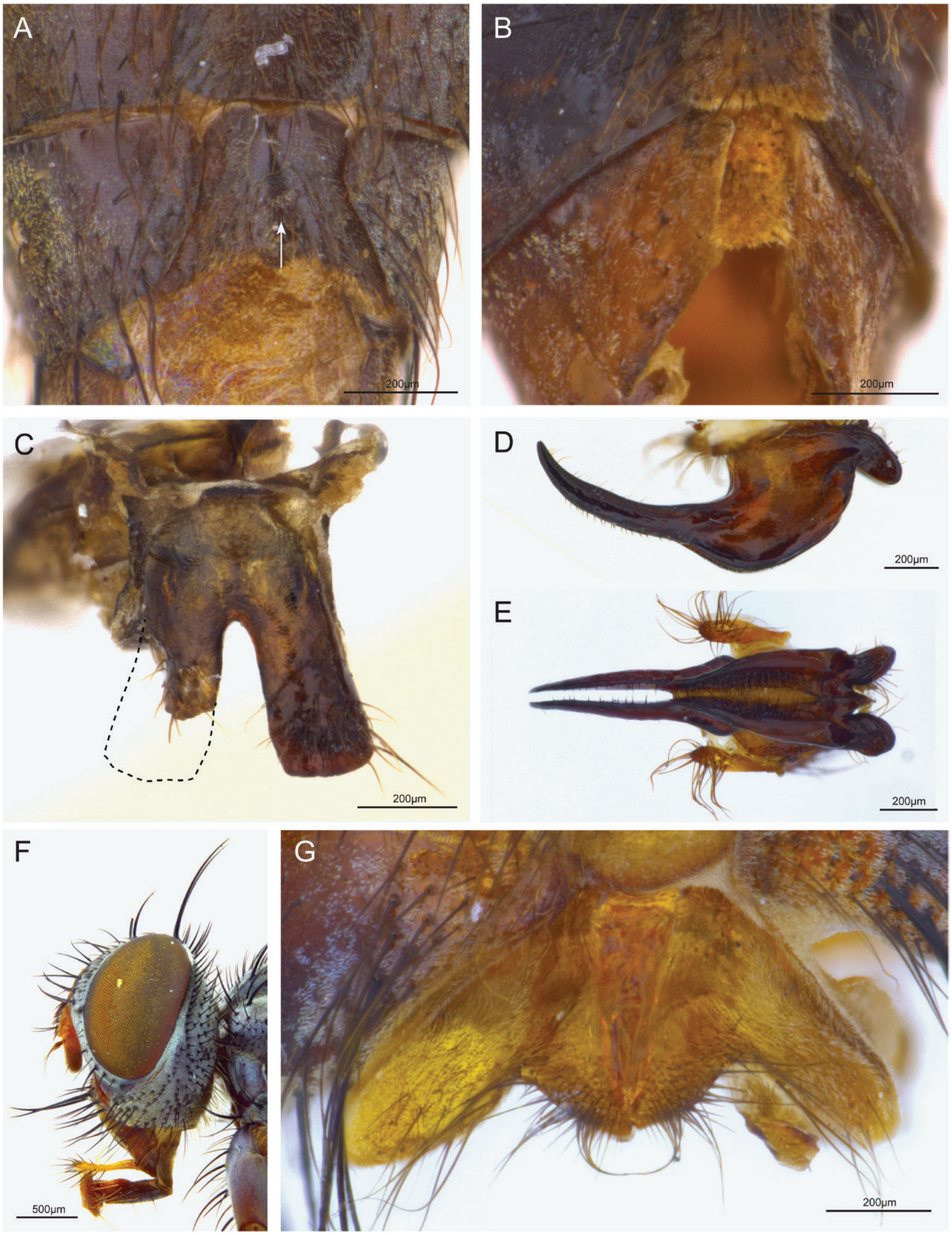

Figure 42. A, male abdominal ST5, ventral view (arrow showing a central a patch of fine setae): *Sarcofahrtiopsis* (*Pacatuba*) *matthewsi*. B, male abdominal ST5, ventral view: *Sarcofahrtiopsis* (*s.s.*) *cuneata*. C, male abdominal ST5, ventral view (stippled outline of broken part): *Sarothromyiops dasycnemis*. D, cercus, left lateral view: *Sarothromyiops dasycnemis*. E, cerci, ventral view: *Sarothromyiops dasycnemis*. F, head with swollen postgena, left lateral view: *Malacophagula neotropica*. G, male abdominal ST5, ventral view: *Argoravinia alvarengai*.

Figure 43. A, habitus, left lateral view: *Malacophagula neotropica*. B, male abdominal ST5, ventral view: *Blaesoxipha* (*Acridiophaga*) *subamericana*. C, male abdominal ST5, ventral view: *Titanogrypa* (*Sarconeiva*) *fimbriata*. D, male terminalia, left lateral view: *Fletcherimyia abdita*. E, male terminalia, left lateral view: *Spirobolomyia singularis*. F, male terminalia, left lateral view: *Comasarcophaga texana*. G, cercus, left lateral view: *Blaesoxipha* (*Acridiophaga*) *subamericana*. H, cercus, left lateral view: *Mecynocorpus salvum*.

Figure 44. A, head, frontal view: *Emblemasoma erro*. B, head and thorax (in part), left lateral view: *Emblemasoma erro*. C, male terminalia, left lateral view: *Lipoptilocnema crispina*. D, male terminalia, dorsal view: *Lipoptilocnema lanei*. E, male abdominal ST5, dorsal view: *Lepidodexia* (*Chlorosarcophaga*) sp. F, head, left lateral view: *Lepidodexia* (*Notochaeta*) *aragua*. G, cercus, left lateral view: *Emblemasoma albicoma*. H, male terminalia, left lateral view: *Engelimyia inops*. I, male genitalia with arrow on the pointed dorsal hump of basiphallus, left lateral view: *Panava peruana*. Abbreviations as in Table 1.

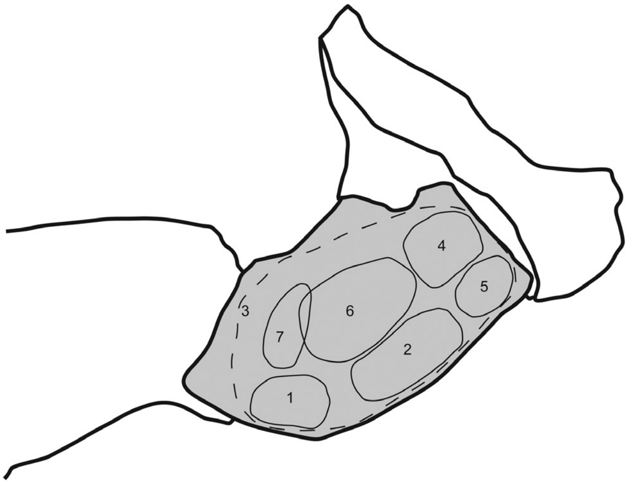

Figure 45. Position of posterior setal patterns on hind trochanter in Sarcophaginae. 1, *Boettcheria*; 2, *Emdenimyia*; 3, *Microcerella* (dashed line); 4, *Sarcophaga*; 5, *Thomazomyia*; 6, *Tulaeopoda*; 7, *Helicobia*.

as non-functional in some genera of the Blaesoxipha clade (i.e. clade 39).

Alternative phylogenetic hypotheses involving genera of the Blaesoxipha clade are found in other studies using morphological and molecular data. In Pape's (1994) morphology-based analysis, the genus *Emdenimyia* emerged in a sister-group relationship with *Boettcheria*, and the clade formed by these two genera was sister to a larger clade composed of (*Fletcherimyia* + ((*Comasarcophaga* + *Spirobolomyia*) + *Blaesoxipha*)). Giroux *et al.* (2010) found slightly different results, with *Blaesoxipha* as paraphyletic with regard to *Spirobolomyia*, and *Comasarcophaga* as sister to *Fletcherimyia*. Our data partially support Pape's (1994) results, since we recover (*Comasarcophaga* + *Spirobolomyia*). However, in both studies the monophyly of the entire clade was supported by a uniquely derived apomorphy, the bent male cercus. A different interpretation of this character in the present study finds the genera *Blaesoxipha* and *Mecynocorpus* as being supported by male cercus with a backward bend in proximal half (Fig. 43G, H), while this bend in the cercus is more distal or subapical in the clade (*Fletcherimyia* + (*Comasarcophaga* + *Spirobolomyia*)) and in *Thomazomyia* (Fig. 43D–F). The molecular phylogenies of Kutty *et al.* (2010) and Piwczyński *et al.* (2014) found radically different topologies for the genera of the Blaesoxipha clade, with species of these genera scattered in several separate clades, while in Stamper *et al.* (2012) three genera of our Blaesoxipha clade emerged as a well-supported monophylum, with *Blaesoxipha* as sister to (*Fletcherimyia* + *Mecynocorpus*); these results are in conflict with our topology, since we recovered *Mecynocorpus* in a trichotomy with two lineages of *Blaesoxipha*.

The first split we found within the Blaesoxipha clade is between clades 40 and 50 (Fig. 2B). Within clade 40, the genera *Villegasia* and *Panava* are monophyletic, while *Sarcodexiopsis* and *Titanogrypa* are paraphyletic. Clade 40 is supported by a homoplasious character state: basiphallus long and slender (Figs 12A, 28E, 34D).

Within clade 40, *Villegasia* is recovered as sister to the remaining genera, i.e. to clade 42. The monophyly of this genus is strongly supported by three autapomorphies: male abdominal ST5 blackish, basiphallus compressed dorso-ventrally (Fig. 34D) and juxta spinose (Fig. 34D–F). Dodge (1966) suggested that this genus is close to *Dexosarcophaga* due to the shared dark colour of the male terminalia, but this character state varies within species of *Villegasia*. Lopes & Tibana (1985) later suggested a close relationship between *Villegasia* and *Emdenimyia* based on male and female terminalia characters. Kutty *et al.* (2010) found *Villegasia* as sister to *Peckia* (*Sarcodexia*) *lambens*.

Sarcodexiopsis is paraphyletic with regard to clade 44, composed of the genera *Panava*, *Promayoa* and *Titanogrypa*. Clade 42 is supported by one autapomorphy: capitis wide and denticulated (Figs 12E, 20C, D, 39E, F). *Sarcodexiopsis* has historically been difficult to define. Roback (1954) placed *Sarcodexiopsis welchi* (Hall, 1930) as closely related to the subtribe Boettcheriina, containing species of the genera *Tripanurga*, *Boettcheria*, *Spirobolomyia*, *Blaesoxipha* and *Titanogrypa*. However, Roback explicitly stressed that this species does not possess many of the features of the Boettcheriina, and he noted a resemblance of its vesical characters to those of *Tripanurga*, although a vesica might not be present in all species of *Sarcodexiopsis*. The lack of diagnostic similarities between species of *Sarcodexiopsis* is evident in Pape (1996), where this is the only genus with 'no diagnosis available'. Providing a definition for *Sarcodexiopsis* is challenging, as its species do not share any apomophies, which would lead to a 'definition' as a 'residual' of those species lacking character states indicating affinities with any other genera. The diagnosis of *Sarcodexiopsis* provided here is based on homoplasies, and with *Sarcodexiopsis* emerging as paraphyletic it calls for revision. A comprehensive phylogenetic analysis incorporating all six currently known species of *Sarcodexiopsis*, as well as representative members of the Blaesoxipha clade, would be required to resolve the limits of this genus.

Clade 44, composed of the genera *Panava*, *Promayoa* and *Titanogrypa*, is supported by one autapomorphy: basiphallus with a dorsal hump at junction with distiphallus (Figs 35G, 39B). Species of *Titanogrypa* are

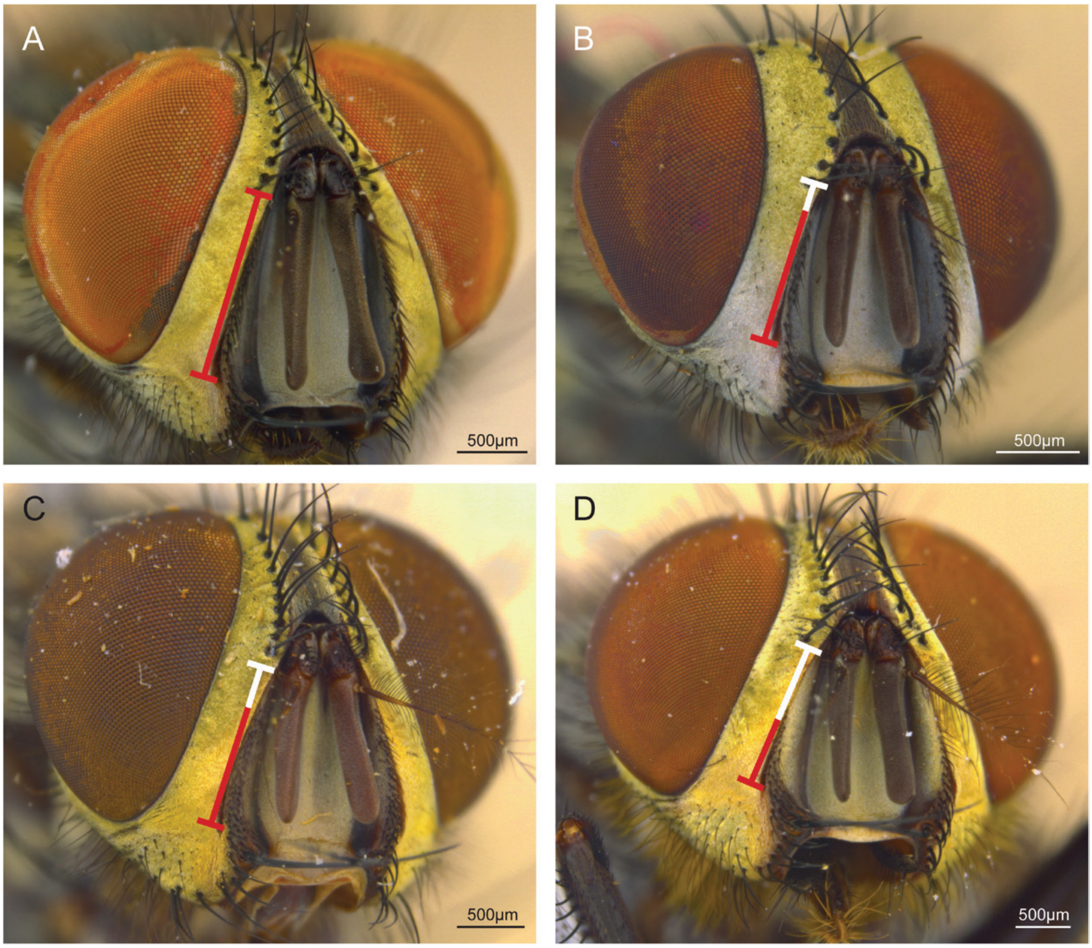

Figure 46. Setosity on facial ridge, red area of bar showing high density of setae. A, head, frontal view: *Emdenimyia limai*. B, head, frontal view: *Duckemyia latifrons*. C, head, frontal view: *Lepidodexia* (*Dexomyophora*) *fascialis*. D, head, frontal view: *Udamopyga* (*s.s.*) *neivai*.

scattered in relationships with non-*Titanogrypa* species, turning this genus paraphyletic. The clades (*P. peculiaris* + *P. ramosa*) and (*Titanogrypa* [*Airypel*] *cryptopyga* Lopes, 1956 + *Titanogrypa* [*Cucullomyia*] *placida*) received strong supports, but all the remaining nodes within clade 44 received mostly weak or no branch supports (Fig. 2B). A conflict of characters of the surstyli, lateral styli and vesica explain the paraphyly of *Titanogrypa*. The shape of the lateral styli as tubular structures (Figs 20C, D, 39B–D) indicates a close relationship between *Titanogrypa* (*Sarconeiva*) *fimbriata* (Aldrich, 1916) and *Promayoa*. The configuration of the vesica as composed of two elongated parts (Fig. 20A, B) supports *Panava* and *Promayoa* as closely related taxa, but the surstylus with an apical patch of short and robust setae supports a monophylum composed of *Panava*, *Promayoa* and the species *T*. (*Sarconeiva*) *fimbriata* and *S. welchi*. Combinations of some homoplasies provide diagnoses for *Panava*, *Promayoa* and *Titanogrypa*, but a more comprehensive phylogenetic analysis, incorporating the type species *Titanogrypa* (*s.s.*) *alata* (Aldrich, 1916) and *Chamayamyia minensis* Lopes, 1980 [listed as subgenerically unplaced within *Titanogrypa* by Pape (1996)] and additional species of *Sarcodexiopsis* will be necessary to elucidate limits among these genera.

The genus *Panava* is recovered as monophyletic, and supported by one autapomorphy: lateral styli fused (Figs 12C, D, 40A), and four homoplasies. It should be stressed that the fusion of the lateral styli does not mean that they form only one conducting structure with a single opening. Instead, in the acrophallus of *Panava* there are three openings corresponding to the three styli (Fig. 12D, E), all of which seem to be functional. The external walls of the lateral styli are fused medially (Fig. 12C, D), and fused to the juxtal plate dorsally (Fig. 12B). The median stylus remains dorsal to the lateral styli as an independent tube (Fig. 12A, E).

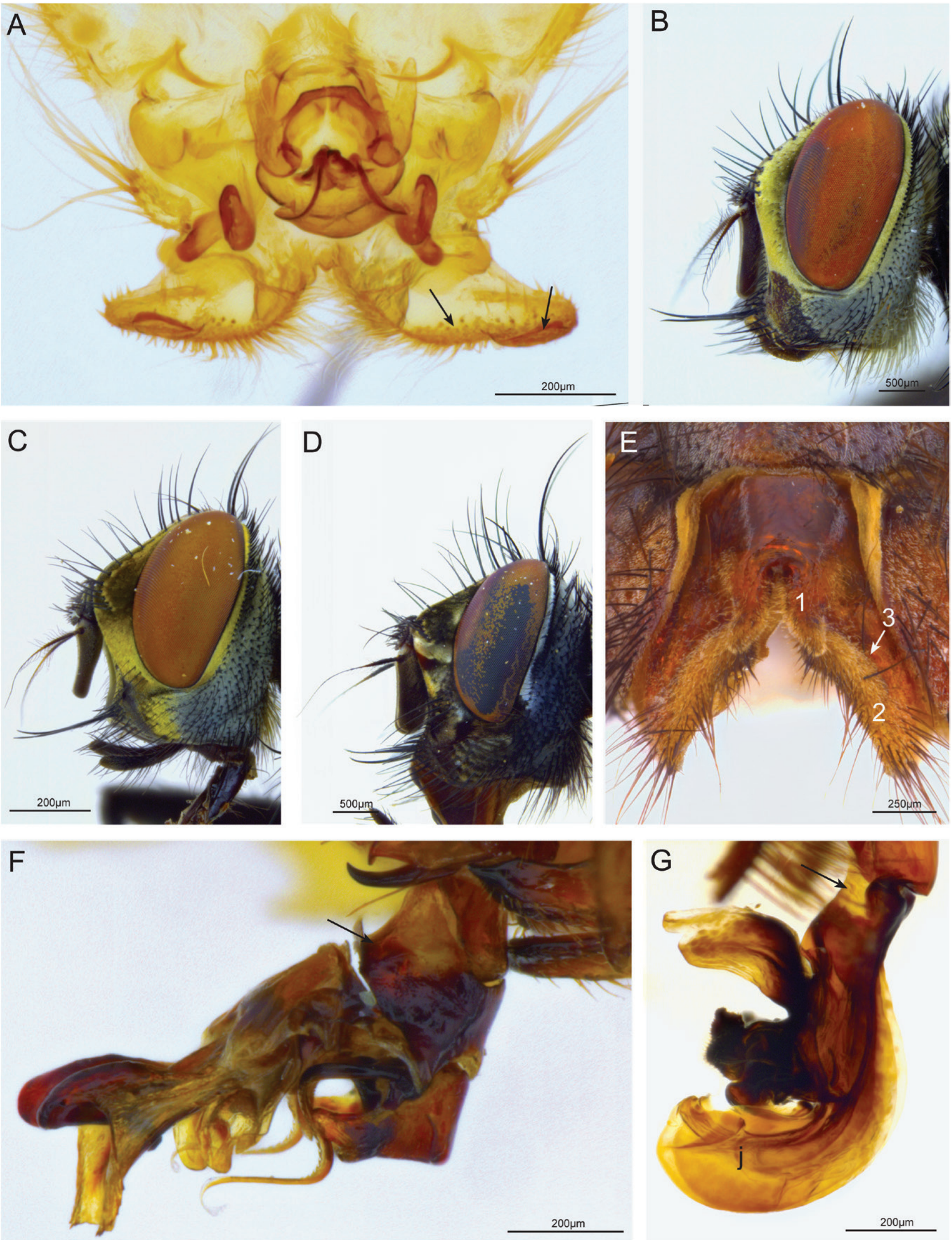

Figure 47. A, male terminalia (arrows showing the two tips of the bi-lobed apex of the cercal prong), ventral view: *Retrocitomyia fluminensis*. B, head, left lateral view: *Peckiamyia abnormalis*. C, head, left lateral view: *Boettcheria praevolans*. D, head, left lateral view: *Microcerella tripartita*. E, male abdominal ST5 in ventral view showing a rounded or pointed lobe on the anterior half (no. 1), margin swollen (no. 2) and a fold along the cleft margin (no. 3): *Boettcheria retroversa*. F, phallus left lateral view (arrow showing paler ventral area between basi- and distiphallus): *Boettcheria latisterna*. G, phallus left lateral view (arrow showing paler ventral area between basi- and distiphallus): *Microcerella adelphe*. Abbreviations as in Table 1.

In frontal view the three acrophallic styli appear to be apically fused (Fig. 40A), but their separation is clear in lateral view (Fig. 40B). Thus, we did not find support for considering the lateral styli as absent in *Panava*, as suggested by Carvalho-Filho & Esposito (2011). Our results are concordant with those of Lopes (1983), who considered *Panava* to be closely related to *Titanogrypa*. Carvalho-Filho & Esposito (2011) argued against *Panava* being closely related to *Rafaelia* and *Titanogrypa* by noting that males of these last two genera possess a dense patch of whitish hair-like setulae on the lateral margins of the scutellum (absent in *Panava*), and that they lack proclinate fronto-orbital setae (present in *Panava*). Interestingly, except for the male proclinate fronto-orbital setae, the other three diagnostic character states of *Panava* proposed by Carvalho-Filho & Esposito (2011) are also shared by one or more species of *Titanogrypa*. Specifically, the setulose wing vein R_1 dorsally is present in *T*. (*Airypel*) *cryptopyga* and *T*. (*Sarconeiva*) *fimbriata*, the phallus divided into a basi- and distiphallus by a hinge is present in all species of *Titanogrypa* and the surstylus with short apical spines is also found in *T*. (*Sarconeiva*) *fimbriata* and *Promayoa*. In conclusion, *Panava* is here found to be monophyletic and with clear limits with regard to *Titanogrypa* although it shares many character states (considered as diagnostic by Carvalho-Filho & Esposito, 2011) with species of this genus. A possible transfer of *Panava* to *Titanogrypa* was suggested by Lopes (1990), based not only on male terminalia features but also on larval characters. However, as the limits of *Titanogrypa* are quite questionable, any transfer of other taxa into this genus would stand as tentative and probably unstable.

The species *P. peculiaris* and *T. ramosa* form a single clade (Fig. 2B) supported by one homoplasy and one autapomorphy, with the latter corresponding to the vesica composed of two elongated parts (Fig. 20A, B). We propose to include *Titanogrypa ramosa* Méndez, Mello-Patiu & Pape, 2008 (as Promayoa ramosa in Fig. 2B) in *Promayoa*, with *Promayoa ramosa* (Méndez, Mello-Patiu & Pape, 2008) as a **new combination**.

The monophyly of *Titanogrypa* is not supported, and we found no clear limits between *Titanogrypa* and other taxa such as *Panava* and *Promayoa*. *Titanogrypa*, as defined by Pape (1996), remains in need of better delimitation. Méndez *et al.* (2008) suggested the non-monophyly of this genus since its species present varying combinations of Pape's (1996) diagnostic character states, and this is corroborated in our study. Giroux *et al.* (2010) included two species of *Titanogrypa*, which formed a monophylum supported by basiphallus with a dorsal hump and scutellum with a patch of whitish hair-like setulae on the lateral margins. However, these character states are also found in some species of *Panava* and *Promayoa*. The molecular studies of Kutty *et al.* (2010) and Piwczyński *et al.* (2014) recovered (*Titanogrypa luculenta* + *Ravinia* sp.) and (*Titanogrypa luculenta* + *Fletcherimyia fletcheri* [Aldrich, 1916]), respectively, although with low branch support. Stamper *et al.* (2012) included two species of *Titanogrypa* and recovered the genus as paraphyletic with regard to the remaining sarcophagines included in their study. Here, the phylogenetic position of this genus as part of the Blaesoxipha clade is well supported, but its monophyly remains unclear.

Clade 50 is supported by two character states: (1) cercal prong bent (reversed in *Emdenimyia*) (Fig. 43D–H), and (2) cercal prong with a proximal hump on dorsal surface (Fig. 43D–H), this being the only autapomorphy. Clade 51 consists of (*Fletcherimyia* + (*Comasarcophaga* + *Spirobolomyia*)) and clade 56 has the genus *Thomazomyia* as sister to clade 58. The latter clade has *Emdenimyia* as sister to a possibly paraphyletic *Blaesoxipha* (including *Mecynocorpus*) (Fig. 2B).

The clade (*Fletcherimyia* + (*Comasarcophaga* + *Spirobolomyia*)) is weakly supported by homoplastic character states, one of them being the presence of a ctenidium. The monophyly of *Fletcherimyia* was explicitly argued by Pape (1990) but is here explicitly tested for the first time, where it receives a weak JK value. Pape (1990) listed two alleged autapomorphies, juxta with pubescence as well as female abdominal tergite 6 strongly convex. *Fletcherimyia* is here supported only by the autapomorphic pubescence of juxta (Figs 22D, E, 43D) because we did not include female characters in the present study, as our knowledge of these is insufficient for an informative optimization. Similar results were presented by Giroux *et al.* (2010), where this genus did not receive high branch support and did not show any autapomorphies, since the pubescence of juxta was not autapomorphic for this genus and the shape of the female abdominal tergite 6 was not included. Although only one of the diagnostic character states proposed by Pape (1996) for this genus came out as autapomorphic, the remaining traits are still useful for diagnosing this genus when used in combination, and the female character state given by Pape (1990) may eventually emerge as autapomorphic when a more complete matrix is assembled and analysed. The genus is well defined biologically as larvae of all species are inhabitants of *Sarracenia* pitchers, which are the modified leaves of a carnivorous plant (Dahlem & Naczi, 2006).

The sister-group relationship between *Comasarcophaga* and *Spirobolomyia* received strong branch support. It is supported by the presence of paraphallic blinkers (Figs 1, 11G, 21H), which is an autapomorphy for these genera. The paraphallic blinkers in *Comasarcophaga* possess a distal sclerotized area ('sa' in Fig. 11G) while in *Spirobolomyia* they have a distal membranous tube-like process ('ts' in Fig. 21H). Lopes (1992) considered *Comasarcophaga* and genera such as *Lepidodexia* as belonging to the tribe Johnsoniini, and recently Giroux *et al.* (2010) supported *Comasarcophaga* as sister to *Fletcherimyia*. Our results did not support either of these hypotheses. Instead, they are concordant with *Spirobolomyia* being sister to *Comasarcophaga*, as found by Pape (1994). Downes (1965) included *Spirobolomyia* as a subgenus of *Blaesoxipha*, and later Pape (1990, 1994) argued against this hypothesis based on differences in the phallic configuration in these genera. Our results support Pape (1990, 1994) in considering *Spirobolomyia* as a genus separate from *Blaesoxipha*.

Pape (1990) synonymized *Archimimus* under *Comasarcophaga*, but later reverted to considering these as different genera (Pape, 1996) and included four species in the genus *Comasarcophaga*, all of which are included in the present study. The monophyly of this genus is supported here by the autapomorphies: (1) length of pedicel more than twice its width, and (2) paraphallic blinkers rounded, with a distal sclerotized area (Fig. 11G). Pape (1996) listed the following five diagnostic character states to define *Comasarcophaga*: (1) male mid-femur with a ctenidium of rounded spines (circular cross section), (2) terminalia red, (3) cercal prong bent backwards (Fig. 43F), (4) juxta slightly displaced ventrally relative to the longitudinal axis of the phallic tube, giving the distiphallus a hump-backed profile (Fig. 11G) and (5) vesica appearing square in lateral view. The fifth character state was reinterpreted in the present study, and the remaining four were included in the present analysis. All of these character states were homoplasies, but they still define *Comasarcophaga* when used in combination.

The monophyly of *Spirobolomyia* was strongly supported by JK values (Fig. 2B), and four autapomorphies: (1) postgonal apodeme elongate, (2) paraphallus with a strong postero-median keel (Fig. 21J), (3) paraphallic blinkers bulbous and tube-shaped (Fig. 21H) and (4) paraphallus with a beak-like projection arching over the juxta (Fig. 21H), and two homoplastic character states: (5) median stylus greatly elongated (Fig. 21I), and (6) median stylus curved (Fig. 21H, I). Character states 1, 3 and 5 were mentioned by Lopes (1975c), who referred to the postgonal apodeme as 'additional forcipes' and homologized the paraphallic blinkers with harpes. Pape (1990, 1996) noted character states 1 and 4, referring to the postgonal apodeme as '[b]asal parameral sclerite' (Pape, 1990) or 'sclerite at base of paramere' (Pape, 1996), and included these two character states in his diagnosis of this genus together with nine other male and female character states.

The first split of clade 56 has a sister-group relationship between the genus *Thomazomyia* and clade 58 (Fig. 2B). *Thomazomyia* is supported by one autapomorphy, i.e. male hind trochanter with a postero-ventral brush-like clump of short, stubby setae proximally (position as no. 5 in Fig. 45), and the homoplasious, distally bifid pregonite. When Lopes (1976b) described *Thomazomyia* he did not suggest any possible phylogenetic affinities with other genera, but later Lopes (1988a) remarked that 'by the redution [reduction] of the mesonotal chaetoraxy [chaetotaxy] and by the structure of the penis the species of *Thomazomyia* remember [resemble] the species of *Lipoptilocnema* in spite of the very different shape of the fifth sternite'. Our study is thus the first to hypothesize the phylogenetic position of *Thomazomyia* within the Sarcophaginae.

Inside clade 58, the monophyletic genus *Emdenimyia* is sister to (*Blaesoxipha* + *Mecynocorpus*) (Fig. 2B). Species of *Emdenimyia* have previously only been included in one cladistic study (Pape, 1994), where this genus was found to be sister to *Boettcheria* due to the presence of a postero-median row of spines on the hind trochanter. A more detailed study of the different setal modifications (spines, short setae and stubby setae) occurring on the hind trochanter revealed the existence of seven patterns or configurations (Fig. 45) found in several genera of Sarcophaginae, including *Emdenimyia* and *Boettcheria*. Due to differences in position on the trochanter, these patterns are here considered as possibly non-homologous and coded separately. Therefore, we do not agree with *Emdenimyia* as sister to *Boettcheria* (Pape, 1994) since the putative synapomorphy appears to consist of non-homologous character states. The monophyly of *Emdenimyia* is supported by five autapomorphies, as follows: (1) facial ridge with dense setosity along its full length (Fig. 46A), (2) male hind trochanter with a postero-ventral brush-like clump of short, stubby setae medially (position as no. 2 in Fig. 45), (3) paraphallus tube-shaped and open dorsally (Fig. 23I), (4) lateral styli directed dorsally (Fig. 23F) and (5) median stylus balloon-like (Fig. 23F–J). The first two were already suggested by Pape (1996), although the second is here reinterpreted.

The monophylum of the genera *Blaesoxipha* and *Mecynocorpus* is here supported by one autapomorphy: the lateral styli fused through a ventro-median bridge proximal to the median stylus ('vb' in Figs 29A, D, E, 30E), but it only received a weak JK value. Our results are concordant with Roback's (1954) arrangement of his subtribe Servaisiina. The study by Giroux *et al.* (2010) supported Downes (1965) in recovering *Blaesoxipha* as paraphyletic with regard to *Spirobolomyia*, which is not consistent with our phylogeny. In Giroux *et al.*'s (2010) tree, the clade of (*Blaesoxipha* + *Spirobolomyia*) was supported by the cercal prong distinctly bent backwards relative to cercal base. As outlined above, this character state is reinterpreted here as two separate character states: (1) male cerci with a soft backwards bend in a distal or subapical position (Fig. 43D–F), and (2) male cerci with a backwards bend in the proximal half (Fig. 43G, H). Character state 1 is found in *Comasarcophaga*, *Fletcherimyia* and *Spirobolomyia*, and character state 2 in *Blaesoxipha* and *Mecynocorpus*. Besides that, species of *Blaesoxipha* and *Mecynocorpus* lack paraphallic blinkers as well as a vesica (Fig. 17H), while these are present in *Spirobolomyia* (Fig. 21H).

Pape (1994, 1996) defined *Blaesoxipha* with the following nine character states: (1) postalar wall setulose, (2) hind trochanter with a postero-median row of spines in both sexes, (3) male mid-femur with a ctenidium of rounded spines (circular cross section), (4) cercus with prong bent backwards, (5) cercus with short spines dorsally on prong, (6) lateral styli fused through a ventro-median bridge proximal to the median stylus, (7) lateral styli collapsed and with no outlet from sperm duct, (8) lateral styli plate-like, with digitate margins, and (9) vesica reduced or not developed. Three character states (1–3) were homoplasious in our analysis, and the remaining six character states were found to support other more inclusive clades within clade 50. Thus, character state 4 supports clade 50 (reversal in *Emdenimyia*), state 5 supports (*Blaesoxipha* + *Mecynocorpus*) but also (*Comasarcophaga* + *Spirobolomyia*), state 7 supports clade 56 and the genus *Villegasia*, state 8 supports the entire Blaesoxipha clade (reversals in clades 53 and 51) and the genus *Panava*, and state 9 supports clade 58 and the genus *Villegasia*. Here, the monophyly of *Mecynocorpus* receives a strong JK value and is supported by one autapomorphy: median stylus cone-shaped and noticeably widened (Fig. 29A–E). The position of this genus as part of the entire Blaesoxipha clade is supported; however, it forms a polytomy with the genus *Blaesoxipha*. Thus, the available morphological evidence and the low branch support for the genus *Blaesoxipha* (including *Mecynocorpus*) provided by our phylogenetic analysis are weak indications to consider these two genera as synonyms. Consequently, we provide generic definitions based on homoplasies, one synapomorphy for (*Blaesoxipha* + *Mecynocorpus*), and one autapomorphy for *Mecynocorpus*, and we highlight the need of better delimitation for these genera.

Clade 63

Two autapomorphies support this clade: (1) male abdominal ST5 with a wide V-shaped cleft, and (2) male abdominal ST5 bearing expansions, pointed and undulated processes. The clade is split into clades 64, 66 and 80. Clade 64 is the Engelimyia clade. Clade 66 consists of a sister-group relationship between clades 67 (Udamopyga clade) and 72 (Peckiamyia clade). Clade 80 is supported by the presence of harpes and consists of a trichotomy of clades 81 (Microcerella clade), 89 (Lepidodexia clade) and 101 (Sarcophaga clade) (Fig. 2B).

Engelimyia clade

The Engelimyia clade (clade 64) is composed of the genera *Engelimyia* and *Tulaeopoda*, which are consistently recovered in a sister-group relationship. The genus *Tulaeopoda* had not yet been included in a phylogenetic analysis. Lopes (1969a) included it in the tribe Sarcophagini and suggested it is most closely related to *Peckia* (Lopes, 1941b, 1975d, 1983). In the last decade, species of *Engelimyia* were included in molecular and morphological phylogenetic analyses, although without a conclusive result on the phylogenetic position of this genus. Pape & Mello-Patiu (2006) did not propose any genus or group of genera as a candidate sister group of *Engelimyia*, but they discussed and rejected any possible phylogenetic relationship of this genus to *Peckia*. However, Giroux *et al.* (2010) found *Engelimyia* as sister to (*Peckia* + (*Sarcodexia lambens* + *Titanogrypa*)). *Engelimyia* has been included in two molecular analyses, where it emerged either in a trichotomy with *Boettcheria* and *Tricharaea* (Kutty *et al.*, 2010), or as sister to *Boettcheria* alone (Piwczyński *et al.*, 2014).

The Engelimyia clade has strong branch support in our analysis. *Engelimyia* and *Tulaeopoda* share ten autapomorphies: (1) male hind femur curved, (2) male abdominal ST3 with one or two patches of dense, erect, black setae, (3) male abdominal ST4 with two patches of dense, erect, black setae, (4) male ST5 with a small pad of stubby setae medially on the inner margin of cleft, (5) cercal prong gradually swollen with a knob-like apex (Fig. 44H), (6) cercal prong with dorsolateral keels, (7) cercal prong with a lateral tuft of long setae, (8) paraphallic tube as long as broad (Figs 22A, 27H), (9) stylar lateral plates present (Fig. 22A) and (10) juxta globose, spinose and denticulated (Figs 22A, B, 27H–J, 34A). Pape (1996) already listed character state 1 in his diagnosis of *Engelimyia*, and he also used a similar interpretation of character state 7 as presented here but restricted it to the diagnosis of *Tulaeopoda*. Character states 4–8, as presented here or slightly modified, are included in the diagnosis of *Engelimyia* by Pape & Mello-Patiu (2006). The present study confirms the presence of stylar lateral plates (character state 9) in both *Engelimyia* and *Tulaeopoda*. Also, the juxta of *Engelimyia* (character state 10) is reinterpreted and homologized with a globose, spinose and denticulated structure, while in previous works (Pape & Mello-Patiu, 2006; Giroux *et al.*, 2010) the juxta was homologized with a sclerotized and smooth bifid structure (Fig. 22C), which is here considered a structure evolved de novo in *Engelimyia*.

Pape & Mello-Patiu (2006) defined *Engelimyia* and discussed its monophyly. Many of the diagnostic character states listed by these authors are reinterpreted here, but *Engelimyia* still emerges as monophyletic in our phylogeny. In a previous phylogenetic study (Buenaventura & Pape, 2015), we provided new interpretations of the uniquely shaped median stylus and capitis of *Engelimyia* (Fig. 22A, B), as well as the description of acrophallic structures such as the stylar membranous lobes and stylar lateral plates (Fig. 22A). As outlined above, only the stylar membranous lobes are autapomorphic for *Engelimyia*, as well as male abdominal ST3 with a single patch of dense, erect, black setae.

Two autapomorphies support *Tulaeopoda*: the posterior surface of the male hind trochanter with a postero-median pad of short setae (position as no. 6 in Fig. 45) and male abdominal ST3 with two patches of dense, erect, black setae. Contrary to what was suggested by Pape (1996), species of *Tulaeopoda* possess well-developed, tubular lateral styli (Fig. 27I, J).

Udamopyga clade

This clade is composed of the genera *Tripanurga* and *Udamopyga* (including *Carinoclypeus*) and is supported by two autapomorphies: (1) juxta slightly recessed within the phallic tube (Figs 27C, D, 34B) and (2) juxta squared with a shallow to deep notch medially (Figs 27E, 34C). A similar position of the juxta with regard to the phallic tube is only found in *Sinopiella*, which has the juxta deeply recessed within the phallic tube (Fig. 21D–F). The reconstructed sister-group relationship between *Tripanurga* and *Udamopyga* (including *Carinoclypeus*) did not receive JK support, but the monophyly of each genus is strongly supported.

Roback (1954) placed *Metoposarcophaga* Townsend (= *Tripanurga*) and genera such as *Rafaelia* and *Boettcheria* in the subtribe Boettcheriina. Lopes (1969a) placed *Carinoclypeus*, *Tripanurga* and *Udamopyga* in the tribe Sarcophagini, but in a subsequent study (Lopes, 1983) he included *Tripanurga* in Sarcophagini, and *Udamopyga* in Cuculomyiini. None of these proposals had been consistently tested, as no study had included representative species of these genera. Stamper *et al.* (2012) found *Tripanurga importuna* (Walker, 1849) to be sister to the genus *Boettcheria*, which somehow supports Roback (1954) in placing *Tripanurga* and *Boettcheria* in the subtribe Boettcheriina. The sister-group relationship between *Tripanurga* and *Boettcheria* received high branch support in Stamper *et al.*'s (2012) phylogeny. Our taxon sample is much more extensive than that analysed by Stamper *et al.* (2012), as we included multiple species of *Boettcheria* and *Tripanurga*. However, the low support for *Tripanurga* as sister to *Udamopyga* (including *Carinoclypeus*) leaves this sister-group relationship as tentative. Future analyses are needed to test which of these alternative topologies is best corroborated.

Pape (1990) proposed a broad concept of the genus *Tripanurga* by including *Erucophaga* Reinhard, *Metoposarcophaga*, *Zygastropyga* Townsend and other genera as synonyms. Pape (1990, 1996) diagnosed *Tripanurga* with seven character states: (1) male cercus with prong bent backwards, (2) ejaculatory apodeme large, (3) parameral (= postgonal) seta slightly flattened, (4) phallus with an epiphallus-like process at base, (5) basiphallus elongated and narrow, (6) distiphallus compact and globular and (7) ventral margin of distiphallus with fringe of filiform processes. Character state 2 is not included here due to difficulties of coding other taxa; 1, 5–7 are reinterpreted, and 3 and 4 came out as autapomorphies. In our phylogenetic analysis *Tripanurga* is monophyletic, supported by five autapomorphies: (1) male abdominal T5 with ventral margin pointed (arrows in Fig. 40E), (2) epandrium higher than wide in lateral view ('epd' in Fig. 40F), (3) postgonal seta slightly compressed (arrows in Fig. 27F, G), (4) basiphallus proximally with a dorsal epiphallus-like process ('ep' in Fig. 27B), (5) vesica with vesical lateral arms ('vla' in Fig. 27B–E), each with an inner denticulated process ('vdp' in Fig. 27E).

The genus *Udamopyga* (including *Carinoclypeus*) is supported by three autapomorphies: (1) posterior margin of the male abdominal ST5 with a slight undulation halfway between the angle and the tip of the V, and a rounded distal expansion (Fig. 40G), (2) cercal prongs fused at least halfway to tip and (3) vesica composed of two petal-like lateral plates, each with a vesical denticulated lobe ('vdl' in Figs 30H, 34B, C, 38A, B). This clade is also supported by two homoplasies: males with rows of frontal setae anteriorly divergent, and basiphallus with a dorsal longitudinal keel. Dodge (1965a) defined the monospecific genus *Carinoclypeus* by the presence of a 'carinate clypeus'. A slightly modified wording for this character state was used by Pape (1996), who diagnosed *Carinoclypeus* by the presence of a 'facial plate with distinct median carina in full length', which here corresponds to the carina parallel in full length to frontogenal suture. Here, no other character states support this genus, which remains defined only by the autapomorphic presence of a median carina on the facial plate, which supports Dodge's (1965a) and Pape's (1996) diagnoses. *Udamopyga* (*s.s.*) is recovered as monophyletic, but it is only supported by one autapomorphy: facial ridge with dense and short setosity on lower 0.50 (Fig. 46D). Based on the strong branch support of the genus *Udamopyga* (including *Carinoclypeus*), and its numerous autapomorphies, we suggest *Carinoclypeus* as a **new junior synonym** of *Udamopyga*. Consequently, we provide a new diagnosis for *Udamopyga* inclusive of *Carinoclypeus*, which is maintained as a subgenus, **new status**.

Peckiamyia clade

This clade, which received aBS but no JK, is composed of the genera *Duckemyia*, *Peckiamyia*, *Retrocitomyia*, *Sinopiella* and *Tapacura*. The Peckiamyia clade splits into clade 73 (genus *Sinopiella*) and clade 74. The latter clade has the genus *Tapacura* as sister to (*Retrocitomyia* + (*Duckemyia* + *Peckiamyia*)). *Duckemyia* (monospecific), *Peckiamyia*, *Sinopiella* and *Tapacura* are recovered as monophyletic. The Peckiamyia clade is supported by one autapomorphy: phallus shorter than or of almost equal length to pregonites. The presence of a three-lobed vesica composed of a proximal section (divided or not) and a pair of vesical lateral arms (Figs 10G, 16F, 21F, 35E, 36B) also supports this clade, although it is not an autapomorphy. Our results are in agreement with Tibana & Lopes (1985), who highlighted similarities in the small size of the phallus of *Peckiamyia*, *Retrocitomyia*, *Sinopiella* and *Tapacura*. These authors also found similarities between *Sinopiella* and the subgenus *Titanogrypa* (*Cucullomyia*), but we did not find support for this assertion. Our results are consistent with those of Piwczyński *et al.* (2014), where *Duckemyia* and *Peckiamyia* emerged as sister groups.

Within the Peckiamyia clade a sister-group relationship was found between the monophyletic *Sinopiella* and the remaining genera, arranged in clade 74. The genus *Sinopiella* is represented in our analysis by its two known species, and it emerges as monophyletic (clade 73 in Fig. 2B). While all other genera of the Peckiamyia clade have hillae, the lateral styli in the genus *Sinopiella* are simple and exhibit no modifications. The monophyly of this genus received strong branch support, and its eight autapomorphies are all in the male terminalia: (1) postgonite slightly swollen, (2) postgonite enlarged, (3) pregonite dorso-ventrally flattened and concave, (4) paraphallus humped postero-distally (Fig. 21D), (5) vesica three-lobed with a proximal section undivided and lobe-shaped (Fig. 21F), (6) vesical lateral arms elongated with rounded apex (Fig. 21F), (7) juxta deeply recessed within the phallic tube (Fig. 21D–F) and (8) juxta squared with ventral margin pointed (Figs 5G, 21F). In the description of this genus, Lopes & Tibana (1982) suggested a close relationship with *Peckiamyia* based on the short phallus, which is supported by our results. In the same publication, these authors also suggested a relationship between *Sinopiella* and *Retrocitomyia* due to both genera sharing enlarged pregonites. Although both these genera are closely related as members of the Peckiamyia clade, this sister-group relationship is not recovered in our phylogeny, as the enlarged pregonites were observed only in *Retrocitomyia*, while *Sinopiella* has normal-sized pregonites and enlarged postgonites. Kutty *et al.* (2010) found strong support for a sister-group relationship between *Sinopiella rotunda* (Lopes & Ferraz, 1991) and *Lepidodexia* (*Notochaeta*) sp., but here all species of *Lepidodexia* form a single clade not closely related to *Sinopiella*. Finally, the three character states (male mid-femur with ctenidium of rounded spines, wing with third costal sector bare ventrally and three conducting styli) listed by Pape (1996) are not diagnostic for this genus.

Clade 74 received weak JK value and is supported by the following autapomorphic character states: (1) hillae directed distally (Figs 16F, G, 35C, E), (2) hillae paddle-like (Figs 16F, 35C–E), (3) only apex of hillae attached to the inner paraphallic wall (Figs 16F) and (4) juxta squared with anterior margin even (Figs 16H, 35F, 36E). The presence of proximal expansions of the lateral styli or hillae in clade 74 is homoplasious in our analysis and appears to have evolved in the ancestor of the Tricharaea grade or earlier, becoming reduced in clade 38, and reappearing in clade 74. Generally, the hillae are visible (Fig. 16F–H) in lateral view in *Duckemyia*, while in *Peckiamyia*, *Retrocitomyia* and *Tapacura* they remain hidden by the lateral wall of the distiphallus. In some species of the last three genera, the hillae are distally attached to the inner wall of the juxta, leaving two low swellings that are visible in dorsal view (arrows in Fig. 28A). Clade 74 is also supported by the presence of a three-lobed vesica, whose proximal section is undivided and arch-shaped in *Duckemyia* (Fig. 16F), *Retrocitomyia* (Fig. 10G) and *Tapacura* (Fig. 36B), while in *Peckiamyia* this section has a shallow proximal division giving two joined lobes (Fig. 35D, E).

Tapacura is reconstructed as a monophyletic taxon with weak JK value but supported by two autapomorphies: (1) vesical lateral arms disc-shaped (Fig. 36A, B) and (2) juxta squared with anterior margin even and flat (Fig. 36E). This genus has very small and distinctive male genitalia, which may carry informative characters for supporting its monophyly. Species of *Tapacura* have lateral plate-like structures completely fused to the paraphallic wall and with a distal cleft (Fig. 36A–C, E). The homology of these structures is uncertain. These plate-like structures are in a similar position than the paraphallic blinkers. However, they lack the landmark for delimiting these blinkers, which is a desclerotized strip between them and the ventral margin of the paraphallus. Also, the lateral plates of *Tapacura* are completely sclerotized, while the paraphallic blinkers are semi-sclerotized.

A sister-group relationship between *Retrocitomyia* (excluding *Retrocitomyia argentina* Lopes, 1988) and (*Duckemyia* + *Peckiamyia*) was recovered in our analysis (clade 76 in Fig. 2B). Clade 76 is supported by two uniquely derived apomorphies: (1) cercal prong S-shaped with uni- or bilobed apex (Fig. 40H) and (2) postgonite directed perpendicular to body axis.

The monophyly of *Retrocitomyia* (excluding *R. argentina*) is strongly supported in our analysis by four autapomorphies: (1) cercal prong bilobed with a blunt tip (see arrows in Fig. 47A), (2) cercal prong without dorso-medial setae, (3) vesical lateral arms paddle-like with a hook-shaped apex and (4) juxta squared with anterior margin even, undulated dorso-ventrally or with a medial folding (Figs 10G, H, 28A). The two tips of the bilobed cercal prong might be more developed in some *Retrocitomyia* species than in others. Lopes (1983) assigned *Retrocitomyia*, together with *Chlorosarcophaga* and *Dexomyophora* (both included in *Lepidodexia* [*s.l.*] by Pape [1996]), and *Udamopyga*, to the subtribe Udamopygina based on various features of the cephaloskeleton of the first-instar larva, a concavity in ST8 of the female, the presence of 'large lateral plates' on the distiphallus and the absence of a vesica. Our results did not support a relationship between *Retrocitomyia*, *Lepidodexia* and *Udamopyga*, and each of these genera emerged within separate, distantly related clades. Also, neither of the diagnostic character states proposed by Lopes (1983) in the description of *Retrocitomyia* nor those suggested by Pape (1996) emerged as autapomorphic for this genus. However, when used in combination, those character states will still be useful for diagnosing this genus.

The sister-group relationship between *Duckemyia* and *Peckiamyia* has moderate branch support and is supported by three autapomorphies: (1) facial ridge with dense setosity on lower 0.85 (Fig. 46B), (2) cercal prong bilobed with a pointed tip (Fig. 40H) and (3) juxta squared, with anterior margin even, flat or slightly concave (Figs 16F, 35E). Of the two genera, only *Peckiamyia* is supported by multiple autapomorphies of the male terminalia and other body parts as follows: (1) postgenal setulae much longer than genal setulae (Fig. 47B), (2) surstylus with a proximal lobe-shaped expansion, (3) surstylus with stubby setae on proximal half, (4) pregonite with strong proximal setae, (5) vesica three-lobed, whose proximal section has a shallow proximal division giving two joined lobes (Fig. 35D, E) and (6) vesical lateral arms trapezoid (Fig. 35C, E). *Duckemyia* shows one autapomorphy: vesical lateral arms ribbon-like (Fig. 16G). Dodge (1966) identified similarities in external characters between *Peckia* and *Peckiamyia*, but he also mentioned *Peckiamyia* as having 'anomalous genitalia' obscuring its affinities. A close relationship between *Peckia* and *Peckiamyia* has not been supported in subsequent studies (Piwczyński *et al.*, 2014; Buenaventura & Pape, 2015), nor in the present study. A comparison of features of *Duckemyia latifrons* Kano & Lopes, 1969 to those of potentially close generic relatives with proclinate fronto-orbital setae in males was provided by Kano & Lopes (1969), who erected a separate genus for this species. The proclinate fronto-orbital setae in males were here found to be a homoplasious character state. In the same publication, these authors also noted the bifurcated cercal prong (Fig. 40H) in *Duckemyia* and *Peckiamyia*, which is also shared with *Retrocitomyia*.

Clade 80

This clade consists of a trichotomy of clades 81 (Microcerella clade), 89 (Lepidodexia clade) and 101 (Sarcophaga clade), and is characterized by the reappearance of the harpes.

Microcerella clade

This clade, represented by the species *R. argentina* and the genera *Austrophyto*, *Boettcheria* and *Microcerella*, received strong JK value and is supported by nine uniquely derived character states including: (1) arista plumose in at most basal half (Fig. 47C, D), (2) thorax with metallic grey/golden stripes (highly contrasting relative to the blackish background), (3) anepimeral area with four strong setae and sparse, weak setulae, (4) male abdominal T5 higher than other abdominal tergites, (5) male ST5 with a rounded or pointed lobe on the anterior half (no. 1 in Fig. 47E), (6) male ST5 with cleft margin swollen (no. 2 in Fig. 47E), (7) male ST5 with a fold along the cleft margin (no. 3 in Fig. 47E), (8) surstylus two to three times longer than wide and (9) phallus with a rigid sclerotized area ventrally between basi- and distiphallus (arrow in Figs 29F, 47F). Three homoplasies also support this clade, including male with rows of frontal setae diverging anteriorly [also found in the genera *Lepidodexia*, *Lipoptilocnema*, *Sarcophaga*, *Spirobolomyia* and *Udamopyga* (including *Carinoclypeus*)], as well as parafacial plate with strong setae (also found in *Helicobia*). From the eight autapomorphies supporting the entire Microcerella clade, character state 8 was included as characteristic for *Boettcheria* species by Dahlem & Downes (1996). Similarly, the character states 1 and 8 were included as diagnostic features for the genus *Microcerella* by

Mulieri *et al.* (2015). Also, both Dahlem & Downes (1996) and Mulieri *et al.* (2015) illustrated the male ST5 with a rounded or pointed lobe on the anterior half (autapomorphy 4) in several species of *Boettcheria* and *Microcerella*, respectively; however, they did not consider it as diagnostic for these genera. Interestingly, a similar lobe on the anterior half of the male ST5 was considered as diagnostic for the genus *Austrophyto* by Mulieri (2017).

Our analysis recovered a monophyletic genus *Boettcheria* as sister to the clade (*Microcerella* + (*Austrophyto* + *R. argentina*)). Based mostly on male terminalia characters, Roback (1954) placed *Boettcheria* close to *Sarcodexiopsis* and *Tripanurga* and included these genera in the subtribe Boettcheriina. Lopes (1983) placed this subtribe within Sarcophagini, but he restricted Boettcheriina to species of *Boettcheria*, and in the same publication he suggested a possible relationship between Boettcheriina and Microcerellini, this last tribe containing species with 'bare or pubescent arista'. In a subsequent publication, Lopes (1989) described *Austrophyto* as a monospecific genus and placed it into the tribe Microcerellini. Pape (1990) synonymized all the generic names included in the Microcerellini of Lopes (1983) under *Microcerella*, excluding only *Cryptosarcophila* Townsend (transferred to *Lepidodexia* as a subgenus) and *Austrophyto*. Pape (1994) found *Boettcheria* as sister to *Emdenimyia*, a relationship supported by the configuration of postero-ventral setae on the trochanter (see discussion of the Blaesoxipha clade), but he did not include *Austrophyto* or any species of *Microcerella*. Based on molecular data, Kutty *et al.* (2010) found *Boettcheria cimbicis* (Townsend, 1892) as part of a trichotomy with *Engelimyia inops* (Walker, 1849) and *Tricharaea femoralis* (Schiner, 1868); Stamper *et al.* (2012) recovered a monophyletic *Boettcheria* as sister to *T. importuna*, and Piwczyński *et al.* (2014) recovered a sister-group relationship between a monophyletic *Boettcheria* and *E. inops*. Thus, molecular data do not yet converge in their phylogenetic estimations with regard to the position of *Boettcheria*, while the morphological data of Giroux *et al.* (2010) coincide with ours in placing *Boettcheria* and *Microcerella* as closely related taxa.

Lopes (1950) revised the species of *Boettcheria* and provided a definition for this genus, where he highlighted the characteristic shape of the male ST5 and the very large vesica. Pape (1989b) redefined this genus and proposed a diagnosis including four character states. In a subsequent revisionary work of the Nearctic species of *Boettcheria*, Dahlem & Downes (1996) provided a generic definition based on three character states. Pape (1996) proposed a diagnosis for *Boettcheria*, in which he included some of his own character states (Pape, 1989b) and also those of Dahlem & Downes (1996). Here we included all of Pape's (1996) diagnostic character states, of which two were reinterpreted and combined into one character state. Our analysis resulted in five autapomorphies supporting this genus. Pape's character state of the modified setae on the male hind trochanter is separated into two character states, with male hind trochanter with a postero-ventral brush-like clump of short, stubby setae distally (position as no. 1 in Fig. 45) coming out as an autapomorphy for *Boettcheria*. The remaining four autapomorphies are: (1) six or more frontal setae below posterior limit of the lunule, (2) male abdominal T5 higher than other abdominal tergites, (3) vesica convoluted (Fig. 30F) and (4) juxta squared with proximal corners slightly elongated (Fig. 30F). Character state 3 may be seen as a simplified way of describing the most complex structure in the male terminalia of species of *Boettcheria*. The vesica in this genus has been previously described as 'trilobed' (Dahlem & Downes, 1996) or 'with more than three lobes' (Giroux *et al.*, 2010); however, any subdivision into lobes or a more detailed definition of this structure would require a homology assessment based on a more inclusive sample of species, which is not the scope of our study. Additional characters with potential phylogenetic content are (1) the unusually larger membranous area between the epandrium and the proximal margin of the surstylus and (2) the L-shaped surstylus in most species of this genus.

The sister-group relationship between (*Austrophyto* + *R. argentina*) and *Microcerella* received strong JK value and is supported by two autapomorphies: (1) male hind trochanter with a pad of short setae covering almost the entire posterior surface (position as no. 3 in Fig. 45) and (2) phallus with a paler ventral area between basi- and distiphallus (arrow in Figs 38E, 47G).

Mulieri (2017) revised *Austrophyto* and provided a definition for this genus, where he highlighted several features, most of them found in many other genera in Sarcophaginae, but also including the (1) postgonite with two long setae, (2) distiphallus with a swollen, desclerotized ventral area proximal to vesica, (3) vesica short and weakly sclerotized, with a microserrated margin and (4) juxta scarcely developed, with apico-lateral membranous lobes and a medial sclerotization (= medial juxtal sclerite) between them. Character state 1 was included here in its original form, while state 2 was included as homologized with paler ventral area between basi- and distiphallus being swollen in *Austrophyto* and *R. argentina*, state 3 was included as vesica with a proximal desclerotized, microserrated and bilobed section ('vbs' in Fig. 38E, G) and state 4 was divided into median juxtal sclerite ('mjs' in Fig. 38F, G) and juxta as two apico-lateral membranous lobes ('jl' in Fig. 38F–H). Mulieri (2017) also highlighted the distiphallus with 'strongly developed harpes', which were not included here due to lack of material. However, the harpes in this genus are conspicuous with a shape not observed in other genera of Sarcophaginae. Mulieri (2017) also compared the reduced juxta of *Austrophyto* with that of *Boettcheria*; however, we do not find support for the latter genus having a juxta reduced nor morphologically similar to that of *Austrophyto*. Some additional comments by Mulieri (2017) on the possible phylogenetic relatedness of *Austrophyto* to *Boettcheria* and *Microcerella* were not endorsed by phylogenetically informative evidence and are considered unsupported. Our analyses reconstructed the monophylum of (*Austrophyto* + *R. argentina*), which received strong JK value and is supported by five autapomorphies: (1) postgonite with two long setae (Fig. 38D), (2) paler ventral area between basi- and distiphallus swollen (arrow in Fig. 38E), (3) vesica with a proximal desclerotized, microserrated and bilobed section ('vbs' in Fig. 38E, G), (4) median juxtal sclerite ('mjs' in Fig. 38F, G) and (5) juxta as two apico-lateral membranous lobes ('jl' in Fig. 38F, G). The affinity of *R. argentina* was uncertain also for Lopes (1988b), who assigned it provisionally to *Retrocitomyia* in spite of the absence of terminalia features typical of that genus. Based on our phylogeny and morphological examinations, we propose to include *R. argentina* in *Austrophyto*, with *Austrophyto argentina* (Lopes, 1988) as a **new combination**.

Previous definitions for *Microcerella* (Macquart, 1851; Hall, 1937; Lopes, 1983; Pape, 1996) were considered as 'skewed', 'based on highly homoplastic characters', and as considering only 'few and unuseful character states' (Mulieri *et al.*, 2015). However, subsequent definitions for this genus included some character states such as 'male without orbital proclinate setae' (Mulieri *et al.*, 2015), which is not diagnostic for this genus, since it is found in at least 37 genera of Sarcophaginae. Outlining a definition for this and other Sarcophaginae genera compels researchers to use homoplasies, which are abundant in the subfamily, as already reported (Giroux *et al.*, 2010). This overwhelming level of homoplasy could have resulted from multiple specializations giving morphologies that retain few clues to their phylogenetic history.

In the description of the genus *Microcerella*, Macquart (1851) used the bare arista to define this taxon, which was also included in definitions proposed by subsequent authors (Hall, 1937; Lopes, 1983; Pape, 1990, 1996). Pape (1990) defined *Microcerella* by the following character states: (1) eyes green, (2) syntergosternite 7 + 8 black, (3) hypandrium swollen at level of pregonite, (4) postgena with at least some black setae close to genal suture, and he also pointed to the (5) syntergosternite 7 + 8 dark brown to black/epandrium red. Pape (1996) added two other character states: (6) strong parafacial setae, and (7) arista almost bare. Mulieri *et al.* (2015) included (8) three strong postsutural dorso-central setae, (9) rigid connection between basi- and distiphallus, fused anteriorly with an incomplete hinge on posterior part, and (10) phallus with a paler anterior (= ventral) area between disti- and basiphallus. From these ten character states, 1, 3 and 5 came out as autapomorphic for this genus in the present study, while character state 2 was also found in *Boettcheria* and 10 was also found in *Austrophyto*, character states 7 and 9 were autapomorphic for the entire Microcerella clade and states 4, 5, 6 and 8 were homoplasious. Besides character states 1, 3 and 5, the monophyly of *Microcerella* was also supported by the paler and flat ventral area between basi- and distiphallus (Fig. 47G) (swollen in *Austrophyto*), and the juxta campanulated to oval (Figs 29F, G, 47G).

Lepidodexia clade

This clade is composed of the genera *Halliosca*, *Emblemasoma* and *Lepidodexia* (including *Archimimus*). It received weak JK value and is supported by three autapomorphies: (1) paraphallic apical expansions present ('pae' in Figs 1B, 9F, 23A, 31C, 32F), (2) juxta squared, with an undulated distal margin (Figs 9H, 31H, 32D) and (3) juxta displaced anteriorly (Figs 31C, E, 32A, F).

The species currently assigned to the genus *Lepidodexia* possess similarities in the phallic morphology, although their diversity in external morphology is remarkable (Lopes, 1951, 1979, 1984, 1985, 1991, 1992). Some of these similarities were noticed by Roback (1954), who considered *Camptops* Aldrich, *Chloronesia* Townsend, *Harpagopyga* Aldrich, *Johnsonia* and *Notochaeta* to be phylogenetically close and placed them in the *Johnsonia* group. Roback (1954) also included *Argoravinia*, *Emblemasoma* and *Helicobia* in this group. Similarly, Lopes (1979, 1984) proposed the tribe Johnsoniini, where he included all the subgenera currently assigned to *Lepidodexia* plus some species currently in the genera *Archimimus* and *Emdenimyia*. The Johnsoniini of Lopes share character states of the head chaetotaxy, female terminalia, labrum of the first-instar larva and male terminalia structures such as the 'spinous lobe of the vesica' (Lopes, 1979, 1984). Lopes (1983) also included *Malacophagula* and *Rafaelia* in the tribe Johnsoniini. Almost all the genera belonging to the Johnsoniini of Lopes were synonymized under *Lepidodexia* by Pape (1995, 1996), being characterized by the vesica bearing a proximal spinous lobe, and only excluding species of *Archimimus* and *Emdenimyia*, to produce a *Lepidodexia* (*sensu lato*) containing 29 subgenera. Many of these are monospecific: *Chloronesia*, *Cryptosarcophila*, *Halliosca*, *Neophytodes* Townsend, *Orodexia* Townsend, *Paramintho* Brauer & Bergenstamm, *Petriana* Lopes and *Stenopygopsis* Townsend; others include only a few species, for example *Abacantha* Hall, *Dexomyophora*, *Eufletcherimyia* Townsend, *Geijskesia* Lopes, *Hallina* and *Travassosisca* Lopes, while only six subgenera have numerous species, i.e. *Chlorosarcophaga*, *Harpagopyga*, *Johnsonia*, *Lepidodexia*, *Neophyto* and *Notochaeta*. Neither the genus *Lepidodexia* nor any of its subgenera have been recently revised. Only three phylogenetic studies have included species of this genus (Lopes, 1984; Giroux *et al.*, 2010; Kutty *et al.*, 2010), and only one of these (Giroux *et al.*, 2010) found *Lepidodexia* as monophyletic, although this clade was supported only by homoplasies. Thus, the monophyly of *Lepidodexia* and its subgenera had not been consistently tested, and there is no phylogenetic hypothesis for relationships within this genus.

In the present study, we included representative species of only six subgenera, i.e. *Lepidodexia* (*Chlorosarcophaga*), *L.* (*Dexomyophora*), *L.* (*Hallina*), *L.* (*Halliosca*), *L.* (*Neophyto*) and *L.* (*Notochaeta*), of which all represented by more than one species emerged as monophyletic within a paraphyletic genus *Lepidodexia* (Fig. 2B).

The only species of *Halliosca* emerges near the base of the Lepidodexia clade as it lacks the two autapomorphies that support this clade: (1) the presence of a hinge between the proximal and distal parts of the harpes [fused in *Halliosca* (Fig. 31E, F)], and (2) juxta angled [arching in *Halliosca* (Fig. 31E)]. *Halliosca* shows several character states shared with the genus *Lipoptilocnema*, including male abdominal ST5 with two pointed black cuticular processes on the angle of the V-shaped cleft, margin of surstylus overlapping the hinge between epandrium and surstylus, and cercal prong bent at mid-length, and with a proximal tuft of long black setae (identical to those of *Lipoptilocnema*). As outlined above, Pape (1996) proposed a broadened concept of *Lepidodexia* (*sensu lato*) containing 29 subgenera, one of these being *Halliosca*. The strong support found for a sister-group relationship between *Emblemasoma* and *Lepidodexia* (exclusive of *Halliosca*) leaves two options: to exclude *Halliosca* as subgenus from the genus *Lepidodexia* (Pape, 1996), or to broaden the definition of the latter to include also *Archimimus* and *Emblemasoma*. We are here resurrecting *Halliosca* as a valid genus, **new status**.

Pape (1996) diagnosed *Lepidodexia* with three character states: (1) postalar wall bare, (2) distiphallus with juxta angled relative to the phallic tube (Fig. 32A) and (3) distiphallus with a spinous lobe proximal to the vesica (no. 1 in Figs 31D, 32C, F). Character state 1 is not particularly diagnostic for *Lepidodexia*, since it is shared only by the subgenera *L.* (*Neophyto*) and *L.* (*Notochaeta*). As mentioned above, character state 2 emerged as autapomorphic for clade 90, as it is shared by all members of the Lepidodexia clade except *Halliosca* (Fig. 31E–G). Character state 3, originally described by Lopes (1979, 1984), is autapomorphic for clade 92, which consists of all subgenera of *Lepidodexia* (including *Archimimus*), together with three uniquely derived synapomorphies: (1) arista almost twice as long as first flagellomere (Fig. 44F), (2) male abdominal ST5 with a rounded expansion taking up the entire posterior half (Fig. 44E), (3) vesica bipartite with a C-shaped medial section (no. 3 in Fig. 32C) and a convex sclerotized distal section (no. 2 in Fig. 32C). A comparison of the proximal spinous lobe of the vesica in various subgenera of *Lepidodexia* shows that this feature can be homologized across the genus (red structure in Fig. 33). A monophyletic *Lepidodexia* can be attained by either raising all subgenera to valid genera, lumping all species into a *Lepidodexia* (*sensu lato*), or a combination of the two. Following the last option, and in order to attain a monophyletic *Lepidodexia*, we choose to include *Archimimus* in this genus, as a subgenus, **new status**, and exclude *Halliosca* and give it the **new status** as a valid genus. This newly circumscribed *Lepidodexia* (including *Archimimus*) received strong branch support and is supported by the conspicuous proximal spinous lobe of the vesica plus the above-mentioned autapomorphies.

The monophyly of and relationships between the subgenera of *Lepidodexia* are partially supported. Thus, *L.* (*Dexomyophora*) is supported by a facial ridge with dense setosity on lower 0.70 (Fig. 46C), while *L.* (*Hallina*), *L.* (*Neophyto*) and *L.* (*Notochaeta*) are only supported by homoplasies.

Three out of five of the currently recognized species of *Archimimus* (*sensu* Pape, 1996) are included in the present study, and they formed a strongly supported monophyletic group that emerged as sister to *L.* (*Neophyto*). The monophyly of *L.* (*Archimimus*) is supported by three autapomorphies: (1) pregonite distally spatulated, (2) median stylus truncated (Fig. 9G) and (3) median stylus with no opening (Fig. 9G). Only five genera and one subgenus of Sarcophaginae have the median stylus strongly modified into an apparently non-conducting stylus or entirely reduced. These are *L.* (*Archimimus*), *Chrysagria*, *Helicobia*, *Lipoptilocnema*, *Peckia* and *Sarcophaga*, and all are characterized by different acrophallic configurations. *Lepidodexia* (*Archimimus*) and *Lipoptilocnema* have both a median stylus and a capitis, but the median stylus is not tubular (Figs 9G, 24B–I); *Chrysagria* has a short capitis and an entirely reduced median stylus (Fig. 11C); *Helicobia* and *Sarcophaga* have an elongated capitis and an entirely reduced median stylus (Fig. 37C, G); and *Peckia* has no trace of either a median stylus or a capitis (Figs 12H, 13H). The sister-group relationship between *L.* (*Archimimus*) and *L.* (*Neophyto*) is supported by one autapomorphy: distance between occiput and antennal base longer than distance between occiput and vibrissal angle.

Roback (1954) included *Emblemasoma* in the *Johnsonia* group, and considered it to be closely related to *Helicobia* and *Johnsonia* (= *Lepidodexia*, in part) due to structural similarities in the male terminalia. *Emblemasoma* was considered as part of the tribe Sarcophagini by Lopes (1969a), but Lopes (1983) later erected the tribe Emblemasomatini for *Emblemasoma* and *Pessoamyia* Lopes. Our results support these assumptions, since *Emblemasoma* is closely related to *Lepidodexia*, as suggested by Roback (1954), and species originally in *Emblemasoma* and *Pessoamyia* constitute a monophylum, as indicated by Lopes (1969a). Lopes (1971) defined *Emblemasoma* and *Pessoamyia* by the presence of an inflated prosternum. Pape (1996) synonymized these two genera and expanded the definition of *Emblemasoma*, which he diagnosed as follows: (1) prosternum enlarged, (2) male mid-femur with a ctenidium of rounded spines (circular cross section) and (3) male cercus distally swollen and with a blunt tip (Fig. 44G). Here, the monophyly of *Emblemasoma* was tested for the first time, and it is supported by seven autapomorphies, mostly from non-terminalia characters. These include character states 1 and 3 of Pape (1996), plus facial plate almost equibroad along its entire length (Fig. 44A), parafacial plate widest at level of lunule (Fig. 44B), palpus with long setae (Fig. 44B), male mid-femur with 1–4 antero-dorsal setae at mid-length and vesica composed of two leaf-shaped lobes (Fig. 23A–E).

Sarcophaga clade

The Sarcophaga clade (clade 101 in Fig. 2B) is formed by *Chrysagria* as sister to (*Helicobia* + (*Peckia* + (*Lipoptilocnema* + *Sarcophaga*))) and all genera were reconstructed as monophyletic. The entire clade has weak support and half of its internal branches have high branch supports. Apart from *Chrysagria* and *Lipoptilocnema*, all genera of the Sarcophaga clade had been included in previous phylogenetic analyses. Giroux *et al.* (2010) found *Sarcophaga* as paraphyletic with regard to *Helicobia*, and *Peckia* as the sister group of (*Sarcodexia* + *Titanogrypa*). Few species of *Helicobia* and *Peckia*, and representatives of 31 subgenera of *Sarcophaga* were included. Kutty *et al.* (2010) found a monophyletic *Helicobia* only distantly related to *Sarcophaga* and to a paraphyletic *Peckia*. Stamper *et al.* (2012) found *Helicobia* as sister to (*Peckia* + *Sarcophaga*), whereas Piwczyński *et al.* (2014) found (*Peckia* [including *Villegasia*] + *Sarcophaga*) as the sister clade of (*Helicobia* + ((*Boettcheria* + *Engelimyia*) + (*Duckemyia* + *Peckiamyia*))). Buenaventura & Pape (2015) discussed the monophyly and phylogenetic relationships of four of the five genera included in the present Sarcophaga clade. These authors included all currently recognized species of *Peckia*, and the resulting topology, with *Peckia* as sister to (*Lipoptilocnema* + (*Helicobia* + *Sarcophaga*)), was generally strongly supported. Buenaventura & Pape (2017) found *Helicobia* as sister to ((*Lipoptilocnema* + *Peckia*) + *Sarcophaga*) based on a data set of four molecular markers and species of all biogeographic regions. Differences to the present study are due to the additional male terminalia character states as discussed below.

The Sarcophaga clade is well supported. Two autapomorphies define this clade: (1) acrophallus with two styli, and (2) median stylus strongly modified into an apparently non-conducting stylus or entirely reduced (capitis present or not). The first split of the Sarcophaga clade shows the genus *Chrysagria* as sister to clade 103, which contains the remaining genera. The genus *Chrysagria* was defined by Lopes & Achoy (1986) by the small 'apical plate' (= juxta) and the styli becoming free, among other male and female character states. Pape (1996) also noticed the particular development of the lateral styli in this genus, as one of the diagnostic character states he proposed for this genus was lateral styli long and curved, reaching beyond the apex of the distiphallus. However, this feature is not exclusively found in *Chrysagria*, but is present also in *Helicobia*, *Peckia* and *Sarcophaga*. Our results are not consistent with those of Lopes (1969a, 1983), who included *Chrysagria* and genera like *Microcerella* in the tribe Microcerellini. The three known species of *Chrysagria* (Pape, 1996), two of which were included in the present study, form a monophylum receiving strong JK value and supported by two autapomorphies: (1) cercal prong with a median tuft of brown and yellow, medially directed setae, and (2) juxta composed of two elongated and smooth segments (Fig. 11C).

The clade (*Helicobia* + (*Peckia* + (*Lipoptilocnema* + *Sarcophaga*))) is supported by three autapomorphies: (1) capitis recurved (Figs 24G, 37C), (2) juxta dome-shaped (Figs 22I, 32F, 37A, D) and (3) juxta with juxtal lateral plates ('jlp' in Figs 13F, 22G, I, 35B, 37E, F). Although the capitis is noticeably developed in *Lipoptilocnema*, *Helicobia* and *Sarcophaga*, it is reduced in *Peckia*. The juxta is generally dome-shaped in this clade; however, in *Lipoptilocnema* it is a membranous expansion covered with sclerotized apical spines (Mulieri *et al.*, 2016), having a recurved shape, and lacking the juxtal lateral plates.

The monophyly of *Helicobia* has been supported by morphological (Giroux *et al.*, 2010; Buenaventura & Pape, 2015) and molecular studies (Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura & Pape, 2017) and it is also strongly supported by our results. Giroux *et al.* (2010) reduced *Helicobia* to a subgenus of *Sarcophaga*, but this was rejected by subsequent studies (Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura & Pape, 2015, 2017), as well as by our results. A single autapomorphy supported this genus: the male hind trochanter with a pad of short setae medially and with a strong seta near its posterior margin (position as no. 7 in Fig. 45). Of the seven apomorphies that supported this taxon in Giroux *et al.*'s (2010) phylogeny, two – posterior and posteroventral setae in the male hind tibia unmodified and dorsal proximal part of wing vein R_1 setulose – were included here, and found not to be uniquely derived in this genus but shared with at least 15 other genera. Another homoplasious character state supporting *Helicobia* is a parafacial plate with strong setae. Similarly, of the six character states defining *Helicobia* in Buenaventura & Pape's (2015) study, five are included here but are not recovered as autapomorphic for this genus. Two of them (ocellar setae strong, vertical setae strong) do not define *Helicobia* in our study, while the three remaining ones correspond to configurations of the vesica that are here reinterpreted. Female T6 with a mid-dorsal desclerotized, fine strip or narrow membranous longitudinal cleft was not included in the present study, due to scarce female data for other Sarcophaginae genera. Despite the homoplastic condition of character states in the present study as well as those of Pape (1996), Giroux *et al.* (2010) and Buenaventura & Pape (2015), we use a combination of these to define *Helicobia*.

The clade (*Peckia* + (*Lipoptilocnema* + *Sarcophaga*)) is supported by one autapomorphy: cercal prong with a subapical saddle-shaped concavity followed by a hump. This clade was also supported by two homoplasies: (1) postgenal setulae white or yellow, and (2) one presutural dorso-central seta. *Peckia* and *Sarcophaga* also share an inner margin of male abdominal ST5 cleft with a large medial pad of long hair-like setulae, or strong and short setae. This setosity pattern is absent in *Lipoptilocnema*, which instead has two pointed black cuticular processes on the angle of the V-shaped cleft of the male abdominal ST5.

Buenaventura & Pape (2015) included all currently recognized species of *Peckia* (*sensu* Buenaventura & Pape, 2013) and provided an extensive discussion on the historical definitions and concepts of this genus by especially Robineau-Desvoidy (Robineau-Desvoidy, 1830), Lopes (1941a, 1943, 1958, 1969a, 1983), Roback (1954) and Pape (1996). Two synapomorphies supported the monophyly of *Peckia* in Buenaventura & Pape (2015): (1) presence of a fringe of long, hair-like setulae along outer margin, extending to – or almost to – the posterior corner of the lower calypter, and (2) reduction of the capitis. These character states, plus paraphallus wider than long (Fig. 13E, F) also support *Peckia* in our analysis. The paraphallic tube in *Peckia* is mostly reduced (except in the subgenus *Pattonella* Enderlein, Fig. 12F), consisting almost only of a sclerotized strip in the proximal part of the distiphallus, whereas the juxta is generally large and complex, particularly in the subgenera *Pattonella* (Fig. 12F), *Peckia* (Fig. 13F–H) and *Sarcodexia* (Fig. 35B). For example, the juxta in the subgenus *Sarcodexia* has one basal and two distal juxtal horns ('bjh' and 'djh' in Figs 13I, J, 35A, B). The genus *Peckia* is also supported by three homoplasies, including the loss of harpes. All groups in basal positions with regard to clade 80 have a distiphallus with no harpes. According to the optimization of this character in our phylogeny, the harpes are considered as primarily absent in the Tricharaea and Dexosarcophaga grades, and the clades Oxysarcodexia, Argoravinia, Blaesoxipha, Engelimyia, Udamopyga and Peckiamyia, but present in clades Microcerella, Lepidodexia and Sarcophaga, while in the genus *Peckia* they are secondarily lost, which may constitute a reduction uniquely derived in this genus.

The clade (*Lipoptilocnema* + *Sarcophaga*) received high JK value and is supported by three uniquely derived character states: margins of surstylus slightly folded or protruding outwards ('sr' in Fig. 44C, D), paraphallic dorsal wall with a longitudinal desclerotized strip with a shallow or deep depression (Figs 24J, 37H) and presence of paraphallic proximal expansions ('ppe' in Figs 24C, 37E, I). This clade was also supported by three homoplasies: male with rows of frontal setae divergent anteriorly, cercus with proximal tuft of long, black, hair-like setulae and harpes protruding dorso-medially over the base of the lateral styli (Fig. 37E, I). Buenaventura & Pape (2015) interpreted the acrophallic structures of the genera of the Sarcophaga clade, such as the reduced median stylus and the elongated capitis, in the same way as here, but some additional character states included in the present analysis resulted in a change in relationships among these genera. Thus, some character states such as the subapical saddle-shaped concavity of the cercal prong followed by a subapical hump support the clade (*Peckia* + (*Lipoptilocnema* + *Sarcophaga*)). Also, the slightly folded or outwards protruding margins of surstylus, the presence of a paraphallic desclerotized strip and the presence of paraphallic proximal expansions support the clade (*Lipoptilocnema* + *Sarcophaga*).

Lipoptilocnema, represented in this analysis by two species, is defined by four autapomorphies in the male terminalia: (1) proximal margin of surstylus overlapping the hinge between epandrium and surstylus (arrow in Fig. 44C), (2) distal part of harpes membranous (Fig. 24B–D, G), (3) juxta recurved (Fig. 24B, G) and (4) juxta triangular with longitudinal keel, laterally membranous, and apically bifid and spinose (Figs 24J, 44D). The position of this genus within the Sarcophaginae was recently analysed by Buenaventura & Pape (2015, 2017), who recovered a monophyletic *Lipoptilocnema* not nested inside any other genus and thereby refuted the proposal of Pape (1996) to include it as a subgenus of *Sarcophaga*. The present phylogeny finds *Lipoptilocnema* as the sister group of *Sarcophaga* as opposed to (*Helicobia* + *Sarcophaga*) of Buenaventura & Pape (2015) and (*Lipoptilocnema* + *Peckia*) of Buenaventura & Pape (2017). Buenaventura & Pape (2015) found *Lipoptilocnema* as supported by four apomorphies: (1) cercal prong with dorsal surface S-shaped, (2) surstylus with anterior and posterior margin slightly folded, (3) paraphallic apical elongated expansion with apical spines and (4) juxta tongue-shaped, broad proximally and gradually getting narrow to the entire apex. Character state 1 was reinterpreted here and found to be also present in *Peckia* and *Sarcophaga*, while character state 2 was included in its original form and found to be also present in *Sarcophaga*. Character states 3 and 4 were also reinterpreted and homologized to the juxta and median stylus, respectively, in agreement with Mulieri *et al.* (2016).

Sarcophaga is recovered as monophyletic, supported by eight autapomorphies including a medio-proximal pad of short setae on the posterior surface of the hind trochanter (position as no. 4 in Fig. 45), a strong seta on postgonite situated distal to middle, paraphallus with a window ('pw' in Fig. 37A), harpes elbowed in proximal part (Fig. 37A, E) and harpes with an apical process ('ah' in Fig. 37F). The characteristic paraphallic window of *Sarcophaga* was first described by Whitmore *et al.* (2013) in a phylogeny of the subgenus *Heteronychia*. Whitmore *et al.* (2013) also described the cercal prong of the subgenus *Heteronychia* with 'a median, saddle-shaped concavity, or a deep hollowing of the dorsal surface, called a dorsal excavation', which is also shared by some species of *Sarcophaga* included here. Its autapomorphic condition is only contradicted by its presence in a few species of the subgenus *Peckia* (*Peckia*). *Sarcophaga* exclusive of *Helicobia* and *Lipoptilocnema* is a monophyletic taxon, as demonstrated in previous molecular (Kutty *et al.*, 2010; Stamper *et al.*, 2012; Piwczyński *et al.*, 2014; Buenaventura *et al.*, 2016; Buenaventura & Pape, 2017) and morphological (Buenaventura & Pape, 2015) studies.

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REFERENCES

Aldrich JM. 1916. *Sarcophaga and allies in North America, Vol. 1*. La Fayette: Entomological Society of America, Thomas Say Foundation.

Andersen S. 1988. Revision of European species of Phytomyptera Rondani (Diptera: Tachinidae). *Entomologica Scandinavica* **19:** 43–80.

Arnqvist G. 1997. The evolution of animal genitalia: distinguishing between hypotheses by single species studies. *Biological Journal of the Linnean Society* **60:** 365–379.

Arnqvist G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature* **393:** 784–786.

Arnqvist G, Rowe L. 2002a. Antagonistic coevolution between the sexes in a group of insects. *Nature* **415:** 787–789.

Arnqvist G, Rowe L. 2002b. Correlated evolution of male and female morphologles in water striders. *Evolution* **56:** 936–947.

Aspoas BR. 1991. Comparative micromorphology of third instar larvae and the breeding biology of some Afrotropical *Sarcophaga* (Diptera: Sarcophagidae). *Medical and Veterinary Entomology* **5:** 437–445.

Augul RSH. 2008. Description of the third instar larva of *Sarcophaga africa* (= *S. haemorrhoidalis*) Fall. (Diptera: Sarcophagidae). *Bulletin of the Iraq Natural History Museum* **10:** 9–20.

Blackith R, Blackith R, Pape T. 1998. Taxonomy and systematics of *Helicophagella* Enderlein, 1928 (Diptera, Sarcophagidae) with the description of a new species and a revised catalogue. *Studia Dipterologica* **4:** 383–434.

Böttcher G. 1912. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten. *Deusche Entomologische Zeitschrift 1912* **Heft V:** 525–544.

Böttcher G. 1913a. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten (Dipt.). *Deusche Entomologische Zeitschrift 1913* **Heft I:** 1–16.

Böttcher G. 1913b. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten (Dipt.). *Deusche Entomologische Zeitschrift 1913* **Heft II:** 115–130.

Böttcher G. 1913c. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten (Dipt.). *Deusche Entomologische Zeitschrift 1913* **Heft III:** 239–254.

Böttcher G. 1913d. Die männlichen Begattungswerkzeuge bei dem Genus *Sarcophaga* Meig. und ihre Bedeutung für die Abgrenzung der Arten (Dipt.). *Deusche Entomologische Zeitschrift 1913* **Heft IV:** 351–377.

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

Buenaventura E. 2013. Morphology of the first and second instars larvae of *Peckia (Peckia) chrysostoma* (Wiedemann, 1830) (Diptera, Sarcophagidae). *Acta Zoológica Mexicana* **29:** 96–104.

Buenaventura E, Camacho G, Garcia A, Wolff M. 2009. Sarcophagidae (Diptera) de importancia forense en Colombia: claves taxonómicas, notas sobre su biología y distribución. *Revista Colombiana de Entomología* **35:** 189–196.

Buenaventura E, Pape T. 2013. Revision of the New World genus *Peckia* Roniveau-Desvoidy (Diptera: Sarcophagidae). *Zootaxa* **3622:** 1–87.

Buenaventura E, Pape T. 2015. Phylogeny of the *Peckia*-genus group: evolution of male genitalia in the major necrophagous guild of Neotropical flesh flies (Diptera: Sarcophagidae). *Organisms Diversity & Evolution* **15:** 301–331.

Buenaventura E, Pape T. 2017. Multilocus and multiregional phylogeny reconstruction of the genus *Sarcophaga* (Diptera, Sarcophagidae). *Molecular Phylogenetics and Evolution* **107:** 619–629.

Buenaventura E, Whitmore D, Pape T. 2016. Molecular phylogeny of the hyperdiverse genus *Sarcophaga* (Diptera: Sarcophagidae), and comparison between algorithms for identification of rogue taxa. *Cladistics* **33:** 109–133.

Carvalho-Filho FDS, Esposito MC. 2011. *Panava* a senior synonym of *Wulpisca*, and description of new species of *Panava* and *Dexosarcophaga* (Bezzisca) from the Brazilian Amazon (Diptera, Sarcophagidae). *Zootaxa* **2808:** 49–56.

Carvalho-Filho FDS, Esposito MC. 2012. Revision of *Argoravinia* Townsend (Diptera: Sarcophagidae) of Brazil with the description of two new species. *Zootaxa* **3256:** 1–26.

Carvalho CJB de, Mello-Patiu CA. 2008. Key to the adults of the most common forensic species of Diptera in South America. *Revista Brasileira de Entomologia* **52:** 390–406.

Carvalho CJB, Rafael JA, Couri MS, Silva VC. 2012. Diptera. In: Rafael JA, Melo GAR, Carvalho CJB, Casari S, Constantino C, eds. *Insetos do Brasil: diversidade e taxonomia*. Ribeirão Preto, São Paulo, Brasil: Holos Editora, 701–743.

Cerretti P, Lo Giudice G, Pape T. 2014. Remarkable Rhinophoridae in a growing generic genealogy (Diptera: Calyptratae, Oestroidea). *Systematic Entomology* **39:** 660–690.

Couri MS, Pont A. 2000. Cladistic analysis of Coenosiini (Diptera: Muscidae: Coenosiinae). *Systematic Entomology* **25:** 373–392.

Cumming JM, Wood DM. 2009. Adult morphology and terminology. In: Brown BV, Borkent A, Cumming JM, Wood DM, Zumbado M, eds. *Manual of Central American Diptera, Vol. 1*. Ottawa, ON, Canada: NRC Research Press, 9–50.

Curran CH. 1934. Sarcophaginae of the American Museum Congo Expedition (Diptera). *American Museum Novitates* **727:** 1–31.

D'Almeida JM. 1994. Ovipositional substrates used by Calyptrate Diptera in Tijuca Forest, Rio de Janeiro. *Memórias do Instituto Oswaldo Cruz* **89:** 261–264.

D'Almeida JM, Almeida JR. 1998. Nichos tróficos em dípteros caliptrados, no Rio de Janeiro, RJ. *Revista Brasileira de Biologia* **58:** 563–570.

Dahlem G, Downes W. 1996. Revision of the genus *Boettcheria* in America North of Mexico (Diptera: Sarcophagidae). *Insecta Mundi* **10**: 77–103.

Dahlem GA, Naczi RFC. 2006. Flesh flies (Diptera: Sarcophagidae) associated with north American Pitcher plants (Sarraceniaceae), with descriptions of three new species. *Annals of the Entomological Society of America* **99:** 218–240.

Darwin CR. 1871. *The descent of man and selection in relation to sex*. London: J. Murray.

Daugeron C, Grootaert P. 2003. Assessment of monophyly of species-groups within Afrotropical Empidini (Diptera: Empididae: Empidinae), with a cladistic analysis of the *Empis setitarsus*-group. *Systematic Entomology* **28:** 339–360.

Dikow T. 2009. Phylogeny of Asilidae inferred from morphological characters of imagines (Insecta: Diptera: Brachycera: Asiloidea). *Bulletin of the American Museum of Natural History* **319:** 1–175.

Dodge HR. 1961. Studies on female sarcophagid flies: I. *Sarcophaga aldrichi* Parker, hinei Aldrich, houghi Aldrich, and *Agria affinis* (Fallén). *The Canadian Entomologist* **93:** 781–785.

Dodge HR. 1965a. The Sarcophagidae (Diptera) of West Indies I. The Bahama Islands. *Annals of the Entomological Society of America* **58:** 474–497.

Dodge HR. 1965b. The Sarcophagidae (Diptera) of the West Indies. II. Jamaica. *Annals of the Entomological Society of America* **58:** 497–517.

Dodge HR. 1966. Some new or little-known Neotropical Sarcophagidae (Diptera), with a review of the genus *Oxysarcodexia*. *Annals of the Entomological Society of America* **59:** 674–701.

Dodge HR. 1967. Some new American Sarcophagidae (Diptera). *Pacific Insects* **9:** 679–686.

Dodge HR. 1968a. Nine new *Nephochaetopteryx* from Brazil (Diptera: Sarcophagidae). *Journal of the Kansas Entomological Society* **61:** 277–287.

Dodge HR. 1968b. The Sarcophagidae of Barro Colorado Island, Panama (Diptera). *Annals of the Entomological Society of America* **61:** 421–450.

Downes W. 1955. Notes on the morphology and classification of the Sarcophagidae and other calyptrates. *Proceedings of the Iowa Academy of Sciences* **62:** 514–538.

Downes W. 1965. Family Sarcophagidae. In: Stone A, Sabrosky CW, Wirth WW, Foote RH, Coulson JR, eds. *A catalog of the Diptera of America north of Mexico*. Washington, DC, USA: U.S. Dept. of Agric., 933–961.

Eberhard WG. 1985. *Sexual selection and animal genitalia*. Boston, MA: Harvard University Press.

Eberhard WG. 1993. Evaluating models of sexual selection: genitalia as a test case. *The American Naturalist* **142:** 564–571.

Eberhard WG. 1996. *Female control: sexual selection by cryptic female choice*. Princeton, NJ, USA: Princeton University Press.

Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12:** 99–124.

Ferrar P. 1979. The immature stages of dung-breeding Muscoid flies in Australia, with notes on the species, and keys to larvae and puparia. *Australian Journal of Zoology* **73:** 1–106.

Fitch WM. 1971. Toward defining course of evolution—minimum change for a specific tree topology. *Systematic Zoology* **20:** 406–416.

Giroux M, Pape T, Wheeler TA. 2010. Towards a phylogeny of the flesh flies (Diptera: Sarcophagidae): morphology and phylogenetic implications of the acrophallus in the subfamily Sarcophaginae. *Zoological Journal of the Linnean Society* **158:** 740–778.

Giroux M, Wheeler TA. 2009. Systematics and phylogeny of the subgenus *Sarcophaga* (*Neobellieria*) (Diptera: Sarcophagidae). *Annals of the Entomological Society of America* **102:** 567–587.

Giroux M, Wheeler TA. 2010. Systematics of *Bulbostyla*, a new subgenus of *Sarcophaga* Meigen, and change of status for *Robackina* Lopes (Diptera: Sarcophagidae). *Zootaxa* **2553:** 35–59.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24:** 774–786.

Guimarães HJL. 2004. Redescrição dos machos de dez espécies neotropicais de *Ravinia* Robineau-Desvoidy 1863 (Diptera, Sarcophagidae). *Arquivos do Museu Nacional, Rio de Janeiro* **62:** 45–66.

Hall DG. 1933. The Sarcophaginae of Panama (Diptera: Calliphoridae). *Bulletin of the American Museum of Natural History* **66:** 251–285.

Hall DG. 1937. Sarcophaginae. *Diptera of Patagonia and South of Chile* **7:** 347–384.

Hennig W. 1973. Ordnung Diptera (Zweifluger). In: Helmcke JG, Starck D, Wermuth H, eds. *Handbuch der Zoologie, Arthropoda - 2. Halfte: Insecta, 2. Teil: Specielles. Vol. 4/2*. Berlin: De Gruyter, 1–337.

Hosken DJ, Stockley P. 2004. Sexual selection and genital evolution. *Trends in Ecology & Evolution* **19:** 87–93.

Ingram KK, Laamanen T, Puniamoorthy N, Meier R. 2008. Lack of morphological coevolution between male forelegs and female wings in *Themira* (Sepsidae: Diptera: Insecta). *Biological Journal of the Linnean Society* **93:** 227–238.

Jirón LF, Bolaños R. 1986. Biology and larval morphology by scanning electron microscopy of *Pattonella intermutans* Walker (Diptera, Sarcophagidae). *Revista Brasileira de Entomologia* **30:** 27–30.

Jordaens K, Sonet G, Richet R, Dupont E, Braet Y, Desmyter S. 2013. Identification of forensically important *Sarcophaga* species (Diptera: Sarcophagidae) using the mitochondrial COI gene. *International Journal of Legal Medicine* **127:** 491–504.

Kano R, Lopes HS. 1969. A new genus of Sarcophagidae from the Amazon (Diptera). *Anais da Academia Brasileira de Ciências* **41:** 91–94.

Kano R, Shinonaga S. 1969. Two new species of sarcophagid flies from Nepal (Diptera: Sarcophagidae). *Pacific Insects* **11:** 191–196.

Kurahashi H, Kano R. 1984. Phylogeny and geographical distribution of the genus *Boettcherisca* Rohdendorf (Diptera: Sarcophagidae). *Japanese Journal of Medical Science & Biology* **37:** 27–34.

Kutty SN, Pape T, Wiegmann BM, Meier R. 2010. Molecular phylogeny of the Calyptratae (Diptera: Cyclorrhapha) with an emphasis on the superfamily Oestroidea and the position of Mystacinobiidae and McAlpine's fly. *Systematic Entomology* **35:** 614–635.

Leite ACR, Lopes HS. 1987. Second contribution to the knowledge of the larvae of the Ravininii (Diptera, Sarcophagidae) based on observations using scanning electron microscope. *Memórias do Instituto Oswaldo Cruz* **82:** 219–226.

Léonide J, Léonide JC. 1986. *Les diptères sarcophagidés endoparasites des orthoptères français - essai biotaxonomie*. Université de Provence (Aix-en-Provence), 301 pp. [Published version of 1984 thesis by J. Léonide with minor changes and an English summary.]

Lopes HS. 1941a. Sobre o aparelho genital feminino dos 'Sarcophagidae' e sua importancia na classificacao (Diptera). *Revista Brasileira de Biologia* **1:** 215–221.

Lopes HS. 1941b. Sôbre alguns sarcofagídeos neotrópicos da coleção do Museu Britânico (Diptera). *Arquivos de Zoologia do Estado de São Paulo* **2:** 357–387.

Lopes HS. 1943. Contribuição ao conhecimento das larvas dos Sarcophagidae com especial referencia ao esqueleto cefálico (Diptera). *Memórias do Instituto Oswaldo Cruz* **38:** 127–163.

Lopes HS. 1945. Sôbre um novo gênero de 'Sarcophagidae' de Surinam (Diptera). *Revista Brasileira de Biologia* **5:** 295–298.

Lopes HS. 1946. Contribuição ao conhecimento das espécies do gênero *Oxysarcodexia* Townsend, 1917 (Diptera Sarcophagidae). *Boletim da Escola Nacional de Veterinária (Rio de Janeiro)* **1:** 62–134.

Lopes HS. 1950. Sôbre os gêneros *Boettcheria* Parker 1914 e *Boettcherimima* n. gen. (Diptera Sarcophagidae). *Memórias do Instituto Oswaldo Cruz* **48:** 687–709.

Lopes HS. 1951. Sôbre o gênero *Lepidodexia* Brauer & Bergestamm, 1891 (Diptera-Sarcophagidae). *Memórias do Instituto Oswaldo Cruz* **49:** 641–658.

Lopes HS. 1958. Considerações sôbre as espécies de *Peckia* Desvoidy, 1830 e de gêneros affins. *Anais da Academia Brasileira de Ciências* **30:** 211–243.

Lopes HS. 1966. Sôbre *Malacophagomyia* g.n. (Diptera, Sarcophagidae) cujas larvas vivem em cadávares de 'Gastropoda' (Mollusca). *Revista Brasileira de Biologia* **26:** 315–321.

Lopes HS. 1968. Sôbre uma espécie nova de *Dexosarcophaga* Townsend, 1917 (Dipt. Sarcophagidae) cujas larvas vivem in ninho de *Camponotus* (Hymenoptera, Formicidae). *Revista Brasileira de Biologia* **28:** 521–523.

Lopes HS. 1969a. Family Sarcophagidae. In: Papavero N, ed. *A catalogue of the Diptera of the Americas South of the United States*. São Paulo, Brasil: Departmento de Zoologia, Secretaria da Agricultura, 1–88.

Lopes HS. 1969b. Neotropical Sarcophagidae reared from Gastropoda by Dr. W. Weyrauch (Diptera). *Studia Entomologia* **12:** 133–160.

Lopes HS. 1971. Notes on *Emblemasoma* and *Pessoamyia* (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **31:** 89–97.

Lopes HS. 1975a. Bredin Archbold Smithsonian Biological Survey of Dominica: the Sarcophagidae of Dominica (Diptera). *Anais da Academia Brasileira de Ciências* **45**: 467–487.

Lopes HS. 1975b. Sarcophagid flies (Diptera) from Pacatuba, State of Ceará. *Revista Brasileira de Biologia* **34:** 271–294.

Lopes HS. 1975c. On some North American Sarcophagidae with red legs (Diptera). *Revista Brasileira de Biologia* **35:** 155–164.

Lopes HS. 1975d. On *Engelimyia*, new genus for *Sarcophaga cassidifera* Engel (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **34:** 425–430.

Lopes HS. 1976a. On the species of *Argoravinia* Townsend (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **36:** 693–696.

Lopes HS. 1976b. *Thomazomyia* a new neotropical genus of Sarcophagidae. *Studia Entomologia* **19:** 503–509.

Lopes HS. 1979. Contribution to the knowledge of the tribe Johnsoniini (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **39:** 919–942.

Lopes HS. 1983. The importance of the mandible and clypeal arch of the first instar larvae in the classification of the Sarcophagidae (Diptera). *Revista Brasileira de Entomologia* **26:** 293–326.

Lopes HS. 1984. A tentative arrangement of the Notochaetina (Diptera, Sarcophagidae), a contribution to the phylogeny of the group. *Anais da Academia Brasileira de Ciências* **56:** 339–350.

Lopes HS. 1985. On *Orodexia*, *Anolisomyia* (revalidated), *Euflettcherimyia* and *Notochaeta* (Diptera, Sarcophagidae), with key to species. *Revista Brasileira de Entomologia* **29:** 559–570.

Lopes HS. 1988a. Old and new neotropical sarcophagidae (Diptera). *Memórias do Instituto Oswaldo Cruz* **83:** 239–251.

Lopes HS. 1988b. On American Sarcophagidae (Diptera), with descriptions of a new genus and three new species. *Revista Brasileira de Biologia* **48:** 915–924.

Lopes HS. 1989. On American Sarcophagidae (Diptera) with descriptions of a new genus and two new species. *Revista Brasileira de Biologia* **49:** 825–835.

Lopes HS. 1990. On the genera of Sarcophagidae (Diptera) showing proclinate frontorbital bristles in males. *Revista Brasileira de Biologia* **50:** 279–292.

Lopes HS. 1991. On *Johnsonia* (Diptera, Sarcophagidae) with description of twelve new species. *Anais da Academia Brasileira de Ciências* **63:** 59–84.

Lopes HS. 1992. Notes on Neotropical Johnsoniini (Diptera, Sarcophagidae), with descriptions of six new species. *Revista Brasileira de Biologia* **52:** 597–607.

Lopes HS, Achoy RM. 1986. On *Chrysagria* (Diptera, Sarcophagidae), with descriptions of two new species, one of them living on larvae of *Altina* sp. (Coleoptera, Chrysomelidae). *Revista Brasileira de Biologia* **46:** 273–276.

Lopes HS, Leite ACR. 1986. Studies on some features of the first instar larvae of *Oxysarcodexia* (Diptera, Sarcophagidae) based on scanning electron microscope observations. *Revista Brasileira de Biologia* **46:** 741–746.

Lopes HS, Leite ACR. 1987. Third contribution to the knowledge of the Raviniini (Diptera: Sarcophagidae) based on observations of the larvae, using scanning electron microscope. *Memórias do Instituto Oswaldo Cruz* **82:** 407–423.

Lopes HS, Leite ACR. 1991. Notes on the male genitalia of species of *Ravinia* and *Chaetoravinia* (Diptera: Sarcophagidae). *Memórias do Instituto Oswaldo Cruz* **86:** 95–101.

Lopes HS, Tibana R. 1982. Sarcophagid flies (Diptera) from Sinop, State of Mato Grosso, Brazil. *Memórias do Instituto Oswaldo Cruz* **77:** 285–298.

Lopes HS, Tibana R. 1988. On Johnsoniini (Diptera, Sarcophagidae), with *Notochaetisca* new name and descriptions of eight new species. *Revista Brasileira de Biologia* **48:** 315–332.

Losos JB. 1999. Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Animal Behaviour* **58:** 1319–1324.

Macquart J. 1851. Diptères exotiquez nouveaux ou peu connus. Suite de 4e supplément publié dans les Mémories de 1849. *Mémories de la Société Nationale des sciences, de L'Agriculture et des Arts, de Lille* **1850:** 134–294.

Maddison WP, Maddison DR. 2011. *Mesquite: a modular system for evolutionary analysis. Version 2.75*. Available at: http://mesquiteproject.org

Matsuda R. 1976. *Morphology and evolution of the insect abdomen*. New York, Oxford, Toronto: Pergamon Press.

McAlpine JF. 1981. Morphology and terminology-adults. In: McAlpine JF, Petersen BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM, eds. *Manual of Nearctic Diptera Volume 1. Agriculture Canada. Monograph 27*. Ottawa, ON, Canada: Canadian Government Publishing Centre, 9–63.

Meiklejohn KA, Wallman JF, Cameron SL, Dowton M. 2012. Comprehensive evaluation of DNA barcoding for the molecular species identification of forensically important Australian Sarcophagidae (Diptera). *Invertebrate Systematics* **26:** 515–525.

Meiklejohn KA, Wallman JF, Dowton M. 2011. DNA-based identification of forensically important Australian Sarcophagidae (Diptera). *International Journal of Legal Medicine* **125:** 27–32.

Meiklejohn KA, Wallman JF, Dowton M. 2013a. DNA barcoding identifies all immature life stages of a forensically important flesh fly (Diptera: Sarcophagidae). *Journal of Forensic Sciences* **58:** 184–187.

Meiklejohn KA, Wallman JF, Pape T, Cameron SL, Dowton M. 2013b. Utility of COI, CAD and morphological data for resolving relationships within the genus *Sarcophaga* (*sensu lato*) (Diptera: Sarcophagidae): a preliminary study. *Molecular Phylogenetics and Evolution* **69:** 133–141.

Mello-Patiu CA. 2000. A new species of *Dexosarcophaga* Townsend from Nicaragua (Diptera, Sarcophagidae, Sarcophaginae). *Boletim do Museu Nacional Rio de Janeiro* **430:** 1–4.

Mello-Patiu CA. 2002. Revision of some *Dexosarcophaga* species described by R. Dodge (Diptera: Sarcophagidae). *Zootaxa* **122:** 1–16.

Mello-Patiu CA, Azevedo AL De. 1998. Redescrição de macho, fêmea e larva de *Rafaelia acanthoptera* (Wulp, 1895) (Diptera, Sarcophagidae). *Boletim do Museu Nacional Rio de Janeiro* **389:** 1–11.

Mello-Patiu CA, Luna-Dias C. 2010. Myiasis in the neotropical amphibian *Hypsiboas beckeri* (Anura: Hylidae) by a new species of Lepidodexia (Diptera: Sarcophagidae). *The Journal of Parasitology* **96:** 685–688.

Mello-Patiu CA, Pape T. 2000. Definitions of *Dexosarcophaga* Townsend 1917 and *Sarcofahrtiopsis* Hall 1933, including to new species and a redescription of *Sarcofahrtiopsis cuneata* (Townsend 1935) (Diptera: Sarcophagidae). *Boletín de Entomología Venezolana* **15:** 181–194.

Mello-Patiu CA, dos Santos JM. 2001. *Nephochaetopteryx* Townsend, 1934: descriptions and comparative morphological notes on the female terminalia (Diptera: Sarcophagidae). *Studia Dipterologica* **8:** 303–315.

Mello-Patiu CA, Soares WF, Silva KP. 2009. Espécies de Sarcophagidae (Insecta: Diptera) registradas no estado do Rio de Janeiro. *Arquivos do Museu Nacional, Rio de Janeiro* **67:** 173–188.

Méndez J, Mello-Patiu CA, Pape T. 2008. New flesh flies (Diptera: Sarcophagidae) from coastal mangroves of Panama with taxonomic notes and keys. *Journal of Natural History* **42:** 249–257.

Mendonça PM, Barbosa RR, Cortinhas LB, Santos-Mallet JR, de Carvalho Queiroz MM. 2013. Ultrastructure of immature stages of *Peckia* (Euboetcheria) collusor (Diptera: Sarcophagidae). *Acta Tropica* **128:** 522–527.

Mooi RD, Gill AC. 2010. Phylogenies without Synapomorphies—a crisis in fish systematics: time to show some character. *Zootaxa* **40:** 26–40.

Moore JC, Pannell JR. 2011. Sexual selection in plants. *Current Biology* **21:** R176–R182.

Morales E. 2000. Estimating phylogenetic inertia in *Tithonia* (Asteraceae): a comparative approach. *Evolution* **54:** 475–484.

Mulieri PR. 2017. Saying goodbye to monotypy in the poorly known genus *Austrophyto* Lopes, 1989 (Diptera: Sarcophagidae): new diagnosis and description of two new species. *Zootaxa* **4268:** 88–100.

Mulieri PR, Mariluis JC. 2011. Description of a new species of *Macronychia* Rondani (Diptera : Sarcophagidae : Miltogramminae), with a key to the New World species of the genus. *Zootaxa* **2832:** 51–55.

Mulieri PR, Mariluis JC, Patitucci LD. 2010. Review of the Sarcophaginae (Diptera: Sarcophagidae) of Buenos Aires Province (Argentina), with a key and description of a new species. *Zootaxa* **2575:** 1–37.

Mulieri PR, Mariluis JC, Patitucci LD, Olea MS. 2015. The Sarcophaginae (Diptera: Sarcophagidae) of Southern South America. I. The species of *Microcerella* Macquart from the Patagonian Region. *Zootaxa* **3933:** 1–88.

Mulieri PR, Mello-Patiu CA. 2013. Revision of the Neotropical genus *Malacophagomyia* (Diptera: Sarcophagidae) with description of a new species. *Zootaxa* **3736:** 368–378.

Mulieri PR, Mello-Patiu CA, Aballay FH. 2016. Taxonomic revision of *Lipoptilocnema* (Diptera: Sarcophagidae), with notes on natural history and forensic importance of its species. *Journal of Medical Entomology* **0:** 1–26.

Nandi BC. 1990. Sarcophagid flies (Diptera: Sarcophagidae) from Bihar, India. *Hexapoda* **2:** 21–28.

Nixon KC, Carpenter JM. 2012. On homology. *Cladistics* **28:** 160–169.

Pandellé L. 1895. Études sur les muscides de France. IIe partie (suite). *Revue d'Entomologie* **14:** 287–351.

Pandellé L. 1896. Études sur les muscides de France. IIe partie. *Revue d'Entomologie* **15:** 1–230.

Pape T. 1989a. Three new species of neotropical Sarcophagidae (Diptera). *Memórias do Instituto Oswaldo Cruz* **84:** 471–476.

Pape T. 1989b. A new species of *Boettcheria* (Diptera: Sarcophagidae) from the Dominican Republic. *Memórias do Instituto Oswaldo Cruz* **84:** 431–434.

Pape T. 1990. Revisionary notes on American Sarcophaginae (Diptera: Sarcophagidae). *Tijdschrift voor Entomologie* **133:** 43–74.

Pape T. 1992. Phylogeny of the Tachinidae family-group (Diptera: Calyptratae). *Tijdschrift voor Entomologie* **135:** 43–86.

Pape T. 1994. The world *Blaesoxipha* Loew, 1861 (Diptera: Sarcophagidae). *Entomologica scandinavica Supplement* **45:** 1–247.

Pape T. 1995. A catalogue of the Sarcophagidae (Insecta: Diptera) described by G. Enderlein. *Steenstrupia* **21:** 1–30.

Pape T. 1996. Catalogue of the Sarcophagidae of the World (Insecta: Diptera). *Memoirs of Entomology International* **8:** 1–558.

Pape T. 1998a. A new genus of Paramacronychiinae (Diptera: Sarcophagidae), argued from a genus-level cladistic analysis. *Systematic Entomology* **23:** 187–200.

Pape T. 1998b. Family Sarcophagidae. In: Papp L, Darvas B, eds. *Manual of Palaearctic Diptera*, Volume 3, Higher Brachycera. Budapest: Science Herald, 649–678.

Pape T, Dahlem G. 2010. Sarcophagidae. In: Zumbado M, Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, eds. *Manual of Central American Diptera, Vol. 2*. Ottawa, ON, Canada: NRC Research Press, 1313–1335.

Pape T, Dechmann D, Vonhof MJ. 2002. A new species of *Sarcofahrtiopsis* Hall (Diptera: Sarcophagidae) living in roosts of Spix's disk-winged bat *Thyroptera tricolor* Spix (Chiroptera) in Costa Rica. *Journal of Natural History* **36:** 991–998.

Pape T, Mello-Patiu CA. 2006. Revision of *Engelimyia* Lopes, 1975 (Diptera: Sarcophagidae). *Zootaxa* **1256:** 21–47.

Pérez-Moreno S, Marcos-García MA, Rojo S. 2006. Comparative morphology of early stages of two Mediterranean *Sarcophaga* Meigen, 1826 (Diptera; Sarcophagidae) and a review of the feeding habits of Palaearctic species. *Micron* **37:** 169–179.

Piwczyński M, Szpila K, Grzywacz A, Pape T. 2014. A large-scale molecular phylogeny of flesh flies (Diptera: Sarcophagidae). *Systematic Entomology* **39:** 783–799.

Povolný D, Verves Y. 1997. The flesh-flies of Central Europe (Insecta, Diptera, Sarcophagidae). *Spixiana, Zeitschrift für Zoology* **24:** 1–263.

Puniamoorthy N, Kotrba M, Meier R. 2010. Unlocking the "Black box": internal female genitalia in Sepsidae (Diptera) evolve fast and are species-specific. *BMC Evolutionary Biology* **10:** 275.

Ramírez-Mora MA, Buenaventura E, Gómez-P LM, Amat E. 2012. Updated checklist and new records of Calyptratae carrion flies (Diptera, Schizophora) from Valle de Aburrá and other localities in Colombia. *Entomotropica* **27:** 27–35.

Richet R, Blackith RM, Pape T. 2011. *Sarcophaga of France (Diptera: Sarcophagidae)*. Sofia, Moscow: Pensoft Publishers.

Roback SS. 1954. The evolution and taxonomy of the Sarcophaginae (Diptera, Sarcophagidae). *Book III, Illinois Biological Monograph* **23:** 1–181.

Robineau-Desvoidy JB. 1830. Essai sur les myodaires. *Mémoires présentés par divers Savans à l'Académie Royale des Sciences de l'Institut de France (Sciences Mathématiques et Physiques)* **2:** 1–813.

Rohdendorf BB. 1937. *Fam. Sarcophagidae. (P. 1). Fauna USSR, 19*. Moscow, Leningrad: Édition de l'Akadémie des Sciences de l'URSS.

Rohdendorf BB. 1965. Composition of the tribe Sarcophagini (Diptera, Sarcophagidae) in Eurasia. *Entomologicheskoe Obozrenie* **44:** 676–695.

Savage J, Wheeler TA, Wiegmann BM. 2004. Phylogenetic analysis of the genus *Thricops* Rondani (Diptera: Muscidae) based on molecular and morphological characters. *Systematic Entomology* **29:** 395–414.

Sharov AG. 1966. *Basic arthropodan stock with special reference to insects*. New York, Oxford, Toronto: Pergamon Press.

Silva KP, Mello-Patiu CA. 2008. Morfologia comparada da terminália masculina de quatro espécies de *Oxysarcodexia* Townsend, 1917 (Diptera, Sarcophagidae). *Arquivos do Museu Nacional, Rio de Janeiro* **66:** 363–372.

Silva KP, Mello-Patiu CA. 2012. Description of the male of *Lepidodexia* (*Xylocamptopsis*) *teffeensis* (Townsend) (Diptera, Sarcophagidae). *Revista Brasileira de Entomologia* **56:** 15–18.

Sinclair BJ. 2000. Morphology and terminology of Diptera male terminalia. In: Papp L, Darvas B, eds. *Contributions to a manual of Palaearctic Diptera with special reference to flies of economic importance. Volume 1. General and applied Dipterology*. Budapest: Science Herald, 53–74.

Sinclair BJ, Brooks SE, Cumming JM. 2013. Male terminalia of Diptera (Insecta): a review of evolutionary trends, homology and phylogenetic implications. *Insect Systematics & Evolution* **44:** 373–415.

Skevington JH, Yeates DK. 2001. Phylogenetic classification of Eudorylini (Diptera: Pipunculidae). *Systematic Entomology* **26:** 421–452.

Snodgrass RE. 1935. *Principles of insect morphology*. New York: McGraw Hill Book Co.

Soares WF, Mello-Patiu CA. 2010. Two new Neotropical species of the genus *Oxysarcodexia* Townsend (Diptera, Sarcophagidae). *Revista Brasileira de Entomologia* **54:** 72–75.

Solodovnikov AY, Newton AF. 2005. Phylogenetic placement of Arrowinini trib. n. within the subfamily Staphylininae (Coleoptera: Staphylinidae), with revision of the relict South African genus Arrowinus and description of its larva. *Systematic Entomology* **30:** 398–441.

Song H, Bucheli SR. 2009. Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. *Cladistics* **26:** 23–35.

Song ZK, Wang XZ, Liang GQ. 2008. Molecular evolution and phylogenetic utility of the internal transcribed spacer 2 (ITS2) in Calyptratae (Diptera: Brachycera). *Journal of Molecular Evolution* **67:** 448–464.

Soulier-Perkins A. 2001. The phylogeny of the Lophopidae and the impact of sexual selection and coevolutionary sexual conflict. *Cladistics* **17:** 56–78.

Stamper T, Dahlem G, Cookman C, Debry R. 2012. Phylogenetic relationships of flesh flies in the subfamily Sarcophaginae based on three mtDNA fragments (Diptera: Sarcophagidae). *Systematic Entomology* **38:** 35–44.

Sugiyama E, Kano R. 1984. Systematics of the Sarcophaginae of the Oriental region based on the comparative morphology of the male genitalia (Diptera, Sarcophagidae). *Japanese Journal of Sanitary Zoology* **34:** 343–356.

Szpila K, Pape T. 2005. Comparative morphology of the first instar of three species of *Metopia* Meigen (Diptera: Sarcophagidae, Miltogramminae). *Acta Zoologica (Stockholm)* **86:** 119–134.

Szpila K, Richet R, Pape T. 2015. Third instar larvae of flesh flies (Diptera: Sarcophagidae) of forensic importance–critical review of characters and key for European species. *Parasitology Research* **114:** 2279–2289.

Tan SH, Rizman-Idid M, Mohd-Aris E, Kurahashi H, Mohamed Z. 2010. DNA-based characterisation and classification of forensically important flesh flies (Diptera: Sarcophagidae) in Malaysia. *Forensic Science International* **199:** 43–49.

Tibana R, Lopes HS. 1985. On Brazilian Sarcophagidae (Diptera) with description of two new genera and four new species. *Revista Brasileira de Entomologia* **29:** 189–198.

Tibana R, Mello-Patiu CA. 1985a. Sobre as fêmeas de 4 espécies de *Helicobia* Coquillett, 1895 (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **54:** 615–620.

Tibana R, Mello-Patiu CA. 1985b. O sintergito 6 + 7 nas fêmeas de *Oxysarcodexia* Townsend, 1917 (Diptera, Sarcophagidae). *Revista Brasileira de Biologia* **45:** 439–445.

Townsend CHT. 1934. New Neotropical oestromuscoid flies. *Revista de Entomologia* **4:** 201–212, 390–406.

Tuxen SL. 1970. *Taxonomist's glossary of genitalia in insects*. Copenhagen: Scandinavian University Press.

Ulrich H. 1974. Das hypopygium der Dolichopodiden (Diptera): homologie und grundplanmerkmale. *Bonner Zoologische Monographien* **5:** 1–60.

Verves Y. 2000. Rational nomenclature of the male genitalia of Sarcophagidae (Diptera). *International Journal of Dipterological Research* **11:** 117–127.

Wells JD, Pape T, Sperling FA. 2001. DNA-based identification and molecular systematics of forensically important Sarcophagidae (Diptera). *Journal of Forensic Sciences* **46:** 1098–1102.

Whitmore D. 2009. A review of the *Sarcophaga* (*Heteronychia*) (Diptera: Sarcophagidae) of Sardinia. *Zootaxa* **2318:** 566–588.

Whitmore D. 2011. New taxonomic and nomenclatural data on *Sarcophaga* (*Heteronychia*) (Diptera: Sarcophagidae), with description of six new species. *Zootaxa* **2778:** 1–57.

Whitmore D, Pape T, Cerretti P. 2013. Phylogeny of *Heteronychia*: the largest lineage of *Sarcophaga* (Diptera: Sarcophagidae). *Zoological Journal of the Linnean Society* **169:** 604–639.

Willmott KR, Lamas G. 2006. A phylogenetic reassessment of *Hyalenna* Forbes and *Dircenna* Doubleday, with a revision of *Hyalenna* (Lepidoptera: Nymphalidae: Ithomiinae). *Systematic Entomology* **31:** 419–468.

Winterton SL, Yang L, Wiegmann BM, Yeates DK. 2001. Phylogenetic revision of Agapophytinae subf. n. (Diptera: Therevidae) based on molecular and morphological evidence. *Systematic Entomology* **26:** 173–211.

Wong ES, Dahlem GA, Stamper TI, DeBry RW. 2015. Discordance between morphological species identification and mtDNA phylogeny in the flesh fly genus *Ravinia* (Diptera: Sarcophagidae). *Invertebrate Systematics* **29:** 1–11.

Wood DM. 1991. Homology and phylogenetic implications of male genitalia in Diptera; the ground plan. In: Weismann L, Országh I, Pont AC, eds. *Proceedings of the Second International Congress of Dipterology*. The Hague, Netherlands: SPB Academic Publishing, 255–284.

Yepes-Gaurisas D, Sánchez-Rodríguez JD, de Mello-Patiu CA, Wolff Echeverri M. 2013. Synanthropy of sarcophagidae (Diptera) in La Pintada, Antioquia-Colombia. *Revista de Biologia Tropical* **61:** 1275–1287.

Yoshizawa K, Johnson KP. 2006. Morphology of male genitalia in lice and their relatives and phylogenetic implications. *Systematic Entomology* **31:** 350–361.

Zerene Systems LLC. 2014. *Zerene Stacker Software*.

Zhang M, Buenaventura E, Pape T, Zhang D. 2016. Molecules and morphology unite *Sarcophaga* (*Stackelbergeola*) Rohdendorf and *S.* (*Rohdendorfisca*) Grunin within megadiverse *Sarcophaga* Meigen (*sensu lato*) (Diptera, Sarcophagidae). *Invertebrate Systematics* **30:** 463–478.

Zhang M, Zhang D. 2013. DNA taxonomy of some *Sarcophaga* species based on the mitochondrial COI gene fragment. *Chinese Journal of Applied Entomology* **50:** 71–85.

Zhang D, Zhang M, Pape T, Gu CW, Wu W. 2013. *Sarcophaga* (*Hoa*)*flexuosa* Ho (Diptera: Sarcophagidae): association of sexes using morphological and molecular approaches, and a redefinition of *Hoa* Rohdendorf. *Zootaxa* **3670:** 71–79.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Taxon sampling. List of species studied.
Table S2. Data matrix. Matrix of morphological characters.
File S1. Character definitions. Morphological characters for phylogenetic analysis.
File S2. Nomenclatural acts. Summary of nomenclatural acts herewith proposed or implied by the new synonymies.