# MORPHOLOGY AND PHYLOGENY OF SARCOPHAGINAE AND THE SYSTEMATICS OF *NEOBELLIERIA* (DIPTERA: SARCOPHAGIDAE)

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# ABSTRACT

A comprehensive Scanning Electron Microscopy (SEM) study of the distal portion of the male phallus (acrophallus), in 42 species of the flesh-fly subfamily Sarcophaginae, was undertaken to clarify its morphology, to homologize its parts and to define male genital characters. In addition, to better understand the phylogenetic implications of the male genitalia, the generic relationships of 19 sarcophagine genera were tested using a parsimony analysis of 72 examplar species, based on 41 male genitalic characters and 33 other morphological characters of larvae, males and females. The monophyly of *Ravinia* Robineau-Desvoidy, *Oxysarcodexia* Townsend, *Titanogrypa* Townsend, *Helicobia* Coquillett, *Lepidodexia* Brauer & Bergenstamm and *Sarcophaga* s.l. Meigen was supported, but *Blaesoxipha* Loew appeared paraphyletic. The genus *Helicobia* was nested within *Sarcophaga* and the subgenus *S. (Neobellieria)* Blanchard was found to be polyphyletic. The analysis also supported a sister-group relationship between the type species of *S.* (*Neobellieria*) and the subgenus *S.* (*Tolucamyia*) Dodge. Based on that cladistic analysis, *S.* (*Tolucamyia*) was synonymized with *S.* (*Neobellieria*) which was redefined to include the five species of the *S.* (*N.*) *polistensis* group, those previously assigned to *S.* (*Tolucamyia*) and one new species. To accommodate the four species of the *S. (N.) semimarginalis* Hall group and four new species, a new subgenus, *S.* (*Bulbostyla*) Giroux & Wheeler, was erected. Finally, *Robackina* Lopes was reinstated as a subgenus of *Sarcophaga* to accommodate the single species *S. triplasia* Wulp.

# RÉSUMÉ

Une étude détaillée de la partie distale du phallus (l'acrophallus) fut entreprise chez 42 espèces de Sarcophaginae, en utilisant la microscopie électronique à balayage (MEB). À l'aide des images produites, la morphologie des acrophallus fut étudiée et les structures homologues identifiées. Des caractères génitaux mâles furent également définis. Afin de vérifier l'implication phylogénétique des génitalia mâles, les relations de 19 genres de Sarcophaginae furent testées à l'aide de la méthode de parcimonie. Au total, 72 espèces exemplaires, 41 caractères génitaux mâles ainsi que 33 autres caractères morphologiques provenant des larves, des mâles et des femelles furent utilisés. La monophylie des genres *Ravinia* Robineau-Desvoidy, *Oxysarcodexia* Townsend, *Titanogrypa* Townsend, *Helicobia* Coquillett, *Lepidodexia* Brauer & Bergenstamm et *Sarcophaga* s.l. Meigen fut confirmée mais le genre *Blaesoxipha* Loew est apparu paraphylétique. Le genre *Helicobia* s'est retrouvé à l'intérieur du genre *Sarcophaga* et le sous-genre *S. (Neobellieria)* Blanchard est apparu polyphylétique. L'analyse a aussi confirmé une relation de groupe-frères entre l'espèce type de *S.* (*Neobellieria*) et le sous-genre *S.* (*Tolucamyia*) Dodge. En se basant sur la phylogénie obtenue, *S.* (*Tolucamyia*) est devenu synonyme de *S.* (*Neobellieria*) lequel fut redéfini pour inclure les cinq espèces du groupe de *S.* (*N.*) *polistensis*, celles du sous-genre *S.* (*Tolucamyia*) et une nouvelle espèce. Afin de classifier les quatre espèces du group de *S. (N.) semimarginalis* Hall et quatre nouvelles espèces le nouveau sous-genre, *S.* (*Bulbostyla*) Giroux & Wheeler, fut érigé. Finallement, *Robackina* Lopes fut rétabli en tant que sous-genre de *Sarcophaga* pour permettre la classification de l'espèce *S. triplasia* Wulp.

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# PREFACE

This thesis is composed of six chapters, three of which are original manuscripts that have been or will be submitted for publication in refereed journals.

## Chapter 1

This chapter consists of a general introduction to the thesis and a literature review of the current knowledge and previous systematics research on sarcophagid flies.

## Chapter 2

This chapter is a manuscript to be submitted to *Zoological Journal of the Linnean Society*: Giroux, M., Pape, T. & T. A. Wheeler. Morphology and phylogenetic implications of the acrophallus in the flesh-fly subfamily Sarcophaginae (Diptera: Sarcophagidae).

## Chapter 3

This chapter is a manuscript submitted to *Annals of the Entomological Society of America*:

Giroux, M. & T. A. Wheeler. 2007. Systematics and phylogeny of the subgenus *Sarcophaga* (*Neobellieria)* Blanchard (Diptera: Sarcophagidae).

## Chapter 4

This chapter is a manuscript in preparation for submission: Giroux, M. and T. A. Wheeler. Systematics of *Bulbostyla,* a new subgenus of *Sarcophaga* (Diptera: Sarcophagidae).

## Chapter 5

This chapter addresses the status of *Sarcophaga triplasia* Wulp and the subgenus *Robackina* Lopes (Diptera: Sarcophagidae).

## Chapter 6

This chapter is a general discussion and conclusion.

## CONTRIBUTION OF AUTHORS

Marjolaine Giroux designed the research for the four manuscripts and carried out specimen preparation, identification, description, illustrations and analysis. She also performed the Scanning Electron Microscopy (SEM) work. Dr. Terry Wheeler supervised the thesis research and edited all manuscripts. He also provided laboratory space and equipment as well as financial support. Dr. Thomas Pape supervised the SEM work and guided M. Giroux within the theoretical and practical approaches of her thesis. He also provided advice about taxonomy and systematics of Sarcophagidae.

# CHAPTER 1. INTRODUCTION AND LITERATURE REVIEW

The Diptera is one of the four largest orders of insects (Stork, 1997; Brown 2005), with more than 125,000 described species worldwide (Brown, 2005). However, many species of flies are still undescribed and much remains to be learned about Diptera at the most fundamental level (Woodley, 1999; Brown, 2005). This is the case with the family Sarcophagidae, or flesh flies, with many species remaining undescribed and with their biological habits largely unknown (Dahlem, 1991; Pape, 1996).

With about 2500 described species worldwide (Pape, 1996; Povolný & Verves 1997), the Sarcophagidae is the second most speciose group of Oestroidea, which also includes the Tachinidae (> 8000 described species worldwide,Wood, 1987a), Calliphoridae (1000 described species worldwide, Shewell, 1987; Rognes, 1997) and two other small families: Oestridae (> 150 described species worldwide, Wood,1987b) , and Rhinophoridae (142 described species, Pape, unpubl.).

The publication of Pape's (1996) world catalogue of Sarcophagidae has provided a useful framework to study the biology and the systematics of these flies. This publication also defined the current magnitude of sarcophagid diversity on a worldwide scale. However, on a regional level, the sarcophagid fauna remains poorly documented. For example, McAlpine *et al.* (1979) recorded 85 species of Sarcophagidae from Canada but Dahlem (2001) listed 120 described species from the country and more probably remain to be described or recorded.

# THE FAMILY SARCOPHAGIDAE

## Description

Sarcophagidae, or flesh flies, are robust grey and black flies, ranging from 2.5 mm to 20 mm in length. They possess a scutum that usually has three dark stripes; a concave subscutellum and an abdomen that is generally checkered, striped, banded, or spotted (Shewell 1987, Pape 1996, 1998). The family is divided into three easily recognizable subfamilies (Pape, 1990, 1996).

Miltogramminae (> 600 described species, Pape, 1998b) are small to medium-sized species with large eyes, broad lower calypteres and an oval or slightly tapering abdomen (Pape 1996). They usually possess a bare or micropubescent arista; a scutum that is almost unicolorous or with indistinct stripes; only two strong notopleural bristles and a suture-like depression, the coxopleural streak, between the meron and the katepimeron (McAlpine 1981; Shewell, 1987; Pape, 1998). The also have postocular setae not or at most slightly alternating in size and the antennal scape flush with the lunule (Pape, 1998a).

Paramacronychiinae (> 84 described species) are generally medium-sized species with the arista showing various degrees of pubescence or plumosity; with three distinct stripes on the scutum; with only two strong notopleural bristles and with a coxopleural streak (Pape, 1996, 1998a). Most species are densely covered with greyish or light brown microtomentum and possess a more or less distinct abdominal pattern of a median stripe and dark lateral spots (Pape, 1996). The male terminalia usually protrude and tergite 6 is fused to syntergosternite 7+8 at a more or less right angle (Pape, 1992; 1998a).

Sarcophaginae (>1800 described species) are mostly large robust species, generally with a uniform colour pattern: a grey thorax with three or more blackish stripes and a checkered abdomen (Pape, 1996). Species of this subfamily also have plumose arista, a fused meron and katepimeron (coxopleural streak absent), a notopleuron usually with two strong primary bristles alternating with two semi-strong subprimary bristles and the hind coxa setose posteriorly (McAlpine, 1981; Pape, 1998a). In contrast to species of the other two subfamilies, the male abdominal sternites 3-4 of sarcophagines are exposed and overlap the margins of the corresponding tergites (Pape, 1998a).

Larvae of Sarcophagidae are white to yellowish, usually elongate cylindrical, pointed at the anterior end and truncate posteriorly (Ferrar, 1987; Shewell, 1987; Szpila & Pape, 2005). The third instar of nearly all species of Sarcophagidae has posterior spiracles within a deep cavity, three more or less vertical and parallel slits, and an incomplete peritreme around the slits (Ferrar, 1987; Dahlem, 1991).

### Distribution

Sarcophagids are cosmopolitan in distribution although their numbers decrease rapidly with latitude, with few subarctic species and none living in the treeless tundra (Shewell, 1987; Pape, 1996). Their diversity is markedly concentrated in tropical and warm temperate, and island faunas are generally very depauperate (Shewell, 1987; Pape, 1996). There is a major deviation between Sarcophagidae diversity of the New World and the Old World, with some marked differences between the subfamilies Miltogramminae and Sarcophaginae (Pape, 1990; 1996; 1998a). Miltogramminae show peaks of diversity in arid parts of Africa and Asia and have a relatively low number of Neotropical species (Pape, 1996; 1998a). In contrast, the Sarcophaginae have their largest concentration of species in the Neotropical region (Shewell, 1987; Pape, 1996; 1998a). Pape (1996; 1998a) hypothesised that the Sarcophaginae arose in the New World with a number of dispersal events bringing New World lineages of *Blaesoxipha* Loew, *Ravinia* Robineau-Desvoidy, and *Sarcophaga* Meigen via a Beringian corridor. Roback (1954) also suggested that Central America represents the area of origin for his tribe Sarcophagini with the ancestral species apparently spread into North and South America. Also, according to Pape, (1998a), nearly 22 Holarctic species are recognized. Only two fossil sarcophagids have been recorded but their identity needs verification.

### Biology

Adult Sarcophagidae can often be observed basking in the sun on foliage, open ground and the sides of buildings. They have pad-like mouthparts for imbibing liquids like nectar (Shewell, 1987; Pape, 1996), honeydew, tree sap and juices from damaged fruits (Downes, 1965). All females are viviparous or ovoviviparous and retain their eggs within a bipouched uterus before depositing first instar larvae on the larval medium or host (Shewell, 1987; Dahlem, 1991). In contrast to their common name (flesh-flies) very few larvae exploit larger vertebrate carrion as a food resource (Dahlem,1991). Many of them show a strong trend for saprophagy, mostly in dead insects and other invertebrates or are parasitoids of live insects (Ferrar, 1987).

The vast majority of Miltogramminae are cleptoparasites of solitary bees (e.g. Andrenidae, Anthophoridae, Halictidae) and wasps (mostly Sphecidae) (Ferrar, 1987). In many cases, the larva eats the host egg or larva (or lets it die from starvation) and feeds on the stored food (arthropod prey or pollen balls) (Ferrar, 1987; Shewell, 1987; Pape, 1998). Several strategies are used by adult miltogrammines to locate their hosts, for example, they trail sphecid wasp to their nest (satellite flies) or search directly for nest entrances (Ferrar, 1987; Pape, 1996). Many host/fly records are listed in Spofford & Kurczewski (1990); Ferrar (1987); Krombein *et al.* (1979) and Allen (1926).

The two other subfamilies display a multitude of life habits. In the Paramacronychiinae, species are mostly predators or parasitoids of Lepidoptera, Orthoptera or Hymenoptera (Pape, 1996, 1998a). Some species of *Wohlfahrtia* Brauer & Bergenstamm also cause myiasis in mammals (Lewis, 1947; Pape, 1996, 1998a; Goddard, 2000). In the Sarcophaginae, members of *Ravinia* and *Oxysarcodexia* Townsend are primarily coprophagous in a wide variety of mammalian dung (Dahlem, 1989; Pape, 1996) and the species of *Fletcherimyia* Townsend are known to feed on trapped insects in pitchers of *Sarracenia* (Pape, 1990; Dahlem & Naczi, 2006). Numerous species of *Blaesoxipha* are parasitoids of Orthoptera (Downes, 1965; Pape, 1994; Miura, 2003) and some species of *Boettcheria* Parker have been reported as parasitoids of adult scarab beetles or of a variety of Lepidoptera (Dahlem & Downes, 1996). According to Pape (1996), the majority of species within the large genus *Sarcophaga* may be scavengers of dead insects, snails or smaller vertebrates. Additional information about breeding habits of Sarcophaginae is listed in Ferrar (1987), Dahlem (1991) and Pape (1996).

## Economic importance

Sarcophagidae are mostly beneficial insects. Adults, especially males, visit flowers (Shewell, 1987; Pape, 1996; Lehnebach & Riveros 2003) and some species act as pollinators (Bänziger & Pape, 2004). Some species, parasites of grasshoppers and locusts, are probably of significance as biological control agents (Ferrar, 1987). The species *Sarcophaga aldrichi* Parker is a common parasitoid of many pest Lepidoptera including the forest tent caterpillar (*Malacosoma disstria* Hübner) and the spruce budworm

(*Choristoneura fumiferana* (Clemens) (Ferrar, 1987; Dahlem, 1991). The non-synanthropic species of *Ravinia* are facultative predators, or competitors, of pestiferous dung-inhabiting flies on cattle feedlots (Pickens, 1981; O'Hara *et al.*, 2000) and are probably the most important decomposers of dog dung in urban communities (Dahlem, 1989). According to Bartosova *et al.* (1997), flesh flies also represent a suitable insect for monitoring pollutant groups (e.g. heavy metals, residues of organochlorine pesticides and polychlorinated biphenyls) in various habitats. In this sense, Sarcophagidae used as forensic indicators, i.e. to estimate postmortem intervals (Byrd & Castner, 2001), can also be used for the detection of various drugs and/or toxins present in the remains (Goff & Lord, 1994).

On the other hand, a few species are harmful to humans and livestock. This is the case for the North American larvae of *Wohlfahrtia vigil* (Walker), which often causes myiasis in humans and young mammals (Dahlem, 1991; Goddard, 2000). A few species have also been reported to be associated with unsanitary conditions and involved in dissemination of human enteropathogens in the environment (e.g., causative agents of gastrointestinal diseases) (Graczyk *et al.*, 2005).

## Systematic position and monophyly

Sarcophagidae are currently classified in the Tachinidae family-group, which also includes the Tachinidae, Rhinophoridae, Oestridae and Calliphoridae (Pape, 1992). These families are united by several characters including the possession of a vertical row of bristles on the meron (McAlpine, 1989; Pape, 1992). Pape (1992, 1996) has corroborated the monophyly of the Sarcophagidae by several autapomorphic character states. He considered the Tachinidae the most probable sister group to the Sarcophagidae although a molecular analysis (Nirmala *et al.*, 2001) indicated that Sarcophagidae are related to Calliphoridae. Pape's (1996) classification basically followed Downes (1955, 1965) and Shewell (1987). However, Downes (1955, 1965) and Shewell (1987) combined the tribes Miltogrammini and Paramacronychiini in a single subfamily (Miltogramminae) that they considered a sister group of Sarcophaginae (Shewell, 1987; Pape, 1998). Pape (1992) considered instead a probable sister-group relationship between the Paramacronychiinae and the Sarcophaginae. The monophyly of the Sarcophaginae is also very well corroborated (Pape, 1996).

Below the subfamily level, because of methodological and conceptual differences among systematists and the remarkable uniformity in external morphology of the species, there is a lack of consensus on the limits of genera (Pape, 1996). For example, Pape (1996) recognized 108 valid genera and Shewell (1987) nearly 400. Shewell (1987) adopted a concept of very small genera. For example, he included the 79 Nearctic species previously listed in the genus *Sarcophaga* by Downes (1965) in 14 different genera, without recognizing the genus *Sarcophaga*. In contrast, Pape (1996) divided some of the larger genera into a number of possibly monophyletic subgenera. For example, the 84 Nearctic species of the genus *Sarcophaga* are listed in 16 subgenera (Pape, 1996). Whether authors prefer to treat sarcophagid taxa at the generic level or at the subgeneric level is entirely subjective. However, contrary to Shewell (1987), Pape (1996) provided generic definitions, based on a list of character states belonging to what he considered as the hypothetical groundplan, to support his phylogenetic hypotheses.

To date, the monophyly of genera in the Miltogramminae and Paramacronychiinae has been reasonably well corroborated (Pape, 1996, 1998b). For the Sarcophaginae, however, there are several competing generic classifications (Downes, 1965; Lopes, 1969, 1982b; Verves, 1986; Shewell, 1987; Pape, 1996; Povolný & Verves, 1997); the classification adopted here is that of Pape (1996). Within this classification, generic and subgeneric concepts are still largely preliminary and more thorough character analyses are needed to corroborate monophyletic groups (Pape, 1990; 1996; 1998; Mello-Patiu & Pape, 2000). However, Pape's generic delimitation is gradually being tested and supported (Pape, 1998) and some of the genera have been recently revised: *Blaesoxipha* (Pape, 1994); *Boettcheria* (Dahlem & Downes, 1996); *Dexosarcophaga* Townsend (Mello-Patiu, 2002). *Fletcherimyia* (Dahlem & Naczi, 2006) and *Engelimyia* Lopes (Pape & Mello-Patiu, 2006). The taxonomy published in the catalogue of Pape (1996) has also been adopted by several authors including Blackith *et al.* (1997), O'Hara *et al.* (2000) and Dahlem (2001), although others do not recognize it (Povolný and Verves,1997; Peris *et al.*, 1998; Kano *et al.*,1999; Kano and Kurahashi, 2000; Verves, 2001; Lehrer, 2002).

## Objectives

As for many groups of Diptera, modern phylogenetic techniques have been rarely applied to test competing generic classifications of the Sarcophaginae. Therefore, the main purpose of this thesis was to cladistically test the monophyly of some genera and subgenera recognized by Pape (1996). To do so, the thesis has been divided into two distinct but related studies.

In the first study (chapter 2) we predicted that the complex structure of the male genitalia, particularly the acrophallus, in Sarcophaginae should provide a suite of phylogenetically informative characters in determining generic relationships within the subfamily. Consequently, a comprehensive Scanning Electron Microscopy (SEM) study of the male acrophallus was undertaken to clarify its morphology, to homologize its parts and to define male genital characters. Those characters were then used, along with other genitalic and non-genitalic morphological characters of adult males and females, as well as larval characters, to construct a hypothesis on phylogenetic relationships between selected genera and subgenera of Sarcophaginae.

In the second study (chapters 3 to 5) a revision of the subgenus *Sarcophaga* (*Neobellieria*) Blanchard was undertaken. Based on the cladistic analysis in chapter 2, it was found that *S.* (*Neobellieria*) was polyphyletic and that its ten species comprised three separate clades. The analysis also supported a sister-group relationship between the type species of S. (*Neobellieria*) and another subgenus, *S.* (*Tolucamyia*) Dodge. Therefore, in chapter 3, the subgenus *S.* (*Neobellieria*) was redefined to include the five species of the *S.* (*N.*) *polistensis* Hall group, the species previously assigned to *S.* (*Tolucamyia*) and one new species. In chapter 4, a new subgenus, *Sarcophaga* (*Bulbostyla*) Giroux & Wheeler, was erected to accommodate the four species of the *S. (N.) semimarginalis* Hall group and four new species. Finally, in chapter 5, the subgenus *Sarcophaga* (*Robackina*) Lopes was reinstated as a subgenus of *Sarcophaga* Meigen to accommodate the single species *Sarcophaga triplasia* Wulp.

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# CHAPTER 2. Morphology and phylogenetic implications of the acrophallus in the flesh-fly subfamily Sarcophaginae (Diptera: Sarcophagidae)

## ABSTRACT

The morphology of the acrophallus, the distal portion of the male phallus, was studied in 42 species of the flesh-fly subfamily Sarcophaginae, using Scanning Electron Microscopy. Terms used to describe the male genitalia were updated based on new interpretations of their homology. Male genitalic characters, combined with other morphological characters of adult males and females and larvae, were used to construct a preliminary phylogeny of 72 exemplar species representing 56 genera and subgenera of Sarcophaginae, as a foundation to a phylogeny of the subfamily. The monophyly of the subfamily was supported, and some generic-level sister group relationships proposed in the literature, but without previous cladistic analyses, were also supported. The genus *Blaesoxipha* Loew may not be monophyletic as currently recognized. The genus *Helicobia* is synonymized with *Sarcophaga* and treated as a subgenus of the latter. The *Sarcophaga* subgenera *Neobellieria* and *Mehria* were not monophyletic. Many of the clades in the analysis were supported primarily or exclusively by male genitalic character states, highlighting the importance of the male genitalia as a source of morphological characters for sarcophagid phylogeny.

**ADDITIONAL KEYWORDS:** cladistics – classification - male genitalia – phylogeny – scanning electron microscopy – systematics.

## INTRODUCTION

While molecular characters are now widely used to reconstruct the phylogeny of Diptera and to test existing phylogenetic hypotheses, several recent studies have also used novel morphological characters with varying degrees of success (Yeates & Wiegmann, 2005), evidence that these character sets are far from exhausted in Diptera systematics. This is especially true of morphological characters that are difficult to study using conventional methods such as light microscopy, or structures for which homology is difficult to establish between taxa. Such characters are a rich potential source of phylogenetic data that still remains to be explored.

The flesh fly subfamily Sarcophaginae is a well-supported monophyletic group that includes about 1800 described species worldwide, divided into 51 genera (Pape, 1992, 1996). Although flies in this subfamily vary greatly in size, they are externally uniform in appearance. In contrast, the male terminalia, especially the phallus, are highly distinctive at the species level and have long been used in species recognition (e.g., Pandellé, 1896; Aldrich, 1916; Patton & Wainwright, 1935; Roback, 1954; Pape, 1987; Dahlem & Downes, 1996; Povolný & Verves, 1997; Mello-Patiu & Pape, 2000).

The male terminalia also provide important characters for phylogenetic reconstruction (Roback, 1954; Pape, 1994, 1998; Blackith *et al*, 1997). However, because sarcophagine male terminalia are highly complex, genitalic characters used in generic diagnoses are often inconsistently defined or with obscure homologies.

Roback (1954) published a detailed morphological study of sarcophagine terminalia and introduced new terms for the phallic structures. He also defined generic relationships within the Sarcophaginae, based primarily on homologies between structures in the male genitalia. Although most of Roback's phylogenetic hypotheses have not been tested cladistically and some aspects of his classification were rejected by subsequent authors (Downes, 1955; Lopes, 1956; Pape, 1994), his work was a major contribution to sarcophagine morphology and many of his terms are still used (e.g., Dahlem & Downes, 1996; Mello-Patiu & Pape, 2000).

Pape (1987, 1994), Povolný & Verves (1997), Verves (2000) and Lehrer (2002b) reviewed and updated the morphology of sarcophagine male genitalia. Nevertheless, the homology of some structures remains ambiguous from genus to genus, which hinders their use in phylogenetic analyses. This is particularly true of the structures that make up the genital opening. In higher Diptera, the acrophallus is the part of the distiphallus bearing the phallotreme (Sinclair, 2000) and provides a reliable landmark (the sperm opening) to homologize genitalia between genera. Because of the complexity and the high degree of sclerotization of the phallus, Scanning Electron Microscopy (SEM) is the most feasible approach for studying its structure. Other than a few studies of selected taxa (e.g., Leite & Lopes, 1989; Lopes & Leite, 1990, 1991) SEM has not been used to homologize genitalic structures across a range of sarcophagine genera.

Because of the complexity of the male genitalia, particularly the acrophallus, in Sarcophaginae, and because of the importance of the male genitalia in species recognition, it is reasonable to predict that these structures provide phylogenetically informative characters in determining generic relationships within the subfamily. There are several competing generic classifications within the Sarcophaginae (Downes, 1965; Lopes, 1969, 1982b; Verves, 1986; Shewell, 1987; Povolný & Verves, 1997), most of which were based on regional faunas and were not tested by cladistic analyses. Pape's (1996) classification included all described species of the family but his concept of very large genera, sometimes with many subgenera, is not shared by most other researchers in the Sarcophagidae (e.g. Povolný and Verves, 1997; Peris *et al.*, 1998; Kano *et al.*, 1999; Kano and Kurahashi, 2000; Verves, 2001; Lehrer, 2002a). To date, there have been few explicit phylogenetic analyses of sarcophagid genera or subgenera. Pape (1994) tested the monophyly of *Blaesoxipha* Loew, but also investigated the phylogenetic relationships of ten sarcophagine genera based on a ground-plan scoring approach (Yeates, 1995). Within the large genus *Sarcophaga* Meigen *s.l.* only the subgenus *Helicophagella* Enderlein has been revised using phylogenetic and phenetic analyses; Blackith *et al.* (1997) analysed genitalic and non-genitalic character sets separately and found that male genitalic characters were more informative for phylogenetic relationships than external morphological characters.

Given that the male genitalia should provide an informative suite of characters for resolving phylogenetic relationships between sarcophagine genera and subgenera, and that explicit cladistic analyses are required to resolve the competing classifications within the subfamily, this study had two primary objectives. The first objective was to conduct a comprehensive SEM study of the sarcophagine phallus to homologize structures across genera, to provide a consistent terminology reflecting that homology, and to assess the potential of those structures in defining genera and subgenera and reconstructing their phylogeny. The second objective was to use those characters, along with other genitalic and non-genitalic morphological characters of adult males and females, as well as larval characters, to construct a hypothesis on phylogenetic relationships among selected genera and subgenera of Sarcophaginae.

## MATERIALS AND METHODS

**Sources of Material and Selection of Taxa.** The study was based on material housed in the Zoological Museum, University of Copenhagen, Denmark (ZMUC), the Canadian National Collection of Insects, Ottawa, ON, Canada (CNC) and the Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM). Given the large number of taxa in the subfamily, an exemplar approach (Yeates, 1995) was used.

For the SEM study, 45 species, representing one genus of Miltogramminae, two genera of Paramacronychiinae and 19 genera of Sarcophaginae were selected. The choice of genera was based on ensuring broad representation across the subfamily, inclusion of some genera whose status relative to other related genera was questionable, and the availability of specimens. For most genera and subgenera, a single species (the type species where possible) was selected (Appendix 1). Multiple species of *Oxysarcodexia* Townsend, *Peckia* Robineau-Desvoidy, *Titanogrypa* Townsend, *Lepidodexia* Brauer & Bergenstamm, *Blaesoxipha, Helicobia* Coquillett and *Ravinia* Robineau-Desvoidy were included because of high morphological variability of the selected species within each genus. Because of the species richness of the genus *Sarcophaga* a broad sampling of subgenera and species was not feasible. Instead, we restricted the sampling to nine species, representing eight subgenera.

The cladistic analysis was based on 72 ingroup exemplar species (Appendix 1) representing 19 sarcophagine genera. The number of species used was the same as in the SEM study for most genera except *Lepidodexia* and *Sarcophaga*. Three additional species of *Lepidodexia* subgenus *Johnsonia* Coquillett were added because of the questionable limits of this genus (Pape, 1996). Because of the size of the genus *Sarcophaga* and the variation in phallic structure, 31 subgenera, as well as the unplaced species *S. aldrichi* Parker, were included. Type species of subgenera were selected where possible (Appendix 1) and all biogeographic regions were represented. Two subgenera, *Neobellieria* Blanchard and *Mehria* Enderlein were represented by multiple species (four and two, respectively) because their monophyly is the focus of a related study by the senior author.

To address intraspecific variability in males, at least three specimens of each species were examined except for *Lepidodexia (Notochaeta) woodi* (Lopes), *Sarcophaga (Kramerea) schuetzei* Kramer, *S. (Phallanthisca) magensi* Kano (two specimens each), *Oxyvinia xanthophora* (Schiner) and *S. (Sinonipponia) hervebazini* Ho (one specimen each). Females of 19 species were not available for examination (see characters 31-33, Appendix 1).

Because Paramacronychiinae is the probable sister-group of Sarcophaginae and Miltogramminae is the probable sister-group of these two (Pape, 1992, 1996), *Brachicoma devia* (Fallén), *Sarcophila* sp. and *Wohlfahrtia vigil* (Walker) (Paramacronychiinae) and *Macronychia aurata* (Coquillett) (Miltogramminae) were included as outgroups in the analysis.

**Preparation and examination of terminalia and larvae.** The abdomen was removed from pinned male specimens, placed in hot 10% KOH for about five minutes, and transferred to glycerin, where the postabdominal structures, including sternite 5, were separated from the abdomen by cutting the membrane between sternite 4 and 5, and the epandrium was then separated from syntergosternite 7+8. If necessary, the terminalia were returned to hot 10% KOH for about 2 minutes for further clearing. The epandrium and hypandrium were usually separated to facilitate examination of the phallus. Female terminalia were separated from the abdomen by cutting the membrane between segments 4 and 5 and were cleared in the same way as males.

All structures were rinsed twice in water, once in 70% ethanol, placed in 20% acetic acid for 5-8 minutes and washed again in 70% ethanol. Once dried, the male abdomen was glued into its original position on the pinned specimen. Terminalia were examined using a compound or a dissecting microscope and illustrated with the aid of a drawing tube, and subsequently stored in glycerin in a plastic microvial pinned below the specimen.

Larvae were removed from pinned females when the latter were dissected, examined in glycerin and then stored in glycerin in a microvial pinned below the specimen. Some larval character states used in the study were taken from the literature.

**Preparation of phallic structures for SEM.** Terminalia were dissected as described above except that the phallus was dissected in 70% ethanol instead of glycerin. The phallus was separated from the hypandrium, pregonite and postgonite and dried in two successive changes of 70% ethanol, followed by two changes of 100% ethanol. In species with a more membranous phallus (*Macronychia aurata*, *Engelimyia inops* (Walker), *Helicobia surrubea* (Wulp)), specimens were critical-point dried, to keep the phallus inflated for study. Each dried phallus was glued to an aluminum stub with double-sided carbon adhesive tape and coated with 20nm of platinum in a high resolution fine coater (Jeol JFC-2300HR). The specimens were examined using a Jeol-JSM-6335F Field emission SEM at the Zoological Museum of Copenhagen, except for specimens in Figs. 6a-c, 8f, h, 10a-c and 18c, f, g, which were gold-coated and examined with a Philips

XL30 Environmental SEM at the Electron Microscope Unit of Agriculture and Agri-Food Canada, Ottawa, Ontario.

Usually, two or three phalli per species were examined. One phallus was kept intact and the others were dissected to make the acrophallus more visible. In species for which only one male specimen was available the coated phallus was first examined intact and then dissected on the stub before being recoated and re-examined.

**Morphology and terminology.** Terminology for adult structures, except the male terminalia, follows McAlpine (1981). Larval terminology follows Szpila & Pape (2005). The complex structure of the sarcophagine male terminalia has given rise to various interpretations of genital homology and, consequently, many workers on Sarcophagidae have defined their own terms or have modified those of earlier authors; these systems of terminology are not always consistent with terms applied to other families of Diptera. We follow the revised epandrial hypothesis summarized by Cumming *et al.* (1995) and Sinclair (2000) (Figs. 1-3).

We define the acrophallus as the division of the distiphallus bearing the phallotreme or sperm exit, and sometimes clothed in small denticles (Sinclair, 2000). The sarcophagine acrophallus comprises the median and lateral styli. To homologise the styli across the selected species, the phallotreme and the microserrations, present on the acrophallus in the groundplan of Miltogramminae and Calliphoridae, were used as landmarks. In addition to some changes in interpretation of homology, the variation in the shape of the vesica, harpes and juxta and the difficulty in delimiting them in some species led us to modify Roback's (1954) original definitions; these changes are outlined in Results.

**Character Matrix and Cladistic Analysis**. Seventy-four characters (63 binary, 11 multistate) were included in the analysis, including 3 larval characters, 27 external adult characters, 41 male genitalic characters and 3 female genitalic characters (Appendix 2). The matrix was compiled using Mesquite version 1.05 (Maddison & Maddison, 2004).

Phylogenetic analyses were performed using the program TNT version 1.0, 2005 (Goloboff et al., 2003). Unweighted and *a posteriori* implied weighting analyses ($k = 3$) (Goloboff, 1993) were conducted under the parsimony criterion. Multistate characters were treated as non-additive. A heuristic search, using tree-bisection-reconnection (TBR) branch swapping, was conducted in both unweighted and weighted analyses. TBR branch swapping was conducted on 1000 random addition sequences, with 10 trees saved per replicate (analyses using different numbers of trees did not provide more conclusive results). Branches were collapsed if the maximum branch length was zero.

The relative degree of support for individual nodes was assessed with bootstrap values calculated from 3000 bootstrap replicates. Relative Bremer support percentages (Goloboff & Farris, 2001) were also used to estimate support for groups recovered in the weighted analysis. Under weighting methods such as implied weighting (Goloboff, 1993), Bremer support may be difficult to compare (Bremer, 1994; Goloboff and Farris, 2001), but relative support is directly comparable (Goloboff and Farris, 2001). We searched for suboptimal trees that were 1-24 steps longer than the optimal trees, and a sample of 40,000 suboptimal trees (1000 random addition replicates X 40 trees saved per replicate) was used for calculating relative Bremer support values.

## RESULTS AND DISCUSSION

## Revised genitalic homologies

The SEM study of a broad sample of genera allowed us to reassess some of Roback's (1954) terminology and homology decisions in the male genitalia. In some cases, these revised interpretations provided additional support for monophyletic taxa within the ingroup.

**Juxta.** Roback (1954) defined the juxta as a ventral appendage of the "corpus" (see phallic tube, below). However, in some taxa, there is no clear demarcation between the juxta and the phallic tube. Thus, Roback referred to species with "free" or "fused" juxta, with intermediates between the two states. We treated the base of the median stylus as a landmark to delimit the site of origin of the juxta and we defined the juxta as any apical extension of the dorsal side of the distiphallus arising from the base of the median stylus. The major phylogenetic implication is that all Paramacronychiinae and Sarcophaginae have a juxta (character state 53:1), whereas Roback considered it absent in Paramacronychiinae and some Sarcophaginae.

**Vesica.** We define the vesica as a lobe-like structure protruding outwards from the anterior surface and originating relatively close to the base of the distiphallus.

**Harpes.** Roback (1954) defined the harpes as a paired, anterodorsal extension of the "corpus" that usually arises at the anterodorsal corners of the "sclerous corpus" (see below) and runs ventromedially from it. We define the harpes as paired, sclerotized processes arising from the anterior margin of the phallic tube distal to the vesica and spreading ventromedially over the base of the lateral styli. As defined by Roback, harpes were present only in his *Sarcophaga*-group (a subset of subgenera currently assigned to *Sarcophaga*) and in *Peckia*. In our definition, harpes are present in *Lepidodexia* and *Sarcophaga*, although their status is not always clear in some *Helicobia* and *Lepidodexia*.

**Phallic tube.** This is the structure that Roback (1954) called the "corpus". He defined the corpus as the tubular basal portion of the phallus and further divided it into the "sclerous corpus" and "membranous corpus". Povolný and Verves (1997) considered the corpus *sensu* Roback equivalent to the distiphallus. Roback (1954) also recognized a structure that he referred to as a phallic tube; however, that structure is an anteroventral prolongation of the membranous corpus present in a small number of Sarcophaginae. It is not homologous with the phallic tube as we define it.

**Capitis.** Roback (1954) defined the capitis as a cap or helmet-like structure on the median process of his *Sarcophaga* group and *Helicobia*. However, this structure is simply a prolongation of the median stylus. The apex of the median stylus is bifurcate in *Sarcophaga* and is sometimes bulbous.

## Tree topology and branch support

The unweighted analysis yielded 110 trees of 393 steps each. The strict consensus tree was poorly resolved and bootstrap and relative Bremer support values were generally low.

The analysis using implied weighting resulted in 140 most parsimonious trees of 413 steps each. The most parsimonious trees differed only in arrangements of some nodes within the genus *Sarcophaga*. Because of this, the strict consensus tree (Figs. 24, 25) was more fully resolved than that from the unweighted analysis. Bootstrap and relative Bremer support values (calculated from 39,840 suboptimal trees) were generally low in the weighted analysis (Figs. 26, 27).

The low bootstrap values and relative Bremer support in many nodes of both analyses was an indication of the amount of homoplasy in the character matrix. Several character states originated multiple times or were secondarily lost in multiple taxa and relatively few monophyletic groups were supported by uniquely derived character states. We do not consider this a weakness in the data matrix arising from the choice of characters or exemplar taxa. Sarcophagidae, like other families of higher Diptera, are subject to extensive homoplasy in morphological characters; this makes it difficult to obtain strong branch support, based on measures like bootstrapping or Bremer support, in cladistic analyses. Nevertheless, the resolution in the weighted trees was high, even though it was based primarily on homoplasious character states.

## Suprageneric relationships

**Subfamily limits.** Because the monophyly of the Sarcophaginae has been well-demonstrated previously (Pape, 1996), testing it was not a primary objective of this study. Thus, known apomorphies for the subfamily were not necessarily included in the matrix. Despite this, monophyly of the Sarcophaginae was supported by multiple character states (Fig. 26). Previous studies (Pape, 1992; Wells *et al.*, 2001) placed Paramacronychiinae as the sister-group of the Sarcophaginae; this relationship was supported by two uniquely derived character states in our analysis: the possession of a juxta (53:1) and a ventrally displaced acrophallus (56:1) (Figs. 21a, 23b-f, 26), as well three other character states: a convex postcranium (7:1), loss of presutural acrostichal setae (14:1) and female tergite 8 vestigial or absent (33:1).

All species of Miltogramminae and Paramacronychiinae have a simple acrophallus, except the miltogrammine *Senotainia trifida* Pape, in which it is tripartite (Pape, 1989). In the Sarcophaginae the acrophallus is generally a complex tripartite structure (Pape 1992, 1996) and Pape (1989) suggested that the presence of a simple acrophallus in some Sarcophaginae represents a secondary loss because the tripartite acrophallus has apparently evolved only twice in the family. Our phylogeny supported this hypothesis in that well-developed lateral styli (57:1) originated once, at the base of the Sarcophaginae (Fig. 26), and were secondarily lost multiple times, in *Titanogrypa alata* (Fig. 22b-c), *Ravinia derelicta* and *R. effrenata* (Fig. 16g-h) and all three species of *Blaesoxipha* (Fig. 4).

The topology of the weighted tree corresponded to that of Wells *et al.* (2001) at the generic and subfamily level, but the trees did not coincide at the subgeneric level within *Sarcophaga*, most likely because of incomplete taxon sampling, rather than conflict between character sets.

***Tricharaea*.** This clade, represented by *T.* (*Sarothromyia*) *simplex*, was the basal ingroup taxon of the Sarcophaginae and was defined on five homoplasious character states (Fig. 26). The basal position of some species of this clade was assumed by some previous authors (Roback, 1954; Lopes, 1982b) and it was placed basally to the rest of the sarcophagine genera in Pape's (1994) phylogenetic analysis. The larvae of *Tricharaea* also have a vestigial, mostly membranous labrum and a clypeal arch situated far from the parastomal bar (Lopes, 1982b).

Six character states, all homoplasious, supported the monophyly of all Sarcophaginae except *Tricharaea* (Fig. 26).

***Ravinia* clade.** The monophyly of *Oxysarcodexia* and *Ravinia* and a sister group relationship between the two genera was supported in the weighted analysis by a uniquely derived character, the male mid femoral ctenidium with flattened spines (30:1) (Fig. 28). This clade is the only one other than the *Tricharaea* clade with a desclerotized strip between the basi-and distiphallus (47:1) (Fig. 26). *Oxysarcodexia* and *Ravinia* have been considered closely related (Roback, 1954; Downes, 1955; Lopes, 1982b) and were sister-groups in Pape's (1994) phylogenetic analysis. The *Oxysarcodexia-Ravinia* clade is also supported by some first-instar larval character states (Downes, 1955: Lopes, 1982b; Leite & Lopes, 1987; Lopes & Leite, 1987; Pape, 1996).

*Oxysarcodexia* was monophyletic (Fig. 26), supported by a uniquely derived apomorphy, the lateral extension above the vesica (51:1) (Fig. 12a), and by four homoplasious character states (Fig. 26)

The monophyly of *Ravinia* was supported by eight apomorphies including the presence of hillae (67:1) (Figs. 14, 15), uniquely derived in this genus. Relationships among the eight species included in the analysis were also well-resolved except for a basal trichotomy (Fig. 26). The clade including *R. errabunda, R. derelicta* and *R. effrenata* was supported by three character states, two of which are uniquely derived: the absence of a membranous bladder (68:1) and absence of a groove (69:1) on the hillae (Figs. 15, 16). These three species have been previously placed (with others not included in the present study) in the subgenus (or genus) *Chaetoravinia* Townsend (Dodge, 1956, Downes, 1965, Lopes, 1969). Similarly, species of the clade *R. columbiana* + *R. rufipes*, supported by one apomorphy, the setose third costal sector (20:1), have previously been assigned to the genus *Andinoravinia* Townsend (Lopes, 1962, 1969).

All genera above the *Ravinia* clade were supported by a uniquely derived apomorphy: a distinct hinge between basiphallus and distiphallus (47:2) (Fig. 26).

***Dexosarcophaga* clade.** A sister-group relationship between *Dexosarcophaga* and *Oxyvinia* was supported in the weighted analysis (Fig. 26), but bootstrap support and relative Bremer support were low. This clade was supported by four homoplasious character states (Fig. 26). These two genera had not previously been considered closely related. Dodge (1968) considered *Dexosarcophaga,* more closely related to *Oxysarcodexia*. Lopes (1982b) included species of those two genera in two different tribes: Cuculomyiini and Raviniini, in which *Oxyvinia* was tentatively placed. Larvae of *Oxyvinia* have a festoon-like oral ridge (Lopes, 1982b; Leite & Lopes, 1987; Pape, 1996) as in the *Ravinia* clade. Unfortunately, larval characters were not very informative because of large amounts of missing data, and we did not include this character in the matrix (Appendix 2). This is one of the regions of the tree where additional larval characters may provide additional, or alternative, resolution for generic relationships.

Although females of the *Desoxarcophaga* clade were not available to be scored in the analysis, Mello-Patiu & Pape (2000) noted an additional apomorphy to those previously listed by Pape (1996) for *Dexosarcophaga*: female tergite 8 with broad and ventrolaterally truncated halves connected medially by a narrow strip.

*Dexosarcophaga* and *Oxyvinia* were each supported by five homoplasious character states (Fig. 26).

***Cistudinomyia.*** The placement of this monotypic genus was unresolved in the unweighted analysis, but in the weighted analysis it was the sister group to all Sarcophaginae above the *Dexosarcophaga* clade, based on a single character state, the presence of a window in male sternite 5 (37:1). This genus was supported by four homoplasious character states (Fig. 26) and its placement within the subfamily did not correspond to that usually given in the literature, probably because of differing interpretations of the connection between basiphallus and distiphallus. We scored *C.*

*cistudinis* as having a distinct hinge (47:2) (Fig. 6d). In contrast, Roback (1954) included *Cistudinomyia* in his subtribe Raviniina, with *Ravinia* and *Oxysarcodexia*, based on the absence of demarcation between the basi- and distiphallus, and Pape (1994), described *C. cistudinis* as having a distinct desclerotized strip between the basi- and distiphallus.

***Blaesoxipha* clade.** This clade included *Comasarcophaga*, *Fletcherimyia*, *Blaesoxipha* and *Spirobolomyia.* The *Blaesoxipha* clade was monophyletic in all trees in the weighted analysis (Fig. 24) and received higher branch support than many other clades (Fig. 26). Its monophyly was supported by a uniquely derived apomorphy, the bent male cerci (42:1), with setae differentiated into spines (43:1). In Pape's (1994) analysis of *Blaesoxipha* the same group of genera were considered most closely related.

A sister-group relationship between *Comasarcophaga* and *Fletcherimyia* was supported by three apomorphies (Fig. 26). Each of the two genera in this clade was supported by multiple apomorphic character states, mostly in the male genitalia (Fig. 26).

*Blaesoxipha* was not monophyletic in any of the analyses, with *Spirobolomyia* consistently treated as the sister group to *B. (Gigantotheca) plinthopyga* + *B. (Kellymyia) kellyi,* and *B. (s. str.) setosa* as the sister group to these three (Figs. 24, 26). This differs from the conclusions of Pape (1994) who found *Blaesoxipha* monophyletic. The grouping of *Spirobolomyia* as sister-group of *B. plinthopyga* + *B. kellyi* was supported by three apomorphies (Fig. 26) including the setosity of the median occipital sclerite (10:1), female tergite 7 absent or vestigial (32.1) and a pair of dome-shaped protuberances on male sternite 5 (36:1).

The relationships and limits of these genera remain unresolved. Roback (1954) originally placed *Kellymyia* close to *Spirobolomyia* based on the shape of male sternite 5.

Downes (1965) included *Fletcherimyia* and *Spirobolomyia* as subgenera of *Blaesoxipha* but omitted *Comasarcophaga*. Lopes (1982b) divided the species included in *Blaesoxipha* by Pape (1994) into two tribes. Pape (1994) treated *Blaesoxipha* as a large genus divided into ten subgenera. Our analysis did not support the monophyly of *Blaesoxipha*; however, our exemplar set included only three of the ten subgenera and a comprehensive phylogenetic analysis incorporating all subgenera, as well as *Spirobolomyia* would be required to resolve the limits of *Blaesoxipha*.

***Peckia* clade.** This clade included *Peckia*, *Sarcodexia* and *Titanogrypa* and was defined by four homoplasious character states (Fig. 26). The monophyly of the individual genera was supported in the weighted analysis (Figs. 24, 26).

*Peckia* was supported by six character states, including three states of male sternite 5 (37:0, 40:1, 41:1).

The weighted analysis placed *Sarcodexia* as the sister group of *Titanogrypa* (Fig. 26). The clade was supported by a larval apomorphy: first instar larva with an elongate clypeal arch reaching the parastomal bar (2:1), as well as one male genitalic character state. The larval character was scored only for *T. alata* and *S. lambens* (Appendix 1). In addition, two species of *Peckia* not included in the analysis, namely *P.* (*s. str.*) *pexata* (Wulp) and *P.* (*Euboettcheria*) *anguilla* (Curran & Walley) have this character state whereas *P.* (*Pattonella*) *intermutans*, included in the matrix, does not (Lopes, 1982b).

Roback (1954) grouped *Sarcodexia* with the genera *Paraphrissopodia* and *Euboettcheria* (both included in *Peckia* by Pape, 1996) but his grouping was primarily based on the possession of 'median filaments'. According to Roback (1954), those filaments resemble the lateral styli but have a different origin; however, we found little evidence of differences in homology between the structures. Roback may have named the structures differently simply because he did not see the median stylus in the species examined. The acrophallus of *S. lambens* and the species of *Peckia* examined are similar in that the median stylus is reduced to an opening surrounded by tubular lateral styli (Figs. 13d, h, 17e-g).

The monophyly of *Titanogrypa* was supported in the weighted analysis by two uniquely derived apomorphies: a basiphallus with a dorsal hump (50:1) and the presence of white setae laterally on the scutellum (16:1) (Fig. 26). The two included species also have five additional apomorphies that are homoplasious.

***Engelimyia.*** This genus, and the next two, made up a pectinate series of clades basal to the *Sarcophaga* clade. Sister group relationships in these branches were each supported by three homoplasious character states (Fig. 26). In contrast, each of the three individual genera was supported by several apomorphic character states. *Engelimyia*, represented by *Engelimyia inops,* was defined on eight apomorphies, six of which were male genitalic character states (Fig. 26). The position of this genus within the Sarcophaginae has not previously been clearly defined. Lopes (1982b) noted that the phallus was similar to that of *Rafaelia* Townsend but because of differences in head morphology and of the absence of first instar larva, he did not reach a taxonomic conclusion.

***Microcerella.*** This clade, represented by *Microcerella spinigena,* was supported by six apomorphies (Fig. 26) only one of which was a male genitalic character state: the reduced, oval postgonal apodeme (46:1). The characteristic shape of the phallic vesica (Fig. 11e) is found in many species of this genus (e.g., Lopes, 1981). Lopes (1982a, 1982b) suggested a sister-group relationship between his tribes Microcerellini and Sarcophagini.

***Boettcheria.*** Dahlem & Downes (1996) revised this genus, but without a cladistic analysis. In our analysis, *Boettcheria* was the sister group of *Lepidodexia* + *Sarcophaga* based on two apomorphies. The genus itself was supported by seven apomorphies including the uniquely derived vesica with more than three lobes (65:4). The presence, on the male hind trochanter, of a ventromedian pad of short bristles (26:1) and of a posteromedian row of spines (27:1) was noted by Dahlem & Downes (1996). However, they noted that the reduction of the anteroventral bristles on the male hind femur to one or two distal bristles (25:1) is unique to *B. latisterna*. Lopes (1982b) included the subtribe Boettcherina in the Sarcophagini but considered that the group may be related to the tribe Microcerellini.

***Sarcophaga* clade.** A sister-group relationship between *Lepidodexia* and *Sarcophaga* was supported in the weighted analysis (Fig. 24), based on the possession of two uniquely derived apomorphies: the juxta fused with the median stylus (52:1) and the presence of harpes (70:1), along with one homoplasious character state: pointed harpes (73:1) (Fig. 26). However, the delimitation of the harpes and the scoring of these characters were difficult in some species, particularly within *Lepidodexia*. Roback (1954) considered harpes present only in the species of his *Sarcophaga* group, which did not include, among others, *Lepidodexia* or *Helicobia*. However, he considered the three genera closely related, mainly because of the similar form of the lateral styli and phallic tube and the point of attachment of the median stylus.

In the weighted analysis *Lepidodexia* was supported by three homoplasious character states; species relationships within *Lepidodexia* were well-resolved, with most clades supported by multiple apomorphic states, even though most were homoplasious (Fig. 26). The monophyly of *L.* (*Johnsonia*) was based on five apomorphies. A setose $CuA_1$ (22:1) is a uniquely derived apomorphy for *L.* (*Johnsonia*) *setosa* + *L.* (*Johnsonia) elegans*.

Pape (1995, 1996) based the monophyly of his broad concept of *Lepidodexia* on similarities in phallic morphology, one of which is the presence of a characteristic spinous lobe proximal to the vesica (see Fig.10a-c, e-f). Similarly, Lopes (1979, 1984) proposed a list of characters for his tribe Johnsoniini and its subtribes mainly based on female and first instar larval features. We did not include all of those characters in the present study, and a revision of *Lepidodexia*, including detailed morphological study of the male genitalia and incorporating female and larval characters, is needed.

The 36 exemplar species of *Sarcophaga* formed a monophyletic group supported by ten apomorphies (Fig. 26), including three uniquely derived character states: the lateral stylus coiled at base (59:1) and a bifurcate median stylus (63:1) with no opening (62:1) (Fig. 18c-h).

Relationships within *Sarcophaga* were largely unresolved in the unweighted analysis but resolution was greater in the weighted analysis. The genus *Helicobia* was monophyletic but was nested within *Sarcophaga* in both analyses.

The subgeneric classification of Pape (1996) largely corresponds to the generic classification of the tribe Sarcophagini of Verves (1986) and Povolný and Verves (1997), divided into 15 subtribes and more than 750 species. Their classification was based on a comparative analysis of morphological and ecological features of the species of

Sarcophagini as outlined by Lopes (1982b) and Rohdendorf (1965). It was not a cladistic analysis and monophyly of the included taxa was not tested. Roback (1954) also treated *Sarcophaga* as a large single genus and included more than 180 species. The 45 species included in the phylogenetic tree of his *Sarcophaga* group were mostly Nearctic and represented 20 of the subgenera recognized by Pape (1996). Sugiyama and Kano (1984) proposed a classification of the tribe Sarcophagini to address generic limits within the Oriental Sarcophaginae. They corroborated the monophyly of *Sarcophaga* with a phylogenetic analysis based on five genitalic characters of 112 species from 35 of the subgenera recognized by Pape (1996). Wells *et al.* (2001) corroborated the monophyly of *Sarcophaga* and clarified some subgeneric relationships within this genus, but their study was not intended as a broad phylogenetic analysis and included only seven species of *Sarcophaga.*

Given the limited sample of species studied by the above authors, as well as in the present study, a more comprehensive study of *Sarcophaga* species, including phylogenetic analyses of more exemplars, is clearly needed.

Aside from *Helicophagella* (Blackith *et al.*, 1997) and *Liopygia* in part (Wells *et al.*, 2001), the monophyly of the 133 subgenera included in *Sarcophaga* has never been cladistically tested. As an indication of the need for these analyses, of the three subgenera represented by multiple species in our analysis, neither *Mehria* nor *Neobellieria* was monophyletic (Fig. 27) and *Helicobia* was monophyletic but had not previously been treated as a subgenus of *Sarcophaga.*

The bifurcate median stylus with no exit opening and the coiled base of the lateral stylus are visible on specimens of *Helicobia* studied (Figs. 8d-h, 9c), as well as in published illustrations of other *Helicobia* species (Tibana, 1981; Tibana & Mello, 1992).

Based on the results of the analysis, the genus *Helicobia* is synonymized with *Sarcophaga* and treated as a subgenus of the latter. The monophyly of *S.* (*Helicobia*) is supported by eight apomorphies including the uniquely derived oval surstylus (45:4) (Fig. 27).

The monophyly of the clade *N. bullata* + *N. polistensis* was supported by two apomorphies: female tergite 8 absent or vestigial (33:1) and male sternite 5 forming a dome-shaped window anteriorly (38:1) (Fig. 27). However, two other species currently assigned to *Neobellieria* (*S.* (*N.) triplasia* and *S. (N.) semimarginalis*) were placed elsewhere in *Sarcophaga,* as sister groups to other subgenera; thus *Neobellieria,* as currently defined, is polyphyletic. A sister-relationship between *N. bullata* + *N. polistensis* and *S.* (*Tolucamyia*) was supported by three character states of the male phallus, one of which, phallic vesica with round lobes bearing thorn-like spines (66:3), was uniquely derived (Fig. 27). A revision of the species currently assigned to *Neobellieria* and *Tolucamyia* is in progress.

## Generic diagnoses and genitalic apomorphies

***Tricharaea.*** A New World genus with 20 described species in three subgenera (Pape, 1996). Three of the species are also found in the Australasian/Oceanian region. *Diagnosis and apomorphies* (Fig. 21d-g): 2 postpronotal setae; 2-3 katepisternal setae (when 3, middle seta reduced); third costal sector setose ventrally; postalar wall bare; surstylus with wide base and narrow elongated apex; dorsal connection between basiphallus and distiphallus reduced to a desclerotized strip; phallic tube well developed and sclerotized; vesica bulbous and sclerotized; styli short with visible longitudinal cleft.

***Oxysarcodexia.*** A New World genus with 81 species. *Oxysarcodexia varia* is also found in the Australasian/Oceanian region (Pape, 1996).

*Diagnosis and apomorphies* (Fig. 12a-h): postcranium concave or flat; mid femur with ctenidium of flattened spines; postalar wall setose; tegula black to dark brown; tergite 5 entirely yellow; terminalia yellow or reddish; dorsal connection between basiphallus and distiphallus reduced to a desclerotized strip; triangular lateral extension of phallic tube, above vesica (Fig. 12a); juxta setose (Fig. 12a); vesica projecting forward and enlarged laterally, shape variable (Fig. 12b, f); lateral styli grooved or tubular; shape of styli also variable, spinulose in O. *timida* and rather smooth in *O. sp.*; median stylus of both examined species well opened dorsally (Fig. 12d, g).

***Ravinia.*** A primarily New World genus with 33 New World species (two of which are also in Hawaii) and one in the Old World. (Pape 1996). Dahlem (1989) revised the genus but that work was a doctoral thesis and the taxonomic decisions have not yet been published under the International Code of Zoological Nomenclature.

*Diagnosis and apomorphies* (Figs. 14a-h, 15a-g, 16a-h): presutural acrostichal seta present; postalar wall setose; tegula light brown to yellowish; mid femur with ctenidium of flattened spines; terminalia bicolored; fifth sternite U-shaped, with a short base and with pads of dense setae on the cleft of posterior margin; dorsal connection between basiphallus and distiphallus reduced to a desclerotized strip; vesica simple, a small flap, slightly expanded distally except in *R. effrenata* where it is rather long (Fig. 14d); hillae present; lateral styli flattened; median stylus short and straight.

Hillae, paired, tube-like structures (sometimes hatchet-like) protruding outwards the anterior surface of the distiphallus (Figs. 14, 15), are unique to the species of this genus. They can be grooved (Fig. 15e) or not (Fig. 15f), with a membranous bladder (Fig. 14a, b, e, f, h) or without it (Fig. 14c, d, g). The hillae have been considered derivatives of lateral styli (Verves, 2000) or the lateral styli themselves. However, we found no evidence supporting that hypothesis and, based on our observations, the hillae are not homologous with the lateral styli (Fig. 15c, g), which are also present, although flattened (Fig. 16a-f ) in some of the selected species, and absent (Fig. 16g-h) in others.

***Dexosarcophaga.*** A Neotropical genus (one species extends into Nearctic) with 43 species (Pape, 1996; Mello-Patiu & Pape, 2000).

*Diagnosis and apomorphies* (Fig. 5c-f): frontal bristles parallel or slightly diverging towards lunule; postcranium concave or flat; presutural acrostichal setae present; postalar wall setose; ctenidium of normal spines present; terminalia brown or blackish; fifth sternite broadly V-shaped with a long base and regularly setose; large vesica and two lateral prolongations of the phallic tube make up a large part of the distiphallus (Fig. 5d); juxta small, covering base of median stylus (Fig. 5c-d) which looks like a distinct curved process ending by a prominent opening (Fig. 5e-f). Lateral styli clearly flattened and lying along lateral side of median stylus; postgonal apodeme reduced to more or less oval dorsal sclerite; bacilliform sclerite developed, rather elongate.

***Oxyvinia.*** A Neotropical genus with 11 species (Pape, 1996).

*Diagnosis and apomorphies* (Fig. 11a-d): frontal bristles parallel or slightly diverging towards lunule; presutural acrostichal setae present; postalar wall setose; ctenidium of normal spines present; terminalia yellow or reddish; hind trochanter with some ventromedian setae forming a pad of spines or short bristles; fifth sternite deeply U-shaped, regularly setose and with a long base; clear articulation between basi- and distiphallus; juxta clearly connected to phallic tube; median stylus clearly curved towards base of phallus; lateral styli flattened, elongated and curved (Fig. 11c) with longitudinal cleft opened all along internal side.

***Cistudinomyia.*** A monotypic Nearctic genus (Pape, 1996).

*Diagnosis and apomorphies* (Fig. 6d-f): frontal bristles parallel or slightly and gradually diverging towards lunule; genal setae black, postgenal setae white/yellow or with at least some white/yellow setae; apical scutellar bristles absent; discal scutellar bristles present; postalar wall setose; ctenidium of normal spines present; bacilliform sclerite developed, rather elongated; fifth tergite entirely yellow; fifth sternite U-shaped, regularly setose and with a short base; vesica claw-shaped in profile; cleft on lateral stylus clearly opened all along internal side; median stylus straight.

***Comasarcophaga.*** A primarily Nearctic genus with four species, one of which extends into Neotropical Mexico (Pape, 1996).

*Diagnosis and apomorphies* (Fig. 6a-c): posterior margin of lower calypter round, lower calypter O-shaped, ctenidium of normal spines present; fifth sternite with pads of short setae on posterior cleft; juxta well-sclerotized and slightly displaced ventrally relative to longitudinal axis of phallic tube (Fig. 6a), giving a humpbacked profile (Pape, 1990; 1996); demarcation between juxta and phallic tube also clearly visible; styli well developed; conspicuous microserrations at apex of styli; cercal prongs distinctly bent backwards and with short spines dorsally; surstylus elongate and narrow.

***Fletcherimyia.*** A Nearctic genus with eight species (Dahlem & Naczi, 2006).

*Diagnosis and apomorphies* (Fig. 7f-i): posterior margin of lower calypter round, lower calypter O-shaped; ctenidium of normal spines present; fifth sternite evenly setose; pubescence on juxtal margin clearly visible; lateral styli flattened; median stylus reduced; surstylus elongate and narrow, more or less triangular; cercal prongs distinctly bent backwards and with short spines dorsally.

The acrophallus is distinct with the lateral styli loop-shaped and the median stylus reduced to an opening (Fig. 7f, h). Roback (1954) named this 'wreath-like structure' the stemmatis and suggested a possible homology of its lateral dorsal projections (the current lateral styli) with the hillae, an autapomorphy for *Ravinia*.

***Blaesoxipha.*** A cosmopolitan genus with over 242 valid species in 10 subgenera (Pape, 1994, 1996, Lehrer, 2002a). Two subgenera are exclusively Neotropical, four are New World and three include Palaearctic species. *Blaesoxipha* s. str. is cosmopolitan (Pape 1996).

*Diagnosis and apomorphies* (Fig. 4a-i): postalar wall setose; hind femur with anteroventral bristles distinctly set off from adjacent seta; vesica not developed; lateral styli not developed or absent; median stylus clearly straight and prominent in *B. plinthopyga* (Fig. 4b) and *B. setosa* (Fig. 4f), reduced in *B. kellyi* (Fig.4i); juxta membranous or weakly sclerotized in *B. setosa* (Fig. 4e-f); postgonal apodeme reduced to a more or less oval dorsal sclerite; surstylus elongate and narrow; cercal prongs distinctly bent backwards and with short spines dorsally.

Pape (1994) stated that the lateral styli were fused each other through a ventromedian bridge proximal to the median stylus. He also homologized the structures on each side of the median stylus (e.g. two digitate structures of *B. plinthopyga*, Fig. 4b) with the lateral styli of other sarcophagine species. However, there is no ventromedian bridge and the structures on each side of the median stylus are not linked with the sperm duct (e.g. Fig 4c-d) as in other species (e.g. Figs. 15g, 22g). Consequently, two of the five apomorphies used by Pape (1994) to support the monophyly of *Blaesoxipha* are not valid. Roback (1954) also misidentified the lateral styli.

***Spirobolomyia.*** A New World genus with five described species (Pape, 1996). *Diagnosis and apomorphies* (Fig. 21a-c): ctenidium of normal spines present; fifth sternite with a pair of closely set half-dome shaped protuberances on disc; three well developed tubular styli; cleft on median stylus distinctly dorsal, microserrations on apex rather long and conspicuous; juxta well sclerotized, connected with the phallic tube and forming a beaklike projection, juxta hooked at apex; postgonal apodeme elongate; hypandrial arms fused in posterior view; surstylus elongate and narrow; cercal prongs distinctly bent backwards and with short spines dorsally.

***Peckia.*** A New World genus with 66 species in four subgenera (Pape, 1996; Pape & Andersson, 2001).

*Diagnosis and apomorphies* (Fig. 13a-h): genal setae with at least a few white/yellow setae close to genal suture, postgenal setae white/yellow; apical scutellar present; discal scutellar absent; some posterior and posteroventral setae of hind tibia elongated, often with wavy tip and forming a more or less dense fringe; fifth sternite V-shaped, with a long base and with pads of short setae on cleft of posterior margin; lateral styli tubular;

median stylus reduced; no demarcation between juxta and phallic tube; vesica entirely sclerotized.

Roback (1954) identified the lateral extension of the phallic tube in *P. chrysostoma* as harpes. Although their position and point of origin agree with our definition, those extensions do not spread ventromedially over the base of the lateral styli as, for example, in species of *Sarcophaga* (Fig. 18a, c, f).

***Sarcodexia.*** A New World genus with two species, one of which has been introduced to Pacific islands (Pape,1996).

*Diagnosis and apomorphies* (Fig. 17a-g): genal setae with at least a few white/yellow setae close to genal suture, postgenal setae white/yellow; presutural acrostichal setae present; apical and discal scutellar present; fifth sternite U-shaped, evenly setose with a short base; terminalia slightly bicolored; phallic tube sclerotized and forming a spherical structure enclosing the median stylus and the base of lateral styli (Fig. 17a-b); lateral styli tubular; median stylus reduced, resembling an opening surrounded by piles of rough hairs (Fig. 17f-g); no hinge between basiphallus and distiphallus; no demarcation between juxta and phallic tube; strong forked arms of juxta forming a spiraling structure similar to pincers (Fig. 17a, c); vesica entirely sclerotized.

Roback (1954) called the lateral styli ‘median filaments’. Leite & Lopes (1989) misidentified the lateral styli and confused them with the small spiraling tubes found within the apex of the juxta. They also noted the reduced median stylus and mentioned the presence of a rounded vesica but it is not clear if they were referring to the small sclerite located at the anterodorsal side of the phallic tube (Fig. 17a).

***Titanogrypa.*** A New World genus with 18 species in four subgenera (Pape, 1996). *Diagnosis and apomorphies* (Fig. 22a-h): gena with at least a few white/yellow setae close to genal suture, postgenal setae white/yellow; frontal bristles parallel or slightly and gradually diverging towards lunule; discal scutellar absent; scutellum with white setae laterally; distinct dorsal hump on basiphallus (Fig. 22d); distinct hinge between juxta and phallic tube; vesica almost half-cylindrical (Fig. 22d-e), with lateral sides strongly sclerotized; three styli clearly linked to the sperm duct (Fig. 22g); cleft on median stylus distinctly dorsal (Fig. 22g); bacilliform sclerites developed, rather elongate; tip of cercal prong rounded.

***Engelimyia.*** A Neotropical genus with four described species (Pape & Mello-Patiu, 2006).

*Diagnosis and apomorphies* (Fig. 7a-e): parafacial plate with weak and even length setae all along, sometimes almost bare; setae on occipital sclerite spreading below the paravertical setae; postalar wall setose; median stylus with a large opening and with small denticles on its dorsal side (Fig. 7a); median stylus curved towards base of phallus; lateral styli large, more or less tubular and with a coil-shaped structure inside (Fig. 7a, e); juxta bulbous and membranous, clearly distinct from phallic tube; vesica reduced or not developed; hypandrial arms fused in posterior view; tip of cercal prong rounded.

***Microcerella.*** A New World genus with 72 described species (Pape, 1996). *Diagnosis and apomorphies* (Fig. 11e-f): genal and postgenal setae black; all occipital setae black; supracervical setae black; postalar wall bare; apical and discal scutellar absent; $R_1$ setose; terminalia clearly bicolored; weak articulation between basi- and distiphallus; vesica flattened, thin and well sclerotized; median stylus clearly curved towards distal end of phallus (Fig.11f); surstylus elongated and narrow.

***Boettcheria.*** A New World genus with 27 described species (Pape, 1996; Dahlem & Downes, 1996; Pape & Dahlem,1998).

*Diagnosis and apomorphies* (Fig. 5a-b): ventral third costal sector setose; hind trochanter with some ventromedian setae forming a pad of spines or short bristles and with posteromedian row of spines; some posterior and posteroventral setae of hind tibia elongated, often with wavy tip and forming a more or less dense fringe; vesica sclerotized and multilobed, very elaborate and elongate, ending with 2 outer lobes apically; lateral styli very long and narrow, extending well past ventral margin of juxta; median stylus with a widely open dorsal cleft.

The anterior juxtal process of Roback (1954) is visible in Fig. 5b. According to Roback (1954), this sclerotized process, present only in subtribe Boettcheriina, is associated with the well-developed median process of that group. Our observations suggest that this process is a prolongation of the juxta, not fused to the base of the median stylus.

***Lepidodexia.*** A New World genus with 187 described species in 32 subgenera (Pape, 1996).

*Diagnosis and apomorphies* (Figs. 10a-g): male apical scutellar bristles absent; posterior margin of lower calypter round; ventral third costal sector setose or not; sternite 5 with a short base; bacilliform sclerites developed, rather elongate; harpes present; base of lateral styli straight, cleft opened on the internal side all along; median stylus fused to juxta and with a clear opening.

### Subgenus *Lepidodexia* (*Johnsonia*)

*Diagnosis and apomorphies* (Fig. 10a-g): frontal bristles parallel or slightly and gradually diverging towards lunule; genal setae black, postgena with at least some white/yellow setae; palpus yellow or brownish yellow; proanepisternum bare; tegula light brown to yellowish; wing vein $R_1$ setose; wing vein $CuA_1$ usually setose; terminalia yellow or reddish; tergite 5 usually entirely yellow; median stylus curved towards distal end of phallus and widely open dorsally (Fig. 10b, d) in both examined species; distinct microserrations at apex of the three styli; vesica well developed but variable: bulbous in *L. tetraptera* (Fig. 10a, c), flattened and thin in *L. woodi* (Fig. 10e-f); hinge between juxta and phallic tube well articulated in *L. woodi* (Fig. 10g); harpes also well developed in this species; surstylus with a wide base and elongated apex.

***Sarcophaga.*** A cosmopolitan genus with more than 790 described species in 133 subgenera (50% of which are monotypic) (Pape, 1996).

*Diagnosis and apomorphies* (Figs. 18-20): posterior margin of lower calypter rather straight, calypter broadly expanded and more angular; phallic tube generally well developed and sclerotized (Figs. 19, 20); vesica and juxta usually developed but shape extremely variable (Figs. 18-20); lateral styli tubular, with a longitudinal cleft, spiralling along stylus (Fig. 18f, h) or opened on internal side only (Fig. 18c, g); base of lateral styli coiled, a simple coil (Fig. 18c, g) to a ring-shaped structure forming a loop apart from the distal part (styli q- or p-shaped) (Fig. 18d); in some species an elongate process arises laterally from the base (parastylus of Verves, 2000) (e.g. *S. destructor,* Fig. 19d; *S. surrubea*, Fig. 9a-b) or lateral membranous toothed extensions are clearly visible (e.g. *S. ruficornis*, Fig. 20b); base of median stylus always fused to juxta and its distal end (capitis of Roback, 1954) free, bifurcated and often recurved (Fig. 18c, e); length of bifurcate tip varies from short tubular processes (Fig.18d) to very long ones (Figs. 18f, h, 19a-b); median stylus with no opening; harpes present, long or short, pointed or rounded (Figs. 18c, 20b); bacilliform sclerites reduced or absent.

**Subgenus *Sarcophaga* (*Helicobia*).** A New World subgenus with 33 described species (Pape, 1996).

*Diagnosis and apomorphies* (Figs. 8a-i, 9a-e): postcranium concave or flat; wing vein $R_1$ setose; phallus with distinct hinge between phallic tube and juxta (Fig. 8c); vesica well developed and membranous (Figs. 8a, i, 9a-b); lateral styli long and filiform; in *S.* (*H.*) *surrubea*, each is enclosed within a sheath and only the apex is visible (Fig. 9c-e); median stylus with bifurcated tips forming two moderately to very long processes; surstylus rather oval; hypandrial arms fused in posterior view.

## Conclusion and recommendations

This study was the first attempt at a broad phylogenetic analysis of the Sarcophaginae using a range of morphological characters. Male genitalia provided apomorphies for almost every node in the tree, confirming the value of this complex structure as a source of phylogenetic characters. This was especially true in the *Sarcophaga* clade, supported by three male genital characters, including two unique apomorphies (Fig. 26). Similarly, the monophyly and some internal relationships within the *Ravinia* clade were supported mainly by male genitalic characters (Fig. 26).

Other morphological character sets also provided synapomorphies at several levels (Figs. 26, 27). Despite comprising a minor fraction of the total character set, larval character states provided synapomorphies for two nodes within the *Peckia* genus group (Fig. 26). Similarly, female character states supported the clades *Sarcophaga*, (*Tolucamyia* + *Neobellieria*) and (*N. bullata* + *N. polistensis*) despite the fact that female characters were not scored for several species in the analysis.

This study provides a preliminary hypothesis of sarcophagine relationships that should be tested in future studies by the incorporation of additional morphological characters and/or exemplar species. Future research should also test this phylogenetic hypothesis using molecular character sets.

By allowing the identification of several monophyletic groups, the current higher level phylogenetic study also provides direction for future revisionary and phylogenetic studies.

The analysis suggested that *Blaesoxipha*, as currently defined, is not monophyletic relative to *Spirobolomyia*. This is in conflict with the conclusions of Pape (1994) who considered *Blaesoxipha* monophyletic. More exemplars and more characters will be required to determine which hypothesis is more likely.

Although *Lepidodexia* and *Sarcophaga* were both monophyletic and were sister-groups in this analysis, both genera are in need of revision at the subgeneric level. Both are large genera containing a number of subgenera (Pape, 1996), whose monophyly and relationships have not been tested cladistically. This is especially true within *Sarcophaga*, where only one of the subgenera represented by more than one species was shown to be monophyletic (*Helicobia*); neither *Neobellieria* nor *Mehria* was monophyletic and this may be the case with many other subgenera.

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**Appendix 1:** Data matrix of morphological characters used in the study. ? = missing data. - = non-comparable data. A = polymorphic 0/1. B = polymorphic 1/2. * = type species of genus , ** = type species of subgenus .

| | 1 | 1111111112 | 2222222223 | 3333333334 | 4444444445 | 5555555556 | 6666666667 | 7777 |
|---|---|---|---|---|---|---|---|---|
| | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234 |
| *Macronychia aurata* | ???0000000 | 001000000A | 000200000- | 0000000 -10 | 0000000000 | 0-0-- 00 - - - | 0000- -0 - -0 | - - - - |
| *Brachicoma devia* * | 1001101000 | 000100000A | 001000001A | 1011000 -00 | 0001- 00100 | 0010010- - - | 0000- -0 - -0 | - - - - |
| *Sarcophila sp.* | ???0001AA0 | 0001000010 | 001000000- | ???1000 -00 | 0001- ?0100 | 0010010- - - | 0000- -0 - -0 | - - - - |
| *Wohlfahrtia vigil* | ???100101A | 0011000010 | 0010000110 | 0011000 -00 | 0001- 00100 | 0010010- - - | 0000- -0 - -0 | - - - - |
| *Blaesoxipha (Gigantotheca) plinthopyga* | 00?1121211 | 1111100000 | 0001011010 | 0110110 -10 | 0110112100 | 0010010- - - | 0000- -0 - -0 | - - - - |
| *Blaesoxipha (Kellymyia) kellyi* ** | 00?1111211 | 1110100000 | 0000011110 | 2110111010 | 0110112100 | 0010110- - - | 3000- -0 - -0 | - - - - |
| *Blaesoxipha (s. str.) setosa* | ???1111A10 | 1110101010 | 00A000000- | 0000001010 | 0110112100 | 0010010- - - | 0000- -0 - -0 | - - - - |
| *Boettcheria latisterna* * | ?0?1111110 | 1000100001 | 000011110- | 0110101010 | 0000502000 | 0011011101 | 1001410 - -0 | - - - - |
| *Cistudinomyia cistudinis* * | ???1011110 | 0111101000 | 0002000010 | ???0001010 | 0000202000 | 0010011102 | 0001110 - -0 | - - - - |
| *Comasarcophaga texana* * | ???111111A | 1111100000 | 0010000110 | ???0101011 | 0110102000 | 0011011102 | 0001110 - -0 | - - - - |
| *Dexosarcophaga transita* * | 0??1000A00 | 1110100000 | 0000000010 | ???0000- 10 | 1000212000 | 001101100? | 2001110 - -0 | - - - - |
| *Engelimyia inops* * | ???1111111 | 1111100100 | 000000010- | ???0001010 | 0000212010 | 0011011100 | 2000- -0 - -0 | - - - - |
| *Fletcherimyia fletcheri* * | ?0?1111110 | 1101100000 | 0010000010 | ???0100- 10 | 0110202000 | 0011111000 | 3001110 - -0 | - - - - |
| *Helicobia morionella* | ???1110210 | 1101100000 | 100100000- | 1110001010 | 0000402110 | 0111011111 | 1111310 - -1 | 01?0 |
| *Helicobia rapax* * | ?0?1110110 | 1101100000 | 100A00000- | 1110001010 | 0000402110 | 0111011111 | 1111310 - -1 | 0110 |
| *Helicobia surrubea* | ???1110110 | 1101100000 | 100101000- | ???0001010 | 1000402110 | 0111011111 | 1111?10 - -1 | 0110 |
| *Lepidodexia (Johnsonia) elegans* ** | ???0011110 | 1001101011 | 111200000- | 0110001010 | 0000502000 | 0111011102 | 0001110 - -1 | 0010 |
| *Lepidodexia (Johnsonia) rufitibia* | ???1011110 | 1101101011 | 101B00010- | 0110001010 | 0000502000 | 0111011102 | 0000- -0 - -1 | 0010 |
| *Lepidodexia (Johnsonia) setosa* | ???0011110 | ?001101011 | 111200000- | ???0001010 | 0000502000 | 0?1101110? | 0001110 - -? | ?? ?? |
| *Lepidodexia (Notochaeta) woodi* | ???1100110 | 1011101001 | 001000000- | ???0001010 | 0000102000 | 0?11011102 | 1001110 - -1 | 0000 |
| *Lepidodexia (s.str.) tetraptera* * | ???1101000 | 1001101000 | 001000000- | 0010001010 | 0000302000 | 0?11011102 | 1001100 - -1 | 0000 |
| *Microcerella spinigena* | 00?1101000 | 1001101100 | 100000000- | 0110001010 | 000011?000 | 0011011101 | 1001110 - -0 | - - - - |
| *Oxysarcodexia sp.* | ???1010110 | 1110100000 | 0002000011 | 0110000- 10 | 0000201000 | 1010111101 | 1001310 - -0 | - - - - |
| *Oxysarcodexia timida* | ???1010210 | 1111101000 | 0002100011 | ???0000- 10 | 0000201000 | 1010111102 | 1001010 - -0 | - - - - |
| *Oxyvinia xanthophora* | ???10011?0 | 1110100000 | 0000010010 | ???0100- 10 | 1000202100 | 0010011102 | 2001010 - -0 | - - - - |
| *Peckia (s.str.) chrysostoma* | ???1121211 | 1111100100 | 000010010 - | 1110000- 11 | 1000202100 | 0010011101 | 3001310 - -0 | - - - - |
| *Peckia (Pattonella) intermutans* ** | 00?1121211 | 1111100100 | 0000000110 | 1110000- 11 | 1000112100 | 0010011101 | 3001110 - -0 | - - - - |
| *Ravinia columbiana* | ???1011110 | 1110101011 | 1000000011 | 0010101011 | 0000211000 | 0010011000 | 0001111000 | - - - - |
| *Ravinia derelicta* | ???1011110 | 1110101010 | 1000000011 | 0000100- 11 | 0000211100 | 0010010- - - | 1001111110 | - - - - |
| *Ravinia effrenata* | ???1011110 | 1110101010 | 100A000011 | ???0100- 11 | 0000211?00 | 0?1?010- - - | 0001111110 | - - - - |
| *Ravinia errabunda* | ???1011110 | 1110101010 | 1000000011 | 0010100- 11 | 0000201100 | 0010011000 | 0001111110 | - - - - |
| *Ravinia heithausi* | ???1011110 | 1100101010 | 0000000011 | 0010100- 11 | 0000201000 | 0010011000 | 0001111000 | - - - - |
| *Ravinia pernix* * | ?0?1011110 | 1100101010 | 0000000011 | 0010100- 11 | 0000201000 | 0010011000 | 0001111000 | - - - - |
| *Ravinia querula* | ???1011110 | 1110101010 | 00000?0011 | 0010100- 11 | 0000201000 | 0010011000 | 0001111000 | - - - - |
| *Ravinia rufipes* | ???1011110 | 1110101011 | 1000000011 | 0010100- 11 | 0000201000 | 0010011000 | 0001111000 | - - - - |
| *Sarcodexia lambens* * | 11?1121211 | 1110100000 | 000000000 - | 0110101010 | 0000111100 | 0010011101 | 3001010 - -0 | - - - - |

|  | 1<br>1234567890 | 1111111112<br>1234567890 | 2222222223<br>1234567890 | 3333333334<br>1234567890 | 4444444445<br>1234567890 | 5555555556<br>1234567890 | 6666666667<br>1234567890 | 7777<br>1234 |
|---|---|---|---|---|---|---|---|---|
| *Sarcophaga (Bellieriomima) uniseta* | ???1111110 | 1101100001 | 00A010010- | ???0001011 | 1000212100 | 0111011111 | 1111110- - 1 | 0100 |
| *Sarcophaga (Bercaea) africa* ** | ???112121A | 1111100000 | 000001010 - | 1110101011 | 1000102100 | 0111011111 | 1111220- - 1 | 1110 |
| *Sarcophaga (Bercaeopsis) tetra* ** | ???111111A | 110110000A | 000001010 - | ???0101011 | 0010202100 | 0111011111 | 1111120- - 1 | 1010 |
| *Sarcophaga (Discachaeta) cucullans* ** | ???1111110 | 1101100100 | 000011010 - | ???0101011 | 0000212100 | 0111011111 | 1111000- - 1 | 1001 |
| *Sarcophaga (Helicophagella) noverca* ** | ???1111110 | 110110010A | 000011010 - | ???0001011 | 0000202100 | 0111011112 | 1110- -0- - 1 | 1010 |
| *Sarcophaga (Heteronychia) haemorrhoa* ** | ???1111110 | 1101100000 | 100011010 - | 0110101011 | 0000202100 | 0111011111 | 1110- -0- - 1 | 1010 |
| *Sarcophaga (Kramerea) schuetzei* ** | ???1111110 | 1110100000 | 000001010 - | 1110101011 | 1010212100 | 011101???? | 11?0- -0- - ? | ???? |
| *Sarcophaga (Krameromyia) anaces* ** | ???1111110 | 110A100001 | 100000000 - | 1110001011 | 1000212100 | 01110111?? | 1110- -0- - 1 | 1001 |
| *Sarcophaga (Leucomyia) alba* ** | 0011121211 | 111A101010 | 000000000 - | 0010001010 | 0000112100 | 0111011111 | 1111000- - 1 | 1010 |
| *Sarcophaga (Liopygia) ruficornis* ** | 00?1121211 | 11111000A0 | 000A01010- | 0110101011 | 0000302100 | 0111011111 | 1111110- - 1 | 1100 |
| *Sarcophaga (Liosarcophaga) pleskei* | ???1111110 | 1111100000 | 000001010 - | 1100101111 | 1000202100 | 0111011111 | 1111110- - 1 | 1011 |
| *Sarcophaga (Mehria) nemoralis* ** | ???1111110 | 1101100001 | 000000010 - | 1110101010 | 1000202100 | 0111011111 | 1111310- - 1 | A010 |
| *Sarcophaga (Mehria) houghi* | ???1111110 | 111A100001 | 000000010 - | 0110101010 | 1000202110 | 0111011112 | 1111210- - 1 | 0100 |
| *Sarcophaga (Neobellieria) polistensis* ** | ???11B1B1A | 11111000A0 | 000A0A010- | 1110101111 | 10002021A0 | 0111011112 | 1111230- - 1 | 1001 |
| *Sarcophaga (Neobellieria) bullata* | 00?11B1211 | 1111100000 | 000A01010- | 1110101111 | 1000202110 | 0111011112 | 1111230- - 1 | 1001 |
| *Sarcophaga (Neobellieria) semimarginalis* | ???1111110 | 1111100000 | 000100010 - | 1010101010 | 1000202100 | 0111011112 | 1111110- - 1 | 1100 |
| *Sarcophaga (Neobellieria) triplasia* | 001111111A | 1111100000 | 000A10010 - | 1110101010 | 0000202100 | 0111011112 | 1111110- - 1 | 0100 |
| *Sarcophaga (Neosarcophaga) occidentalis* ** | ???111111A | 1111100000 | 000A01010 - | 1110101010 | 1000202100 | 0111011111 | 1111100- - 1 | 1110 |
| *Sarcophaga (Parasarcophaga) taenionota* ** | 0011121211 | 1111100000 | 000001010 - | 1010101010 | 1000202100 | 0111011111 | 1111110- - 1 | 1010 |
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| *Sarcophaga (Phytosarcophaga) destructor* ** | 0011111211 | 1101100000 | 100100000 - | 0110001010 | 1000212100 | 0110011111 | 1110- - 0- -1 | 1001 |
| *Sarcophaga (Pseudothyrsocnema) spinosa* ** | ???1121110 | 1111100000 | 000000000 - | 1100101011 | 1000202110 | 0111011111 | 1111110- - 1 | 1101 |
| *Sarcophaga (Robineauella) caerulescens* ** | 0011111110 | 1111100001 | 000001010 - | 1110101010 | 0000202100 | 011101111? | 1111100- - 1 | 1110 |
| *Sarcophaga (Rosellea) aratrix* ** | 001111111A | 111110000A | 000001010 - | 1110101110 | 1000202100 | 0111011112 | 1111110- - 1 | 1000 |
| *Sarcophaga (s.str.) carnaria* * | 001111111A | 1111100000 | 000001010 - | 0110101010 | 1000212100 | 0111011112 | 1111100- - 1 | 1010 |
| *Sarcophaga (Sarcorohdendorfia) impatiens* | ???1121211 | 1110100000 | 000001010 - | 1110101010 | 1010302100 | 0111011111 | 1111110- - 1 | 1100 |
| *Sarcophaga (Seniorwhitea) orientalis* | 0011111111 | 1111100000 | 0000A1010 - | 0000101011 | 1000212100 | 0111011111 | 1111110- - 1 | 0100 |
| *Sarcophaga (Sinonipponia) hervebazini* ** | ???1111110 | 111010000A | 000001010 - | 1110?0?011 | 1000202100 | 0111011111 | 1111110- - 1 | 1010 |
| *Sarcophaga (Thyrsocnema) incisilobata* ** | ???1111110 | 1101100000 | 000001010 - | 1110101111 | 1000212100 | 0110011111 | 1111110- - 1 | 0010 |
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| *Sarcophaga (Wohlfahrtiopsis) johnsoni* ** | 00111B1B1A | 1111101100 | 000000010 - | 1110100 -11 | 0010302100 | 0111011111 | 1111110- - 1 | 1000 |
| *Sarcophaga aldrichi* | 0??1111110 | 1110100000 | 000000010 - | ???0101010 | 1000202100 | 0111011112 | 1111110- - 1 | 1100 |
| *Spirobolomyia singularis* * | ???1111111 | 1110100010 | 0001000110 | 0110011010 | 0110122110 | 0010011101 | 1001120- - 0 | - - - - |
| *Titanogrypa (Cucullomyia) placida* | ???1021211 | 1111111100 | 0002000010 | 1010001011 | 0000102001 | 0011011101 | 1001010- - 0 | - - - - |
| *Titanogrypa (s.str.) alata* * | 0101021210 | 0101110100 | 10A001000 - | 1110001011 | 0000102001 | 0011010- - - | 0001010- - 0 | - - - - |
| *Tricharaea (Sarothromyia) simplex* | 0??0011110 | 1001101001 | 000000000 - | 1010000 -10 | 0000501000 | 0010011101 | 0001000- - 0 | - - - - |

**Appendix 2:** Characters used in phylogenetic analysis.

**Larvae**

1. First instar larva, clypeal arch: (0) well developed and forming a bridgelike dorsal connection; (1) reduced.
2. First instar larva, clypeal arch elongate and reaching parastomal bar: (0) absent; (1) present.
3. First instar larva, rim of spiracular cavity: (0) bare; (1) microtrichose.

**Head**

4. Male proclinate orbital setae: (0) present; (1) absent.
5. Frontal bristles: (0) rows parallel or gradually diverging near lunule; (1) strongly diverging near lunule.
6. Gena and postgena setae, colour: (0) black; (1) genal setae black, postgena with at least some white or yellow setae; (2) gena with a least a few white or yellow setae close to genal suture, postgenal setae white or yellow.
7. Postcranium, shape: (0) concave or flat; (1) convex.
8. Occipital setae, colour: (0) black; (1) setae around occipital foramen white or yellowish, outer setae black; (2) white or yellowish.
9. Supracervical setae, colour: (0) black; (1) white, yellow or golden yellow.
10. Median occipital sclerite, setosity: (0) setae never extending below paravertical setae; (1) setae extending below paravertical setae.

**Thorax**

11. Prosternum, setosity: (0) bare; (1) setose.
12. Postalar wall, setosity: (0) bare; (1) setose.
13. Postsutural dorsocentral bristles, number: (0) three; (1) not three.

14. Presutural acrostichal seta: (0) present; (1) absent.

15. Coxopleural streak: (0) present; (1) absent.

16. Scutellum, white setae laterally: (0) absent; (1) present.

17. Male apical scutellar bristles: (0) present; (1) absent.

18. Male discal scutellar bristles: (0) present; (1) absent.

**Wing**

19. Tegula, colour: (0) black to dark brown; (1) light brown to yellowish.

20. Ventral surface of costa between Sc and $R_1$: (0) bare; (1) setose.

    Minute equidistant setae often present on the ventral third costal sector are not considered here. We consider an irregular row of spines extending to or just past $R_1$.

21. Dorsal, proximal part of $R_1$: (0) bare; (1) setose.

22. First anterior branch of $CuA_1$: (0) bare; (1) setose.

23. Lower calypter, shape: (0) posterior margin rather straight, calypter broadly expanded and more angular; (1) posterior margin round.

**Abdomen**

24. Tergite 5, colour. (0) same as other abdominal tergites; (1) with yellow margin of variable width; (2) entirely yellow.

**Leg**

25. Male hind femur, anteroventral bristles: (0) present and distinct; (1) absent or reduced to one or two distal bristles.

26. Male hind trochanter, ventromedian setae: (0) unmodified; (1) some setae forming pad of spines or short bristles.

27. Hind trochanter, posteromedian setae: (0) unmodified; (1) forming a row of spines.

28. Male hind tibia, posterior and posteroventral setae: (0) unmodified; (1) at least some setae elongated, often with wavy tip and forming a more or less dense fringe.

29. Male mid femur, apical posteroventral setae (ctenidium): (0) absent; (1) present.

30. Male mid femur, ctenidium, shape of spines: (0) rounded; (1) flattened (Fig. 29).

**Female terminalia**

31. Female tergite 6, dorsal surface: (0) even; (1) narrowly membranous or mid dorsal line present; (2) with a pair of depressions.

32. Female tergite 7: (0) present; (1) absent or vestigial.

33. Female tergite 8: (0) present; (1) absent or vestigial.

**Male terminalia**

34. Syntergosternite 7+8, fusion: (0) free; (1) fused with tergite 6.

35. Syntergosternite 7+8, anterodorsal emargination: (0) absent; (1) present (Fig. 3a-b);.

36. Sternite 5, posteromedian surface of disc: (0) even (Fig. 1b); (1) with a pair of closely set dome-shaped protuberances.

37. Sternite 5, window: (0) absent; (1) present (Fig. 1b).

38. Sternite 5, window: (0) even with rest of base (Fig. 1b); (1) forming a dome-shaped elevation anteriorly.

39. Sternite 5, posterior emargination: (0) shallow; (1) deep (Fig. 1b).

40. Sternite 5, cleft of posterior margin, setosity: (0) regularly setose (Fig. 1b); (1) forming pads.

41. Sternite 5; length of base: (0) short; (1) long (Fig. 1b).

42. Male cercus, orientation of prong relative to base: (0) straight, at most distal part of prong evenly curved or bent (Fig. 1c,d); (1) prong distinctly bent backwards relative to base.

43. Male cercal prong, setae: (0) all setae slender, similar to those on cercal base, often shorter; (1) at least some setae differentiated into spines.

44. Male surstylus: (0) articulated with epandrium (Fig. 1a); (1) fused to epandrium.

45. Male surstylus, shape: (0) very long and wide; (1) elongated and narrow; (2) roughly triangular (Fig. 1a); (3) rounded; (4) oval; (5) wide base with elongated process(es).

46. Postgonal apodeme, configuration: (0) spreading anteriorly along base of postgonite; (1) not spreading, reduced to oval dorsal scerite; (2) not spreading, forming a long process.

47. Phallus, dorsal connection between basi- and distiphallus: (0) continuous (Fig.23 a-e); (1) with desclerotized strip (Fig.4a-b); (2) with distinct hinge (Figs.21a, c & 22 d, e).

48. Bacilliform sclerites, shape: (0) developed, elongate; (1) reduced or absent (Fig. 1c).

49. Hypandrial arms, degree of fusion posterior view: (0) free; (1) fused.

50. Basiphallus, dorsal hump: (0) absent; (1) present (Fig. 22d).

51. Phallic tube, lateral extension above the vesica: (0) absent; (1) present (Fig. 12a).

52. Juxta, degree of fusion to median stylus: (0) free; (1) fused (Figs. 8d-f & 18c-g).

53. Juxta: (0) absent (Fig.23a); (1) present.

54. Juxta, dorsal connection with phallic tube: (0) demarcation absent (Fig. 21a); (1) demarcation present.

55. Juxta, texture: (0) bare; (1) setose (Fig. 12a).

56. Acrophallus, position: (0) terminal (Fig. 23a); (1) ventral surface of phallus (Figs. 22d & 23d).

57. Lateral styli: (0) not developed or absent (Fig. 4); (1) separate structures connected to rest of acrophallus only at their base.

58. Lateral styli, shape: (0) flattened (Fig. 13); (1) grooved or tubular (Fig. 22g).

59. Lateral styli, shape of base: (0) straight (Fig. 22d); (1) coiled or spiraling (Fig. 18d).

60. Lateral styli, longitudinal cleft: (0) absent; (1) spiraling all along (Fig. 13h); (2) opened on internal side all along (Fig. 18c, g).

61. Median stylus, shape: (0) straight (Fig. 21g); (1) curved towards distal end of phallus (Fig. 18 c-h); (2) curved towards the base of phallus (Fig. 11d); (3) reduced (Fig. 13 d, h).

62. Median stylus: (0) with clear opening (Fig. 5b,c,f); (1) no opening (Fig. 18c-h).

63. Median stylus, tip: (0) not bifurcate (Fig. 6c,f); (1) bifurcate (Fig. 18c-h).

64. Phallic vesica: (0) reduced or not developed (Fig.4a); (1) developed (Fig. 5a).

65. Phallic vesica, number of lobes: (0) one (Fig. 21d-e); (1) bilobed (Fig. 10c, f); (2) two separate lobes; (3) trilobed (Fig.8b); (4) more than three lobes (Fig. 5a).

66. Phallic vesica, shape of lobes: (0) bulbous (Fig. 21d-e); (1) flattened and thin (Fig. 10f); (2) tubular; (3) rounded and bearing thorn-like spines.

67. Hillae: (0) absent; (1) present (Fig.14).

68. Hillae membranous bladder: (0) present (Fig. 14a,b) ; (1) absent (Fig. 14g).

69. Hillae groove: (0) present (Fig. 15e); (1) absent (Fig. 15f).

70. Harpes: (0) absent; (1) present (Figs 18-20).

71. Harpes, degree of fusion to phallic tube: (0) free; (1) fused.

72. Harpes, length: (0) long (Fig. 18a); (1) short.

73. Harpes, shape of tip: (0) rounded; (1) pointed (Fig. 18a).

74. Harpes, shape: (0) flattened dorsoventrally, (1) flattened laterally.

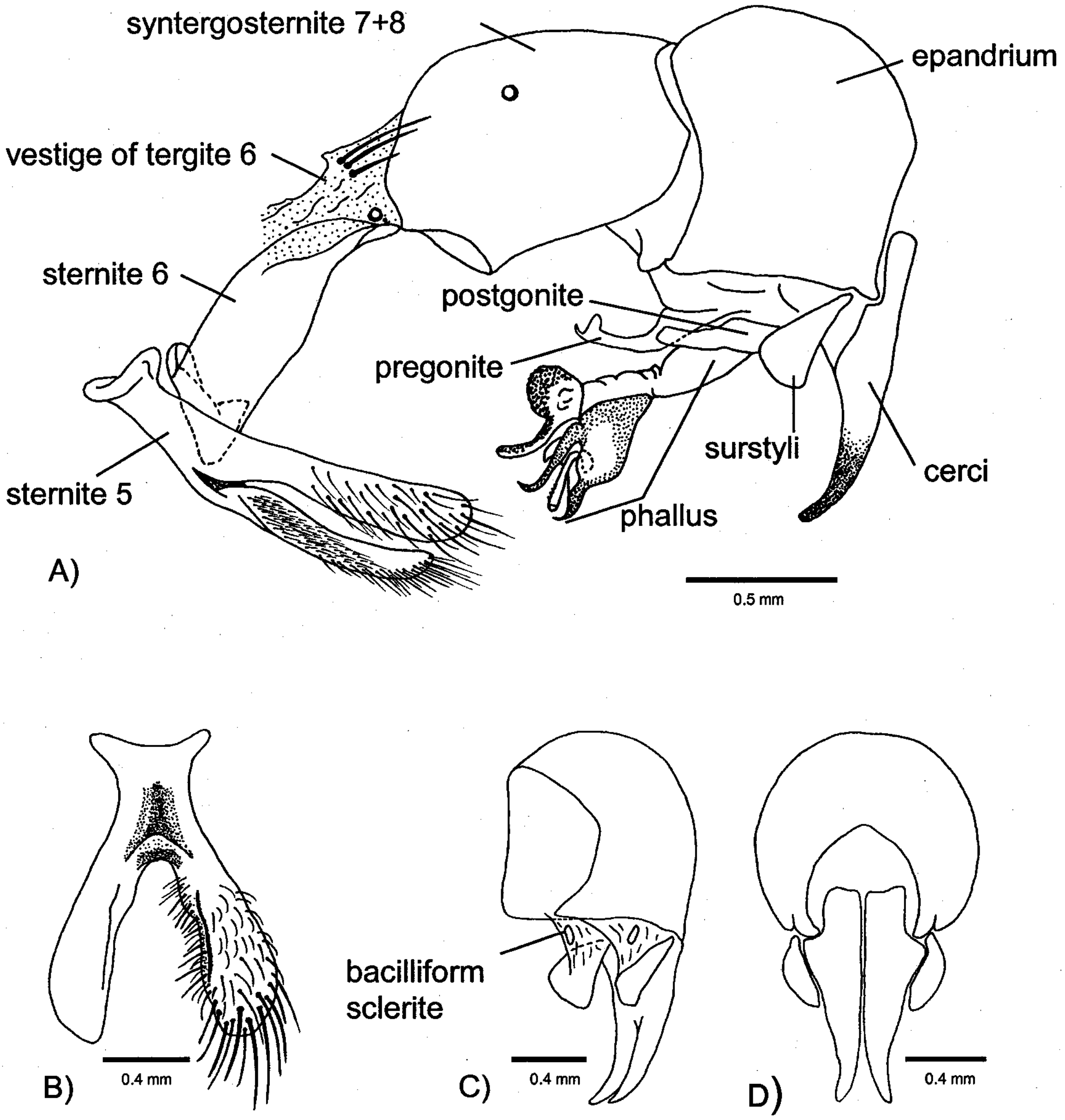

**Figure 1.** *Sarcophaga (Neosarcophaga) occidentalis*: a) male terminalia, left lateral view; b) sternite 5, ventral view; c) bacilliform sclerites, anterolateral view; d) epandrium, cerci and surstyli, posterior view

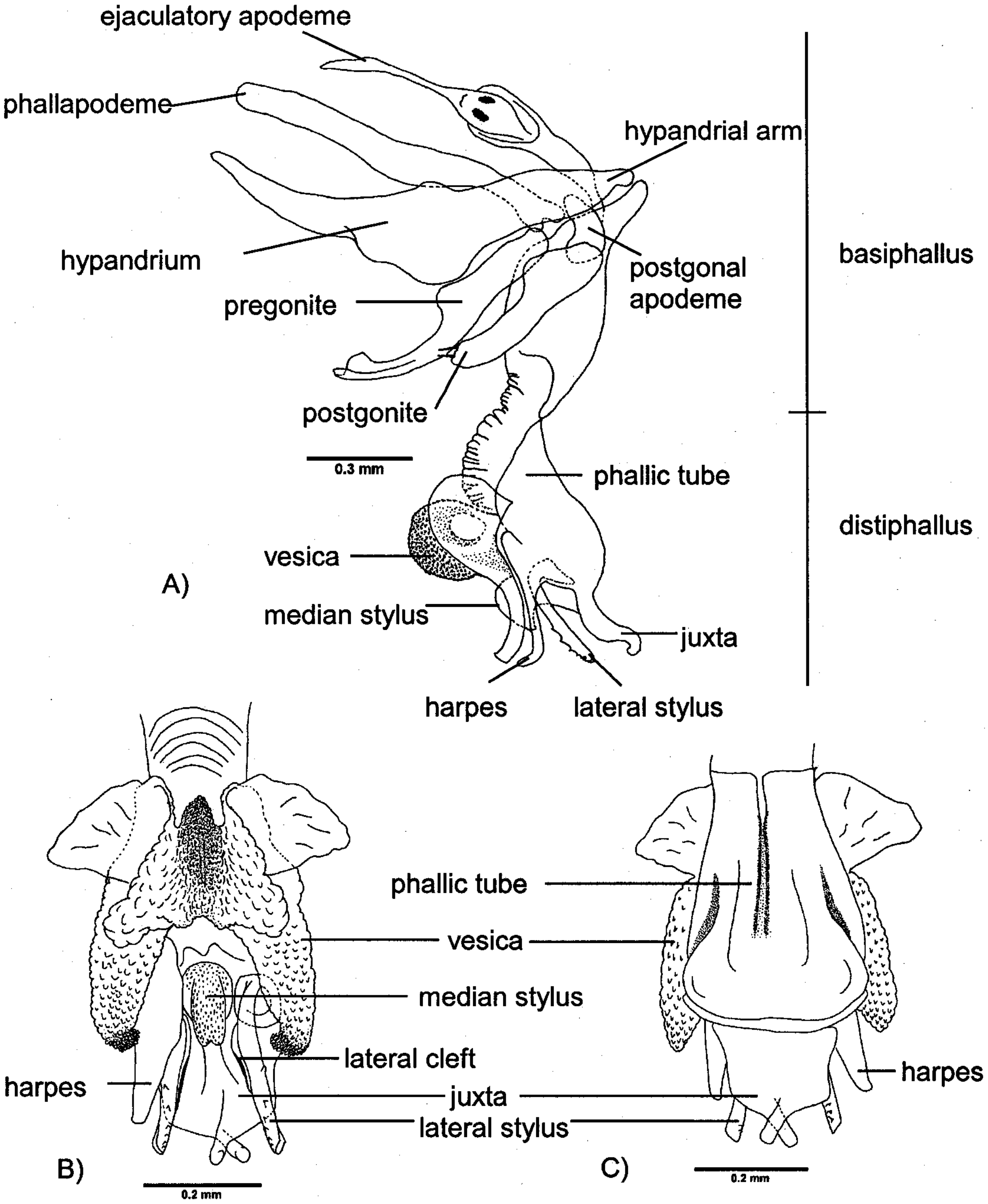

**Figure 2.** *Sarcophaga (Neosarcophaga) occidentalis*: a) phallus, left lateral; b) distiphallus, ventral view, left harpes removed; c) distiphallus, dorsal view

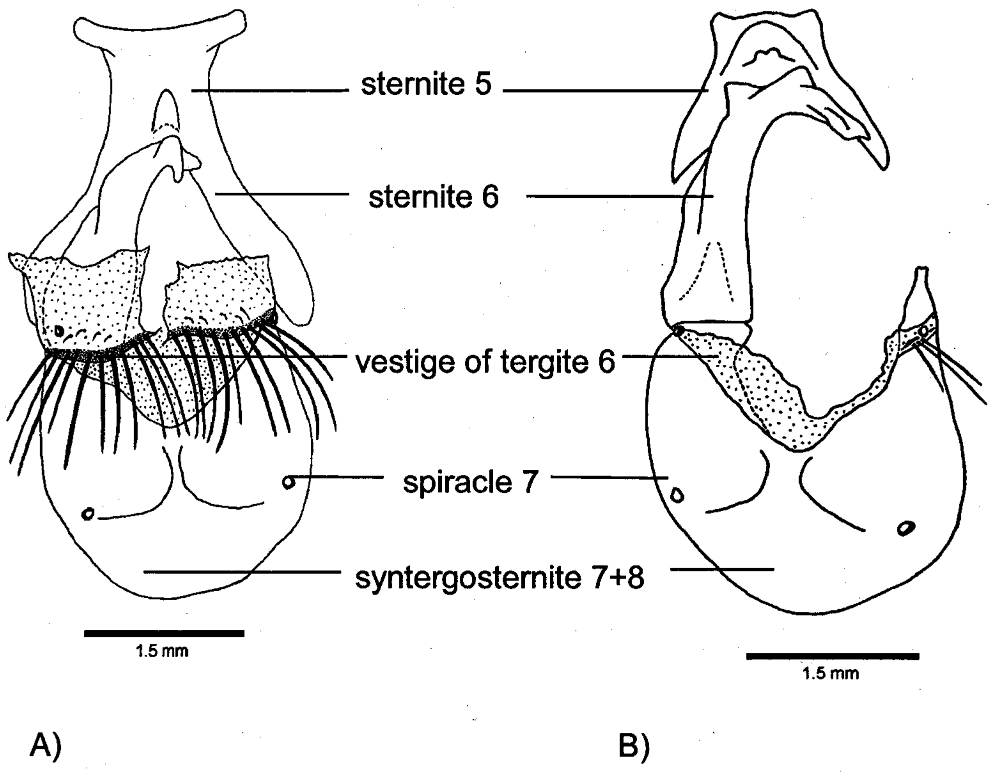

**Figure 3.** *Sarcophaga* (*s.str.*) *carnaria* a), *S. (Neobellieria) triplasia* b): male terminalia, dorsal view

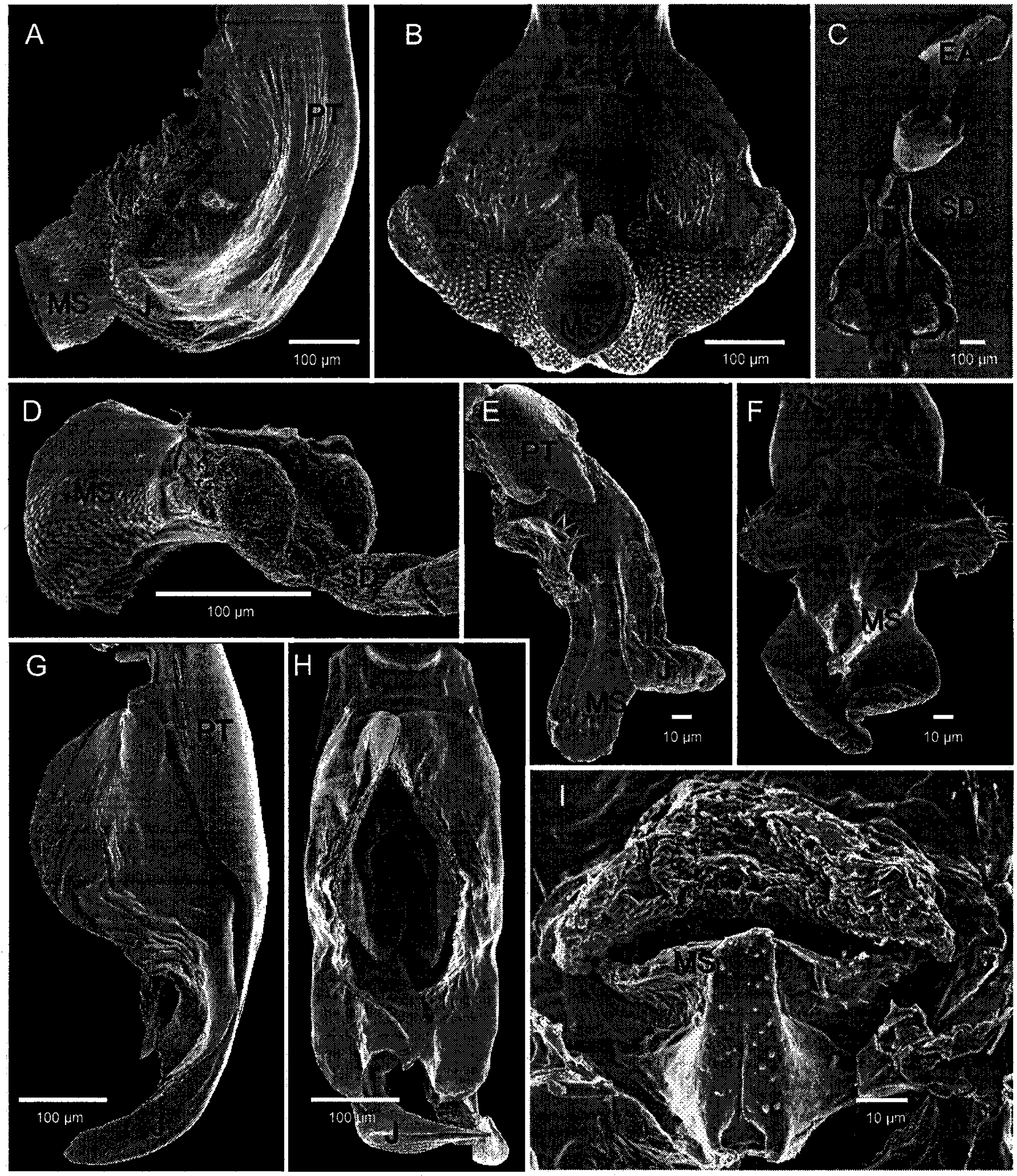

**Figure 4.** *Blaesoxipha (Gigantotheca) plinthopyga* (a-d): a) distiphallus, lateral view; b) distiphallus, frontal view; c) dissected phallus, frontal view d) median stylus and sperm duct, posteroventral view. *B. (s.str.) setosa* (e-f): e) distiphallus lateral view; f) distiphallus frontal view. *B. (Kellymyia) kellyi* (g-i): g) distiphallus, lateral view; h) distiphallus frontal view; i) median stylus. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

**Figure 5.** *Boettcheria latisterna* (a-b): a) distiphallus, lateral view; b) styli, frontal view. *Dexosarcophaga transita* (c-f): c) styli, frontal view; d) distiphallus, lateral view; e) styli, lateral view; f) median stylus, frontal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

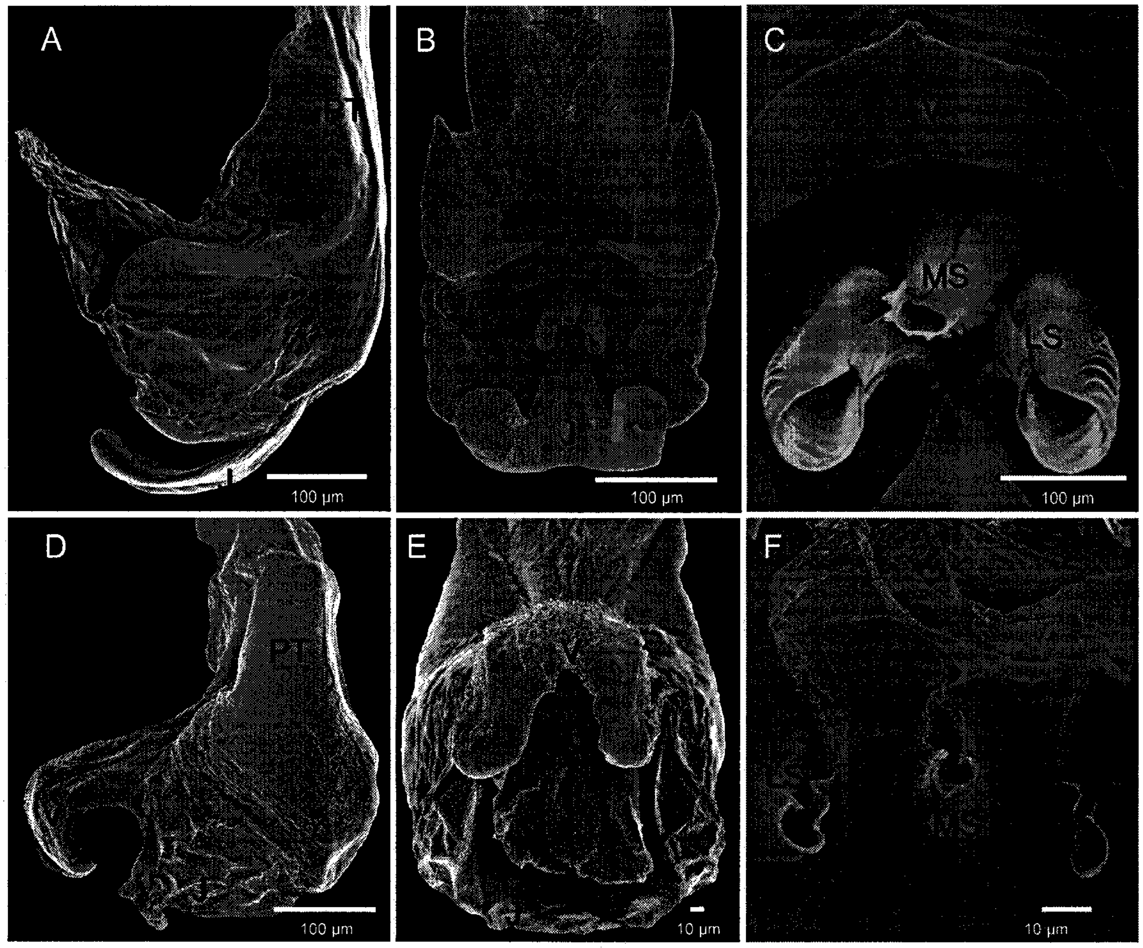

**Figure 6.** *Comasarcophaga texana* (a-c): a) distiphallus lateral view; b) distiphallus frontal view; c) styli frontal view. *Cistudinomyia cistudinis* (d-f): d) distiphallus lateral view; e) distiphallus frontal view; f) styli frontal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

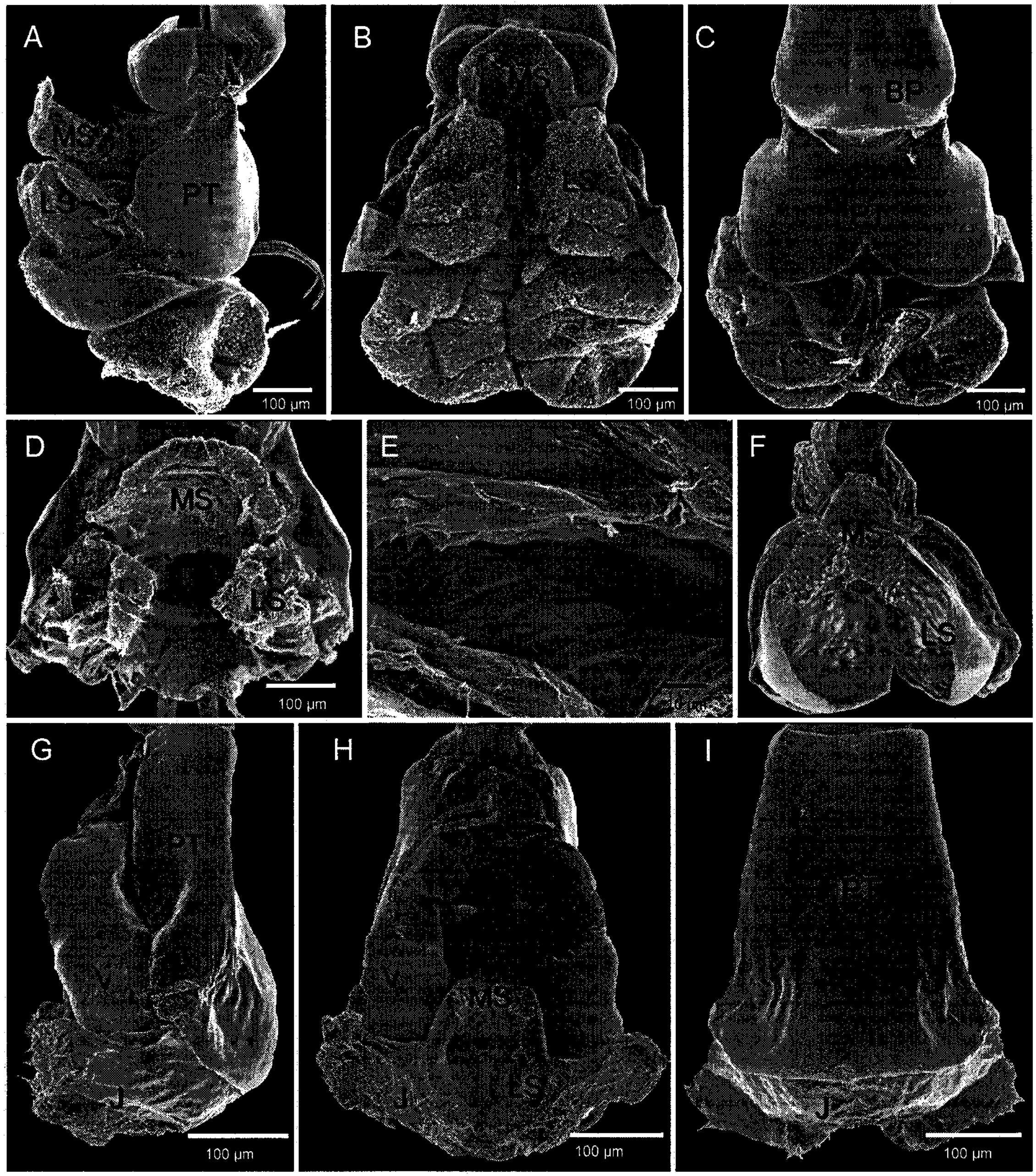

**Figure 7.** *Engelimyia inops* (a-e): a) distiphallus, lateral view; b) distiphallus, frontal view; c) distiphallus, dorsal view; d) distiphallus frontal view, juxta removed; e) lateral styli. *Fletcherimyia fletcheri* (f-i): f) styli; g) distiphallus, lateral view; h) distiphallus, frontal view; i) distiphallus, dorsal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

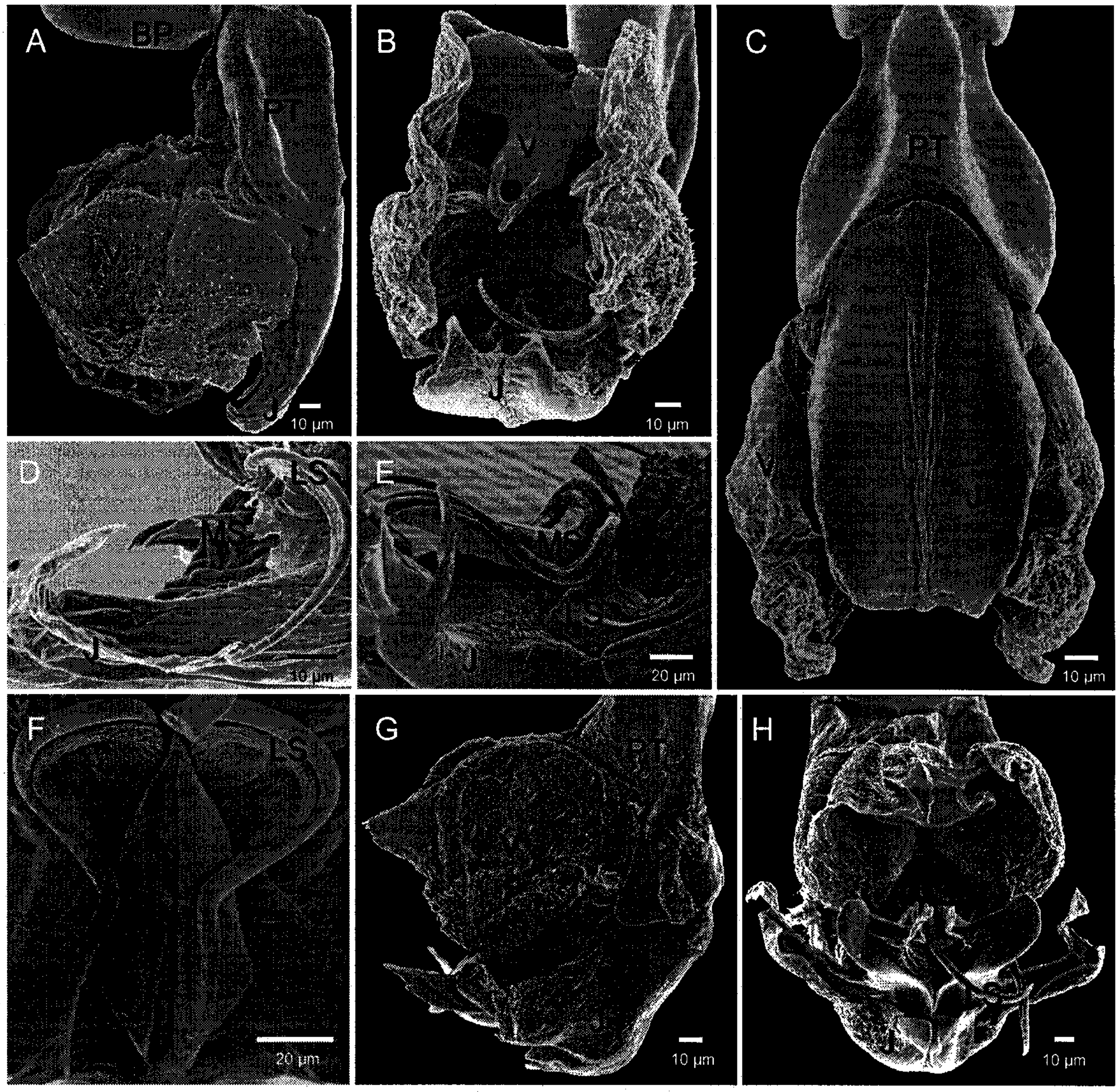

**Figure 8.** *Sarcophaga* (*Helicobia) morionella* (a-e): a) distiphallus lateral view; b) distiphallus frontal view; c) distiphallus dorsal view; d) styli lateral view; e) styli anterior view. *S.* (*Helicobia) rapax* (f-i) f) styli lateral view; g) distiphallus lateral view; h) styli anterior view; i) distiphallus frontal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

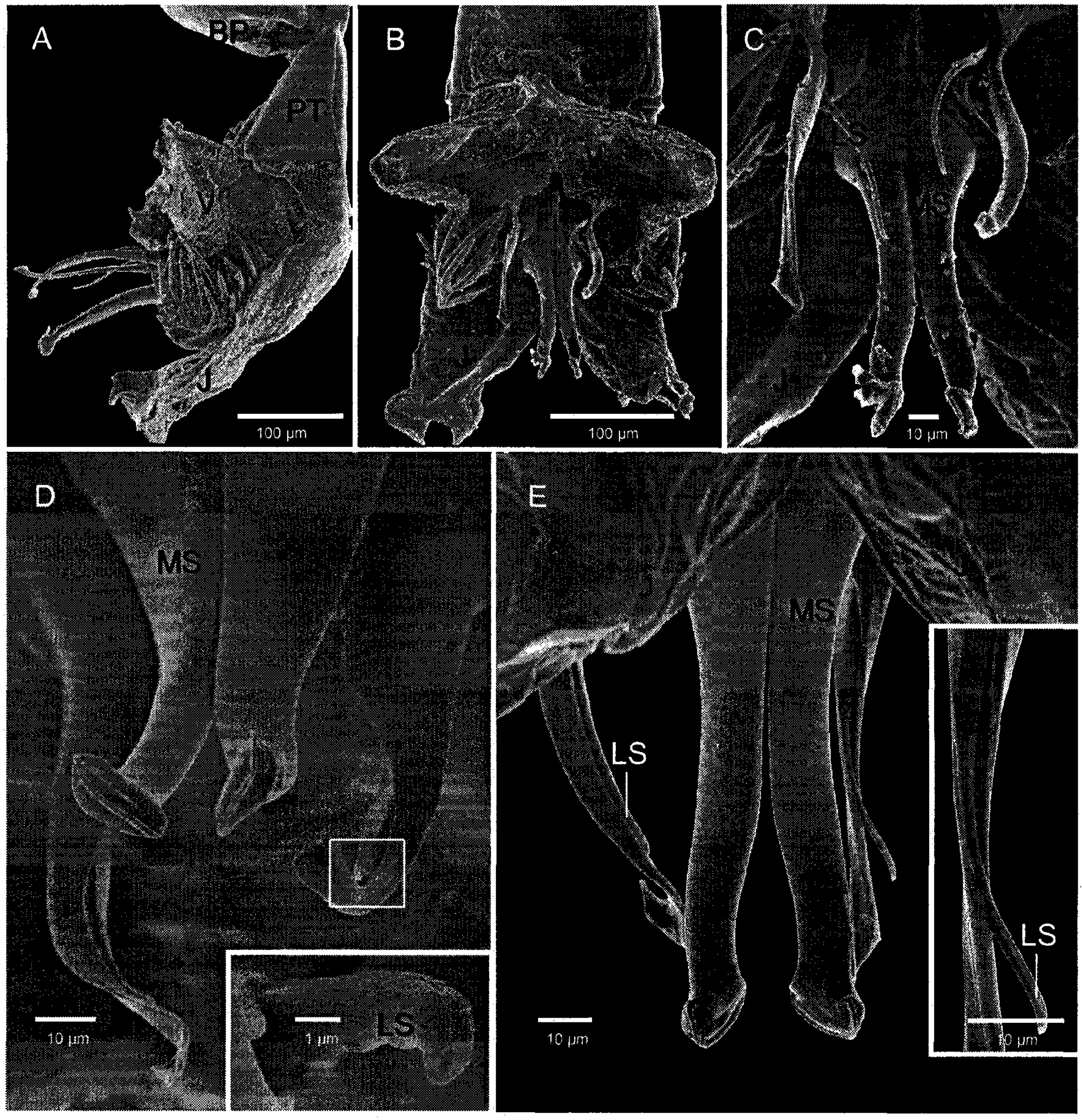

**Figure 9.** *Sarcophaga* (*Helicobia) surrubea*: a) distiphallus lateral view; b) distiphallus frontal view; c) styli ventral view; d) apex of styli, frontal view; e) lateral styli within their sheaths, dorsal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

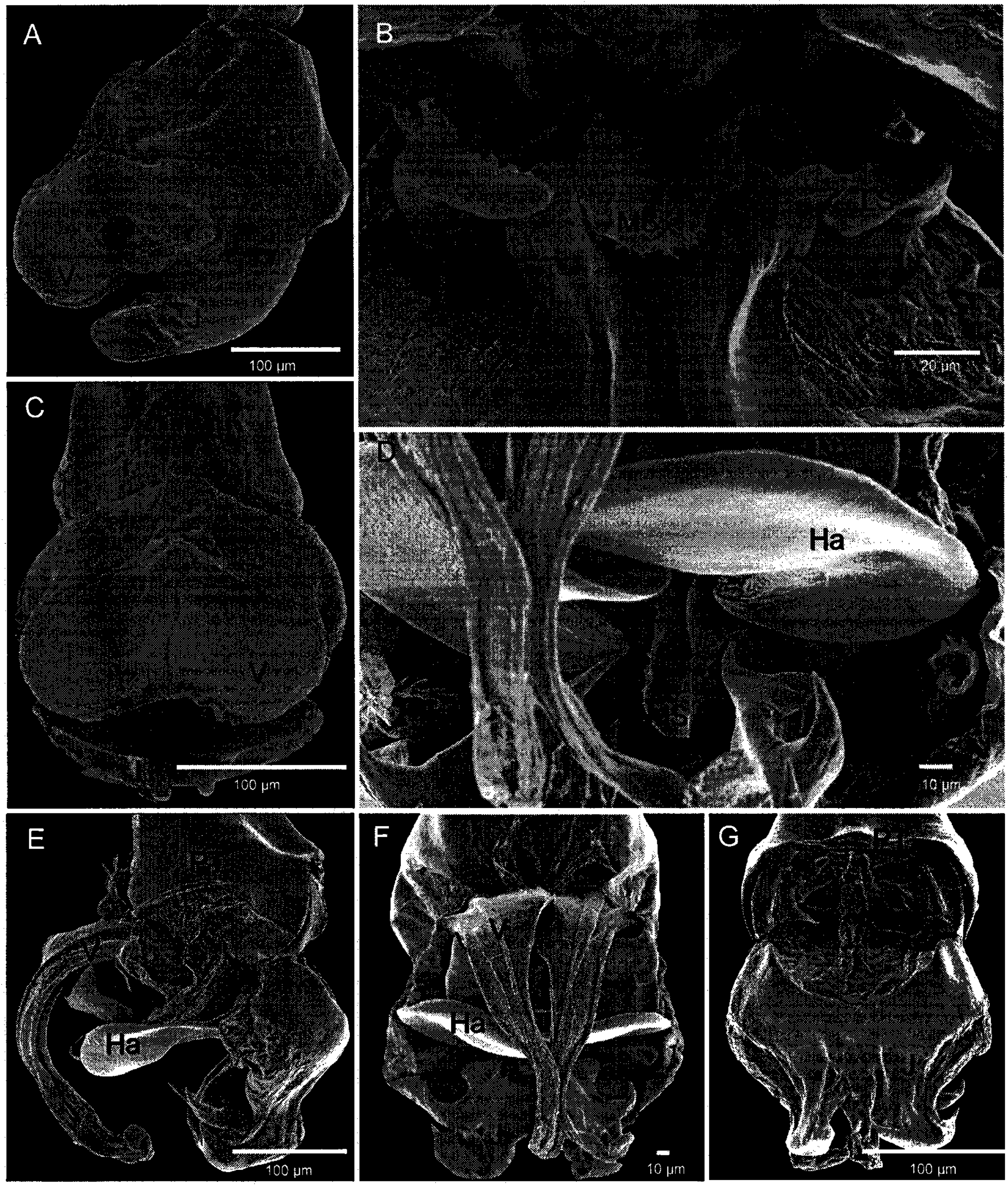

**Figure 10.** *Lepidodexia (s. str.) tetraptera* (a-c): a) distiphallus lateral view; b) styli ventral view; c) distiphallus frontal view. *Lepidodexia (Notochaeta) woodi*. (d-g) d) styli ventral view; e) distiphallus lateral view; f) distiphallus frontal view; g) distiphallus, dorsal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

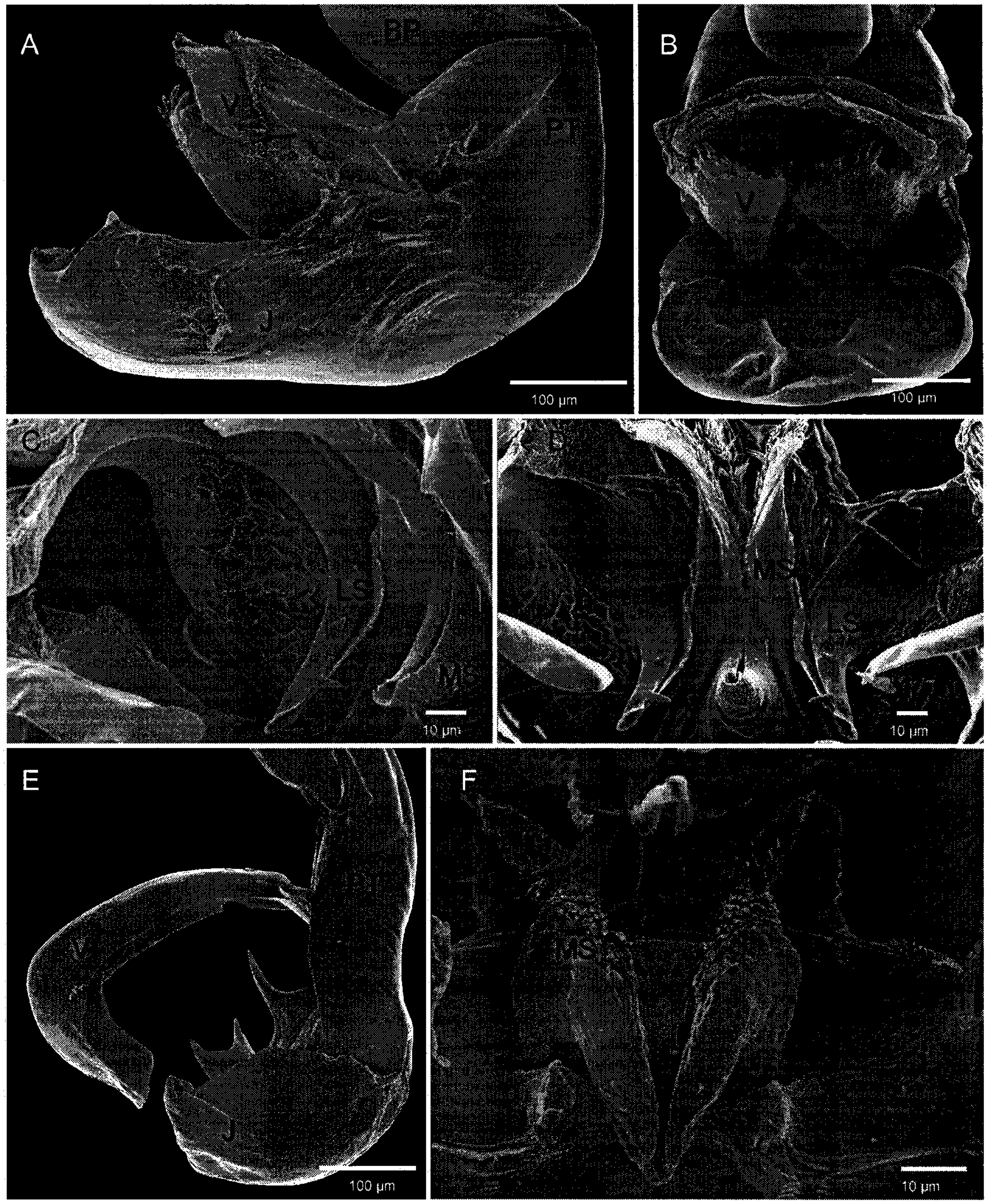

**Figure 11.** *Oxyvinia xanthophora* (a-d): a) distiphallus lateral view; b) distiphallus frontal view; c) styli fronto-lateral view; d) styli frontal view. *Microcerella spinigena* (e-f): e) distiphallus lateral view; f) styli frontal view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

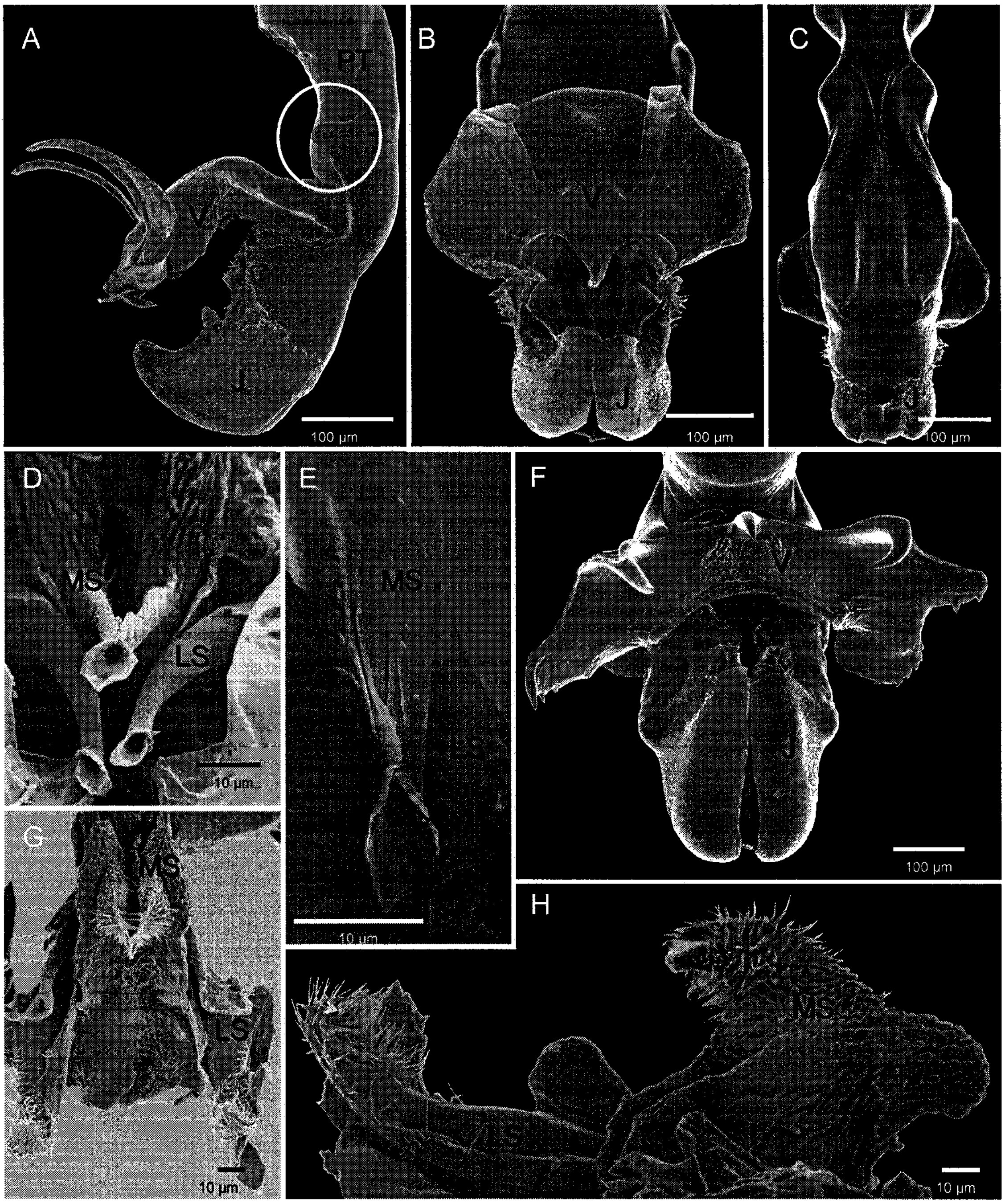

**Figure 12.** *Oxysarcodexia sp.* (a-e): a) distiphallus lateral view, the lateral extension above the vesica (char. 62) is circled ; b) distiphallus frontal view; c) distiphallus dorsal view; d) styli frontal view; e) styli dorsal view. *O. timida* (f-h): f) distiphallus frontal view; g) styli frontal view; h) styli lateral view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

**Figure 13.** *Peckia (s. str.) chrysostoma* (a-d): a) distiphallus lateral view; b) distiphallus frontal view; c) styli and part of the vesica; d) styli. *Peckia (Pattonella) intermutans* (e-h): e) distiphallus lateral view; f) distiphallus frontal view; g) styli dorsal view h) styli ventral view. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

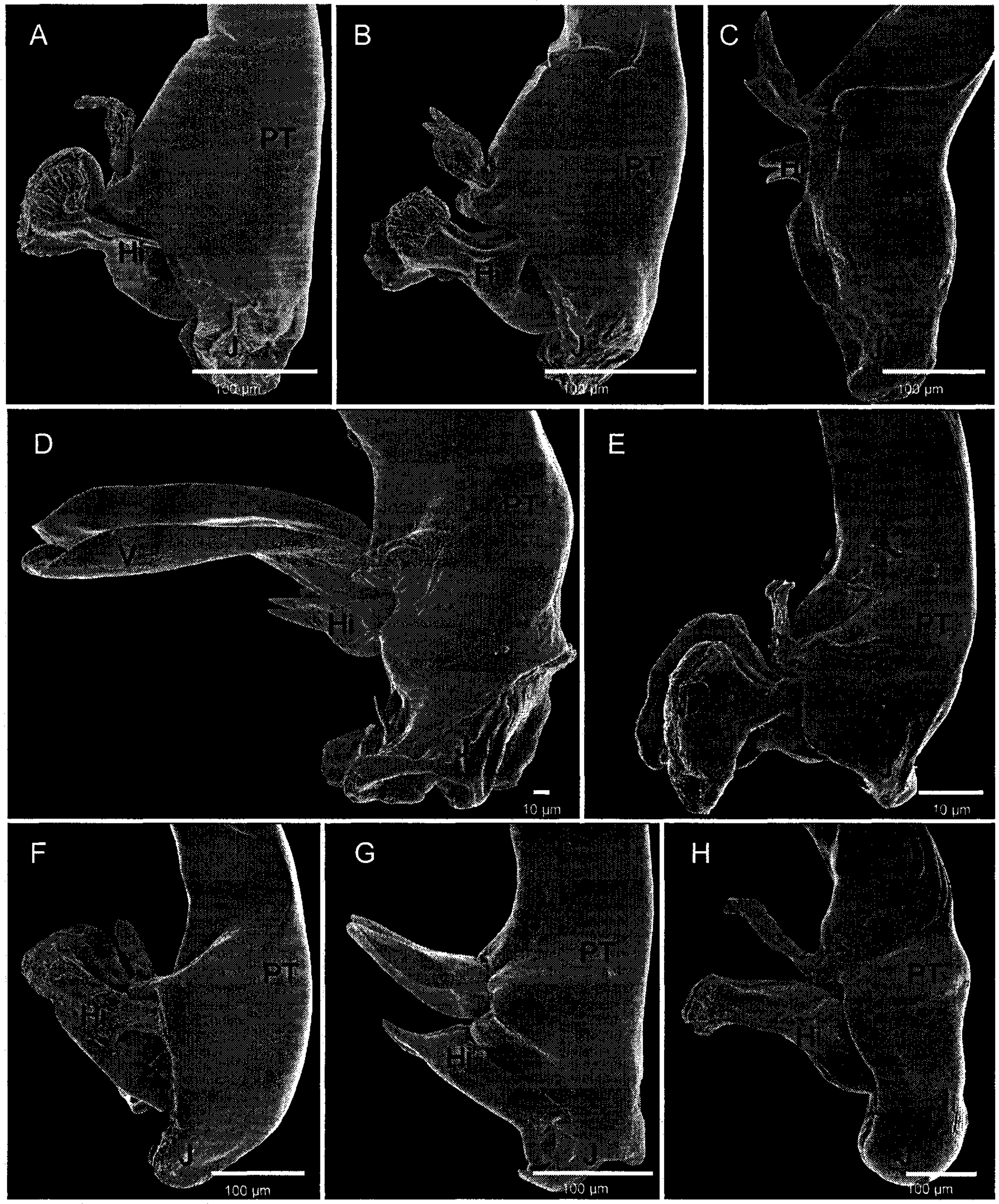

**Figure 14.** *Ravinia*. Distiphallus lateral view: a) *R. columbiana*; b) *R. rufipes*; c) *R. errabunda*; d) *R. effrenata*; e) *R. heithausi*; f) *R. pernix*; g) *R. derelicta*; h) *R. querula*. Abbreviations (Figs. 4-23): *Ha* - harpes; *Hi* - hillae; *EA* - ejaculatory apodeme; *J* - juxta; *LS* - lateral stylus; *MS* - median stylus; *PT* - phallic tube; *SD* - sperm duct; *V* - vesica

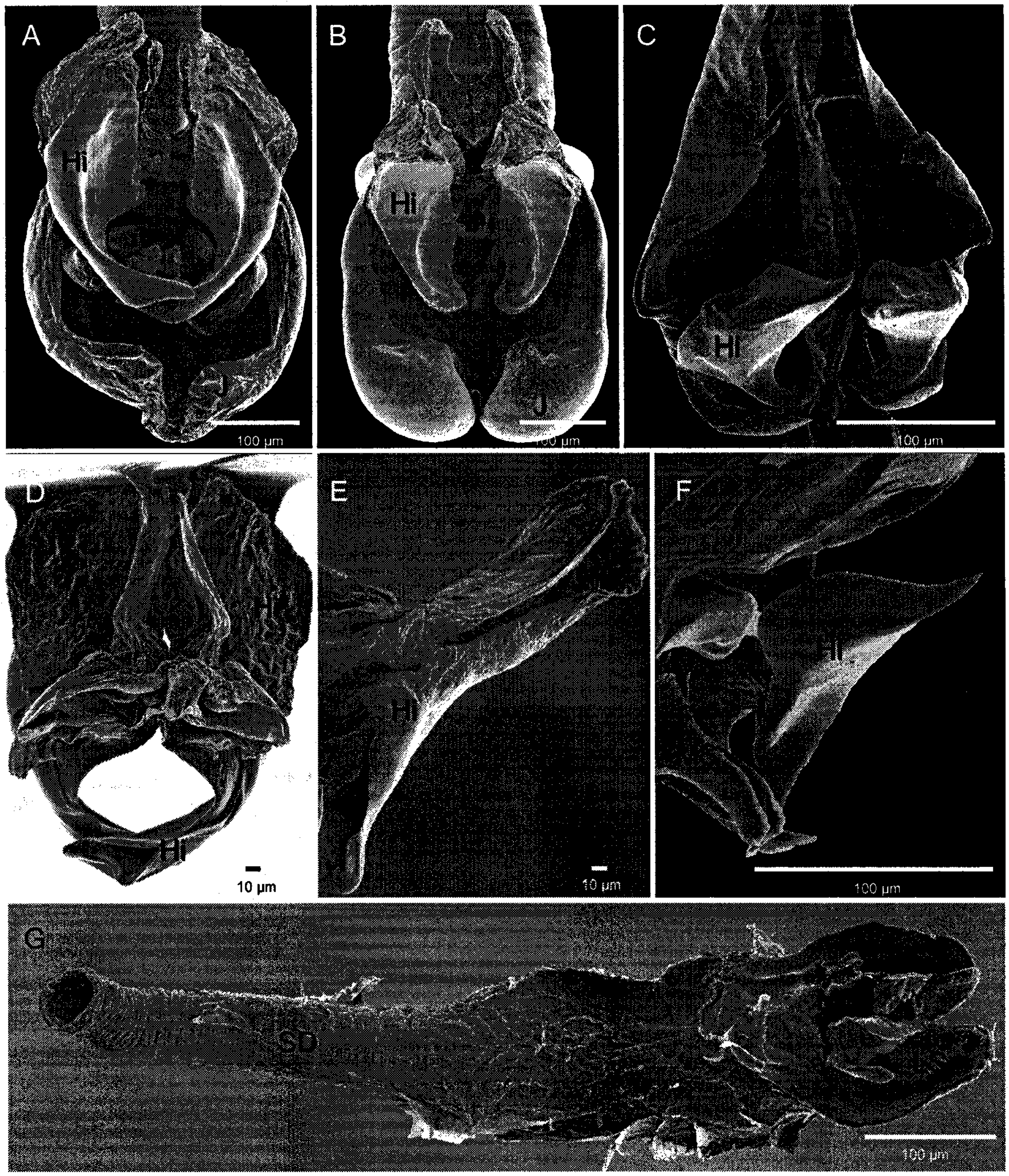

**Figure 15.** *Ravinia*. Distiphallus frontal view: a) *R. pernix*; b) *R. querula*. c) *R. derelicta,* phallic tube has been dissected to show sperm duct. d) *R. pernix,* hillae dorsal view; e) *R. querula,* left hillae lateral view; f) *R. derelicta*, left hillae lateral view; g) *R. pernix*, phallic tube has been removed to show sperm duct

**Figure 16.** *Ravinia*. Styli a) *R. querula*; b) *R. pernix*; c) *R. heithausi*; d) *R. errabunda*; e) *R. rufipes*; f) *R. columbiana*; g) *R. derelicta*; h) *R. effreneta*

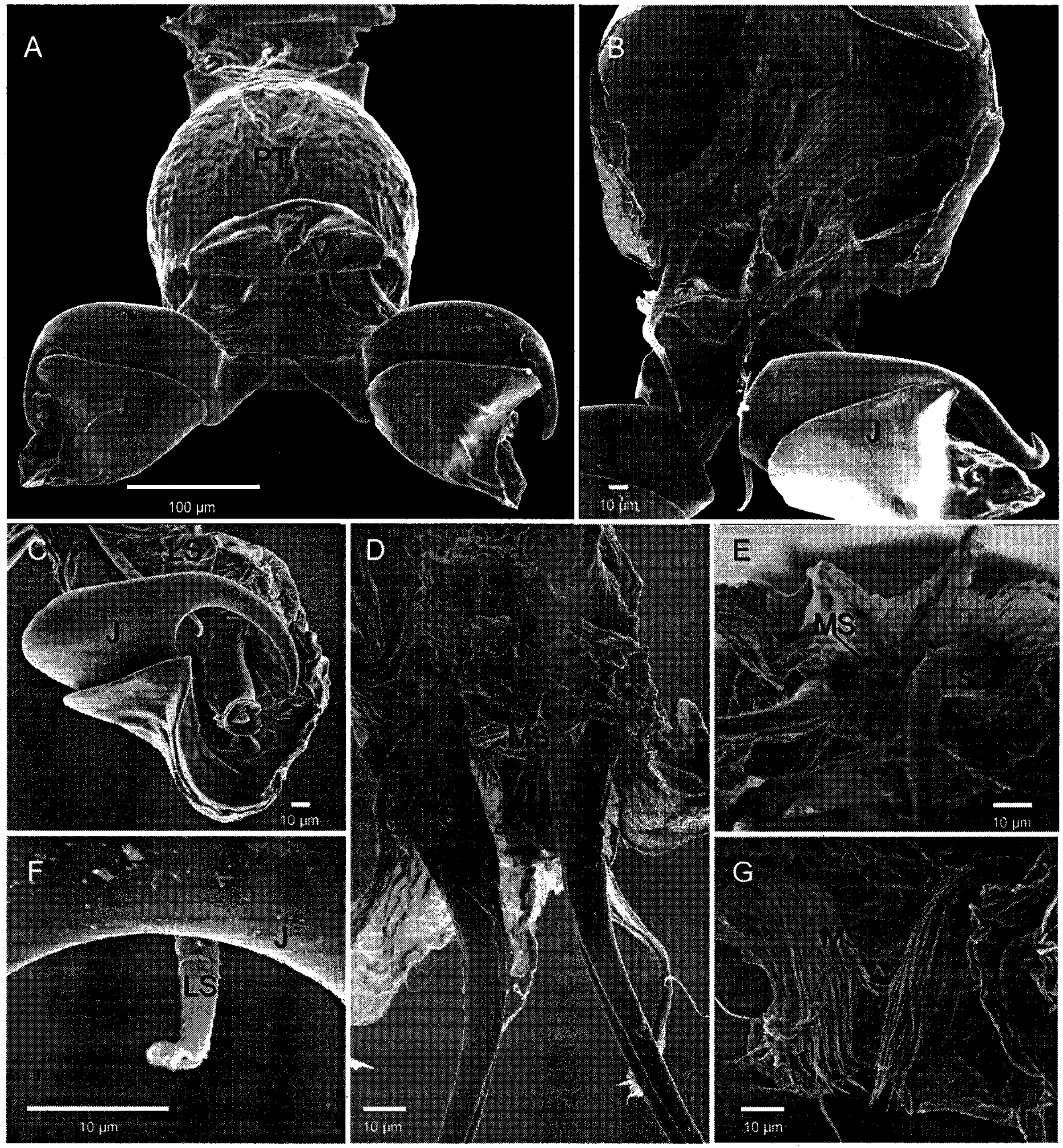

**Figure 17.** *Sarcodexia lambens*: a) distiphallus frontal view; b) distiphallus frontal view, vesica and phallic tube removed; c) lateral stylus in the apex of juxta arm; d) apex of lateral stylus; e) styli; f) median stylus opening; g) median stylus

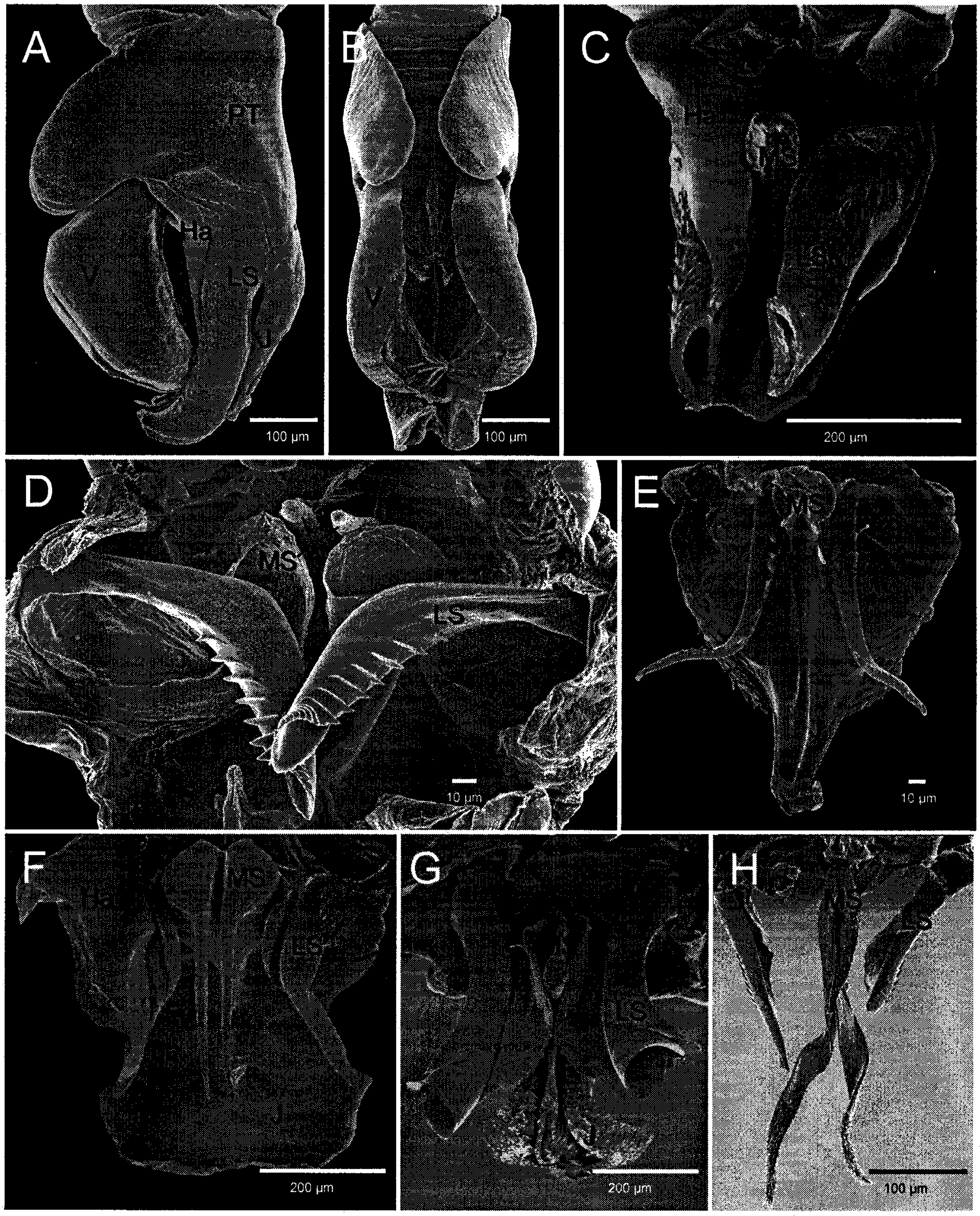

**Figure 18.** *Sarcophaga* (*s. str.*) *carnaria* (a-c): a) distiphallus lateral view; b) distiphallus frontal view; c) distiphallus frontal view, left harpe and vesica removed. Styli, harpes and vesica removed: d) *S.* (*Parasarcophaga*) *taenionota;* e) *S.* (*Phytosarcophaga) destructor;* f) *S.* (*Wohlfahrtiopsis*) *johnsoni,* right harpe preserved. g) *S.* (*Mehria) houghi*; h) *S.* (*Serniorwhitea) orientalis*

**Figure 19.** *Sarcophaga* (*Thyrsocnema) incisilobata* (a-c): a) distiphallus lateral view; b) distiphallus frontal view; c) distiphallus dorsal view. *S.* (*Phytosarcophaga) destructor*) (d-f): d) distiphallus lateral view; e) distiphallus frontal view; f) distiphallus dorsal view. *S.* (*Seniorwhitea) orientalis* (g-i): g) distiphallus lateral view; h) distiphallus frontal view (asymmetrical) ; i) distiphallus dorsal view

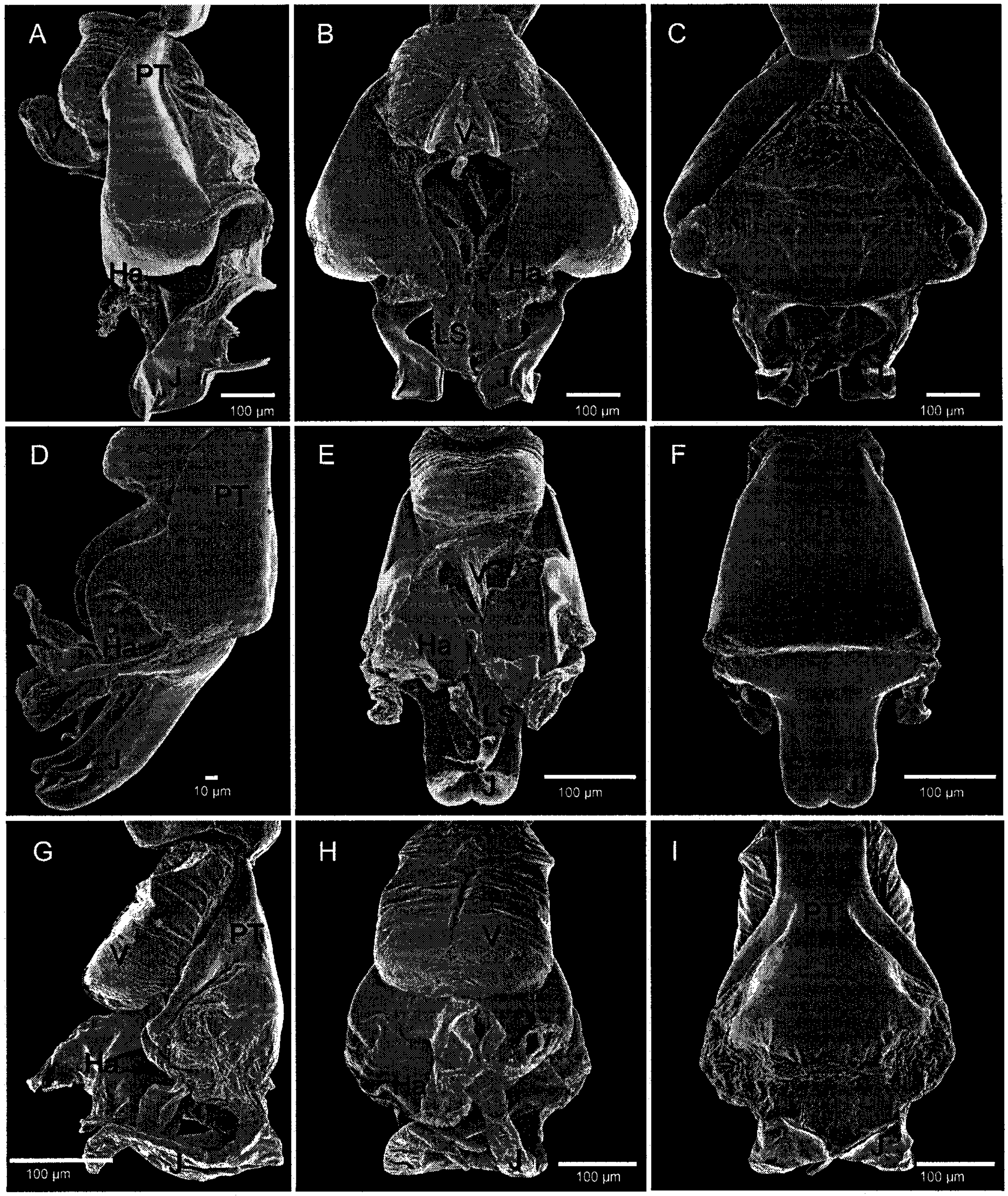

**Figure 20** *Sarcophaga* (*Liopygia) ruficornis* (a-c): a) distiphallus lateral view; b) distiphallus frontal view; c) distiphallus dorsal view. *S.* (*Heteronychia) haemorrhoa* (d-f): d) distiphallus lateral view; e) distiphallus frontal view; f) distiphallus dorsal view. *S.* (*Parasarcophaga*) *taenionota* (g-i): g) distiphallus lateral view; h) distiphallus frontal view; i) distiphallus dorsal view

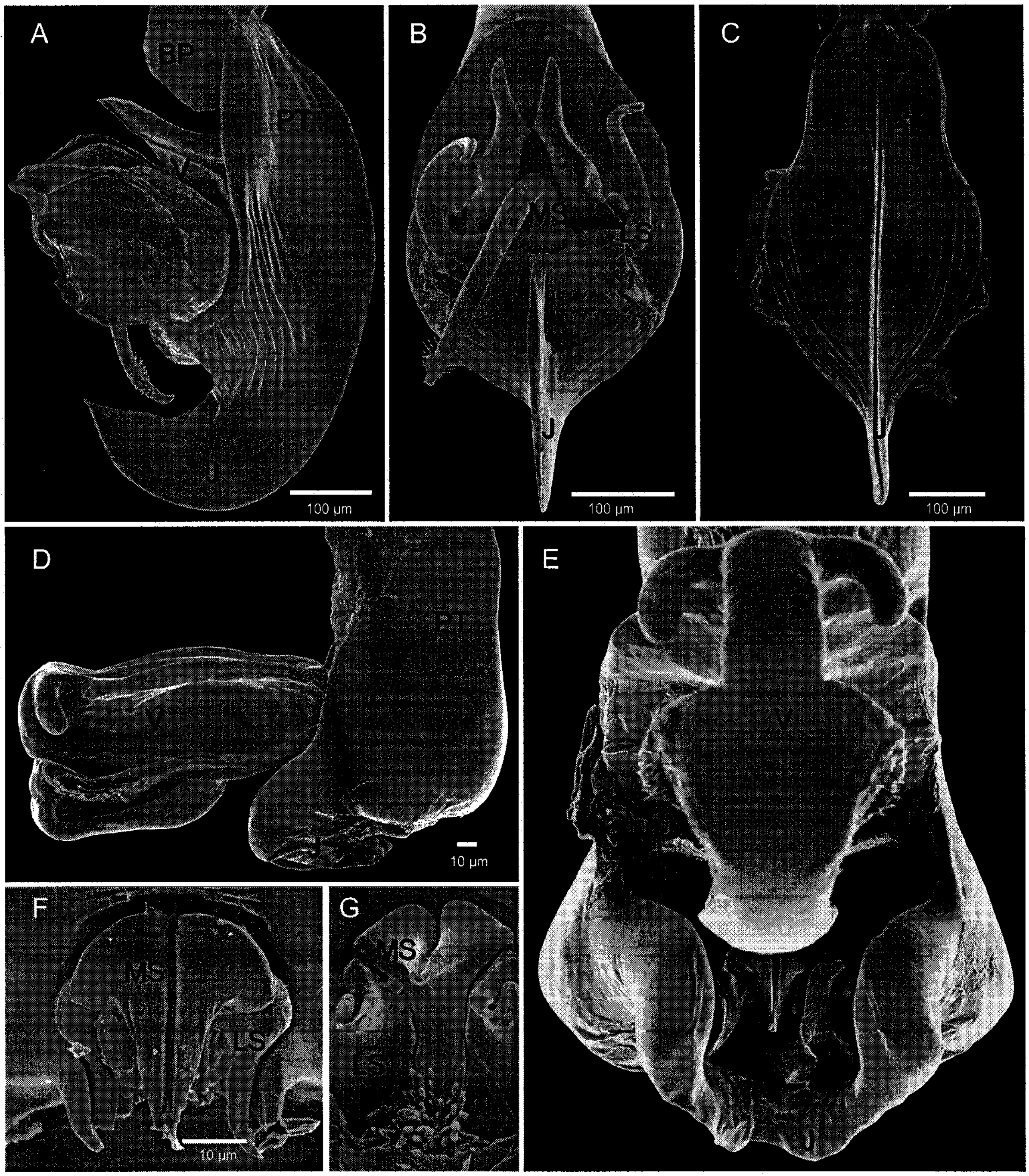

**Figure 21.** *Spirobolomyia singularis* (a-c): a) distiphallus lateral view; b) distiphallus frontal view, part of vesica removed; c) distiphallus dorsal view. *Tricharaea (Sarthromyia) simplex* (d-g): d) distiphallus lateral view; e) distiphallus frontal view; f) styli dorsoventral view; g) styli frontoventral view

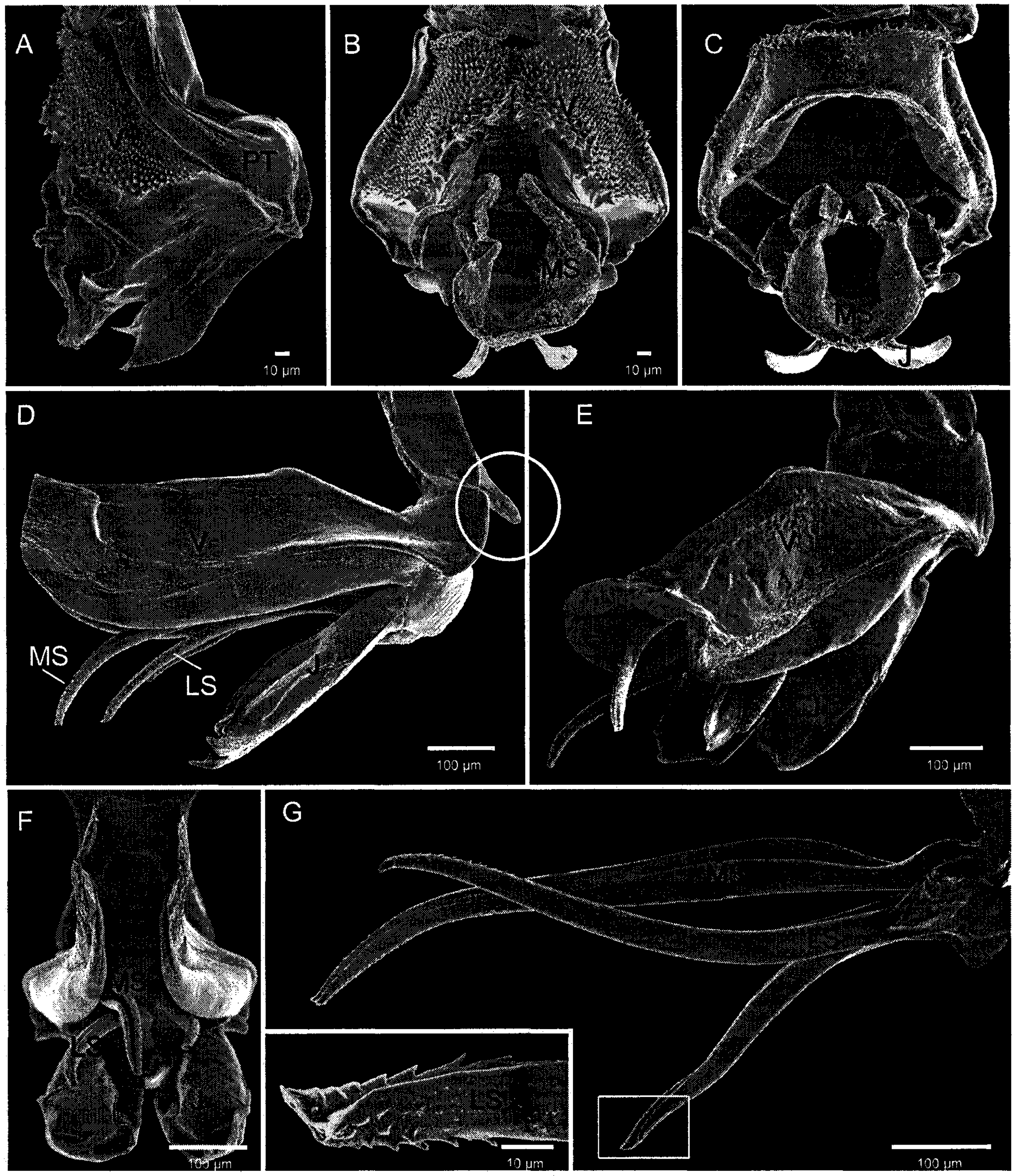

**Figure 22.** *Titanogrypa (s. str.) alata* (a-c): a) distiphallus lateral view; b) distiphallus frontal view; c) distiphallus frontal view, vesica removed. *Titanogrypa (Cucullomyia) placida* (d-g): d) distiphallus lateral view, dorsal hump (char. 61) is circled; e) distiphallus dorso-lateral view; f) distiphallus frontal view; g) styli

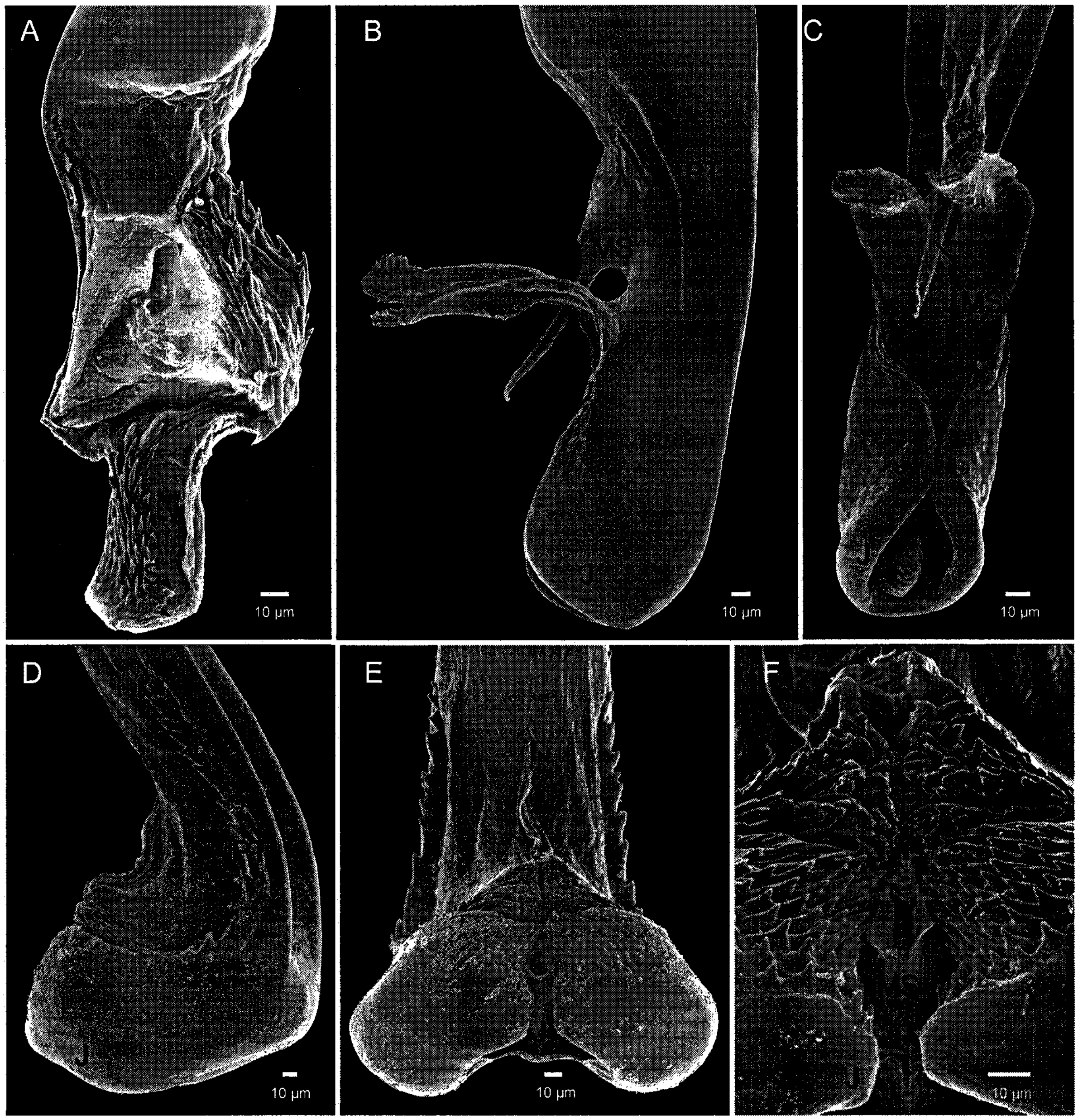

**Figure 23.** *Macronychia aurata* (Miltogramminae): a) acrophallus lateral view. *Sarcophila sp.* (Paramacronychiinae): b) acrophallus lateral view; c) acrophallus frontal view. *Brachicoma devia* (Paramacronychiinae): d) acrophallus lateral view; e) acrophallus frontal view; f) median stylus frontal view

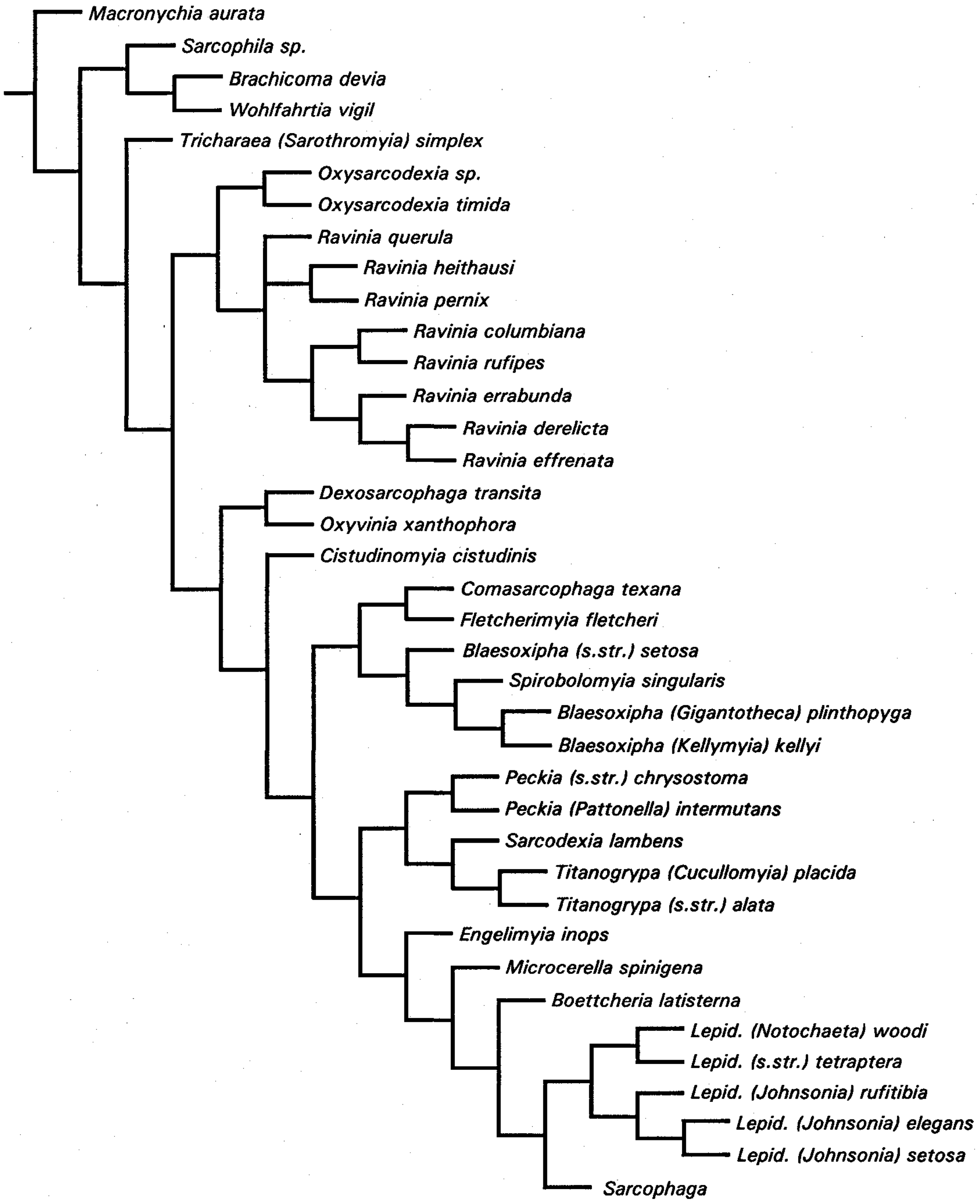

**Fig. 24.** Strict consensus tree of 140 most parsimonious trees (length 413) obtained from analysis under implied weights (k=3). Values of bootstrap (3000 replicates) (in bold and italics) and relative Bremer support (in italics) are given below branches.

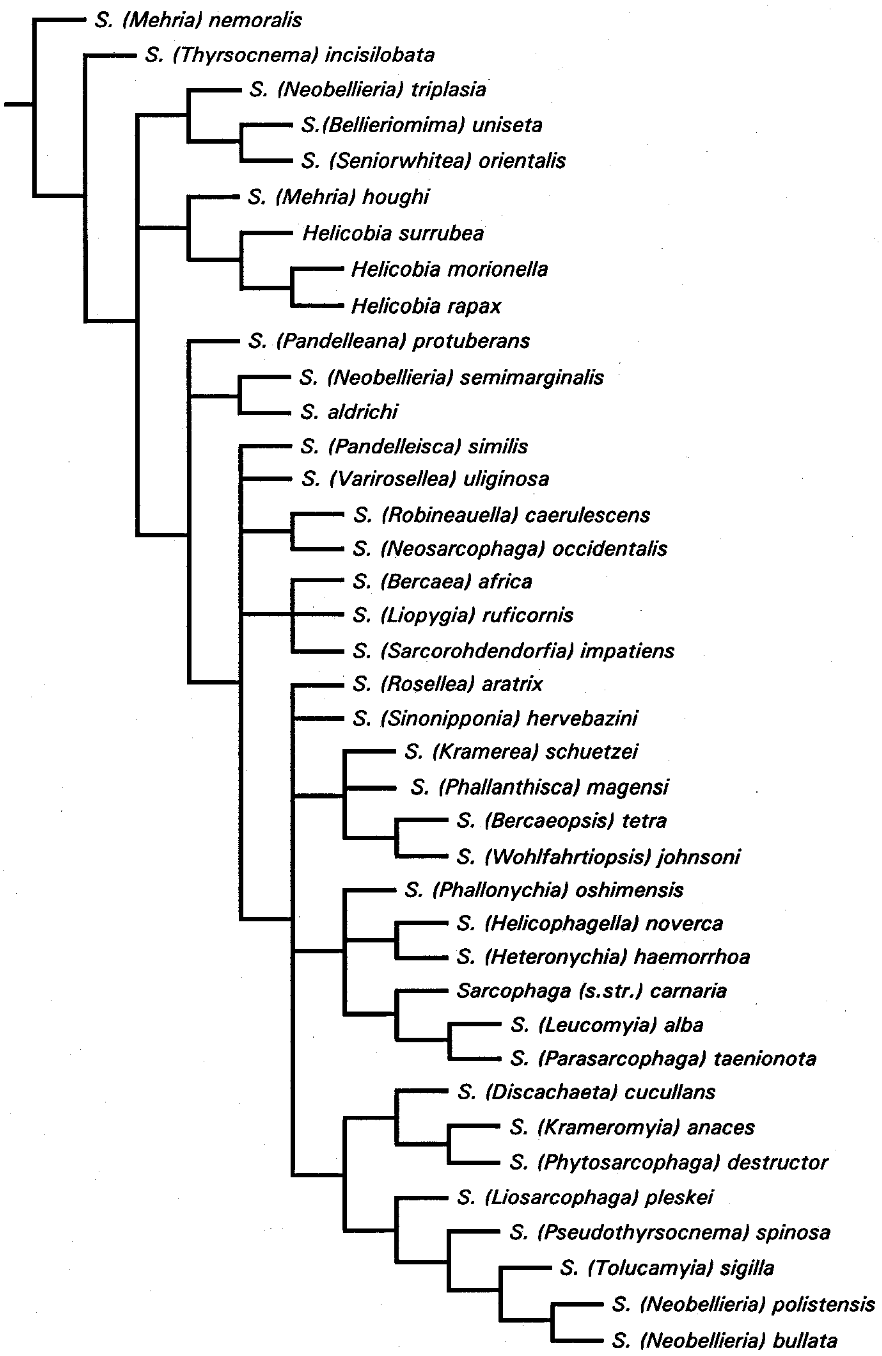

**Fig. 25.** Strict consensus tree of 140 most parsimonious trees (length 413) obtained from analysis under implied weights (k=3) showing topology within *Sarcophaga* s.l. Values of bootstrap (3000 replicates) (in bold and italics) and relative Bremer support (in italics) are given below branches.

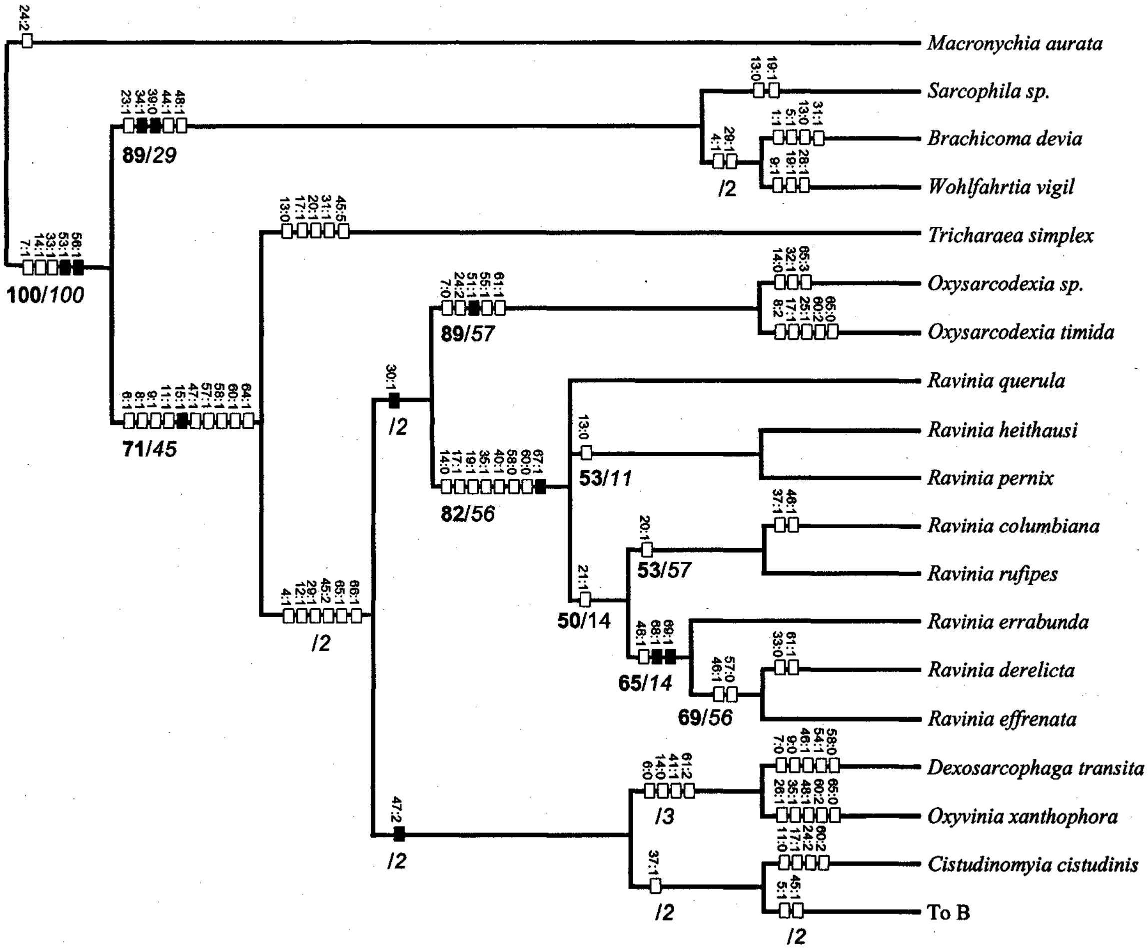

**Fig. 26a.** One of 140 most parsimonious trees obtained from analysis under implied weights (k=3) showing character distibution. Black hashmarks represent uniquely derived character states; white hashmarks represent homoplasious character states.

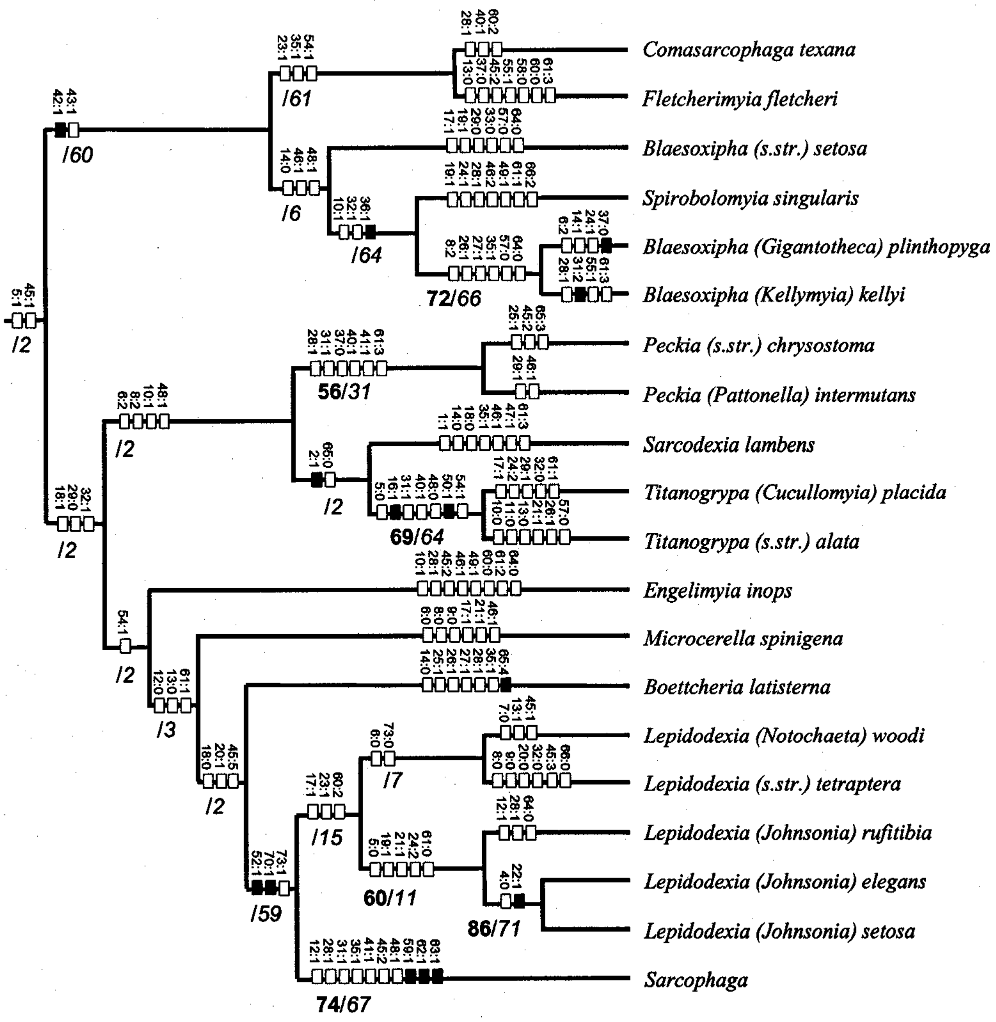

**Fig. 26b.** One of 140 most parsimonious trees obtained from analysis under implied weights (k=3) showing character distibution. Black hashmarks represent uniquely derived character states; white hashmarks represent homoplasious character states.

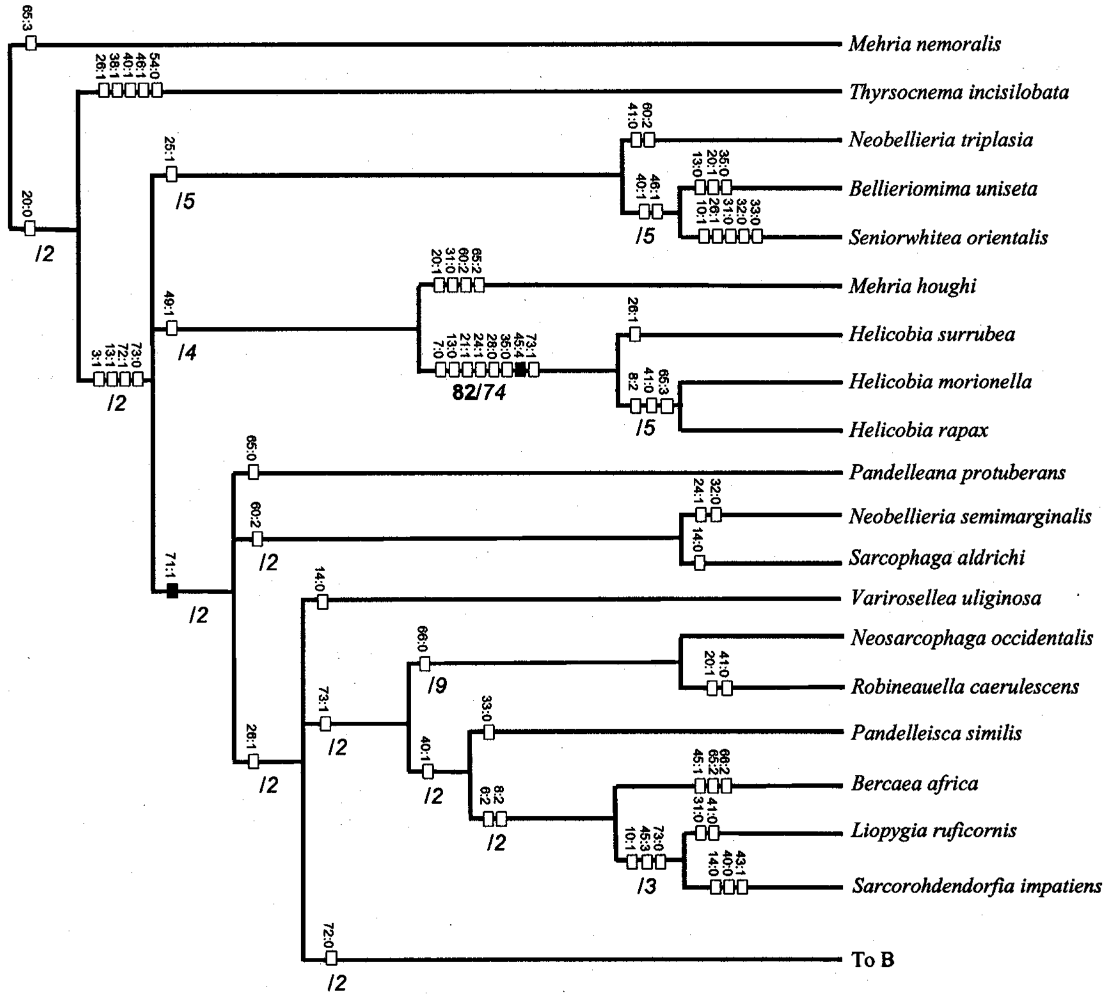

**Fig. 27a.** One of 140 most parsimonious trees obtained from the analysis under implied weights (k=3) showing character distribution within *Sarcophaga* s.l. Black hashmarks represent uniquely derived character states; white hashmarks represent homoplasious character states.

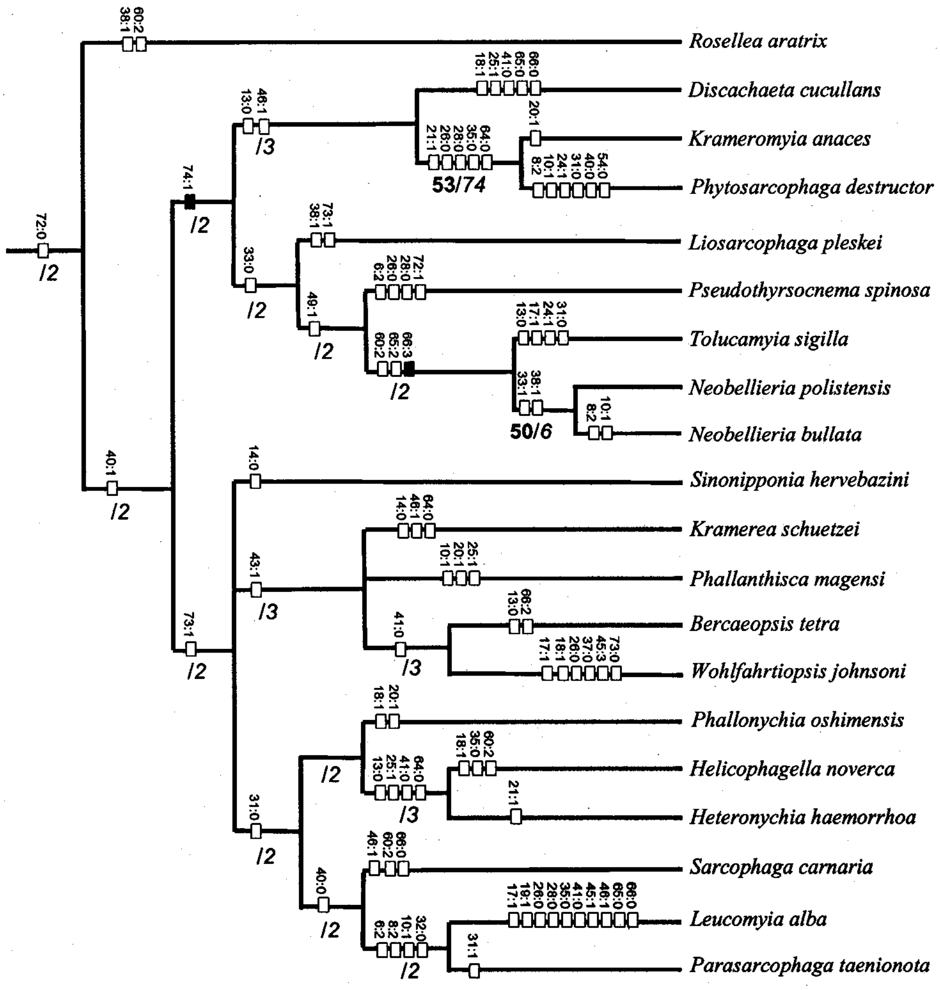

**Fig. 27b.** One of 140 most parsimonious trees obtained from the analysis under implied weights (k=3) showing character distribution within *Sarcophaga* s.l. Black hashmarks represent uniquely derived character states; white hashmarks represent homoplasious character states.

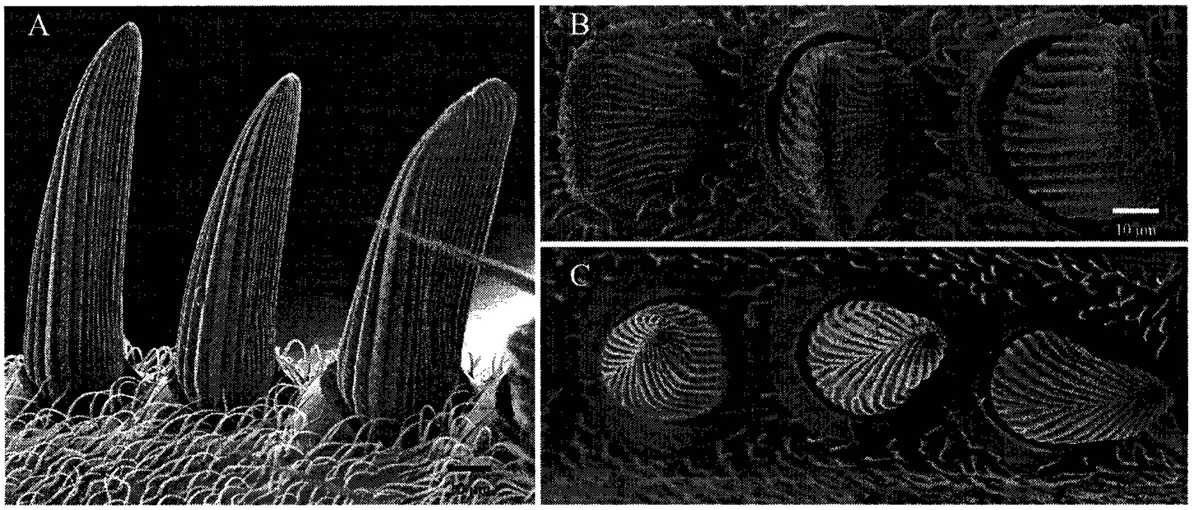

**Figure 29.** *Ravinia heithausi*: a) flattened spines of mid femoral ctenidium, lateral view; b) ventral view. *Dexosarcophaga transita*: c) rounded spines of mid femoral ctenidium, ventral view

## CONNECTING STATEMENT

The phylogenetic analysis presented in chapter 2 put the genus *Sarcophaga* s.l. Meigen in the context of its subfamily and provided support for its monophyly. *Sarcophaga* is the largest genus of Sarcophaginae and the monophyly of most of its 133 subgenera has never been tested cladistically. However, Chapter 2 demonstrated that the exclusively New World subgenus *S.* (*Neobellieria*) Blanchard is polyphyletic since the species *S.* (*N.*) *triplasia* Wulp and *S.* (*N.*) *semimarginalis* Hall form two separate species groups not related to the type species *S.* (*N.*) *polistensis* Hall. The analysis also supported a sister-group relationship between the *S.* (*N.*) *polistensis* species group and the New World subgenus *S.* (*Tolucamyia*) Dodge. In chapter 3 the subgenus *S.* (*Neobellieria*) is redefined to include the five species of the *S.* (*N.*) *polistensis* group, the species previously assigned to *S.* (*Tolucamyia*) and one new species. This chapter consists of a species-level revision in which all of the included species are redescribed and illustrated.

# CHAPTER 3. Systematics and phylogeny of the subgenus *Sarcophaga* (*Neobellieria)* Blanchard (Diptera: Sarcophagidae)

**ABSTRACT** The subgenus *Sarcophaga* (*Neobellieria*) Blanchard is revised. The subgenus as previously recognized, was polyphyletic. *Sarcophaga triplasia* Wulp and the four species of the *Sarcophaga semimarginalis* species group are removed from the subgenus. The remaining species of *Neobellieria* are paraphyletic relative to the subgenus *Tolucamyia* Dodge; accordingly, *Tolucamyia* is synonymized with *Neobellieria*. *Neobellieria* is redefined to include five species previously assigned to *Neobellieria* (*Sarcophaga bullata* Parker, *S. citellivora* Shewell, *S. cooleyi* Parker, *S. libera* Aldrich, *S. polistensis* Hall), three species previously assigned to *Tolucamyia* (*Sarcophaga cavagnaroi* (Dodge), *S. schrameli* Dodge, *S. sigilla* Reinhard) and one new species, *S.* (*Neobellieria*) *longisterna* Giroux and Wheeler. *Sarcophaga marstoniana* (Dodge) is synonymized with *S. sigilla*. Lectotypes are designated for *Sarcophaga bullata* and *S. cooleyi*. Although there are relatively few rearing records for most *Neobellieria* species, the species at the base of the tree develop primarily in vertebrates or vertebrate carrion; this group includes myiasis-causing species and species useful in forensic entomology. Two species nested higher in the tree (*S. libera, S. polistensis*) are associated with nests of Hymenoptera. *Neobellieria* apparently originated in the Nearctic region and the recently derived lineages subsequently colonized the northern Neotropical region.

**KEY WORDS** Diptera, *Neobellieria, Tolucamyia, Sarcophaga,* systematics, myiasis, forensic

With over 790 described species, *Sarcophaga* Meigen is the largest genus in the flesh fly family Sarcophagidae (Pape 1996). The genus is divided into 133 subgenera, approximately half of which are monotypic. Although a comprehensive phylogenetic analysis is needed to corroborate the monophyly and subgeneric-level phylogenetic relationships of *Sarcophaga* (Pape 1996; 1998), an exemplar-based phylogenetic analysis including 36 exemplar species in 31 subgenera, provided good support for its monophyly (Giroux 2006).

Aside from *S.* (*Helicophagella*) Enderlein (Blackith et al. 1997) the monophyly of most of the subgenera within *Sarcophaga* has not been tested. This is the case with the subgenus *Neobellieria* Blanchard. *Neobellieria*, as currently defined, comprises ten New World species (Pape 1996), primarily in the Nearctic region. The phylogenetic analysis of Giroux (2006) found that *Neobellieria*, represented by four exemplar species, was polyphyletic. The monophyly of the clade *S.* (*N.*) *bullata* Parker + *S.* (*N.*) *polistensis* Hall was supported but *S.* (*N.*) *triplasia* Wulp and *S.* (*N.*) *semimarginalis* Hall were placed elsewhere in *Sarcophaga*: *S.* (*N.*) *triplasia* and the clade *S.* (*Bellieriomima*) *uniseta* Baranov + *S.* (*Seniorwhitea*) *orientalis* Parker were sister-groups whereas *S.* (*N.*) *semimarginalis* + *Sarcophaga aldrichi* Parker formed a separate clade. The phylogenetic analysis also supported a sister-group relationship between the clade *S.* (*N.*) *bullata* + *S.* (*N.*) *polistensis* and *Tolucamyia sigilla* Reinhard as well as a sister-group relationships between this latter grouping and representatives of two Old World subgenera: *S.* (*Pseudothyrsocnema*) *spinosa* Villeneuve and *S.* (*Liosarcophaga*) *pleskei* (Rohdendorf).

The biology of *Neobellieria* species is incompletely known but some of them are economically important. *Sarcophaga* (*N.*) *bullata*, *S.* (*N.*) *citellivora* Shewell and *S.* (*N.*) *cooleyi* Parker cause myiasis and are of medical and veterinary significance (Stewart

1934, James 1947, Curtis 1956, Michener 1993). The species *S.* (*N.*) *bullata* and *S.* (*N.*) *cooleyi* are associated with vertebrate carrion and are likely to be collected on decaying human remains (Byrd and Castner 2001, Wells et al. 2001). *Sarcophaga* (*N.*) *bullata* is also frequently used as a study species for basic entomological research (e.g., Perfectti and Werren, 2001, Dacks et al. 2003).

Many species of *Sarcophaga* may be collected during the first and/or second wave of insects associated with decomposing human and animal cadavers (Smith 1986, Goff 1993, Byrd and Castner 2001) but there are few suitable identification keys for these species and their identification is difficult (Goff 1993, Byrd and Castner 2001, Wells et al. 2001, Zehner et al. 2004). Species identification of sarcophagids collected from corpses could provide evidence for the postmortem interval (Wells and Lamotte 2001), antemortem abuse or neglect (Wells et al. 2001) or postmortem transport of a corpse (Benecke 1998). In light of the potential importance of *Neobellieria* species as forensic indicators, a revision of the subgenus is necessary and relevant. *Neobellieria* is here redefined to include the five species of the *S.* (*N.*) *polistensis* group, the species previously assigned to *S.* (*Tolucamyia*) and one new species. The four species of the *S.* (*N.*) *semimarginalis* group and *S.* (*N.*) *triplasia* are removed from *Neobellieria.*

This revision is based on characters of adult flies. Illustrations and descriptions of larvae and puparia of *S.* (*N.*) *bullata* and *S.* (*N.*) *cooleyi* have been published by Knipling (1936), Sanjean (1957), Sivasubramanian and Biagi (1983) and Dahlem (1991).

## Materials and Methods

This revision was based on specimens housed in the following institutions: American Museum of Natural History, New York, NY, USA (AMNH); California Academy of

Sciences, San Francisco, CA, USA (CASC); Canadian National Collection of Insects, Ottawa, ON, Canada (CNC); Field Museum of Natural History, Chicago, IL, USA (FMNH); Personal collection of Gregory A. Dahlem (GD); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); Museu Nacional/Universidade Federal do Rio de Janeiro, São Cristóvão, Rio de Janeiro, Brazil (MNRJ); Montana State University, Bozeman, MT, USA (MTEC); Northern Forestry Centre, Canadian Forest Service, Edmonton, AB, Canada (NFC); Université de Montréal, Montreal, QC, Canada (QMOR); Royal Ontario Museum, Toronto, ON, Canada (ROM); Snow Entomology Collection, University of Kansas, Lawrence, KS, USA (SEMC); Swedish Museum of Natural History, Stockholm, Sweden (SMNH); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); University of Minnesota, St. Paul, MN, USA (UMSP); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). The label data of primary types are given verbatim with data from a single label enclosed in single quotation marks and line changes on a label shown by a slash.

For examination of terminalia, the abdomen was removed from pinned male specimens, placed in hot 10% KOH for about five minutes, and transferred to glycerin for dissection (more details in Giroux 2006). Female terminalia were separated from the abdomen by cutting the membrane between segments 4 and 5 and were cleared in the same way as males. All structures were rinsed twice in water, once in 70% ethanol, placed in 20% acetic acid for 5-8 minutes and washed again in 70% ethanol. For SEM study, terminalia were dissected as described above except that the phallus was dissected in 70% ethanol instead of glycerin and dried in two successive changes of 70% ethanol, followed by two changes of 100% ethanol. Each dried phallus was coated with 20nm of platinum and examined using a Jeol-JSM-6335F Field emission SEM at the Zoological Museum of Copenhagen. Line drawings were made using a compound or dissecting microscope equipped with a drawing tube. Female terminalia were photographed using a digital camera on a dissecting microscope. Females were associated with males by mating pairs collected in copula, and through agreement in collecting localities and dates with identifiable males. Body length was measured from the anterior margin of the head, excluding antennae, to the posterior margin of abdominal tergite 5, thus excluding terminalia. This method removes apparent variation in total length based on whether or not male terminalia were extended prior to pinning, but also gives a length measurement that is lower than the "total length" of the specimen. Thus, this measurement should be used with caution.

A character matrix was compiled using Mesquite version 1.05 (Maddison and Maddison 2004). Twenty-seven characters (26 binary, 1 multistate treated as non-additive) were included in the analysis, including 7 external characters of adults, 16 characters of male terminalia and 4 characters of female terminalia. *Sarcophaga* (*Pseudothyrsocnema*) *spinosa* and *S.* (*Liosarcophaga*) *pleskei* were used as outgroups based on the results of the phylogenetic analysis of Giroux (2006). Trees were generated using the program TNT version 1.0, 2005 (Goloboff et al. 2003). Unweighted analyses were conducted under the parsimony criterion. Cases of character state polymorphism in terminal taxa were treated as independent changes of states within each taxon, adding extra steps to the overall tree length. An exhaustive search was conducted and branches were collapsed if maximum branch length was zero. The relative degree of support for individual nodes was assessed with bootstrap values calculated from 1000 bootstrap replicates and Bremer support (Bremer 1994) performed using a sample of 30,000 suboptimal trees that were 1 to 7 steps longer than the optimal trees.

## ***Sarcophaga* (*Neobellieria*) Blanchard**

*Neobellieria* Blanchard 1939: 822 (type species: *Neobellieria brethesi* Blanchard 1939 [= *Sarcophaga polistensis* Hall 1933] by original designation).

*Sapromyia* Roback 1954: 64 (type species: *Sarcophaga bullata* Parker 1916, by original designation) (synonymized with *Sarcophaga* by Downes 1965: 957, with *Neobellieria* by Lopes 1969: 51).

*Tolucamyia* Dodge 1965: 256 (type species: *Tolucamyia marstoniana* Dodge 1965, by original designation) **new synonym.**

*Sarcophaga* (*Neobellieria*): Pape (1996: 366).

*Sarcophaga* (*Tolucamyia*): Pape (1996: 411).

**Diagnosis.** *Neobellieria* may be distinguished from other subgenera of *Sarcophaga* only by male and female genitalic characters Males have two rounded vesical lobes bearing thorn-like spines and with horn-shaped lateral styli The dome-shaped window of male sternite 5 will distinguish *S. bullata*, *S. citellivora*, *S. cooleyi*, *S. libera*, and *S. polistensis*. Females are characterized by the depression of the central part of sternite 7.

**Male.** Body length 5.5-14.0 mm. Head: ground color black or brown usually with bronze, silvery or yellowish pruinosity; postocellar setae forming a group of medium to long proclinate hair-like setae and setae extending to or beyond level of paravertical setae;

inner vertical seta reclinate; outer vertical seta as long as or slightly longer than upper postocular; proclinate orbital setae absent; upper orbital setae reclinate; number of medioclinate frontal and interfrontal setae variable; frontal vitta dark brown; fronto-orbital plate with scattered black hairs; parafacial yellowish, greyish or brownish pruinose, with scattered black hairs; color of genal and postgenal hairs variable; most occipital setae white, usually 1-2 rows of black setae below postocular setae; antenna dark to light brown, junction between pedicel and first flagellomere sometimes orange-red; palpus pale to dark brown, often slightly clavate. Thorax: ground color black or brown, usually with grey, white, bronze or silvery pruinosity; presutural acrostichal setae absent; 1 pair of prescutellar acrostichal setae; 4-5 presutural dorsocentral setae, slightly stronger than adjacent clothing setae; number of postsutural dorsocentral setae variable; 1-2 presutural intra-alar setae (anterior one stronger) + 1-2 postsutural intra-alar setae (posterior one stronger); 1-2 + 3-4 supra-alar setae; anterior postpronotal seta present; 2 basal postpronotal setae; proanepisternum usually bare; 2 postalar setae; intrapostalar setae reduced or absent; postalar wall haired; scutellum with 1 strong and long subapical, 1 basal and 1 discal pair of setae; variable number of strong anepisternal setae, upper two always shorter and declinate; 2-3 katepisternal setae, if three then middle one usually smaller; infrasquamal setae present; posterior spiracle subtriangular with anterior fin-shaped fringe usually dark brown and posterior fringe usually paler. Wing membrane hyaline; veins pale-brown; tegula dark, brown pruinose, setulose on about half of its surface, with a short black bristle on outer margin and 2 long black bristles on inner margin; basicosta pale, golden-beige pruinose; C extending to $M_{1+2}$, the base strongly bristled with 2-3 stout bristles close to costagial break, usually with ventral row of equidistant minute setae extending to or just beyond $R_1$; weak costagial, humeral and subcostal breaks; costal spine absent or vestigial; subcostal sclerite and stem-vein golden-brown pruinose; base of stem-vein with cluster of golden-brown hairs; axillary sclerites golden-beige pruinose; $R_{4+5}$ setulose at base dorsally and ventrally, ventral row often extending to proximal half; bend of M acute, sometimes right-angled, bent part concave relative to cell $R_{4+5}$, extension at bend sometimes sclerotized but usually present as a short fold darkened by dense microtrichia; crossvein r-m sometimes slightly infuscated; $CuA_1$ ending at wing margin as a fold with dense microtrichia; $A_1$+$CuA_2$ not reaching wing margin; A distinct as a fold darkened by dense microtrichia; lateral margin of alula with fringe of dark hairs; calypteres creamy white; upper calypter rather rounded, posterior margin with white or brown short hairs; lower calypter broadly expanded and angular, posterior margin rather straight; hairs fringing calypteres extending to lateral margin of lower calypter. Legs: ground color pale to dark brown or black; fore and mid coxa covered with long hairs and strong setae; hind coxa covered with long hairs and 2-3 strong setae on lateral side; trochanters shining brown; hind trochanter usually with dense, ventral, strong setae (less dense on small specimens); fore femur usually with long ventral wavy hairs on proximal half or third, with complete row of strong dorsal and ventral setae (longer in middle) and complete row of shorter posterodorsal setae; fore tibia with 1 dorsal, 1 posterodorsal, 1 posterior and 1 posteroventral setae apically, 1-2 posterior setae on proximal two-thirds, 2-4 strong anterodorsal setae on proximal part; mid femur usually with row of short posteroventral setae on apical half or third, with a complete row of long anteroventral setae, with 3-5 strong mid anterior setae and with 2-3 strong posterodorsal setae apically; mid tibia usually with long ventral, anteroventral and posteroventral hair-like setae on distal half, with 2-5 short posterodorsal setae on proximal third, with 1-3 short to long mid anterodorsal setae, with 1 long anteroventral, 1 dorsal, 1 posterodorsal setae on apical third and setae of various lengths around apex; hind femur and tibia straight to slightly curved ventrally, usually with numerous long anteroventral, ventral, posteroventral and posterior wavy hairs (smaller and less dense on small specimens and on *S. citellivora*); hind femur sometimes slightly swollen, usually with 1 row of long anteroventral setae, with 2-3 dorsal and posterodorsal setae on apical third, with 1 complete row of long anterodorsal setae, with second restricted to proximal two-thirds; hind tibia with 2-3 anterodorsal and posterodorsal setae (anterodorsal row with weaker setae interspersed), with 1 strong and sometimes 1-2 weaker anteroventral setae at or before apical third, with 1 dorsal, 1 anterodorsal, 1 anterior, 1 anteroventral and 1 ventral setae of various lengths apically, apex with small pad of fine brown or black posteroventral and posterior setae; tarsomere length: 1>2>3>4<5, first and second hind tarsomeres with pad of fine bronze posteroventral and posterior setae. Abdomen elongate and slightly conical posteriorly; ground color black or brown with grey, bronze, silvery or yellowish pruinosity; tergites covered with small black setae dorsally and relatively long hairs ventrally; number of lateral marginal setae variable between tergites and between specimens; usually a pair of median marginal setae on tergite 4; margin of tergite 5 usually partly orange-reddish and with a marginal row of strong setae. Male terminalia: ground color yellowish-orange, black setulose; sternite 5 with V-shaped emargination posteriorly and usually with long base anteriorly, cleft of posterior margin with pad of black rounded stout bristles, innermost ones longer, window usually present and sometimes forming a prominent dome-shaped elevation anteriorly on base; tergite 6 vestigial or absent, syntergosternite 7+8 sometimes darker than epandrium, with anterodorsal emargination and with spiracle 7 dorsolateral; epandrium shining and globose, square in lateral view but usually with posteroventral extension covering a small portion of cerci in lateral view; surstylus triangular, proximal surface bare; cercal base clothed with long black hairs; cercal prong tapering and curving anteriorly, black on distal half, some species with dense brush of short stiff hairs on medial margin; bacilliform sclerites reduced or absent, hypandrial arms sometimes fused in posterior view and thus forming a ring, postgonal apodeme tapering along base of postgonite; pregonite with minute setulae along posterior surface, postgonite with a bristle usually near the middle, rarely at the base, of the anterior surface; vesica sclerotized, with two separate lobes bearing thorn-like spines apically, harpes well developed, fused or partly fused to phallic tube, laterally compressed, sclerotized on proximal part, membranous distally, covered with small teeth; lateral styli coiled at base, horn-shaped, with microserrations on distal part and with longitudinal cleft opened all along internal side, median stylus bifurcate, forming two short processes and with no opening; juxta fused to median stylus, partly or entirely sclerotized, separation from phallic tube is either a desclerotized strip or hinge-like.

**Female.** Body length 7.0-13.5 mm. Differs from male as follows: Head: outer vertical setae strong and well developed; proclinate orbital setae present; medioclinate frontal and interfrontal setae sometimes fewer than in male. Thorax: apical scutellar setae absent; 2-4 katepisternal setae, middle 1-2 usually smaller than others. Legs: hairs on distal half of mid tibia absent; mid femur with row of short posteroventral setae on apical half or third but setae thinner, no wavy hairs but 1 row of strong and long posteroventral setae in proximal half; hind femur without long ventral, anteroventral and posteroventral wavy hairs, second long anterodorsal setae on proximal two-thirds absent or reduced to 1-2 proximal setae, 3-4 strong posteroventral setae on proximal half; hind tibia with 1 strong and sometimes 2-3 weaker anteroventral setae at or before apical half. Abdomen rounded and slightly conical posteriorly; tergites covered with small black setae dorsally and ventrally, with relatively long hairs restricted to sternites and ventral margins of tergites. Margin of sternite 2 usually with 4 strong bristles. Margin of sternite 3 sometimes with a few strong bristles. Female terminalia: tergite 6 narrowly membranous mid-dorsally except in *S. sigilla* Reinhard, with variable number of marginal setae stronger dorsally than ventrally; spiracle 6 and 7 distinct on each plate of tergite 6; tergite 7 absent; tergite 8 absent, except in *S. sigilla*; sternites 6-8 not fused; central part of sternite 7 slightly to deeply depressed; sternite 8 reduced to a narrow sclerite covered with minute setae and usually with 1 long black seta laterally; cerci distinct.

**Remarks.** *Neobellieria* was described by Blanchard (1939) for *N. brethesi* Blanchard, which was later synonymized with *Sarcophaga polistensis* Hall. Roback (1954) assigned *S. polistensis*, *S. polistensis offecta, S. bullata, S. cooleyi* and *S. libera* Aldrich to the new genus *Sapromyia*, but Downes (1965) treated *Sapromyia* as a junior synonym of *Sarcophaga.* Lopes (1969) synonymized *N. brethesi* with *S. polistensis offecta* and included them in *Neobellieria* along with *S. triplasia*. Shewell (1987: 1169) and Pape (1996) included *Sapromyia* in *Neobellieria. Tolucamyia* was erected by Dodge (1965) who noted the similarity in the shape of the male cerci and sternite 5 between the two included species and *S. bullata*. Pape (1996) treated *Tolucamyia* as a subgenus of *Sarcophaga.*

### Key to males of *Sarcophaga* (*Neobellieria*)

Females are unknown for *S. cavagnaroi* (Dodge), *S. longisterna* n. sp., and *S. schrameli*

Dodge.

1. Postsutural dorsocentral bristles usually 3 (if 4, third one from scutellum reduced); male apical scutellar bristles absent; window of male sternite 5, if present, even with rest of base (Figs. 24, 49) (window absent in *S. longisterna*); demarcation between juxta and phallic tube a desclerotized strip ................................... 2

- Postsutural dorsocentral bristles 4 or more, posterior 2 stronger and longer than anterior 2; male apical scutellar bristles present; window of male sternite 5, if present, forming a dome-shaped elevation anteriorly (Fig. 36) (window absent in *S. schrameli*); demarcation between juxta and phallic tube a distinct hinge ........ 4

2. Postsutural dorsocentral bristles 3; dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; lateral margins of juxta straight (Figs. 20, 45) .......................................................................... 3

- Postsutural dorsocentral bristles 3 or 4 (if 4, third one from scutellum reduced); dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; lateral margins of juxta clearly concave (Fig. 64) ............................................................... S. (*Neobellieria*) *sigilla*

3. Syntergosternite 7+8 elongate (Fig. 49); male sternite 5 without window (Fig. 48); short stiff hairs restricted to medial margin of cercal prong . ............................................................ . *S.* (*Neobellieria*) *longisterna*

- Syntergosternite 7+8 not elongate (Fig. 24); sternite 5 with window (Fig. 23);

short stiff hairs covering cercal prong (Figs. 21, 22)

…………………………………………………… *S.* (*Neobellieria*) *cavagnaroi*

4. Moderately long costal spine usually present; margin of tergite 5 same color as rest of tergite; sternite 5 without window (Fig. 62); cercal prong abruptly narrowed apically (Figs. 60, 61); harpes strongly bent in lateral view (Fig. 57); juxta partly sclerotized ……………………………… *S.* (*Neobellieria*) *schrameli*

\- Long costal spine absent; margin of tergite 5 usually partly orange-red; sternite 5 with window forming a dome-shaped elevation anteriorly (Fig. 36); cercal prong not sharply narrowed apically (Figs. 53, 54); harpes straight in lateral view (Figs. 4, 25, 31, 38, 50); juxta entirely sclerotized ……………………………………… 5

5. Dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; hairs fringing calypter at fold creamy-white; base of male sternite 5 short (Figs. 35, 36) …………………………………………………………………… 6

\- Dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypter at fold pale brown or yellow; base of male sternite 5 long (Fig. 55)

……………………………………………………………………………………7

6. Window of sternite 5 forming sharply defined dome-shaped elevation anteriorly (Fig. 36); juxta as long as wide (Fig. 32); vesical lobes invaginated in lateral view (Fig. 31) ……………………………………………… *S.* (*Neobellieria*) *cooleyi*

\- Window of sternite 5 forming small dome-shaped elevation anteriorly; juxta wider than long (Fig. 26); vesical lobes not invaginated in lateral view.........................................................*S.* (*Neobellieria*) *citellivora*

7. Black, horn-like structure arising laterally from base of harpes (Figs. 3-5) ................................................................. *S.* (*Neobellieria*) *bullata*

- Black, horn-like structure at base of harpes absent (Figs. 38, 50, 51) .............. 8

8. Posterior margin of tergite 5 usually partly orange-red; apex of juxta longer than base, juxta deeply concave dorsally at base and with sinuous dorsal margin in lateral view (Fig. 38) .......................................... *S.* (*Neobellieria*) *libera*

- Tergite 5 usually entirely orange-red, with yellowish pruinosity; apex of juxta same length or shorter than base, juxta weakly concave dorsally and with dorsal margin not sinuous in lateral view (Fig. 50) .......................*S.* (*Neobellieria*) *polistensis*

***Sarcophaga* (*Neobellieria*) *bullata*** **Parker**

(Figs. 3-12)

*Sarcophaga georgina* Wiedemann of Felt (1913: 80) (misidentification).

*Sarcophaga* sp. of Parker (1914: 422).

*Sarcophaga bullata* Parker 1916: 359; Downes (1965: 957).

*Sarcophaga bison* Aldrich 1916: Plate 12, Fig.110. *Nomen nudum*

*Sapromyia bullata*: Roback (1954: 65).

*Neobellieria bullata*: Shewell (1987: 1176).

*Sarcophaga* (*Neobellieria*) *bullata*: Pape (1996: 366).

**Male.** Body length 7.0-14 mm. Head: 9 to 14 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-4 pairs of weak interfrontal setae, posterior ones usually better developed; gena usually black-haired with white setae close to genal suture; postgena white-haired. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior 2-3, apical scutellar setae present. Wing: lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe; posterior margin of upper calypter with white or brown short hairs; hairs fringing calypteres long and pale brown at fold. Legs: grey-white pruinosity; strong ventral setae on hind trochanter denser on large specimens; mid femur usually with long ventral wavy hairs on proximal half or third. Terminalia: window of sternite 5 forming a dome-shaped elevation anteriorly; harpes with well-developed black projection laterally, shape varying from sabre-shaped to antler-shaped (many intermediate forms) with or without covering of minute teeth (Fig. 3-4); distinct hinge between juxta and phallic tube; juxta short and straight (Fig. 5); short stiff hairs on medial margin of cercal prong moderately dense.

**Female.** Body length 7.5-13.5 mm. Differs from male as follows: Head: 8-12 medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-3 weak interfrontal setae, posterior ones better developed. Legs: mid femoral organ (Fig. 11) present. Abdomen: margin of sternite 3 often with 6-8 strong bristles, particularly on large specimens. Terminalia (Figs. 10, 12): posterior margin of tergite 6 with 6-8 strong marginal setae on each side, evenly spaced, about equal in size and restricted to dorsal half; sternite 6 deeply depressed, with numerous small setae posteriorly and laterally, with 6 to 8 long black setae on posterior margin; sternite 7 with 6 long and weak black setae on posterior margin; sternite 10 present and membranous, covered with short setae.

**Types.** LECTOTYPE (by present designation): ♂ labelled '714'; 'Cold Spring / Harbor. L. I.'; 'Type / M.A.C.'; 'Sarcophaga ♂ / bullata R.Pkr / det R.r. Parker' (USNM). PARALECTOTYPES(by present designation): USA: New York: Long Island, Cold Spring Harbor (5♂, 7♀, USNM); Nassau, 21.ix.1912 (1♀, USNM); New York, 77th St., bred (1♀, USNM); Rockland, 24.vii.1913 (1♂, USNM); Massachusetts: Amherst (1♂, USNM); Springfield, 18.viii.1913, on human excrement (1♂, USNM); Gloucester, 30.viii.1912, C.W. Johnson (2♂, MCZ); 1♂ Massachusetts Agricultural College (not examined); 2♂, 2♀ AMNH (not examined); 1♂, 1♀, Cornell University (not examined); 1♀, R. R. Parker Collection (not examined).

**Other material examined.** Over 800 ♂ and ♀ from many localities in the following states and provinces: **CANADA**: British Columbia; Manitoba; Ontario; Quebec; **MEXICO**: Morelos; **UNITED STATES**: Alabama; Arkansas; California; Connecticut; District of Columbia; Delaware; Florida; Georgia; Idaho; Illinois; Indiana; Iowa; Kansas; Kentucky; Louisiana; Maryland; Massachusetts; Michigan; Minnesota; Missouri; Mississippi; Montana; New Hampshire; New Jersey; New Mexico; New York; North Carolina; North Dakota; Ohio; Oklahoma; Oregon; Pennsylvania; South Carolina; South Dakota; Tennessee; Texas; Utah; Vermont; Virginia; Washington; Wisconsin (CNC, DEBU, GD, LEM, MNRJ, MTEC, QMOR, ROM, USNM, UMSP).

**Distribution.** Widespread Nearctic.

**Biology.** The larvae are saprophagous and breed in carrion (Aldrich 1916, Graenicher

1931, Dahlem 1991). Adults are often collected flying around decaying material such as cow dung and human excrement. Because of its carrion-breeding habits, *S. bullata* is often associated with human remains in forensic entomology (Byrd and Castner 2001, Wells et al. 2001). It has been documented as causing intestinal and cutaneous myiasis (Watson 1942, James 1947). *Sarcophaga bullata* is also used as a model species in physiological and behavioral studies (e.g., Bylemans et al. 1998, Cheung and Smith 1998, Franssens et al. 2005).

**Remarks.** Parker (1916) designated two specimens, a male and a female, as "types" in addition to 26 paratypes. Aldrich (1916) treated Parker's two "types" as holotype and allotype, but did not clearly state which of the specimens he considered the holotype; thus, this cannot be considered fixation of a lectotype by inference of holotype (ICZN 1999, Recommendation 73F). Because more than one specimen was designated as 'type' and because no holotype or lectotype was previously fixed for this species the male type has been designated as lectotype to fix the identity of *Sarcophaga bullata*.

### *Sarcophaga* (*Neobellieria*) *cavagnaroi* (Dodge)

(Figs. 18-24)

*Tolucamyia cavagnaroi* Dodge 1965: 259.

*Sarcophaga* (*Tolucamyia*) *cavagnaroi*: Pape (1996: 411).

**Male.** Body length 5.5-11.0 mm. Head: 9-13 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; 3-6 pairs of interfrontal setae, posterior ones usually better developed; fronto-orbital plate and parafacial with yellow pruinosity; fronto-orbital plate with few scattered black hairs; parafacial setosity often limited to single row close to eye and with 1-3 strong setae just before genal groove; gena black-haired; postgena black-haired with white setae posteriorly. Thorax: pruinescence often golden or shining yellow; 3 postsutural dorsocentral setae; proanepisternum usually setose, sometimes bare; apical scutellar setae absent. Wing: lateral margin of alula with fringe of dark hairs longer than those on anterior margin of anal lobe; posterior margin of upper calypter with white or pale brown short hairs; hairs fringing calypteres long and pale brown at fold. Legs: mid femur usually with long ventral and posteroventral wavy hairs on proximal half or third; long anteroventral setae on hind femur reduced to 2-4 setae apically, some setae slightly stronger than adjacent clothing hairs. Terminalia: window of sternite 5 even with rest of base (Figs. 23-24); horns on harpes reduced or absent; harpes strongly bent in lateral view (Fig. 18); desclerotized strip between juxta and phallic tube (Fig. 20); dense short stiff hairs covering cercal prong (Figs. 21-22).

**Female.** Unknown.

**Types.** HOLOTYPE: ♂ labelled 'Guatemala / Panajachel / VIII-19-1963'; 'D. Q. Cavagnaro / and M. E. Irwin / collectors'; 'Tolucamyia / cavagnaroi / Holotype / Det. H. R. Dodge 1964'; 'California Academy / of Sciences / type No. 8891' (CASC).

**Other material examined. MEXICO**: **Chiapas**: Yerba Buena, 5200', 9-10.vi.1969 (1♂, CNC); Yerba Buena, Hwy 195, 24.vi.1969 (1♂, CNC); San Cristobal, 7000', 1-7.vi.1969 (1♂, CNC); San Cristobal de Las Casas, 7087', 13.vi.1969 (1♂, CNC); same except 11.vi.1969 (1♂, CNC); same except 7200', 14.v.1969 (1♂, CNC); 3 mi NE San Cristobal, 27.vi.1969 (1♂, CNC); 3 mi N San Cristobal, 7000', 4.vi.1969 (1♂, CNC).

**Distribution:** Neotropical: Chiapas, Mexico.

### ***Sarcophaga (Neobellieria) citellivora*** **Shewell**

(Figs. 14, 25-30)

*Sarcophaga citellivora* Shewell 1950: 245; Downes (1965: 958).

*Neobellieria citellivora*: Michener (1993: 148).

*Sarcophaga* (*Neobellieria*) *citellivora*: Pape (1996: 367).

**Male.** Body length 9.0-11.0 mm. Head: 9 -12 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-3 pairs of weak interfrontal setae; parafacial greyish, brownish or pinkish pruinose; gena usually black-haired with white setae close to genal suture; postgena white-haired; junction between pedicel and first flagellomere usually brownred; palpus dark brown to black. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones; prescutellar acrostichal sometimes absent; infrasquamal setae present but sometimes very sparse; apical scutellar setae present. Legs: grey-white pruinosity; fore femur with few long ventral wavy hairs on proximal part; mid femur with few long ventral wavy hairs on proximal half or third; mid tibia without long ventral, anteroventral and posteroventral bristlelike hairs on distal half and with second row of long anterodorsal setae on proximal two-thirds sometimes absent or reduced to 1-2 proximal setae. Wing: basicosta ivory-white pruinose, lateral margin of alula with fringe of dark hairs longer than those on anterior margin of anal lobe; posterior margin of upper calypter with white short hairs; hairs fringing calypteres long and creamy-white at fold. Abdomen: margin of tergite 5 sometimes partly orange-reddish. Terminalia: window of sternite 5 forming a small dome-shaped elevation anteriorly; harpes with sabre-shaped, short black horn laterally (Fig. 25); distinct hinge between juxta and phallic tube; juxta short, apex concave relative to base in lateral view (Figs. 25-26); cercal prong moderately curving forward; short stiff hairs on medial margin of cercal prong moderately dense.

**Female.** Body length 7.0-9.5 mm. Differs from male as follows: Head: 9-11 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule. Usually 2-3 pairs of weak or minute interfrontal setae. Leg: mid femoral organ absent. Terminalia (Figs. 14, 23): tergite 6 with moderately strong setae laterally, evenly spaced and about equal in size; sternite 6 slightly depressed; sternites 6 and 7 usually with 6 long and weak setae on posterior margin; sternite 8 rather broad compared to that of other species of subgenus; sternite 10 membranous and covered with short setae.

**Types.** HOLOTYPE: ♂ labelled 'Vavenby, B. C. / Ex. Citellus / columbianus'; 'Livestock Insect Lab. / Kamloops, B.C. / Reared 7 Aug 1950'; 'Sarc. / HOLOTYPE / citellivora / Shew. / No 5921' (CNC). ALLOTYPE: same data as holotype (1♀, CNC). PARATYPES: same data as holotype (1♂, 2♀, CNC; 1♂, USNM); same data as holotype except 10.viii.1950 (2♂, CNC); Alberta: Lethbridge, 18.vi.1926 (1♂, CNC); British Columbia: Kamloops, Livestock Insect Lab (2 larvae, not examined).

**Other material examined. CANADA**: **Alberta**: 5 km E, 1 km S Picture Butte (49°52'N, 112°43'W), reared from *Spermophilus richardsonii,* G. R. Michener (102♂, 109♀, LEM); Picture Butte, 30.viii.1990 (1♂, CNC); same except 29.viii.1990 (2♂, CNC); same except 6.xi.1990 (2♂, CNC); same except 3.xii.1990 (1♂, CNC); same except 31.x.1990 (2♂, 1♀, CNC); same except 20.vii.1989 (1♂, 1♀, CNC); same except 28.viii.1990 (1♀, CNC); Fort McLeod, 7.vii.1967, ex. scalp wound in child (2♂, 4♀, CNC); Longview, 11 mi. S. Turner Vall., 12.viii.1976, ex. male juvenile *S. richardsonii* (1♂, 1♀, CNC); Edmonton, from ear of Indian boy at Camsell Hosp., 7.x.1954, pupated en route, emerged Kamloops B.C., 15.iii.1955 (1♂, CNC); **Saskatchewan**: Pleasant Cr., 13.vii.1937 (1♂, CNC).

**Distribution.** Western Nearctic: Alberta, Saskatchewan

**Biology.** This species is primarily a parasite of ground squirrels (Shewell 1950, Michener 1993) and the LEM specimens were reared from Richardson's ground squirrels. There are also multiple recorded cases of human myiasis (Curtis 1956).

**Remarks.** A puparium is pinned below all type specimens except the paratype from Lethbridge, Alberta. Two additional specimens not listed in the original publication are also labelled as paratypes; they have the same data as holotype but do not have associated puparia.

### *Sarcophaga (Neobellieria) cooleyi* Parker

(Figs. 13, 31- 37)

*Sarcophaga cooleyi* Parker 1914: 417; Downes (1965: 958).

*Sapromyia cooleyi*: Roback (1954: 65)

*Sarcophaga* (*Neobellieria*) *cooleyi*: Pape (1996: 367).

**Male.** Body length 8.5-14 mm. Head: 7-10 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-3 pairs of weak interfrontal setae, gena usually black-haired, sometimes with white setae close to genal suture; postgena white-haired. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones: apical scutellar setae present. Wing: lateral margin of alula with fringe of dark hairs longer than those on anterior margin of anal lobe; posterior margin of upper calypter with white short hairs; hairs fringing calypteres long and creamy-white at fold. Legs: grey-white, brownish pruinosity; strong ventral setae on hind trochanter, denser on large specimens; mid femur usually with long ventral wavy hairs on proximal half or third. Abdomen: pair of median marginal setae usually absent on tergite 4; margin of tergite 5 sometimes partly orange-reddish. Terminalia: sternite 5 with window forming a sharply defined dome-shaped elevation anteriorly on base (Fig. 36); vesical lobes slightly invaginated in lateral view (Fig. 35); harpes with well-developed sabre-shaped black horn laterally which is not covered with minute teeth, apex of harpes rather bulbous (Fig. 31); distinct hinge between juxta and phallic tube; juxta long, curved in lateral view, apex split into two diverging parts (Fig. 32); short stiff hairs on medial margin of cercal prong moderately dense.

**Female.** Body length 8.0 -14.0 mm. Differs from male as follows: Head: 7-9 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-3 pairs of weak or minute interfrontal setae. Thorax: 4 katepisternal setae, middle two smaller than the others. Leg: mid femoral organ sometimes present. Abdomen: relatively long hairs on sternites and on ventral margin of tergites rarely present. Terminalia (Figs. 13, 37): tergite 6 with 7-9 strong marginal setae on each side, evenly but closely spaced, about equal in size and concentrated on dorsal half; sternite 6 flattened, covered with small setae on posterior half, with 6-8 long black setae on posterior margin; sternite 7 with 6 long, weak black setae on posterior margin; sternite 10 vestigial.

**Types.** LECTOTYPE (by present designation): ♂ labelled 'Laurel Mont. / 8-3-1914'; 'Type / M.A.C.'; 'Sarcophaga / cooleyi ♂ / det. R. R. Parker' (USNM). PARALECTOTYPES: USA: Montana: Laurel, 19.ix.1914 (1♀, USNM); same except 29.vii.1914 (1♂, 2♀, USNM; 2♀, MTEC); same except 02.viii.1914, bred fish (5♂, 3♀, USNM, 1♂, MTEC); same except 01.viii.1914 (2♂, USNM; 1♂, MTEC); same except 19.vii.1914 (1♂, USNM); same except 23.vii.1914 (2♀, USNM; 1♀, MTEC); same except 27.vii.1914 (1♂, MTEC; 1♀, USNM); same except 12.ix.1914 (1♀, USNM).

**Other material examined.** Over 300 ♂ and ♀: **CANADA**: **Alberta**: Lethbridge, Claresholm, Brooks, Orion, Cowley, Onefour, Purple Springs; **British Columbia**: Lillooet, Fountain Valley, Kamloops, 7 mi N Oliver, McGillivray Falls, Keremeos, Medicine; **Manitoba**: Lyleton; **Saskatchewan**: Allan, Indian Head, Saskatoon, Langenburg, Earl Grey, Pheasant Cr., Swift Current, Burnham, Strongfield, Hughton, Willows, Great Deer, Abernethy, Dollard, Maymont, Pike Lake, St. Louis, Melfort, Fort Qu'Appelle, Echo Valley Prov. Pk.; **Ontario**: Ottawa; **Yukon Territory**: Kluane N.P., Whitehorse; **UNITED STATES**: **California**: Nice, Modoc Co., Eureka, Sacramento, Coachella, Indio, Mecca, Siskiyou Co., El Dorado, Inyo Co., 7 mi. SE Truckee;

**Colorado**: Estes Park, Grand Junction, Garfield Co.; **District of Columbia**: Washington; **Idaho**: Moscow, Burley, Rigby; **Indiana**: Montgomery Co.; **Michigan**: Hillsdale Co.; **Montana**: Laurel, Miles City, Bigfork, Florence, Park Co., Billings, Powder Co., Glacier Nat. Pk.; **Nevada**: Reno, 12 mi SW Wells; **North Dakota**: Beach, Minot, Bottineau, Mandan, Bismark, Valley City; **Oregon**: Boardman, Dixie, Newport, Boiler Bay, Lake Co., Klamath Co., Lower Klamath Lake, Deschutes Co., Rainier, Tillamook Co., Adrian, Neskowin, Grant Co.; **Utah**: Cache Co., Logan, Great Salt Lake, Bryce Canyon, Stockton, Washington Co., Utah Lake, Panguitch, Dividend; **Washington**: Pullman, Ritzville, Seaview, Wenatchee, Copalis, Oysterville, Mount Rainier N. P., Ilwaco, Colfax, Tucannon, Asotin, Vantage; **Wisconsin**: Stratford, Brooks, Yellowstone Lake, Elbe; **Wyoming**: Park Co., Cody, Mountain View (CNC, FMNH, GD, MNRJ, MTEC, NFC, ROM, UMSP, USNM).

**Distribution.** Primarily western Nearctic: Yukon Territory to California, east to Saskatchewan, Wisconsin, Michigan and Indiana (eastern records from Ottawa and Washington D.C.)

**Remarks.** One of the male syntypes has been designated as the lectotype to fix the identity of this species.

**Biology.** Larvae of *S. cooleyi* have been reared from a range of decaying substrates including vertebrate carrion (Parker 1914, Dahlem 1991) and invertebrates. They have been identified as a parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) (Coppel 1960) and larvae have also been recorded from adult

Noctuidae (Lepidoptera) (unpublished specimen record in CNC) although the label data do not indicate whether the specimens were reared from the noctuid or dissected from the host. There are records of *S. cooleyi* larvae causing myiasis, including human cases (Stewart 1934, James 1947).

***Sarcophaga* (*Neobellieria*) *libera* Aldrich**

(Figs. 15, 38-43)

*Sarcophaga libera* Aldrich 1916: 235; Downes (1965: 958).

*Sapromyia libera*: Roback (1954: 65).

*Sarcophaga* (*Neobellieria*) *libera*: Pape (1996: 367).

**Male.** Body length 8.5-12.5 mm. Head: 9-13 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-3 pairs of weak interfrontal setae, posterior ones usually better developed; gena usually black-haired, sometimes with white setae close to genal suture; postgena white-haired. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones; apical scutellar setae present. Wing: lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe; posterior margin of upper calypter with white or brown short hairs; hairs fringing calypteres long and pale brown at fold. Legs: grey-white pruinosity; strong ventral setae on hind trochanter, denser on large specimens; mid femur usually with long ventral wavy hairs on proximal half or third; mid tibia sometimes without long ventral, anteroventral and posteroventral bristle-like hairs on distal half. Terminalia: window of sternite 5 forming a dome-shaped elevation anteriorly; horns on harpes reduced or absent; distinct hinge between juxta and phallic tube; juxta long, apex longer than base, base usually concave relative to apex in lateral view (Fig. 38); short stiff hairs on medial margin of cercal prong moderately dense.

**Female.** Body length 9.5 -11.0 mm. Differs from male as follows: Head: 8-12 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 2-4 pairs of weak interfrontal setae, posterior ones sometimes better developed; parafacial greyish, brownish or pinkish pruinose. Legs: mid femoral organ absent. Terminalia (Figs. 15, 43): tergite 6 with moderately strong setae on each side evenly spaced and about equal in size; sternite 6 slightly depressed, covered with short to long setae and hairs on posterior two-thirds, with 8-10 long black setae on posterior margin; sternite 7 with few weak and short black setae on posterior margin; sternite 10 membranous and covered with short setae.

**Types.** HOLOTYPE: ♂ labelled ' Beaver Creek, / MONT. 6300 ft. / S. J. Hunter. / August, 1913.'; 'Sarcophaga / libera / Type 1916 Ald.' (SEMC).

**Other material examined.** 152♂ and 10♀: **CANADA**: **British Columbia**: Burnaby, Vancouver Island, Thetis Pk., Mission City, Badger Lake, near Knouff Lake, Savary Island; **Manitoba**: Gillan; **Northwest Territories**: Hyndman Lake, Yellowknife, Rd. nr. Stoke Lake; **Ontario**: 7 mi E Griffith, Kenora District, Macdiarmid, Lake Nipigon Provincial Park, Thunder Bay; **Quebec**: Mont Rigaud, Gt. Whale R.; Sakami; **Yukon Territory**: Kluane Lake, Dempster Hwy (Mi 87, km 400, km 416, km 465), Carcross Sand Dunes; Russel Mt.; **UNITED STATES**: **Arkansas**: Crawford Co.; **Florida**: South, Lacoochee, Lake Jovita; **Georgia**: Dekalb Co., Stone Mt., Chatham Co., Macon, Thomasville, Head River, 1 mi N Pine Mountain, Savannah; **Illinois**: Mason Co., Mason

State Forest, near Forest City, 5 mi W Manito, ca. 4 mi W Monticello; **Idaho**: Mt. Moscow, Custer Co., 25 mi W of Stanley; **Indiana**: Montgomery Co., Shades State Park, Pulaski Co., Tippecanoe River State Park, Putnam Co., Lieber St. Pk.; **Louisiana**: Denham Springs; **Michigan**: Lansing, Otsego Co., Pigeon River, Clinton Co., Rose Lake Cons. Area, Shiawassee Co., Rose Lake Wildlife Exp. Stn., Black River, Marquette Co., 15 mi S Ishpeming; **Mississippi**: Washington Co., 3 mi N Leland; **Missouri**: Hillsboro; 5 mi N Hillsboro, Atherton; **Minnesota**: Duluth; **Montana**: Missoula, Mt. Sentinel; **North Carolina**: Watauga Co., Camp Broadstone, near Boone, Smokemont, Highlands, Whitesides Mtn.; **New York**: Fleetwood; **Ohio**: Amherst; **Oregon**: Benton Co., Corvallis, Wallowa Co., Hat Point, 21 km W Corvallis; **Tennessee**: Sevier Co., Chilhowee Mountains, Great Smoky Mountains Nat. Pk., Cades Cove; **Texas**: Pittsburg; **Washington**: White River, Mt Rainier; Puyallup (CNC, DEBU, FMNH, GD, LEM, MNRJ, ROM, USNM).

**Distribution.** Widespread Nearctic.

**Biology.** Although rearing records are few, there are records of larvae as predators of the pupae of *Dolichovespula arenaria* (Fabricius) (Hymenoptera: Vespidae) (specimen data in CNC and USNM). The males from Rigaud, QC were collected at a hilltop.

**Remarks.** A female specimen is pinned above the holotype. The left front leg of the holotype is glued to a label below the specimens.

***Sarcophaga* (*Neobellieria*) *longisterna* Giroux and Wheeler n. sp.**

(Figs. 44-49)

**Male.** Body length 11.5 mm. Head: postocellar setae extending as far as paravertical setae, 10 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; 3 pairs of minute interfrontal setae; fronto-orbital plate with few scattered black hairs; parafacial setosity limited to a few setae close to eye and with 2 strong setae just before genal groove; gena blackhaired; postgena white-haired with some black setae close to oral margin; occipital setae white and with 3 rows of black setae ventral to postocular setae. Thorax: 3 postsutural dorsocentral setae; apical scutellar setae absent. Wing: lateral margin of alula with fringe of dark hairs longer than those on anterior margin of anal lobe; posterior margin of upper calypter with white or pale brown short hairs; hairs fringing calypteres long and pale pale brown at fold. Legs: mid femur with long ventral and posteroventral wavy hairs on proximal half or third, posteroventral row on apical half with long and slightly stronger setae than adjacent clothing hairs; mid tibia with long ventral and posteroventral wavy hairs; long anteroventral setae on hind femur restricted to 2 setae apically. Abdomen: margin of tergite 5 with some orange-reddish color. Terminalia: sternite 5 without window (Fig. 48); syntergosternite 7+8 1.5 times longer than that of other species of the subgenus (Fig. 49); horns on harpes reduced or absent; harpes strongly bent in lateral view (Fig. 44); desclerotized strip between juxta and phallic tube; short stiff hairs on medial margin of cercal prong dense.

**Female.** unknown.

**Type.** HOLOTYPE: ♂ labelled 'Big Bend N. P. TEX. / Pine Can. 5-6000' / May 10 1959 / J. F. McAlpine' (CNC).

**Etymology.** From the Latin *longus* (long) and *sterna* (sternite). The name refers to the long syntergosternite 7+8 of this species.

**Distribution.** Southern Nearctic: Texas

***Sarcophaga* (*Neobellieria*) *polistensis* Hall**

(Figs. 16, 50-56)

*Sarcophaga polistensis* Hall 1933: 110; Downes (1965: 959).

*Sarcophaga polistensis offecta* Lopes 1938: 342.

*Neobellieria brethesi* Blanchard 1939: 823.

*Sapromyia polistensis*: Roback (1954: 65)

*Sapromyia polistensis offecta*: Roback (1954: 65)

*Neobellieria offecta*: Lopes (1969: 51).

*Sarcophaga* (*Neobellieria*) *polistensis*: Pape (1996: 367).

**Male.** Body length 7.0-12.0 mm. Head: ground color brown with whitish, yellowish or shining yellow pruinosity, sometimes with bronze or silvery pruinosity. 8-12 medioclinate pairs of frontal setae, row distinctly curving outwards at lunule; usually 2-3 pairs of weak interfrontal setae, posterior ones usually better developed; frontal vitta sometimes pale brown or reddishbrown; parafacial yellowish or brownish pruinose, sometimes bright yellow; gena usually blackhaired with white or yellow setae close to genal suture;

postgena white or yellow-haired; antenna dark to light brown, sometimes yellow. Thorax: pruinescence often golden or shining yellow; 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones; apical scutellar setae present. Wing: lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe; posterior margin of upper calypter with white or brown short hairs; hairs fringing calypteres long, pale brown or yellow at fold. Legs: grey-white or yellow pruinosity; fore femur with few or without long ventral wavy hairs on proximal part; fore tibia usually with 2-3 strong anterodorsal setae on proximal part; mid femur with few long ventral wavy hairs on proximal half or third; mid tibia without long ventral, anteroventral and posteroventral bristlelike hairs on distal half, second row of long anterodorsal setae on proximal two-thirds sometimes absent or reduced to 1-2 proximal setae. Abdomen: tergite 5 usually entirely orange-reddish and covered with yellowish pruinosity. Terminalia: window of sternite 5 forming a dome-shaped elevation anteriorly; horns on harpes reduced or absent; distinct hinge between juxta and phallic tube; apex of juxta same length or shorter than base, base rather straight relative to apex in lateral view (Fig. 50); short stiff hairs on medial margin of cercal prong moderately dense (Figs. 53, 54).

**Female.** Body length 9.0-10.5 mm. Differs from male as follows: Head: 7-10 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; interfrontal setae usually absent or minute. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones; sometimes 4 katepisternal setae, middle two smaller than others. Legs: mid femoral organ absent. Terminalia (Figs. 16, 56): Tergite 6 with 5-6 moderately strong setae on each side, concentrated on dorsal half; sternite 6 slightly depressed, covered with short setae on posterior third, usually with 6 long black setae on posterior margin; sternite 7 with few weak and short black setae on posterior margin; sternite 10 membranous and covered with short setae.

**Types.** HOLOTYPE: ♂ labelled 'H. B. Parks / collector'; 'Bexar Co. Texas / 8-24-1931'; 'Hall coll. / Sarcophagidae'; 'Holotype / *Sarcophaga* / *polistensis* / Hall' (USNM). ALLOTYPE: Texas: Bexar Co., 24.viii.1932 (1♀, USNM). PARATYPES: same data as allotype (1♂, USNM; 1♂, CNC); same except 5.iv.1929 (1♂, CNC); same except 16.viii.1932 (1♀, CNC); Oklahoma: Stillwater, 28.vii1932 (1♂, 1♀, USNM); Payne Co., 30.ix.1932 (1♂, USNM); same except 28.ix.1932 (1♀, CNC). HOLOTYPE of *S. polistensis offecta*: ♂ labelled 'Cantareira / Horto [Horto Florestal], S. Paulo / S. Lopes, III-1936' (MNRJ). PARATYPES: Itatiaia, 800 ms., xii.1933 (1♂, MNRJ); Angra E. do Rio / Japuhyba, ii.1935(1♂, MNRJ); same except i.1936 (1♂, MNRJ); Corcovado, Rio, x.1932 (1♂, MNRJ); Ch. da Floresta / Gavea [Rio de Janeiro], ix.1935 (1♂, MNRJ); Brasilien, Nova Teutonia, Sta. Catharina, 27 °11′S. 52° 23′W, 22.i.1937 (1♂, MNRJ; 1♂, CNC); Rio de Janeiro (Grajahú), 20.ii.1938 (3♂, not examined).

**Other material examined.** 78♂ and 13♀: **BRAZIL**: **Bahia**: Encruzilhada; **Maranhão**: Grajahu; **Mato Grosso**: Juína, Sinop; **Rio de Janeiro**: Itaguaí, Itatiaia; Instituto Oswaldo Cruz; **Rio Grande do Sul**: 15 de Novembro; **Santa Catarina**: Nova Teutonia, Therezopolis; **COLOMBIA**: Valle, near Candelaria; **COSTA RICA**: Guanacaste (Santa Rosa N. P.); **ECUADOR**: **El Oro**: Zaruma; **PANAMA**: Emperador Rd. km10, Canal Zone, near Frijoles; **MEXICO**: **Durango**: 5 mi W Durango; **Morelos**: Acatlipa; **Veracruz**: 8 mi W Sontecomapan; **UNITED STATES**: **Arizona**: Arizona City, Santa Rita Mts., Baboquivari Mt.; **Florida**: Miami, Dade City, 11 mi NW Copeland, Homestead, Royal Palm Pk.; **Illinois**: Carbondale; **Oklahoma**: Stillwater; **Texas**: Brownsville, Port Lavaca, Big Bend Nat. Pk., Dallas, College Station, Hidalgo Co., Austin, Castroville; **Virginia**: Dismal Swamp (CNC, MNRJ, SMNH, USNM).

**Distribution.** Southern Nearctic and Neotropical. Arizona to Virginia, south to Ecuador and Brazil.

**Biology.** Larvae inhabit nests of several species of *Polistes* Latreille (Hymenoptera: Vespidae) (Hall 1933, Blanchard 1939).

**Remarks.** Lopes (1938) distinguished *S. polistensis offecta* from *S. polistensis* by the absence of the ctenidium on the mid femur and by small details of the phallus. Pape (1996) did not consider *S. polistensis offecta* distinct and we found no consistent differences in either of the characters.

***Sarcophaga* (*Neobellieria*) *schrameli* Dodge**

(Figs. 57-62)

*Sarcophaga schrameli* Dodge 1967: 685.

*Sarcophaga* (*Tolucamyia*) *schrameli*: Pape (1996: 411).

**Male.** Body length 7.0-9.5 mm. Head: 8-11 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; 0-4 pairs of interfrontal setae, posterior ones usually better developed; gena black-haired; postgena white-haired with few black setae close to oral margin. Thorax: 4-5 postsutural dorsocentral setae, posterior two stronger than anterior ones; apical scutellar setae present. Wing: lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe; posterior margin of upper calypter with white or pale brown short hairs; hairs fringing calypteres long and pale brown at fold; long costal spine usually present. Legs: fore femur with few or without long ventral wavy hairs on proximal part; mid femur with few long ventral wavy hairs on proximal half or third and with a complete row of setae posteroventrally; numerous long or very long ventral, anteroventral and posteroventral wavy hairs absent on hind femur. Abdomen: margin of tergite 5 same color as other abdominal tergites. Terminalia: sternite 5 without window (Fig. 62); horns on harpes reduced or absent; harpes strongly bent in lateral view (Fig. 57); desclerotized strip between juxta and phallic tube; apex of cercal prong distinctly tapering; short stiff hairs on medial margin of cercal prong dense (Figs. 60, 61).

**Female.** Unknown.

**Types.** HOLOTYPE: ♂ labelled 'Matachic, Chih. / Mex. VII- 7 - 47'; 'D. Rockefeller / Exp. Schramel'; 'Sarcophaga / schrameli / Holotype / Det. H. R. Dodge 1966' (AMNH). PARATYPES: same data as holotype (2♂, not examined); same data as holotype except D. Rockefeller Exp. Cazier (1♂, AMNH); MEXICO: Chihuahua; San Jose Babicora, 7700ft., 04.vii.1947, D. Rockefeller / Exp. Michener (1♂, AMNH).

**Other material examined. MEXICO: Chiapas**, San Pedro Madero, *Coreopsis* stems, 29.viii.1909 (2♂, USNM); **Mexico**, 22 mi N Altacomulco, 8100', 18.viii.1964 (1♂, CNC); **Durango**, 11 mi W Durango, 7000', 13.vii.1964 (1♂, CNC); 20 mi NE Durango, 6400', 24.vi.1964 (1♂, CNC); 3 mi E El Salto, 8200', 4.vii.1964 (1♂, MNRJ).

**Distribution.** Southern Nearctic to Neotropical: Durango to Chiapas, Mexico.

**Biology.** Unknown.

### *Sarcophaga* (*Neobellieria*) *sigilla* Reinhard

(Figs. 17, 63-68)

*Sarcophaga sigilla* Reinhard 1947: 118; Downes (1965: 959).

*Tolucamyia marstoniana* Dodge 1965: 256. **New synonym**

*Sarcophaga* (*Tolucamyia*) *sigilla*: Pape (1996: 411).

*Sarcophaga* (*Tolucamyia*) *marstoniana*: Pape (1996: 411).

**Male.** Body length 6.0-11.0 mm. Head: 7-12 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; 2-5 pairs of interfrontal setae, posterior ones usually better developed; fronto-orbital plate with few scattered black hairs; parafacial setosity often limited to single row close to eye and with 0-3 strong setae just before genal groove; gena black-haired; postgena black-haired with white setae posteriorly, sometimes entirely black-haired; occipital setae white and with 2-3 rows of black setae ventral to postocular setae. Thorax: 3-4 postsutural dorsocentral setae, if 4, the third one from scutellum reduced; proanepisternum setose or bare; apical scutellar setae absent. Wing: sometimes a few spines extending to R1 ventrally on C; lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe; posterior margin of upper calypter with white short hairs; hairs fringing calypteres long and pale brown at fold. Legs: mid femur usually with long ventral and posteroventral wavy hairs on proximal half or third;

number of long anteroventral setae on hind femur ranging from 3-4 apical setae to an almost complete row. Terminalia: sternite 5 with window even with rest of base; horns on harpes reduced or absent; harpes strongly bent in lateral view (Fig. 63); desclerotized strip between juxta and phallic tube; short stiff hairs on medial margin of cercal prong dense.

**Female.** Body length 8.0-9.0 mm. Differs from male as follows: Head: 8-9 pairs of medioclinate frontal setae, row distinctly curving outwards at lunule; usually 3-5 weak interfrontal setae, posterior ones better developed. Wing: hairs fringing calypteres sometimes creamy-white at fold. Legs: mid femoral organ present. Terminalia (Figs. 17, 68): dorsal surface of tergite 6 even, with no setae dorsally, with moderately strong to weak setae on each side evenly spaced and about equal in size; tergite 8 present; sternite 7 slightly depressed; sternite 6 usually with 4-6 long and strong setae on posterior margin; sternite 7 with two long and strong setae on each side of posterior margin; sternite 8 with a row of tiny setae, slightly broader than those of other species of subgenus; sternite 10 membranous and covered with short setae.

**Types.** HOLOTYPE: ♂ labelled 'Huachuca Ms. / Ar. 7-8-32 / J. D. Beamer'; 'Holotype / S. sigilla / Reinhard'; 'Sarcophaga / sigilla / R. Rnh' (USNM).

HOLOTYPE of *Tolucamyia marstoniana*: ♂ labelled 'Mexico: Mexico / 20 mi. E. Toluca / July 31, 1962 / N. Marston -34'; 'Tolucamyia / marstoniana / Holotype / Det. H. R. Dodge 1964' (USNM). ALLOTYPE: ♀ same data as holotype.

**Other material examined. MEXICO**: **Mexico**, 3.5 mi. N. Teotihuacan, 30.vi -

01.vii.1982, 7300' (1♂, GD); same except 6.3 mi. E. summit Rt. 15, 8000', Bosencheve, 7-8.vii.1982, bark and logs conifer for. (1♂, GD); **Durango**, 14 mi. SW. El Salto, 8000', 9.vi.1964 (2♂, CNC); same except 24 mi. W. La Ciudad, 7000', 17.vii.1964 (1♂, CNC); same except 21.vii.1964 (1♂, CNC); **Sinaloa**, 4.5 mi. W. El Palmito, 6300', 25.vii.1964 (1♂, CNC); **Oaxaca**, Tehuantepec, 6.ix.1947 (1♀, CNC); **Michoacán**. Quiroga, 14.ix.1947 (1♂, MNRJ); Atzcap'co, 31.viii.1922 (1♂, USNM); **UNITED STATES**: **Arizona**: Huachuca Mtns. Ramsey Canyon, Hamburg trail (31° 26.3' N, 110°19.2' W), ca. 6300', 11.viii.1999 (5♂, GD); same except ca. 1.4 mi. along Hamburg trail, 23.ix.1994 (3♂, CNC); same except Carr Peak, 9200' (31° 24.8' N, 110°18.3' W), 12.viii.1999 (1♂, CNC); same except trail to Carr Peak from Reff Townsite, 7500'-8500' (1♂, CNC); Cochise Co., Rustlers Pk., 8000', 18.vi.1956 (1♂, CNC).

**Distribution.** Southern Nearctic to Neotropical: Arizona to Oaxaca and Michoacán, Mexico.

**Remarks.** The apex of the abdomen (tergites and sternites 4-5) of the holotype of *Tolucamyia marstoniana* is glued to the label. The only discernable differences between the holotype of *T. marstoniana* and that of *S. sigilla* were too minor to justify separation of the two species.

## Discussion

The phylogenetic analysis yielded 18 most parsimonious trees of 47 steps each. The monophyly of *Neobellieria* is supported by 11 synapomorphies (Fig. 2), three of which are uniquely derived within *Sarcophaga,* based on the exemplar study (Giroux 2006):

horn-shaped lateral styli (21:1) and two rounded vesical lobes (23:1) bearing thorn-like spines (24:1). In addition to the subgenera included in the exemplar study, the senior author also examined the type species of half the subgenera within *Sarcophaga* and none had the horn-shaped lateral styli (21:1). In addition to strong morphological support for the monophyly of *Neobellieria*, Wells et al. (2001) found that *S. (N.) bullata* and *S. (N.) cooleyi* were sister species based on mitochondrial DNA analysis, although their taxon sampling was limited: two species of *Neobellieria* and five other species of *Sarcophaga* were included in their analysis. Molecular analysis of additional species of *Neobellieria* would test our phylogenetic hypothesis and might also provide molecular tools to identify specimens, including females and larvae. The 18 most parsimonious trees differed in the placement of the five basal taxa of *Neobellieria*. The strict consensus tree is shown in Fig. 1. The clade *Sarcophaga citellivora* and *S. cooleyi* was treated either as the sister group to rest of the subgenus (as in Fig. 2) or as separate branches at the base of the tree. Both *S. citellivora* and *S. cooleyi* have sternite 5 with a short base (14:1) and free hypandrial arms (17:1). Both of these species also share the lateral sabre-shaped horn on the harpes (27:1) with *S. bullata*; *S. cooleyi* and *S. bullata* also have similarities in size and setosity of female tergite 6 (Figs. 12-13) as well as the absence of female tergite 8 (10:1) (Fig. 2). The former subgenus *Tolucamyia* is monophyletic (Fig. 2), supported by three autapomorphies: harpes strongly bent in lateral view (26:1), a partly sclerotized juxta (18:1) and black genal setae, with at least some white setae on the postgena (1:0). The latter character is, however, polymorphic in *S. bullata, S. polistensis* and *S. libera.* Although *Tolucamyia* is monophyletic, its recognition as a distinct subgenus would makes the five species currently assigned to *Neobellieria* paraphyletic and thus the synonymy of the two subgenera is justified.

*Sarcophaga citellivora, S. cooleyi* and *S. bullata* have similar ecological habits; larvae of all three species have been reared from vertebrate hosts and may opportunistically cause human myiasis (Stewart 1934, Watson 1942, Curtis 1956). The latter two species are also likely to be found feeding on human cadavers (Wells et al. 2001). Thus, development in vertebrate hosts may be plesiomorphic for *Neobellieria* species, although more outgroup comparisons, based on broader taxon sampling, would be required to provide support for this.

The three species of *Neobellieria* discussed above are the only members of the subgenus recorded from vertebrates. Larvae of *S. polistensis* and *S. libera* have been reared from nests of Vespidae, where they are apparently predaceous on the pupae. Although *S. cooleyi* has also been recorded in association with invertebrate hosts, those records are all from Lepidoptera, and the association with Hymenoptera nests may provide additional support for a sister-group relationship between *S. polistensis* and *S. libera*.

The biology of the four species of the former subgenus *Tolucamyia* is unknown and given their placement on the tree (Fig. 2), it is difficult to predict whether they are associated with vertebrate or invertebrate hosts.

*Sarcophaga* is most species-rich in the Old World, with only about 100 New World species (Pape 1996, 1998). The New World species do not form a monophyletic group (Giroux 2006), suggesting multiple connections between the Old and New Worlds. *Neobellieria* is restricted to the New World, which suggests that the subgenus originated in this region. The most likely route to the New World for the ancestor of the lineage was from the northern Palearctic to the Nearctic, probably via Beringia. The clade *S. citellivora* + *S. cooleyi* contains two western Nearctic species, which provides some support for a Beringian route. *Sarcophaga bullata* and *S. libera* are widespread Nearctic species but *S. polistensis* is southern Nearctic and widespread in the Neotropical region from Mexico to Brazil. Species previously assigned to *Tolucamyia* are restricted to Arizona, Texas, Mexico and Guatemala, predominantly at high elevations.

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## Appendix 1: Characters used in phylogenetic analysis.

1. Genal and postgenal setae: (0) genal setae black, some postgenal setae white or yellow; (1) some genal setae white or yellow close to genal suture, postgenal setae white or yellow.
2. Postsutural dorsocentral bristles: (0) four or more, posterior two stronger and longer than anterior two; (1) three or four (third one from scutellum reduced or absent); (2) three well developed.
3. Male apical scutellar bristles: (0) present; (1) absent.
4. Marginal hairs on alula: (0) longer than anterior marginal hairs of anal lobe; (1) as long as anterior marginal hairs of anal lobe.
5. Hairs fringing calypteres at fold: (0) creamy-white; (1) pale brown.
6. Female mid femoral organ: (0) absent; (1) present.
7. Female sternites 6-8; fusion: (0) at least some sternites fused; (1) sternites 6-8 free.
8. Female sternite 6: (0) even (1) depressed
9. Female sternite 7: (0) even (1) depressed
10. Female tergite 8: (0) present; (1) absent or vestigial.
11. Male sternite 5,window: (0) present; (1) absent.
12. Male sternite 5, window: (0) forming a dome-shaped elevation anteriorly; (1) flat.
13. Male sternite 5, emargination: (0) U-shaped; (1) V-shaped.
14. Male sternite 5; length of base: (0) long; (1) short.
15. Male terminalia, color: (0) dark brown or black; (1) yellow or reddish.
16. Male cercal prong, short stiff hairs on medial margin: (0) sparse; (1) dense.
17. Hypandrial arms, degree of fusion, posterior view: (0) fused; (1) free.

18. Juxta, degree of sclerotization: (0) well sclerotized; (1) partly sclerotized.

19. Juxta, demarcation with phallic tube: (0) distinct hinge; (1) desclerotized strip.

20. Juxta, shape in dorsal view: (0) as long as wide; (1) wider than long.

21. Lateral styli, shape: (0) tubular or filiform (1) horn-shaped.

22. Lateral styli, longitudinal cleft: (0) closed, spiraling along length; (1) opened on internal side along length.

23. Phallic vesica, number of lobes: (0) bilobed structure; (1) two separate lobes;

24. Phallic vesica, shape of lobes: (0) flattened and thin; (1) rounded with thorn-like spines.

25. Phallic vesica, sclerotization: (0) partly sclerotized; (1) entirely sclerotized.

26. Harpes, shape in lateral view: (0) straight; (1) bent at roughly a right-angle.

27. Harpes, black lateral horns: (0) reduced or absent; (1) present.

**Appendix 2:** Data matrix of character states used in analysis. ?, missing data; -, inapplicable character; A, polymorphic 0/1.

| | 1 | 1111111112 | 2222222 |
|---|---|---|---|
| | 1234567890 | 1234567890 | 1234567 |
| *Liosarcophaga pleskei* | 0000010000 | 0000001000 | 0000000 |
| *Pseudothyrsocnema spinosa* | 1000000000 | 0100000000 | 0000000 |
| *Neobellieria bullata* | A001111111 | 0010110001 | 1111101 |
| *Neobellieria cavagnaroi* | 02101????? | 0110110111 | 1111110 |
| *Neobellieria citellivora* | 1000001111 | 0011101001 | 1111101 |
| *Neobellieria cooleyi* | 10000A1011 | 0011111000 | 1111101 |
| *Neobellieria libera* | A001101111 | 0010110001 | 1111100 |
| *Neobellieria longisterna* | 02101????? | 1-10110111 | 1111110 |
| *Neobellieria polistensis* | A001101111 | 001011A001 | 1111100 |
| *Neobellieria schrameli* | 00011????? | 1-10111101 | 1111110 |
| *Neobellieria sigilla* | 0111111010 | 01?0110111 | 1111110 |

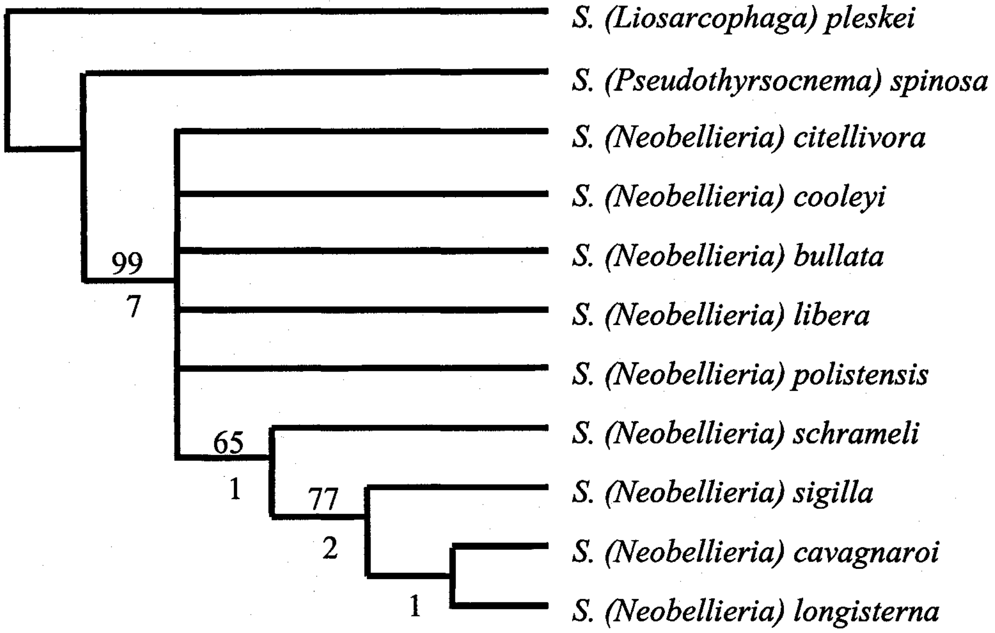


**Fig. 1.** Strict consensus tree from phylogenetic analysis. Bootstrap and Bremer support values are given above and below branches, respectively.

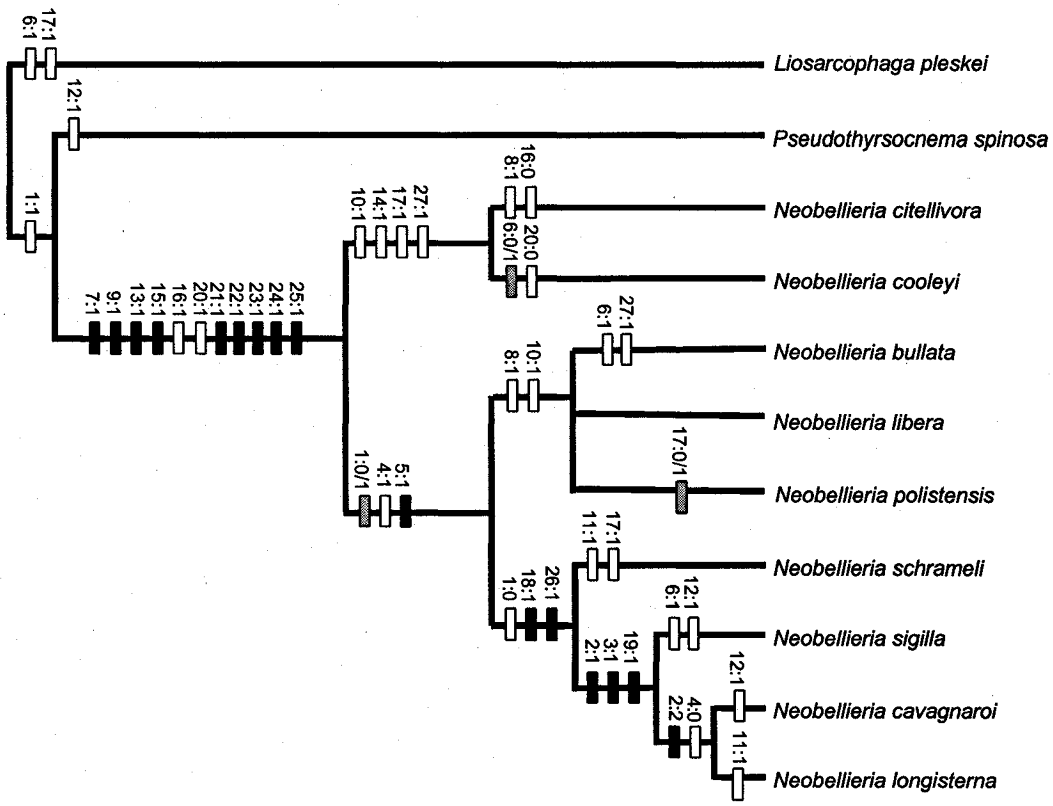
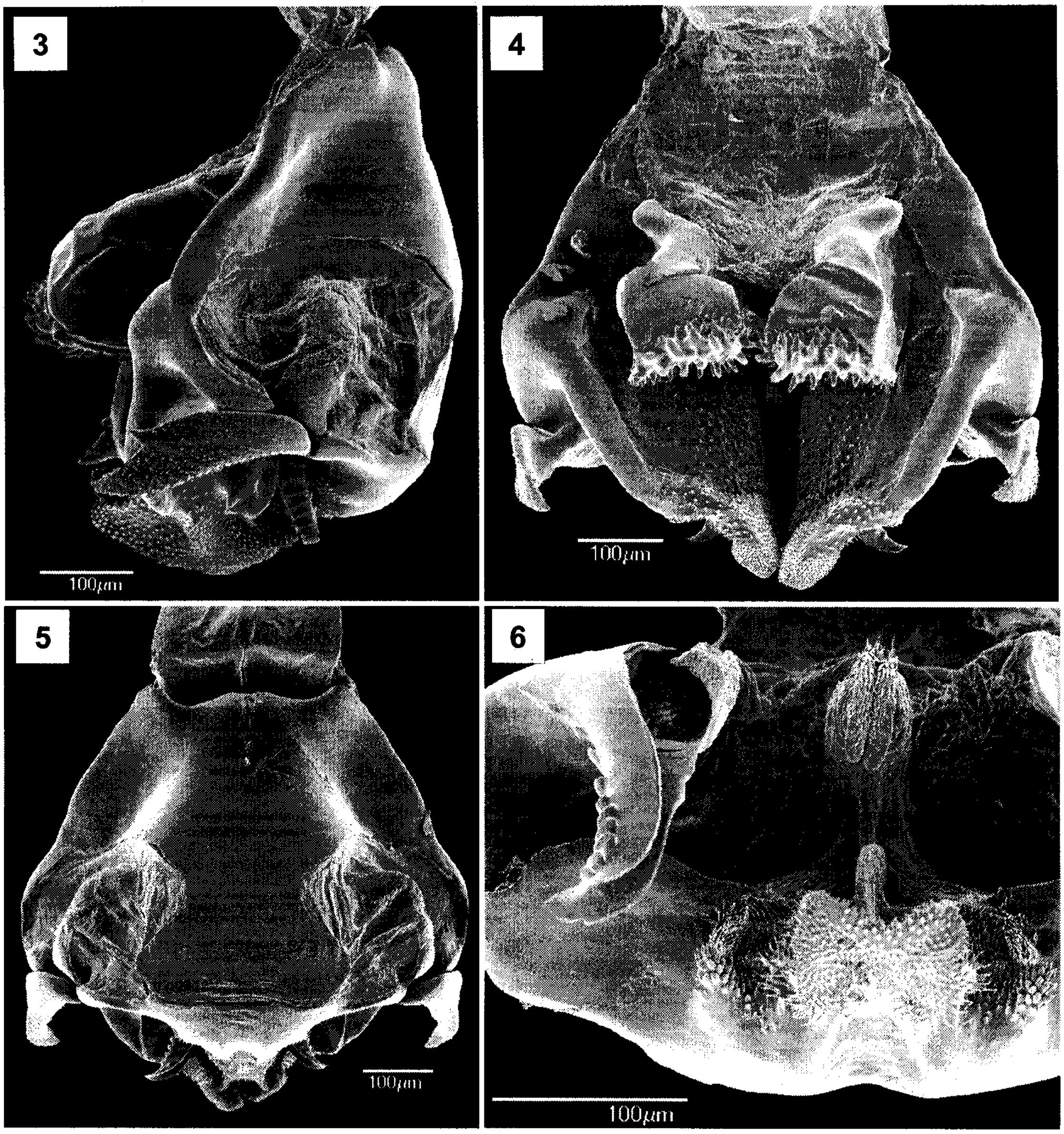
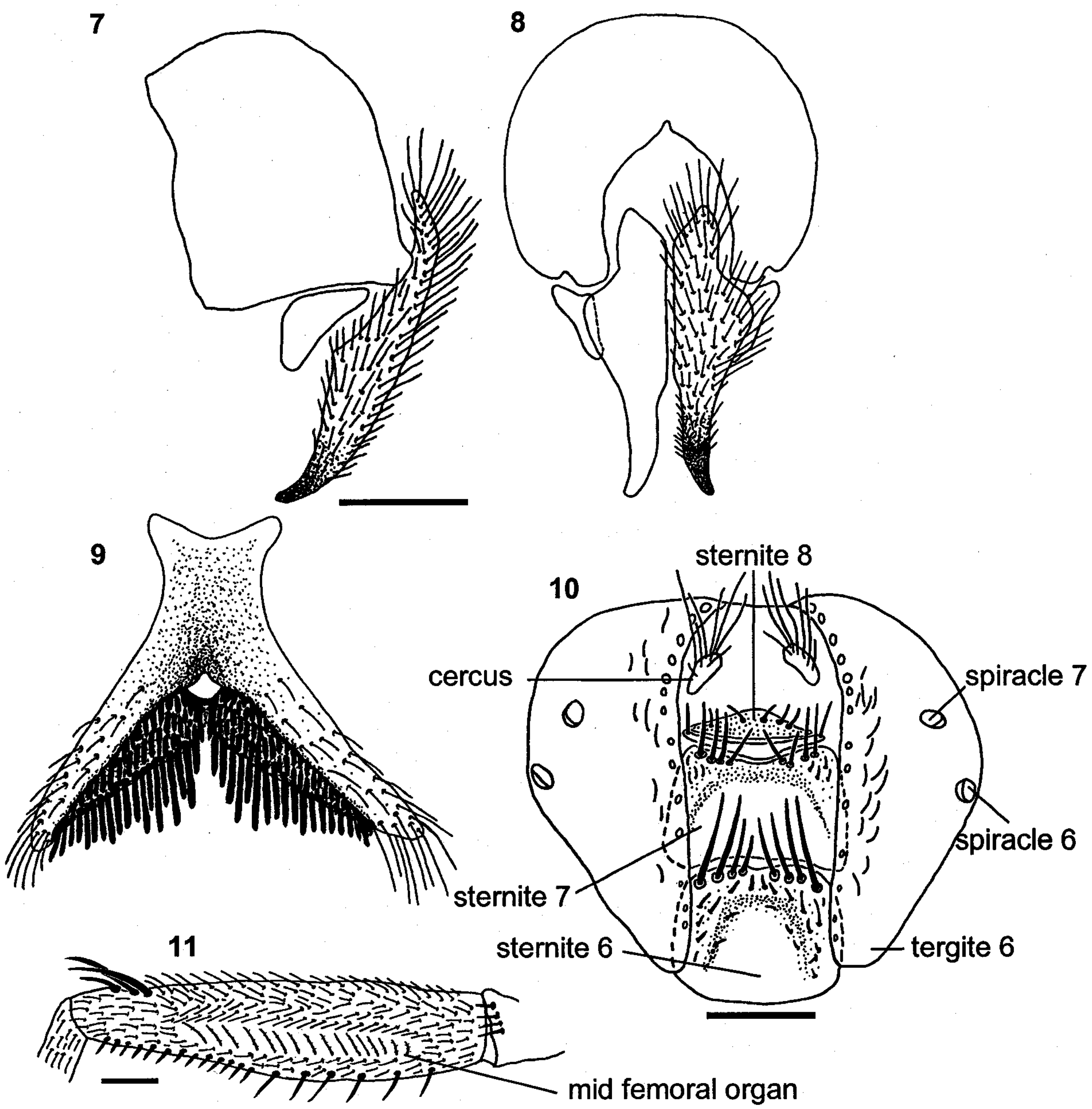


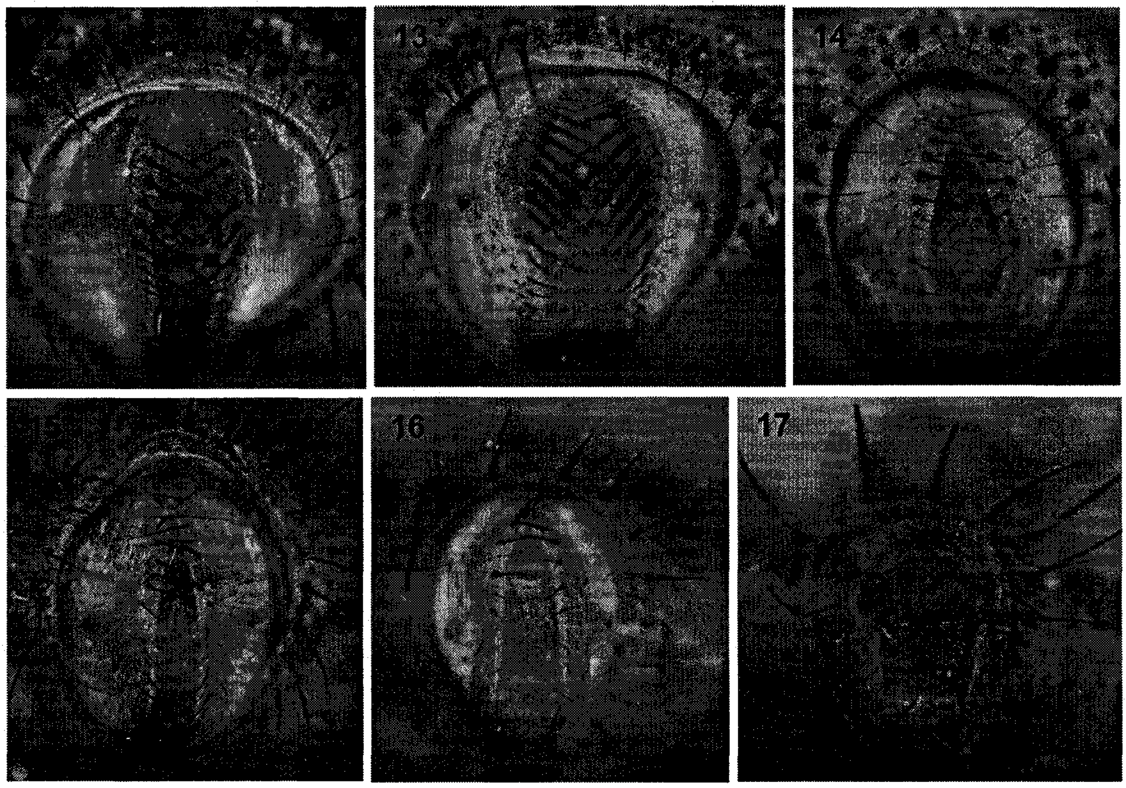
**Fig. 2.** One of 18 most parsimonious trees showing character state distribution in *Neobellieria*. Uniquely derived states in black, homoplasious states in white, polymorphic states in gray.



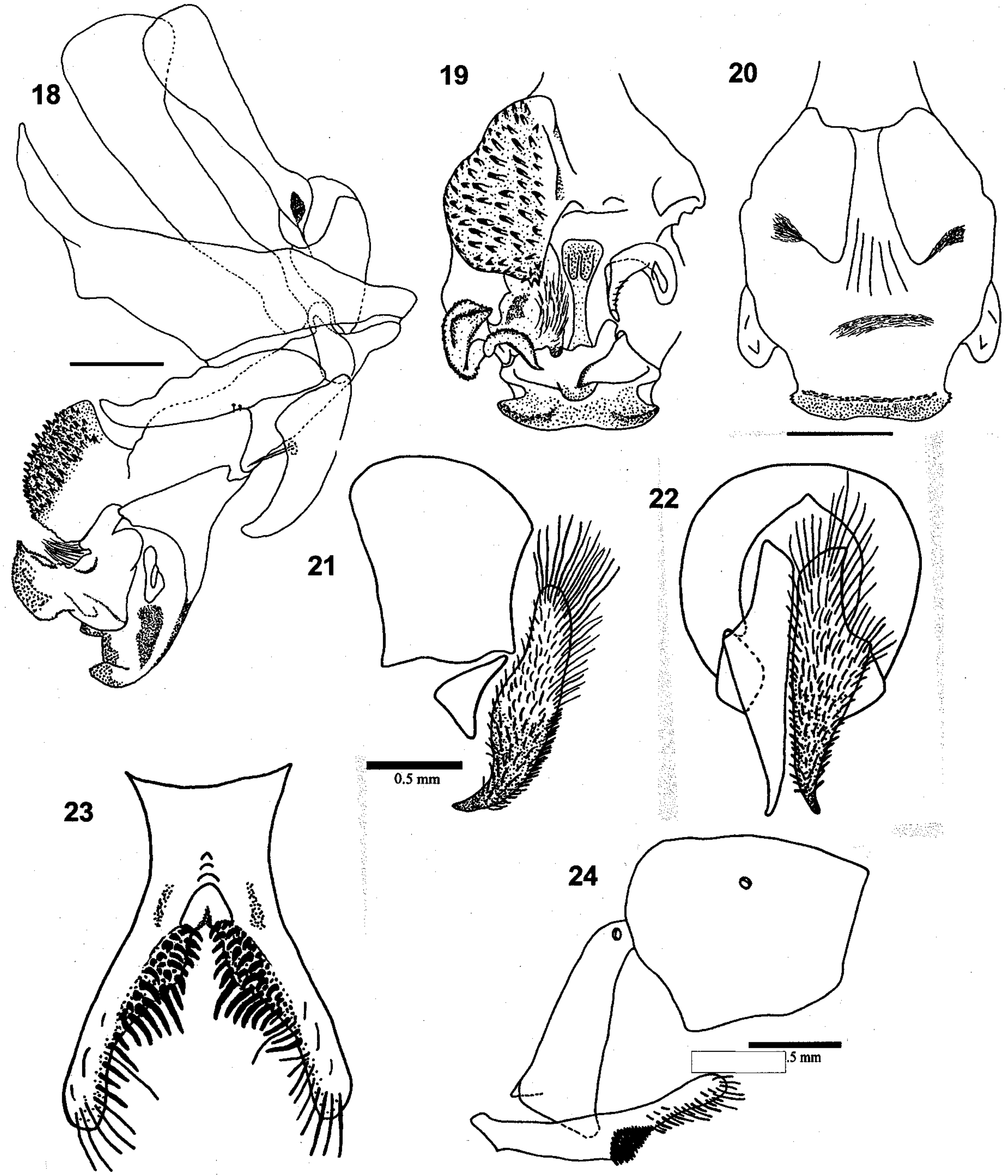
**Figs. 3-6.** *Neobellieria bullata*. (3) acrophallus, lateral. (4) acrophallus, anterior. (5) acrophallus, posterior. (6) styli and juxta.



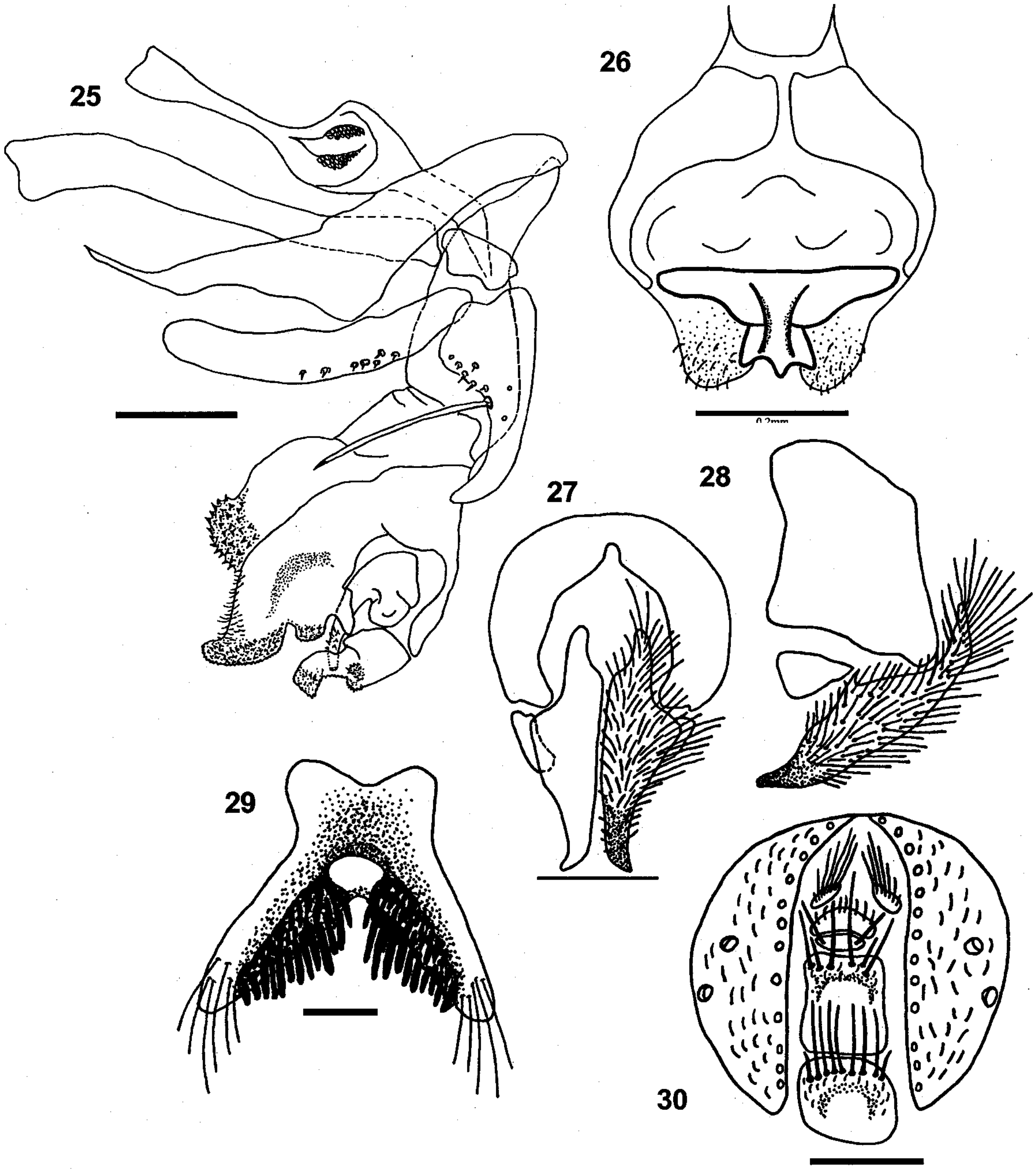
**Figs. 7-11.** *Neobellieria bullata.* (7) epandrium, surstylus and cerci, lateral. (8) epandrium, surstylus and cerci, posterior. (9) male sternite 5, ventral. (10) Female genitalia, posteroventral. (11) female mid femoral organ (left femur, posterior view). Scale: 0.5 mm.



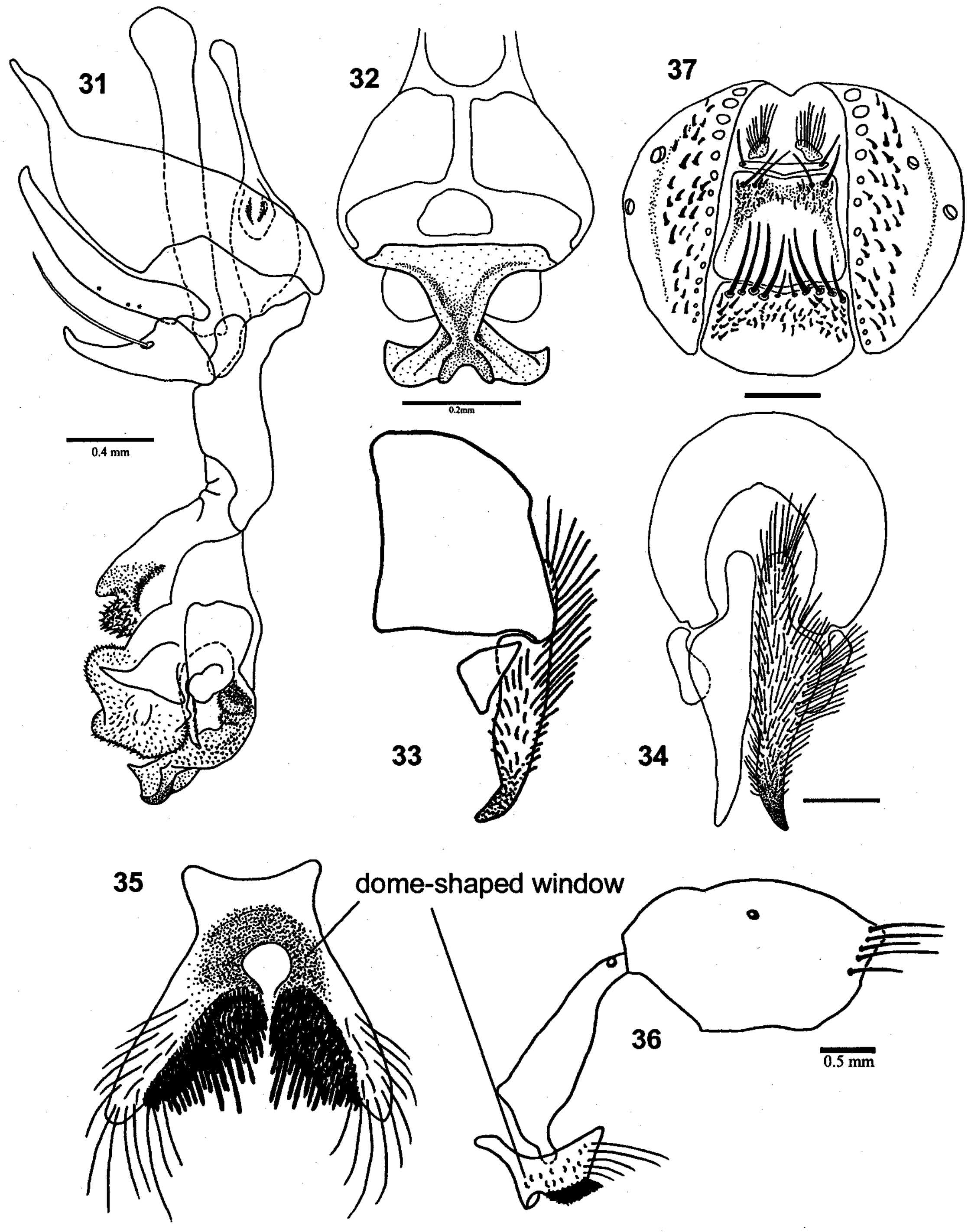
**Figs. 12-17.** *Neobellieria*, female genitalia, posterior. (12) *N. bullata*. (13) *N. cooleyi*. (14) *N. citellivora*. (15) *N. libera*. (16) *N. polistensis*. (17) *N. sigilla*.



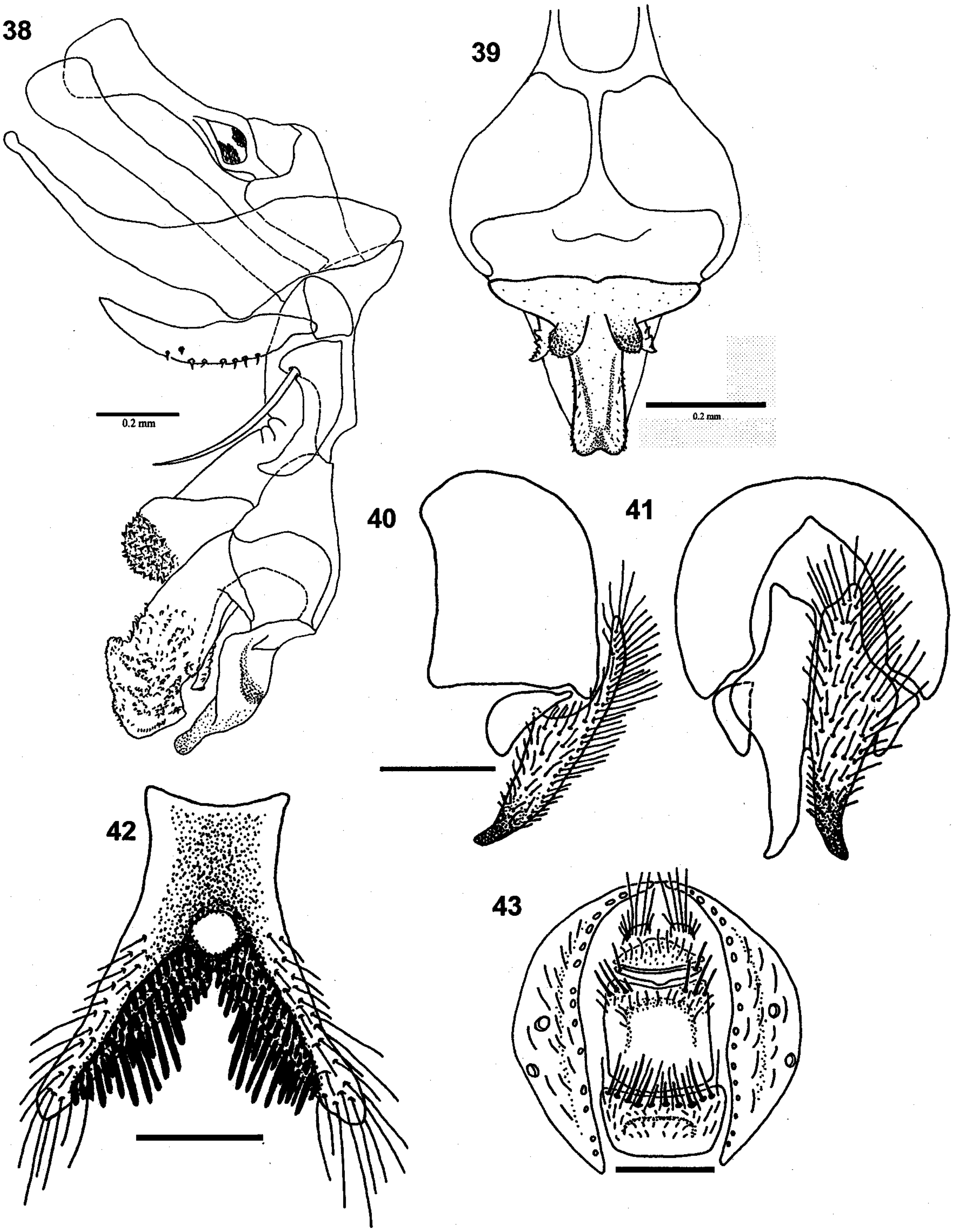
**Figs. 18-24.** *Neobellieria cavagnaroi.* (18) phallus, left lateral. (19) acrophallus, anterior. (20) acrophallus, posterior. (21) epandrium, surstylus and cerci, lateral. (22) epandrium, surstylus and cerci, posterior. (23) male sternite 5, ventral. (24) male sternites 5-6, syntergosternite 7+8, lateral. Scale: 0.2 mm (Figs. 18-20); 0.5 mm (Figs. 21-24).



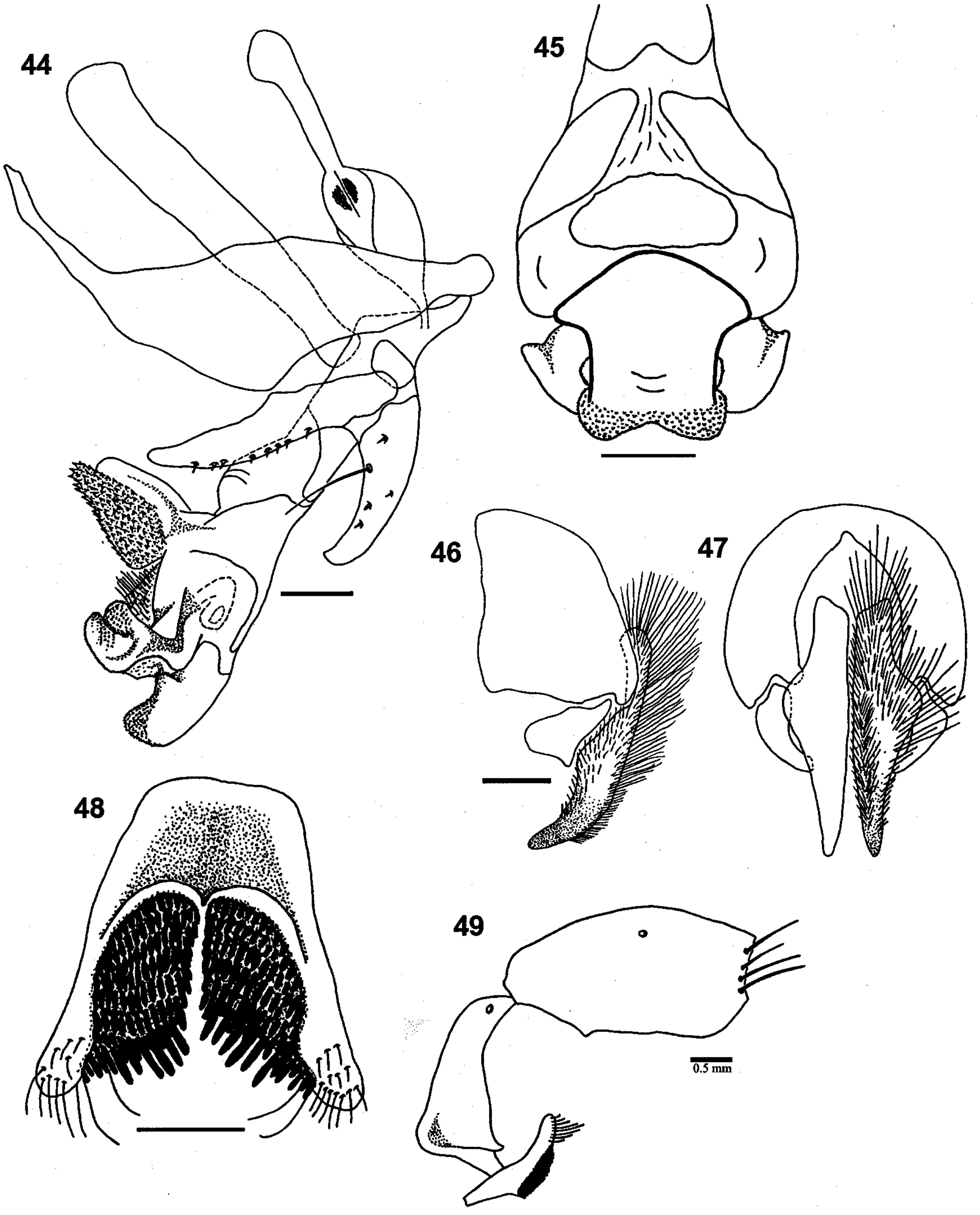
**Figs. 25-30.** *Neobellieria citellivora*. (25) phallus, left lateral. (26) acrophallus, posterior. (27) epandrium, surstylus and cerci, lateral. (28) epandrium, surstylus and cerci, posterior. (29) male sternite 5, ventral. (30) Female genitalia, posteroventral. Scale: 0.2 mm (Figs. 25-26); 0.5 mm (Figs. 27-30).



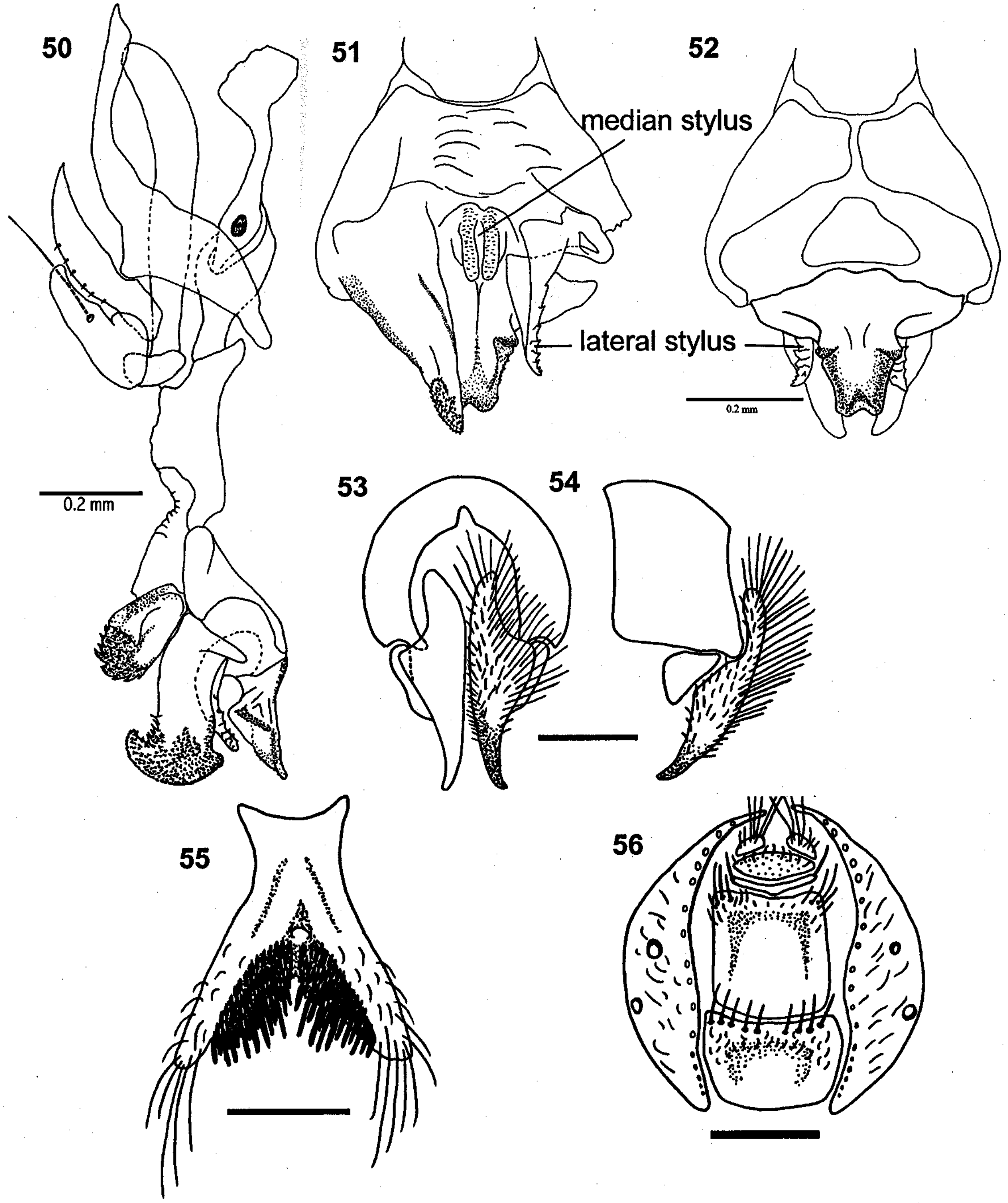
**Figs. 31-37.** *Neobellieria cooleyi.* (31) phallus, left lateral. (32) acrophallus, posterior. (33) epandrium, surstylus and cerci, lateral. (34) epandrium, surstylus and cerci, posterior. (35) male sternite 5, ventral. (36) male sternites 5-6, syntergosternite 7+8, lateral. (37) female genitalia, posteroventral. Scale: 0.2 mm (Fig. 31); 0.4 mm (Fig. 32); 0.5 mm (Figs. 33-37).



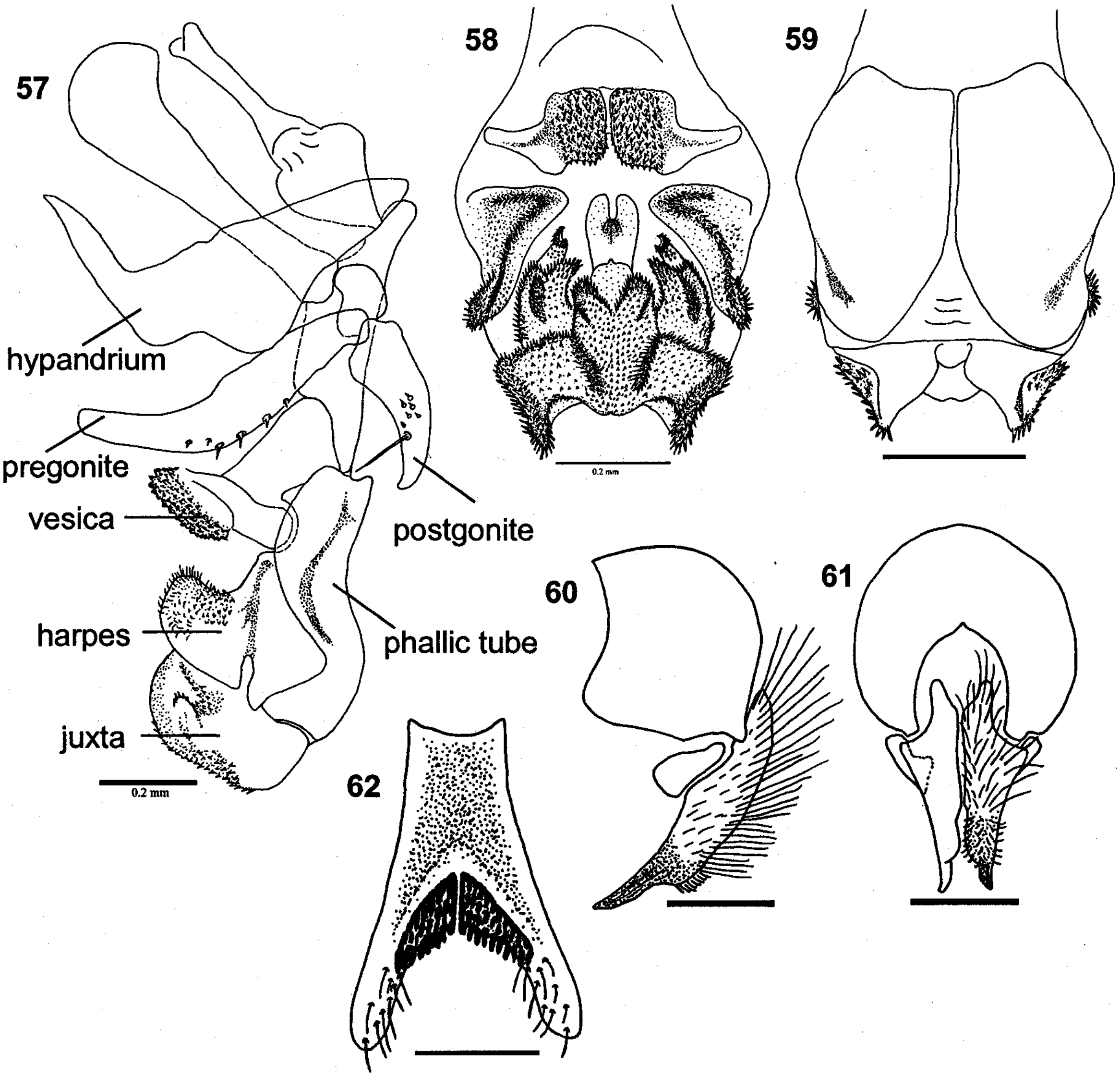
**Figs. 38-43.** *Neobellieria libera.* (38) phallus, left lateral. (39) acrophallus, posterior. (40) epandrium, surstylus and cerci, lateral. (41) epandrium, surstylus and cerci, posterior. (42) male sternite 5, ventral. (43) female genitalia, posteroventral. Scale: 0.2 mm (Figs. 38-39); 0.5 mm (Fig. 40-43).



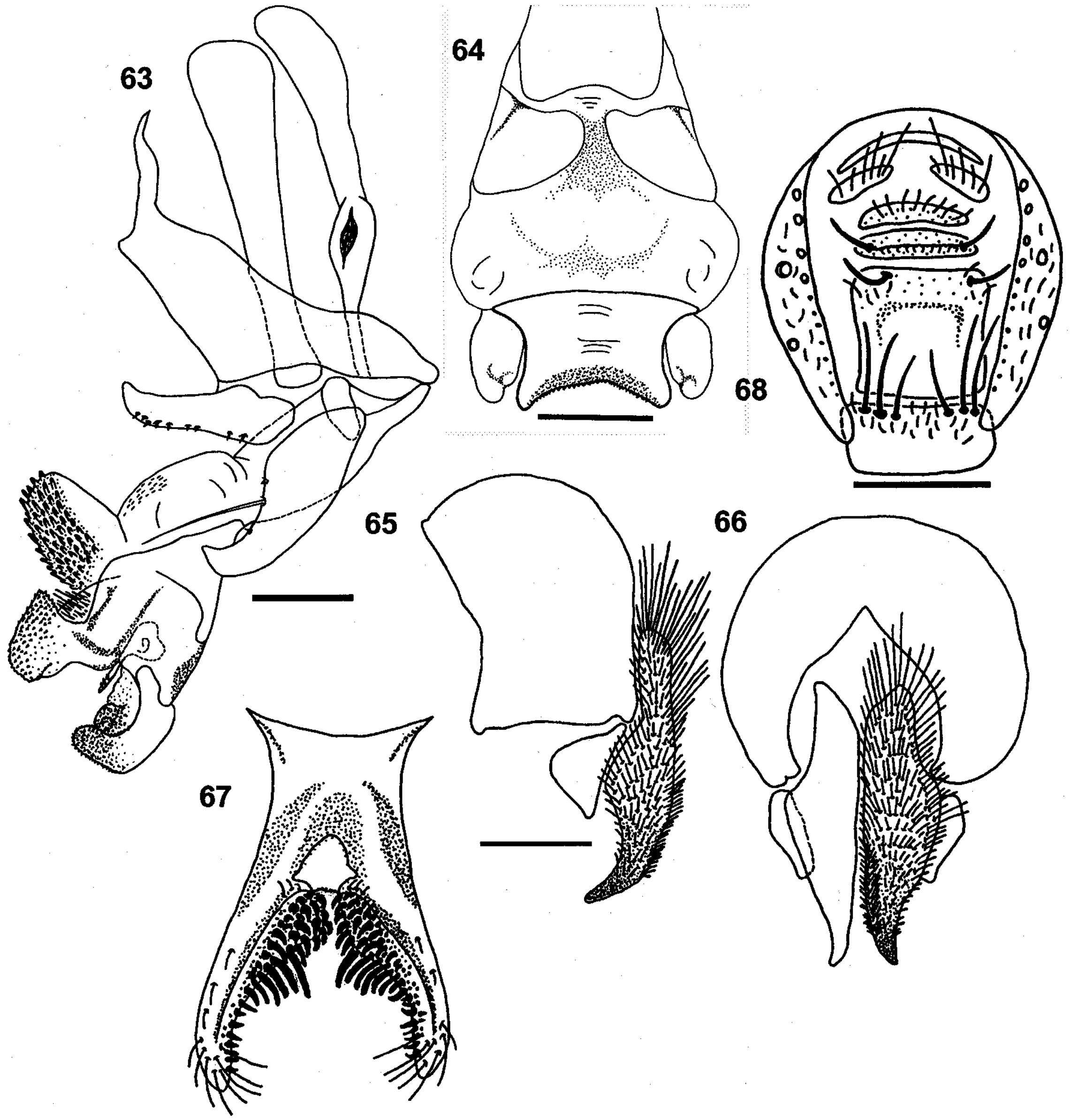
**Figs. 44-49.** *Neobellieria longisterna*. (44) phallus, left lateral. (45) acrophallus, posterior. (46) epandrium, surstylus and cerci, lateral. (47) epandrium, surstylus and cerci, posterior. (48) male sternite 5, ventral. (49) male sternites 5-6, syntergosternite 7+8, lateral. Scale: 0.2 mm (Figs. 44-45); 0.5 mm (Figs. 46-49).



**Figs. 50-56.** *Neobellieria polistensis*. (50) phallus, left lateral, (51) acrophallus, anterior. (52) acrophallus, posterior. (53) epandrium, surstylus and cerci, lateral. (54) epandrium, surstylus and cerci, posterior. (55) male sternite 5, ventral. (56) female genitalia, posteroventral. Scale: 0.2 mm (Figs. 50-52); 0.5 mm (Figs. 53-56).



**Figs. 57-62.** *Neobellieria schrameli.* (57) phallus, left lateral. (58), acrophallus, anterior. (59) acrophallus, posterior. (60) epandrium, surstylus and cerci, lateral. (61) epandrium, surstylus and cerci, posterior. (62) male sternite 5, ventral. Scale: 0.2 mm (Figs. 57-59); 0.5 mm (Figs. 60-62).



**Figs. 63-68.** *Neobellieria sigilla*. (63) phallus, left lateral. (64) acrophallus, posterior. (65) epandrium, surstylus and cerci, lateral. (66) epandrium, surstylus and cerci, posterior. (67) male sternite 5, ventral. (68) female genitalia, posteroventral. Scale: 0.2 mm (Figs. 63-64); 0.5 mm (Fig. 65-68).

# CONNECTING STATEMENT

In the phylogenetic analysis of the Sarcophaginae presented in chapter 2, it was demonstrated that *Sarcophaga* (*Neobellieria*) Blanchard is one of the currently recognized subgenera whose monophyly is not supported. It was also found that the species previously assigned to *S.* (*Neobellieria*) form three separate clades, one of which is the *S. (N.) semimarginalis* Hall species group. In chapter 4, the new subgenus *Sarcophaga* (*Bulbostyla*) Giroux & Wheeler has been erected to accommodate the four species of the *S. (N.) semimarginalis* species group and four new species. A species-level revision is provided

# CHAPTER 4. Systematics of *Bulbostyla*, a new subgenus of *Sarcophaga* (Diptera: Sarcophagidae)

## Abstract

*Sarcophaga (Bulbostyla)* Giroux & Wheeler is erected as a new subgenus of *Sarcophaga* Meigen to accommodate some species previously assigned to the subgenus *S. (Neobellieria)* Blanchard. The subgenus, as currently recognized contains eight species: *S. airosalis* **sp. n.**; *S. cadyi* **sp. n.** (type species), *S. cuautla* **sp. n.**, *S. ironalis* **sp. n.**, *S. semimarginalis* Hall, *S. sternalis* (Reinhard), *S. subdiscalis* Aldrich and *S. yorkii* Parker. All species are described and illustrated and a key to the species is provided. The species within the subgenus are morphologically uniform and are distinguished mostly on male genitalic characters. Thus, phylogenetic resolution of species relationships within *Bulbostyla* will require consideration of additional characters, such as molecular sequence data.

## Introduction

The genus *Sarcophaga* Meigen contains 133 subgenera, most of which have not been corroborated as monophyletic groups (Pape 1996; 1998). A preliminary phylogenetic analysis of the Sarcophaginae, including 31 subgenera of *Sarcophaga* (Giroux *et al.,* submitted) addressed the monophyly of at least some of those subgenera, one of which, *Neobellieria* Blanchard, was found to be polyphyletic since two species, *S. (N.) triplasia* Wulp and *S. (N.) semimarginalis* Hall, were not closely related to the type species *S.* (*N.) polistensis* Hall.

*Sarcophaga semimarginalis* is closely related to three other described species previously assigned to *Neobellieria*: *S. sternalis* (Reinhard), *S. subdiscalis* Aldrich and *S. yorkii* Parker. Because there is no subgeneric name available for these four species, and because they cannot easily be accommodated within another existing subgenus of *Sarcophaga* based on current phylogenetic knowledge, a new subgenus-group name was warranted.

The purpose of this paper is to describe the new subgenus *Sarcophaga* (*Bulbostyla*) Giroux & Wheeler to accommodate the four species of the *S. (N.) semimarginalis* group and four new species.

## Materials and Methods

This revision was based on specimens housed in the following institutions: Canadian National Collection of Insects, Ottawa, ON, Canada (CNC); Personal collection of Greg A. Dahlem, Highland Heights, KY, USA (GD); Florida State Collection of Arthropods, Gainesville, Florida (FSMA); Museu Nacional/Universidade Federal do Rio de Janeiro, São Cristóvão, Brazil (MNRJ); Université de Montréal, Montreal, QC, Canada (QMOR); Royal Ontario Museum, Toronto, ON, Canada (ROM); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Females were associated with males through correspondence in collecting localities and dates with identifiable males. Preparation and examination of male and female terminalia and production of SEM micrographs follow Giroux *et al.* (submitted). Illustrations were made using a compound or a dissecting microscope equipped with a drawing tube.

Terminology follows McAlpine (1981) for external characters and female genitalia, and Giroux *et al.* (submitted) for male terminalia. Body length was measured from the anterior margin of the head, excluding antennae, to the apex of the abdomen, excluding genitalia. The label data of primary type material is given verbatim with '/' showing a line change and ';' representing a change in label.

### ***Sarcophaga* (*Bulbostyla*) Giroux & Wheeler subgen.n.**

*Type species: Sarcophaga* (*Bulbostyla*) *cadyi* Giroux & Wheeler sp. n.

*Diagnosis: Bulbostyla* may be distinguished from other subgenera of *Sarcophaga* by male genitalic characters only. Males have the juxta wider than long and the hinge between juxta and the phallic tube invaginated; the lateral styli have a wide diameter and the tip of the median stylus is swollen; the phallic vesica has two lateral moderately long and sclerotized processes.

*Description:*

Male: body length 9.0-13.0 mm.

*Head:* ground color black or brown usually with bronze or silvery pruinosity, sometimes yellowish or pinkish depending on the incidence of light; postocellar setae forming a group of medium to long proclinate hairs and setae extending to level of paravertical setae; inner vertical setae reclinate; outer vertical setae as long or slightly longer than upper postocular; proclinate orbital setae absent; upper orbital setae reclinate; number of medioclinate frontal setae variable, row distinctly curving outwards at lunule, often ending by more than one row of setae; weak interfrontal setae all along frontal vitta, sometimes spreading interiorly on the vitta; frontal vitta dark brown or black; fronto-orbital plate with numerous scattered black hairs; parafacial bronze or silvery pruinose, sometimes yellowish or pinkish depending on the incidence of light, with scattered black small hairs followed by long hairs just before genal groove; color distribution of hairs on gena and postgena variable; inner occipital setae white and usually with 2-4 rows of black setae below postocular setae; antenna dark to light brown, length of first flagellomere about 1.5 X length of pedicel; palpus pale to dark brown (yellowish in *S. semimarginalis*).

*Thorax:* ground color black or brown usually with bronze or silvery pruinescence, sometimes yellowish or pinkish depending on the incidence of light; presutural acrostichal setae absent; 1 pair prescutellar acrostichal setae; 4-5 presutural dorsocentrals, slightly stronger than adjacent clothing setae; 4-5 postsutural dorsocentral setae, posterior two stronger than anterior 2-3; 1-2 presutural intra-alar setae (anterior one stronger) + 1-3 postsutural intra-alar setae (posterior one stronger); 1-2 + 3-4 supra-alar setae; anterior postpronotal seta present; 2 basal postpronotal setae; proanepisternum usually bare; 2 postalar setae; intrapostalar setae reduced or absent; postalar wall haired; scutellum with 1 apical, 1 strong and long subapical, 2 basal (anterior one weaker) and 1 discal pair of setae; variable number of strong anepisternal setae, upper two always shorter and declinate; 3 katepisternal setae, occasionally 2 or 4; infrasquamal setae present; posterior spiracle subtriangular with anterior fin-shaped fringe usually dark brown (usually bronze on *S. yorkii*) and posterior fringe usually paler.

*Wing:* membrane hyaline, cells at base often darkened by brown microtrichia (particularly on *S. yorkii*); veins pale to dark-brown; tegula dark, pale to dark-brown pruinose, bristled on about half of its surface, with a short black bristle on outer margin and 2 long black bristles on inner margin; basicosta pale, golden-beige pruinose; C extending to $M_{1+2}$, the base strongly bristled with 2-3 stout bristles close to costagial break, usually with ventral row of equidistant minute setae extending to or just beyond $R_1$; weak costagial, humeral and subcostal breaks; costal spine absent or vestigial; subcostal sclerite and stem-vein golden-brown pruinose (dark brown to black pruinose on *S. yorkii*); base of stem-vein with cluster of golden-brown hairs; axillary sclerites golden-beige pruinose (darker on *S. yorkii*); $R_{4+5}$ setulose at base dorsally and ventrally, ventral row often extending to proximal half; bend of M acute, sometimes right-angled, bent part concave relative to cell $R_{4+5}$, extension at bend usually present as a short fold darkened by dense microtrichia; crossvein r-m sometimes slightly infuscated; $CuA_1$ ending at wing margin as a fold with dense microtrichia; $A_1$+$CuA_2$ not reaching wing margin; $A_2$ distinct as a fold darkened by dense microtrichia; lateral margin of alula with fringe of hairs of various lengths; calypters creamy white; upper calypter rather rounded, posterior margin with white or brown short hairs; lower calypter broadly expanded and angular, posterior margin rather straight; hairs fringing calypters extending to distal margin of lower calypter.

*Legs:* background color dark brown or black; fore and mid coxae covered with long hairs and strong setae; hind coxa with 2-3 strong setae on lateral side, covered with long hairs, sometimes very dense; hind trochanter with ventral moderately long setae; fore femur usually with moderately long ventral hairs, with complete row of strong dorsal and ventral setae (longer in middle), with complete row of shorter posterodorsal setae and sometimes with 4-6 weak posterior setae apically; fore tibia with 1 anterodorsal, 1 dorsal, 1 posterodorsal, 1 posterior, 1 posteroventral and usually 1 short ventral setae apically, 1 posterior setae on apical third, 3-5 strong anterodorsal setae on proximal part; mid femur with moderately long ventral hairs on proximal part, with row of moderately long posteroventral setae on apical half or third, with a complete row of moderately long to long anteroventral setae, with 3-5 strong mid anterior setae and with 2-4 strong posterodorsal setae apically; mid tibia with 1-2 moderately long posterodorsal setae on proximal third sometimes with weaker setae interspersed, with 1-3 moderately long mid anterodorsal setae, sometimes with 1 moderately long to long anteroventral, 1 dorsal, 1 posterodorsal setae on apical third and setae of various lengths around apex; hind femur and tibia straight, usually with moderately long anteroventral, ventral, and posteroventral hairs; hind femur with 1 row of moderately long to long anteroventral setae, with 1 row of moderately long to long posteroventral setae, with 2-3 dorsal and posterodorsal setae on apical third, with 1 complete row of moderately long to long anterodorsal setae, with second restricted to proximal two-thirds (sometimes reduced or absent on *S. cadyi* and *S. semimarginalis*); hind tibia with 2-3 strong anterodorsal and posterodorsal setae (anterodorsal row with weaker setae interspersed), with 1 strong and sometimes 1-2 weaker anteroventral setae on apical half or third, with 1 dorsal, 1 anterodorsal, 1 anterior, 1 anteroventral, 1 ventral and 1 posteroventral setae of various lengths apically, apex with small pad of fine brown or black posteroventral and posterior setae; tarsomere length: 1>2>3>4<5, first and second hind tarsomeres with pad of fine bronze posteroventral and posterior setae.

*Abdomen:* elongated and slightly conical posteriorly; ground color black or brown with grey, bronze or silvery pruinosity; tergites covered with small black setae dorsally, moderately long wavy hairs restricted to sternites 1-2 and ventral margin of tergites 3-5; number of lateral marginal setae variable between tergites and between specimens; median marginal setae on tergite 4 always present; margin of tergite 5 often partly orange-reddish, row of setae at posterior margin often forming half circle spreading on apical third.

*Terminalia:* background color yellowish but with cerci and syntergosternite 7+8 often darker than epandrium; sternite 5 with V-shaped emargination posteriorly and with a relatively long base anteriorly, cleft of posterior margin with moderately dense, strong black setae, apical parts with long hairs, window present and sometimes forming an elevation anteriorly on base; tergite 6 vestigial or absent; syntergosternite 7+8 with anterodorsal emargination and with spiracle 7 dorsolateral; epandrium globose, square in lateral view but with posteroventral extension partly covering cerci in lateral view; surstylus triangular, proximal surface bare; cercal base clothed with long black hairs, cercal prong stout and blunt, straight in profile, cover of short to moderately long hairs; bacilliform sclerites reduced or absent; hypandrial arms not fused in posterior view; postgonal apodeme reduced to a more or less oval dorsal sclerite; pregonite with minute setulae along ventral surface, usually with a pointed lateral extension, postgonite with a short bristle arising from basal anterior surface and with a number of small setulae dorsally; vesica sclerotized, with two lateral moderately long and sclerotized processes;

harpes sclerotized, short and rather round, fused or partly fused to phallic tube; lateral styli coiled at base, with wide diameter (particularly obvious on dried specimens) and covered with strong microserrations, longitudinal cleft opened all along internal side; median stylus bifurcate, with no opening, bulbous and forming two short processes apically; hinge between juxta and phallic tube invaginated, juxta sclerotized, fused to median stylus and wider than long.

Female: body length 10.0-11.5 mm. Differs from male as follows: *Head:* outer vertical setae strong and well developed; proclinate orbital setae present; number of medioclinate frontal and interfrontal setae sometimes fewer than in male. *Thorax:* apical scutellar setae absent. *Legs:* fore femur without moderately long ventral hairs; mid femoral organ present; hind tibia without long posteroventral wavy hairs. *Abdomen:* rounded and slightly conical posteriorly; tergites covered with small black setae dorsally and ventrally, with relatively long hairs restricted to ventral margin of tergites. Margin of sternite 2 usually with 4 strong bristles. Margin of sternite 3 sometimes with a few strong bristles.

*Terminalia:* tergite 6 narrowly membranous mid-dorsally; spiracle 6 and 7 distinct on each plate of tergite 6; sternites 6-8 not fused; sternite 8 reduced to a sclerotized patch covered with moderately long hairs on mid posterior margin; sternite 10 membranous and covered with short setae; cerci distinct.

*Etymology: :* From the Latin *bulbosus* (bulb) and *stylus*. The name refers to the swollen tip of the median stylus. The subgeneric name is feminine.

*Remarks:* Tergites 4 and 5 are partially fused in the only female of *S. cadyi*, although this is apparently an aberrant specimen. We also examined 12 other females that probably belong to *Bulbostyla* but we were unable to associate them with males. Three of the females were dissected and all have sternite 8 reduced to a sclerotized patch covered with moderately long hairs on mid posterior margin and sternite 7 desclerotized on its middle part (as on *S. semimarginalis*). Those character states are possibly synapomorphic for the subgenus although further investigation is needed.

**Key to males of described species of *Sarcophaga* (*Bulbostyla*)**

1. Hind tibia with long posteroventral wavy hairs . . . 2
- Hind tibia without long posteroventral wavy hairs . . . 5
2. Window of sternite 5 not protruding; male pregonite with pointed lateral extension; vesica and juxta not as in Figs.14-15 . . . 3
- Window of sternite 5 protruding; male pregonite without pointed lateral extension; vesica and juxta as in Figs.14-15 . . . S. *(Bulbostyla) ironalis*
3. Strong setae on margin of tergite 5 not marginal but forming half circle spreading on apical third, vesica and juxta not as in Figs.17-19 . . . 4
- Margin of tergite 5 with a marginal row of strong strong setae, sometimes two middle ones slightly anterior to the others, vesica as in Figs.17-18, juxta with two deep invaginations in dorsal view (Fig. 19) . . . *S. (Bulbostyla) semimarginalis*
4. Dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; hairs fringing calypters at fold creamy-white; vesica and juxta as in Figs. 1-2 . . . *S. (Bulbostyla) airosalis*

- Dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters at fold pale to dark brown or black; vesica and juxta as in Figs. 25-26 . . . *S. (Bulbostyla) subdiscalis*

5. Window of sternite 5 not protruding; vesica and juxta not as in Figs. 22-23 . . . 6

- Window of sternite 5 protruding; vesica and juxta as in Figs. 22-23 . . . *S.(Bulbostyla) sternalis*

6. Dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; strong setae on margin of tergite 5 not marginal but forming half circle spreading on apical third; syntergosternite 7+8 darker than epandrium; vesica and juxta not as in Figs.11-12 . . . 7

- Dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; margin of tergite 5 with a marginal row of strong strong setae, sometimes two middle ones slightly anterior to the others; syntergosternite 7+8 same color as epandrium; vesica and juxta as in Figs. 11-12 . . . *S. (Bulbostyla) cuautla*

7. Genal setae black, postgena with a least some white setae; hairs fringing calypters at fold pale brown; male pregonite without pointed lateral extension, vesica and juxta as in Figs. 4-5 . . . *S. (Bulbostyla) cadyi*

- Genal setae black, lateral part of postgena with black setae; hairs fringing calypters at fold dark brown or black; male pregonite with pointed lateral extension; vesica and juxta as in Figs. 28-29. . . *S. (Bulbostyla) yorkii*

### ***Sarcophaga* (*Bulbostyla*) *airosalis* Giroux & Wheeler sp. n.** (Figs. 1-3)

*Type material:* Holotype: ♂ labelled ' Pachuca, 1700'/ Hidalgo, Mex. / 29-VII-1954 /J. G. Chillcott ' (CNC).

*Description:*

Male: body length 10 mm. *Head:* 9 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; hairs fringing calypters creamy-white. *Legs:* hind tibia with long posteroventral wavy hairs. *Abdomen:* Tergite 5 with a orange-yellow margin on apical half or third, sometimes entirely yellow, row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia*: window on sternite 5 almost even with rest of base; pregonite with pointed lateral extension; vesica and juxta as in Figs. 1-2.

Female: unknown.

*Etymology:* Pachuca, the type locality, is also known as " *la bella airosa* " or "the windy one " because of frequent strong winds in the region.

### ***Sarcophaga* (*Bulbostyla*) *cadyi* Giroux & Wheeler sp. n.** (Figs. 4- 10)

*Type material:* Holotype: ♂ labelled 'QUE Cté Vaudreuil / summit Mt Rigaud / 6:30-7 AM, 21.vii.96 / D. M. Wood 220m' (CNC). Allotype: Ontario: Leeds Co. Chaffeys

Locks, 14.vi.1970 (CNC). Paratypes: same data as holotype (3♂, CNC); Quebec: Cté Vaudreuil, summit Mt Rigaud, 6.vii.2001, 220m (1♂, CNC); La Trappe [ Parc d'Oka ] 4.viii.1935 (1♂, QMOR); Ontario: Leeds Co. Chaffeys Locks, 6.viii.1970 (1♂, ROM); same data except 8.viii.1969 (1♂, ROM); same data except 5.viii.1969 (1♂, ROM); Georgian Bay Is. NP, 13.viii.1983, dry Malaise (1♂, DEBU).

*Description:*

Male: body length 9.5-11.5 mm. *Head:* 11-16 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters pale-brown. *Legs:* hind tibia without long posteroventral wavy hairs. *Abdomen:* Tergite 5 with a orange-yellow margin on apical half or third, sometimes entirely yellow, row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia:* cerci and syntergosternite 7+8 darker than epandrium; window on sternite 5 almost even with rest of base; pregonite without pointed lateral extension; vesica and juxta as in Figs. 4-5.

Female: body length 11.5 mm.

*Terminalia* (Fig. 6): tergite 6 with moderately strong setae on each side evenly spaced and about equal in size, with long hairs interspersed; tergite 7 and 8 absent; sternite 6 and 7 covered with short to moderately long setae and hairs on distal margin, sternite 7 slightly concave.

*Etymology: Cady* is a diminutive of Yvon Cadieux, the man who shares M. Giroux' life. The species was named to express her gratitude for his moral and financial support during her PhD studies.

***Sarcophaga* (*Bulbostyla*) *cuautla* Giroux & Wheeler sp. n.** (Figs. 11-13)

*Type material:* Holotype: ♂ labelled 'Cuautla Mx / June 5 '22 / EG Smith' ; '♂' ; 'GN' ; 'David G. Hall / COLL.' ; 'N. Gen ? / Sp.N. / Det. D. G. Hall' (USNM).

*Description:*

Male: body length 11.0 mm. *Head:* 12-14 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula longer than those on anterior margin of anal lobe; hairs fringing calypters pale-brown. *Legs:* hind tibia without long posteroventral wavy hairs. *Abdomen:* Tergite 5 same color as other abdominal tergites or with a pale brown margin, margin with a marginal row of strong setae, two middle ones sometimes slightly anterior to the others.

*Terminalia:* window on sternite 5 almost even with rest of base; vesica and juxta as in Figs. 11-12.

Female: unknown.

*Etymology:* The species name is a noun in apposition based on the type locality.

***Sarcophaga* (*Bulbostyla*) *ironalis* Giroux & Wheeler sp. n.** (Figs. 14-16)

*Type material:* Holotype: ♂ labelled ' Biol. Note # / 385 / Wm. Downes' ; 'Pilot Knob Mt. nr. / Pilot Knob, Mo. / 12.vi.1968 / Wm. L. Downes' (FSCA); Paratypes: Mexico, Xochimilco, D.F., 20.viii.1948 (1♂, MNRJ); same data except Amanalco, 5.v.1950 (1♂, CNC); same data except Jalisco, Guadalupe, 26.vii.1931 (1♂, CNC).

*Description:*

Male: body length 8.0-11.0 mm. *Head:* 9-15 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula as long as or longer than those on anterior margin of anal lobe; hairs fringing calypters creamy-white to pale-brown. *Legs:* hind tibia with long posteroventral wavy hairs. *Abdomen:* Tergite 5 same color as other abdominal tergites or with a pale brown margin or with a orange-yellow margin on apical half or third, margin with a marginal row of strong setae, sometimes two middle ones slightly anterior to the others or sometimes row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia:* window of sternite 5 forming an elevation anteriorly on base; pregonite without pointed lateral extension; vesica and juxta as in Figs. 14-15.

*Etymology:* Pilot Knob Mountain is in Iron County, Missouri and is the site of an old iron mine. The species name is an adjective referring to that the county and the past history of the area.

***Sarcophaga* (*Bulbostyla*) *semimarginalis* Hall** (Figs. 17- 21)

*Sarcophaga semimarginalis* Hall 1931: 283.

*Sarcophaga* (*Neobellieria*) *semimarginalis*: Pape 1996: 367.

*Type material:* Holotype ♂ labelled 'Menard Tex. / 15-24-VII-1929'; 'E. C. Cushing / Collector'; 'Type No. / 43867 / U.S.N.M.'; ' Sarcophaga / semimarginalis Hall ' (USNM). Paratype ♂, same data as holotype except 11-21.vii.1930, Parish collector (not examined).

*Other material examined:* USA: Arizona: Graham Co. Cyclone Hill, 3.3 mi w. on Hwy. 366 from Hwy. 191, ca. 4000', 23.viii.1993 (3♂, CNC); Texas: Big Bend N.P., Santa Elena can., 5.v.1959, 2100' (3♂, CNC); Davis Mts St. Pk., Jeff Davis Co., 25-08-1968 (10♂, GD); same data except 23-08-1968 (1♂, GD); Bexar Co., 29.ix.1936 (1♂, CNC); Presidio Co., 11.vii.1929 (1♂, 1♀, CNC); MEXICO: Nuevo Leon, Mamulique pass 2km., NE on microwave rd., 17-18.vi.1982, 2000', dry wash (1♂, GD).

*Description:*

Male: body length 9.0-12.0 mm. *Head.* 8-11 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae; palpus pale brown-yellow. *Wing:* dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters creamy-white. *Legs:* hind tibia with long posteroventral wavy hairs. *Abdomen:* Tergite 5 same color as other abdominal tergites or with a pale brown margin or with a orange-yellow margin on apical half or third, margin with a marginal row of strong setae, sometimes two middle ones slightly anterior to the others.

*Terminalia:* window on sternite 5 almost even with rest of base; vesica as in Figs.17-18, juxta with two deep invaginations in dorsal view (Fig. 20).

Female: body length 10 mm.

*Terminalia* (Fig.21): tergite 6 with moderately strong setae on each side evenly spaced and about equal in size; tergite 7 present; tergite 8 vestigial: sternite 6 with 8 moderately strong setae on distal margin; sternite 7 desclerotized on its middle part, with 6 weak setae on distal margin.

### ***Sarcophaga* (*Bulbostyla*) *sternalis* (Reinhard)** (Figs. 22-24)

*Emblemasoma sternalis* Reinhard 1939: 62

*Archimimus sternalis*: Reinhard 1952: 141

*Sarcophaga* (*Neobellieria*) *sternalis*: Pape 1996: 367.

*Type material:* Holotype ♂ labelled 'Donna / 5-18-1932 Tx'; 'Holotype / *E.* / *sternalis* / Reinhard'; 'Emblemasoma / sternalis / Rein. det. H. J. Reinhard' ; 'Holotype / Archimimus / sternalis / Reinhard'; 'Archimimus / sternalis /Rnh.'; 'Holotype / CNC No. 10735' (CNC). Paratype ♂, same data as holotype (not examined).

*Other material examined:* USA: California: Kern Co., 16.x.1937 (1♂, CNC); MEXICO: Nuevo Leon, Mamulique pass 2km., NE on microwave rd., 17-18.vi.1982, 2000', dry wash (1♂, GD).

*Description:*

Male: body length 12.0 - 13.0 mm. *Head.* 9-13 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters creamy-white to pale brown. *Legs:* hind tibia without long posteroventral wavy hairs. *Abdomen:* Tergite 5 same color as other abdominal tergites or with a pale brown margin or with a orange-yellow margin on apical half or third, margin with a marginal row of strong setae, sometimes two middle ones slightly anterior to the others or sometimes row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia:* window of sternite 5 forming an elevation anteriorly on base; vesica and juxta as in Figs.22-23.

***Sarcophaga (Bulbostyla) subdiscalis* Aldrich** (Figs. 25-27)

*Sarcophaga subdiscalis* Aldrich 1916: 219.

*Sarcophaga* (*Neobellieria*) *subdiscalis*: Pape 1996: 367.

*Type material:* Holotype ♂ labelled 'Anglesea / 6-11-05 NJ.' ; 'HbK' ; 'gen dr' ; 'Type No. / 20548 / U. S. N. M.' ; 'Sarcophaga / subdiscalis / Ald.' (USNM).

*Other material examined:* USA: Maryland: nr. Laurel, Patuxent Wildl. Ref., 8.vi.1967, Malaise trap (1♂, USNM); North Carolina: Highlands, 3000-5000 ft, Apr-May 1936 (1♂, USNM);

*Description:*

Male: body length 10.5-12.5 mm. *Head.* 12-16 pairs of medioclinate frontal setae; genal setae black, postgena with at least some white or yellow setae. *Wing:* dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters pale to dark brown or black. *Legs:* hind tibia with long posteroventral wavy hairs. *Abdomen:* Tergite 5 with a orange-yellow margin on apical half or third, sometimes entirely yellow, row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia:* window on sternite 5 almost even with rest of base; vesica and juxta as in Figs. 25-26.

*Remarks:* The right wing and the epandrium (with cerci, surstylus and phallus) are glued on the third label of the holotype specimen.

***Sarcophaga* (*Bulbostyla*) *yorkii* Parker** (Figs. 28-30)

*Sarcophaga yorkii* Parker 1919: 265.

*Sarcophaga* (*Neobellieria*) *yorkii*: Pape 1996: 367.

*Type material:* Holotype ♂ labelled ' Niagara Falls / June 25 NY' ; 'PARKER COLL. / SARCOPHAGIDAE / purchased Dec. 1937 / David G. Hall.'; 'Sarcophaga / yorkii R. PKc. / Holotype' (USNM). Paratype: same data as holotype (1♂, USNM).

*Other material examined:* Canada: Quebec: summit of Mt. Rigaud, Vaudreuil Co., 23.vi.93 (2♂, DEBU); USA: North Carolina: Burke Co., Pisgah Nat. Forest., Summit of Hawksbill Mt., 27.v.1999, 4020 ft (9♂, GD).

*Description:*

Male: body length 9.5-13.0 mm. *Head.* 11-17 pairs of medioclinate frontal setae; frontal vitta usually matt black; genal and postgenal setae black, white postgenal setae, when present, restricted to inner posterior part of oral margin. *Thorax:* proanepisternum setose. *Wing:* dark hairs on lateral margin of alula as long as those on anterior margin of anal lobe; hairs fringing calypters dark brown or black. *Legs:* hind tibia without long posteroventral wavy hairs. *Abdomen:* Tergite 5 with a orange-yellow margin on apical half or third, sometimes entirely yellow, row of strong setae not marginal but forming half circle spreading on apical third.

*Terminalia:* cerci and syntergosternite 7+8 darker than epandrium; window on sternite 5 almost even with rest of base; vesica and juxta as in Figs. 28-29.

*Remarks:* The paratype specimen has lost its genitalia but sternite 5 is still present.

## Discussion:

Based on comparison to the related subgenera *Varirosellea* Xue and *Pandelleana* Rohdendorf (see Giroux *et al.* submitted), the monophyly of *Bulbostyla* is supported by seven synapomorphic character states, six of which are male genitalia states: the invaginated hinge between the juxta and the phallic tube; the swollen tip of the median stylus; the wide diameter of the lateral styli; a longitudinal cleft opened on internal side all along the lateral styli; the juxta wider than long; and the phallic vesica with two lateral, moderately long and sclerotized processes. One non-genitalic character state, male fore femur without long ventral wavy hairs, also supports the monophyly of *Bulbostyla*.

Although support for the monophyly of the subgenus was strong, a preliminary phylogenetic analysis based on morphological characters produced no clear resolution of species relationships within the genus. This is mainly because the differences between the species are based mostly on differences in the shape of the vesica and juxta, differences that are difficult to score in a matrix. Other character states show homoplasy across the subgenus. Because morphological divergence is so minor between the species, resolution of relationships within *Bulbostyla* may require analysis of molecular data.

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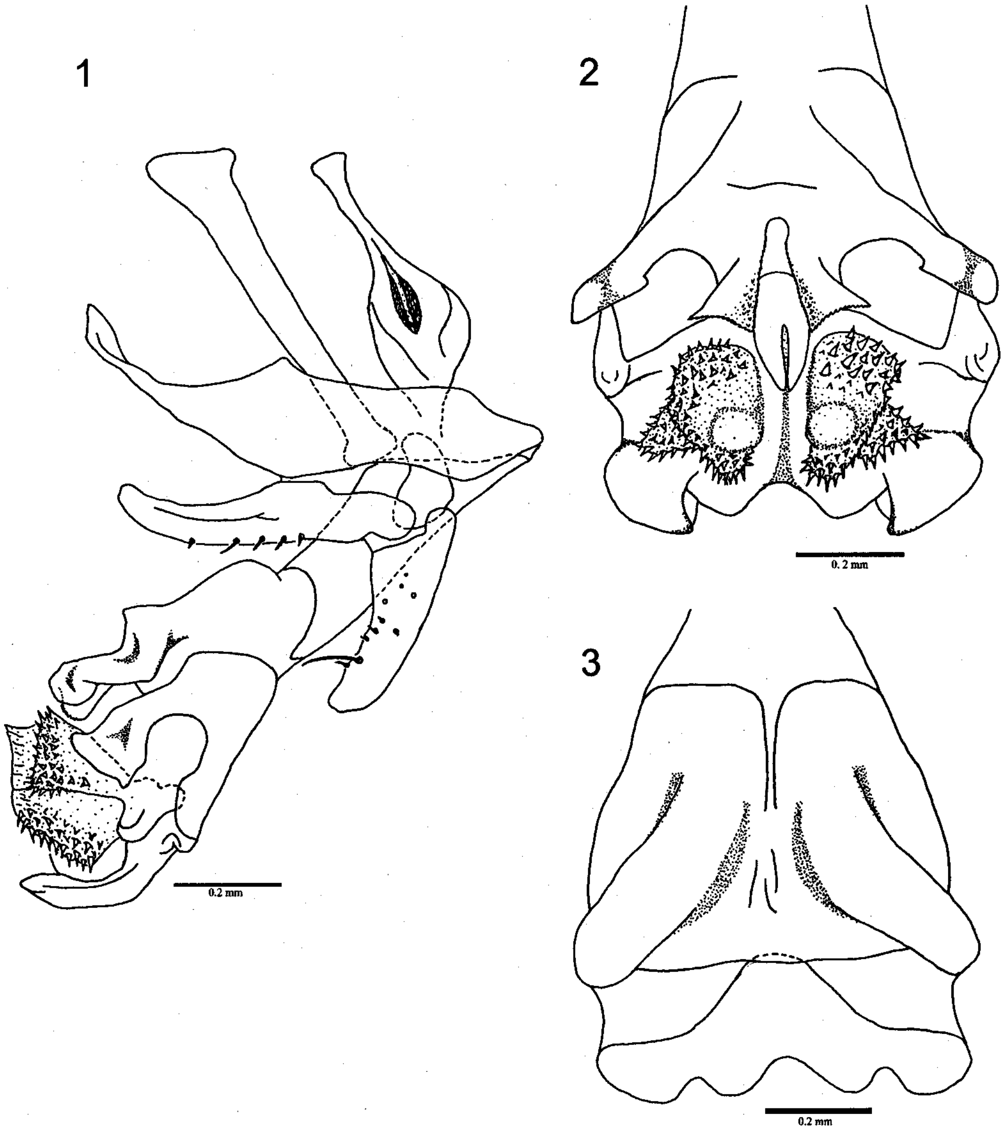
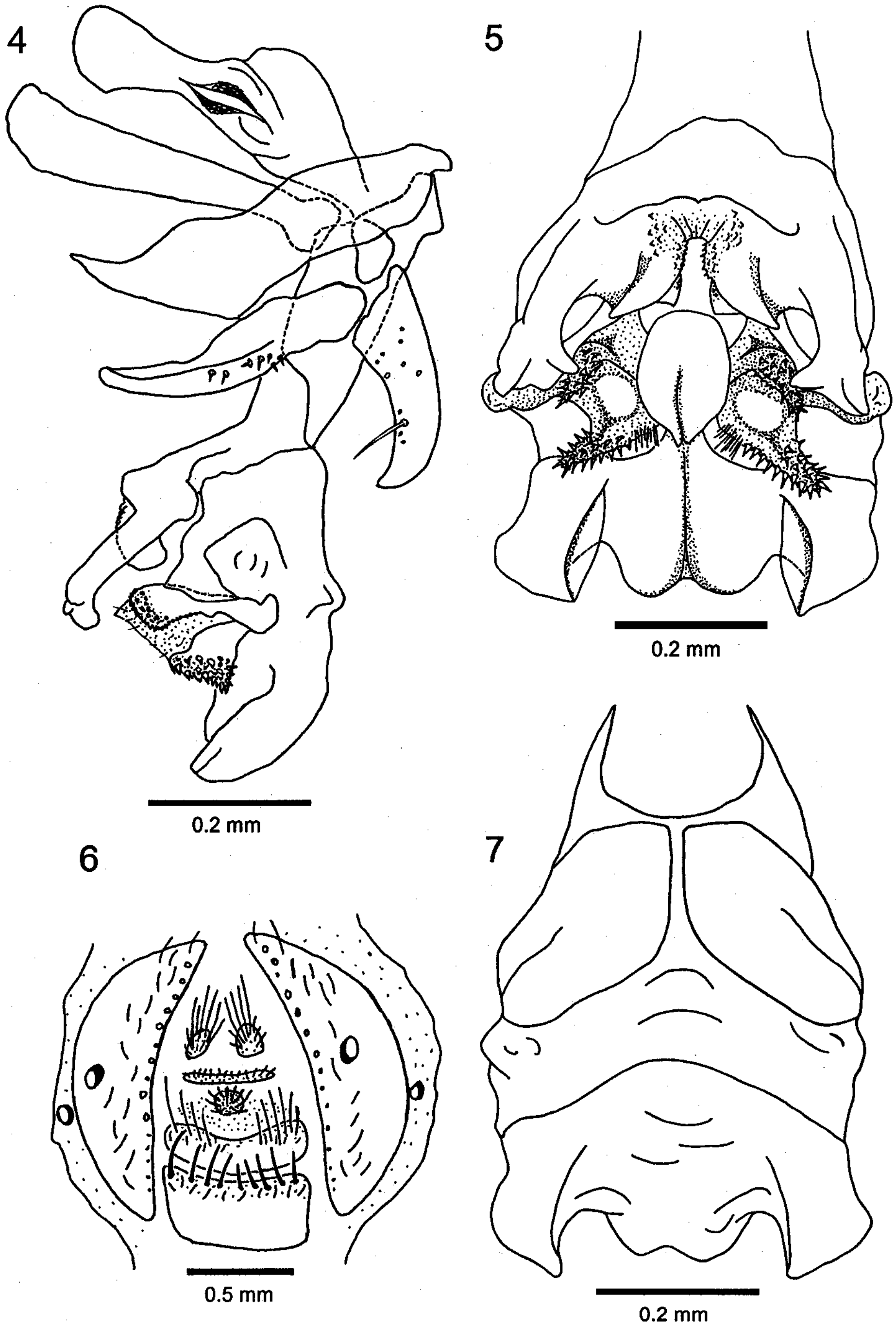
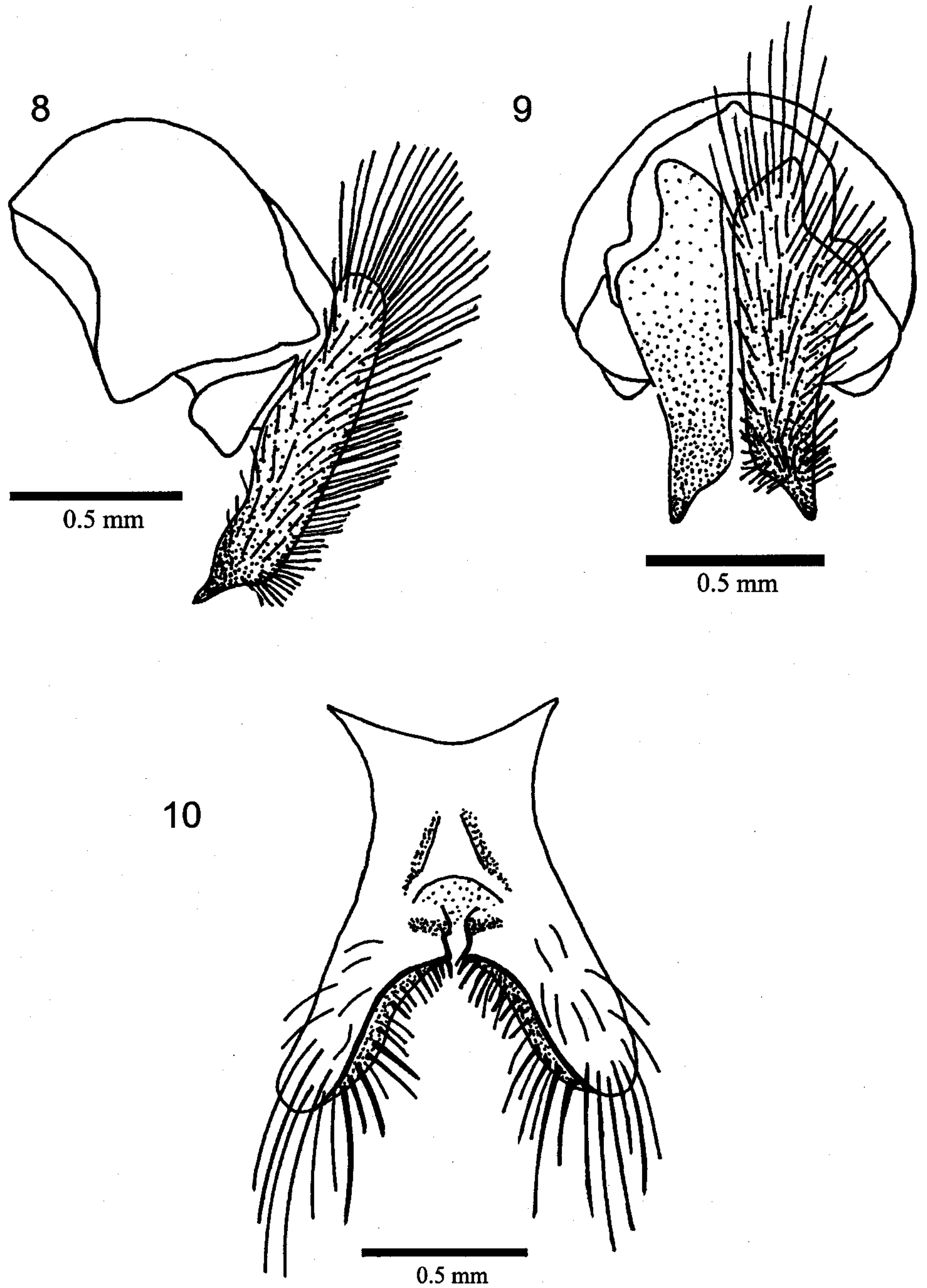


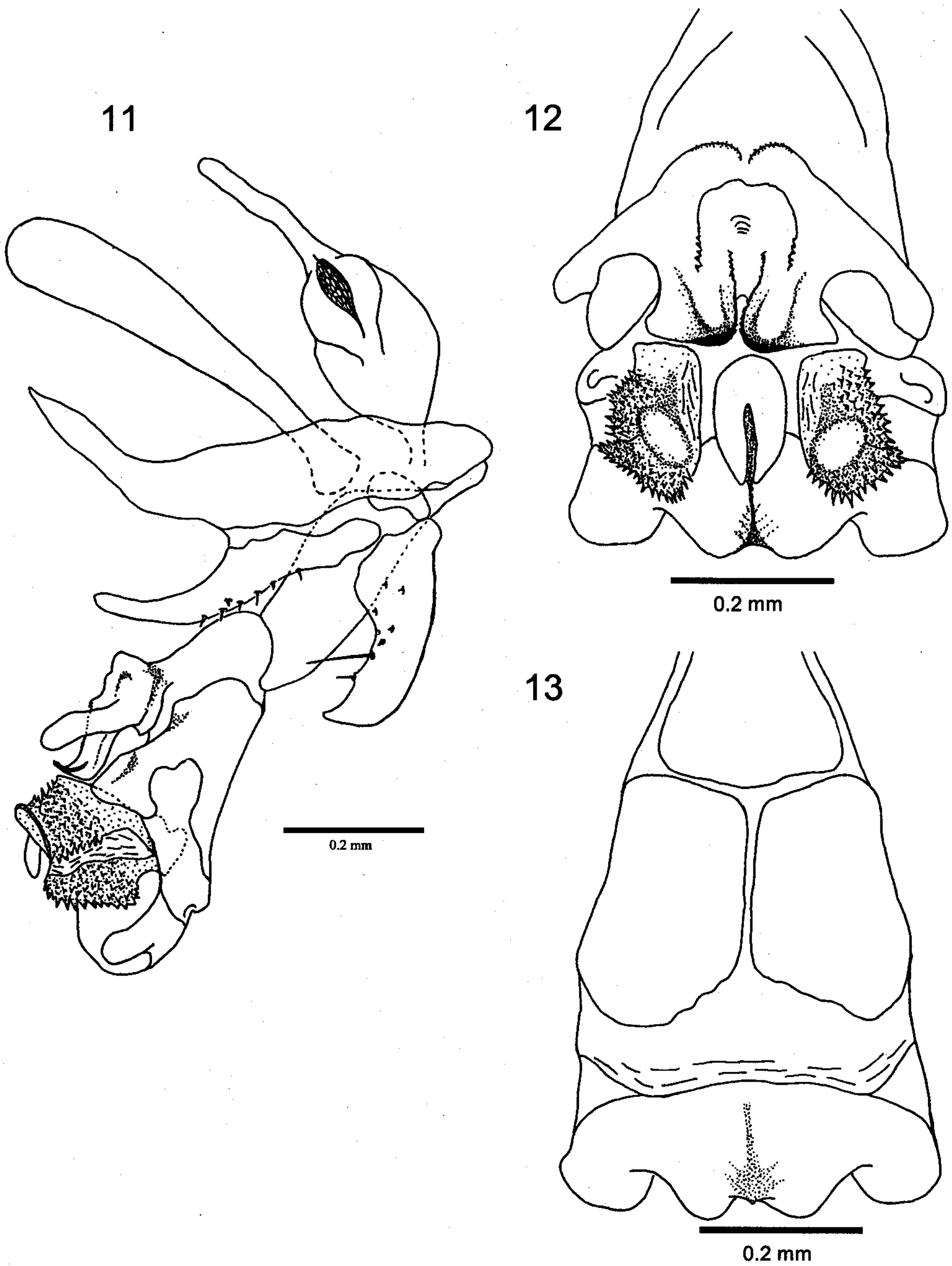
**Figures 1-3**. *Sarcophaga (Bulbostyla) airosalis*: (1) Phallus, lateral. (2) Acrophallus, anterior. (3) Acrophallus, posterior



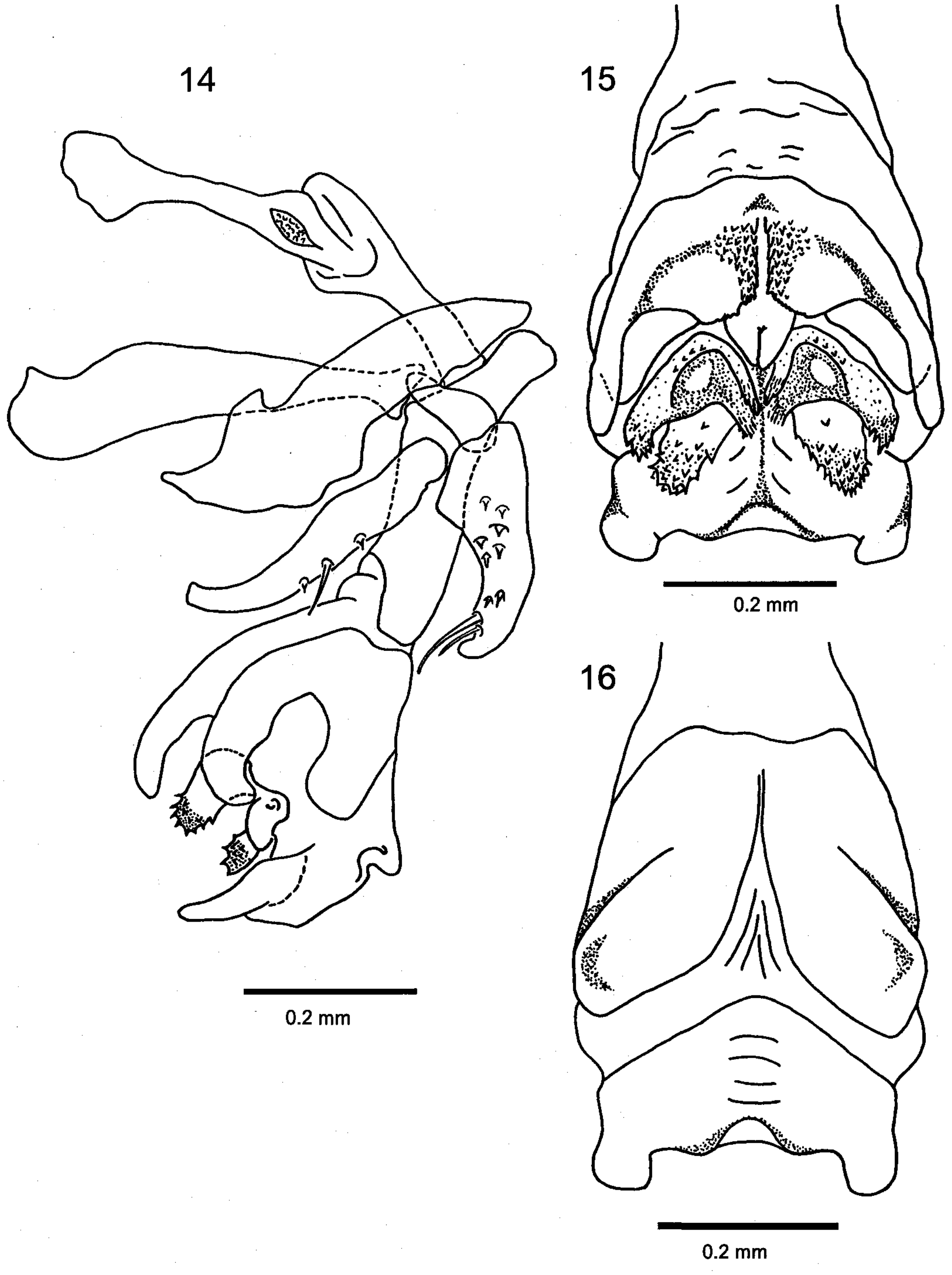
**Figures 4-7.** *Sarcophaga (Bulbostyla) cadyi*: (4) Phallus, lateral. (5) Acrophallus, anterior. (6) Acrophallus, posterior. (7) Female genitalia, posteroventral



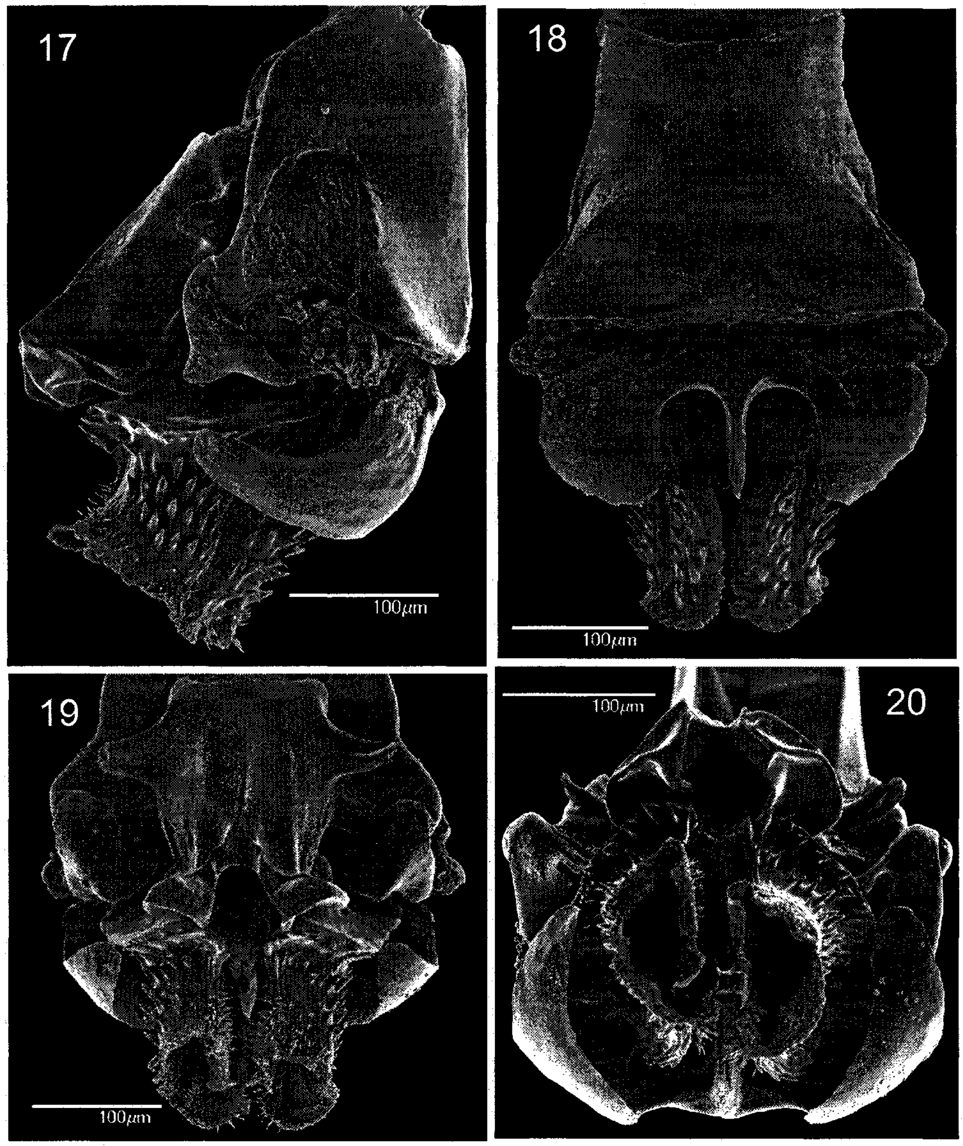
**Figures 8-10.** *Sarcophaga (Bulbostyla) cadyi*: (8) Epandrium, surstylus and cerci, lateral. (9) Epandrium, surstylus and cerci, posterior. (10) Sternite 5 ventral



**Figures 11-13.** *Sarcophaga (Bulbostyla) cuautla*: (11) Phallus, lateral. (12) Acrophallus, anterior. (13) Acrophallus, posterior



**Figures 14-16.** *Sarcophaga (Bulbostyla) ironalis*: (14) Phallus, lateral. (15) Acrophallus, anterior. (16) Acrophallus, posterior



**Figures 17-20.** *Sarcophaga (Bulbostyla) semimarginalis*: (17) Phallus, lateral. (18) Acrophallus, anterior. (19) Acrophallus, posterior. (20) Styli and juxta, anterior

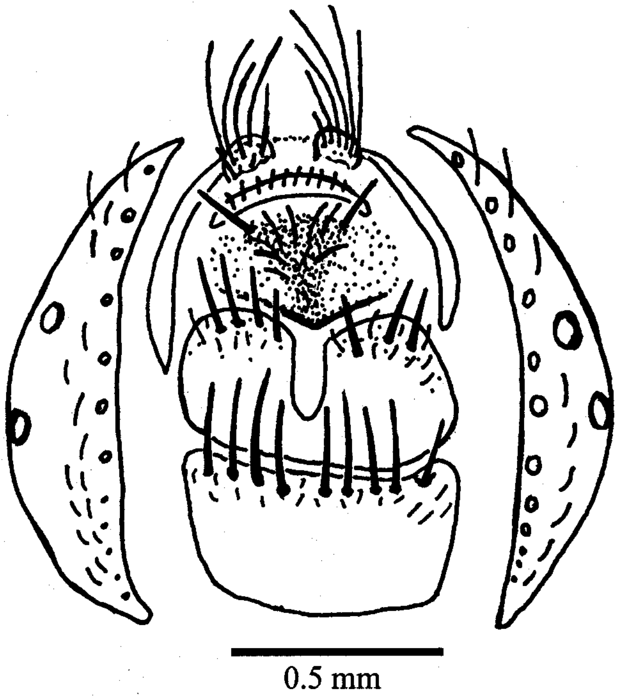
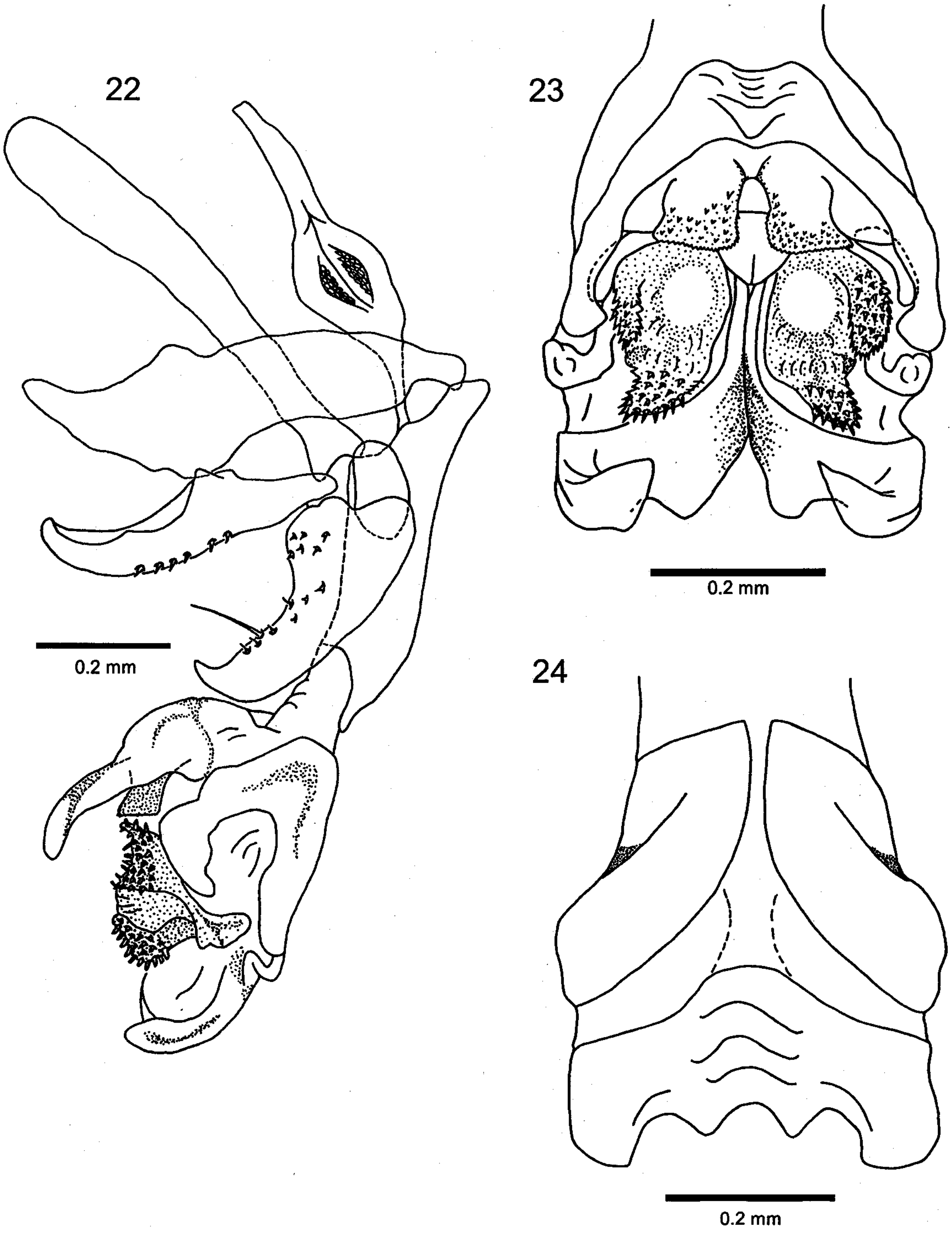
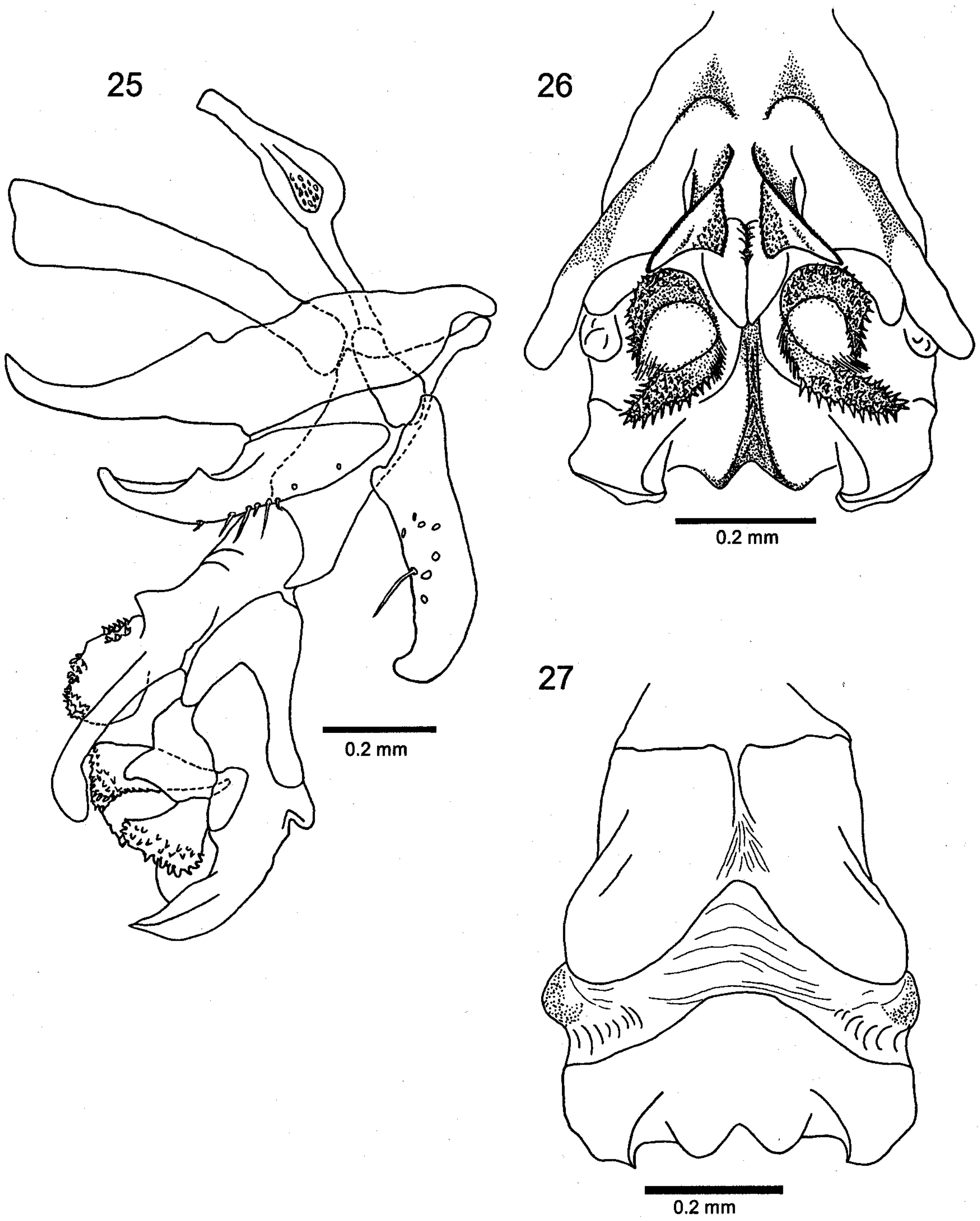


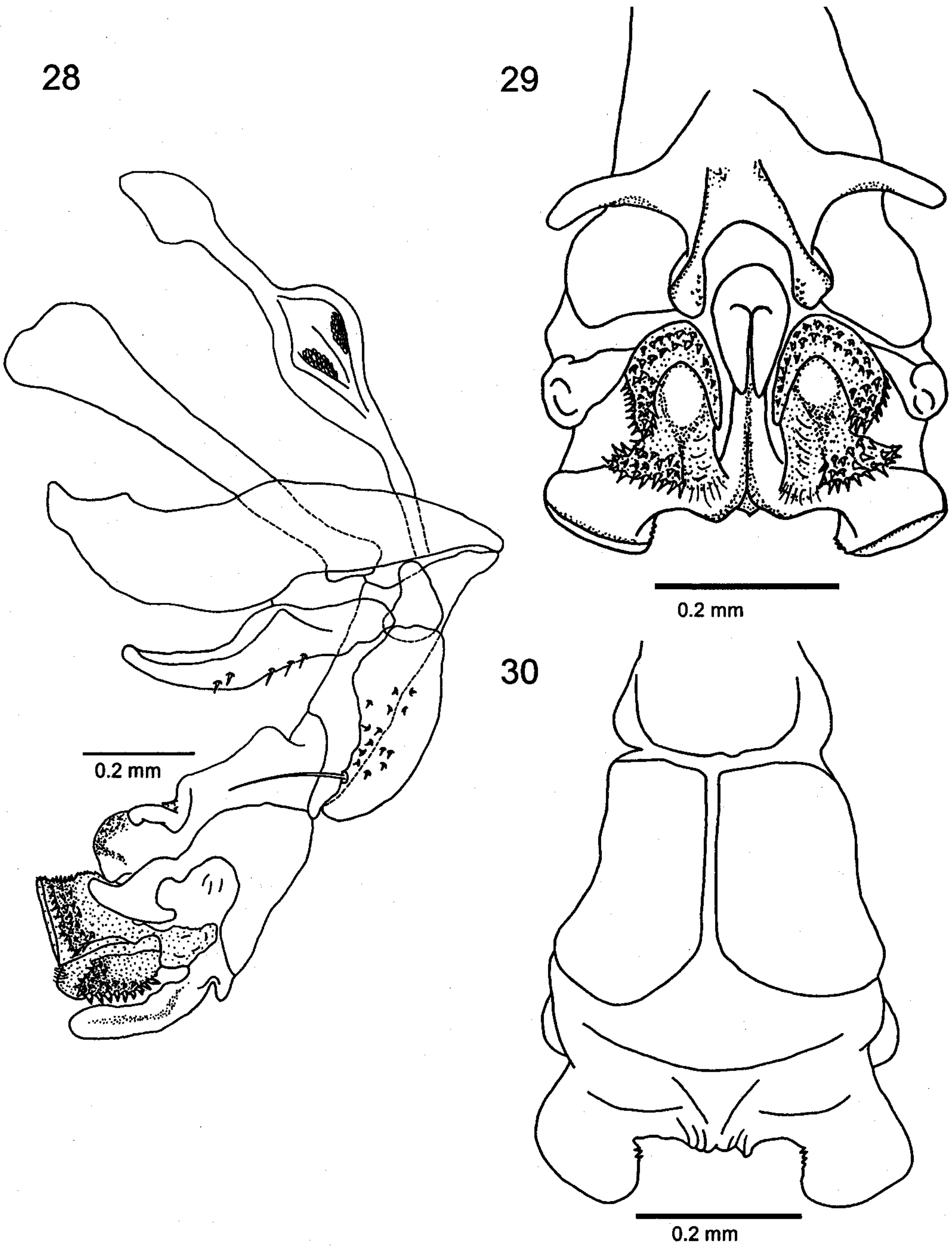
**Figure 21.** *Sarcophaga (Bulbostyla) semimarginalis*. Female genitalia, posteroventral



**Figures 22-24.** *Sarcophaga (Bulbostyla) sternalis*: (22) Phallus, lateral. (23) Acrophallus, anterior. (24) Acrophallus, posterior



**Figures 25-27.** *Sarcophaga (Bulbostyla) subdiscalis*: (25) Phallus, lateral. (26) Acrophallus, anterior. (27) Acrophallus, posterior



**Figures 28-30.** *Sarcophaga (Bulbostyla) yorkii*: (28) Phallus, lateral. (29) Acrophallus, anterior. (30) Acrophallus, posterior

## CONNECTING STATEMENT

The non-monophyly of *S.* (*Neobellieria*) was demonstrated in chapter 2. For this reason, and to accommodate the single New World species *Sarcophaga triplasia* Wulp, the genus *Robackina* Lopes was removed from synonymy with the subgenus *Sarcophaga* (*Neobellieria*) Blanchard and reinstated as a subgenus of *Sarcophaga* Meigen. The following chapter gives this new status to *S.* (*Robackina*) and its single species is redescribed.

# CHAPTER 5. Taxonomy of *Sarcophaga Triplasia* Wulp and the status of *Robackina* Lopes (Diptera: Sarcophagidae)

**Abstract.** *Robackina* Lopes is removed from synonymy with the subgenus *Sarcophaga* (*Neobellieria*) Blanchard and reinstated as a subgenus of *Sarcophaga* Meigen to accommodate the single New World species *Sarcophaga triplasia* Wulp. The subgenus and species are redescribed and illustrated.

## Introduction

The cosmopolitan genus *Sarcophaga* Meigen includes 133 subgenera (Pape 1996). The monophyly and relationships of most of these subgenera have not been tested cladistically. In a preliminary phylogenetic analysis of the Sarcophaginae, including 31 subgenera of *Sarcophaga*, we have found that *Neobellieria* Blanchard is one of the currently recognized subgenera whose monophyly is not supported. The species assigned to *Neobellieria* by Pape (1996) comprise three separate clades, one of which contains only the species *Sarcophaga* (*Neobellieria) triplasia* Wulp, the type species of *Robackina* Lopes.

*Sarcophaga triplasia* was first made available in a key (Wulp 1895) and a complete description was published the next year (Wulp 1896). Lopes (1975) transferred *S. triplasia* to the new genus *Robackina*. Subsequently, Pape (1996) synonymized *Robackina* with the subgenus *Sarcophaga* (*Neobellieria*).

Because of the non-monophyly of *Neobellieria*, the purpose of this paper is to reinstate the genus group name *Robackina* as a subgenus of *Sarcophaga* and to revise the type, and only included, species *Sarcophaga* (*Robackina) triplasia*.

## Materials and Methods

This revision was based on specimens from the following institutions: Natural History Museum, London, England (BMNH); Canadian National Collection of Insects, Ottawa, ON, Canada (CNC); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); Field Museum of Natural History, Chicago, IL, USA (FMNH); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ);

Personal collection of Greg A. Dahlem, Highland Heights, KY, USA (GD); Royal Ontario Museum, Toronto, ON, Canada (ROM); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

The abdomen was removed from pinned male specimens, placed in hot 10% KOH for about five minutes, and transferred to glycerin, where the postabdomen, including sternite 5, was separated by cutting the membrane between sternite 4 and 5, and the epandrium was then separated from syntergosternite 7+8. If necessary, genitalia were returned to hot 10% KOH for about two minutes. The epandrium and hypandrium were usually separated to facilitate examination of the phallus. Female terminalia were removed from pinned specimens by cutting the membrane between abdominal segments 4 and 5; the postabdomen was cleared in the same way as males. All structures were rinsed in water (twice), 70% ethanol, 20% acetic acid (5-8 minutes), and 70% ethanol. Once dried, the male abdomen was glued into its original position on the pinned specimen and male or female terminalia were stored in glycerin in a plastic microvial pinned below the specimen. Illustrations were made using a compound or a dissecting microscope equipped with a drawing tube. Female terminalia were photographed using a Nikon Coolpix 4500 camera on a Nikon SMZ 1500 microscope.

Terminalia for scanning electron microscopy were dissected as above except that the phallus was dissected in 70% ethanol instead of glycerin. The phallus was separated from the hypandrial complex and dried in two changes of 70% ethanol, followed by two changes of 100% ethanol. The phallus was glued to an aluminum stub with double-sided carbon tape, coated with 20nm of platinum in a high resolution fine coater (Jeol JFC-2300HR) and examined using a Jeol-JSM-6335F Field emission SEM.

Body length was measured from the anterior margin of the head, excluding antennae, to the apex of the abdomen, excluding genitalia. The label data of primary type material is given verbatim with '/' showing a line change and ';' representing a change in label.

*Sarcophaga* (*Robackina)* Lopes, **stat. n.**

*Robackina* Lopes, 1975: 159 (type species: *Sarcophaga triplasia* Wulp by original designation)

*Sarcophaga* (*Neobellieria*) in part: Pape, 1996: 366.

Diagnosis: *Robackina* may be distinguished from other subgenera of *Sarcophaga* by the strong anteroventral setae on the apical part of the hind femur (Fig. 10-13), the tapering and anteriorly curved apex of the male cercal prong in lateral view (Fig. 3) and male sternite 5 with a short base and a pad-like patch of black bristles on the posterior margin (Fig. 4).

Description (male):

Head: ground color black or brown usually with bronze, silvery or yellowish pruinosity. Postocellar setae forming a group of medium to long proclinate hairs and setae extending to or beyond level of paravertical setae; inner vertical setae reclinate; outer vertical setae as long or slightly longer than upper postocular; proclinate orbital setae absent; upper orbital setae reclinate; fronto-orbital plate with scattered black hairs, often forming a single row close to eye; parafacial bronze, brownish or yellowish pruinose, with scattered black hairs; occipital setae white except 1-2 rows of black setae ventral to postocular setae.

Thorax: ground color black or brown, bronze, grey or silvery pruinose. Presutural acrostichal setae absent; 1 pair prescutellar acrostichal seta; 4-5 presutural dorsocentrals, slightly stronger than adjacent clothing setae; 1 + 2 intra-alar setae, posterior one stronger; 1-2 + 3-4 supra-alar setae; anterior postpronotal seta present; 2 basal postpronotal setae, inner one sometimes reduced; 2 postalar setae; intrapostalar setae reduced or absent.; postalar wall haired. Usually 5-8 strong anepisternal setae, upper two shorter and declinate; dorsal and anterodorsal parts of anepisternum and dorsal part of katepisternum with moderately long to long wavy hairs. Infrasquamal setae present. Posterior spiracle subtriangular with anterior fin-shaped fringe usually dark brown and posterior fringe usually paler.

Wing membrane hyaline; veins dark brown, pale-brown or yellowish. Tegula dark, brown pruinose, bristled on about half of its surface, with a short black bristle on outer margin and 2 long black bristles on inner margin. Basicosta pale, golden-beige pruinose. C extending to $M_{1+2}$, base strongly bristled with 2-3 stout bristles close to costagial break, usually with ventral row of equidistant tiny setae extending to or just beyond $R_1$. Weak costagial, humeral and subcostal breaks. Costal spine absent or vestigial. Subcostal sclerite and stem-vein golden-brown pruinose. Base of stem-vein with cluster of golden-brown hairs. Axillary sclerites golden-beige pruinose. $R_{4+5}$ setulose at base dorsally and ventrally, ventral row often extending to proximal half. Bend of M acute, sometimes right-angled, bent part concave relative to cell $R_{4+5}$, extension at bend usually present as short fold darkened by dense microtrichia. $CuA_1$ ending at wing margin as small fold with dense microtrichia. $A_1$+$CuA_2$ not reaching wing margin. $A_2$ present as a fold darkened by dense microtrichia. Calypters creamy white; upper calypter rounded; lower calypter broadly expanded and angular, posterior margin straight.

Legs: background color yellow to black, grey-white pruinose. Trochanters usually shining brown. Hind trochanter with ventral patch of short, strong setae. Fore femur with complete row of strong dorsal and ventral setae (longer in middle) and complete row of shorter posterodorsal setae. Fore tibia usually with 3-4 strong anterodorsal setae proximally, 1 posterior setae on distal third, 1 dorsal, 1 posterodorsal, 1 posterior and 1 posteroventral setae apically. Mid femur with row of short posteroventral setae on apical half or third (sometimes slightly stronger than adjacent clothing hairs), with almost complete row of moderately long anteroventral setae, 3-5 strong mid anterior setae and 2-3 stong posterodorsal setae apically. Mid tibia with 2-4 short posterior setae on proximal half or third, with 1-3 short to moderately long mid anterodorsal setae, usually with 1 moderately long posterior, 1 posterodorsal seta on apical third (sometimes a ventral seta also present), and setae of various lengths around apex. Hind femur and tibia straight to slightly curved ventrally (Fig 10). Hind femur with 1 strong anteroventral setae on apical part, 1 complete row of anterodorsal setae, with second anterior row restricted to proximal half or third (Fig. 10) and with posterodorsal row of 4-5 setae, the distalmost being almost posterior relative to the others. Hind tibia with 2-5 posterodorsal setae on proximal half and with 1 dorsal, 1 anterodorsal, 1 anterior, 1 anteroventral setae apically. Tarsomere length: 1>2>3>4<5, first fore tarsomere and first and second hind tarsomeres with pad of fine bronze posteroventral and posterior setae.

Abdomen elongate, slightly conical posteriorly. Ground color black or brown with grey, bronze or silvery pruinosity. Tergites covered with small black setae dorsally and longer hairs ventrally. Number of lateral marginal setae variable between tergites and between specimens.

Terminalia: background color yellowish-orange, black setulose. Sternite 5 with V-shaped emargination posteriorly and with short base anteriorly, cleft of posterior margin with dense patch of moderately long to long black bristles, window present (Fig. 4). Tergite 6 absent. Syntergosternite 7+8 with anterodorsal emargination and with spiracle 7 dorsolateral. Epandrium shining and globose, square in lateral view (Fig. 3) but with posteroventral extension partly covering cerci in dorsal view (Fig. 2). Surstylus triangular (Figs. 2-3), proximal surface bare. Cercal base clothed with typical black long hairs, cercal prong black on distal half (Fig. 3). Bacilliform sclerites reduced or absent. Hypandrial arms not fused in posterior view. Postgonal apodeme reduced to a more or less oval dorsal sclerite. Pregonite with tiny setulae along ventral surface. Postgonite with a short bristle arising from basal anterior surface. Lateral stylus coiled at base and with a longitudinal cleft opened all along internal side (Figs. 1, 6-7). Median stylus bifurcate and with no opening (Figs. 1, 6-7). Juxta fused to median stylus.

Female: As in male except as follows: Head: outer vertical setae strong. Proclinate orbital setae present. Thorax: apical scutellar setae absent. Usually 3 katepisternal setae, middle one smaller than the others. Hairs on dorsal and anterodorsal parts of anepisternum and dorsal part of katepisternum shorter and less dense. Legs moderately long to long anteroventral, ventral and posteroventral wavy hairs absent on all femora and tibiae. Mid femoral organ present. Mid femur with 1 row of moderately strong posteroventral setae in proximal half or third. Mid tibia with moderately long ventral seta on apical third always present. Hind femur and tibia always straight. Hind femur with a more or less regular row of anteroventral setae along length, with 3-4 ventral setae. Abdomen rounded and slighty conical posteriorly. Tergites 1-5 covered with small black setae dorsally and ventrally, with longer hairs restricted to sternites and ventral margin of tergites.

Terminalia (Figs. 5, 9): tergite 6 narrowly membranous mid-dorsally, sometimes with a secondarily sclerotized membrane. Spiracle 6 and 7 distinct on each plate of tergite 6. Sternites 6-8 not fused. Cerci distinct.

*Sarcophaga* (*Robackina) triplasia* Wulp (Figs. 1-13)

*Sarcophaga triplasia* Wulp, 1895: 269; Wulp, 1896: 283.

*Sarcophaga fulvipes nigra* Parker, 1914: 38 (junior secondary homonym of *Myophora nigra* Robineau-Desvoidy, 1830).

*Sarcophaga fulvipes* Macquart of Aldrich, 1916 and Roback, 1954 (misidentification).

*Sarcophaga fulvipes dissidia* Parker, 1917: 157 (replacement name for *Sarcophaga fulvipes nigra*).

*Robackina triplasia*: Lopes, 1975: 161; Lopes, 1980: 229.

*Sarcophaga* (*Neobellieria*) *triplasia*: Pape, 1996: 367.

Type material: Lectotype (by present designation): ♂ labelled 'Mexico, Amula, in Guerrero, 6000 feet' (H.H. Smith) (BMNH); Paralectotypes: 3 ♀ same data as lectotype (BMNH).

Type material of *Sarcophaga fulvipes dissidia*: Holotype: ♂ labelled 'Niagara Falls / June 24 NY'; 'Type'; 'Type / 7770'; '*Sarcophaga / fulvipes / dissidia* R. Pkr. / det. R. R. Parker'; 'may become / S. dissidia (RPkr.)'; 'collection / C. W. Johnson' (MCZ).

Other material examined: **CANADA**: **Ontario:** St-Lawrence Islands Nat. Park, Camelot Island, 10.viii.1976 (1♂, 1♀, CNC); same data except Thwartway Isl., 29.vi.1976 (1♂, CNC); same data except 5-23.viii.1976 (6♂, 4♀, CNC); Frontenac Co., Perth Road, 25.vii.1957 (1♂, CNC); same data except 4.viii.1970 (1♀, ROM); Renfrew Co., Calabogie, roadside, 27.vi.1978 (1♀, ROM); same data except abandoned road, 15.vi.1978 (1♂, ROM); same data except on *Salix* leaves, 14.vi.1978 (1♀, ROM); Leeds Co., Chaffeys Locks, 26-27.vi.1969 (1♂, 1♀, ROM); same data except 03-30.vii.1969 (4♂, 2♀, ROM); Leeds Co., 8 mi. N.Westport, on Co. road 10, plants by roadside, 13.viii.1978 (1♂, ROM); Georgian Bay Islands Nat. Pk., 5.ix.1983 (1♀, DEBU); **Quebec:** Mont St-Hilaire, 25.vi-2.vii.2001 (1♀, LEM); Old Chelsea, King Mt., 16.vi.1961 (1♂, CNC); same data except 13.viii.1969 (1♂, CNC); same data except 22.vii.1970 (1♂, CNC); Mont Rigaud, 800', 11.vi.1981 (3♂, CNC); same data except 25.ix.1985 (1♂, CNC); same data except 16.viii.2005 (4♂, LEM); **USA: Arizona:** Pima Co., Madera Canyon, Santa Rita Mts., 6.vii.1958, 5000' (1♂, 1♀, CNC); **Arkansas:** Washington Co. 27.v.1928 (1♀, USNM); **Florida:** Sanford, 8.viii.1939 (1♀, CNC); Wildwood, 2.viii.1930 (1♂, CNC); Palm Beach Co., 14.ix.1952 (1♂, USNM); St. Augustine (1♂, USNM, 1♂, MCZ, 1♂, CNC); same data except 16.iv.1919 (1♀, MCZ); Branford, 31.vii.1930 (1♀, CNC); **Georgia:** Towns Co./White Co., Chattahouchee National Forest, summit of Tray Mountain (34° 47'N. 83°40'W), 4430', 26.v.2000, 11AM to 3PM (23♂, GD); Union White/Lumpkin Co's, summit of Cowrock Mountain (34°

43'N. 83°51'W), 3841', 25.v.2000, 11AM to 12:30PM (35♂, GD); Rabun Co., summit of Rabun Bald (34° 58'N. 83°18'W), 4696', 22.v.2000, 10AM to 1PM (7♂, GD); Rabun Bald, 12.vii.1952 (1♂, GD); same data except 24.viii.1949 (1♂, USNM); Tray Mountain, 19.vi.1936 (1♂, USNM); **Indiana:** Orange Co., Pioneer Mothers Memorial Forest, 12.vii.1989 (1♂, DEBU); Cobb Co., Kennesaw Mt. Nat. Battlefield Pk, summit of Kennesaw Mountain (33° 58'N. 84°34'W), 1808', 21.v.2000, 12:30PM to 1:30PM (2♂, GD); **Iowa:** Boone Co, Ledges St. Pk. 25.ix.1950 (1♀, GD) same data except 8.vii.1950 (1♂, 3♀ GD); **Kentucky:** Marion Co., Rohan Knob, 19.v.1985 (31♂, GD); **Louisiana:** Opelousas, iii.1997 (1♂, FMNH); **Maryland:** Beltsville, 06.viii.1916 (1♂, USNM); Laurel, 4.vi.1967 (1♂, USNM); same data except 1.vi.1965, Malaise trap (1♀, CNC); Plummers Island, 20.ix.1917 (1♂, USNM); **Mississippi:** Lafayette Co., spring 1943 (2♂, CNC); **Missouri:** Pilot Knob, Pilot Knob Mt. nr., 21-22.viii.1967 (4♂, GD); Reynolds Co., Johnson's Shut-ins St. Pk., 11.vi.1968 (2♂, GD); **New Mexico:** Bernalillo Co., 7 mi. S. Tijeras, 7400', 23-26.viii.1975, ponderosa pine-pinyon-juniper wood (1♂, FMNH); **New York:** Bear Mountain, 2.viii.1925 (1♀, FMNH); same data except 21.vi.1925 (1♂, USNM); same data except 18.v.1941 (1♀, USNM); Jefferson Co., Butterfield, 2.viii.1970 (1, ROM); Tuxedo, 29.vii.1912 (1♂, USNM); **North Carolina:** Otto, Cunningham Cr., Coweeta Hyd. Lab., 17.v.1961 (1♂, CNC); Base of Wayah Bald, 10.viii.1957 (1♂, CNC); Burke Co., Pisgah National Forest, summit of Hawksbill Mt., 4020', 16.viii.1999, 12h30 to 14h30 (11♂, GD); same data except 27.v.1999 (4♂, GD); **Ohio:** Sugar Grove, 8.vi.1926 (1♂, USNM); same data except 10.vi.1928 (1♀, USNM); **Pennsylvania:** Schuylkill Co., Auburn, 9.viii.1993 (1♂, DEBU); Inglenook, 3.vii.1917 (1♂, USNM); **South Carolina:** Clemson, 26.v.1962 (1♂, USNM); **Tennessee:** Great Smoky Mountains Nat. Pk.. Ramsey Cascades, 12.vi.1946 (1♂, USNM); same data except Chimneys camp, 11vi.1946 (1♂, USNM); same data except Chimneys, 20.vi.1941 (1♀, USNM); **Texas:** Menard, 1929 (2♂, USNM); Sonora, 22.ix.1920 (1♂, USNM); Jeff Davis Co., Davis Mts St. Pk., 23.viii.1968 (1♂, GD); Sheffield, 10.vi.1949 (2♂, CNC); Big Bend Nat. Pk., Dugout Wells, 3000', 13.v.1959 (1♂, CNC); Chisos Mts. 17.vii.1936 (1♀, CNC); **Virginia:** Hardy Co., Lost River St. Pk., 1-14.viii.1960 (1♂, USNM); Augusta Co., George Washington N. F. Great North Mt., at ridge line, 2600' (38° 5'1"N, 79°26'2"W), 11.vii.2001 (1♂, CNC); Shenandoah, Big Meadows, 15.vi.1941 (1♂, USNM); same data except Lewis Falls, vii.1939 (1♂, USNM); Cacapon St. Pk, 31.viii.1955 (1♂, USNM); **MEXICO: Durango:** 5-25 mi W. Durango, between 6500' and 7200', 14.vi-10.viii.1964 (17♂, 3♀, CNC); same data except 10 mi W. El Salto, 9000' (1♀ CNC); 20 mi. E. Concordia, 3000', 8.viii.1964 (1♂, CNC); **Nuevo Leon:** Mamulique Pass 2km NE on microwave road, 17-18.vi.1982, dry wash, 2000' (1♂, 2♀, GD).

Description (male): body length 7.5-16.0 mm.

Head: 8-12 pairs of medioclinate frontal setae, row curving outwards at lunule. Usually 3-6 pairs of weak interfrontal setae, posterior ones longer and stronger. Frontal vitta pale brown, dark brown or black. Gena black-haired. Postgena white-haired. Antenna dark to light brown, middle of arista usually light brown. Palpus pale to dark brown, sometimes yellow, clavate.

Thorax: 4-5 postsutural dorsocentrals, posterior two stronger. Scutellum with 1 short apical (sometimes weak), 1 strong and long subapical, 1 basal and 1 moderately long discal pair of setae. Usually 2 katepisternal setae, if 3 then middle one usually smaller than others.

Wing: Lateral margin of alula with fringe of dark hairs as long as those on anterior margin of anal lobe. Posterior margin of upper calypter with short white hairs. Hairs fringing calypters at fold long, whitish, sometimes golden-brown, extending to distal margin of lower calypter.

Legs: tibiae and femora yellow to black, tibiae often paler than femora and femora sometimes with a rounded dark area anteriorly and posteriorly at apex. All femora and tibiae except fore tibia usually with moderately long to long anteroventral, ventral and posteroventral wavy hairs (denser on hind legs). Hind femur sometimes moderately swollen (see Remarks).

Abdomen: usually 1 pair of median marginal setae on tergite 4. Posterior margin of tergite 5 usually partly orange-reddish and with marginal row of strong setae.

Terminalia: cercal prong tapering and curving anteriorly (Fig. 3). Vesica sclerotized, forming a bilobed structure with small teeth on apical margin. Harpes reduced and not fused to phallic tube (Fig. 1). Lateral stylus well developed, with numerous microserrations on exterior margins and long slender hook laterally (Figs. 1, 6-7). Median stylus forming two very long tubular processes apically (Fig. 1,7). Juxta as long as wide in dorsal view and entirely sclerotized (Fig. 8). Demarcation with phallic tube distinct.

Female: body length 8.0 - 12.0 mm. As in male except as follows: Head: pedicel sometimes yellow. Legs: hind femur never swollen and with second row of anterodorsal setae on proximal half or third usually missing or reduced. Hind tibia sometimes with a third anteroventral setae. Abdomen: posterior margin of sternite 2 usually with 3-4 strong bristles. Posterior margin of sternite 3 sometimes with few strong bristles.

Terminalia: tergite 6 well developed and forming two distinct plates separated dorsally by a secondarily sclerotized membrane, plates clasp-like and usually covering other genital sclerites (Fig. 9). Sternite 6 concave and covered with small setae on distal half (Fig. 5). Sternite 7 flattened, rounded with row of short setae on distal margin (Fig. 5). Sternite 8 reduced. Sternite 10 membranous and with row of short setae on distal margin (Fig. 5).

Remarks: Wulp (1896) based his description on four syntypes, a male and three females. Neither Aldrich (1916, 1930) nor Lopes (1975) designated a lectotype although Aldrich (1930) noted that one of the female syntypes is not conspecific with the others. Accordingly, the male syntype has been designated as lectotype to fix the identity of *Sarcophaga triplasia*.

There is geographic variation in the shape and chaetotaxy of the hind femur and tibia (Figs. 10-13). Specimens from Durango, Mexico and Menard, Sheffield and Sonora, Texas have long, dense, wavy anteroventral, ventral and posteroventral hairs on all legs (except fore tibia). The hind femur is strongly swollen and the hind tibia strongly curved. The second row of anterodorsal setae is absent on specimens from Durango, Sheffield and Menard (Figs. 11, 13) but present on a specimen from Sonora (Fig. 12). The two anteroventral setae of the hind tibia are absent in specimens from Durango (Fig.11) and one is present on specimens from Texas (Figs. 12,13). Specimens from Durango also have a dense pad of ventral setae on the hind trochanter. There are intermediates between the most extreme type (Fig. 11) and the typical Nearctic form (Fig. 10) and the specimens do not differ in other characters.

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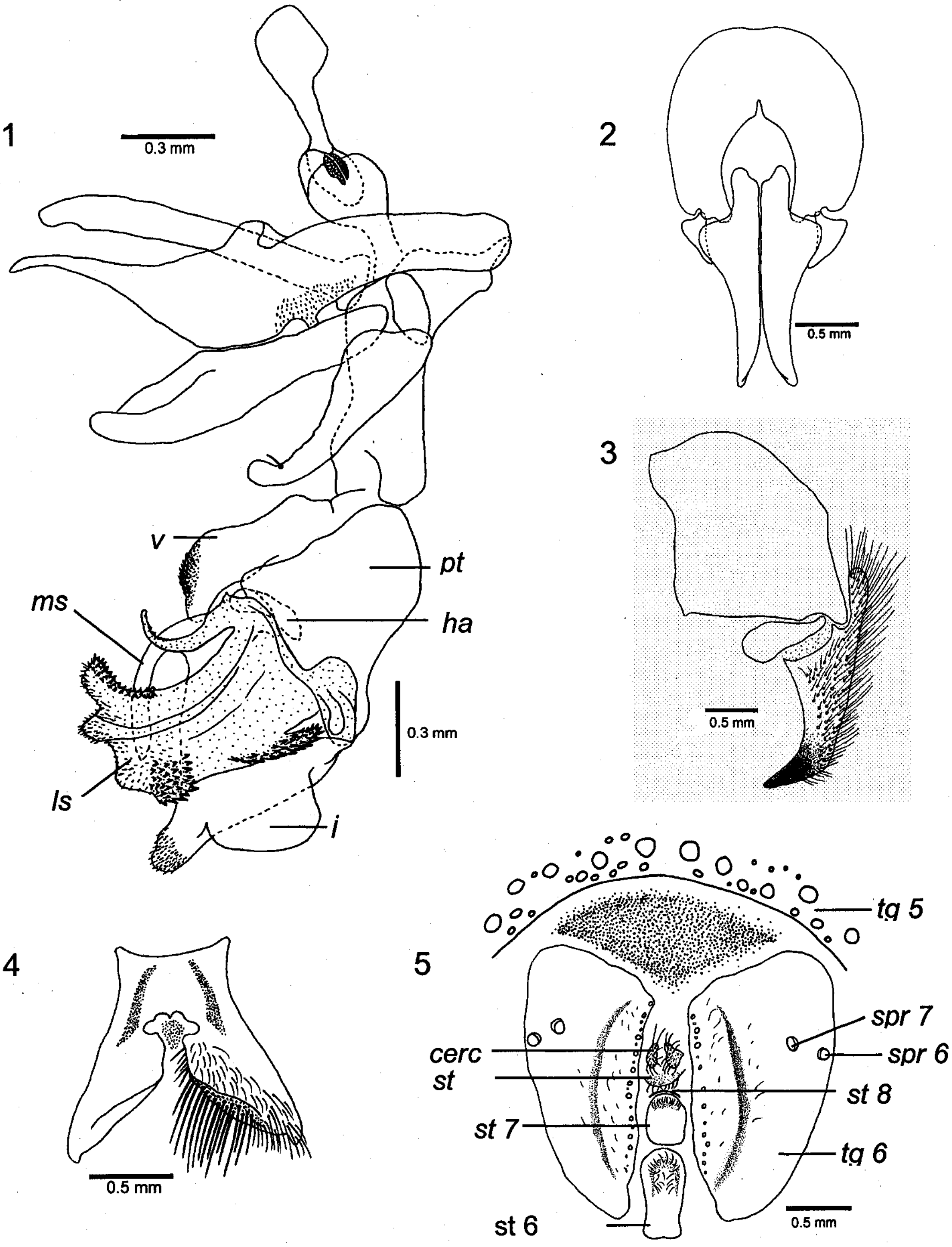
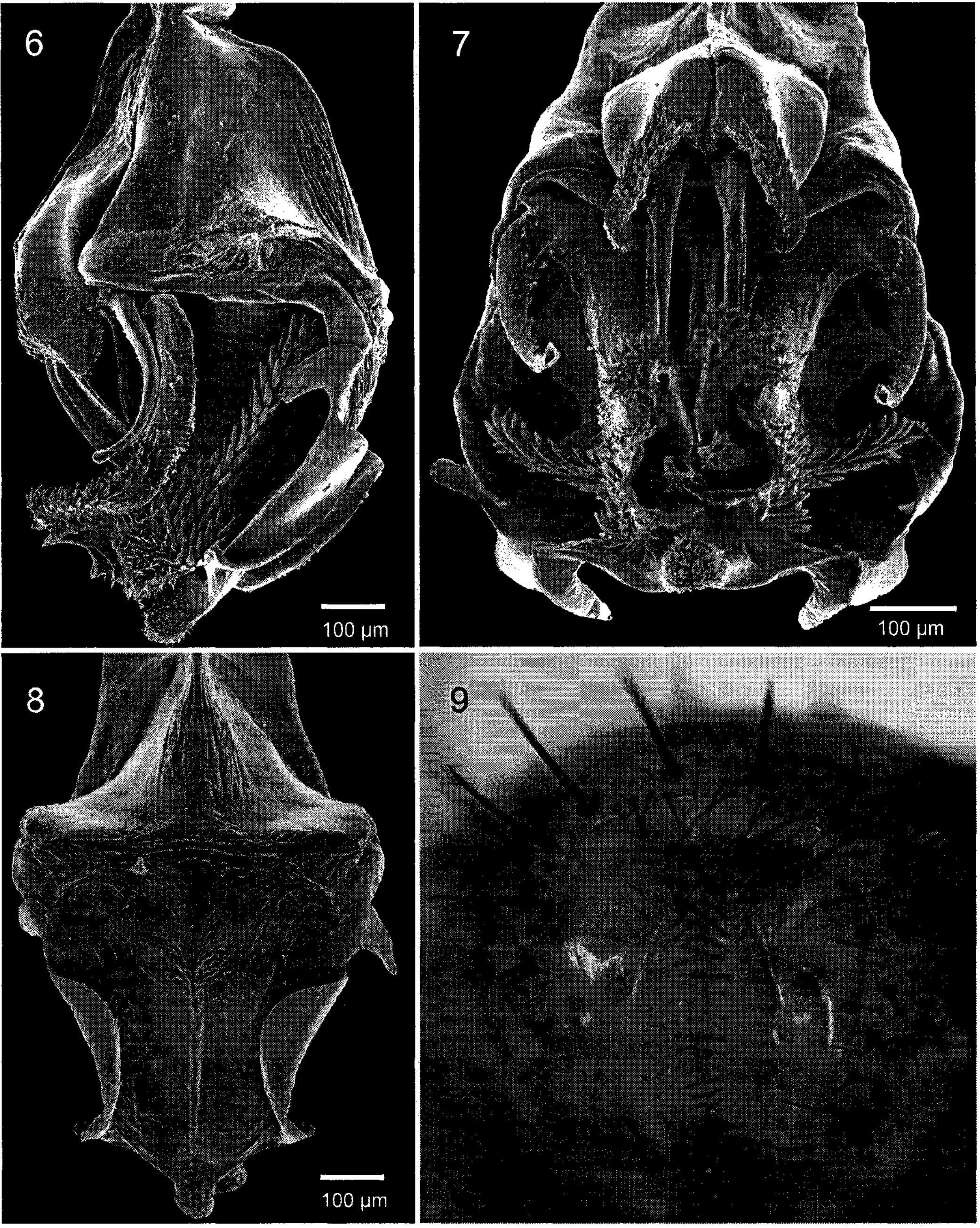
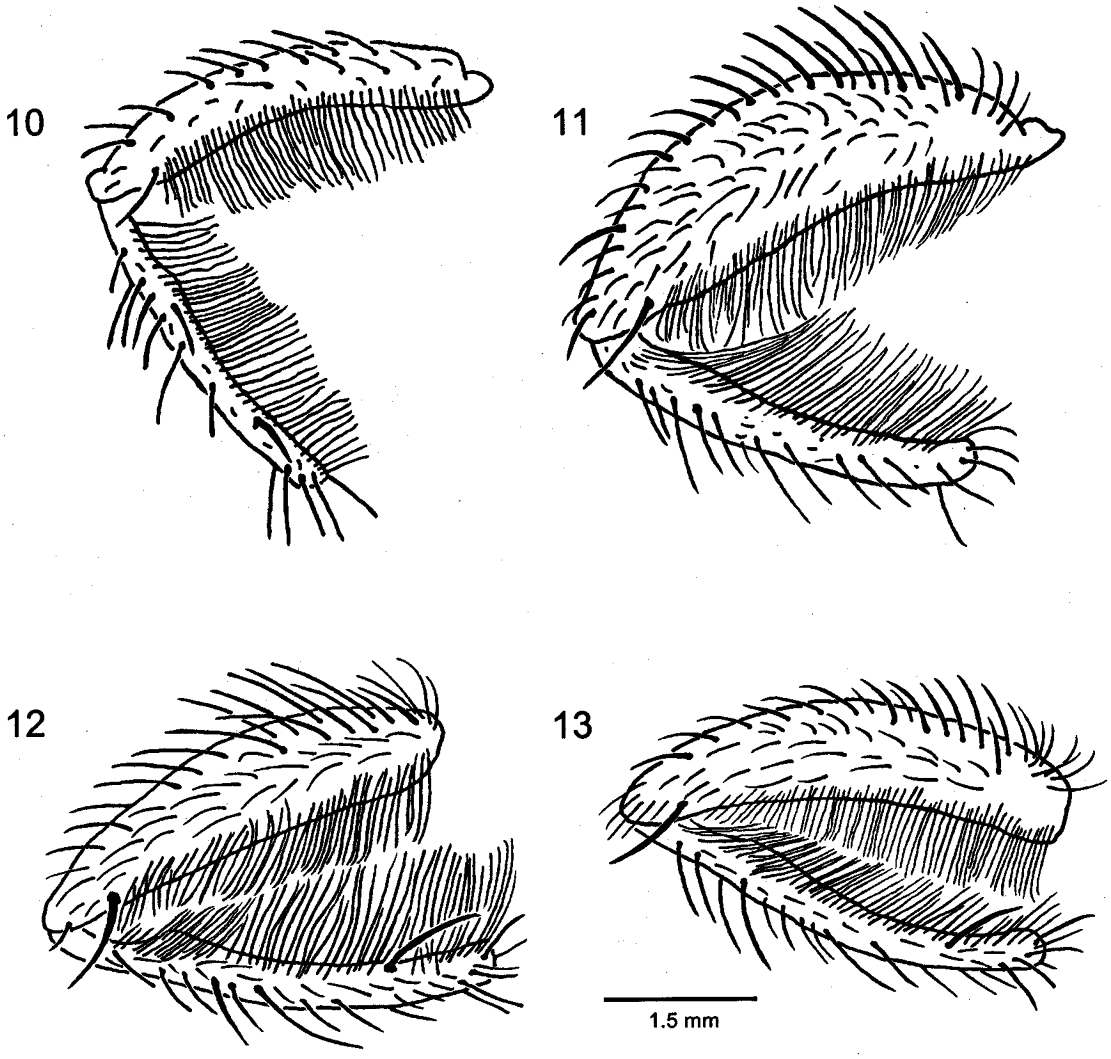


**Figures 1-5.** *S. (Robackina) triplasia* male and female genitalia. 1. Phallus, left lateral. 2. Male epandrium, surstylus and cerci, posterior view. 3. Male epandrium, surstylus and cerci, lateral view. 4. Male sternite 5. 5. Female genitalia, posteroventral view. Abbreviations: *cerc* = cercus, *ha* = harpes, *j* = juxta, *ls* = lateral styli, *ms* = lateral styli, *pt* = phallic tube, *spr* = spiracle, *st* = sternite, *tg* = tergite, *v* = vesica



**Figures 6-9.** *S. (Robackina) triplasia* male and female genitalia. 6. Male acrophallus, lateral view. 7. Male acrophallus, ventral view. 8. Male acrophallus, posterior view. 9. Female genitalia posterior view



**Figures 10-13.** Geographic variation in hind femur and tibia of *S. (Robackina) triplasia.* 10. Typical Nearctic form. 11. Specimen from Durango, Mexico. 12. Specimen from Sonora, Texas. 13. Specimen from Sheffield, Texas

# GENERAL CONCLUSION

The study presented here has made a major contributions to the knowledge and the systematics of the subfamily Sarcophaginae. It provided the first comprehensive Scanning Electron Microscopy (SEM) documentation of the sarcophagine male genitalia and one of the first explicit phylogenetic analyses clarifying sarcophagine generic classification, based on morphological characters. The male genitalic morphology was highlighted as an important source of informative phylogenetic characters and some priority areas for further systematic studies were also identified (chapter 2).

Although this phylogeny represents a significant step forward in our understanding of sarcophagine relationships, it should be keep in mind that it is a preliminary hypothesis. Other morphological studies need to be done to complete this work in which many small sarcophagine genera were not included. To achieve this goal, the addition of examplar species, particularly from the Neotropical region, the possible area of origin of the sarcophagine ancestor, will contribute to resolving the basal relationship of the subfamily.

Because flesh-flies are among the first insects to invade carrion, some Sarcophagidae can be particularly useful in forensic sciences. Because of this, the revision of *S.* (*Neobellieria*), including illustrations and photograph of male and female genitalia (chapter 3), was a prerequisite to facilitating the use of these species in forensic investigations. With the recent resurgence of interest in the use of insects as evidence in legal issues, such morphological work should be conducted in future to provide new tools for medico-legal investigators. The revision of *S.* (*Neobellieria*), one of the 133 subgenera included within *Sarcophaga*, also gave a good idea of the non-stability of the classification within this speciose genus. A detailed study of the male genitalic structures will be required to resolve phylogenetic relationships within *Sarcophaga* and many changes in the status of currently recognized subgenera may be expected. Phylogenetic studies based on morphology alone provide valuable phylogenetic information but new data from DNA sequences should also be exploited within *Sarcophaga* to clarify relationships at the subgeneric and species level. Molecular data sources are now widely used in Diptera phylogeny. However, to date, molecular techniques have been rarely used within Sarcophagidae and no attempts have been made to produce species or subgeneric-level phylogenies based on combination of molecular and morphological characters. The new subgenus *S.* (*Bulbostyla*) for which the species are quite similar and seem to show little morphological divergence (chapter 4) should be a good candidate for such investigations and to demonstrate the usefulness of molecular characters to resolve problematic species-group relationships. In addition to resolving relationships between very similar species, molecular analyses may also prove useful in resolving sister-group relationships in highly autapomorphic species such *S.* (*Robackina*) *triplasia* (chapter 5).