Phylogeny and classification of Muscini (Diptera, Muscidae)

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Worldwide in distribution, the tribe Muscini comprises 21 accepted genera and about 350 species. In the present study, a cladistic analysis based upon adult morphological characters is carried out in order to discuss the monophyly of the tribe and its genera, the intergeneric relationships and, in some cases, also the intrageneric relationships. As a result, Muscini is supported as a monophyletic tribe sister-group of Stomoxyini. Except for *Morellia* Robineau-Desvoidy, *Curranosia* Paterson, and *Eudasyphora* Townsend, all the remaining genera are monophyletic. The results are dubious for *Polietes* Rondani, which was then provisionally kept unchanged. *Morellia* was broadened to include the Neotropical endemic genera *Parapyrellia* Townsend, *Trichomorellia* Stein, and *Xenomorellia* Malloch. Therefore, a new classification is proposed for *Morellia* in which it is divided into four subgenera: *Morellia s.s.*, *Parapyrellia*, *Trichomorellia*, and *Xenomorellia*. Furthermore, the previously proposed subgenus *Dasysterna* Zimin is given new status as a genus; however, as it is preoccupied by *Dasysterna* Dejean, the new replacement name *Ziminellia* **nom. nov.** is proposed herewith. *Eudasyphora* was found to be a paraphyletic group relative to *Dasyphora* Robineau-Desvoidy; both genera are hence synonymized, and *Dasyphora* is classified in three subgenera: *Dasyphora s.s.*, *Eudasyphora*, and *Rypellia* Malloch. The analysis demonstrated that the traditional classification of *Musca* Linnaeus into subgenera is artificial and, moreover, that the use of characters from male genitalia could be strongly informative for classifying the genus in phylogeny-supported species groups. Finally, the new classification proposal for Muscini recognizes 18 genera and, furthermore, two undescribed genus-ranked taxa are indicated. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **149**, 493–532.

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INTRODUCTION

Muscidae is a large dipteran family comprising about 4500 described species in 180 genera (de Carvalho *et al.*, 2005), and is divided into seven subfamilies following the classification proposed by de Carvalho (1989b). Two tribes, Muscini and Stomoxyini, are in the subfamily Muscinae, which is considered to be among the most basal subfamilies (de Carvalho, 1989b; Couri & de Carvalho, 2003). The tribe Muscini, worldwide in distribution, exhibits a wide diversity in both morphology and ecology. Examples include reproductive strategies that may be oviparity, ovolarviparity, or larviparity (Meier, Kotrba & Ferrar, 1999), and feeding habits of larvae, which may be saprophagy,

coprophagy, and carnivory, whereas adults may be saprophagous, coprophagous, nectarivorous, or haematophagous (Skidmore, 1985; Ferrar, 1987). Adults are metallic, blackish, or brown–yellowish in colour. The morphology of male terminalia is also quite variable.

The classification of Muscini is still debated and controversial. One of the reasons for the controversy results from the uncertain definition of the subfamily, and of the family Muscidae and its allied groups. Some of these groups are now widely accepted as separate families (e.g. Anthomyiidae, Calliphoridae, Tachinidae, etc.) and most of the characters traditionally used to classify Muscinae are now known as homoplasies: for example, the posteriorly enlarged lower calypter and the M vein bent forward to R_{4+5}. The original definition for Muscinae (Schiner, 1862) included

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genera with the following features: M vein bent forward to R_{4+5}, arista plumose, abdomen short and oval without strong setae, and legs relatively short. This broad characterization includes many genera now recognized as belonging to Tachinidae and Calliphoridae. Subsequently, several classifications were proposed for Muscinae (Girschner, 1893; Bezzi & Stein, 1907; Schnabl & Dziedzicki, 1911; Malloch, 1925; Ringdahl, 1929).

The contributions of Hennig (1964a, b) to taxonomy, and particularly his pioneer study of Muscidae using the phylogenetic approach (Hennig, 1965), drove current discussions of definitions and delimitations for the Muscinae and the tribe Muscini in new directions. Hennig (1965) proposed the anepimeron setulae, plumose arista, and posterior spiracles with sinuous ridges in larvae as synapomorphies of the Muscini.

Current classification of the Muscini follows Hennig (1965), with additional contributions by Skidmore (1985) and de Carvalho (1989b). At present, the tribe Muscini includes 21 genera and about 350 species, and can be diagnosed by the following characters: plumose arista (Figs 1, 8, 9), flexible and retractile proboscis, sinuous subcostal vein (Figs 6, 7), the apical portion of the M vein usually bent forward to R_{4+5} (Figs 6, 7), lower calypter posteriorly enlarged (Fig. 4) or glossiform, female usually with developed proclinate frontoorbital seta (Figs 1, 2), fronto-orbital plate setulose on its upper half or entirely, setulose anepimeron (Figs 4, 5), and usually present calcar (Figs 27, 28).

Here, we carried out a cladistic analysis of the tribe Muscini based on the study of morphological characters from 82 exemplar species representing all 21 recognized genera. Characters supporting the tribe monophyly and the monophyly and phylogenetic relationships of the genera are presented and discussed. A phylogeny-supported classification of Muscini into genera, and eventually into subgenera and species groups, is proposed.

MATERIAL AND METHODS

EXAMINED MATERIAL

The material examined belongs to the following institutions (with their respective curators): Australian National Insect Collection, CSIRO, Canberra, Australia (Graham Crompton); California Academy of Sciences, San Francisco, CA, USA (Robert Zuparko); Colección Boliviana de Fauna, La Paz, Bolivia (Jaime Sarmiento); Coleção Entomológica, Centro de Pesquisa Agropecuária dos Cerrados, EMBRAPA, Planaltina, Brazil (Amabílio J. A. Camargo); Colección Instituto Alexander von Humboldt, Bogotá, Colombia (José Enrique Castillo); Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (Claudio J. B. de Carvalho); Entomology Section, University of Colorado Museum, Boulder, CO, USA (Virginia Scott); Hope Entomological Collections, University Museum of Natural History, Oxford, UK (Adrian C. Pont); Insect Research Collection, University of Wisconsin, Madison, WI, USA (Steven Krauth); Instituto Miguel Lillo, Universidad Nacional de Tucuman, Tucuman, Argentina (Guillermo L. Claps); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (Manuel Zumbado); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (José A. Rafael); Instituto de Biociências, Universidade Federal do Mato Grosso, Cuiabá, Brazil (Rosina D. Miyazaki); Maurice T. James Entomological Collection, Washington State University, Pullman, WA, USA (Richard Zack); Museo Entomologico, Leon, Nicaragua (Jean-Michel Maes); Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz de la Sierra, Bolivia (María Julieta Ledezma); Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (Hilda A. O. Gastal); Museu Nacional, Rio de Janeiro, Brazil (Márcia S. Couri); Museu Paraense Em'lio Goeldi, Belém, Brazil (Ana Y. Harada); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sônia A. Casari); Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (Joachim Ziegler); Natal Museum, Pietermaritzburg, South Africa (David Barraclough); The Natural History Museum, London, UK (David Notton).

TAXONOMIC SAMPLING

All 21 currently recognized genera of Muscini were included in the analysis. A total of 82 exemplar species were included in the ingroup and six species were included in the outgroup (see Table 1). The choice of exemplar species for the ingroup to represent each genus was based primarily on morphological diversity. Hence, our sampled taxa were an attempt to represent the spectrum of morphological diversity as well as the spectrum of their geographical distributions. Only *Mitroplatia* was under-represented in the analysis, as no species from the Oriental region were studied. When genera were previously classified into species groups (e.g. *Musca* and *Neomyia*), taxa were also sampled to represent the infrageneric groups. When possible, the type species of a genus was chosen as an exemplar species, and only *Mitroplatia* and *Pyrellina* were not represented by their type species. Two undescribed species were studied: *Mesembrina* sp. 1 from Costa Rica, and *Xenomorellia* sp. 1 from Bolivia and Colombia.

The choice of terminal taxa for the outgroup was based on phylogenetic background existing in the literature. The choice of *Delia platura* (Anthomyiidae) to root the resulting cladograms was based on

Table 1. List of genera and exemplar species used in the cladistic analysis (the numbers in square brackets indicates the total number of species within each genus; asterisk indicates the type species)

Ingroup	Distribution
Biopyrellia [1 sp.]	
B. bipuncta (Wiedemann, 1830)*	Neotropical
Curranosia [7 spp.]	
C. gemma (Bigot, 1878)	Afrotropical
C. prima (Curran, 1935)	Afrotropical
C. spekei (Jaennicke, 1867)*	Afrotropical
Dasyphora [17 spp.]	
D. albofasciata (Macquart, 1839)	Palaearctic
D. gussakovskii Zimin, 1947	Oriental, Palaearctic
D. pratorum (Meigen, 1826)*	Palaearctic
Deltotus [3 spp.]	
D. facetus Séguy, 1935*	Afrotropical
Eudasyphora [15 spp.]	
E. cyanella (Meigen, 1826)*	Palaearctic
E. cyanicolor (Zetterstedt, 1845)	Oriental, Palaearctic
E. flavipes (Malloch, 1931)	Oriental, Palaearctic
E. kempi Emden, 1965	Oriental
E. zimini (Hennig, 1963)	Palaearctic
Hennigmyia [3 spp.]	
H. setinervis (Stein, 1913)*	Afrotropical
Mesembrina [12 spp.]	
M. latreillii Robineau-Desvoidy, 1830	Nearctic, Palaearctic
M. meridiana (Linnaeus, 1758)*	Oriental, Palaearctic
M. mystacea (Linnaeus, 1758)	Palaearctic
Mesembrina sp. 1.	Neotropical
Mitroplatia [15 spp.]	
M. mouschi Zielke, 1971	Afrotropical
M. pyrellioides (Curran, 1928)	Afrotropical
M. smaragdina (Séguy, 1935)	Afrotropical
Morellia [*c.* 55 spp.]	
M. abdominalis Stein, 1918	Afrotropical
M. aenescens Robineau-Desvoidy, 1830	Palaearctic
M. basalis (Walker, 1853)	Neotropical
M. calyptrata Stein, 1913	Afrotropical
M. hortensia (Wiedemann, 1824)	Australasian, Oriental, Palaearctic
M. hortorum (Fallén, 1817)*	Oriental, Palaearctic
M. humeralis (Stein, 1918)	Neotropical
M. micans (Macquart, 1855)	Nearctic
M. nigricosta Hough, 1900	Neotropical
M. nigrisquama Malloch, 1928	Oriental
M. paulistensis Pamplona & Mendes, 1995	Neotropical
M. podagrica (Loew, 1857)	Nearctic, Palaearctic
M. xanthoptera Pamplona, 1986	Neotropical
Musca [*c.* 67 spp.]	
M. albina Wiedemann, 1830	Afrotropical, Oriental, Palaearctic
M. alpesa Walker, 1849	Afrotropical
M. autumnalis De Geer, 1776	Afrotropical, Oriental, Nearctic, Neotropical, Palaearctic
M. cassara Pont, 1973	Australasian, Oriental
M. domestica Linnaeus, 1758*	cosmopolitan
M. fergusoni Johnston & Bancroft, 1920	Australasian
M. larvipara Portschinsky, 1910	Palaearctic
M. lasiophthalma Thomson, 1869	Afrotropical
M. lusoria Wiedemann, 1824	Afrotropical, Oriental, Palaearctic
M. pattoni Austen, 1910	Oriental
M. vetustissima Walker, 1849	Australasian
Myiophaea [1 sp.]	
M. spissa (Walker, 1858)*	Australasian

Table 1. *Continued*

Ingroup	Distribution
Neomyia [c. 75 spp.]	
N. australis (Macquart, 1848)	Australasian
N. cornicina (Fabricius, 1781)	Oriental, Nearctic, Neotropical, Palaearctic
N. dubia (Malloch, 1923)	Afrotropical
N. gavisa (Walker, 1859)*	Oriental
N. lauta (Wiedemann, 1830)	Australasian, Oriental, Palaearctic
N. laxifrons (Villeneuve, 1916)	Afrotropical
N. limbata (Villeneuve, 1916)	Afrotropical
N. macrops (Curran, 1935)	Afrotropical
N. nudissima (Loew, 1852)	Afrotropical
N. rhingiaeformis (Villeneuve, 1914)	Afrotropical
N. sperata (Walker, 1859)	Oriental
N. timorensis (Robineau-Desvoidy, 1830)	Australasian, Oriental, Palaearctic
N. viridescens (Robineau-Desvoidy, 1830)	Palaearctic
Neorypellia [1 sp.]	
N. neglecta (Townsend, 1939)*	Neotropical
Parapyrellia [2 spp.]	
P. maculipennis (Macquart, 1846)*	Neotropical
Polietes [11 spp.]	
P. domitor (Harris, 1780)	Palaearctic
P. hirticrura Meade, 1887	Nearctic, Palaearctic
P. lardaria (Fabricius, 1781)*	Palaearctic
P. steinii (Ringdahl, 1913)	Palaearctic
Polietina [15 spp.]	
P. concinna (Wulp, 1896)*	Nearctic, Neotropical
P. flavidicincta (Stein, 1904)	Neotropical
P. rubella (Wulp, 1896)	Neotropical
P. steini (Enderlein, 1927)	Neotropical
Pyrellia [22 spp.]	
P. albocuprea Villeneuve, 1914	Afrotropical
P. rapax (Harris, 1780)	Palaearctic
P. scintillans Bigot, 1888	Afrotropical, Oriental
P. tasmaniae Macquart, 1846	Australasian
P. vivida Robineau-Desvoidy, 1830*	Nearctic, Oriental, Palaearctic
Pyrellina [12 spp.]	
P. distincta (Walker, 1853)	Afrotropical
P. marsya (Walker, 1849)	Afrotropical
Sarcopromusca [2 spp.]	
S. pruna (Shannon & Del Ponte, 1926)*	Neotropical
S. sarcophagina (Wulp, 1896)	Neotropical
Trichomorellia [8 spp.]	
T. seguyi (Pamplona, 1983)	Neotropical
T. trichops (Malloch, 1923)*	Neotropical
Xenomorellia [2 spp.]	
X. holti Malloch, 1923*	Neotropical
Xenomorellia sp. 1	Neotropical

Outgroup	Distribution
Muscoidea: Anthomyiidae	
Delia platura (Meigen, 1826)	Cosmopolitan
Muscidae: Azeliinae: Azeliini	
Drymeia hamata (Fallén, 1823)	Palaearctic
Thricops semicinereus (Wiedemann, 1817)	Palaearctic
Muscidae: Azeliinae: Reinwardtiini	
Muscina stabulans (Fallén, 1817)	Cosmopolitan
Muscidae: Muscinae: Stomoxyini	
Haematobia irritans (Linnaeus, 1758*)*	Cosmopolitan
Stomoxys calcitrans (Linnaeus, 1758)	Cosmopolitan

phylogenetic hypotheses for Muscoidea (Vossbrinck & Friedman, 1989; Michelsen, 1991) in which Muscidae and Anthomyiidae are sister groups. For the selection of muscid taxa, we used the phylogenetic studies of Muscidae carried out by de Carvalho (1989b) and Couri & de Carvalho (2003): *Haematobia irritans* and *Stomoxys calcitrans* belong to Stomoxyini, the sister group for Muscini; *Drymeia hamata* and *Thricops semicinereus* belong to Azeliinae, a group closely related to Muscinae, and with a more basal position within the Muscidae.

CHARACTERS

Only adult morphological characters were used in the analysis, as characters from immature stages are mostly unavailable in the literature for Muscini. All characters are defined as unordered and polymorphic characters are coded following the 'polymorphic' coding of Wiens (1998). The program WINCLADA (Nixon, 2002) was used for data matrix editing. Adult morphological terminology follows McAlpine (1981), except for some traditional terms following de Carvalho (1989a): humeral callus (for postpronotum of McAlpine, 1981), humeral setae (for postpronotal setae), posthumeral and presutural setae (for presutural intra-alar setae), prealar seta (for the first postsutural supra-alar setae; Fig. 3), and calcar (for the developed seta at the apical third of the posterodorsal surface of hind tibia; Figs 27, 28). In addition, a few other terms were adopted here: median and marginal spined processes of cercal plate (Fig. 32 for superior and inferior spined processes, respectively, of Couri & de Carvalho, 1997; following Nihei, 2004); accessory proclinate fronto-orbital seta (for the weak seta immediately above the strong proclinate fronto-orbital seta see Figs 1, 2; several authors had numbered the fronto-orbital setae as one, two). As for the setae next to the humeral callus, we used two terms, posthumeral and parahumeral setae (Fig. 3). The posthumeral seta is located posteriorly to the humeral callus, and this is considered as the true posthumeral seta. The parahumeral seta is located beside the humeral callus and obliquely in front of the true posthumeral seta; its insertion is not actually posterior to the humeral callus as is the posthumeral seta. This terminology was preferred to avoid confusion and to clearly state unambiguous hypotheses of homology. Both setae had previously been numbered as either one or two posthumeral setae (thereby grouping them), or as presutural intra-alar setae, also numbered as one or two, although they are not regularly aligned.

CLADISTIC ANALYSIS

NONA version 2.0 (Goloboff, 1993a) and XPEE-WEE version 1.3 (Goloboff, 1997) were used for cladogram searching. In both, the following commands were used: hold10000, mult*200, generating a heuristic search by 'tree bisection-reconnection branch-swapping' and 'random addition sequence', with 200 replicates.

Characters were treated with three-character weighting schemes to test the self-consistency of the cladograms obtained under different weighting approaches. The character weighting schemes applied were: equal (EW), successive (SW), and implied weighting (IW).

The SW approach (Farris, 1969; Carpenter, 1988, 1994) is an iterative weighting scheme that applies different weights to characters according to either their performance or fitness (interpreted as *phylogenetic reliability* by Carpenter, 1994) in the initial analysis with equal weights. Character performance can be quantified by several character indexes (e.g. consistency index (CI), retention index (RI), or rescaled consistency index). The program NONA implements SW when associated with the 'swt.run' module (distributed in the NONA package), and applies differential weights according to the CI of the characters.

The IW (Goloboff, 1993c) applies weights to characters simultaneously with the tree reconstruction, i.e. the weighting does not depend on any previous analysis, as in the above approach. Weights are estimated by the character fit in each given tree, not including any other tree (as occurs when one uses SW, which estimates the weight for a character according to some index calculated over all the set of equally parsimonious trees resulting from an initial analysis with EW). The character fit varies according to the value previously defined for the concavity constant k (see Goloboff, 1993c, 1995; Turner & Zandee, 1995). Here we used different values for k (within the range 1–6, allowed by the program XPEE-WEE) to examine its impact on the number and topology of the resulting cladograms. The program XPEE-WEE (Goloboff, 1997) was used for the cladogram search under IW. This program implements the character fit and cladogram fitness calculations by using the *floating point* in the arithmetical procedure (Goloboff, 1997), and is more precise than the program PEE-WEE (Goloboff, 1993b).

The program WINCLADA (Nixon, 2002) was used for the tree viewing and editing and for the character optimization.

CHARACTER DESCRIPTIONS

1. Proclinate fronto-orbital seta on female: (0) absent; (1) present (Figs 1, 2).
2. Accessory proclinate fronto-orbital seta on female: (0) absent; (1) present (Figs 1, 2).
3. Setulae on female fronto-orbital plate: (0) absent; (1) present, on its upper half; (2) present, on its entire extension.

4. Interfrontal seta on female: (0) absent; (1) present (Fig. 2).

5. Setulae on female frontal vitta: (0) absent (Fig. 2); (1) present, on its upper half; (2) present, on its entire extension.

6. Upward setae on gena: (0) absent; (1) present (Fig. 1). The exact position of these setae is clearly above the subvibrissal setae (Fig. 1). In some taxa one or two subvibrissal setae orientate upwards, however, these cases were not considered homologous to the character treated here.

7. Proboscis: (0) flexible and retractile; (1) strongly sclerotized (not flexible) and not retractile.

8. Arista: (0) plumose, with long setulae on both dorsal and ventral surfaces (Figs 1, 8, 9), (1) plumose, with long setulae on dorsal surface; (2) pubescent, with short setulae on both dorsal and ventral surfaces. Setulae length was classified as follows: short setulae, not longer than the basal width of arista; long setulae, conspicuously longer than the basal width of arista.

9. Secondary setulae on inner-dorsal surface of arista: (0) absent; (1) present as pubescence (Fig. 9); (2) present, conspicuously developed (Figs 1, 8). Setulae length was classified as described above.

10. Eyes: (0) with sparse setulae (short); (1) with dense setulae (either short or long).

11. Relative size of the anterointernal ommatidia on male: (0) developed, slightly larger than the other ommatidia; (1) conspicuously developed, clearly larger than the other ommatidia and with the same size as anterior ocellus. State 1 is clearly recognizable as the exaggerated enlargement of the anterointernal ommatidia gives the impression that the eye is separated into two parts (as described by Malloch, 1923 for some *Neomyia* species): one upper portion with the ommatidia strongly enlarged and one lower portion with the ommatidia slightly enlarged.

12. Length of female ocellar triangle: (0) short (not reaching the middle of the frons); (1) long (either reaching or surpassing the middle of the frons).

13. Size of vibrissa: (0) strongly developed, clearly distinct from the subvibrissal setae (Fig. 1); (1) weakly developed, slightly distinct from the subvibrissal setae. State 1 is present in *Biopyrellia* and some *Mesembrina*. In the former, the vibrissa is reduced as the subvibrissal setae, whereas in some *Mesembrina* species the vibrissa is reduced but the subvibrissal setae are developed. In this study, these two observed variations were considered as similar.

14. Insertion of vibrissa: (0) inserted at the level of oral margin (Fig. 1); (1) inserted above the level of oral margin.

15. Row of frontal setae of female at the lowermost level: (0) reaching the level of lunula; (1) not reaching the level of lunula; (2) reaching the median level of pedicel.

16. Male eyes: (0) dichoptic; (1) holoptic, the fronto-orbital plates in contact; (2) holoptic, the fronto-orbital plates not in contact.

17. Female anterior ocellar seta: (0) developed; (1) reduced.

18. Male anterior ocellar seta: (0) developed; (1) reduced.

19. Enlargement of the basal portion of arista: (0) weak and slightly distinct (Fig. 8); (1) strong and conspicuous (Fig. 9). In state 0, the base of arista is slightly larger than its remaining portion, with a gradual narrowing from the base and a rectilinear appearance to the arista; the conspicuous enlargement of the basal portion of arista in state 1 gives the arista the appearance of a median concavity.

20. Setulae on facialia, above the oral margin: (0) absent; (1) present.

21. Thorax surface: (0) glabrous; (1) rough. The rough surface refers to a kind of perforated appearance to the thorax surface, with perforations coincident with the insertions of the ground setulae.

22. Presutural acrostichal setae: (0) not developed; (1) two pairs; (2) one anterior pair; (3) one posterior pair; (4) three pairs; (5) four pairs; (6) multiple irregular pairs.

23. Postsutural acrostichal setae: (0) absent; (1) one prescutellar pair; (2) two pairs; (3) three pairs; (4) four pairs; (5) five pairs.

24. Humeral setae: (0) two; (1) three; (2) four.

25. Notopleural setae: (0) two (Fig. 10), (1) three, with an additional median seta (Fig. 12), (2) three, with an additional posterior seta (Fig. 11).

26. Posthumeral seta (Fig. 3): (0) absent; (1) present.

27. Parahumeral seta (Fig. 3): (0) absent; (1) developed.

28. Presutural seta (Fig. 3): (0) absent; (1) present.

29. Postsutural intra-alar setae: (0) absent; (1) one; (2) two; (3) three; (4) four.

30. Intrapostalar seta (Fig. 3): (0) absent; (1) present.

31. Prealar seta: (0) absent; (1) present.

32. Setulae on postalar wall: (0) absent; (1) present.

33. Setulae on anterior supra-squamal ridge: (0) absent; (1) present.

34. Setulae on posterior supra-squamal ridge: (0) absent; (1) present.

35. Setulae on proepisternum: (0) absent; (1) present.

36. Upward seta at the upper anterior corner of anepisternum: (0) absent; (1) one developed seta; (2) more than one developed seta, forming an irregular row.
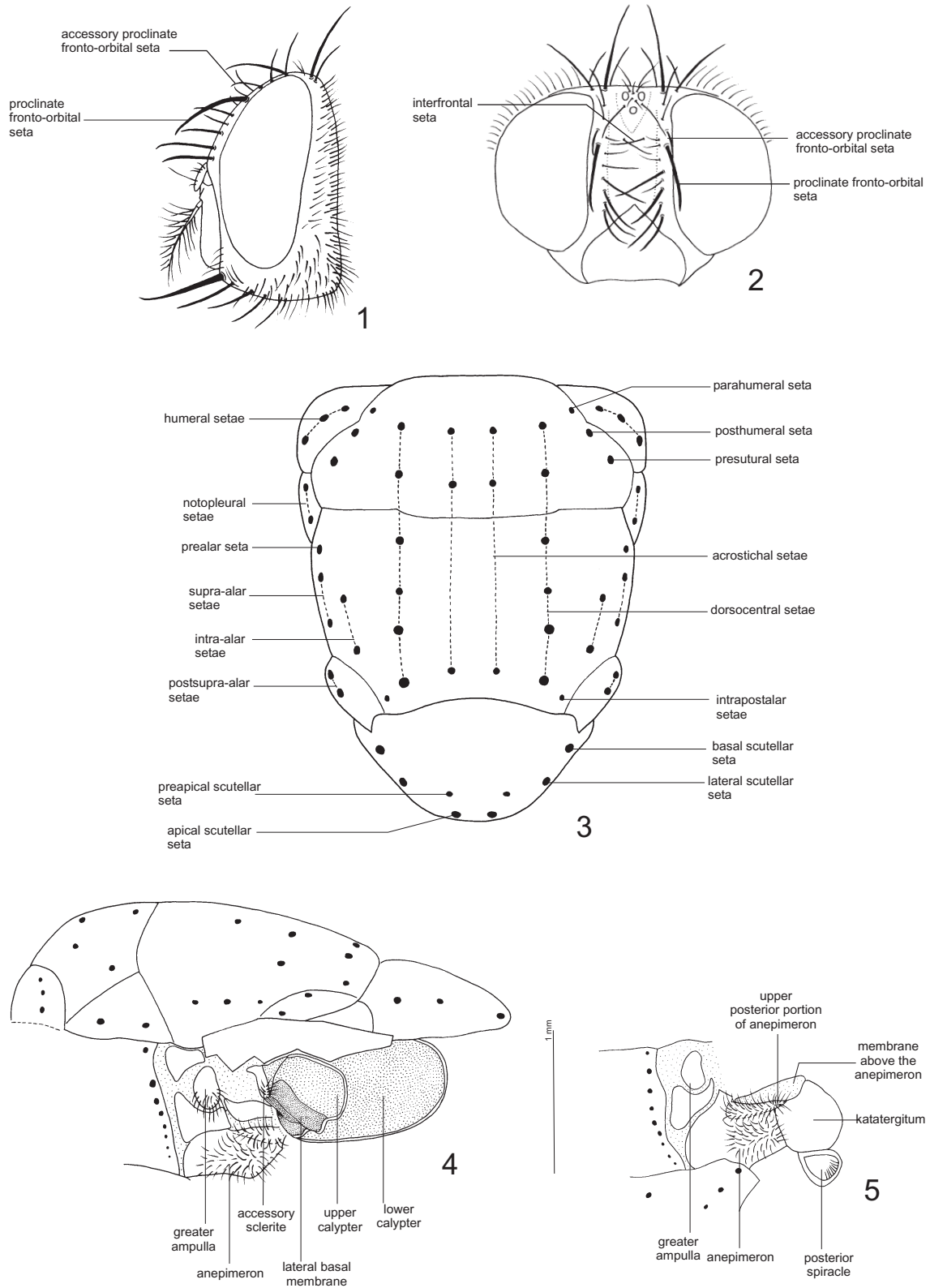
Figures 1–5. Morphological characters: 1, head, female, lateral view, *Polietina orbitalis*; 2, same, upper-frontal view; 3, thorax scheme for Muscini, dorsal view; 4, thorax (partial), lateral view, *Neomyia cornicina*; 5, thorax (partial), lateral view, *Pyrellina distincta*.

37. Greater ampulla: (0) pubescent; (1) setulose at the lower portion (Fig. 4).
38. Anepimeron: (0) bare; (1) posteriorly setulose (Fig. 5); (2) widely setulose (Fig. 4).
39. Upper setulae on anepimeron: (0) normally developed (setulae-like); (1) strongly developed (setae-like).
40. Setulae on upper-posterior portion of anepimeron (which borders partially the katatergitum at the upper portion): (0) absent; (1) present (Fig. 5).
41. Anterior katepisternal seta: (0) absent; (1) present (Figs 18, 19, 20).
42. Posterior katepisternal setae: (0) absent; (1) one; (2) two (Figs 18, 19), (3) three (Fig. 20).
43. Relative distance between the anterior and posterior katepisternal setae: (0) the anterior seta nearly equidistant to the upper and lower posterior setae (Fig. 18), (1) the anterior seta clearly closer to the lower posterior than to the upper one (Figs 19, 20).
44. Setulae on hind spiracle: (0) absent; (1) present, on posterior margin (Fig. 5).
45. Setulae on katepimeron: (0) absent; (1) present.
46. Setulae on meron: (0) absent; (1) present, below the hind spiracle.
47. Setulae on metakatepisternum: (0) absent; (1) present, above the hind coxa.
48. Setulae on prosternum: (0) absent; (1) present.
49. Setulae on anatergitum: (0) absent; (1) present. The setulae on anatergitum are sparsely present immediately below the lower calypter.
50. Lateral of scutellum at the basal portion with downward setulae: (0) absent; (1) present.
51. Lateral of scutellum with row(s) of downward setulae until the apex: (0) absent; (1) present.
52. Setulae on ventral surface of scutellum: (0) absent; (1) present.
53. Preapical scutellar seta (Fig. 3): (0) absent; (1) present.
54. Shape of lower calypter: (0) glossiform; (1) enlarged posteriorly but not extending under scutellum; (2) enlarged posteriorly and extending under scutellum.
55. Lateral-basal membrane connecting the upper and lower calypter: (0) present (Fig. 4); (1) absent.
56. Ventral setulae on subcostal sclerite: (0) absent; (1) present (Figs 13–17).
57. Median ventral setulae on subcostal sclerite: (0) absent; (1) present (Fig. 15).
58. Anterior ventral setulae on subcostal sclerite: (0) absent; (1) present (Figs 13, 16, 17).
59. Posterior ventral setulae on subcostal sclerite: (0) absent; (1) present (Figs 14, 16, 17).
60. Fine setulae on the accessory sclerite at the base of upper calypter (Fig. 4): (0) absent; (1) present.

61. Setulae on the membrane above the anepimeron and below the lower calypter (Fig. 5): (0) absent; (1) present. This character is difficult to observe because the membrane is often hidden under the lower calypter; its exact position is below the lower calypter and above the upper-posterior portion of anepimeron. The setulae, when present, are restricted to the posterior portion of the membrane.
62. Brown macula on humeral vein: (0) absent; (1) present.
63. Brown macula on apex of Sc and R_1 veins: (0) absent; (1) present.
64. Brown macula on apex of R_{2+3} vein: (0) absent; (1) present.
65. Brown macula on r-m crossvein: (0) absent; (1) present.
66. Brown macula on dm-cu crossvein: (0) absent; (1) present.
67. Intense colouration on basal third of wing and calypters: (0) absent; (1) present, goldish–yellow colouration; (2) present, blackish colouration. This intense colouration is quite different from the wing spot pattern commonly observed on many muscids (viz. characters 62–66) and differs from the former by its intensity and texture, making the alar membrane opaque, whereas the spots, even when conspicuously dark brown, may make the membrane translucent.
68. Costal vein ventrally: (0) bare; (1) setulose until the subcostal vein; (2) setulose almost until the apex.
69. Median sinuosity on subcostal vein: (0) absent; (1) present (Figs 6, 7).
70. Basal portion of stem-vein dorsally (Fig. 6): (0) bare; (1) setulose.
71. Basal portion of stem-vein ventrally: (0) bare; (1) setulose.
72. Apical portion of stem-vein dorsally (Fig. 6): (0) bare; (1) setulose.
73. Apical portion of stem-vein ventrally: (0) bare; (1) setulose.
74. R_1 vein dorsally: (0) bare; (1) setulose.
75. R_1 vein ventrally: (0) bare; (1) setulose.
76. Rs node dorsally (Fig. 6): (0) bare; (1) setulose.
77. Rs node ventrally: (0) bare; (1) setulose.
78. R_{4+5} vein dorsally: (0) bare; (1) setulose at the portion before the r-m crossvein (but not reaching r-m); (2) setulose to, or rarely slightly past, the r-m crossvein; (3) setulose almost entirely.
79. R_{4+5} vein ventrally: (0) bare; (1) setulose at the portion before the r-m crossvein (but not reaching r-m); (2) setulose to, or rarely slightly past, the r-m crossvein; (3) setulose almost entirely.
80. Vein M ventrally: (0) bare; (1) setulose between the crossveins r-m and dm-cu.

81. Apical portion of M vein: (0) straight (subparallel to R_{4+5}); (1) slightly bent forward to R_{4+5} (Fig. 6); (2) sharply bent forward to R_{4+5}, with an angled curve (Fig. 7).

82. Length of A_1 vein: (0) short, not reaching the margin of wing; (1) long, reaching the margin of wing.

83. Microtrichiae on alar membrane: (0) present on all the membrane; (1) absent on some portions.

84. Male fore tibia on posteroventral surface: (0) bare; (1) with a submedian seta; (2) with a series of setae on apical half; (3) series of setae on median third; (4) series of setae on the entire surface, longer setae on apical half.

85. Male fore tibia on posterior to posteroventral surface: (0) bare; (1) series of setae on apical half or two-thirds.

86. Male mid femur on dorsal surface: (0) without preapical protuberance (Figs 22, 23), (1) with preapical protuberance covered by unmodified setae (Figs 25, 26), (2) with preapical protuberance covered by modified hook-shaped setae (Fig. 24).

87. Male mid femur with a series of developed setae on the median third of the anterior surface: (0) absent; (1) present (Fig. 21).

88. Male mid tibia on anterodorsal surface with a series of backward setae: (0) absent; (1) present (Figs 24, 26).

89. Male mid tibia on posteroventral to ventral surface: (0) bare; (1) with a strong submedian seta (Fig. 22), (2) with a series of setae on apical half; (3) with a series of fine and dense setae on entire surface.

90. Female mid tibia on anterodorsal surface: (0) without a submedian seta; (1) with a submedian seta.

91. Female mid tibia on apical third of anterodorsal surface: (0) bare; (1) setulose.

92. Hind coxa with setulae on posterior margin: (0) absent; (1) present.

93. Hind tibia with one seta (calcar) on apical third of posterodorsal surface: (0) absent; (1) weak (shorter than tibia width) (Fig. 27), (2) strong (distinctly longer than tibia width) (Fig. 28).

94. First abdominal sternite: (0) bare; (1) setulose on lateral borders; (2) widely setulose.

95. Cercal plate on ventral face with the median spined process: (0) absent (Figs 35, 36), (1) present (Figs 32, 33, 34, 37, 38).

96. Cercal plate on ventral face with the marginal spined process at the lower lobe: (0) absent (Figs 34, 35, 36), (1) present (Figs 32, 33, 37, 38).

97. Surstylus with an inward projection on the median portion of posterior surface: (0) absent; (1) present (Figs 43, 44).

98. Surstylus with an outward apical projection on the outer side of posterior surface: (0) absent; (1) present (Fig. 45).

99. Hypandrium with the anterior margin: (0) narrow (Figs 29, 30), (1) widened (Fig 31).

100. Shape of paramere, in lateral view: (0) developed, simple shape (slightly bent downwards) (Figs 39, 40, 42), (1) developed, hook-shaped (Fig. 41), (2) reduced (button-shaped).

101. Inferior base of aedeagus apodeme: (0) without an anterior intergonopodal projection; (1) with an anterior intergonopodal projection (Fig. 42). This projection extends forward from the base of aedeagus apodeme and between the gonopods (see Fig. 42), and may be fused to the gonopods to a greater or lesser extent. It also varies in shape: wider in *Neomyia* and narrower in most other genera.

102. Shape of distiphallus, in lateral view: (0) campanulate (Figs 39, 40, 42), (1) trapezoidal (Fig. 41).

103. Lateral-apical membrane of distiphallus: (0) bare; (1) with spinules reduced and weakly sclerotized
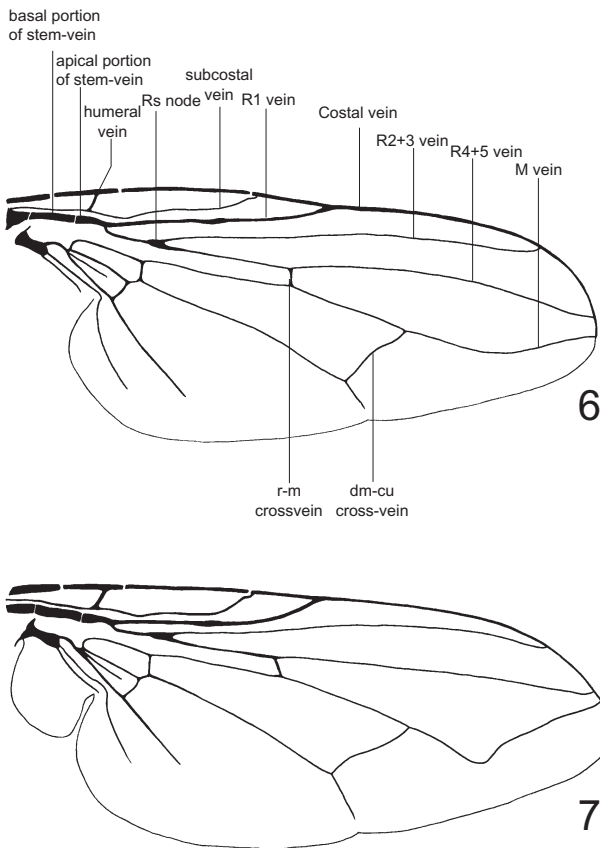
Figures 6–7. Morphological characters: 6, wing, *Morellia podagrica*; 7, wing, *Neomyia cornicina*.

(Figs 39, 40), (2) with spinules developed and strongly sclerotized (Fig. 42). This character is difficult to visualize, particularly when the spinules are reduced (state 1) and sparsely distributed in low number, although in most species the spinules are densely present. In any case, depending on the treatment for the cleaning and diaphanization of genitalia (using KOH solution), the visualization of these spinules may be difficult.

104. Anterior membrane of distiphallus: (0) bare; (1) with spinules reduced and weakly sclerotized (Fig. 40). Also a difficult character to visualize, because of the same problem described above.

105. Anterior portion of distiphallus apically with horned sclerite: (0) absent; (1) present.

106. Sixth pair of spiracles on female terminalia: (0) absent; (1) present.

107. Female terminalia with microtrichiae on intersegmental membrane 6–7: (0) absent; (1) present.

108. Female terminalia with microtrichiae on intersegmental membrane 7–8: (0) absent; (1) present.

109. Female terminalia with spine-like setae on posterior margin of the 7th abdominal tergite: (0) absent; (1) present.

110. Shape of female cerci: (0) digitiform; (1) triangular (subacuminate); (2) semicircular (half-moon-shaped); (3) acuminate. The acuminate cerci are distinctly different from the triangular cerci, as the latter, despite being triangular, maintain a slightly rounded apex, whereas the acuminate cerci (present only in *Eudasyphora cyanella* in the studied taxa) possess a conspicuous point. The semicircular cerci include forms present by convergence in *Neomyia*, *Musca*, and some few *Morellia*. The forms observed in *Neomyia* and *Musca* are doubtless similar but, on the other hand, the forms present in *Morellia* species perhaps should be treated under a separate state. However, as this question remains, both forms are hypothesized herein as one character state.

111. Shape of epiproctum in the female terminalia: (0) nail-shaped (elongated longitudinally); (1) campanulate (widened at base).

112. Number of spermathecae: (0) three; (1) two .

ON THE USE OF DIFFERENTIAL CHARACTER WEIGHTING

From the data matrix (88 taxa × 112 characters) presented in Table 2, several cladogram searches were carried out under the application of different character weighting approaches, and the searches are summarized in Table 3.

We assert that differential character weighting is necessary in phylogenetic reconstruction using parsimony analysis, contrary to the views of some authors (e.g. Kluge, 1997, 1998). Under a Popperian refutationist perspective, Kluge (1997, 1998) argues that every character provides equally strong evidence of relationship and that the treatment of characters under the EW regime is correct. However, based on their experience, most practising systematists do otherwise (Kitching, 2002). Differential weighting begins in any case, however, when a choice of characters is made, by the researcher, who gives preference for a qualitative rather than a quantitative continuous character to be included in the analysis. Therefore, character examination and the subsequent recognition of homologies by one systematist involves several steps where the subjective decision is made successively, and, in this process, that systematist applies differential weighting when examining and deciding about continuous variation, colouration changes, polymorphic characters, etc.

Because not all characters used in a phylogenetic analysis have the same information content and predictive value, it is clear that not all characters included in an analysis provide equally strong evidence for phylogenetic inference. Rather, this serves as a foundation for the application of differential weights so that we may insure that each character will be given its appropriate weight. Hence, researchers should be concerned with appropriate a posteriori methods of character weighting to guarantee that the postulated primary homologies (*sensu* De Pinna, 1991) will have their information content used in the appropriate way. Cladograms made by attributing a posteriori weights to characters, based on their relative degrees of homoplasy, explain the data better than cladograms in which an extra step in a very homoplastic character is considered as important as an extra step in a character that fits the tree topology almost perfectly (Farris, 1969).

Here, we used three approaches for character weighting: equal (EW), successive (SW) and implied weighting (IW). These weighting schemes generated partially congruent results, except for IW when a concavity constant (k) of either 1 or 2 was used. The EW strict consensus (Fig. 46) resulted in a very similar topology to that under SW (Figs 47, 48) . The difference was restricted to the lower resolution of the former, yet the main generic and suprageneric groups are the same in both.

As a result of the dependence on a prior analysis using equal weights followed by differential weights, the SW generated topologies very similar to the topologies found under EW. This dependency would not be a problem if the application of differential weights for a given character was not determined by a character statistical index (CI and RI) estimated over all sets of cladograms. For example, for a character i in the present analysis to be given a weight according to its
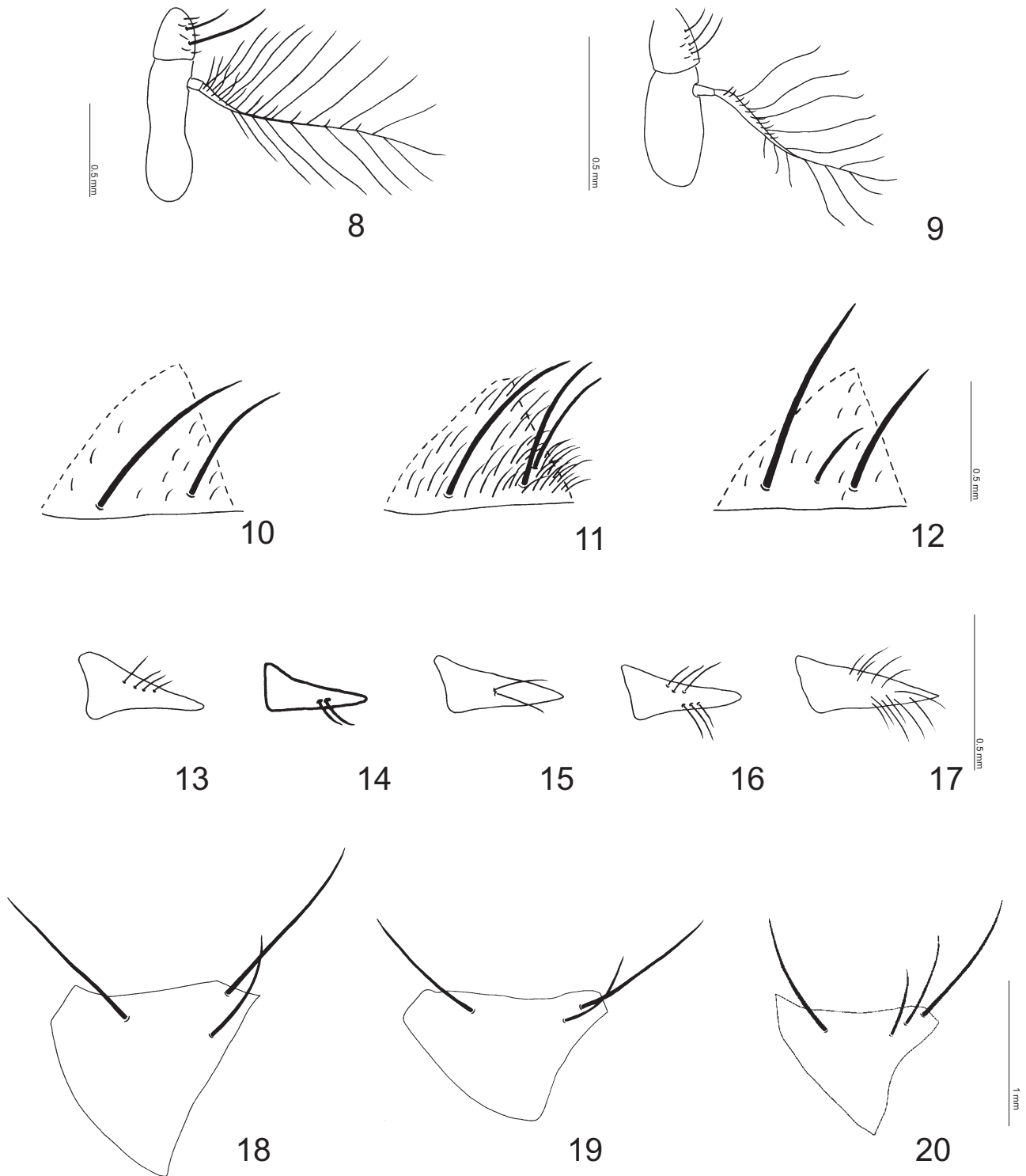
Figures 8–20. Morphological characters: 8, antenna, inner-lateral view, *Polietina flavithorax*; 9, same, *Pyrellia albocuprea*; 10, notopleuron, lateral view, *Myiophaea spissa*; 11, same, *Polietes domitor*; 12, same, *P. flavithorax*; 13, subcostal sclerite, ventral view, *Neomyia lauta*; 14, same, *P. albocuprea*; 15, same, *P. flavithorax*; 16, same, *Neomyia laxifrons*; 17, same, *Curranosia gemma*; 18, katepisternum, lateral view, *P. flavithorax*; 19, same, *Mitroplatia smaragdina*; 20, same, *Sarcopromusca pruna*.
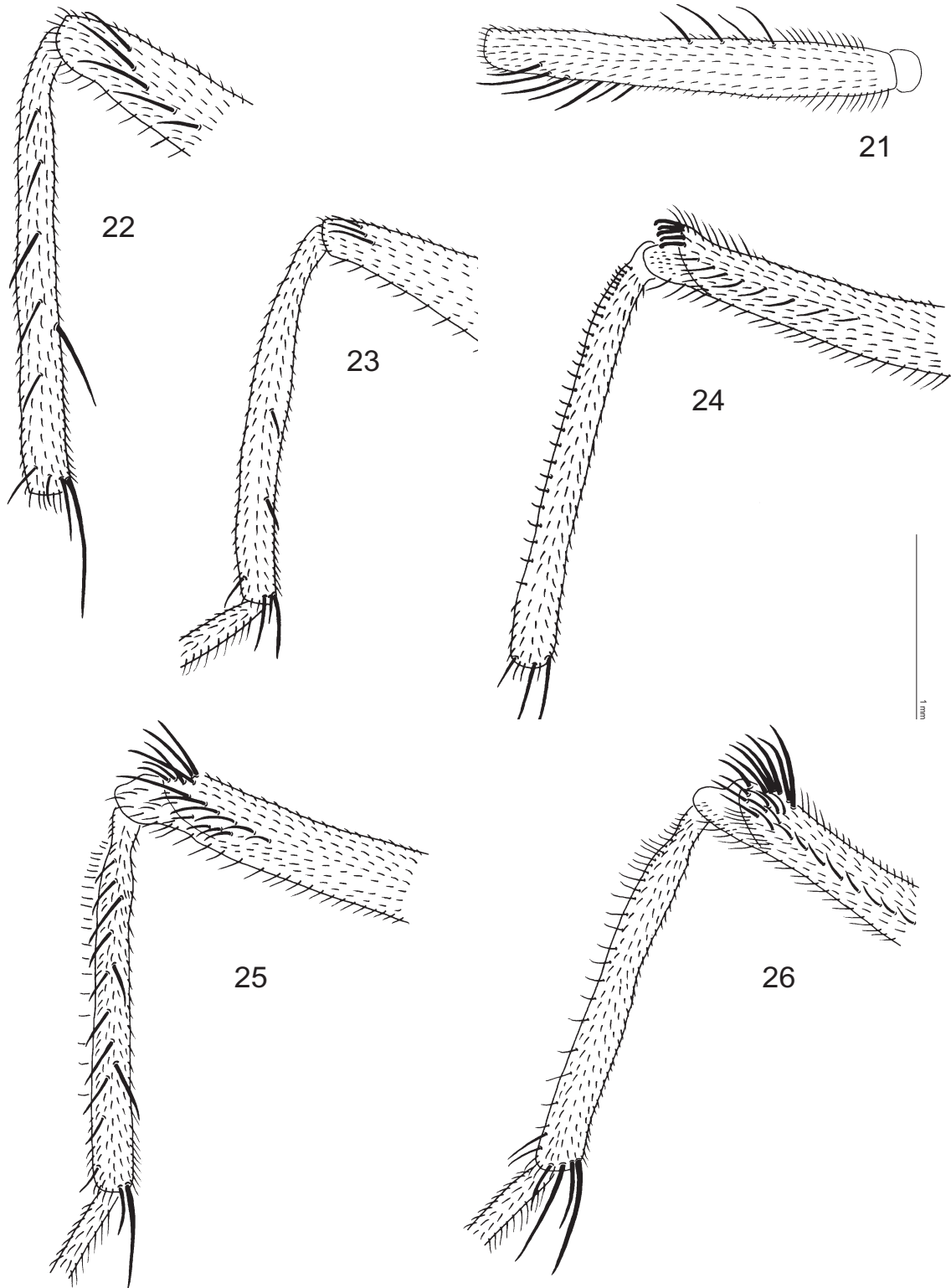
Figures 21–26. Morphological characters: 21, mid femur, female, dorsal view, *Pyrellia albocuprea*; 22, apex of mid femur and tibia, male, posterior view, *Pyrellina distincta*; 23, same, *Biopyrellia bipuncta*; 24, same, anterior view, *Parapyrellia maculipennis*; 25, same, posterior view, *Morellia podagrica*; 26, same, anterior view, *Morellia podagrica* (all figures are on the same scale).
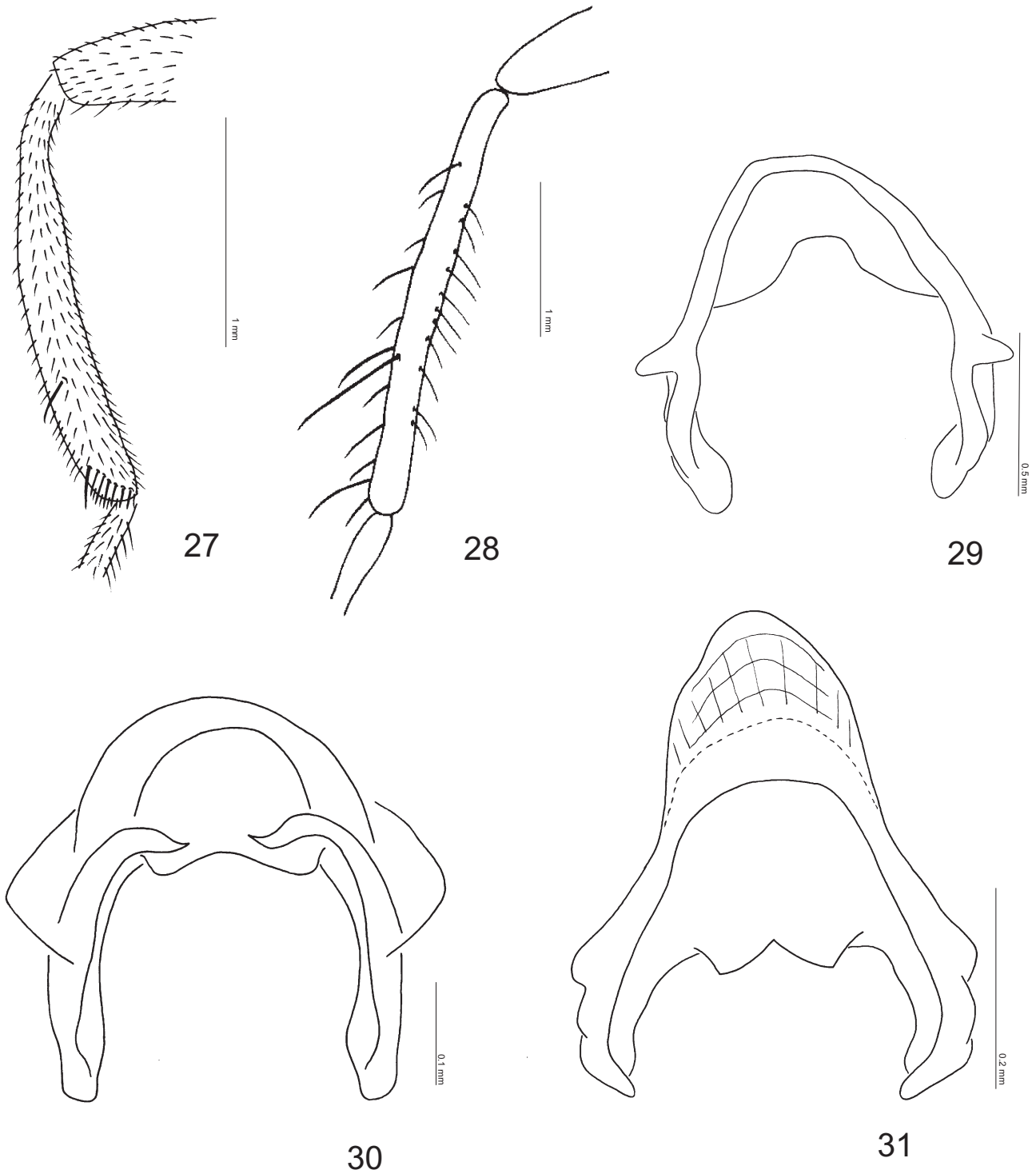
Figures 27–31. Morphological characters: 27, hind tibia, female, posterior view, *Biopyrellia bipuncta*; 28, same, male, *Polietina major* (after Nihei, 2002); 29, hypandrium, dorsal view, *Drymeia hamata*; 30, same, *Musca larvipara*; 31, same, *Pyrellia vivida*.

median
spined
process

marginal
spined
process
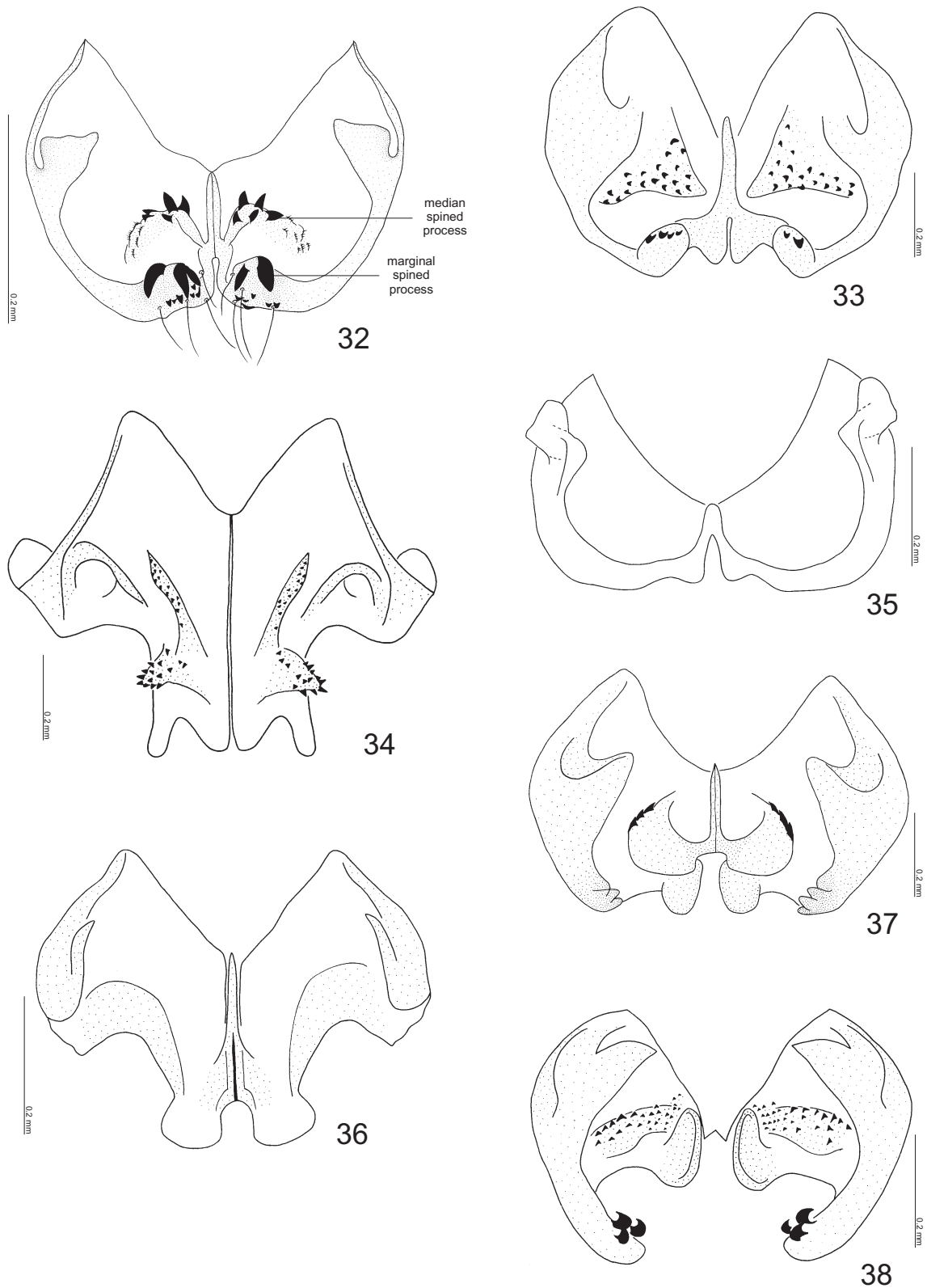
Figures 32–38. Morphological characters: 32, male cercal plate, ventral face, *Polietina flavidicincta* (modified from Nihei, 2004); 33, *Polietes steinii*; 34, *Mesembrina mystacea*; 35, *Musca larvipara*; 36, *Neomyia viridescens*; 37, *Dasyphora pratorum*; 38, *Eudasyphora cyanella*.
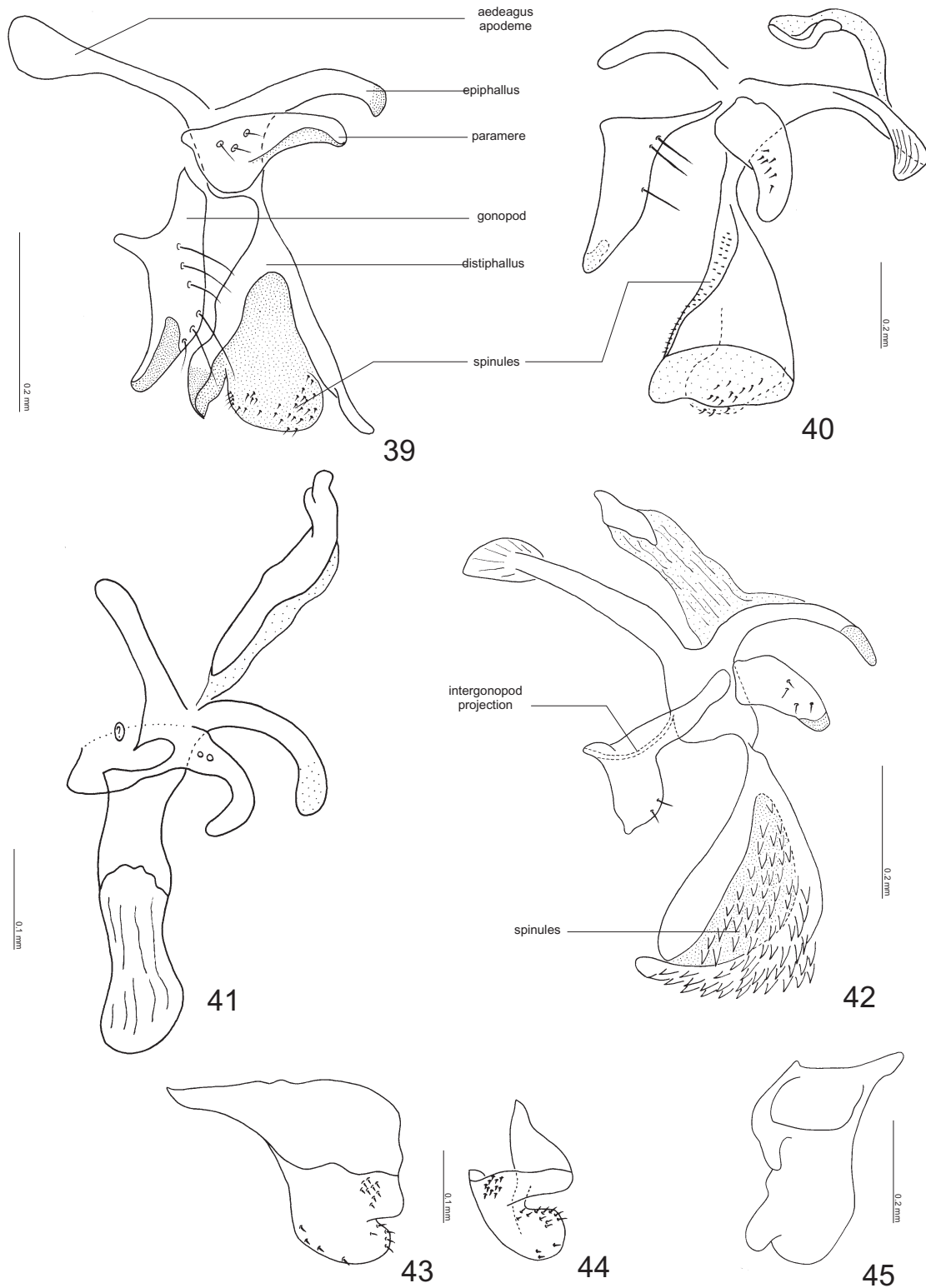
Figures 39–45. Morphological characters: 39, male terminalia, aedeagus, *Polietina flavidicincta* (modified from Nihei, 2004); 40, same, *Mesembrina mystacea*; 41, same, *Musca larvipara*; 42, same, *Neomyia viridescens*; 43, left surstylus, outer lateral view, *Neomyia macrops*; 44, left surstylus, posterior view, *Neomyia macrops*; 45, right surstylus, outer lateral view, *Xenomorellia* sp. 1.

Table 2. Data matrix used in the cladistic analysis

Terminal taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Delia platura	1	0	0	1	0	1	0	0	0	2	1	0	0	0	0/1	0	2	0	1	0	0	6	4/5	0	1	0	1	2	1	1	0	0	0	0	0	0	0	0	–	0	1	2	2	0	0	0	0	0	0	0	0	1	0	0	0
Muscina stabulans	0	0	2	1	1	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	4/5	1	1	0	1	0	1	2	1	1	0	0	0	0	1	0	0	–	0	1	2	0	0	0	0	0	0	0	0	1	0	0	2	0
Haematobia irritans	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	2	1	0	1	0	1	?	0	0	0	0	0	0	0	0	1	–	0	1	1	1	0	0	0	0	1	0	0	0	0	0	2	0
Stomoxys calcitrans	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1/2	1	0	1	0	0	1	–	1	0	0	1	0	0	0	0	0	0	0	0
Thricops semicinereus	1	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	2	1	1	0	0	0	0	1	0	0	–	0	1	3	0	0	1	0	0	0	1	0	0	0	1	2	0
Drymeia hamata	1	0	0	1	0	1	0	0	2	1	0	0	0	0	0	2	0	1	0	0	0	0	1	1	1	1	0	1	2	0	1	0	0	0	2	1	0	0	–	1	1	3	0	0	1	0	0	1	1	0	1	0	1	2	0
Biopyrellia bipuncta	0	1	1	0	0	0	0	0	2	0	1	0	1	1	1	2	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	1	0	1	0	1	0	1	0	1	–	0	0	0	0	1	1	1	1	0	0	2	0
Curranosia gemma	0	1	0	0	0	0	0	0	2	0	0	1	1	1	1	2	0	1	1	0	0	0	1	0	1	0	0	1	2	1	1	0	0	1	1	1	1	0	0	0	1	3	1	1	0	0	0	1	1	1	1	0	0	2	0
Curranosia prima	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	2	0	1	1	0	0	0	1	1	0	1	0	1	2	1	1	0	0	1	0	1	0	1	0	1	1	2	1	1	0	0	0	1	1	1	1	0	0	2	0
Curranosia spekei	0/1	1	0	1	0	0	0	0	2	0	0	1	0	0	0	2	0	1	1	0	0	1	1	1	0	1	0	0	1/2	1	1	0	0	1	0	0	0	0	0	1	1	2	1	1	1	0	0	1	1	1	1	0	0	2	0
Trichomorellia seguyi	1	1	2	0	1	0	0	0	2	1	0	0	0	0	0	2	0	1	0	0	0	1	3	2	0	1	1	1	1/3	1	1	0	0	1	0	0	0	0	0	1	1	2	1	1	1	0	0	1	1	1	1	0	1	1	0
Trichomorellia trichops	1	1	1	0	0	0	0	0	2	1	0	0	0	0	0	2	0	1	0	0	0	1	1	2	0	1	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	2	1	1	1	0	0	1	1	1	1	0	1	1	0
Deltotus facetus	1	0	1	0	0	0	0	0	2	1	0	0	0	0	2	2	0	0	0	0	0	2	2	2	0	1	0	1	2	1	1	0	0	0	0	0	0	1	0	0	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Hennigmyia setinervis	1	0	0	1	0	1	0	0	2	0	1	1	0	0	0	2	0	0	0	0	0	4	4	1	0	1	0	1	2	1	1	1	0	0	0	1	0	0	0	0	1	3	1	0	1	0	0	1	1	1	1	0	1	2	0
Dasyphora albofasciata	1	1	1	0	0	0	0	0	2	1	0	0	0	0	0	2	0	1	0	0	0	1	1	1	0	1	0	1	2	1	1	0	0	0	0	1	0	0	–	1	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Dasyphora flavipes	1	1	1	0	0	0	0	0	2	1	0	1	1	0	0	2	0	1	0	0	0	1	1	1	1	0	1	0	2	1	1	0	0	0	0	1	0	1	0	0	1	3	1	1	0	0	0	1	1	1	1	0	0	2	0
Eudasyphora zimini	1	1	1	0	1	0	0	0	2	1	0	1	0	0	0	2	0	1	0	0	0	0	1	1	0	1	0	1	2	1	1	0	0	0	0	0	0	1	0	1	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Eudasyphora zimini	1	1	1	0	1	0	0	0	2	1	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	1	0	2	1	1	0	0	0	0	0	0	0	1	0	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Dasyphora pratorum	1	2	0	1	0	0	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	0	0	0	1	?	1	1	3	1	1	0	0	0	1	1	1	1	?	1	2	0
Dasyphora gussakovskii	1	1	0	1	0	0	0	0	2	1	0	0	0	0	0	2	0	1	1	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	0	1	0	1	0	1	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Eudasyphora cyanella	1	1	1	0	1	0	0	0	2	1	0	1	0	0	0	2	0	0	0	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	0	0	0	0	1	0	1	3	1	1	1	0	0	1	1	1	1	0	1	2	0
Eudasyphora cyanicolor	1	1	1	0	1	0	0	0	2	1	0	1	0	0	0	2	0	0	1	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	0	1	0	1	0	1	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Eudasyphora kempi	1	1	1	0	1	0	0	0	2	1	0	1	0	0	0	2	0	1	1	0	0	0	1	1	0	1	1	1	2	1	1	0	0	0	0	0	0	1	0	1	1	3	1	1	0	0	0	1	1	1	1	0	1	2	0
Polietes domitor	1	1	2	1	1	1	0	0	2	1	0	0	0	0	0	2	0	0	0	0	4	4	3	1	2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	3	3	0	0	0	0	0	1	1	0	1	0	0	2	0
Polietes hirticrura	1	2	1	1	1	1	0	0	2	1	0	1	0	0	0	2	0	0	0	0	4	4	1	1	0	1	0	1	3	0	1	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	0	1	1	0	1	0	1	2	0
Polietes lardaria	1	2	1	1	1	1	0	0	2	1	0	0	0	0	0	2	0	0	0	0	4	4	3	1	0	1	0	1	2	1	1	0	0	0	0	0	0	1	0	1	0	1	–	0	1	0	0	1	1	0	1	0	1	2	0
Polietes steinii	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	1	0	0	0	0	4	3	3	1	0	1	0	1	3	0	1	0	0	0	0	2	0	1	0	0	2	1	0	1	0	0	0	1	1	0	1	0	2	2	0
Mesembrina latreillii	1	1	2	0	1	0	0	0	2	0	?	0	0	0	0	?	0	?	1	0	3	3	3	1	2	1	0	1	2	0	1	0	0	0	0	0	2	0	1	1	3	1	1	0	0	0	0	1	1	1	1	?	2	2	1
Mesembrina meridiana	1	2	1	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	3	1	2	0	0	0	0	1	0	0	0	0	0	0	2	0	1	0	1	1	–	0	0	0	0	1	1	1	1	0	2	2	1
Mesembrina mystacea	1	2	1	1	0	0	0	0	2	0	0	0	1	0	0	2	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0	1	1	1	–	1	0	0	0	1	1	1	1	0	2	2	1
Mesembrina sp. 1	0	2	1	1	0	0	0	0	2	0	0	0	0	1	0	2	0	0	1	0	0	0	2	1	0	0	1	0	1	0	0	0	0	0	0	0	2	0	0	1	0	1	–	1	0	0	0	1	1	1	1	0	2	2	1
Mitroplatia mouschi	0	0	0	0	0	0	0	0	1	0	?	0	0	0	0	?	1	?	0	0	0	0	1	?	0	0	0	0	0	1	0	0	0	0	0	0	0	1	?	0	0	1	–	1	0	0	0	1	1	0	0	0	0	0	0
Mitroplatia pyrellioides	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	2	1	1	0	0	0	1	1	1	1	0	0	2	0
Mitroplatia smaragdina	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0	1	2	1	0	1	0	1	0	1	0	0	0	0	2	0	1	0	1	2	2	1	1	0	0	0	1	1	0	0	0	0	2	0
Morellia abdominalis	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	1	1	1	1	1	1	0	0	0	0	2	0	1	0	1	2	2	1	1	0	0	0	1	1	1	1	0	0	2	0
Morellia aenescens	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	1	0	1	1	1	1	0	0	0	0	2	0	1	0	1	1	2	1	1	0	0	0	1	1	1	1	0	0	2	0
Morellia basalis	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	2	1	0	1	1	1	2	1	1	1	0	0	1	1	1	1	0	0	2	0
Morellia calyptrata	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	2	2	0	1	0	1	1	1	1	0	0	0	0	2	0	1	0	1	2	2	1	1	1	0	0	1	1	1	1	0	0	2	0
Morellia hortensia	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	0	0	0	2	0	1	1	1	2	2	1	1	1	0	0	1	1	1	1	0	0	2	0
Morellia hortorum	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	3	1	1	0	1	0	1	1	0	1	0	0	0	0	2	0	0	0	1	1	2	1	1	0	0	1	0	1	1	1	0	1	2	0
Morellia humeralis	0	1	0	1	0	0	0	0	2	0	0	0	0	1	0	2	0	1	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0/1	0	0	1	1	1	2	1	1	1	0	1	1	1	0	1	?	0	2	0
Morellia micans	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	2	0	1	0	1	1	2	1	1	1	0	0	1	1	1	1	0	0	2	0
Morellia nigricosta	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	0	1	1	1	0	1	0	0	0	0	2	0	1	0	1	1	2	1	1	1	0	1	1	1	1	1	0	0	2	0
Morellia nigrisquama	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	1	1	1	1	1	1	0	0	0	0	2	0	1	0	1	1	2	1	1	1	0	0	1	1	1	0	1	1	2	0

Terminal taxa	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	0	1	2	3	4	5	6	7	8	9	10	11	12
Delia platura	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	–	1	0	0	2	1/2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Muscina stabulans	0	–	–	–	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	–	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
Haematobia irritans	0	–	–	–	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	–	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1
Stomoxys calcitrans	0	–	–	–	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	–	0	0	0	0	1/2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1
Thricops semicinereus	0	–	–	–	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	–	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Drymeia hamata	0	–	–	–	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	–	1	1	0	2	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0
Biopyrellia bipuncta	0	1	1	1	0	0	0	1	0	0	0	0	2	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Curranosia gemma	1	0	1	1	0	0	1	1	0	0	0	0	2	1	0	0	1	0	0	2	0	0	2	2	0	1	0	1	0	0	0	0	0	1	0	0	0	2	2	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0
Curranosia prima	1	0	1	1	0	0	1	0	0	0	0	0	2	1	0	0	1	1	1	0	1	1	2	2	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0
Curranosia spekei	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	2	1	?	1	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0
Trichomorellia seguyi	0	–	–	–	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	2	0	1	2	3	0	1	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0
Trichomorellia trichops	0	–	–	–	1	0	1	0	0	0	0	0	2	1	0	1	1	1	0	2	0	1	3	3	1	1	0	0	0	0	0	0	1	0	0	0	0	2	1	?	1	0	1	1	0	1	0	?	0	1	0	0	1	0	0	0	0
Deltotus facetus	1	1	1	1	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	1	0	1	3	3	1	1	0	0	3	0	0	0	0	1	0	1	0	2	1	?	1	0	1	?	0	1	0	?	?	0	0	1	0	0	0	1	0
Hennigmyia setinervis	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	2	0	1	2	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Dasyphora albofasciata	1	0	0	1	0	0	0	0	0	0	0	0	2	1	1	0	1	1	1	3	0	1	3	3	1	0	0	0	0	0	0	0	1	1	0	0	0	2	1	?	1	0	1	1	0	1	0	?	?	0	0	0	0	1	1	1	0
Eudasyphora flavipes	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	3	0	1	3	3	1	1	0	0	0	0	1	0	1	1	0	1	0	2	1	1	1	0	1	1	0	1	0	?	?	0	0	1	0	1	0	1	0
Eudasyphora zimini	1	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3	0	1	3	3	0	1	0	0	0	0	0	0	1	0	0	1	0	2	1	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0
Dasyphora pratorum	1	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3	0	1	3	3	0	1	0	0	0	0	0	0	1	1	0	1	0	2	2	?	1	0	1	1	0	1	0	?	0	0	0	0	0	0	1	1	0
Dasyphora gussakovskii	1	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3	0	1	3	3	0	1	0	0	0	0	0	0	1	1	0	1	0	2	2	1	1	0	1	1	0	1	0	0	0	1	3	1	0	1	1	1	0
Eudasyphora cyanella	1	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3	0	1	3	3	0	1	0	0	0	0	0	0	1	1	0	1	0	2	1	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0
Eudasyphora cyanicolor	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	3	0	1	3	3	0	1	0	0	0	0	0	0	1	1	0	1	0	2	2	0	1	0	1	1	0	1	0	0	1	1	0	0	0	1	1	1	0
Eudasyphora kempi	1	0	0	1	0	0	1	0	0	0	0	0	2	1	0	1	1	1	1	3	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	2	2	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0
Polietes domitor	0	–	–	–	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polietes hirticrura	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	2	1	?	1	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polietes lardaria	0	–	–	–	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polietes steinii	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Mesembrina latreillii	0	–	–	–	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	?	?	0	1	0	?	1	1	0	2	2	?	?	0	?	?	0	1	1	0	1	0	0	1	1	0	0	0	0
Mesembrina meridiana	0	–	–	–	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	2	2	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	1	0
Mesembrina mystacea	0	–	–	–	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	3	3	1	1	0	2	2	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0
Mesembrina sp. 1	0	–	–	–	0	0	0	0	0	0	0	2	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	3	3	0	1	0	2	2	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0
Mitroplatia mouschi	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	?	1	1	0	?	1	1	0	1	0	1	?	?	0	0	0	?	0	0	0	2	2	?	?	0	?	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Mitroplatia pyrellioides	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	2	?	1	0	?	1	0	1	0	0	0	0	0	1	0	1	0	1	0
Mitroplatia smaragdina	0	–	–	–	0	0	1	0	0	0	0	0	2	1	0	0	1	1	1	3	1	1	3	2	0	1	0	0	0	0	0	0	0	0	0	2	0	2	2	0	1	0	1	0	0	1	0	0	1	1	0	1	1	0	1	0	0
Morellia abdominalis	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	2	1	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0
Morellia aenescens	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	1	0	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	2	0	0	0
Morellia basalis	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	1	0	3	1	1	3	1	0	1	0	0	0	0	2	1	1	0	0	0	0	2	2	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0
Morellia calyptrata	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	2	0	0	1	2	0	1	0	1	0	0	2	1	1	0	0	0	0	2	2	0	1	0	1	1	0	1	0	0	0	0	0	0	0	2	1	0	0
Morellia hortensia	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	1	0	1	2	1	1	1	2	0	1	0	0	0	0	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0
Morellia hortorum	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	2	2	0	1	1	1	1	0	1	0	0	0	0	0	1	0	2	0	0	0
Morellia humeralis	0	–	–	–	0	0	1	0	0	1	0	0	2	1	0	1	1	1	0	2	1	1	3	0	0	1	0	0	4	0	0	1	1	0	0	0	0	2	2	0	1	0	1	1	0	1	0	1	0	1	1	2	0	2	1	1	0
Morellia micans	0	–	–	–	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	2	0	0	2	1	0	1	0	0	0	0	0	1	1	0	0	0	0	2	2	1	1	1	1	1	0	0	0	0	0	1	2	0	0	0	0	0	0
Morellia nigricosta	0	–	–	–	0	0	1	1	0	1	0	0	2	1	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	2	0	1	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	0
Morellia nigrisquama	0	–	–	–	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	4	0	0	0	1	0	0	0	0	2	2	0	0	1	1	1	0	1	0	1	1	1	2	0	1	1	0	0	0

Table 2. *Continued*

Terminal taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Morellia paulistensis	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	2	0	1	1	1	1	1	1	0	0	0	0	2	0	1	0	1	1	2	1	1	0	0	1	1	1	1	1	0	0	2	0
Morellia podagrica	1	1	1	0	0	0	0	0	2	0	0	0	0	0	2	0	1	0	0	0	0	0	1/2	1	0	1	0	1	1	1	1	1	0	0	0	2	0	1	0	1	1	2	1	1	0	0	1	0	0	1	1	0	1	2	0
Morellia xanthoptera	0	0	2	0	0	0	0	0	2	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	0	0/1	0	1	0	1	1	2	1	1	1	1	0	1	0	1	1	0	0	2	0
Musca albina	0	0	2	2	0	0	0	0	0	1	0	0	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	—	1	1	1	1	0	1	0	1	0	0	0	2	0
Musca alpesa	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca autumnalis	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca cassara	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	0	?	0	0	1	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca domestica	0	0	2	2	0	0	0	0	0	0	0	0	0	0	?	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	1	1	0	1	2	1	1	0	0	1	1	1	1	1	0	0	2	0
Musca fergusoni	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0	1	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca larvipara	0	0	2	2	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1	0	1	1	1	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca lasiophthalma	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0/1	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca lusoria	0	0	2	2	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca pattoni	0	0	2	2	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Musca vetustissima	1	1	2	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia australis	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	0	1	0	1	0	0	1	3	1	1	0	0	1	1	1	1	1	0	0	2	0
Neomyia cornicina	1	0	2	0	0	0	0	0	2	0	0	0	0	1	1	0	1	0	1	0	0	2	0	1	0	1	0	1	1	1	1	0	1	1	0	0/1	2	0	0	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia dubia	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	1	1	2	0	0	0	1	2	—	1	0	0	1	1	1	1	1	0	0	2	0
Neomyia gavisa	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	2	1	1	0	1	0	1	1	1	0	0	2	0
Neomyia lauta	1	0	2	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	?	1	0	0	2	0	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia laxifrons	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia limbata	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia macrops	0	0	2	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	1	0	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia nudissima	0	0	2	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0/1	2	0	0	0	1	2	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia rhingiaeformis	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	2	1	1	0	1	1	0	1	1	1	0	0	2	0
Neomyia sperata	1	0	2	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia timorensis	1	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Neomyia viridescens	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0/1	2	0	?	0	1	2	1	1	0	0	0	0	1	1	1	0	0	2	0
Pyrellina distincta	1	0	2	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	1	1	1	2	1	1	1	0	0	0	1	0	1	0	1	1	3	1	1	0	1	0	0	1	1	1	1	1	0	0
Pyrellina marsya	1	0	2	0	0	1	0	0	2	1	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	1	1	1	2	1	1	0	1	0	0	0	1	0	0	1	1	3	1	1	0	1	0	0	1	0	1	1	1	0	0
Pyrellia albocuprea	1	1	1	0	0	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0	0	0	1	0	1	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Pyrellia rapax	1	1	2	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0	1	0	1	0	0	1	3	1	1	0	1	1	0	1	1	1	0	0	2	0
Pyrellia scintillans	1	1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	0	0	0	0	0	0	1	0	0	1	3	1	1	0	1	0	0	1	0	1	0	1	0	0
Pyrellia tasmaniae	1	1	1	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	1	0	0	1	3	1	0	1	0	0	0	1	1	1	0	0	2	0
Pyrellia vivida	1	1	2	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	3	1	1	0	0	1	0	1	1	1	0	0	2	0
Myiophaea spissa	1	0	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2	0	1	0	1	2	1	0	1	0	0	0	0	0	1	0	1	1	2	1	1	0	1	0	0	1	1	1	0	0	1	0
Neorypellia neglecta	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2	0	1	1	1	2	1	1	0	1	0	0	0	0	0	0	1	1	2	1	0	1	0	0	0	1	1	1	0	0	2	0
Parapyrellia maculipennis	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	1	0	0	0	1	0	1	2	1	1	0	1	0	0	1	1	1	0	0	2	0
Sarcopromusca pruna	1	1	1	0	0	0	0	0	2	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	3	1	1	1	0	0	0	1	0	1	0	0	0	0
Sarcopromusca sarcophagina	1	1	1	0	0	0	0	0	2	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	1	3	1	1	1	0	0	0	1	0	1	0	0	0	0
Xenomorellia holti	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	2	2	0	1	1	1	2	1	0	1	0	1	0	0	0	0	1	1	1	2	1	1	1	0	0	0	1	1	1	0	1	0	0
Xenomorellia sp 1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	2	0	0	0	0	0	0	1	1	2	0	1	1	1	2	1	0	1	0	1	0	0	0	1	0	1	1	2	1	1	1	0	0	0	1	0	1	0	1	0	0
Polietina concinna	1	1	1	1	0	1	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0	1	1	1	1	2	0	1	1	1	1	0	0	1	1	0	1	0	0
Polietina flavidicincta	1	0	1	1	1	0	1	0	2	0	0	0	0	0	?	0	0	0	0	0	0	1	1	1	1	1	1	1	2	0	1	1	1	0	0	1	1	0	1	1	1	2	0	1	1	0	1	0	0	1	1	0	1	0	0
Polietina rubella	1	0	1	1	1	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	1	1	1	1	1	1	2	0	1	1	1	0	0	1	0	1	0	1	1	2	0	1	1	1	1	1	0	0	1	0	1	0	0
Polietina steini	1	0	1	1	0	1	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0/1	1	1	1	1	1	1	2	1	1	1	0	0	0	1	0	1	0	1	1	2	0	1	—	1	1	1	0	0	1	0	1	0	0

Terminal taxa	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112
Morellia paulistensis	0	–	–	–	0	0	1	0	0	0	0	0	2	1	1	0	1	1	0	0	1	1	3	3	0	1	0	0	0	0	2	1	1	0	0	0	0	2	2	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	1	2	0
Morellia podagrica	0	–	–	–	0	0	0	1	0	0	1	0	2	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	4	1	1	1	1	0	0	0	0	2	2	1	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0
Morellia xanthoptera	0	–	–	–	0	1	1	1	1	1	1	0	2	1	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Musca albina	0	–	–	–	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	2	1	0
Musca alpesa	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	2	2	1	0
Musca autumnalis	0	–	–	–	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	1	0	2	2	1	1	0
Musca cassara	0	–	–	–	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	1	1	0	2	0	2	1	0
Musca domestica	0	–	–	–	0	0	0	0	0	0	0	1	2	1	1	0	0	0	0	0	0	1	1	0/1	2	2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	1	1	0	2	0	2	1	0
Musca fergusoni	0	–	–	–	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	2	2	2	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	2	1	2	1	0
Musca larvipara	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	2	2	2	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	?	?	?	?	?	?
Musca lasiophthalma	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0	0	0	0/1	0/1	0	0	1	0	2	0	1	0	0	0	1	1	?	?	?	2	1	?
Musca lusoria	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	3	0	2	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	1	0	2	1	2	1	0
Musca pattoni	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	2	2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	1	1	0	2	1	2	1	?
Musca vetustissima	0	–	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	1	1	0	2	0	2	1	0
Neomyia australis	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	2	2	0	2	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	2	0	1	1	0	2	1	2	1	0
Neomyia cornicina	1	0	1	1	0	1	0	0	0	0	0	2	0	1	0	0	0	1	0	0	1	1	2	2	0/1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	2	0	2	0	1	1	0	2	1	2	1	0
Neomyia dubia	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	2	2	0	2	0	1	0	0	0	1	0	0	0	0	1	0	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia gavisa	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	2	0	1	0	1	0	0	0	0	1	0	0	0	1	1	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia lauta	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	2	0	1	0	0	0	0	1	0	0	0	1	2	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia laxifrons	1	0	1	1	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0	0	1	2	2	2	2	2	0	0	0	0	0	1	0	0	0	0	1	2	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia limbata	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	1	2	2	0	2	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	1	0	1	0	2	0	1	1	1	1	?	2	1	2	1	?
Neomyia macrops	1	0	1	1	1	1	0	0	0	0	0	2	0	1	1	0	0	1	0	0	1	2	3	3	0	2	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia nudissima	1	0	1	1	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0/1	0	0	1	2	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia rhingiaeformis	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	2	2	2	0	2	0	0	0	0	0	1	0	0	0	0	1	2	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Neomyia sperata	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	2	2	0	2	0	0	0	0	0	1	0	0	0	0	1	2	2	0	0	0	0	1	0	2	0	1	0	0	1	0	2	1	2	1	0
Neomyia timorensis	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	2	2	0	2	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	1	0	1	0	2	0	1	1	1	1	0	2	1	2	1	0
Neomyia viridescens	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	2	2	2	0	2	0	0	0	0	0	1	0	0	0	0	1	1	2	0	0	1	0	1	0	2	0	1	0	1	1	0	2	1	2	1	0
Pyrellina distincta	0	–	–	–	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0/1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	2	2	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	1	0	0
Pyrellina marsya	0	–	–	–	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0	2	2	?	?	0	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0
Pyrellia albocuprea	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	1	0	0	0	2	0	0	1	1	0	1	0	0	2	1	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	0	0	?
Pyrellia rapax	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	1	1	1	2	2	1	1	0	0	2	0	0	1	0	0	1	0	0	2	1	?	?	1	0	1	0	1	0	0	0	0	0	?	0	0	0	0	?
Pyrellia scintillans	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0/1	0	1	1	1	1	1	0	1	0	0/1	0	0	0	1	0	0	1	0	0	1	2	1	0	1	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0
Pyrellia tasmaniae	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	1	1	3	3	2	0	0	0	0	0	0	0	1	0	0	1	0	0	2	2	1	0	1	?	1	0	1	0	0	0	1	0	1	0	0	1	0	0
Pyrellia vivida	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	3	3	1	0	1	0	0	0	0	0	1	1	0	1	0	0	2	2	1	0	1	?	1	0	1	0	0	0	1	0	1	0	0	1	0	0
Myiophaea spissa	1	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	1	0	1	3	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0
Neorypellia neglecta	0	–	–	–	0	1	1	1	0	1	0	0	2	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	1	1	1	0	1	0	0	0	1	0	1	0	0	1	0	0
Parapyrellia maculipennis	0	–	–	–	0	0	0	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	2	0	1	1	0	0	2	0	2	2	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Sarcopromusca pruna	0	–	–	–	0	0	0	0	1	1	0	2	1	0	1	1	0	0	1	0	0	0	1	0/1	1	0	0	0	1	0	0	0	0	0	0	0	0	2	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Sarcopromusca sarcophagina	0	–	–	–	0	0	0	0	1	1	0	2	1	0	1	1	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	2	2	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
Xenomorellia holti	1	0	1	1	0	1	0	0	0	0	1	2	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	2	1	1	0	1	1	1	0	2	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0
Xenomorellia sp 1	1	0	0	0	0	1	0	1	1	1	0	2	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	2	1	1	0	1	0	0	0	0	2	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0
Polietina concinna	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	1	3	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Polietina flavidicincta	1	1	0	0	0	0	1	1	1	1	0	2	0	0	0	0	1	1	1	1	1	3	2	0	1	0	0	1	–	0	0	–	0	?	0	0	0	2	2	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0
Polietina rubella	1	1	0	0	0	0	1	1	1	1	0	2	0	1	0	0	0	0	1	0	1	3	2	1	1	1	0	1	?	?	?	?	?	?	0	0	0	2	2	?	?	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0
Polietina steini	1	1	0	0	0	0	0	1	1	1	0	2	1	0	1	0	0	1	1	0	0	1	3	2	1	0	0	1	1	0	0	–	0	1	0	0	0	2	2	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0

?, missing data; –, inapplicable data.

Table 3. Summary of the cladogram searches applying different character weighting schemes

	Character weighting schemes							
	Equal	Successive	Implied ($k = 1$)	Implied ($k = 2$)	Implied ($k = 3$)	Implied ($k = 4$)	Implied ($k = 5$)	Implied ($k = 6$)
Number of cladograms	860	7	4	2	3	4	4	4
Length	671	674	745	726–728	692	688	688	683
Fitness	5374.87–5400.30*	5471.03	5451.46	5484.03–5485.40	5514.71	5513.27	5513.27	5507.78
CI	22	22	20	21	22	22	22	22
RI	73	73	69	70	72	72	72	72

*The software X-PEE-WEE only supports the opening of '.tre' files with up to 50 cladograms, therefore these values were estimated on the basis of the first 50. CI, consistency index; RI, retention index.

CI, the character i would potentially have 860 values for CI, and the weight could be given by using either the highest value among those 860 values (if using NONA), or either the highest, average or lowest value (if using PAUP version 4.0b10; Swofford, 2001). Therefore, Goloboff (1993c) suggested the use of IW, which, unlike SW, gives differential weights for characters concomitantly with tree reconstruction and for each cladogram. Thus, a given character i is assigned a weight according to its value of fit for a given cladogram.

In XPEE-WEE, the fit value for any character i is estimated by the equation $f_i = k/(k + es)$, where k is the concavity constant and es is the number of extra-steps for the character (Goloboff, 1993b; Goloboff, 1997). The lower the value for k, the higher the fit difference among the characters with and without extra-steps will be, resulting in a more strict and radical weighting. On the other hand, as k increases the fit will be lower, with a weighting closer to that of EW (if k reached infinity, their values would be equal). The effects of using different values for k have been exhaustively examined by Goloboff (1993c, 1995) and experimentally investigated by Turner & Zandee (1995), but no clear suggestions for the most adequate values are given by these authors.

Here, the IW approach is preferred for several reasons. (1) It finds trees in one stage, and the solution obtained is not influenced by the initial weights attributed to the characters (Kaila, 1999). (2) The self-consistency of the final cladograms is not defined with respect to a pooled set of topologies (Harbach & Kitching, 1998). (3) The *fit* function used does not have a lower bound of zero, and so the chance of dismissing evidence by entirely excluding characters is minimized (Bosselaers & Jocqué, 2002). (4) The approach does not downweight multistate characters (Goloboff, 1993c).

The SW can be equally self-consistent if the use of differential weights occurs on each cladogram independent of the remaining set. However, weight assignment based on either CI or RI would be downweighting for some characters (reversions, multistate characters, etc.) compared with weight assignment based on the fit equation above (Goloboff, 1993c).

Herein, we used several values for k (see results in Table 3). Lower values for k tend to generate longer cladograms because they favour characters with higher fit (Goloboff, 1993c, 1995; Turner & Zandee, 1995). Also, greater values of k will result in greater similarities among the resulting cladograms and those obtained under EW and SW.

The IW analysis using $k = 3$ generated three cladograms with the best fit (5514.71) and a length of 692 steps (Figs 49, 50, 51, 52) . Figures show strict consensus of those three most parsimonious cladograms under unambiguous optimization (Figs 49, 50), and under *acctran* optimization (Figs 51, 52). The main differences among the three cladograms were restricted to the clade including *Musca*, whereas the remaining clades stayed the same. Therefore, the strict consensus (Figs 49, 50) was used for the discussion of supra and infrageneric relationships. Discussion on internal relationships of *Musca* was based on the strict consensus as well as on the variations found among the other three cladograms (Fig. 53).

PHYLOGENETIC RELATIONSHIPS

Genera within Muscini appear as the sister group of the clade comprising *H. irritans* and *S. calcitrans* (Figs 49, 50), thereby supporting the sister-group relationship between Muscini and Stomoxyini (de Carvalho, 1989b; Couri & de Carvalho, 2003). Monophyly of Muscini was supported by the following characters. (1) Developed secondary setulae on the inner-dorsal surface of arista (character 9): this feature is not exclusive to muscine taxa, it is found widely within other muscids (see Couri & de Carvalho, 2003). (2) Cercal plate with ventral median spined process (character 95): this spined process is exclusive to Muscini, and so is the marginal spined process
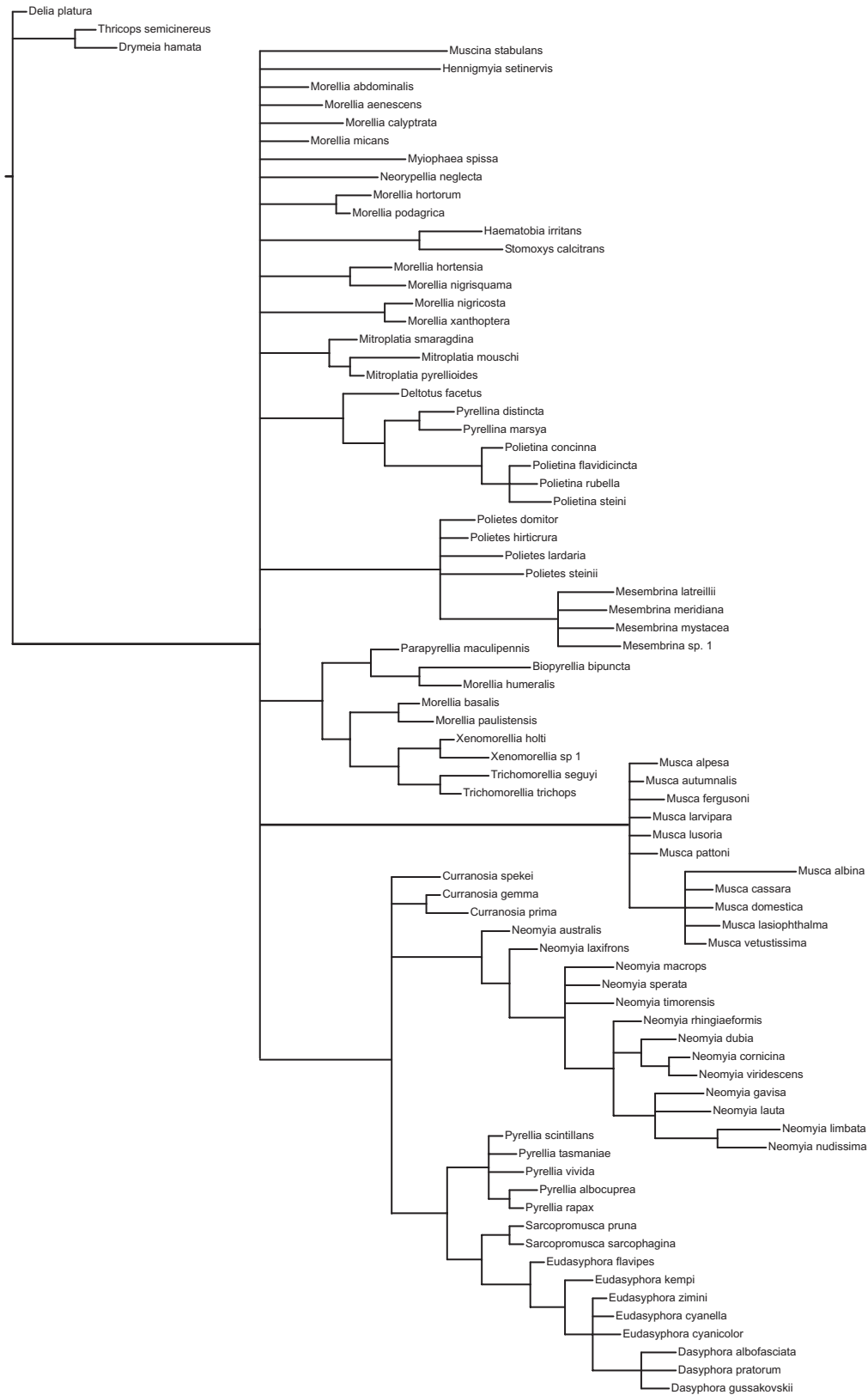
Figure 46. Strict consensus of 860 most parsimonious cladograms with equal weighting, with unambiguous optimization.
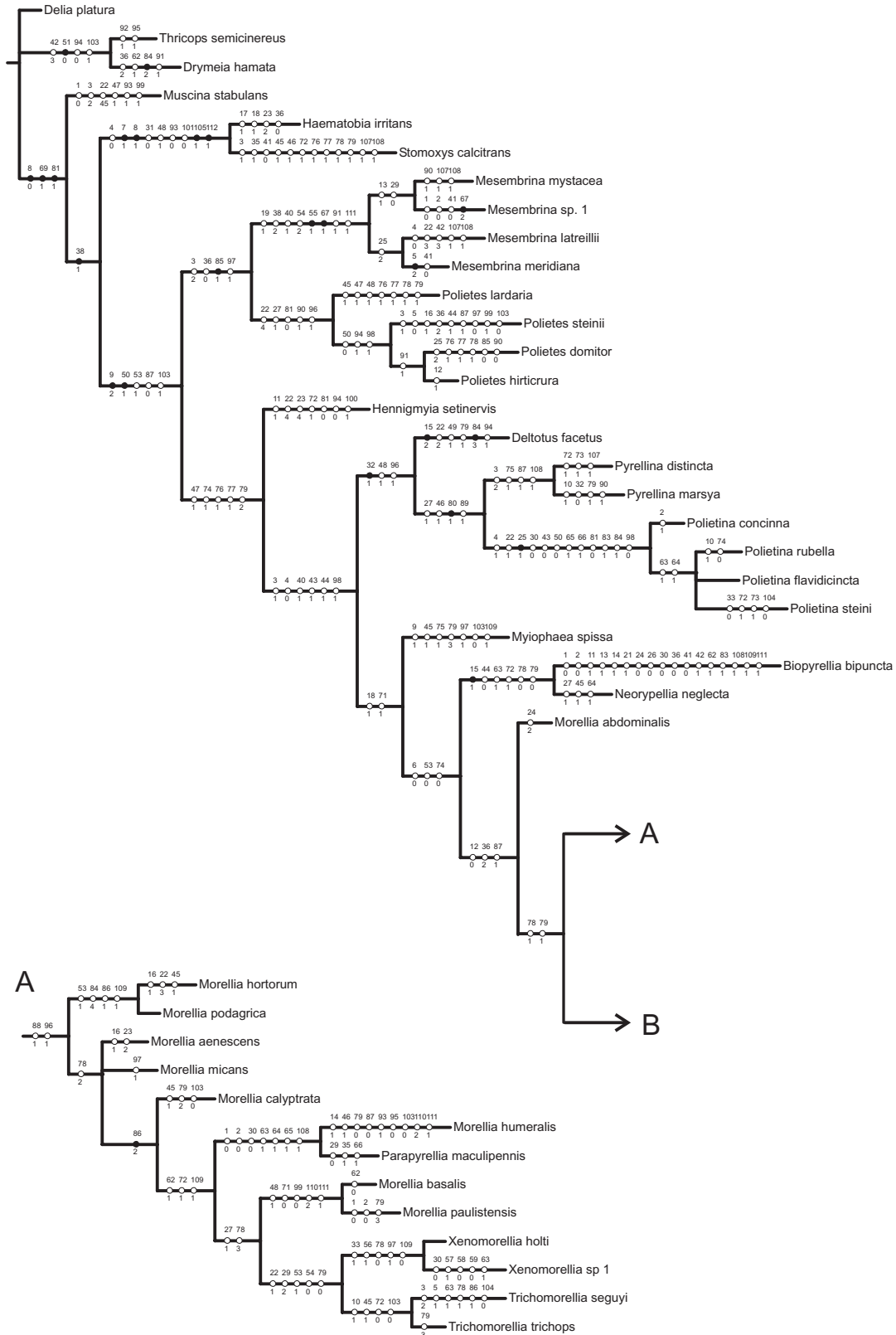
Figure 47. Strict consensus of seven most parsimonious cladograms with successive weighting, with unambiguous optimization (continued in Fig. 48).

Figure 48. (continued from Fig. 47). Strict consensus of seven most parsimonious cladograms with successive weighting, with unambiguous optimization.

(character 96) found in several taxa, although not in the ground-plan of the tribe. (3) Distiphallus with reduced spinules on lateral-apical membrane (character 103): these spinules are also found in many Azeliini and were indicated in the ground-plan of the tribe (Savage & Wheeler, 2004). The adult characters previously considered as synapomorphies of Muscini (Hennig, 1965) were not supported. The plumose arista (character 8) is present at the base of cladogram, shared by *Muscina stabulans* (Reinwardtiini) and all Muscini taxa; the setulose anepimeron (character 38) is shared by Muscini and Stomoxyini. However, Hennig (1965) recognized the problem with those characters and suggested a convergence, at least, of those characters shared by Muscini and Stomoxyini.

The genera *Mesembrina* and *Polietes* are within the most basal Muscini, and the monophyly of *Polietes* is not supported, although in both EW and SW it was monophyletic and a sister-group of *Mesembrina*. *Polietes* is quite heterogeneous in morphology, comprising a mosaic of characters; apparently there are neither synapomorphies nor diagnostic characters that support this genus as a natural group. Being the only Holarctic representative with glossiform lower calypter and the M vein straight toward the apex facilitates its diagnosis and identification as a taxonomic group; however, in a global perspective, that group has no clear support.

Several genera have been proposed bearing *Polietes* species as genotypes (e.g. *Pseudophaonia* Malloch, 1918; *Polietella* Ringdahl, 1922, *Pseudomorellia* Ringdahl, 1929). Peris & Llorente (1963) suggested the 'group' *Polietes* to gather the genera *Polietes s.s.*, *Pseudophaonia*, and *Pseudomorellia*. They commented, however, on the possibility that these genera may be grouped into one genus, which was indeed consolidated in taxonomic studies of the Palaearctic Muscidae (Hennig, 1964b). Shinonaga & Kano (1971) and Shinonaga (2003) divided *Polietes* into two subgenera: *Polietes s.s.*, with a setulose prosternum; and *Pseudomorellia*, with a bare prosternum. Based on our results (Fig. 49), *Polietes s.s.* is probably monophyletic, including *Polietes lardaria* and *Polietes nigrolimbata* (Bonsdorff, 1866), and possibly a few more species, whereas *Pseudomorellia* is paraphyletic by the incongruent position of *Polietes domitor* and *Polietes steinii*. However, the SW analysis (Fig. 47) indicated *Pseudomorellia* as monophyletic and a sister group of *P. lardaria*, a representative of *Polietes s.s.*

Polietes was also divided into the subgenera *Pseudophaonia (*with *Polietes hirticrura* and *Polietes orichalceoides*) and *Polietes s.s.* (*P. lardaria*, *P. nigrolimbata*, and *P. domitor*) based on characters of immature stages (Skidmore, 1985). Our analysis (Fig. 49) supports monophyly for *Pseudophaonia*, but this requires the inclusion of *P. steinii* (a type species

of *Polietella*), making *Polietes s.s.* paraphyletic. Even in the SW strict consensus (Fig. 47), none of Skidmore's subgenera were supported.

Here, *Polietes* is divided into three parts: *P. hirticrura* and *P. steini* (the genus becoming *Polietella*), *P. domitor* (in the genus *Pseudomorellia*) and *P. lardaria* (representing *Polietes s.s.*; Fig. 49). However, we prefer here to maintain *Polietes* provisionally as a valid genus, contrary to results of the IW analysis, but consistent with EW and SW analyses. Clearly, further systematic studies examining all *Polietes* species could either validate its monophyly or split the genus and revalidate the generic names included under its synonymy.

Mesembrina, on the other hand, is easily diagnosed with several characters that strongly support monophyly. The basal position of *Mesembrina*, *Polietes*, and *Hennigmyia* within Muscini is in agreement with Hennig (1965) and Skidmore (1985). Those three genera together would be a sister group to all remaining Muscini (Hennig, 1965). Skidmore (1985), studying characters from immature stages, proposed the tribe Mesembrinini to group the three genera, with that tribe composing Muscinae along with Muscini *s.s.* Here, we corroborate the basal position of these genera but do not support their grouping forming a clade. *Hennigmyia*, an Afrotropical genus with three species (Pont, 1980), is apparently isolated from *Polietes* and *Mesembrina*, but is a sister group of all the other Muscini. Its characters are very distinctive, particularly its cercal plate without ventral spined processes (characters 95 and 96), thereby presenting a more simple conformation than those of closely related genera (*Polietes*, *Mesembrina*, *Deltotus*, *Pyrellina*, and *Polietina*). Furthermore, its aedeagus resembles that present in some *Musca* species, especially with its hook-shaped paramere (character 100) as observed in *Musca cassara*, *Musca domestica*, etc.

The clade *Deltotus* + (*Pyrellina* + *Polietina*) is strongly supported (Fig. 49) and the close relationship between *Deltotus* and *Pyrellina* corroborates the findings of Hennig (1965). The glossiform lower calypter (character 54) of *Pyrellina* would approximate it from *Polietes* and would cause the main uncertainty regarding its relationship within the Muscini (Hennig, 1965). The position of *Polietina* was also uncertain. Originally described in Phaoniinae close to *Polietes* (Schnabl & Dziedzicki, 1911), *Polietina* did not accompany *Polietes* when the latter was placed in Muscini (Collin, 1948). Thereafter it was included in Cyrtoneurininae but distant from the other genera in that subfamily (Hennig, 1965). The genus was later placed in Muscini (Couri & de Carvalho, 1997), and that placement was supported by cladistic analysis (Couri & de Carvalho, 2003). Here we corroborate this placement and show the supporting characters and the

Figure 49. Strict consensus of three most parsimonious cladograms with implied weighting ($k = 3$), with unambiguous optimization (continued in Fig. 50).
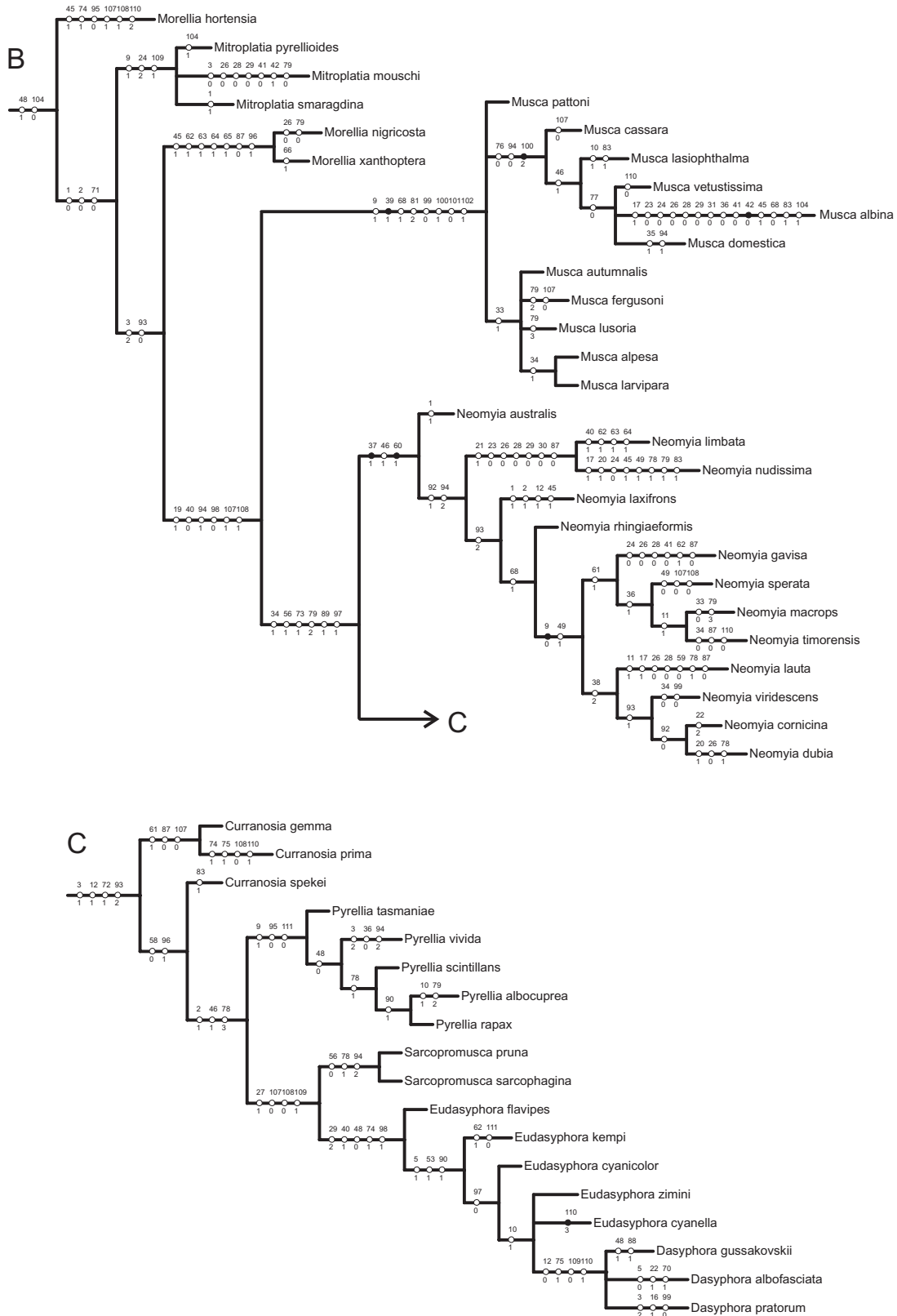
Figure 50. (continued from Fig. 49). Strict consensus of three most parsimonious cladograms with implied weighting ($k = 3$), with unambiguous optimization.

Figure 51. Strict consensus of three most parsimonious cladograms with implied weighting (*k* = 3), with *acctran* optimization (continued in Fig. 52).
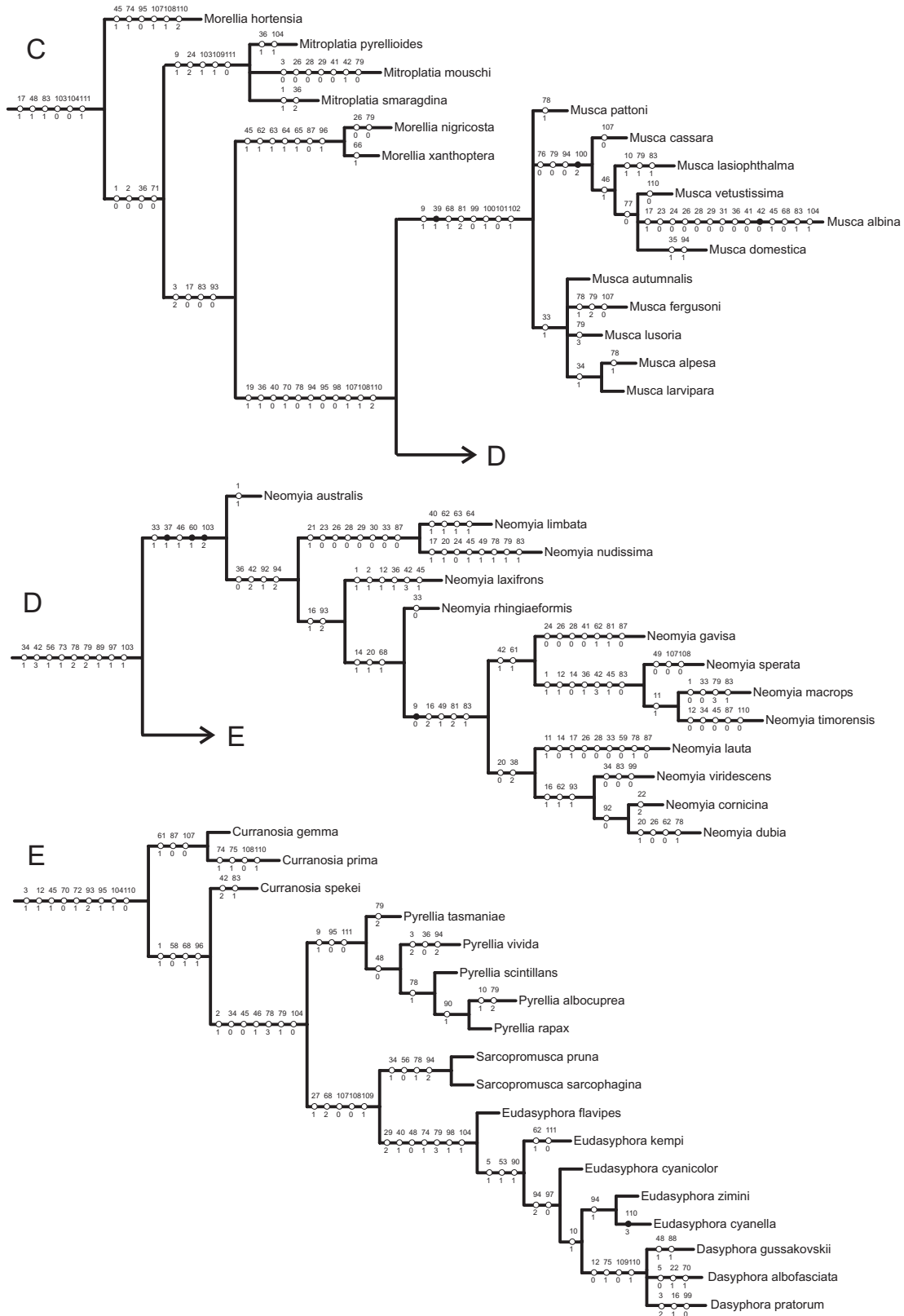
Figure 52. (continued from Fig. 51). Strict consensus of three most parsimonious cladograms with implied weighting (*k* = 3), with *acctran* optimization.
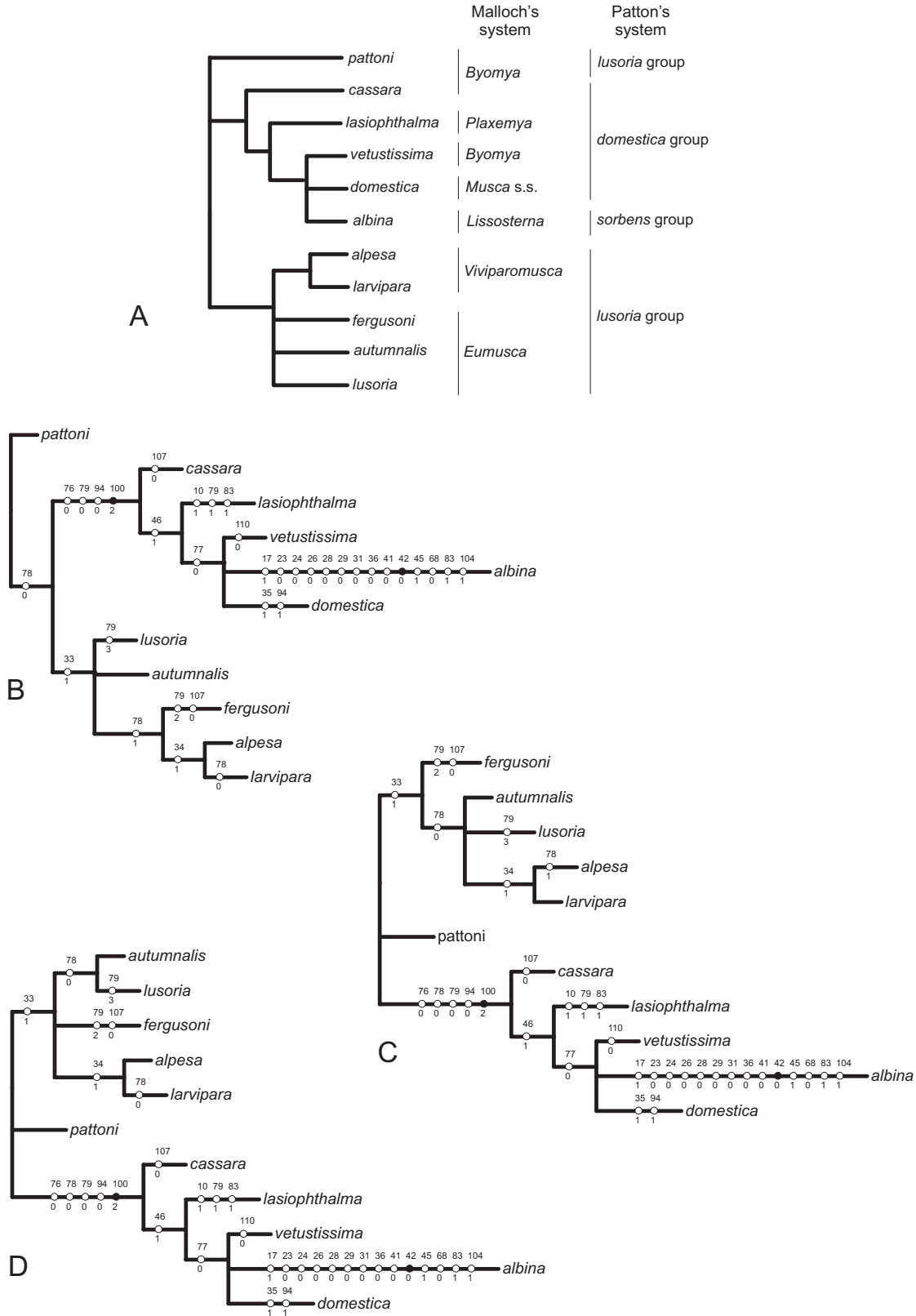
Figure 53. Internal relationship of *Musca*. A, *Musca* clade from the strict consensus and the classification systems of Malloch (1925, 1928, 1929) and Patton (1932); B–E, differences in the clade *Musca* within the three most parsimonious cladograms with implied weighting (*k* = 3), and with *acctran* optimization.

phylogenetic relationship with other genera. Setulae on the postalar wall (character 32), reported as a probable synapomorphy for *Polietina* (de Carvalho & Couri, 2002), is a synapomorphy, but for the entire *Deltotus* + (*Pyrellina* + *Polietina*) clade.

The Australasian monotypic genus *Myiophaea* appears isolated and close to *Morellia* and allied genera. *Myiophaea* would be related to *Rypellia* (= *Eudasyphora*; see discussion below), and a little distant from *Dasyphora* and *Neomyia* (referred to as *Orthellia* Robineau-Desvoidy, 1830) (Pont, 1967). Despite that, *Myiophaea* shares some characters of the leg chaetotaxy with *Morellia* (e.g. absence of posteroventral seta on mid tibia), and its relationship with *Rypellia*, *Dasyphora*, and *Neomyia* would be supported by the setulose subcostal sclerite (character 56 in the analysis). Pont (1967) emphasized this character because of its rarity in Muscidae. However, it is reasonably common within the Muscini, being present (under a variety of forms) either in basal (*Deltotus* and *Polietina*), intermediate (*Xenomorellia*) or more apical genera (*Pyrellia*, *Curranosia*, *Eudasyphora*, *Dasyphora*, and *Neomyia*). The large and bare prosternum in *Myiophaea* resembles *Rypellia* (Pont, 1967). The bare prosternum (character 48) is shared independently by several groups of Muscini (inclusive of *Morellia s.l.*). The prosternum shape was not used here, particularly because of the difficulty in coding the wide variability in shape that occurs in Muscini. However, the prosternum shape in *Myiophaea* is the same shape mainly present in Muscini, including *Morellia s.l.* (as commented by Pont, 1967), the basal genera *Deltotus*, *Pyrellina*, *Polietina*, *Polietes*, etc. and the apical genera *Neomyia*, *Eudasyphora*, etc.

Morellia and allied genera are located in the intermediate portion of the cladogram (Figs 49, 50); most of these genera were included in *Morellia* in the past but are considered valid to date. *Biopyrellia* and *Neorypellia* together comprise a Neotropical clade, separate from *Morellia s.l.* This is contrary to the orthodox view in which *Biopyrellia bipuncta* is part of *Morellia* (e.g. Séguy, 1935; Albuquerque, 1956; Pont, 1972). This relationship is also contrary to that of Townsend (1932), who described *Biopyrellia* close to *Parapyrellia*, and Hennig (1965), who proposed a monophyletic group comprising *Parapyrellia* and *Chaetopyrellia* Townsend, 1932 (= *Morellia*). Hennig (1965) also argued for the affinity of this group with some large Old World genus other than *Morellia* (not supported here). The treatment of *Biopyrellia* as independent from *Morellia* corroborates the taxonomic revalidation made by Pamplona (1986a) and followed by subsequent authors (e.g. de Carvalho & Couri, 2002; de Carvalho *et al.*, 2005).

On the other hand, *Morellia*, *Parapyrellia*, *Xenomorellia*, and *Trichomorellia* (the latter revalidated by

Pont, Nihei & de Carvalho, 2005; with *Dasymorellia* Malloch, 1923 as junior synonym) were grouped together in a large clade. Also, some species of *Morellia* were not included in that clade: *Morellia abdominalis* was positioned outside at the base, whereas *Morellia hortensia* and *Morellia nigricosta* + *Morellia xanthoptera* were placed closer to *Mitroplatia* Enderlein, 1935 and other genera (*Musca*, *Neomyia*, etc.). Consequently, we broaden the definition of *Morellia* to include the Neotropical genera *Parapyrellia*, *Xenomorellia*, and *Trichomorellia*. Hence, here, these genera are considered new synonyms of *Morellia s.l.* and, moreover, a subgeneric division for *Morellia* is proposed. The taxonomic changes proposed can be seen in Figure 54 and in the 'Summary of taxonomic changes proposed' at the end of the text.

Morellia s.l. is divided here into four subgenera: *Morellia s.s.*, *Parapyrellia*, *Xenomorellia*, and *Trichomorellia*. The three latter subgenera, geographically restricted to the Neotropics, are certainly monophyletic. The question of the monophyletic status of *Morellia s.s.* remains. Two species groups arise within *Morellia s.s.*: the *hortorum* and the *basalis* groups, with the remaining species provisionally allocated into this subgenus without a defined group. *Morellia aenescens*, *Morellia micans* and *Morellia calyptrata* are more closely related to the Neotropical clade composed of *Parapyrellia*, *Xenomorellia*, and *Trichomorellia*, and the *basalis* group. *M. aenescens* and *M. micans* are probably part of a same group comprising Holarctic representatives, or they might be separated into distinct species groups, whereas *M. calyptrata* might be part of an Afrotropical group. Skidmore (1985) suggested the lower affinity between the larval morphology of *M. aenescens* and other Palaearctic species.

The placement of *M. abdominalis*, indicated here outside *Morellia s.l.*, remains an open question. We do not know whether there are additional species closely related to this Afrotropical species. Here *M. abdominalis* was conserved within *Morellia* just for convenience, and was not given a subgeneric placement (as *incertae sedis*). The need for a more comprehensive study of *Morellia* from across the world in order to understand its limits and internal relationships is evident.

Earlier classification of *Morellia* into species groups divided *Morellia* into three groups (Pont, 1973): *hortorum* (with prosternum wide and bare), *simplex* (prosternum wide and setulose), and *pyrellioides* (prosternum conspicuously widened anteriorly). This study supports the *hortorum* group. The *pyrellioides* group was first recognized by Peris (1967) and subsequently segregated from *Morellia* (Zielke, 1971) into the new genus *Weyerellia* (= *Mitroplatia*), which was placed outside the limits of *Morellia s.l.* in the present analysis. The *simplex* group was segregated by Zimin
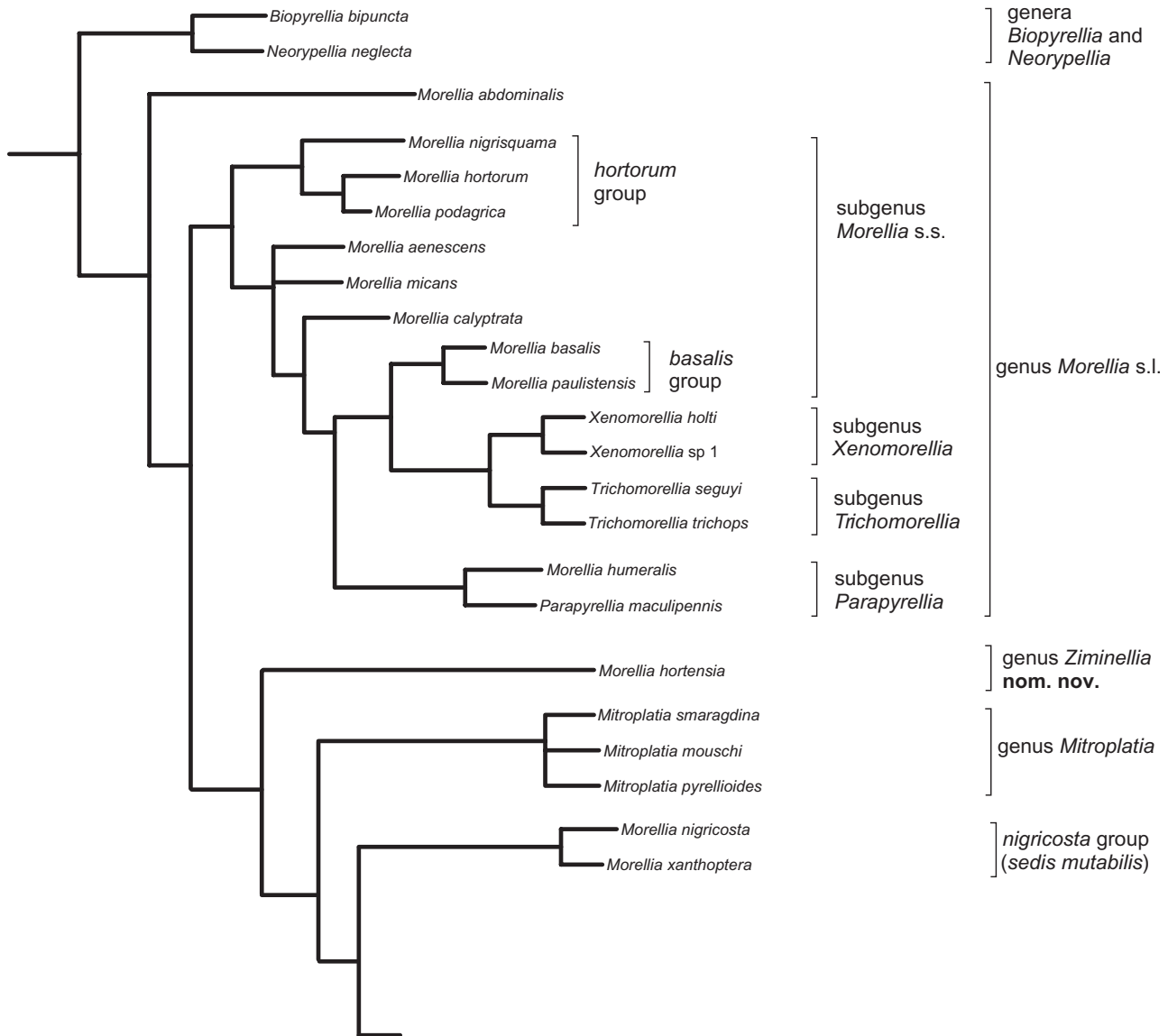
Figure 54. Partial strict consensus (from Figs 49, 50) summarizing the taxonomic changes proposed in this study for *Morellia* and allied taxa (see the explanation in the text).

(1951) into the subgenus *Dasysterna*, basically to include the species of *Morellia* with setulose prosternum. Here, *Dasysterna* was represented by *M. hortensia* and fell outside *Morellia s.l.* Thus, we support the validity of the *simplex* group (or subgenus *Dasysterna*) as a genus-ranked grouping. As *Dasysterna* Zimin, 1951 is preoccupied by *Dasysterna* Dejean, 1833, we propose herewith the new replacement name *Ziminellia* nom. nov. Nihei & de Carvalho, for *Dasysterna* Zimin. The type species is *Cyrtoneura simplex* Loew (1857).

With regard to the clade *M. nigricosta* + *M. xanthoptera*, named here as the *nigricosta* group, it is closely related to *Mitroplatia*, an Afro-Oriental genus. Resemblance among the Neotropical and two Afrotropical *Morellia* species (*Morellia pyrellioides* and *Morellia smaragdina*, now included in *Mitroplatia*) was based solely on colouration (Albuquerque, 1956). *Mitroplatia* and the *nigricosta* group are distinguished from *Morellia s.l.* by the following characters: absence of proclinate fronto-orbital seta on female (character 1), absence of accessory proclinate fronto-orbital seta on female (character 2), and basal portion of stem-vein bare on ventral face (character 71). Furthermore, the *nigricosta* group differs from *Morellia s.l.* mainly by the absent calcar (character 93). Previously, Pamplona (1986b) commented on the similarity between *M. xanthoptera* and *M. nigricosta* [referred to

as *Morellia nitida* (Wiedemann, 1830)]. Together, *Ziminellia* nom. nov., *nigricosta* group and *Mitroplatia* differ from *Morellia s.l.* mainly by the setulose prosternum (also present in the *basalis* group and *Morellia nigrisquama*). As well as *Ziminellia* nom. nov., the *nigricosta* group is also indicated here as a genus-ranked grouping, but it will be properly described in a future study. The *nigricosta* group was provisionally kept in *Morellia s.l.* as *sedis mutabilis*.

The monophyly of *Morellia* (Fig. 54) was supported by the backward-orientated setae on the anterodorsal surface of male mid tibia (character 88) and the ventral marginal spined process on the cercal plate (character 96, *acctran* optimization). Although Hennig (1965) considered *Morellia* a 'well supported' monophyletic group, the group did not include *Parapyrellia*, *Xenomorellia*, or *Trichomorellia*, although he suspected that *Sarcopromusca* should be included in *Morellia*. The hypothesis of monophyly argued by Hennig (1965) was based on the posterior larval extremity, although he did not examine all *Morellia* species. Perhaps, this character, and others, from immature stages may provide valuable information in future studies, hence contributing to support the monophyly of *Morellia*, either in the broad sense proposed here or as proposed by Hennig (1965).

The close relationship between *Xenomorellia* and *Trichomorellia* supports Albuquerque (1952) in that *Trichomorellia* (referred to as *Dasymorellia*) is 'closely related to *Xenomorellia* Mall., from which it can be easily separated by the dorsal chaetotaxy of stem-vein and pilosity of the eyes'. Here, these characters support the separation of both subgenera: in *Xenomorellia*, the apical portion of the stem-vein is dorsally setulose (character 72) and the eyes are short and sparsely setulose (character 10); whereas in *Trichomorellia*, the apical portion of the stem-vein is bare and the eyes are long and densely setulose.

The broadening of *Morellia* so that it comprises the Neotropical endemic taxa is a return to the traditional concept of the genus defined by Séguy (1935), Albuquerque (1956) and Pont (1972). However, on the one hand, the concept is broadened to include three Neotropical groups, whereas on the other hand, it is narrowed by segregating out a Palaearctic-Oriental (*Ziminellia* nom. nov.) and a Neotropical (*nigricosta*) group. Therefore, the concept proposed here for *Morellia* and allied genera can be summarized as follows: (1) *Biopyrellia* is a valid genus; (2) *Parapyrellia*, *Trichomorellia*, and *Xenomorellia* are synonyms of *Morellia* and are redefined as subgenera; (3) *Mitroplatia* is a valid genus; (4) *Dasysterna* Zimin is given new status as genus and the new replacement name *Ziminellia* nom. nov. is proposed; and (5) the *nigricosta* group is indicated as a genus-ranked group that must be separated from *Morellia*.

In this analysis we included five characters related to the pattern of wing spotting (characters 62–66). Wing spotting is highly homoplasic within Muscidae and most of the spotted-winged taxa occur in the tropics, mainly in Neotropical, Afrotropical, and Oriental regions. Within *Morellia s.l.*, only the Neotropical species possess conspicuous wing spots, including the *nigricosta* group (and also the Oriental species of *Mitroplatia*; Van Emden, 1965). Thirteen out of 18 Neotropical species of *Morellia s.l.* have spotted wings (Pamplona & Couri, 1995). We performed a cladogram search excluding characters 62–66 using IW ($k = 3$) with results very similar to the analysis in which those characters were included. The search generated four equally parsimonious cladograms (strict consensus in Fig. 55), with 663 steps length, fitness 5508.29, CI 22, and RI 72. Therefore, there was no overestimation of those characters for the cladograms obtained and discussed here.

Monophyly of *Musca* (Fig. 50) was supported by a number of characters. The only exclusive character is setae-like setulae in the upper portion of anepimeron (character 39). Other supporting characters were reduced setulae (pubescence) on the inner-dorsal surface of arista (character 9), as also seen in *Pyrellia*, *Mitroplatia*, and *Myiophaea*; a costal vein that is ventrally setulose up to the subcostal vein (character 68), as also seen in *Mesembrina*, some *Neomyia*, and *Pyrellia*; the M vein bent forward to the R_{4+5} vein forming an angled curve (character 81), as also seen in some *Neomyia*; hypandrium that is not enlarged at the anterior margin (character 99), as also seen in *Mesembrina*, some *Polietes*, *Myiophaea*, and some *Morellia*; the lack of an anterior intergonopodal projection at the inferior base of the aedeagus apodeme (character 101), this projection is found in all remaining Muscini and in the outgroup Muscidae, except for *H. irritans* and *S. calcitrans* (Stomoxyini); and trapezoidal distiphallus (character 102), whereas all remaining Muscini examined have a campanulate (bell-shaped, triangular) distiphallus.

Including approximately 67 species, the genus *Musca* is present in all biogeographical regions, although its occurrence in Nearctic and Neotropical regions is a result of recent dispersion (Krafsur & Moon, 1997). Its classification has been addressed by several authors and, consequently, has suffered splitting classifications according to a number of different systems. For example, Malloch (1925, 1928, 1929) divided *Musca* into several small genera, using names previously proposed by earlier authors. Based only on chaetotaxy, his classification recognized eight genera: *Musca s.s.*; *Byomya* Robineau-Desvoidy, 1830; *Plaxemya* Robineau-Desvoidy, 1830; *Eumusca* Townsend, 1911; *Viviparomusca* Townsend, 1915; *Philaematomyia* Austen, 1909; *Ptilolepis* Bezzi, 1921 and *Lissos-*

Figure 55. Strict consensus of three most parsimonious cladograms with implied weighting ($k = 3$), excluding characters of the pattern of wing spotting (characters 62–66), with unambiguous optimization.

terna Bezzi, 1923. The 11 species of *Musca* included in the analysis are representative of six genera as shown in Figure 53A. The monotypic genera *Philaematomyia* (with *Musca crassirostris* Stein, 1903) and *Ptilolepis* (with *Musca inferior* Stein, 1909) were not represented.

This analysis concurred with some relationships of Malloch's classification proposal, but more importantly showed that his was a fragile classification, the division of which does not reflect natural groups. The clade *Musca alpesa* + *Musca larvipara* supports *Viviparomusca* and is closely related to the nonmonophyletic *Eumusca*. Within the three cladograms from IW analysis ($k = 3$) there is evidence for a close relationship of either *Musca fergusoni* (Fig. 53B) or *Musca autumnalis* and *Musca lusoria* (Fig. 53C) with the clade *M. alpesa* + *M. larvipara*. *Lissosterna* and *Musca s.s.* are monotypic and their representatives (*Musca albina* and *Musca domestica*, respectively) form a polytomic clade together with *Musca vetustissima* (representing *Byomya*). This clade is related to *Musca lasiophthalma* and *Musca cassara*, representing *Plaxemya* and *Byomya*, respectively. Besides *M. vetustissima* and *M. cassara*, the third representative of *Byomya* in the analysis, *Musca pattoni*, was placed either in a basal polytomy (Fig. 53C, D) or as sister group of *Musca s.l.* (Fig. 53B), showing that *Byomya* is not a natural group.

Patton (1932) considered Malloch's classification as fragile, particularly because it is based on characters from chaetotaxy and is not concerned about the structure of the male abdominal terminalia. Based on the male abdominal terminalia (primarily, the shape of the paramere, and secondarily, the shape of the epiphallus, cercal plate and fifth sternite), Patton (1932) proposed the division of *Musca* into three species groups: *domestica* (with the simplest form of genitalia), *sorbens* (with the intermediate form) and *lusoria* (with the most specialized form). These three groups were represented in the analysis (Fig. 53A). Both *M. cassara* and *M. lasiophthalma* were interpreted here as belonging to the *domestica* group; their terminalia agrees with the group description of Patton (1932), although *M. lasiophthalma* has some elements from the genitalia described for the *sorbens* group.

In contrast to Malloch's system, our study more strongly corroborated Patton's system (Fig. 53A–D). The primary character, the paramere shape, is character number 100, where a simple and developed paramere (state 0) is the form commonly present in all the remaining Muscini, whereas a hook-shaped and developed paramere (state 1) is found in *M. pattoni* and in the clade comprising *M. autumnalis*, *M. fergusoni*, *M. lusoria*, *M. alpesa* and *M. larvipara* (also present in *Hennigmyia* by convergence). This clade supports the *lusoria* group, except for the position of *M. pattoni*. Finally, a reduced and button-shaped paramere (state 2) occurs in the clade with *M. cassara*, *M.*

lasiophthalma, *M. vetustissima*, *M. albina*, and *M. domestica*, all belonging to the *domestica* group, with the exception of *M. albina* from the *sorbens* group. Our results support the division of *Musca* into two species groups: the *lusoria* and *domestica* groups. The *sorbens* group seems to fall within the *domestica* group, which demonstrates its intermediate nature (as originally emphasized by Patton, 1932), and is interpreted here as a morphological variation within the *domestica* group.

The secondary characters of Patton's system are in epiphallus shape. In the *domestica* group, the epiphallus is slightly concave (in lateral view) and narrow (in dorsal view); in the *sorbens* group, it is also slightly concave but widened (with no bifurcation, and at most with a widening at the apex); whereas, in the *lusoria* group, it is strongly concave (hook-shaped, see Fig. 41) and is widened and distinctly bifurcate. These morphological variations observed in the shape of the epiphallus were not explored in the present analysis and we feel that they represent modification in shape and size through a continuous gradient, which is difficult to code for use as a phylogenetic character. Perhaps, because of their continuous variation, they were considered secondary characters by Patton (1932).

The remaining genera (*Pyrellia*, *Curranosia*, *Sarcopromusca*, *Eudasyphora*, *Dasyphora*, and *Neomyia*) are grouped in an apical clade (Fig. 50) by setulae on the posterior supra-squamal ridge (character 34), three posterior katepisternal setae (character 42, *acctran* optimization; but several *Neomyia* with two setae), ventral setulae on subcostal sclerite (character 56; but bare in *Sarcorpromusca*), apical portion of stem-vein setulose on ventral face (character 73), mid tibia with a strong submedian seta on posteroventral to ventral surface (character 89), and a distinct inward projection at the median-posterior portion of surstylus (character 97; absent in *Dasyphora* and some *Eudasyphora*). Of the above, character 89 is important because of its presence in the entire clade, although it also appears independently in *Pyrellina* + *Polietina*. This large clade supports Skidmore (1985), who proposed the affinity among *Neomyia*, *Eudasyphora*, and part of *Pyrellia*, but despite that *Neomyia* also shares larval characters with *Musca*.

Neomyia is strongly supported as a monophyletic group. Malloch (1923) stressed the setulae on the posterior supra-squamal ridge to distinguish it from *Pyrellia*. Later Curran (1935) added setulae on the greater ampulla as a character exclusive to *Neomyia*. In fact, the setulose greater ampulla (character 37) is exclusive to *Neomyia*. On the other hand, the setulose posterior supra-squamal ridge (character 34) segregates *Neomyia* from *Pyrellia*, whereas it is present in *Curranosia* and *Sarcopromusca* (see the discussion below). *Neomyia* is also supported by the following characters: (1) setulose meron (character 46), present

by convergence in *Pyrellina*, *Polietina*, some *Musca*, and in the clade bearing *Pyrellia*, *Sarcopromusca*, *Eudasyphora*, and *Dasyphora*; (2) fine setulae on the accessory sclerite at the base of the upper calypter (character 60), a character exclusive to *Neomyia* and shared by all studied species; (3) setulose anterior supra-squamal ridge (character 33, *acctran* optimization), also present in *Deltotus*, *Polietina*, *Xenomorellia*, and in some *Musca*; (4) strongly sclerotized spinules at the apex of distiphallus (character 103, *acctran* optimization), the character previously used by Paterson (1957) to segregate *Curranosia* from *Neomyia*, but is not uniquely derived as it was regarded similar to the condition found in some Azeliini (Savage & Wheeler, 2004); and (5) semicircular cerci on the female (character 110, *deltran* optimization), also present by convergence in *Musca* and some species of *Morellia* (see comments in the 'List of characters').

Earlier studies that split *Neomyia* into small groups were partially supported by our results. Van Emden (1939) divided *Neomyia* in three groupings, which were later elevated to subgenera by Peris (1967): *Neomyia s.s.*, *Pseudogymnosoma* Townsend, 1918, and *Lasiopyrellia* Villeneuve, 1913. We included here species that represented those three subgenera: *Neomyia cornicina*, *Neomyia dubia*, *Neomyia gavisa*, *Neomyia sperata*, *Neomyia australis*, *Neomyia macrops*, *Neomyia lauta*, *Neomyia laxifrons*, *Neomyia timorensis*, *Neomyia viridescens* (in *Neomyia s.s*); *Neomyia nudissima*, and *Neomyia limbata* (in *Pseudogymnosoma*); and *Neomyia rhingiaeformis* (in *Lasiopyrellia*). As a result, at least *Pseudogymnosoma* is monophyletic, whereas *Neomyia s.s.* is clearly polyphyletic. The status of *Lasiopyrellia*, represented only by *N. rhingiaeformis*, is still uncertain, yet its close relationship with *Neomyia s.s.* (except for some basal species: *N. australis* and *N. laxifrons*) supports Peris (1967). Also, the basal position of *N. australis* supports Pont (1973), who argued that this species should be isolated from all other *Neomyia*.

Paterson (1957) described *Curranosia* after Curran (1935) observed that two African *Neomyia* species have a bare greater ampulla, and so should be removed from the genus. Our analysis (Fig. 50) supported the separation of *Curranosia* from *Neomyia*, but without supporting its monophyly and with the genus divided into two groups: *Curranosia spekei* (type species) and *Curranosia gemma* + *Curranosia prima*. Zielke (1973, 1974) recognized at least one species group within the genus (the *spekei* group, stated as *pilarara* group), and he distinguished the *spekei* group in contrast to an unnamed group of species including *C. gemma* and *C. prima*. The main difference distinguishing those groups, and which places the *spekei* group more closely related to *Pyrellia*, *Sarcopromusca*, and *Dasyphora s.l.*, is the marginal spined process on the cercal plate

(character 96) and the loss of anterior ventral setulae on the subcostal sclerite (character 58). The group formed by *C. gemma* and *C. prima*, named herein as the *gemma* group, lacks the marginal spined process, and the subcostal sclerite is still anteroventrally setulose. Furthermore, the cercal plate is structurally different between the two groups, as emphasized by Zielke (1973, 1974). The *gemma* group, indicated here as a genus-ranked taxon, will be properly described in a future study. It was provisionally kept in *Curranosia* as *sedis mutabilis*. The composition of each species group is presented below in the 'Summary of taxonomic changes proposed'.

Sarcopromusca is a Neotropical genus with an as yet dubious placement, with its two species frequently allocated into *Morellia*, *Pyrellia*, or *Neomyia* (see de Carvalho *et al.*, 2005). Pamplona (1992) revalidated the genus retiring it from the synonymy proposed by Pont (1972) under *Morellia* (in agreement with Hennig, 1965). Our cladistic analysis here supports the validity of *Sarcopromusca*.

Eudasyphora comprises a paraphyletic group that includes *Dasyphora* as an apical clade. This clade has several characters that separate it from *Eudasyphora*, but *Eudasyphora* per se is not a natural group if it does not include the *Dasyphora* species. Skidmore (1985) stressed the differences in larval morphology and habits of the two genera, but also commented that *Dasyphora* would be closely related to *Musca*. Moreover, *Eudasyphora flavipes* (type species of *Rypellia* Malloch, 1931, =*Eudasyphora*) is placed at the base of the clade *Eudasyphora* + *Dasyphora*. Therefore, we propose a new synonymy between *Eudasyphora* Townsend, 1911 and *Dasyphora* Robineau-Desvoidy, 1830. In addition, we present a classification of *Dasyphora s.l.* divided into three subgenera: *Dasyphora s.s.*, *Eudasyphora*, and *Rypellia* (see below the 'Summary of the taxonomic changes proposed'). The analysis supports the monophyly of *Dasyphora s.s.* and probably *Rypellia* as well.

Rypellia is a sister group to *Eudasyphora* + *Dasyphora s.s.*, and it may be elevated to generic status, as Hennig (1964b) suggested. In the phylogenetic study performed by Cuny (1980), *Eudasyphora* was distinctly divided into two clades ranked as subgenera: *Eudasyphora s.s.* and *Rypellia*. *Eudasyphora* was described by Townsend (1911) as gathering a group of species placed partly in *Dasyphora s.s.*, and partly in *Pyrellia*. That genus, according to Cuny (1980), was based on characters such as the glossy abdomen (also in *Pyrellia*) and the almost entirely setulose R_{4+5} vein (also in *Dasyphora s.s.*), and the female terminalia with some modifications adapted to larviparity in *Dasyphora s.s.*, unlike the oviparous *Eudasyphora* and *Pyrellia*. Zimin (1951) and Hennig (1964b) considered Townsend's splitting unjustified and then placed all the species of *Eudasyphora* in *Dasyphora*. Cuny (1980)

argued about the sister-group relationship between *Eudasyphora* and *Pyrellia* based on characters from male cercal plate, namely, the outer lower lobe being longer than the inner, and the inwards inner lobe. Those two characters were examined here but not included in the analysis as they are clearly continuous quantitative characters (e.g. with overlapping character states). There are several taxa with intermediate forms and hence coding is difficult for these characters. For example, in *Pyrellia* and *Eudasyphora*, the outer lower lobe is distinctly more developed than the inner lobe (which gives an M-shaped appearance to the cercal plate, as it presents distinct downwardly orientated lateral processes; see Fig. 38), which is also the case in *Sarcopromusca* and *M. micans*. Also, the outer lower lobe is either undeveloped or as developed as the inner lobe, states that are found widely within the Muscini (see Figs 32, 33, 35). Between these two are several intermediate forms causing doubtful coding. For example, *Dasyphora* (Fig. 37) resembles *Eudasyphora* (Fig. 38), with respect to the outer lobes, which close inwardly and concavely, and the outer lobes are as developed as the inner lobes. Yet, the form is different from that present in either *Musca* (Fig. 35) or *Polietina* (Fig. 32). Another interesting example is *Curranosia spekei* (see Zielke, 1971: fig. 16A,B) in which an intermediate form occurs between *Polietina* and *Eudasyphora*, but is more similar to *Polietina* in that it is somewhat flattened, unlike the 'capsulate' (concave) shape of *Dasyphora*, which is distinctly more similar to *Eudasyphora*. Also, in *Morellia (Trichomorellia)* (see Pamplona, 1983: figs 10, 15) an intermediate form exists between *Polietina* and *Eudasyphora*, but differs from *C. spekei*. Other interesting forms are present in most species of *Neomyia* (see Fig. 36), in which the outer lobe is developed forming a pronounced process, but the inner lobe is also developed and conspicuous. Yet, the cercal plate of *Neomyia* has a flattened, not capsulate, shape. In *Morellia (Parapyrellia)* (see Albuquerque & Lopes, 1979: fig. 4), instead of the outer lobe forming a concave process, it forms a digitiform process that is orientated inwardly. This digitiform process also occurs (but is reduced) in *Biopyrellia* and *M. (M.) nigrisquama*.

Similarly, the inward inner lobe cited by Cuny (1980) also represents a continuous quantitative character. It is more conspicuous in *Pyrellia* and *Dasyphora s.l.* (Figs 37, 38), and less conspicuous in *Curranosia* and *Sarcopromusca* (see illustrations in Pamplona, 1992). The inner lobe of *Neomyia* (Fig. 36) is also questionable because it is very developed and under a different degree of inward curvature, although not so inward as in *Eudasyphora* (Fig. 38). This shape variation was not included in the analysis and, unless it is fully understood (including all transformation steps), it will continue posing problems to the character coding.

Contrary to Cuny (1980), the sister-group relationship between *Pyrellia* and *Eudasyphora* was not supported here, which indicated that *Pyrellia* should be more basal. However, we found species relationships within *Eudasyphora* similar to those obtained by Cuny (1980) (Fig. 50). The main difference was regarding the position of *Dasyphora s.s.* as apical to *Rypellia* and *Eudasyphora*.

Dasyphoromima was originally described by Zimin (1951) as a subgenus of *Pyrellia* and has been placed in a variety of locations and ranks by subsequent authors: as genus by Peris & Llorente (1963); as synonym of *Dasyphora* but with subgeneric status uncertain by Hennig (1964b); as subgenus of *Pyrellia* by Cuny (1980); and as synonym of *Eudasyphora* by Pont (1986). The major problem is that its type species (*Pyrellia pavlovskyi* Zimin, 1951) is known only from the female holotype and was not examined by anyone besides Zimin (1951) (reported by Peris & Llorente, 1963 and Hennig (1964b). Peris & Llorente (1963) described *Dasyphoromima occidentalis* based on only one male, which was posteriorly recognized as an erroneously identified male of *Eudasyphora cyanicolor* (Peris, 1990). Previously, Hennig (1965) commented on the dubious relationship between one European species (*D. occidentalis*) and another from far eastern Russia (*P. pavlovskyi*). The placement of *P. pavlovskyi*, here assumed conservatively in the subgenus *Eudasyphora* (following the most recent placement, given by Pont, 1986), will only be clarified after a detailed study of specimens of both sexes.

A cladogram summarizing the intergeneric relationships is presented in Fig. 56. Below, a summary of the taxonomic changes proposed in this study is presented, followed by the new classification proposal of Muscini, according to the morphology-based phylogenetic hypothesis herein discussed. In the new classification 18 genera are recognized in the tribe Muscini.

SUMMARY OF THE TAXONOMIC CHANGES PROPOSED
MORELLIA ROBINEAU-DESVOIDY, 1830

Subgenus *Morellia s.s.*

Group *hortorum*: *Morellia (Morellia) hortorum* (type species), *M. (M.) nigrisquama*, *M. (M.) podagrica*.

Group *basalis*: *M. (M.) basalis*, *M. (M.) paulistensis*.

Incertae sedis (doubtful species group placement) – *M. (M.) micans*, *M. (M.) aenescens*, *M. (M.) calyptrata*, and other species not examined.

Subgenus *Parapyrellia* Townsend, 1915 **syn. nov., stat. nov.** Species included: *Morellia (Parapyrellia) maculipennis* (Macquart, 1846) (type species) **comb. nov.**; *M. (P.) oportuna* (Albuquerque & Lopes, 1979) **comb. nov.**; *M. (P.) humeralis* (Stein, 1918).
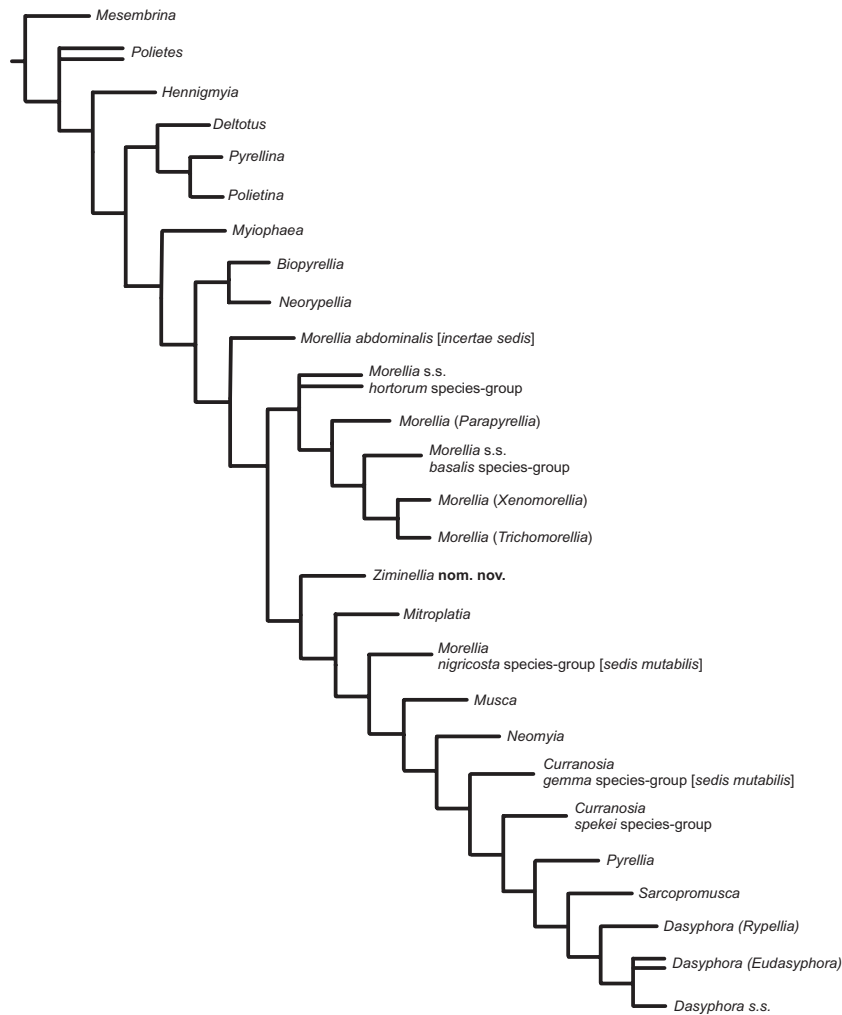
Figure 56. Cladogram summarizing the phylogenetic relationships of Muscini taxa.

Subgenus *Trichomorellia* Stein, 1918 **syn. nov., stat. nov.** Species included: *Morellia* (*Trichomorellia*) *trichops* (Malloch, 1923) (type species) **comb. nov.**, *M.* (*T.*) *benoisti* (Pamplona, 1983) **comb. nov.**; *M.* (*T.*) *callidimera* (Bigot, 1887) **comb. nov.** (with *fulvipes* Bigot, 1887 as junior synonym; see Pont, 2000: 14); *M.* (*T.*) *flavipalpis* (Pamplona, 1983) **comb. nov.**; *M.* (*T.*) *nigritibia* (Snyder, 1949) **comb. nov.**; *M.* (*T.*) *saphirina* (Séguy, 1935) **comb. nov.**; *M.* (*T.*) *seguyi* (Pamplona, 1983) **comb. nov.**; *M.* (*T.*) *spinifera* (Wulp, 1883) **comb. nov.**

Subgenus *Xenomorellia* Malloch, 1923 **syn. nov., stat. nov.** Species included: *Morellia* (*Xenomorellia*) *holti* (Malloch, 1923) (type species) **comb. nov.**; *M.* (*X.*) *montanhesa* (Albuquerque, 1952) **comb. nov.**

Incertae sedis – *M. abdominalis*.

Sedis mutabilis (genus-ranked taxon) – group *nigricosta*: *M. nigricosta* Hough, 1900, *M. xanthoptera* Pamplona, 1986.

ZIMINELLIA NIHEI & DE CARVALHO **NOM. NOV.**

Ziminellia Nihei & de Carvalho, **nom. nov.** *Dasysterna* Zimin, 1951 (preocc. *Dasysterna* Dejean, 1833). Species included: *Ziminellia simplex* (Loew, 1857) (type species) **comb. nov.**, *Z. hortensia* (Wiedemann, 1824) **comb. nov.**, *Z. asetosa* (Baranoff, 1925) **comb. nov.**

DASYPHORA ROBINEAU-DESVOIDY, 1830

Subgenus *Dasyphora s.s.* Species included: *Dasyphora* (*Dasyphora*) *pratorum* (Meigen, 1826) (type species); *D.* (*D.*) *albofasciata* (Macquart, 1839); *D.* (*D.*) *apicotaeniata* Ni, 1982; *D.* (*D.*) *asiatica* Zimin, 1947; *D.* (*D.*) *gansuensis* Ni, 1982; *D.* (*D.*) *gussakovskii* Zimin, 1947; *D.* (*D.*) *himalayensis* Pont, 1972; *D.* (*D.*) *latifrons* Zimin, 1951; *D.* (*D.*) *meridionalis* Zimin, 1951; *D.* (*D.*) *paraversicolor* Zimin, 1951; *D.* (*D.*) *penicillata* (Egger, 1865); *D.* (*D.*) *quadrisetosa* Zimin, 1951; *D.* (*D.*) *setitibia* Zimin, 1951; *D.* (*D.*) *similis* Zimin, 1951; *D.* (*D.*)

stackelbergiana Sychevskaya, 1967; *D. (D.) tianshanensis* Ni, 1982; *D. (D.) trichosterna* Zimin, 1951.

Subgenus *Eudasyphora* Townsend, 1911 **syn. nov., stat. nov.** Species included: *Dasyphora (Eudasyphora) cyanella* (Meigen, 1826) (type species) **comb. nov.**; *D. (E.) canadiana* (Cuny, 1980) **comb. nov.**; *D. (E.) cordilleriana* (Cuny, 1980) **comb. nov.**; *D. (E.) cyanicolor* (Zetterstedt, 1845) **comb. nov.**; *D. (E.) kempi* (Emden, 1965) **comb. nov.**; *D. (E.) pavlovskyi* (Zimin, 1951) **comb. nov.**; *D. (E.) setosa* (Loew, 1869) **comb. nov.**; *D. (E.) tateyamensis* (Shinonaga, 1976) **comb. nov.**; *D. (E.) zimini* Hennig, 1963 **comb. nov.;** *D. (E.) dasyprosterna* (Fan & Qian, 1992) **comb. nov.**

Subgenus *Rypellia* Malloch, 1931 **syn. nov., stat. nov.** Species included: *Dasyphora (Rypellia) flavipes* (Malloch, 1931) (type species) **comb. nov.**; *D. (R.) dissimilis* (Malloch, 1932) **comb. nov.**; *D. (R.) flavipennis* (Emden, 1965) **comb. nov.**; *D. (R.) montana* (Malloch, 1932) **comb. nov.**; *D. (R.) semilutea* (Malloch, 1923) **comb. nov.**

CURRANOSIA PATERSON, 1957

Group *spekei*: *Curranosia spekei* (Jaennicke, 1867) (type species), *C. congoensis* Zielke, 1974, *C. vockerothi* Zielke, 1973.

Sedis mutabilis (genus-ranked taxon) – group *gemma*: *C. gemma* (Bigot, 1878), *C. prima* (Curran, 1935), *C. cerciformis* Zielke, 1971, *C. cooksoni* Zielke, 1971.

GENERA OF MUSCINI PROPOSED IN THE NEW CLASSIFICATION

Biopyrellia Townsend, 1932
Curranosia Paterson, 1957
  spekei group
  gemma group (genus-ranked taxon, to be described)
Dasyphora Robineau-Desvoidy, 1830
  Subgenus *Dasyphora s.s.*
  Subgenus *Eudasyphora* Townsend, 1911 **syn. nov., stat. nov.**
  Subgenus *Rypellia* Malloch, 1931 **syn. nov., stat. nov.**
Deltotus Séguy, 1935
Hennigmyia Peris, 1967
Mesembrina Meigen, 1826
Mitroplatia Enderlein, 1935
Morellia Robineau-Desvoidy, 1830
  Subgenus *Morellia s.s.*
  Subgenus *Parapyrellia* Townsend, 1915 **syn. nov., stat. nov.**
  Subgenus *Trichomorellia* Stein, 1918 **syn. nov., stat. nov.**
  Subgenus *Xenomorellia* Malloch, 1923 **syn. nov., stat. nov.**
  nigricosta group (genus-ranked taxon, to be described)

Musca Linnaeus, 1758
Myiophaea Enderlein, 1935
Neomyia Walker, 1859
Neorypellia Pont, 1972
Polietes Rondani, 1866
Polietina Schnabl & Dziedzicki, 1911
Pyrellia Robineau-Desvoidy, 1830
Pyrellina Malloch, 1923
Sarcopromusca Townsend, 1927
Ziminellia Nihei & de Carvalho, **nom. nov.**

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