Phylogeny of genus *Wyeomyia* (Diptera: Culicidae) inferred from morphological and allozyme data

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Abstract—Phylogenetic relationships within the genus *Wyeomyia* Theobald are presented, based on a cladistic analysis of 88 morphological characters (from adults, larvae, and pupae) of 38 named species and 1 unnamed species and 46 allozyme markers from a subset of 19 of these species. Two taxa are used as outgroup (*Sabethes aurescens* Lutz and *Limatus durhami* Theobald). The analysis indicates that, as currently defined, the genus *Wyeomyia* is not a monophyletic lineage: firstly, the genus *Onirion* Peyton and Harbach is nested within the genus *Wyeomyia*, and secondly, the subgenus *Phoniomyia* Theobald is a monophyletic lineage outside the genus *Wyeomyia*. Our results also demonstrate that the subgenera *Cruzmyia* Lane and Cerqueira, *Decamyia* Dyar, *Dendromyia* Theobald, *Spilonympha* Motta and Lourenço-de-Oliveira, and *Prosopolepis* Lutz are monophyletic lineages nested within the genus *Wyeomyia*. *Triamyia* Dyar is resurrected as a subgenus of *Wyeomyia* to include *W. aporonoma* Dyar and Knab and *W. staminifera* Lourenço-de-Oliveira, Motta, and Castro. The subgenus *Miamyia* Dyar is resurrected to include seven species: *W. codiocampa* Dyar and Knab, *W. lutzi* (Costa Lima), *W. limai* Lane and Cerqueira, *W. serrata* (Lutz), *W. hosautos* Dyar and Knab, *W. oblita* (Lutz), and *W. sabethea* Lane and Cerqueira.

Résumé—Nous présentons les relations phylogénétiques au sein du genre *Wyeomyia* Theobald d'après une analyse cladistique de 88 caractères morphologiques (des adultes, des larves et des nymphes) chez 38 espèces nominales et une espèce inédite, ainsi que de 46 marqueurs allozymes chez un sous-ensemble de 19 de ces espèces. Deux taxons (*Sabethes aurescens* Lutz et *Limatus durhami* Theobald) servent de groupes externes. L'analyse indique que, dans sa définition courante, le genre *Wyeomyia* ne forme pas une lignée monophylétique: (*a*) le genre *Onirion* Peyton et Harbach s'emboîte dans le genre *Wyeomyia* et (*b*) le sous-genre *Phoniomyia* Theobald est une lignée monophylétique qui se situe hors du genre *Wyeomyia*. Nos résultats démontrent aussi que les sous-genres *Cruzmyia* Lane et Cerqueira, *Decamyia* Dyar, *Dendromyia* Theobald, *Spilonympha* Motta et Lourenço-de-Oliveira et *Prosopolepis* Lutz sont des lignées monophylétiques au sein du genre *Wyeomyia*. Nous tirons de la synonymie le nom de *Triamyia* Dyar pour servir de sous-genre de *Wyeomyia* et regrouper *W. aporonoma* Dyar et Knab et *W. staminifera* Lourenço-de-Oliveira, Motta et Castro, ainsi que le nom du sous-genre *Miamyia* Dyar pour inclure 7 espèces: *W. codiocampa* Dyar et Knab, *W. lutzi* (Costa Lima), *W. limai* Lane et Cerqueira, *W. serrata* (Lutz), *W. hosautos* Dyar et Knab, *W. oblita* (Lutz) et *W. sabethea* Lane et Cerqueira.

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Introduction

The tribe Sabethini not only contains some of the most striking mosquitoes among the Neotropical Diptera: Culicidae, but is also the group that is most diverse in morphology and behavior. The tribe comprises 13 genera: 8 are restricted to the Neotropical region, 1 is found

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in both the Neotropical and Neartic regions, 2 are from the Australian and Oriental regions, 1 is restricted to the Australian region, and 1 is found in the Ethiopian/Oriental region. A recent investigation of cladistic relationships within the Sabethini was done by Judd (1996), who demonstrated that the Sabethini was a monophyletic group but the genera *Wyeomyia* Theobald, *Tripteroides* Giles, and *Runchomyia* Theobald were not. In an extensive morphological cladistic analysis within Culicidae, Harbach and Kitching (1998) corroborated the monophyly of the Sabethini.

Wyeomyia is the largest of all the Neotropical genera of Sabethini. It includes species that are sylvatic and characterized by phytotelmatic immature stages. Mosquitoes belonging to the genus *Wyeomyia* collected in tropical rain forests have been found to be infected with several arboviruses: Iaco and Maguari viruses were isolated from *Wyeomyia* sp., Taiassui and Tucunduba viruses from *Wyeomyia* sp. and *Wyeomyia aporonoma*, and Una and Triniti viruses from *Wyeomyia* sp. (Hervé *et al.* 1986; Vasconcelos *et al.* 2001).

The genus *Wyeomyia* includes more than 100 species, currently comprising 15 subgenera (Knight and Stone 1977; Judd 1998*a*; Motta and Lourenço-de-Oliveira 2005). However, few mosquito taxa are as poorly studied as this genus. Until recently, the internal classification of *Wyeomyia* was based mainly on the revision of Lane and Cerqueira (1942). The name *Wyeomyia* was proposed by Theobald (1901) to include 7 species; however, this description was based on adult females only and was consequently brief and inconsistent. Dyar (1928) hypothesized a new classification for *Wyeomyia*, proposing four genera and 19 subgenera that included 66 species. Subsequently, Edwards (1932) restricted Dyar's four genera to *Wyeomyia*, which was subdivided into 4 subgenera. Later, Lane (1953) proposed that *Wyeomyia* comprised 7 subgenera.

The scant knowledge of immature stages and the absence of reliable characters in the adult stage confuse the classification of *Wyeomyia*. Belkin *et al.* (1970) noted that the organization of the genus was unnatural and recommended an exhaustive study of the immature stages to reveal monophyletic lines. Recent studies employing morphological characters from all life stages established some small and better defined groups, the subgenera *Caenomyiella* and *Decamyia* (Harbach and Peyton 1990*a*), *Exallomyia* (Harbach and Peyton 1992), *Prosopolepis* (Lourenço-de-Oliveira *et al.* 1999), *Dendromyia* (Motta and Lourenço-de-Oliveira 2000), *Spilonympha* (Motta and Lourenço-de-Oliveira 2005), and *Hystatomyia* (Judd 1998*a*). However, the subgeneric boundary of *Wyeomyia*, the largest subgenus, remains unclear because there are conflicting definitions, owing to the use of inconsistent morphological characters. Moreover, numerous species previously included in *Dendromyia* are currently without subgeneric placement (Motta and Lourenço-de-Oliveira 2000). Except for Judd's study on the Sabethini (Judd 1996, 1998*a*, 1998*b*), nearly all hypotheses concerning subgenera of *Wyeomyia* have been formulated without the support of a phylogenetic analysis: neither the monophyly of the genus nor relationships among subgenera have been tested using phylogenetic methodology. Interestingly, the results of Judd's (1996) cladistic analysis suggest that the genus *Wyeomyia*, as traditionally defined, is paraphyletic because it does not include the genera *Phoniomyia* Theobald and *Limatus* Theobald; the author recovered these two genera nested within the *Wyeomyia* clade. The main objectives of the present study are to test the monophyly of the genus *Wyeomyia* as currently defined by Judd (1998*a*) and Harbach and Kitching (1998) and to estimate the phylogenetic relationships within the genus.

Materials and methods

Selection of taxa

Morphological analysis

Using morphology, phylogenetic analyses were conducted for 41 species (Table 1). The ingroup consisted of 38 named species and 1 unnamed species of the genus *Wyeomyia*, representing 11 of 15 currently recognized subgenera. Nine species are without subgeneric assignment. We selected at least 2 species of each of the following subgenera: *Cruzmyia*, *Decamyia*, *Dendromyia*, *Phoniomyia*, *Spilonympha*, and *Wyeomyia*. We examined only 1 species of the subgenera *Dodecamyia*, *Menolepis*, and *Prosopolepis* because they are monotypic, and the subgenus *Exallomyia* for which only 1 species is available. Considering the availability of the three life stages (fourth-instar larva, pupa, and adult) for the subgenus *Antunesmyia*, *W. alani* was included because it is the only species for which the immature stages are described. The outgroup included *Sabethes aurescens* and *Limatus durhami*, which were

Table 1. The 41 species examined in the morphological analysis.

Genus	Subgenus	Species
Wyeomyia	*Spilonympha*	*W. aningae** Motta and Lourenço–de–Oliveira
		*W. mystes** Dyar
		*W. bourrouli** (Lutz)
		W. forcipenis Lourenço-de-Oliveira and Silva
		*W. airosai** Lane and Cerqueira
		*W. finlayi** Lane and Cerqueira
		W. howardi Lane and Cerqueira
	Dendromyia	*W. ypsipola** Dyar
		*W. testei** Sevenet and Abonnenc
		W. luteoventralis Theobald
		W. jocosa (Dyar and Knab)
		W. complosa (Dyar)
	Decamyia	*W. ulocoma* (Theobald)
		W. felicia (Dyar and Nunez-Tovar)
	Antunesmyia	*W. alani* Lane and Cerqueira
	Prosopolepis	*W. confusa* (Lutz)
	Dodecamyia	*W. aphobema** (Dyar)
	Cruzmyia	*W. forattinii* Clastrier
		W. dyari Lane and Cerqueira
	Exallomyia	*W. tarsata* Lane and Cerqueira
	Wyeomyia	*W. lutzi** (Costa Lima)
		W. sabethea Lane and Cerqueira
		*W. oblita** (Lutz)
		*W. arthrostigma** (Lutz)
		*W. medioalbipes** Lutz
		W. limai Lane and Cerqueira
	Menolepis	*W. leucostigma** Lutz
	Without subgeneric placement	*W. melanocephala** Dyar and Knab
		W. surinamensis Bruijning
		W. flui Bonne-Wepster and Bonne
		Wyeomyia sp. 4
		W. argenteorostris Bonne-Wepster and Bonne
		*W. aporonoma** Dyar and Knab
		W. staminifera Lourenço-de-Oliveira, Motta, and Castro
		*W. negrensis** Gordon and Evans
		W. chalcocephala Dyar and Knab
	Phoniomyia	*W. palmata** Lane and Cerqueira
		W. edwardsi Lane and Cerqueira
Onirion		*O. personatum** (Lutz)
Sabethes		*S. aurescens* Theobald
Limatus		*L. durhami* Theobald

Note: Species for which data from both morphological and allozyme analyses were available are indicated by an asterisk.

reconstructed as sister groups of the genus *Wyeomyia* in Harbach and Kitching's (1998) study. *Onirion personatum* was also included in the analysis to evaluate its phylogenetic relationship with the genus *Wyeomyia*.

The specimens examined for this study were from the collections of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; the Faculdade de Saúde Pública, Universidade de São Paulo, São Paulo, Brazil; and the National Museum of Natural History, Washington, D.C., United States of America.

Allozyme analysis

An allozyme study was conducted for 19 species (Table 1) because fresh specimens were not

Table 2. Data matrix for 41 taxa and 134 characters used in this analysis.

Species/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
S. aurescens	3	1	1	1	0	1	1	0	0	1	1	3	0	0	0
L. durhami	3	0	1	0	0	0	1	0	0	0	1	2	0	0	0
W. edwardsi	1	0	1	1	1	3	0	0	0	0	0	1	1	0	1
W. howardi	2	0	0	1	0	0	1	1	0	0	1	1	0	0	0
W. luteoventralis	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. jocosa	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. complosa	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. ulocoma	2	0	0	1	0	0	1	0	0	?	1	1	0	0	0
W. felicia	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. alani	2	0	0	1	0	4	1	1	0	0	1	2	0	0	0
W. confusa	0	0	—	—	—	2	—	0	1	0	1	1	0	0	0
W. forattinii	1	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. dyari	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. tarsata	1	0	1	1	0	3	1	2	0	0	1	1	0	1	0
W. sabethea	3	0	1	1	0	4	1	1	0	0	1	1	0	0	0
W. limai	2	0	0	1	0	4	1	2	0	0	1	1	0	0	0
W. surinamensis	2	0	1	1	0	1	1	0	0	0	1	1	0	0	0
W. flui	2	0	1	1	0	1	1	0	0	0	1	1	0	0	0
W. sp. 4	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. argenteorostris	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. staminifera	2	0	1	1	0	0	1	1	0	0	1	1	0	0	0
W. chalcocephala	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. palmata	1	0	1	1	1	3	0	0	0	0	0	1	1	0	1
O. personatum	2	0	1	1	0	0	1	0	0	1	1	0	0	0	0
W. aningae	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. mystes	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. bourrouli	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. forcipenis	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. airosai	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. finlayi	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. ypsipola	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. testei	3	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. aphobema	1	0	1	1	0	3	1	0	0	0	1	1	0	0	0
W. lutzi	2	0	0	1	0	4	1	2	0	0	1	1	0	0	0
W. oblita	2	0	1	1	0	4	1	2	0	0	1	1	0	0	0
W. arthrostigma	2	0	1	1	0	1	1	0	0	0	1	1	0	0	0
W. medioalbipes	2	0	1	1	0	1	1	0	0	0	1	1	0	0	0
W. leucostigma	1	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. melanocephala	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0
W. aporonoma	2	0	1	1	0	0	1	1	0	0	1	1	0	0	0
W. negrensis	2	0	1	1	0	0	1	0	0	0	1	1	0	0	0

available for all the 41 species used in the morphological analysis. All mosquitoes examined were collected as either larvae or adults in separate localities in the Brazilian states of Rondônia, Amazonas, Mato Grosso, Bahia, and Rio de Janeiro. We included in the analysis only the female adult stage, and the number of assayed individuals varied among species (Table 4).

Agarose gels were stained for 23 different enzymes, of which only 10 (coded by 11 loci) gave interpretable and reproducible bands. The enzymes tested were malate dehydrogenase (MDH), EC 1.1.1.37; malic enzyme (ME), EC 1.1.1.40; phosphoglucose isomerase (PGI), EC 5.3.1.9; phosphoglucomutase (GM), EC 5.4.2.2; isocitrate dehydrogenase (IDH), EC 1.1.1.42; hexokinase (K), EC 2.7.1.1; adenylate kinase (AK), EC 2.7.4.3; glycerol-3-phosphate dehydrogenase (αPGD), EC 1.1.1.8; fumarate hydratase (FUM), EC 4.2.1.2; and 6-phosphogluconate dehydrogenase (PGDH), EC

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
0	1	1	1	1	2	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1
1	0	0	0	0	1	0	1	0	0	1	0	0	1	?	0	1	1	0	0	1
1	0	0	0	0	1	1	?	0	1	0	0	0	0	0	0	0	1	0	0	1
1	1	1	1	1	1	0	1	1	1	1	0	0	0	?	0	1	1	1	0	0
0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2
0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2
1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1
1	1	0	0	1	1	0	1	0	1	1	1	0	0	1	0	1	0	0	0	1
1	1	1	1	1	1	0	1	0	1	1	0	0	0	1	0	1	0	0	0	1
1	1	0	0	1	1	0	1	1	0	1	1	0	1	?	0	1	1	0	0	0
1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1
1	0	0	0	0	1	0	1	1	1	1	0	0	0	?	1	1	0	0	0	0
1	1	0	0	0	1	0	1	1	0	1	0	0	0	?	0	1	1	0	0	0
1	0	0	0	0	1	0	1	0	1	1	0	1	1	?	0	1	1	0	0	1
0	0	0	0	0	2	0	2	0	0	0	0	0	1	?	0	1	1	0	0	1
2	0	0	0	0	2	0	2	1	1	?	1	0	0	?	0	1	?	1	0	1
1	1	1	1	1	2	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1
1	1	1	1	1	2	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1
1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	1	1	0	0	1
1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	1
1	1	0	0	0	1	0	1	0	0	0	0	0	0	?	0	1	1	0	0	1
1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	1	1	0	0	1
1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1
1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1
1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	1	0	0	0
1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	1	1	0	0	0
1	1	1	1	1	1	0	1	1	1	1	0	0	0	?	0	1	1	1	0	0
1	1	1	1	1	1	0	1	1	1	1	0	0	0	?	0	1	1	1	0	0
1	1	1	1	1	1	0	1	1	1	1	0	0	0	?	0	1	1	1	0	0
1	1	1	1	1	1	0	1	1	1	1	0	0	0	?	0	1	1	1	0	0
0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2
0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2
1	0	0	0	0	1	0	?	0	1	1	0	0	0	1	0	1	1	0	0	1
2	0	0	0	0	2	0	2	1	1	1	1	0	0	?	0	1	1	1	0	1
2	0	0	0	0	2	0	2	1	1	1	1	0	0	?	1	1	1	0	0	1
1	0	0	0	1	1	0	1	1	0	1	0	0	0	?	0	1	1	0	0	1
1	0	0	0	0	1	0	1	0	0	1	0	0	0	?	0	1	1	0	0	1
1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0	1	0	0	0	1
1	1	1	1	1	0	0	0	0	0	1	0	0/1	1	0	0	1	0	1	0	1
1	1	0	0	0	1	0	1	0	0	0	0	0	0	?	0	1	1	0	0	1
1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0	1	1	0	0	1

1.1.1.44. Enzyme electrophoresis was carried out in agarose gels following Hjerten's (1961) protocol with the modifications proposed by Salles *et al.* (1986) and Rosa-Freitas *et al.* (1990).

Morphology

Eighty-eight characters from three life stages were included in the analysis, 39 from the fourth-instar larva, 15 from the pupa, and 34 from the adult male and female. Seventy-four characters were coded as binary and 14 as multistate. All characters were initially treated as unweighted and unordered. Fourteen autapomorphies, which are parsimony non-informative, were excluded from all cladistic analyses; consequently they did not contribute to tree statistics. All 14 autapomorphies are indicated with an asterisk (*) in the character list. When more than one character state was observed in a single taxon, these are scored in the

Table 2 (*continued*).

Species/Character	37	38	39	40	41	42	43	44	45	46	47	48	49	50
S. aurescens	0	0	0	0	1	0	0	1	1	0	1	1	1	0
L. durhami	0	0	0	0	1	1	0	1	1	0	1	0	1	1
W. edwardsi	0	1	1	1	1	0	0	0	1	0	1	0	1	1
W. howardi	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. luteoventralis	0	0	0	1	0	0	0	1	1	0	1	0	0	?
W. jocosa	0	?	?	1	0	0	0	1	1	0	1	0	0	?
W. complosa	0	0	0	1	0	0	0	1	1	0	1	0	0	?
W. ulocoma	0	?	?	1	0	0	0	1	1	0	1	0	1	1
W. felicia	0	?	?	1	0	0	1	1	1	0	1	0	1	0
W. alani	0	?	?	1	0	0	0	1	1	0	1	1	0	?
W. confusa	0	0	0	1	0	0	0	1	1	0	1	0	1	0
W. forattinii	0	?	?	1	0	0	0	1	0	0	1	0	1	1
W. dyari	0	?	?	1	0	0	1	1	0	0	1	0	1	1
W. tarsata	0	0	0	1	0	0	0	1	1	0	1	0	1	1
W. sabethea	0	0	0	1	0	0	0	1	1	0	1	1	0	?
W. limai	0	?	?	1	0	0	1	1	1	0	1	1	0	?
W. surinamensis	0	?	?	1	0	0	1	1	1	1	1	0	1	1
W. flui	0	0	0	1	0	0	1	1	1	1	1	0	1	1
W. sp. 4	0	0	1	1	0	0	0	1	1	0	1	0	0	?
W. argenteorostris	0	0	0	1	0	0	0	1	1	0	1	0	1	1
W. staminifera	0	0	0	1	0	0	0	1	1	0	1	0	1	1
W. chalcocephala	0	?	?	1	0	0	0	1	1	0	1	0	1	1
W. palmata	0	1	1	1	1	0	0	0	1	0	1	0	1	1
O. personatum	0	0	0	1	0	0	0	1	1	0	0	0	1	1
W. aningae	1	0	0	1	0	0	0	1	1	0	0	0	1	1
W. mystes	1	0	0	1	0	0	0	1	1	0	0	0	1	1
W. bourrouli	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. forcipenis	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. airosai	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. finlayi	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. ypsipola	0	0	0	1	0	0	0	1	1	0	1	0	0	?
W. testei	0	0	0	1	0	0	0	1	1	0	1	0	0	?
W. aphobema	1	0	0	1	0	0	0	1	1	0	1	0	1	1
W. lutzi	0	0	0	1	0	0	1	1	0	0	1	1	0	?
W. oblita	0	0	0	1	0	0	1	1	0	0	1	1	0	?
W. arthrostigma	0	0	0	1	0	0	0	1	0	0	1	1	1	1
W. medioalbipes	1	0	0	1	0	0	0	1	0	0	1	1	1	1
W. leucostigma	0	0	0	1	1	0	0	1	1	0	0	0	1	1
W. melanocephala	0	0	0	1	0	0	0	1	1	0	1	0	1	1
W. aporonoma	0	0	0	1	0	0	0	1	1	0	1	0	1	1
W. negrensis	0	0	0	1	0	0	0	1	1	0	1	0	0	?

data matrix as polymorphic. Missing values are represented by a question mark (?) and were employed when the character-state assignments were not applicable or the condition of the available specimens precluded observation of that character. A dash (—) indicates that the character-state homology could not be established.

Characters listed by Judd (1996), Harbach and Kitching (1998), and Sallum *et al.* (2000) were included or reinterpreted. Additional characters, particularly those distinguishing subgenera, were also used. Except for designations of gonostylar lobes (Belkin *et al.* 1970), the morphological terminology follows that of Harbach and Knight (1980).

51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	2
0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	2	1	0	0
0	0	0	0	?	2	1	0	1	1	1	0	1	0	0	0	?	0	0	0	0
0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	1
0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1
0	1	0	1	1	1	1	1	1	0	0	0	1	1	0	0	1	?	1	1	1
0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1
0	0	0	1	0	0	1	?	1	?	0	1	1	0	0	0	1	0	1	0	1
0	1	0	1	0	0	1	1	1	1	0	1	1	1	0	0	1	?	1	0	1
1	0	0	1	1	0	1	1	1	0	1	0	1	?	0	0	1	?	1	0	1
0	1	0	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	1	1	1
0	0	0	1	0	0	1	1	1	1	0	0	1	?	0	0	0	0	1	0	0
0	0	0	1	?	0	1	1	1	1	0	0	1	?	0	0	1	0	1	0	0
0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1
1	1	0	1	?	0	1	1	1	1	0	0	1	0	1	0	1	1	1	0	1
1	2	0	1	0	0	1	1	1	1	1	0	0	0	1	0	1	1	1	0	1
0	0	0	2	1	0	1	1	1	1	0	0	1	1	0	0	1	0	1	2	1
0	0	0	2	1	0	1	1	1	1	0	0	1	1	0	0	1	0	1	2	1
0	0	0	0	1	0	1	1	1	1	0	0	1	1	0	0	1	0	1	0	1
0	2	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	2	1	0	1
0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1
0	0	0	2	0	0	1	?	1	1	?	0	1	1	0	0	1	0	1	0	1
0	0	0	0	0	1	1	0	1	1	1	0	1	0	0	0	1	2	0	0	0
0	0	0	1	0	2	1	1	1	0	0	0	1	1	0	1	1	0	1	0	0
0	0	0	2	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	1
0	0	0	2	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	1
0	0	0	1	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0	1
0	0	0	1	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0	1
0	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	1
0	0	0	1	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0	1
0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1
0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1
0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	0	1	0	1	0	1
1	2	0	1	0	0	1	1	1	1	1	0	0	0	1	0	1	1	1	0	1
1	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	1	1	1	0	1
1	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1
0	2	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1
0	0	0	1	0	2	1	1	1	0	0	0	1	?	0	0	1	1	1	0	1
0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0	1	0	1	0	1
0	0	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1
0	1	0	1	0	1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1

Cladistic analysis

Morphological and allozyme data were combined in a single matrix and analyzed using the parsimony criterion in PAUP version 4.0 (Swofford 2002).

The data matrix was constructed using MacClade version 4 (Maddison and Maddison 2002), and characters were identified as morphological (1–88) or allozyme (89–134). Two sets of taxa were determined in MacClade: group 1 contained 22 species from which we collected only morphological data and group 2 contained 19 species with both morphological and allozyme data. For the allozyme data, individual alleles were scored as characters for presence and absence as alternative states (binary character).

Table 2 (*continued*).

Species/Character	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86
S. aurescens	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0
L. durhami	1	0	0	1	1	0	1	1	?	0	0	1	1	3	0
W. edwardsi	1	1	0	1	0	1	1	0	1	?	0	0	0	0	0
W. howardi	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. luteoventralis	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0
W. jocosa	1	1	1	1	0	1	0	1	1	?	1	0	1	1	0
W. complosa	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0
W. ulocoma	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0
W. felicia	1	1	1	1	1	1	0	0	1	0	1	0	1	1	0
W. alani	1	1	1	?	1	1	0	0	1	0	0	0	0	0	0
W. confusa	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. forattinii	1	1	0	1	0	1	0	0	1	1	0	1	0	0	0
W. dyari	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0
W. tarsata	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0
W. sabethea	1	1	1	1	1	1	0	0	1	1	0	1	1	3	0
W. limai	1	1	1	1	0	1	0	0	1	1	0	1	1	3	0
W. surinamensis	1	1	1	1	0	1	0	2	1	0	1	0	1	1	0
W. flui	1	1	1	1	0	1	0	2	1	0	1	0	1	1	0
W. sp. 4	1	1	1	1	0	1	0	2	1	0	1	0	1	1	0
W. argenteorostris	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0
W. staminifera	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0
W. chalcocephala	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0
W. palmata	1	1	0	1	0	1	1	0	1	1	0	0	0	0	0
O. personatum	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0
W. aningae	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0
W. mystes	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0
W. bourrouli	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. forcipenis	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. airosai	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. finlayi	1	1	1	1	0	1	0	0	1	0	0	0	1	3	0
W. ypsipola	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0
W. testei	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0
W. aphobema	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0
W. lutzi	1	1	1	1	1	1	0	0	1	1	0	1	1	3	0
W. oblita	1	1	1	1	1	1	0	0	1	1	0	1	1	3	0
W. arthrostigma	1	0	1	1	1	1	0	1	0	1	0	1	1	3	0
W. medioalbipes	1	1	1	1	0	1	0	0	1	1	0	1	1	3	0
W. leucostigma	1	0	0	1	0	1	0	2	1	0	0	0	1	3	0
W. melanocephala	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0
W. aporonoma	1	1	1	1	0	1	0	0	1	0	0	0	1	1	0
W. negrensis	1	1	1	1	1	1	0	2	1	1	0	0	1	2	1

The data sets were analyzed as follows. Initially the morphology data set with 41 taxa and 88 characters (Table 2) was analyzed under the parsimony method, with 74 parsimony-informative characters treated as unordered and unweighted. Tree searches were conducted using the heuristic search option, tree bisection and reconnection branch-swapping, and 10 000 random stepwise addition replicates. To test the monophyly of the ingroup, the outgroup was not initially used to root the trees. After that, the same heuristic search criterion was applied to the set of equally parsimonious result trees, with unweighted, unordered search and 10 random-addition replicates per search, and five rounds of successive approximations character weighting (Farris 1969; Carpenter 1994). Character weights were based on the

87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104
1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	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	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	?	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	1
1	0	1	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0
0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0
0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0
0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1
0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0
0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0
0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0
1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0
0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0
1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0	0
0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0
0	0	0	1	0	0	0	0	1	0	1	0	1	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	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0
0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0

maximum value of the rescaled consistency index (CI) (Farris 1989).

The combined morphological and allozyme character data set (Table 2) for the 19 species (group 2) was analyzed under the parsimony criterion with 95 parsimony-informative characters treated as unordered and unweighted. Tree searches were conducted using the method described above.

To evaluate the relative robustness of clades recovered in the parsimony analyses, bootstrap (Felsenstein 1985) values were calculated in PAUP. Bootstrap analyses consisted of 1000 pseudoreplicates and employed heuristic search with tree bisection and reconnection branch-swapping and 10 random-addition replicates per bootstrap pseudoreplicate. Bremer support values (Bremer 1994) for clades were also estimated using PAUP.

Table 2 (*concluded*).

Species/Character	105	106	107	108	109	110	111	112	113	114	115	116	117	118
S. aurescens	?	?	?	?	?	?	?	?	?	?	?	?	?	?
L. durhami	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. edwardsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. howardi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. luteoventralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. jocosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. complosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. ulocoma	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. felicia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. alani	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. confusa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. forattinii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. dyari	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. tarsata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. sabethea	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. limai	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. surinamensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. flui	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. sp. 4	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. argenteorostris	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. staminifera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. chalcocephala	?	?	?	?	?	?	?	?	?	?	?	?	?	?
W. palmata	0	0	1	0	0	0	0	1	0	1	0	0	0	0
O. personatum	1	0	0	0	1	0	0	0	0	0	0	1	0	1
W. aningae	1	0	0	0	0	0	1	0	0	1	0	0	1	0
W. mystes	0	0	0	1	0	0	1	0	0	1	0	0	1	0
W. bourrouli	0	0	1	0	0	0	1	0	1	1	0	0	0	1
W. forcipenis	0	0	1	0	0	0	1	0	1	1	0	0	0	1
W. airosai	0	0	1	0	0	0	1	0	0	1	0	0	0	0
W. finlayi	0	0	0	0	0	0	1	0	1	1	0	0	0	1
W. ypsipola	0	0	1	0	0	1	0	0	0	1	1	0	0	0
W. testei	0	0	1	0	0	1	0	0	0	0	0	0	0	0
W. aphobema	1	0	0	0	0	1	0	0	0	1	0	0	0	0
W. lutzi	0	0	1	1	0	0	1	0	0	0	0	0	0	0
W. oblita	0	0	0	1	0	0	1	0	0	1	0	0	0	0
W. arthrostigma	0	0	0	1	0	0	0	1	0	0	1	0	0	0
W. medioalbipes	0	1	0	0	1	0	1	0	1	0	0	0	0	0
W. leucostigma	1	0	0	0	1	0	0	0	1	0	0	0	0	0
W. melanocephala	0	0	1	0	1	0	0	0	0	0	0	0	0	1
W. aporonoma	0	0	0	0	0	0	0	0	0	0	0	1	0	0
W. negrensis	0	1	0	0	0	0	0	0	1	1	0	0	0	0

Allozyme

Individual genotype data were used to estimate gene frequencies for 19 ingroup taxa. We also estimated pairwise genetic identities and distances (Nei 1978). Identity values were used to construct a UPGMA phenetic dendrogram (Sneath and Sokal 1973) with the BIOSYS-1 program, version 2.0 (Swofford and Selander 1981) (Fig. 1).

Character descriptions

Morphological characters

Larva

(1) Maxilla, laciniarastrum 1 (CI = 0.375): absent (0) (Fig. 2*a*); spiculate with flexible apex (1) (Fig. 2*b*); spiculate with stiff apex (2) (Fig. 2*c*); denticular (3) (Fig. 2*d*).

119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
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0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
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0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0
0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1

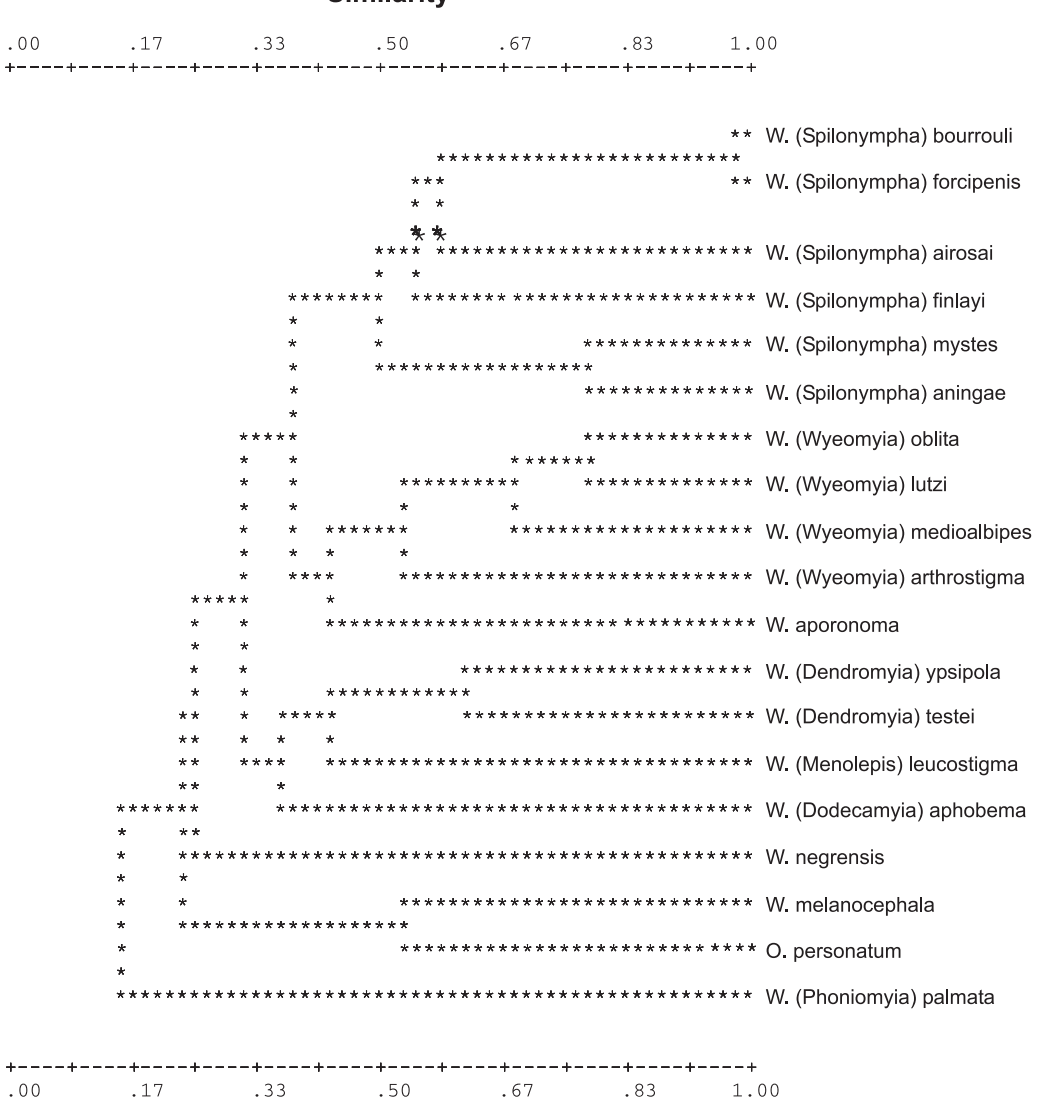
A denticular laciniarastrum (3) occurs in the outgroup, *Dendromyia*, two species of *Spilonympha*, and *W. sabethea* Lane and Cerqueira. Judd (1995) suggested that the denticular condition is primitive within the Sabethini.

(2) Maxillary palpus (*): with 3 apical setae (0); with 4 apical setae (1). Only members of the genus *Sabethes* show a maxillary palpus with 4 apical setae. All other species, including those in *Limatus*, possess a maxillary palpus with 3 apical setae. Condition 1 is an autapomorphy for *Sabethes*, and thus it is uninformative for the analysis.

(3) Seta 1-Mx, position (CI = 0.250): apical (0); displaced slightly basally (1).

Apical position was considered only when seta 1-Mx was inserted on the anterior margin of the maxillary body; all other basal positions were assigned to condition 1.

Fig. 1. UPGMA phenetic dendrogram generated using Nei's (1978) pairwise unbiased genetic identities.



(4) Seta 1-Mx, development (*): elongate (0); short (1).

Among all taxa examined, *Limatus* is the only taxon in which seta 1-Mx is elongate. Because condition (0) is an autapomorphy for *Limatus*, character 4 was excluded from the analysis.

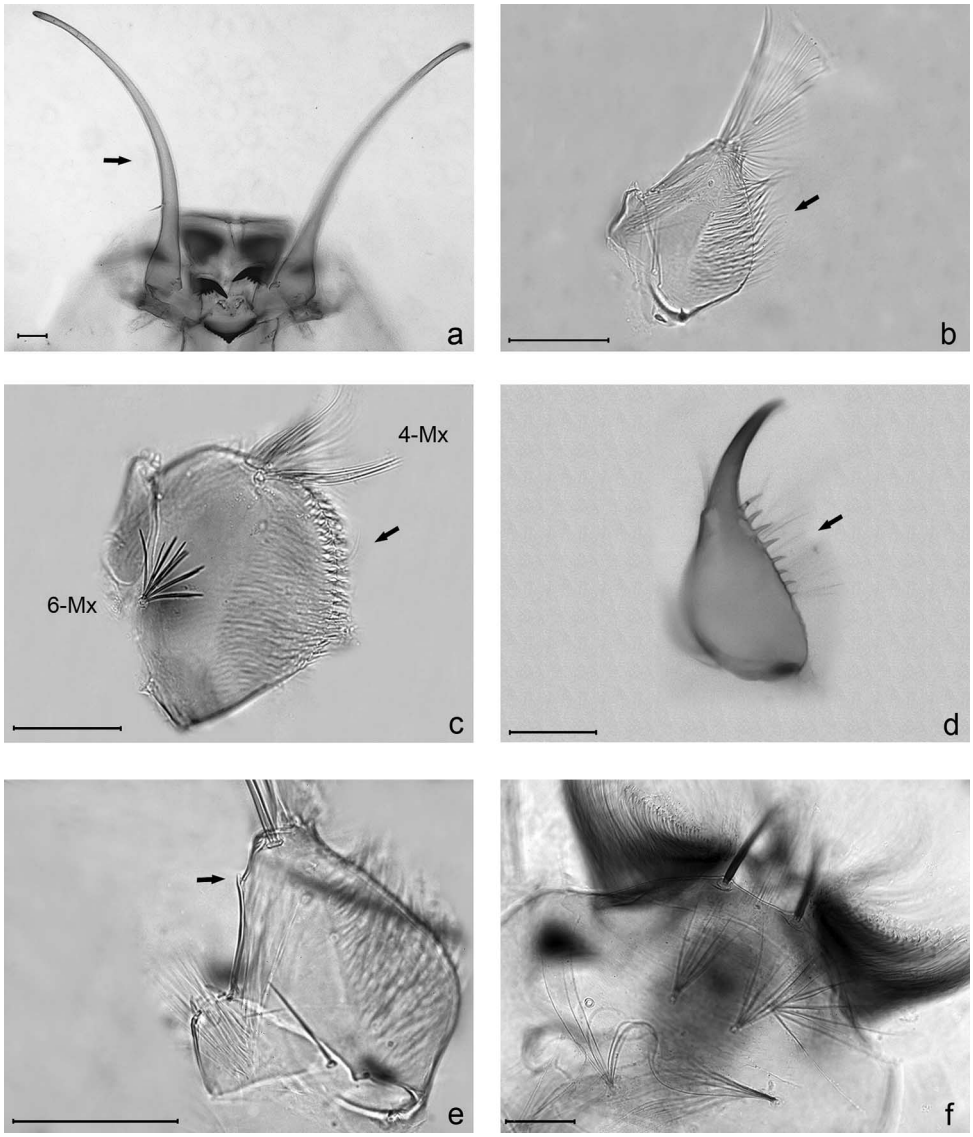
(5) Maxilla, lateral notch containing seta 3-Mx (CI = 1.000): absent (0); present (1) (Fig. 2*e*).

In some species, seta 3-Mx arises from the outer margin of the maxilla in a cuplike extension of the cuticle called the maxilla lateral notch. In the present study, only *Phoniomyia* species possess condition 1. According to Judd (1996, 1998*a*), *Phoniomyia* and *Hystatomyia* have seta 3-Mx arising from this notch.

(6) Seta 4-Mx, development (CI = 0.571): single, pointed (0); single, truncate (1); spinelike (2); brush-tipped (3); forked (4) (Fig. 2*c*).

A forked seta 4-Mx occurs in the majority of species of the subgenus *Wyeomyia*. In *Phoniomyia* species, seta 4-Mx is brush-tipped, a condition shared with *Dodecamyia* and *Exallomyia*. Seta 4-Mx is slightly stronger in *Exallomyia* species than in *Dodecamyia* and *Phoniomyia* species.

Fig. 2. Maxillae of fourth-instar larvae of *Wyeomyia confusa* (*a*), *W. palmata* (*b*), *W. lutzi*, showing maxillary setae 4-Mx and 6-Mx (*c*), *W. ypsipola* (*d*), *W. palmata* (*e*); and anterior margin of the head of *W. palmata* (*f*). The arrows indicate some character states. Scale bars = 0.1 mm.



(7) Seta 4-Mx, position (CI = 1.000): on anterolateral margin (0); posterior (1).

In *Phoniomyia*, seta 4-Mx is located on the anterolateral margin of the maxillary body, directly lateral to the maxillary brush. In the remaining species examined, seta 4-Mx arises posteriorly on the maxillary body.

(8) Seta 6-Mx, development (CI = 0.400): single (0); branched (1); stellate (2) (Fig. 2*c*).

Seta 6-Mx is produced as a single seta in the majority of species included in this analysis, but is stellate in some species of the subgenus *Wyeomyia*. Judd (1995) observed that a simple, unbranched seta 6-Mx is present in most sabethines.

(9) Dorsomentum, position (*): arising posteriorly, beyond middle of head (0); arising anteriorly, beyond middle of head (1).

In *W. confusa*, in which the larva displays predatory behavior, the dorsomentum is located well to the anterior. Condition 1 is an autapomorphy for *W. confusa*.

(10) Anterior edge of dorsomentum (CI = 0.500): median tooth prominent, lateral teeth smaller (0); median and lateral teeth prominent (1).

The dorsomentum with prominent median and lateral teeth occurs only in *Sabethes* and *Onirion*. All other species possess only a prominent median tooth.

(11) Anterior margin of head (CI = 1.000): somewhat triangular (0) (Fig. 2*f*); rounded (1).

Larvae of *Phoniomyia* have a unique feature that distinguishes them from all other sabethines. The mesal anterior part of the head is pronounced and thus the anterior area of the head is triangular.

(12) Occipital foramen (CI = 0.750): circular (0) (Fig. 3*c*); transverse, slit-like, extending anterolaterally (1) (Fig. 3*d*); transverse, not extending laterally (2) (Fig. 3*a*); transverse, slit-like, extending dorsolaterally (3) (Fig. 3*b*).

The occipital foramen in *Onirion* species is circular, whereas in the remaining species examined it is transverse. In *L. durhami* and *W. alani*, the occipital foramen is transverse, not extending laterally, whereas in the remaining *Wyeomyia* and *Phoniomyia* species it is slit-like, extending anterolaterally, not toward the ventral or dorsal surface as in *Sabethes*.

(13) Seta 1-A, development (CI = 1.000): flexible (0); stiff (1).

In *Phoniomyia*, antennal seta 1-A consists of a branched stiff seta, whereas in all other species examined seta 1-A is normally single and always flexible.

(14) Seta 1-A, placement (*): apical (0); midlength (1).

Seta 1-A arises from the apical third of the antenna in all species examined; only in *Exallomyia* was seta 1-A placed in the middle of the antennal shaft, as assigned by Harbach and Peyton (1992). Condition 1 is an autapomorphy for *W. tarsata*.

(15) Seta 4-C, position (CI = 1.000): anterior, on dorsal apotome, slightly posterior to median labral plate (0); posterior, on dorsal apotome, directly mesal to antennal prominence (1).

In *Phoniomyia*, seta 4-C arises more posteriorly, directly mesal to the antennal prominence. In all other species examined, seta 4-C is anterior, arising near to the median labral plate.

(16) Seta 15-C, position (CI = 0.400): between anterior border of labiogula and termination of hypostomal ridge (0); posterior to termination of hypostomal ridge at middle of labiogula (1); well posterior to termination of hypostomal ridge, close to posterior end of hypostomal suture (2).

Except for *W. complosa*, all *Dendromyia* species have seta 15-C between the anterior border of the labiogula and the termination of the hypostomal ridge. Only *W. lutzi*, *W. oblita*, and *W. limai* have seta 15-C arising close to the posterior end of the hypostomal suture.

(17) Seta 4-P, development (CI = 0.250): aciculate, aciculae similar in development to those of seta 7-P (0); strongly aciculate, aciculae considerably more developed than those of seta 7-P (1).

Because seta 7-P is nearly identical in the taxa included in the study, it was used as a landmark to define the development of seta 4-P. In the majority of *Wyeomyia* species seta 4-P is strongly aciculate, mainly in the middle of the branches, and thus different from the other prothoracic setae.

(18) Seta 11-P (CI = 0.250): hairlike (0); spiniform (1).

(19) Seta 11-M, development (CI = 0.250): hairlike (0); spiniform (1).

(20) Seta 11-T, development (CI = 0.250): hairlike (0); spiniform (1).

Seta 11-T is spiniform in the majority of the *Wyeomyia* species.

(21) Seta 13-I, development (CI = 0.500): single (0); branched, with flexible branches (1); stellate (2).

Wyeomyia melanocephala and *W. confusa* share condition 1 (seta 13-I single) with *Onirion*. In the majority of *Wyeomyia* species, seta 13-I is branched and flexible, although stellate setae occur within the subgenus *Wyeomyia* and in the outgroup taxa.

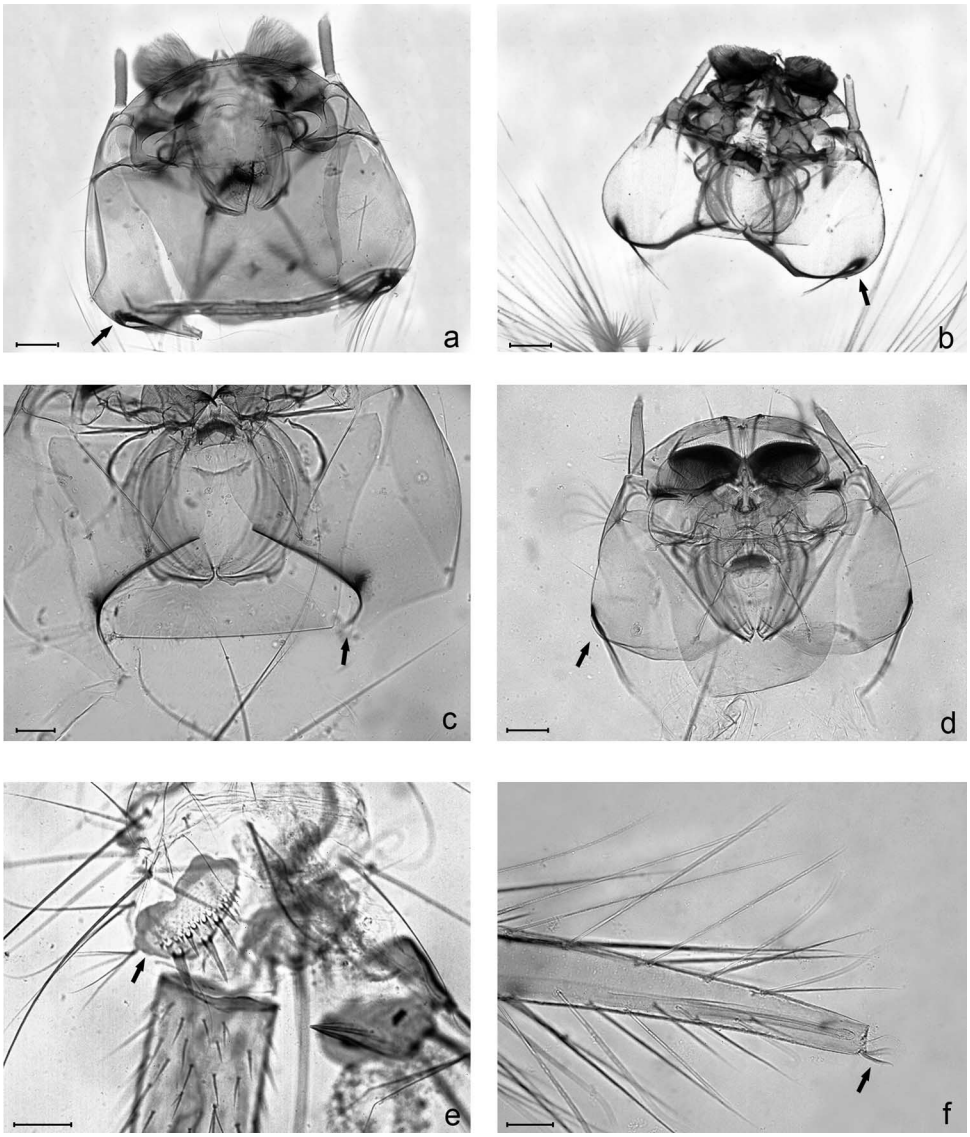
(22) Setae 6,7-III position (CI = 1.000): inserted on separate plates (0); inserted on same plate (1).

Except for *Phoniomyia* species, all species examined have setae 6,7-III arising from separate plates.

(23) Seta 1-VIII, development (CI = 0.667): branched, short (0); branched (2); stellate (2).

The length of the comb scales was used as a landmark to determine the length of seta 1-VIII. Consequently, in those species in which seta 1-VIII was longer than the comb scales it was scored as state 1. In both states (0; 1) the setae were not stellate. According to Harbach and Knight (1980), a stellate seta has numerous stiff branches projecting at various angles from a single base.

Fig. 3. Heads of fourth-instar larvae of *Limatus durhami* (*a*) *Sabethes aurescens* (*b*), *Onirion personatum* (*c*), and *Wyeomyia airosai* (*d*), sclerotized plate on segment VIII of *W. airosai* (*e*), and siphon apex of *W. palmata* (*f*). The arrows indicate some character states. Scale bars = 0.1 mm.



(24) Segment VIII, sclerotized plate (CI = 0.250): absent (0); present (1) (Fig 3*e*).

All *Spilonympha* species have a sclerotized plate on segment VIII, although this condition also occurs in members of the subgenera *Cruzmyia*, *Wyeomyia*, and *Antunesmyia*.

(25) Comb scales (CI = 0.167): in a single row (0); in several rows (1).

The scales arising from a plate were assigned as condition 1. In *Phoniomyia*, *Decamyia*, *Dodecamyia*, *Exallomyia*, and *Menolepis*, *W. surinamensis*, *Wyeomyia* sp. 4, *W. chalcocephala*, and *W. negrensis*, the comb scales arise in several rows from the integument, not from a plate.

(26) Segment X, saddle (CI = 0.167): covering dorsal half of segment X (0); covering more than dorsal half of segment X (1).

In some species, the saddle is small and covers only the dorsal half of segment X. This condition is observed in all *Dendromyia* species.

(27) Spines on posterolateral margin of saddle (CI = 0.250): absent (0); present (1).

Based on the outgroup taxa, the primitive condition is the absence of spines on the

posterolateral margin and this condition is observed in the majority of species examined. The saddle has spines on the posterolateral margin in species of the subgenera *Wyeomyia*, *Antunesmyia*, and *Decamyia* and in *W. argenteorostris*.

(28) Seta 4-X, development (*): branched (0); single (1).

A single seta 4-X is observed only in *W. tarsata* and *W. melanocephala*. The polymorphic condition for seta 4-X was observed in *W. melanocephala*.

(29) Seta 4-X, development (CI = 0.125): less than 0.5 of seta 1-X length (0); more than 0.5 of seta 1-X length (1).

The majority of *Wyeomyia* species have a short seta 4-X. Based on the outgroup comparison, the primitive condition is a long seta 4-X.

(30) Pecten spines, development (CI = 0.250): a single row (0); more than one row (1).

Missing values were assigned for this character in species where pecten spines are absent.

(31) Spicules on siphon (CI = 0.250): absent (0); present (1).

All *Dendromyia* species possess spicules on the siphon; with the exception of *W. forattinii* and *W. oblita*, the remaining species have no conspicuous spicules on the siphon. In the outgroup taxa, only *Sabethes* possesses spines on the siphon.

(32) Siphon, apex (CI = 0.500): narrow, as wide as seta 2-S length (0) (Fig. 3*f*); broad, wider than seta 2-S length (1).

Seta 2-S was used as a landmark to define the width of the siphon apex. Seta 2-S varies in length in some species, but only *Phoniomyia* and *Sabethes* species have the siphon apex as wide as seta 2-S length.

(33) Seta 1-S, development (CI = 0.250): single (0); branched (1).

The majority of species examined have seta 1-S branched; only *W. ulocoma*, *W. felicia*, *W. forattinii*, *W. leucostigma*, and *W. melanocephala* have seta 1-S single.

(34) Seta 1-S, position (CI = 0.250): arising basally (0); arising beyond basal 0.3 (1).

The position of seta 1-S varies among the *Wyeomyia* species. The basal margin of the siphon was used as a landmark for the position of seta 1-S. Only setae that arise from the base of the siphon were considered to exhibit condition 0. The majority of *Wyeomyia* species have seta 1-S arising basally.

(35) Seta 2-S, anterior margin (CI = 0.500): smooth (0); spiculate (1) (Fig. 4*b*).

Seta 2-S has a spiculate margin only in *Onirion* and *Sabethes*. All *Wyeomyia* species have seta 2-S with a smooth margin.

(36) Siphon (CI = 0.400): without seta 2a-S (0); with hairlike seta 2a-S (1); with strong, stout and sclerotized seta 2a-S (2).

Harbach and Peyton (1990*a*, 1992) considered 2a-S to be the seta that arises in a similar position on the dorsal surface of the siphon. Only in *Dendromyia* species is seta 2a-S strong, stout and sclerotized (1); it is absent in *Spilonympha* species.

(37) Numerous accessory setae on siphon (CI = 0.333): absent (0); present (1) (Fig. 4*a*)

Condition 1 was defined as the presence of numerous setae dispersed on all surfaces of the siphon.

(38) Feeding behavior (CI = 1.000): ventral side down (0); ventral side up (1).

Feeding ventral side up is characteristic of *Phoniomyia* species and until now has not been observed in any other Neotropical Sabethini.

(39) Larval pigmentation (CI = 0.500): absent (0); present (1).

The occurrence of pigmentation in larvae of *Wyeomyia* species is rare, at least in larvae reared under laboratory conditions; reddish pigmentation was observed only in the unnamed *Wyeomyia* sp. 4. The larvae of *Phoniomyia* species are always colored.

Pupa

(40) Seta 1-CT, development (CI = 1.000): straight (0) (Fig. 4*d*); sigmoidal (1) (Fig. 4*c*).

Harbach and Peyton (1990*a*) pointed out the sigmoidal development of seta 1-CT in *Wyeomyia* species. All *Wyeomyia* species examined for this study have a sigmoidal seta 1-CT.

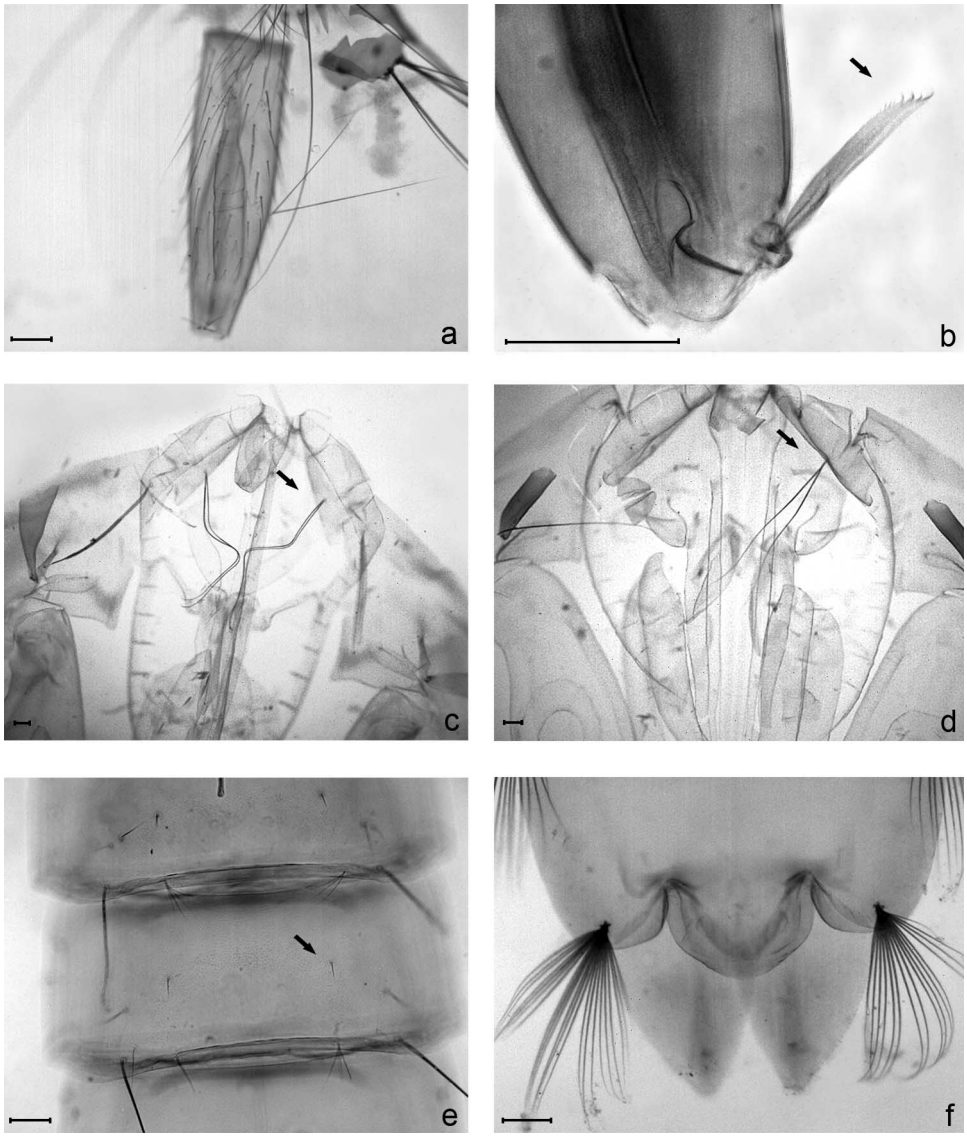
(41) Apex of seta 1-CT (CI = 0.500): hooked (0); straight (1).

This character was used by Judd (1996) for the Sabethini, taking into consideration the degree to which the apex is hooked. However, in *Wyeomyia* species the apex varies, so it is difficult to determine the degree to which it is hooked. We therefore considered only two states for the apex of seta 1-CT.

(42) Seta 5-CT, development (*): strong, more developed than seta 4-CT (0); hairlike, similar in degree of development to seta 4-CT (1).

In *L. durhami*, seta 5-CT is hairlike, whereas in all other species examined for this study, seta 5-CT is strongly developed.

Fig. 4. Siphonal accessory setae of *W. airosai* (*a*), seta 2-S of the fourth-instar larva of *O. personatum* (*b*), pupal seta 1-CT of *W. felicia* (*c*), pupal seta 1-CT of *S. aurescens* (*d*), *pupal seta 2-V of W. oblita* (*e*), and posterolateral angle of segment VIII of the pupa of *W. oblita* (*f*). The arrows indicate the character states. Scale bars = 0.1 mm.



(43) Setae 10,11-CT, placement (CI = 0.250): mesal to seta 11-CT (0); directly posterior to seta 11-CT (1).

(44) Seta 5-IV, position (CI = 1.000): arising close to setae 1 and 2-IV (0); arising far from setae 1 and 2-IV (1).

In *Phoniomyia* species, seta 5-IV arises mesally, close to setae 1 and 2-IV.

(45) Seta 2-V, position (CI = 0.200): displaced well anterior to seta 1-V (0) (Fig. 4*e*); not displaced anterior to seta 1-V (1).

In species in the subgenera *Cruzmyia* and *Wyeomyia*, seta 2-V is placed anteriorly. In all other species, seta 2-V occurs roughly at the level of setae 1 and 5-V.

(46) Seta 6-V,VI, development (CI = 1.000): normal, similar to that of seta 3-V,VI (0); strongly dissimilar to that of seta 3-V,VI (1).

Seta 6-V,VI similar in aspect to seta 3-V,VI was considered normal (condition 0). Only *W. flui* and *W. surinamensis* have seta 6-V,VI strong.

(47) Seta 5-VI, development (CI = 0.333): shorter than tergum VI (0); longer than tergum VI (1).

The majority of *Wyeomyia* species have a long seta 5-VI.

(48) Seta 9-VI, development (CI = 0.500): hairlike (0); stout (1).

All members of the subgenera *Wyeomyia* and *Antunesmyia* possess a stout seta 9-VI. In the outgroup taxon *S. aurescens*, seta 9-VI is multiply branched but equally strong.

(49) Seta 6-VII, position (CI = 0.333): ventral (0); dorsal (1).

This character varies among the *Wyeomyia* species; however, in all *Spilonympha* species seta 6-VII arises dorsally, whereas in all *Dendromyia* species it is ventral.

(50) Seta 6-VII, position (CI = 0.333): anterior to seta 9-VII (0); posterior to seta 9-VII (1).

Seta 9-VII was used as a landmark to define the position of seta 6-VII. Taxa in which seta 6-VII arises ventrally were scored as not applicable.

(51) Posterolateral angle of segment VIII, development (CI = 1.000): not produced (0); produced as a posterior lobe (1) (Fig. 4*f*).

In taxa where segment VIII does not possess a posterior lobe, the posterior margin of segment VIII is slightly projected. In *Antunesmyia* and *Wyeomyia* species (except for *W. medioalbipes*), segment VIII forms a distinct lobe from which seta 9-VIII arises.

(52) Seta 9-VIII, position (CI = 0.286): at posterolateral angle (0); directly mesal to posterolateral angle (1); directly anterior to posterolateral angle (2).

(53) Paddle, outer margin, position (*): in line with insertion of seta 9-VIII (0); displaced well mesal to insertion of seta 9-VIII (1).

(54) Paddle apex (CI = 0.400): rounded (0); triangular (1); truncate (2).

A paddle with a rounded apex was observed in the outgroup taxon *Limatus*, in *Phoniomyia* species, and in *Wyeomyia* sp. 4. Except for five species that have a truncate apex, all *Wyeomyia* species have a paddle with a somewhat triangular apex.

(55) Male genital lobe, distal margin (CI = 0.143): without fingerlike projection (0); with fingerlike projection (1) (Fig. 5*a*).

Adult

(56) Gonostylus (CI = 0.250): branched at apex (0); branched at base (1); simple (2).

All conditions of this character are observed in *Wyeomyia* species. However, in the majority of species examined for the study, the gonostylus is branched at the apex (with stem), which is also the condition in the outgroup taxa.

(57) Lobe C of gonostylus, development (CI = 1.000): ladle-like (0); not ladle-like (1).

The development of lobe C of the gonostylus varies among *Wyeomyia* species, but in *Spilonympha*, lobe C is distinguished by its unique ladle-like shape.

(58) Aedeagus (CI = 1.000): elongate (0); rounded (1).

The shape of the aedeagus is determined by the projection of the median sternal plate. Only *Phoniomyia* species possess an elongate aedeagus.

(59) Apical tergal arm of aedeagus, development (*): with tooth-like projection on mesal margin (0); without tooth-like projection (1).

A tooth-like projection on the mesal margin of the apical tergal arm is an autapomorphy for *Limatus*.

(60) Apical tergal arm of aedeagus, development (CI = 0.111): fused mesally to arm of opposite side (0); separate (1).

Apical tergal arms fused mesally in an apical tergal bridge was scored as condition 0. All *Dendromyia* species have fused apical tergal arms, but this character varies within the subgenus *Wyeomyia*.

(61) Aedeagal median sternal plate (CI = 0.200): barely extending beyond tergal arm (0); extending well beyond tergal arm (1).

The majority of the species examined in this study have the aedeagal median sternal plate barely extending beyond the tergal arm.

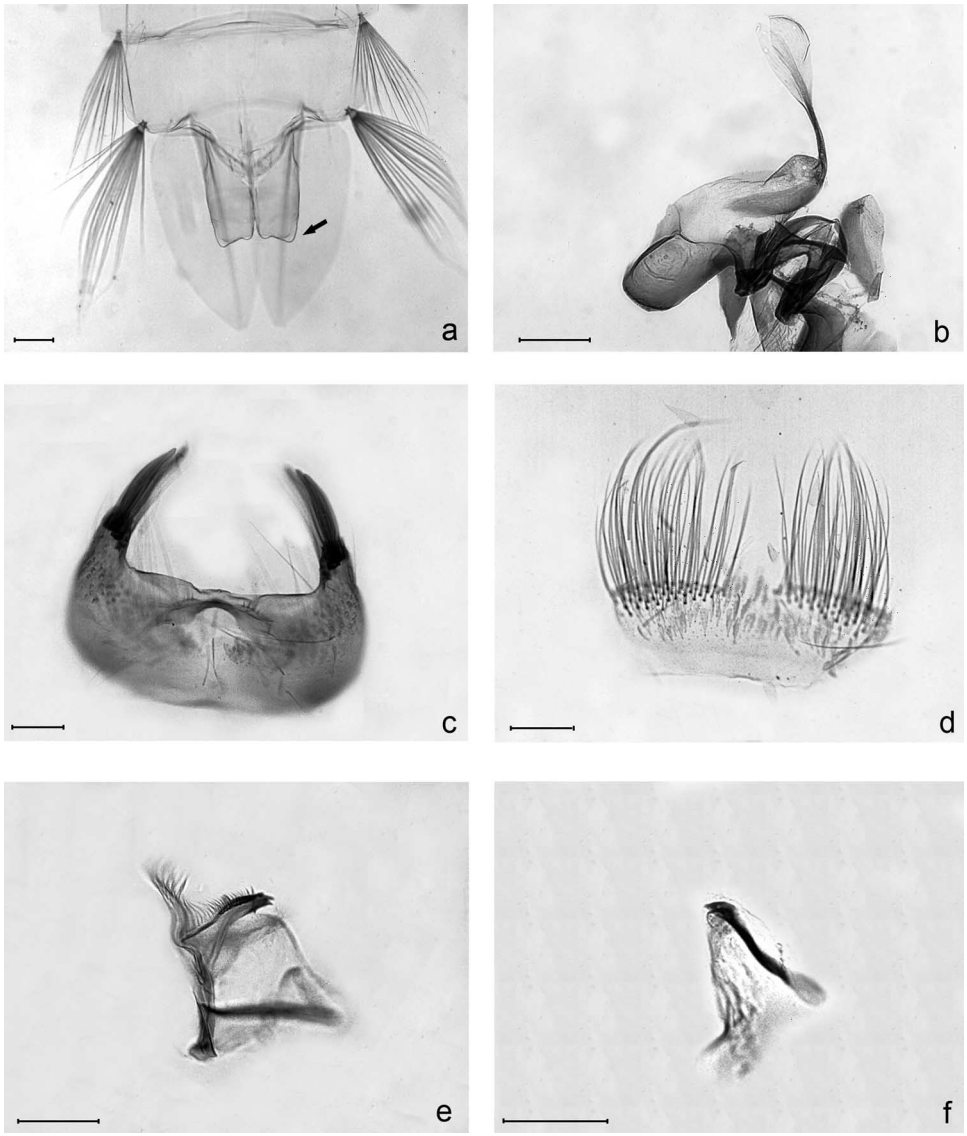
(62) Basal plate (CI = 1.000): without leaf-like seta (0); with leaf-like seta (1) (Fig. 5*b*).

Only *Decamyia* species (*W. ulocoma* and *W. felicia*) have a basal plate with leaf-like setae.

(63) Tergum VIII, thick and sclerotized setae on posterolateral margin (CI = 1.000): present (0) (Fig. 5*c*); absent (1) (Fig. 5*d*).

Thick and sclerotized setae on the posterolateral margin of tergum VIII is a distinct feature present in three of the six species of the subgenus *Wyeomyia* examined (*W. lutzi*, *W. oblita*, and *W. limai*). *Wyeomyia arthrostigma* has posterolateral setae that are not developed as in the above species, therefore this was scored as condition 1.

Fig. 5. Genital lobe of the pupa of *W. airosai* (*a*), basal plate of aedeagus of *W. felicia* (*b*), tergum VIII of male genitalia of *W. lutzi* (*c*), tergum VIII of *W. ypsipola* (*d*), *proctiger of W. lutzi* (*e*), and proctiger of *W. bourrouli* (*f*). The arrow indicates the character state. Scales = 0.1 mm.



(64) Tergum VIII, posterolateral lobe (CI = 0.250): present (0); absent (1).

(65) Proctiger (CI = 1.000): without filamentous projection (0) (Fig. 5*f*); with filamentous projection (1) (Fig. 5*e*)

A proctiger with a filamentous projection occurs only in *W. lutzi*, *W. sabethea*, *W. oblita*, and *W. limai*. In *W. oblita*, this filamentous projection forms a strong structure, fused basally.

(66) Cercal setae (*): normal, short (0); exceptionally long (1).

Among the species examined, only *Onirion* possesses a paraproct with exceptionally long cercal setae, so this is an autapomorphy for *Onirion*. Harbach and Peyton (2000) assigned condition 1 as a distinctive state for *Onirion*.

(67) Semi-erect forked scales on head (*): absent (0); present (1).

The majority of the *Wyeomyia* species possess short, semi-erect, usually pale, forked scales disposed in a single transverse row on the occiput. These scales are absent only in *Wyeomyia* (*Cruzmyia*) *forattinii* (autapomorphy).

(68) Interocular space (CI = 0.286): narrow (0); broad (1); very broad (2).

Spilonympha, *Dendromyia*, *Exallomyia*, and *Menolepis* species possess a broad interocular space, whereas the other species have a narrow interocular space, though *W. palmata*, *W. argenteorostris*, and *Limatus* have a broader interocular space than the other species examined.

(69) Proboscis (CI = 1.000): very long (0); short (1).

A proboscis more than twice the antennal length was considered very long. Only *Phoniomyia* species possess a very long proboscis. Although *Cruzmyia* species possess a long proboscis, it is not similar in proportion.

(70) Clypeus (CI = 0.667): bare (0); with scales on dorsal surface (1); with scales on distal margin of dorsal surface (2).

Scales on the clypeus was subdivided into two states determined by the distribution of scales. *W. jocosa*, *W. complosa*, and *W. confusa* have scales on the dorsal surface, whereas *W. flui* and *W. surinamensis* have scales only on the distal margin of the dorsal surface. The clypeus of the remaining species is bare.

(71) Antepronota (CI = 0.750): more widely separated (0); moderately approximated (1); approximated (2).

The antepronota are more approximated in *Sabethes*, in which they nearly touch dorsally. These structures are separate in *Limatus* and *Phoniomyia*, whereas they are somewhat separated but still close together in all *Wyeomyia* species.

(72) Antepronotum (*): with a conspicuous apicomesal angle (0); without a conspicuous apicomesal angle (1).

Huang (2002) pointed out the development of the antepronotum in *Sabethes*, which possesses an apicomesal angle. Condition 0 is an autapomorphy for *Sabethes*.

(73) Postpronotal scales (CI = 0.167): continuous (0); discontinuous (1).

Continuous postpronotal scales resemble a unique cover of fused scales. The outgroup taxa and few Wyeomyia species exhibit condition 0.

(74) Scutum, profile in lateral view (CI = 0.333): somewhat round anteriorly (0); somewhat flat anteriorly (1).

A slightly convex scutum is a synapomorphy for *Limatus*, *Phoniomyia*, *Cruzmyia*, and *Menolepis*.

(75) Scutal scales, condition (*): broad, overlapping scales (0); moderately broad, slightly overlapping scales (1).

Sabethes species are unique in having broad, flat, overlapping scales on the scutum, whereas all other species possess moderately broad, slightly overlapping scales. Condition 0 is an autapomorphy for *Sabethes*.

(76) Paratergite (CI = 0.143): bare (0); with scales (1).

Harbach and Kitching (1998) pointed out that no sabethine has paratergal scales or setae. However, we observed paratergal scales in the outgroup taxa, as well as in the subgenera *Antunesmyia*, *Decamyia*, *Wyeomyia*, and *Exallomyia*, and in *W. melanocephala* and *W. negrensis*.

(77) Prespiracular area (*): with scales (0); with setae (1).

The presence of prespiracular scales is an autapomorphy for *Limatus*. All other species examined possess prespiracular seta.

(78) Metallic-colored scutal scales (CI = 1.000): absent (0); present (1).

This may not be a strong character in itself, but considering the overall observations from other studies on *Wyeomyia* species that are known for their dull scutal scaling, it would be valid. Color is usually distinctive for sabethine species (Dyar 1919; Lane and Cerqueira 1942). Harbach and Peyton (1990*b*) took it into consideration when they transferred a species of *Wyeomyia* to the genus *Sabethes*. Belkin *et al.* (1970) also distinguished adults of *Wyeomyia* species from those of other sabethines by the dull appearance of the scutal scales. Harbach (1991) suggested that dull scutal scales was a plesiomorphic condition among sabethine species. Furthermore, in their cladistic analysis of the Culicidae, Harbach and Kitching (1998) restored the relationship between *Limatus* and *Sabethes* because of the strong metallic sheen of the scutelar scales.

(79) Mesopostnotal area (CI = 0.250): without scales (0); with scales intermixed with setae (1); with scales anterior to mesopostnotal setae (2).

The presence of scales was scored as two states: one state with only a few scales intermixed with mesopostnotal setae and a second for those species that possess a tuft of scales located anterior to the mesopostnotal setae. Condition 2 occurs in *W. negrensis*, *W. leucostigma*, *W. flui*, and *W. surinamensis*.

(80) Mesokatepisternal scales (CI = 0.500): covering entire mesokatepisternum (0); covering posterior 0.5 of mesokatepisternum (1).

(81) Lower mesokatepisternal setae (CI = 0.250): extending above dorsal margin of mesomeron (0); not extending above dorsal margin of mesomeron (1).

Lower mesokatepisternal setae not extending above the dorsal margin of the mesomeron was used by Dyar (1928) as a diagnostic character for species of the subgenus *Wyeomyia*. In our analysis, condition 1 was observed in members of the subgenera *Wyeomyia*, *Dodecamyia*, *Cruzmyia*, and *Exallomyia*.

(82) Wing, upper calypter (CI = 0.333): without marginal setae (0); with marginal setae (1).

In the Sabethini, marginal setae on the upper calypter are usually represented by two setae. Condition 1 was observed in *Onirion*, *Dendromyia*, *Decamyia*, *W. surinamensis*, *W. flui*, *Wyeomyia* sp. 4, and *W. chalcocephala*.

(83) Vein R_s (CI = 0.200): without proximal spur (0); with proximal spur (1).

A proximal spur is present in the subgenera *Wyeomyia*, *Dodecamyia*, and *Cruzmyia*.

(84) Vein M, anterior scales on proximal 0.5 of dorsal surface (CI = 0.333): decumbent (0); anteriorly projected (1).

Scales on the proximal 0.5 of the dorsal surface of vein M can arise parallel to the vein on the anterior side. The majority of *Wyeomyia* species have scales projecting anteriorly to the longitudinal axis of vein M.

(85) Condition of scales on dorsal surface of proximal 0.5 of vein M (CI = 0.375): narrow spatulate (0); moderately broad spatulate (1); broad spatulate (2); ligulate (3).

Species of the subgenera *Wyeomyia*, *Prosopolepis*, and *Spilonympha* have narrow, elongate, spatulate scales on the dorsal surface of the proximal 0.5 of vein M. The states moderately broad spatulate, broad spatulate, and narrow spatulate are defined according to Figure 82 I, l/m, k in Harbach and Knight (1980, page 321).

(86) Condition of posterior scales on dorsal surface of proximal 0.5 of vein M (*): decumbent (0); posteriorly projected (1).

Among the species examined for the study, only *W. negrensis* has the posterior scales on the proximal half of vein M projecting posteriorly.

(87) Crossvein mcu (CI = 0.250): proximal to crossvein rm (0); adjacent to rm (1).

(88) Number of spermathecal capsules (CI = 0.500): 3 (0); 1 (1).

Female mosquitoes possess either one or three spermathecal capsules (Harbach and Kitching 1998). Three spermathecal capsules were observed in the outgroup taxa and also in the majority of *Wyeomyia* species. One spermathecal capsule was observed in *W. flui*, *W. surinamensis*, *W. chalcocephala*, *Wyeomyia* sp. 4, and *W. negrensis*. Judd (1996) observed one spermathecal capsule in *W. albosquamata* and *W. phroso*. Within the Sabethini, *Tripteroides* and *Topomyia* (Oriental and Australasian) possess one spermathecal capsule.

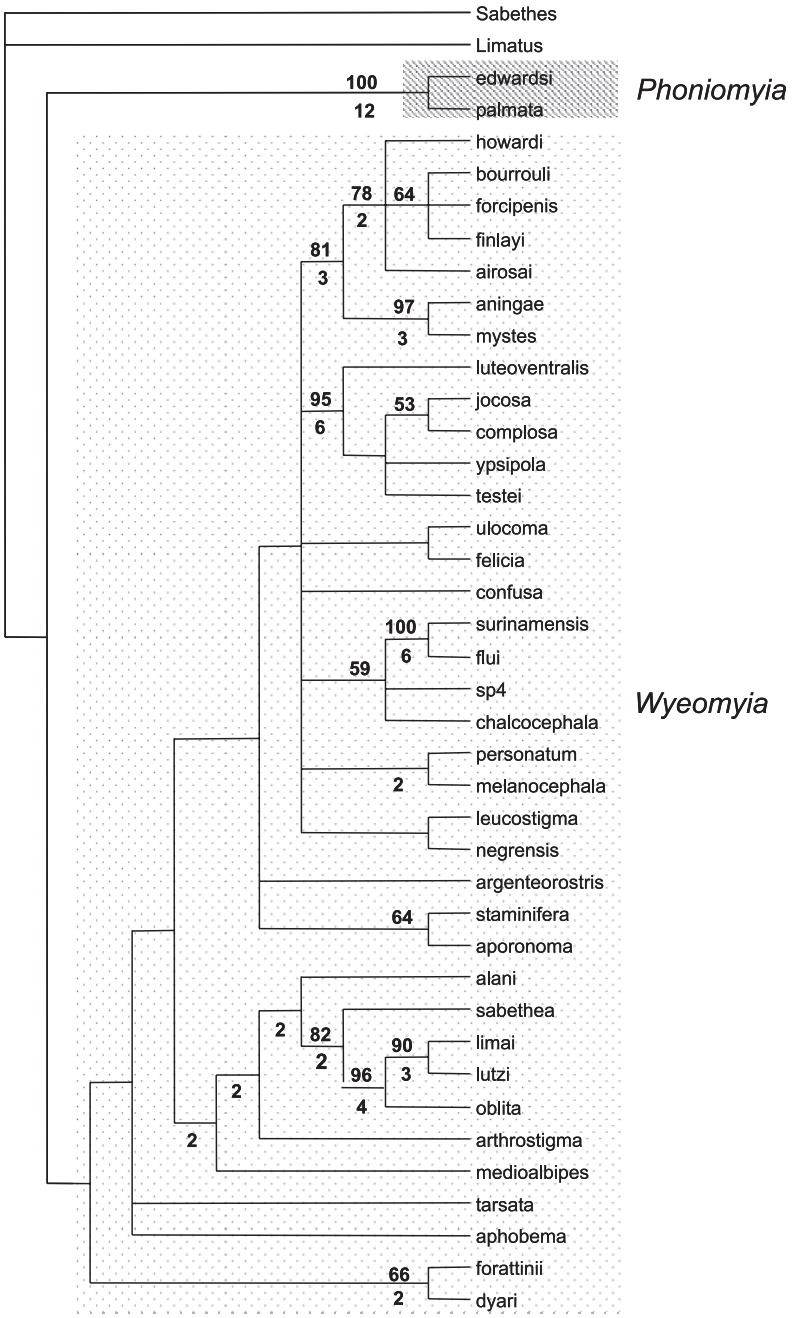
Results and discussion

The discussion about monophyletic lineages within the genus *Wyeomyia* is based on the strict-consensus topology of 31 equally parsimonious trees (length = 267 steps, CI = 0.355, and retention index (RI) = 0.644) obtained in the unweighted, unordered character data analysis of 41 species of Sabethini. The strict-consensus tree of those trees is shown in Figure 6. Using the successive approximations character weighting method, the character weights stabilized after three rounds and identified a set of four equally parsimonious trees with a weighted length of 61.69326. These four trees are not a subset of those 30 unweighted trees, and the strict consensus is shown in Figure 7.

The analysis of the combined morphological and allozyme data for the 19 species included 95 parsimony-informative characters. The unweighted parsimony analysis of combined data sets resulted in a single topology of 250 steps (CI = 0.440, RI = 0.588). In the successive approximations weighting analyses, character weights stabilized in the first round resulting in one successive approximations character weighting tree with a weighted length of 64.347 62. The unweighted and weighted topologies are identical (Fig. 8).

The results of all cladistic analyses were largely topologically congruent. Minor differences were observed in the phylogenetic positions of *W. negrensis*, *W. leucostigma* (*W. aporonoma*, *W. staminifera*), *W. argenteorostris*, and *W. confusa*. Similarly, relationships among *Dodecamyia* and *Exallomyia* species show variable arrangements, with weak bootstrap support values in any method and data set adopted. Parsimony bootstrap analysis

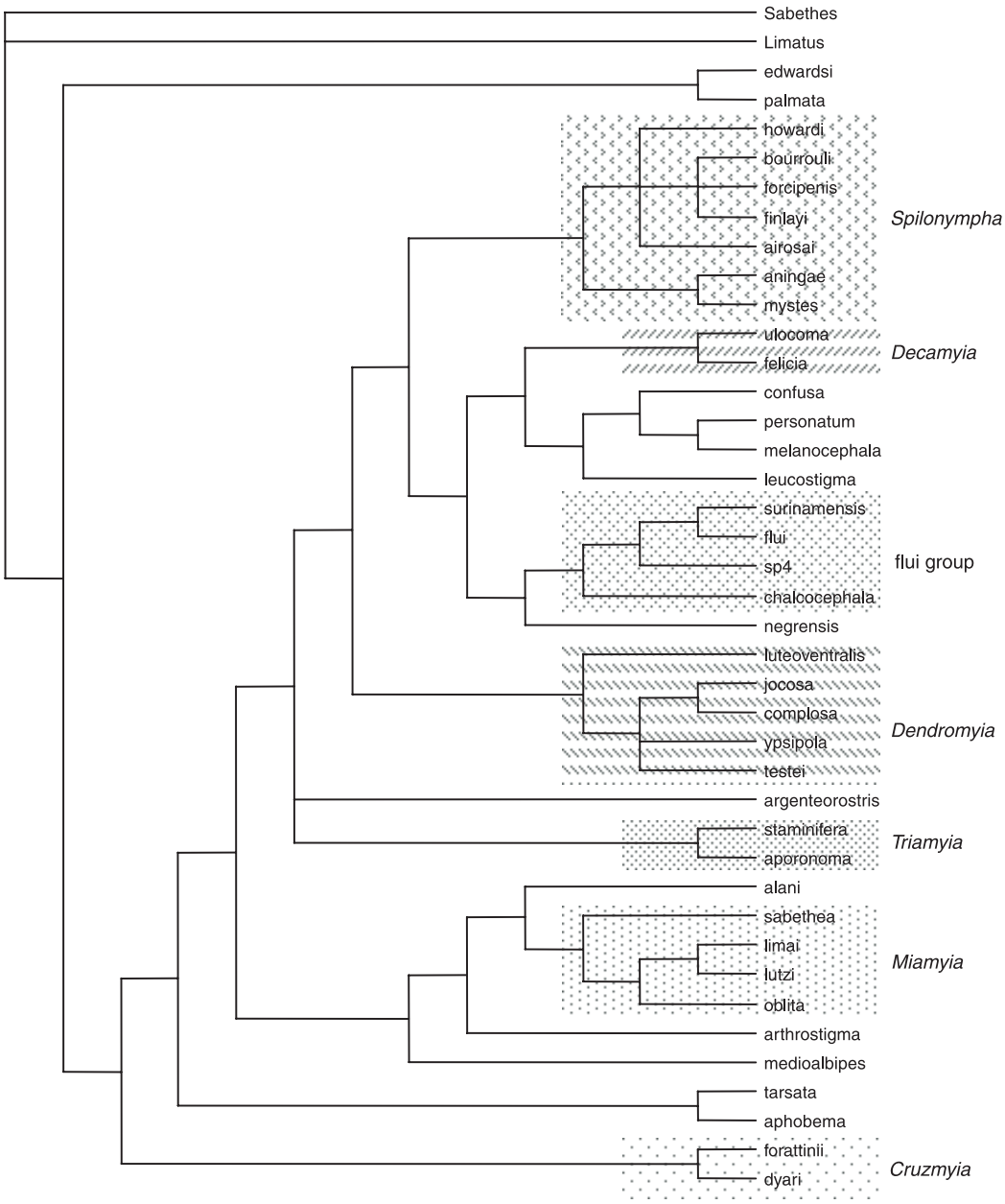
Fig. 6. Strict-consensus topology of the 30 most parsimonious trees recovered in the unweighted, unordered analysis of morphological data for 41 species. The number in boldface type above each branch indicates the percentage of bootstrap pseudoreplicates in which that node is supported, and the number below indicates the Bremer support value. The shaded areas denote monophyletic groups within the genus *Wyeomyia*, the former genus *Phoniomyia*, and *Wyeomyia*.



of the combined morphological and allozyme data sets (Fig. 8) better supported the monophyletic groups found in the morphological analysis.

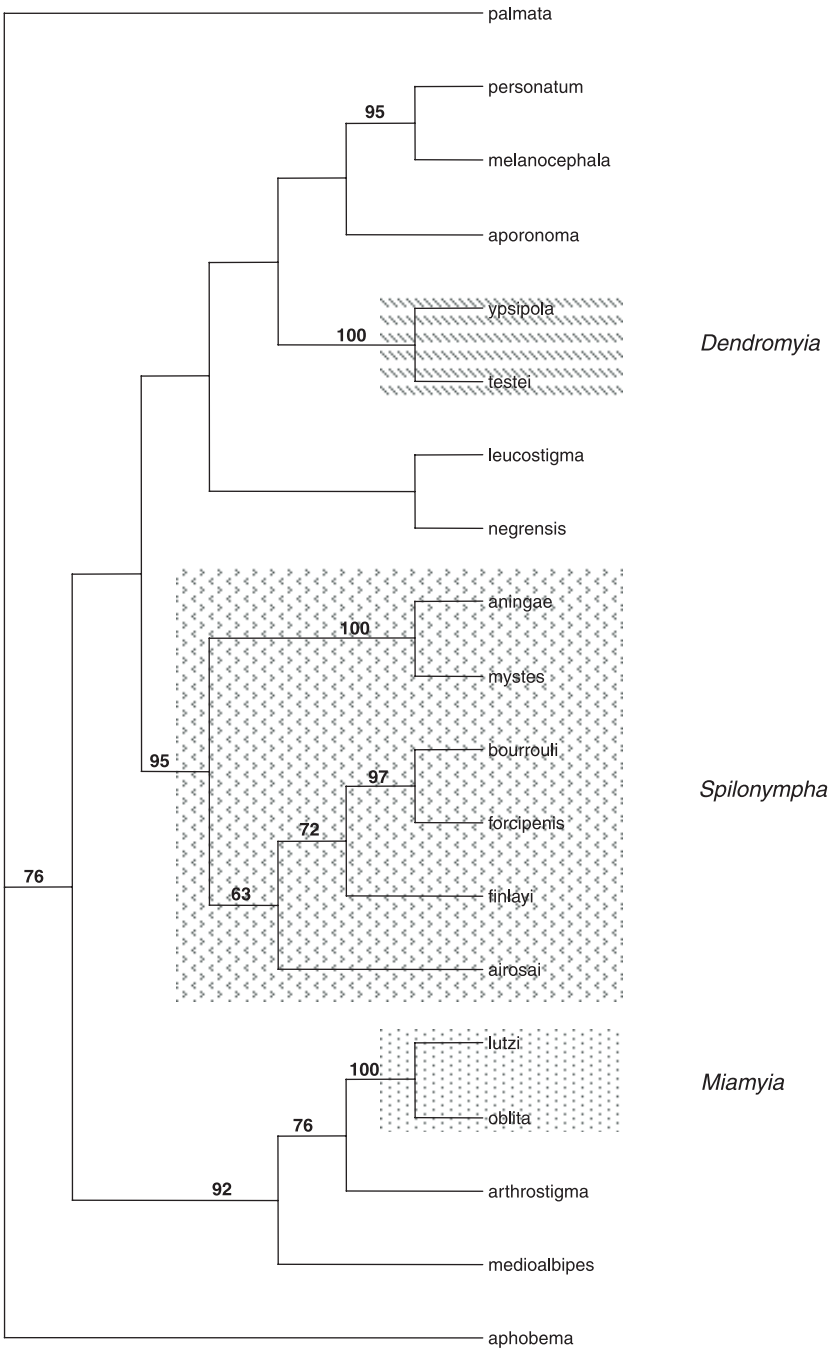
Parsimony character optimization (Table 3) was done in a topology recovered in the unweighted, unordered analysis shown in Figure 9.

Fig. 7. Strict-consensus topology of four equally parsimonious trees recovered in the successive approximations weighting analyses using the rescaled consistency index to down-weight homoplastic morphological characters based on morphological data for 41 species. The shaded areas denote monophyletic subgenera of *Wyeomyia*, except for the "flui group".



The results of all analyses did not recover the genus *Wyeomyia* in the way it is currently defined, as a monophyletic lineage, because the genus *Onirion* is embedded within *Wyeomyia* as the sister of *W. melanocephala*. Also, the results partially contradict those of Judd (1996) relative to the genera *Wyeomyia* and *Limatus* and the subgenus *Phoniomyia*. Judd (1996) found that the genus *Wyeomyia* was a paraphyletic assemblage, with *Limatus* and *Phoniomyia* embedded within the clade formed by *Wyeomyia* species. One of three synapomorphies for *Wyeomyia*, *Phoniomyia*,

Fig. 8. The single most parsimonious tree recovered in the unweighted, unordered analysis of morphological and allozymic data for 19 species. The number in boldface type above each branch indicates the percentage of the bootstrap pseudoreplicates in which that node is supported, and the number below indicates the Bremer support value. The shaded areas denote monophyletic subgenera of *Wyeomyia*.



and *Limatus* (Judd 1996) was herein redefined and tested using the present data set (seta 14,15-C located midway between the anterior margin of the labial sclerite and the posterior tentorial pit), and a second synapomorphy was employed for all 41 species as defined by that author. However, phylogenetic signal was lost following the inclusion of additional species because these characters

Table 3. Optimization of character states using the tree shown in Figure 9 generated in the unweighted, unordered analysis (length = 267, consistency index (CI) = 0.3558, retention index = 0.6614*).

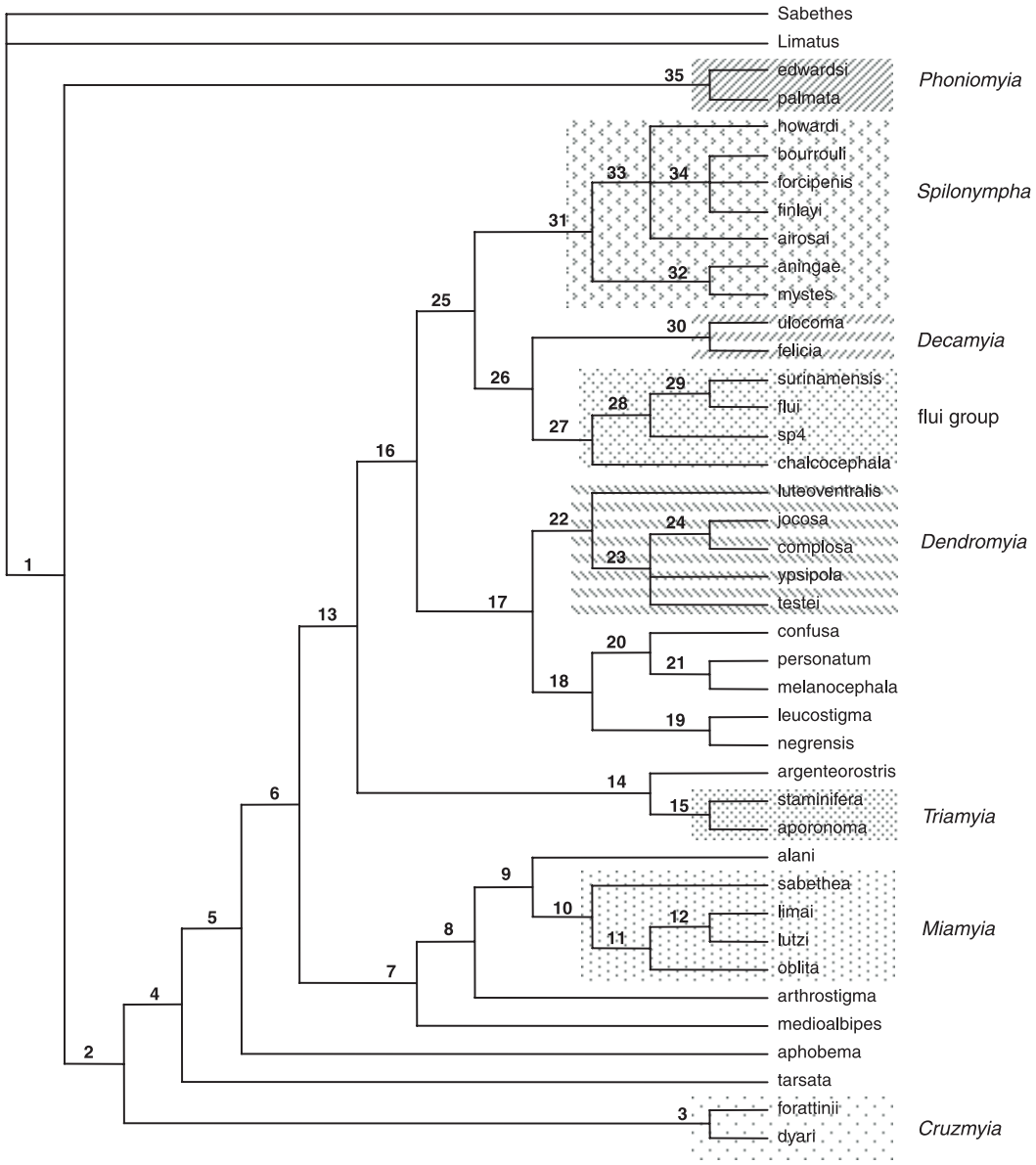
Node	Character	CI	Stage change
3	6	0.500	3→0
	24	0.250	0→1
	36	0.400	1→0
	45	0.200	1→0
10	16	0.400	1→0
	20	0.250	1→0
	21	0.500	1→2
	23	0.667	1→2
	52	0.250	0→1
	55	0.200	1→0
	65	1.000	0→1
11	8	0.400	1→2
	16	0.400	0→2
	25	0.167	0→1
	29	0.167	1→0
	43	0.250	0→1
	45	0.200	1→0
	63	1.000	1→0
12	3	0.250	1→0
	34	0.250	0→1
	52	0.250	1→2
	61	0.200	0→1
15	8	0.400	0→1
	60	0.143	1→0
22	1	0.375	2→3
	16	0.400	1→0
	26	0.167	1→0
	30	0.250	1→0
	31	0.250	0→1
	36	0.400	1→2
	49	0.250	1→0
	68	0.250	0→1
27	30	0.250	1→0
	54	0.400	1→2
	79	0.286	0→1
	88	0.500	0→1
29	6	0.500	0→1
	21	0.500	1→2
	23	0.667	1→0
	29	0.167	0→1
	43	0.250	0→1
	46	1.000	0→1
	70	0.667	0→2
31	24	0.250	0→1
	36	0.400	1→0
	37	0.333	0→1
	57	1.000	0→1
	68	0.250	0→1
32	1	0.375	2→3
	47	0.333	1→0
	54	0.400	1→2
	79	0.286	0→1
33	34	0.250	0→1
	85	0.375	1→2
34	61	0.200	0→1
35	5	1.000	0→1
	7	1.000	1→0
	11	1.000	1→0
	13	1.000	0→1
	15	1.000	0→1
	22	1.000	0→1
	38	1.000	0→1
	39	0.500	0→1
	44	1.000	1→0
	56	0.250	0→1
	58	1.000	1→0
	61	0.200	0→1
	69	1.000	1→0

*Includes only nodes that are supported by ≥50% bootstrap proportion.

were inconsistent within *Wyeomyia*. Our results show the genus *Limatus* and the subgenus *Phoniomyia* as separate lineages arising outside the genus *Wyeomyia*, although the bootstrap support is weak (<50%).

Phoniomyia was proposed as a genus by Theobald (1903). Its taxonomic position changed several times (Bonne-Wepster and Bonne 1921; Dyar 1924; Edwards 1932) and finally Lane and Cerqueira (1942) defined it as a genus. The taxonomic instability of the group has been caused mainly by the fact that most of the species descriptions were based on the adult stages with no association with immature stages, despite adult characters being generally conservative in all *Phoniomyia* species. Judd (1998*a*) recovered the genus *Phoniomyia* as the sister of the subgenus *Hystatomyia*. Thus, the genus *Wyeomyia*, as it was defined by Lane and Cerqueira (1942), was a paraphyletic lineage. As a result, Judd (1998*a*) reduced *Phoniomyia* to a subgenus of *Wyeomyia*. Because no specimen of the subgenus *Hystatomyia* was available for the present study, the sister-group relationship between *Phoniomyia* and *Hystatomyia* could not be tested using the present morphological data set. It is important to point out that the placement of *Phoniomyia* outside *Wyeomyia*

Fig. 9. One of the most parsimonious unweighted, unordered trees generated using the morphological data for 41 species. This topology was employed for parsimony character optimization (Table 3) and shows the nodes. The shaded areas denote monophyletic subgenera of *Wyeomyia*, except for the "flui group".



may also be a result of not having any *Hystatomyia* species in the data set. However, *Phoniomyia* as either a genus or subgenus of *Wyeomyia* is a distinct phylogenetic lineage, which is well supported by 100% bootstrap and a Bremer support value of 12. The monophyly of *Phoniomyia* is supported by 10 consistent synapomorphies: maxilla with a lateral notch containing seta 3-Mx (character 5); larval seta 4-Mx on the anterolateral margin, directly lateral to the maxillary brush (character 7); anterior margin of the head somewhat triangular (character 11); seta 1-A stiff (character 13); seta 4-C arising posteriorly on the dorsal apotome directly mesal to the antennal prominence (character 15); setae 6,7-III inserted on the same plate (character 22); larva feeds ventral side up (character 38); pupal seta 5-IV inserted

close to seta 1-IV (character 44); aedeagus elongate (character 58); and proboscis twice as long as antenna (character 69).

Within *Wyeomyia*, the basal clade (node 3) (Fig. 9) leads to *Cruzmyia* species (*W. forattinii* and *W. dyari*). Four synapomorphies support the *Cruzmyia* clade: larval seta 4-Mx single, pointed (character 6); presence of a sclerotized plate on segment VIII (character 24); absence of seta 2a-S (character 36); and pupal seta 2-V displaced well anterior to seta 1-V (character 45). Judd (1996) recovered *Cruzmyia* and *Limatus* as sister groups. *Cruzmyia* was proposed as a subgenus of *Wyeomyia* by Lane and Cerqueira (1942), based mainly on adult characters (wing and proboscis features), and the results of the present study corroborate this hypothesis, being supported by a 66% bootstrap proportion and a Bremer support value of 2.

Nodes 4 and 5 show the subgenera *Dodecamyia* (*W. aphobema*) and *Exallomyia* (*W. tarsata*) as sister taxa of a major clade (node 6). In the topology generated using the successive approximations weighting method (Fig. 7), *Dodecamyia* and *Exallomyia* were recovered as sister groups, supported by a single synapomorphy (larval seta 4-Mx brush-tipped (character 6)). The bootstrap proportion for the *Dodecamyia* plus *Exallomyia* clade is <50%.

Monophyly of the nominal subgenus *Wyeomyia* was not corroborated by the results of the present analysis (node 7) because the subgenus *Antunesmyia* (*W. alani*) arises among members of the subgenus *Wyeomyia*. Placement of *Antunesmyia* within the subgenus *Wyeomyia* corroborates Judd's (1996) hypothesis that the subgenus *Wyeomyia* is a polyphyletic lineage. *Antunesmyia* plus *Wyeomyia* (node 8) is the sister to a clade leading to (*Antunesmyia*, *W. lutzi*, *W. limai*, *W. oblita*, *W. sabethea*). The relationship between *Antunesmyia* and *Wyeomyia* is supported by five synapomorphies: fourth-instar larvae with seta 4-Mx forked (character 6); seta 6-Mx stellate (character 8); presence of spines on the posterolateral margin of the saddle (character 27); larval seta 4-X longer than 0.5 of seta 1-X length (character 29); pupa with seta 2-V displaced well anterior to seta 1-V (character 45), and seta 6-VII ventral (character 49). However, these characters are not entirely consistent, so the *Wyeomyia* plus *Antunesmyia* arrangement is only weakly supported by a <50% bootstrap proportion.

Antunesmyia was proposed as a subgenus of *Wyeomyia* by Lane and Cerqueira (1942) to include three species. While the fourth-instar larva and pupa of *W. alani* are described, the two other species were defined on the basis of adult female characters. Some larval and pupal features of *W. alani* are similar to those of species of the subgenus *Wyeomyia*. Members of both *Antunesmyia* and *Wyeomyia* inhabit bamboo-internode habitats.

The clade formed by *W. lutzi*, *W. limai*, *W. oblita*, and *W. sabethea* (node 10) is monophyletic and supported by six synapomorphies: larval seta 15-C arises well posterior to the hypostomal ridge, close to the posterior end of the hypostomal suture (character 16); seta 11-T hairlike (character 20); larval seta 13-I stellate with stiff branches (character 21); pupal seta 1-VIII stellate (character 23); seta 9-VIII anterior to posterolateral angle of tergum VIII (character 52); male genital lobe of pupa with distal margin without a fingerlike projection (character 55) and proctiger with filamentous projections (character 65). Parsimony bootstrap support for node 10 is moderate (82%), with a Bremer support value of 2. Dyar (1928) defined the subgenus *Miamyia* to include *W. codiocampa* Dyar and Knab, *W. serrata* (Lutz), and *W. hosautos* Dyar and Knab. However, *Miamyia* has been treated as a junior synonym of the subgenus *Wyeomyia* since Edwards (1932). *Wyeomyia lutzi*, *W. limai*, *W. codiocampa*, and *W. serrata* were also included in the "serrata series" within the subgenus *Wyeomyia* by Lane and Cerqueira (1942). Recently, Judd (1996) found *W. codiocampa* in a sister relationship with *W. oblita*. Our results corroborate Judd's (1995, 1996) hypotheses and support the recognition of *Miamyia* as a subgenus of the genus *Wyeomyia*. We therefore formally resurrect the subgenus *Miamyia* from synonymy with the subgenus *Wyeomyia*. The species comprising the subgenus *Miamyia* are *W. codiocampa*, *W. serrata*, *W. hosautos*, *W. lutzi*, *W. limai*, *W. oblita*, and *W. sabethea*.

A major clade (node 13) is formed mainly by species that are placed in the subgenera *Dendromyia* (*sensu* Lane and Cerqueira 1942) and *Menolepis*. Within this major clade there is a secondary group defined by node 14, which includes *W. aporonoma* plus *W. staminifera* as the sister of *W. argenteorostris*. This arrangement is supported by a synapomorphy, larva with saddle covering the dorsal half of segment X (character

26), and supported by a bootstrap proportion of <50%. In contrast, node 15 leading to *W. aporonoma* and *W. staminifera* is supported by a 64% bootstrap value, a Bremer support value of 1, and two synapomorphies: seta 6-Mx branched (character 8); and apical tergal arm of the aedeagus fused mesally (character 60). A hypothesis about the monophyly and definition of a group formed by *W. aporonoma* and *W. staminifera* became evident to us during a study that included the description of *W. staminifera* (Lourenço-de-Oliveira *et al.* 1992). Because the results of the present analysis corroborate the monophyly of the group formed by *W. aporonoma* and *W. staminifera*, and the split leading to it is moderately supported, we consider that the group may be defined as a subgenus within the genus *Wyeomyia*. Dyar (1928) defined the subgenus *Triamyia* to include *W. aporonoma* and *W. personata* (Lutz), based on adult female and male genitalia characters. Later, Edwards (1932) included these species in the subgenus *Dendromyia*. Here we propose to resurrect *Triamyia* as a subgenus of genus *Wyeomyia* to include *W. aporonoma* and *W. staminifera*.

Node 18 defines a clade formed by *W. leucostigma* plus *W. negrensis* as the sister group of *W. melanocephala* plus *O. personatum* as the sister group of *W. confusa*. Node 18 is supported by larval seta 4-X longer than 0.5 of seta 1-X length (character 29); male genital lobe without a fingerlike projection (character 55); anterior scales on dorsal surface of proximal 0.5 of vein M elongate and ligulate (character 85).

Node 19 leads to a clade formed by *W. negrensis* and *W.* (*Menolepis*) *leucostigma*. Two homoplastic synapomorphies support the split: larval comb scales inserted in several rows (character 25) and mesopostnotal area with scales anterior to mesopostnotal setae (character 79). In the successive weighting analysis (Fig. 7), *W. negrenis* was recovered as the sister of *W. chalcocephala*, *W. surinamensis*, *W. flui*, and *Wyeomyia* sp. 4 ("flui group"). In the analysis with combined morphology and allozyme data from 19 species (Fig. 8), we observed the arrangement *W. negrensis* plus *W. leucostigma*, but the bootstrap value was low (<50%). The phylogenetic position of *W. negrensis* remains unresolved, mainly because its position varies in the topologies generated using different methods of analysis. *Wyeomyia leucostigma* also appears as the sister to *W. confusa* and *W. melanocephala* plus *O. personatum* in the successive weighting analysis; however, this arrangement is poorly supported.

The subgenus *Prosopolepis* (*W. confusa*) was recovered as a sister lineage of *W. melanocephala* plus *O. personatum* (node 20). This arrangement is supported by three synapo-morphies: larval seta 13-I single (character 21); seta 1-VIII branched (character 23); pupa with posterolateral lobe of tergum VIII present (character 64); parsimony bootstrap support <50%. *Prosopolepis* was proposed as a genus of the Sabethini by Lutz (1905) to include a single species named *Prosopolepis confusus*. Dyar (1928) included this species and three others in the genus *Dendromyia* Theobald. Subsequently, Edwards (1932) recognized *Dendromyia* as a subgenus of genus *Wyeomyia* and Lane (1953) retained this change of status. As a consequence of the revision of the subgenus *Dendromyia* (Motta and Lourenço-de-Oliveira 2000), *W. confusa* was removed from the subgenus and left without subgeneric placement in the genus *Wyeomyia*. Later, Lourenço-de-Oliveira *et al.* (1999) resurrected *Prosopolepis* from synonymy with the subgenus *Dendromyia* to include *W. confusa*.

The clade formed by *O. personatum* and *W. melanocephala* (node 21) is supported by six synapomorphies: larva with pecten spines disposed in a single row (character 30); seta 1-S single (character 33); seta 1-S arising beyond the basal 0.3 (character 34); pupal seta 9-VIII arising from posterolateral angle of tergum VIII (character 52); male genitalia with gonostylus simple (character 56); dorsal surface of proximal 0.5 of vein M with moderately broad spatulate scales (character 85). Bootstrap support for the relationship between *O. personatum* and *W. melanocephala* is weak.

In the present analysis, the branch leading to *Onirion* plus *Wyeomyia* (node 2) is supported by six synapomorphies: larva with pecten spines disposed in one row (character 30); siphon with a broad apex, wider than length of seta 2-S (character 32); segment X with saddle covering more than dorsal half of segment (character 26); apex of pupal seta 1-CT hooked (character 41); apex of paddle triangular (character 54); scutal scales without metallic sheen (character 78). This arrangement disagrees with that of Harbach and Peyton (2000) regarding the placement of the genus *Onirion*, which was

recovered embedded within the genus *Wyeomyia* in this study, whereas in Harbach and Peyton (2000), the taxon was placed outside it in an unresolved relationship with genera *Isostomyia* Coquillett plus *Shannoniana* Lane and Cerqueira and *Wyeomyia* plus *Limatus* and *Sabethes*. The following morphological characters were used to distinguish *Onirion* from other Sabethini: larva with circular occipital foramen; concentration of aciculae on one side of the branches of setae 4-P and 7-T; stout seta 11-T with multiple apical spikes; strong development and placement of seta 13-IV,V lateral to setae 11 and 12; presence of a dense filamentous pecten extending the length of the siphon; the presence of punctures on abdominal segments III and IV of the pupa; and strong development of the cercal setae on the male genitalia (Harbach and Peyton 2000). In the cladistic analysis, we scored two characters, the circular occipital foramen of the fourth-instar larva and development of the cercal setae of the male genitalia; however, because they were autapomorphies for *Onirion* they were excluded from all analyses. Although the autapomorphies are not informative in terms of resolving relationships, they are arrayed as unique characters that are not contradicted, and thus give a clear indication of the degree of morphological divergence. The presence of a circular occipital foramen in *Onirion* is shared with other genera of Sabethini, including *Shannoniana* and *Trichoprosopon* Theobald. However, it is a distinctive character for *Onirion* in comparison with other *Wyeomyia* species. None of the taxa with a circular occipital foramen were used as outgroup in our analysis and this character could have affected the relationship of *Onirion* with *Wyeomyia*. Similarly, *O. personatum* was placed in an unresolved relationship in the cladistic analysis of the Sabethini by Judd (1996). This taxon appears as a separate lineage arising between *W. melanocephala* and a group comprised of *Limatus*, *Phoniomyia*, and *Wyeomyia* species.

The phylogenetic position of *Onirion* within the Sabethini is ambiguous. Consequently, it is suggestive of two scenarios. According to the principle of equivalent rank, *Onirion* can be retained as a genus of the Sabethini, and thus certain subgenera of *Wyeomyia* might be elevated to generic rank. An alternative scenario would be to regard *Onirion* as a subgenus of *Wyeomyia*. However, we consider that it is premature to make any taxonomic change, as more detailed studies are necessary. As a consequence, we choose to maintain the generic status of *Onirion* and the subgeneric status of all monophyletic lineages recovered in the study. Furthermore, elevation to generic rank and excessive splitting of tribe could cause taxonomic instability.

The subgenus *Dendromyia* (node 22) was confirmed as a monophyletic group within *Wyeomyia*, supported by eight synapomorphies: larva with maxilla with a denticular laciniarastrum 1 (character 1); seta 15-C inserted between the anterior border of the labiogula and the termination of the hypostomal ridge (character 16); segment X with the saddle covering half of segment X (character 26); pecten spines disposed in a single row (character 30); presence of spicules on the siphon (character 31); siphon with seta 2a-S very strong, stout, and sclerotized (character 36); pupal seta 6-VII ventral (character 49); and a broad interocular space (character 68). Bootstrap support for the *Dendromyia* clade is 95% and the Bremer support value is 6. The subgenus *Dendromyia* was redefined by Motta and Lourenço-de-Oliveira (1995, 2000) on the basis of morphological and allozyme data (Motta *et al.* 1998), but its phylogenetic position within *Wyeomyia* has not been tested until now.

Node 26 defines a clade formed by (*W. chalcocephala*, *W. surinamensis*, *W. flui*, and *Wyeomyia* sp. 4) plus (*W. ulocoma* and *W. felicia*), supported by two synapomorphies: male genital lobe without a fingerlike projection (character 65) and upper calypter with marginal setae (character 82). The clade (node 27) composed of *W. chalcocephala*, *W. surinamensis*, *W. flui*, and *Wyeomyia* sp. 4 ("flui group") is supported by four synapomorphies: larva with pecten spines disposed in a single row (character 30); paddle apex truncate (character 54); adult with mesopostnotal scales anterior to mesopostnotal setae (character 79); and presence of one spermathecal capsule (character 88). Bootstrap support for the split leading to this group is 59%. Although bootstrap support is not strong, the results of the study suggest that *W. chalcocephala*, *W. surinamensis*, *W. flui*, and *Wyeomyia* sp. 4 belong to a phylogenetic lineage that can be defined as a new, unnamed subgenus, which will be defined in a future publication (M.A. Motta, in preparation).

The subgenus *Decamyia* (*W. ulocoma* and *W. felicia*) forms a clade (node 30) supported by two synapomorphies (larval seta 1-S single

Table 4. Allele frequencies for 11 loci in 19 species studied.

	Population									
Locus	1	2	3	4	5	6	7	8	9	10
MDH										
n	29	27	23	19	7	1	26	16	29	15
A	0.000	0.000	**0.457**	0.000		0.000	0.000	0.000	0.000	0.000
B	1.000	1.000	0.543	0.000	1.000	1.000	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	0.000	0.000	0.000	1.000	0.000	0.000	1.000	1.000	1.000	1.000
E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGM										
n	24	22	27	20	7	2	29	16	26	17
A	0.146	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.000	0.000
B	0.542	0.205	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.750	0.324
D	0.313	0.795	0.000	0.175	0.000	0.000	0.086	0.750	0.000	0.000
E	0.000	0.000	1.000	0.825	1.000	0.750	0.000	0.000	0.250	0.265
F	0.000	0.000	0.000	0.000	0.000	0.000	0.810	0.250	0.000	0.000
G	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H	0.000	0.000	0.000	0.000	0.000	0.000	0.103	0.000	0.000	0.412
I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
IDH-1										
n	28	29	27	20	5	2	31	17	29	18
A	0.054	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.028
B	0.000	0.000	0.500	0.000	0.000	0.250	0.161	0.029	0.000	0.972
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	0.946	0.931	0.500	1.000	1.000	0.750	0.839	0.971	0.000	0.000
E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
F	0.000	0.069	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
IDH-2										
n	28	27	2	21	7	1	31	17	30	19
A	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
D	1.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000
E	0.000	0.000	1.000	0.000	0.000	0.000	1.000	0.000	0.000	1.000
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
FUM										
n	25	22	24	14	7	2	25	17	20	18
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	0.000	0.000	0.000	**0.214**	0.000	0.000	0.000	0.000	0.000	0.000
E	1.000	1.000	1.000	0.786	1.000	1.000	1.000	1.000	1.000	0.000
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
GPI										
n	32	27	30	21	7	2	27	16	29	14
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
C	0.172	0.315	0.000	0.833	0.000	0.000	0.000	0.000	0.190	0.000
D	0.828	0.685	1.000	0.167	1.000	1.000	0.000	0.000	0.810	0.000
E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000

11	12	13	14	15	16	17	18	19
26	26	26	29	12	28	24	29	31
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.952
0.000	0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000
1.000	1.000	1.000	0.000	0.000	0.000	0.938	1.000	0.048
0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	**0.063**	0.000	0.000
25	28	26	30	12	28	28	29	28
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.107	0.000	0.339
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.880	0.214	0.000	0.667	0.292	0.036	0.000	0.017	0.661
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.120	0.786	0.058	0.333	0.708	0.929	0.000	0.879	0.000
0.000	0.000	0.942	0.000	0.000	0.036	0.893	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.103**	0.000
27	28	29	26	12	29	29	30	29
0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000
0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.083	0.983	0.000	0.000	1.000
0.000	0.000	0.603	1.000	0.000	0.000	0.000	0.917	0.000
0.000	0.000	0.000	0.000	**0.917**	0.000	0.000	0.000	0.000
1.000	0.000	0.397	0.000	0.000	0.000	1.000	0.000	0.000
26	28	25	27	12	29	29	20	28
0.000	0.000	0.000	0.000	0.000	0.000	0.000	.000	0.161
0.000	0.000	0.000	0.000	0.000	1.000	1.000	1.000	0.000
0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
1.000	1.000	0.000	0.000	1.000	0.000	0.000	0.000	0.839
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000	0.000
26	24	20	28	12	24	24	26	24
0.000	0.000	**1.000**	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000
1.000	1.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
26	22	25	25	12	25	30	25	27
0.000	0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.040	0.000	0.000	0.000	0.000	1.000	0.000
0.712	0.000	0.960	0.000	0.000	0.000	1.000	0.000	1.000
0.288	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 4 (*concluded*).

	Population									
Locus	1	2	3	4	5	6	7	8	9	10
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G	0.000	0.000	0.000	0.000	0.000	0.000	**0.870**	0.000	0.000	0.000
H	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
I	0.000	0.000	0.000	0.000	0.000	0.000	**0.130**	0.000	0.000	0.000
6PG										
n	17	17	29	14	1	2	32	18	32	14
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
D	0.559	0.559	0.000	0.500	0.000	0.000	0.000	0.000	0.000	0.000
E	0.441	0.441	0.000	0.500	1.000	0.000	1.000	1.000	1.000	1.000
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
AK										
n	22	22	19	17	7	2	13	9	14	16
A	0.000	0.000	0.000	0.000	**0.214**	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	1.000	1.000	1.000	0.882	0.000	0.000	0.000	0.000	0.000	0.000
D	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
F	0.000	0.000	0.000	0.118	0.786	0.000	0.923	1.000	1.000	0.000
G	0.000	0.000	0.000	0.000	0.000	0.000	0.077	0.000	0.000	1.000
GPD										
n	28	30	32	20	7	2	32	18	31	19
A	0.000	0.000	0.000	**0.050**	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.056	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	1.000	1.000	1.000	0.850	0.000	1.000	1.000	0.944	1.000	1.000
E	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
HK										
n	31	30	28	20	7	2	28	14	25	18
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	1.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
D	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ME										
n	23	22	28	20	6	2	26	12	26	17
A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	000
D	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
E	0.000	0.091	1.000	0.000	0.167	1.000	0.000	0.000	0.000	0.000
F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G	0.739	0.659	0.000	1.000	0.833	0.000	0.000	0.000	0.000	0.000
H	0.261	0.250	0.000	0.000	0.000	0.000	1.000	1.000	1.000	1.000
I	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
J	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Note: *n* is the sample size per locus. Alleles shown in boldface type were not considered for cladistic analysis.

11	12	13	14	15	16	17	18	19
0.000	0.000	0.000	1.000	0.000	1.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	**1.000**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
13	20	17	15	1	21	14	20	15
0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	1.000	1.000	0.000	0.000	0.000
1.000	1.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
0.000	0.000	**1.000**	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000	0.000
21	17	15	22	12	19	23	20	21
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000	1.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1.000	1.000	0.000	0.000	0.000	0.000	0.478	1.000	0.000
0.000	0.000	0.000	0.000	**1.000**	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	1.000	0.522	0.000	0.000
0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
28	30	28	31	13	29	30	29	29
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.911	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**
0.089	1.000	0.000	1.000	1.000	1.000	0.967	1.000	0.000
0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
25	28	24	28	13	28	28	24	22
0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	1.000	1.000	1.000	1.000	1.000	.000	1.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**
25	22	21	20	13	22	29	16	28
0.000	0.000	0.000	0.000	0.000	0.000	**0.310**	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	**0.690**	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.911**
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.089**
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	1.000	1.000	0.000	0.000	0.000
1.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.810	0.000	0.000	0.000	0.000	1.000	0.000
0.000	0.000	0.190	0.000	0.000	0.000	0.000	0.000	0.000

Table 5. Estimates of Neis (1978) unbiased genetic identity (above the diagonal) and genetic distance (below

	Population								
	1	2	3	4	5	6	7	8	9
1: bourr	*****	0.981	0.508	0.555	0.601	0.479	0.369	0.492	0.352
2: forci	0.019	*****	0.503	0.565	0.580	0.469	0.371	0.527	0.349
3: myste	0.677	0.688	*****	0.527	0.513	0.780	0.450	0.337	0.400
4: finla	0.589	0.572	0.641	*****	0.538	0.438	0.535	0.545	0.492
5: airos	0.509	0.544	0.668	0.621	*****	0.557	0.449	0.554	0.470
6: aning	0.735	0.756	0.248	0.825	0.584	*****	0.367	0.360	0.394
7: oblit	0.997	0.991	0.798	0.626	0.802	1.003	*****	0.778	0.681
8: lutzi	0.709	0.640	1.087	0.606	0.591	1.022	0.252	*****	0.669
9: medio	1.045	1.053	0.915	0.710	0.756	0.932	0.384	0.401	*****
10: arthr	1.736	1.742	0.993	0.995	1.515	1.423	0.480	0.734	661
11: ypsip	0.915	0.944	1.792	1.034	0.842	1.412	1.577	1.192	0.970
12: teste	1.114	1.155	1.539	0.775	0.953	1.184	0.949	0.758	950
13: negre	1.939	2.024	1.486	1.225	1.049	1.422	1.347	1.375	0.887
14: aporo	1.117	1.124	0.901	0.849	1.046	0.882	0.738	0.759	0.917
15: melan	1.336	1.335	1.493	1.322	1.510	1.526	1.630	1.265	1.609
16: perso	1.356	1.355	1.391	1.378	1.322	0.948	1.268	1.284	1.256
17: aphob	1.654	1.695	1.609	1.550	1.959	1.049	1.379	1.443	0.839
18: leuco	1.376	1.326	1.426	0.652	1.273	0.785	0.772	0.779	0.914
19: palma	1.293	1.348	1.524	2.336	1.081	1.408	5.332	2.444	2.072

(character 33) and male genitalia with a basal plate with a leaf-like seta (character 62)) and is supported by a bootstrap value of <50%. *Decamyia* was proposed as a genus by Dyar (1919) and has been treated as a synonym of *Dendromyia* since Edwards (1932) until Harbach and Peyton (1990*a*) resurrected it as a subgenus of *Wyeomyia*. Although bootstrap support for the *Decamyia* clade is weak (<50%), it is supported by a non-homoplastic synapomorphy (basal plate with a leaf-like seta). Also, the results of the present analysis corroborate the monophyly of *Decamyia* and its placement as a subgenus of *Wyeomyia*.

The current analysis also supports the monophyly of the subgenus *Spilonympha* (node 31), corroborating the previous taxonomic status of this group (Motta and Lourenço-de-Oliveira 2005). The subgenus *Spilonympha* is supported by four synapomorphies: larval segment VIII with a sclerotized plate (character 24); absence of seta 2a-S (character 36); presence of numerous accessory setae on the siphon (character 37); lobe C of the gonostylus somewhat ladle-like (character 57); and a broad interocular space (character 68). This arrangement is supported by a bootstrap value of 81%.

Analysis of allozyme data from 19 species by means of the BIOSYS program yielded the dendrogram shown in Figure 1. Allele frequencies of 11 loci in the 19 species studied (Table 4) produced genetic identity values (*I*) that were used to construct the UPGMA dendrogram. This analysis resulted in an arrangement similar to that of *Spilonympha*, *Wyeomyia*, *Dendromyia*, *Phoniomyia*, and the genus *Onirion* in the cladistic analysis. In the allozyme analysis *W. palmata* and *W. aphobema* appeared to be the most divergent species in the group, which partially agrees with the results of the morphological cladistic analysis. The *I* values between *W. palmata* and other *Wyeomyia* species were low (0.005–0.339). As is noted in Table 5, the limits of *I* values varied from one group to another; consequently, it is difficult to fix a range for each taxon. However, in reviews of the relationships of *I* values in the systematic diversity of different groups, Thorpe (1982) and Thorpe and Solé-Cava (1994) concluded that among congeneric species the usual range is 0.30–0.85. Thus, the *I* values obtained for species of the subgenera *Phoniomyia* and *Wyeomyia* suggest that they belong to distinct groups.

Onirion personatum formed a cluster with *W. melanocephala* in the allozyme analysis, and the levels of identity observed between them were similar to those defined for congeneric species ($I = 0.54$). The internal organization of *Spilonympha* shows that *W. mystes* is more

the diagonal) for pairwise comparisons between 19 species.

10	11	12	13	14	15	16	17	18	19
0.176	0.400	0.328	0.144	0.327	0.263	0.258	0.191	0.253	0.274
0.175	0.389	0.315	0.132	0.325	0.263	0.258	0.184	0.266	0.260
0.370	0.167	0.215	0.226	0.406	0.225	0.249	0.200	0.240	0.218
0.370	0.356	0.461	0.294	0.428	0.267	0.252	0.212	0.521	0.097
0.220	0.431	0.386	0.350	0.351	0.221	0.267	0.141	0.280	0.339
0.241	0.244	0.306	0.241	0.414	0.217	0.387	0.350	0.456	0.245
0.619	0.207	0.387	0.260	0.478	0.196	0.281	0.252	0.462	0.005
0.480	0.304	0.469	0.253	0.468	0.282	0.277	0.236	0.459	0.087
0.516	0.379	0.387	0.412	0.400	0.200	0.285	0.432	0.401	0.126
*****	0.255	0.390	0.236	0.401	0.201	0.194	0.231	0.384	0.131
1.366	*****	0.611	0.207	0.069	0.139	0.022	0.427	0.308	0.216
0.940	0.492	*****	0.198	0.227	0.344	0.255	0.333	0.543	0.100
1.446	1.577	1.619	*****	0.158	0.102	0.104	0.319	0.335	0.201
0.913	2.673	1.484	1.846	*****	0.232	0.312	0.096	0.304	0.043
1.605	1.974	1.068	2.283	1.461	*****	0.542	0.096	0.345	0.109
1.642	3.813	1.367	2.259	1.165	0.613	*****	0.246	0.449	0.188
1.464	0.850	1.099	1.144	2.347	2.340	1.401	****	0.334	0.110
0.958	1.177	0.611	1.094	1.190	1.064	0.800	1.098	*****	0.006
2.029	1.533	2.306	1.606	3.150	2.214	1.671	2.208	5.150	*****

closely related to *W. aningae* (Fig. 1), as was observed in the cladistic analysis (Fig. 6), and the level of identity among *Spilonympha* species varied from 0.43 to 0.98. Species of the subgenus *Wyeomyia* are included in a distinct cluster that is separate from the remaining species included in the present study. The most closely related species were *W. oblita* and *W. lutzi*, which corroborates the results of the cladistic analysis (Fig. 6). Analysis of the allozyme data failed to resolve relationships among *W. aporonoma*, *W. aphobema*, *W. leucostigma*, and the remaining species included in the study, probably because of sample sizes.

As has been observed by several authors (Dyar and Knab 1906; Dyar 1919, 1928; Belkin *et al.* 1970; Judd 1998*b*), knowledge of all life stages, primarily the larva, is of considerable value for making phylogenetic inferences concerning taxa. However, problems with life-stage incongruence have been observed since Dyar and Knab (1906). Judd (1998*b*) discussed this problem. Different life stages are subject to different environmental selection pressures that can account for observed morphological differences (Judd 1998*b*); such as in the sabethines, which are restricted to developing and ovipositing in one type of habitat.

Significant structural modifications occur mainly in the larval stage and are probably influenced by adaptation. This is a possible source of homoplasy and masks phylogenetic relationships. In the sabethines, we observed that those species that develop in bromeliads have similar morphological characteristics. *Phoniomyia* species, which inhabit bromeliads, possess morphological features in the larval and pupal stages similar to those of bromeliad-inhabiting *Wyeomyia* species (*e.g.*, the subgenus *Hystatomyia*).

Our results also suggest that *Cruzmyia*, *Decamyia*, *Dendromyia*, *Spilonympha*, and *Prosopolepis* are monophyletic lineages within the genus *Wyeomyia*. In the present study, hypotheses concerning phylogenetic relationships within the genus *Wyeomyia* have been proposed on the basis of synapomorphies that are unique or have the least amount of homoplasy. Based on the results of morphological and allozyme analyses, this study indicates that, as currently defined, the genus *Wyeomyia* is not a monophyletic lineage. We propose two main changes in the current classification of the genus: (1) resurrection of subgenus *Triamyia* Dyar to include *W. aporonoma* and *W. staminifera*; (2) resurrection of the subgenus *Miamyia* Dyar to include seven species, *W. codiocampa*, *W. lutzi*, *W. limai*, *W. serrata*, *W. hosautos*, *W. oblita*, and *W. sabethea*. We also suggest that *W. flui*, *W. surinamensis*, *W. chalcoceplala*, and

Wyeomyia sp. 4 belong to a distinct unnamed subgenus. The relationships of *W. negrensis* and *W. argenteorostris* varied, and for this reason they will continue to be without subgeneric assignment in the genus *Wyeomyia*.

The present analysis of *Wyeomyia* is a start toward resolving the evolutionary history of the genus, a first step in establishing a natural classification. Moreover, there are numerous partially described species without subgeneric placement and several undescribed species. Also,better knowledge of the genus *Wyeomyia* will provide a footing for establishing relationships within the Sabethini.

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