First phylogeny of predatory flower flies (Diptera, Syrphidae, Syrphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the current tribal classification

Ximo Mengual[a]*, Gunilla Ståhls[b] and Santos Rojo[a]

[a]*Dpto. de Ciencias Ambientales/Instituto Universitario CIBIO, Universidad de Alicante, Apdo 99. E-03080 Alicante, Spain;* [b]*Finnish Museum of Natural History, PO Box 17, FI-00014 University of Helsinki, Finland*

Abstract

The family Syrphidae (Diptera) is traditionally divided into three subfamilies. The aim of this study was to address the monophyly of the tribes within the subfamily Syrphinae (virtually all with predaceous habits), as well as the phylogenetic placement of particular genera using molecular characters. Sequence data from the mitochondrial protein-coding gene *cytochrome c oxidase subunit I* (*COI*) and the nuclear *28S ribosomal RNA* gene of 98 Syrphinae taxa were analyzed using optimization alignment to explore phylogenetic relationships among included taxa. *Volucella pellucens* was used as outgroup, and representatives of the tribe Pipizini (Eristalinae), with similar larval feeding mode, were also included. Congruence of our results with current tribal classification of Syrphinae is discussed. Our results include the tribe Toxomerini resolved as monophyletic but placed in a clade with genera *Ocyptamus* and *Eosalpingogaster*. Some genera traditionally placed into Syrphini were resolved outside of this tribe, as the sister groups to other tribes or genera. The tribe Bacchini was resolved into several different clades. We recovered Paragini as a monophyletic group, and sister group of the genus *Allobaccha*. The present results highlight the need of a reclassification of Syrphinae.

© The Willi Hennig Society 2008.

Syrphidae (Diptera: Cyclorrhapha) commonly called hover or flower flies, comprise almost 6000 described species and is a speciose family of Diptera (Thompson, 2006). Almost all adult syrphids visit flowers for pollen and nectar. Larvae, on the other hand, are found in a very diverse array of habitats, including fungal fruiting bodies (mycophagy), dung, nests of social Hymenoptera, decaying wood and water bodies of several types (saprophagy), mining in leafs and stems of numerous plant families (phytophagy), and as predators of arthropods. Three subfamilies, Microdontinae, Eristalinae and Syrphinae, and 14 tribes are currently recognized in the family (Thompson and Rotheray, 1998).

Ståhls et al. (2003) presented the most recent phylogenetic study on Syrphidae. They used a combined analysis of molecular and morphological characters, and addressed the systematic position of the disputed elements in the intrafamilial classification of Syrphidae, namely the monophyly of Eristalinae and the placement of Microdontinae and Pipizini. Their study showed that the Microdontinae (including the genus *Spheginobaccha*) formed a clade, and Pipizini and Syrphinae were placed as the sister groups, except in the equal weight parsimony analysis where Pipizini was resolved as the sister group to Eristalinae + Syrphinae.

Larval feeding modes of Syrphidae

Immature stages of Microdontinae are inquilines in ants' nests feeding on eggs, larvae and pupae, whereas larvae of Eristalinae include saprophages in a wide range of decaying media from dung to dead wood, while some species of the genus *Volucella* are wasp- and

*Corresponding author:
E-mail address:* xmengual@ua.es

bee-brood predators, and *Nepenthosyrphus* larvae are sit-and-wait aquatic predators in the water-filled leaves of *Nepenthes* in South-east Asia (Mogi and Chan, 1996; Rotheray, 2003). Larvae of Syrphinae are mostly predaceous on soft-bodied Hemiptera (*sensu* Sorensen et al., 1995) such as aphids, coccids and psyllids, but some species feed on Thysanoptera, immature Coleoptera and/or Lepidoptera (Rotheray, 1993; see Rojo et al., 2003 for a review).

A recent finding shows that not all larvae of Syrphinae are predators, as phytophagy was found in the genus *Allograpta* (Nishida et al. 2002) and the larvae of the species *Toxomerus politus* is known to also feed on pollen (see comments in Rojo et al., 2003). Moreover, there are new prey groups recently discovered for predatory syrphid larvae, e.g., larvae of *Ocyptamus wulpianus* feed on soft-bodied larvae of craneflies (Tipulidae), mosquitoes (Culicidae) and aquatic beetles (Coleoptera, Helodidae) (Rotheray et al., 2000).

Subfamily Syrphinae: taxonomic history

The subfamily Syrphinae has been defined many times including different tribes and genera. The first subfamilial classification of Syrphidae was by Newman (1834), who divided the family in Chrysitoxites and Syrphites, and suggested the division of Syrphites into four subgroups: Syrphities, Eristalites, Volucellites and Rhingites. Williston (1887) established three subfamilies (Syrphinae, Eristalinae and Cerinae) and subfamily Syrphinae was divided into seven tribes. Shannon's (1921, 1922, 1923) comprehensive studies on North American taxa recognized 10 subfamilies, including a well-defined Syrphinae with four tribes (Melanostomini, Syrphini, Paragini and Bacchini); and Hull (1949a) classified syrphids into 14 subfamilies and divided Syrphinae into three tribes: Syrphini, Bacchini and Melanostomini.

Goffe (1952) used adult characters and divided Syrphinae in four tribes: Sphaerophorini (including genera *Baccha* and *Sphaerophoria*), Stenosyrphini (with genera *Melanostoma*, *Platycheirus* and others), Chrysotoxini and Syrphini (including genus *Paragus*). Wirth et al. (1965) recognized six tribes: Bacchini, Melanostomini, Paragini, Chrysotoxini, Syrphini and Pipizini, the latter was earlier included in the subfamily Eristalinae. Two years later, Dusek and Laska (1967), using larval and adult characters, divided the subfamily into seven tribes (Sphaerophorini, Melanostomini, Xanthogrammini, Chrysotoxini, Paragini, Dideini and Syrphini), and tribe Pipizini was treated as a part of the subfamily Eristalinae. Vockeroth (1969) recognized six tribes based on male terminalia and immature stages: Paragini, Chrysotoxini, Bacchini, Melanostomini, Toxomerini and Syrphini. He was the

first to discuss Neotropical Syrphinae, establishing the monogeneric tribe Toxomerini, and considered Pipizini as a member of Eristalinae. These two latter papers form the basis of the current classification of Syrphinae. Vockeroth (1992) adjusted his classification recognizing only four tribes in Syrphinae (including *Chrysotoxum* in the Syrphini and placing Melanostomini under Bacchini), and transferred genus *Ocyptamus* from the Bacchini to the Syrphini. For the Manual of Palaearctic Diptera, Thompson and Rotheray (1998) followed him and four tribes are recognized currently in the subfamily Syrphinae: Bacchini, Paragini, Syrphini and Toxomerini. Genera currently classified into Syrphinae are listed in Table 1 based mainly in Thompson (2006).

Target taxa of the present study

The genus *Allograpta* is distributed almost worldwide, absent only in northern Nearctic and western Palaearctic areas. Vockeroth (1969, 1973a) described it as one of the most variable genera of the tribe Syrphini based on the external morphology of adults, but with consistent aedeagal characters of the male genitalia. Because of the great variation in body size, shape of abdomen, body color pattern, and head shape of adults within the genus, a number of generic or subgeneric segregates were proposed. Immature stages of most known *Allograpta* species are predators of aphids and psyllids (reviewed in Rojo et al., 2003), and it is the only genus in Syrphini containing completely non-predaceous species, i.e., *Allograpta centropogonis* (Nishida et al. 2002). This switch in larval feeding biology found in *Allograpta* is relevant and interesting in the study of the evolution of larval feeding modes in Syrphinae.

Ocyptamus is a New World genus distributed in Nearctic and Neotropical regions. Species of this genus show much greater variation in color pattern and body shape than do those of any other genus of the tribe, and they also show more variation in the male genitalia than do those of most genera (Vockeroth, 1969). Many species of this genus were described in genera as different as *Syrphus*, *Episyrphus*, *Epistrophe*, *Melangyna* (all Syrphini) and *Baccha* (Hull, 1949a,b; Fluke, 1956). This huge variation in placement of particular taxa prompted us to study the phylogenetic relationships of taxa of *Ocyptamus*, by including as many morphologically diverse taxa as possible.

The taxonomical borders and contents of the tribe Bacchini and genus *Baccha* has changed considerably since the description of genus *Baccha* by Fabricius (1805) as *Syrphus elongatus*. We were particularly interested in how molecular characters would resolve the tribal classification and attempted to include as much taxonomical diversity as possible.

Table 1
Attempted synthesis of generic and subgeneric names in Syrphinae (using current classification in four tribes)

Name	Author	Type species
Tribe Bacchini		
Argentinomyia	Lynch Arribalzaga 1891	*Argentinomyia testaceipes* Lynch Arribalzaga, 1891
Baccha	Fabricius 1805	*Baccha elongata* (Fabricius, 1775)
Leucopodella	Hull 1949	*Leucopodella bigoti* (Austen, 1893)
Melanostoma	Schiner 1860	*Melanostoma mellinum* (Linnaeus, 1758)
Platycheirus	Lepeletier & Serville 1828	*Platycheirus (Platycheirus) scutatus* (Meigen, 1822)
*Platycheirus (Carposcalis)**	Enderlein 1937	*Platycheirus (Carposcalis) stegnus* (Say, 1829)
*Platycheirus (Eocheilosia)**	Hull 1949	*Platycheirus (Eocheilosia) ronana* (Miller, 1921)
*Platycheirus (Pachysphyria)**	Enderlein 1937	*Platycheirus (Pachysphyria) dexter* (Harris, 1780)
Pseudoplatychirus	Doesburg 1955	*Pseudoplatychirus peteri* Doesburg, 1955
Pyrophaena	Schiner 1860	*Platycheirus (Pyrophaena) rosarum* (Fabricius, 1787)
Rohdendorfia	Smirnov 1924	*Rohdendorfia dimorpha* Smirnov, 1924
Spazigaster	Rondani 1843	*Spazigaster apennini* Rondani, 1843
Syrphocheilosia	Stackelberg 1964	*Syrphocheilosia aterrima* Stackelberg, 1964
*Talahua**	Fluke 1945	*Talahua fervida* (Fluke, 1945)
*Tuberculanostoma**	Fluke 1943	*Tuberculanostoma antennatum* Fluke, 1943
Xanthandrus	Verrall 1901	*Xanthandrus (Xanthandrus) comtus* (Harris, 1780)
*Xanthandrus (Androsyrphus)**	Thompson 1981	*Xanthandrus (Androsyrphus) setifemoratus* Thompson, 1981
Tribe Syrphini		
*Afrosyrphus**	Curran 1927	*Afrosyrphus varipes* Curran, 1927
*Agnisyrphus**	Ghorpade 1994	*Agnisyrphus angara* Ghorpade, 1994
Allobaccha	Curran 1928	*Allobaccha rubella* (Wulp, 1898)
Allograpta	Osten Sacken 1875	*Allograpta (Allograpta) obliqua* (Say, 1823)
*Allograpta (Antillus)**	Vockeroth 1969	*Allograpta (Antillus) ascita* (Vockeroth, 1969)
Allograpta (Fazia)	Shannon 1927	*Allograpta (Fazia) decemmaculata* (Rondani, 1863)
*Allograpta (Rhinoprosopa)**	Hull 1942	*Allograpta (Rhinoprosopa) aenea* (Hull, 1937)
Asarkina	Macquart 1834	*Asarkina (Asarkina) rostrata* (Wiedemann, 1824)
*Asarkina (Achoanus)**	Munro 1924	*Asarkina (Achoanus) hulleyi* (Munro, 1924)
*Asiodidea**	Stackelberg 1930	*Asiodidea nikkoensis* (Matsumura, 1916)
*Betasyrphus**	Matsumura 1917	*Betasyrphus serarius* (Wiedemann, 1830)
Chrysotoxum	Meigen 1803	*Chrysotoxum bicinctum* (Linnaeus, 1758)
*Citrogramma**	Vockeroth	*Citrogramma hervebazini* (Curran, 1928)
Dasysyrphus	Enderlein 1937	*Dasysyrphus albostriatus* (Fallen, 1817)
Dideoides	Brunetti 1908	*Dideoides ovatus* Brunetti, 1908
*Dideomima**	Vockeroth 1969	*Dideomima coquilletti* (Williston, 1891)
Dideopsis	Matsumura 1917	*Dideopsis aegrota* (Fabricius, 1805)
*Doros**	Meigen 1803	*Doros profuges* (Harris, 1780)
*Eosphaerophoria**	Frey 1946	*Eosphaerophoria marginata* Frey, 1946
Epistrophe	Walker 1852	*Epistrophe grossulariae* (Meigen, 1822)
Epistrophella	Dusek & Laska 1967	*Epistrophella euchroma* (Kowarz, 1885)
Episyrphus	Matsumura & Adachi 1917	*Episyrphus (Episyrphus) balteatus* (De Geer, 1776)
*Episyrphus (Asiobaccha)**	Violovitsh 1976	*Episyrphus (Asiobaccha) nubilipennis* (Austen, 1893)
Eriozona	Schiner 1860	*Eriozona syrphoides* (Fallen, 1817)
*Eupeodes**	Osten Sacken 1877	*Eupeodes (Eupeodes) volucris* Osten Sacken, 1877
Eupeodes (Lapposyrphus)	Dusek & Laska 1967	*Eupeodes (Lapposyrphus) lapponicus* (Zetterstedt, 1838)
Eupeodes (Macrosyphus)	Matsumura & Adachi 1917	*Eupeodes (Macrosyrphus) okinawensis* (Matsumura, 1916)
Eupeodes (Metasyrphus)	Matsumura 1917	*Eupeodes (Metasyrphus) corollae* (Fabricius, 1794)
*Exallandra**	Vockeroth 1969	*Exallandra cinctifacies* (Speiser, 1910)
Fagisyrphus	Dusek & Laska 1967	*Fagisyrphus cinctus* (Fallen, 1817)
*Giluwea**	Vockeroth 1969	*Giluwea flavomacula* Vockeroth, 1969
*Lamellidorsum**	Huo & Zheng 2005	*Lamellidorsum piliflavum* Huo & Zheng, 2005
Leucozona	Schiner 1860	*Leucozona (Leucozona) lucorum* (Linnaeus, 1758)
Leucozona (Ischyrosyrphus)	Bigot 1882	*Leucozona (Ischyrosyrphus) sivae* (Bigot, 1882)
Megasyrphus	Dusek & Laska 1967	*Megasyrphus erraticus* (Linnaeus, 1758)
Melangyna	Verrall 1901	*Melangyna (Melangyna) quadrimaculata* (Verrall, 1873)
*Melangyna (Austrosyrphus)**	Vockeroth 1969	*Melangyna (Austrosyrphus) novaezealandiae* (Macquart, 1855)
*Melangyna (Melanosyrphus)**	Vockeroth 1969	*Melangyna (Melanosyrphus) dichoptica* Vockeroth, 1969
Meligramma	Frey 1946	*Meligramma guttata* (Fallen, 1817)
Meliscaeva	Frey 1946	*Meliscaeva cinctella* (Zetterstedt, 1843)
*Notosyrphus**	Vockeroth 1969	*Notosyrphus goldbachi* (Fluke, 1950)
Ocyptamus	Macquart 1834	*Ocyptamus (Ocyptamus) fuscipennis* (Say, 1823)
Ocyptamus (Hermesomyia)	Vockeroth 1969	*Ocyptamus (Hermesomyia) wulpianus* (Lynch Arribalzaga, 1891)

Table 1
(Continued)

Name	Author	Type species
*Ocyptamus (Mimocalla)**	Hull 1943	*Ocyptamus (Mimocalla) capitatus* (Loew, 1863)
Parasyrphus	Matsumura 1917	*Parasyrphus aeneostoma* (Matsumura, 1917)
*Pelloloma**	Vockeroth 1973	*Pelloloma nigrifacies* Vockeroth, 1973
*Pseudodoros**	Becker 1903	*Pseudodoros (Pseudodoros) nigricollis* Becker, 1903
Pseudodoros (Dioprosopa)	Hull 1949	*Pseudodoros (Dioprosopa) clavatus* (Fabricius, 1794)
*Rhinobaccha**	Meijere 1908	*Rhinobaccha gracilis* Meijere, 1908
*Salpingogaster**	Schiner 1868	*Salpingogaster (Salpingogaster) pygophora* Schiner, 1868
Salpingogaster (Eosalpingogaster)	Hull 1949	*Salpingogaster (Eosalpingogaster) conopida* (Philippi, 1865)
Scaeva	Fabricius 1805	*Scaeva (Scaeva) pyrastri* (Linnaeus, 1758)
Scaeva (Semiscaeva)	Kuznetzov 1985	*Scaeva (Semiscaeva) selenitica* (Meigen, 1822)
Simosyrphus	Bigot 1882	*Simosyrphus grandicornis* (Macquart, 1842)
Sphaerophoria	Lepeletier & Serville 1828	*Sphaerophoria (Sphaerophoria) scripta* (Linnaeus, 1758)
*Sphaerophoria (Loveridgeana)**	Doesburg & Doesburg 1977	*Sphaerophoria (Loveridgeana) beattiei* (Doesburg & Doesburg, 1977)
Syrphus	Fabricius 1775	*Syrphus ribesii* (Linnaeus, 1758)
*Vockerothiella**	Ghorpade 1994	*Vockerothiella laticornis* (Curran, 1928)
Xanthogramma	Schiner 1860	*Xanthogramma pedissequum* (Harris, 1776)
Tribe Paragini		
Paragus	Latreille 1804	*Paragus (Paragus) bicolor* (Fabricius, 1794)
*Paragus (Afroparagus)**	Vujic & Radenkovic, 2008	*Paragus (Afroparagus) borbonicus* Macquart, 1842
Paragus (Pandasyopthalmus)	Stuckenberg 1954	*Paragus (Pandasyopthalmus) longiventris* Loew, 1858
Paragus (Serratoparagus)	Vujic & Radenkovic, 2008	*Paragus (Serratoparagus) pusillus* Stuckenberg, 1954
Tribe Toxomerini		
Toxomerus	Macquart 1855	*Toxomerus geminatus* (Say, 1823)

*Genera and subgenera not included in the present analysis. As a type species, current valid name is given.

Tribe Pipizini

Tribe Pipizini has been treated as a member of the subfamily Eristalinae using the traditional evidence from adult morphological characters (see Thompson, 1969, 1972). Vockeroth (1969) referred the tribe Pipizini to Eristalinae on the basis of characters of the adults, and World Catalogues (Vockeroth and Thompson, 1987; Thompson and Vockeroth, 1989; Thompson and Rotheray, 1998) followed him recognizing four tribes for Syrphinae: Bacchini, Toxomerini, Syrphini and Paragini.

Rotheray and Gilbert (1989) included the tribe Pipizini into subfamily Syrphinae using larval characters and recognized four other tribes (Bacchini, Paragini, Syrphini and Melanostomini). This paper was the first to use larval characters in a cladistic analysis to establish the classification of the Pipizini, prior to other papers estimating the placement of Pipizini using molecular data (Cheng et al., 2000; Ståhls et al., 2003). The present study does not aim to address the placement of Pipizini, but the tribe is included as additional taxa because of the similarity in larval feeding mode.

The aim of this study was to address the monophyly of the tribes within the subfamily Syrphinae, as well as the phylogenetic position of particular genera (*Allograpta, Paragus, Baccha, Ocyptamus*) using molecular characters. The mitochondrial protein-coding gene *cytochrome c oxidase subunit I* (COI) was chosen for sequencing, as well as the nuclear *28S ribosomal RNA* gene because both have proved to be informative for species-level and genus-level analyses, as demonstrated in a large number of studies of insect evolutionary relationships (e.g., Ståhls and Nyblom, 2000; Caterino et al., 2001; Ståhls et al., 2003, 2004; Arevalo et al., 2004; Mengual et al., 2006; Ståhls, 2006; Brammer and Dohlen, 2007; Winterton et al., 2007). The present study is the most comprehensively sampled phylogenetic study of Syrphinae, and it is the first to use molecular characters for subfamily Syrphinae to address tribal relationships.

Materials and methods

Taxa and characters

The taxon sampling covered as much taxonomic diversity as possible for Syrphinae. Most included species have Palaearctic or Holarctic distributions, but a fair number of samples of taxa from other biogeographical regions were also available or obtained for molecular work (Table 2). We also included representatives of the tribe Pipizini. *Volucella pellucens* (Syrphidae: Eristalinae: Volucellini) was chosen as the outgroup. Nomenclature follows mainly the Biosystematic Database of World Diptera for species name (Thompson, 2006).

Table 2
Taxon sampling used in the molecular analysis, including GenBank accession numbers. Four tribes are recognized following Thompson and Rotheray (1998); genera are listed in alphabetical order

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Bacchini				
Allobaccha sapphirina (Wiedemann, 1830)	S87	Thailand, Chiang Mai, IV.2001 Leg.: D. Quicke & N. Laurenne	EF127349	EF127430
Allobaccha sp. 1	S150	Tanzania, Amani Hills, 2001	EF127347	EF127428
Allobaccha sp. 2	S166	Malaysia, 2001.	EF127369	EF127449
Argentinomyia cf. *neotropica* (Curran, 1937)	Y208	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; Malaise trap in wooded, damp wash. 24°27.25′ S, 65°17.83′ W, 1278 m, 27.X/14.XI.2003. Leg.: M.E. Irwin, F.D. Parker	EF127363	EF501963
Argentinomyia CR-12 Thompson, *in litt*	XP17	Costa Rica, Páramo, Cerro de la Muerte 14.I.2005. Leg.: F.C. Thompson	EF127296	EF127374
Baccha elongata (Fabricius, 1775)	Y242	Finland, Ta: Vesijako, VII.2004, Malaise trap Leg.: J. Jakovlev	EF127326	EF127407
Leucopodella gracilis (Williston, 1891)	S488	Costa Rica, PN Tapanti, 1600 m, 12.I.2005. Leg.: S. Rojo	EF127365	EF127444
Leucopodella sp.	S78	Brazil, 2000	EF127331	EF127412
Melanostoma annulipes (Macquart, 1842)	XP53	Madagascar, Fianarantsoa Prov., road from Valbio to Ranomafana. 25.XI.2004. Leg.: X. Mengual	EF127320	EF127399
Melanostoma scalare(Fabricius, 1794)	G324	Finland, Al: Åland islands, 10.VI.1999 Leg.: G. Ståhls	AY212799	EF127417
Melanostoma sp.	S564	The Netherlands, Leiden, Meijendel dune area, 5.IX.2005, Leg.: excursion participants	EF127322	EF127401
Melanostoma univittatum (Wiedemann, 1824)	XP47	Indonesia, Northern Sulawesi, Tumarates, Langowan [Lagoon]. 1°08′N 124°50′E. 13/20. VIII.2004. Leg.: M. Meray, M.F. & C. Dien	EF127314	EF127393
Platycheirus peltatus (Meigen, 1822)	G245	Finland, N: Helsinki region, 11.VI.1998 Leg.: G. Ståhls	AY261706	AY261753
Platycheirus albimanus (Fabricius, 1781)	E38	Sweden, 2000. Leg.: J. van Steenis	EF127351	EF127432
Platycheirus nielseni Vockeroth, 1986	E36	Sweden, 2000. Leg.: J. van Steenis	EF127352	EF127433
Pseudoplatycheirus glupovi Barkalov *in litt*	S561	Russia, Altai, Plateau Ukok, VII.2005 Leg.: A.V. Barkalov	EF127317	EF127394
Pyrophaena granditarsa (Foster, 1771)	S563	The Netherlands, Leiden, IX. 2005 Leg.: J. van Steenis	EF127321	EF127400
Rohdendorfia alpina Sack, 1938	G344	Italy, South Tirol, Stelvio Pass, 28.VII.1999 Leg.: G. Ståhls	EF127338	EF127420
Rohdendorfia dimorpha Smirnov, 1924	S562	Russia, Altai, Plateau Ukok, VII.2005 Leg.: A.V. Barkalov	–	EF127395
Spazigaster ambulans (Fabricius, 1798)	S158	Austria, Imst. Leg.: J. van Steenis	EF127350	EF127431
Syrphocheilosia claviventris (Strobl, 1910)	G327	Italy, South Tirol, Stelvio Pass, 28.VII.1999 Leg.: G. Ståhls	EF127334	EF127415
Xanthandrus (Xanthandrus) comtus (Harris, 1780)	S121	Greece, Lesbos island, IV.2001 Leg.: S. Rojo & C. Pérez (L2)	EF127340	EF127422

Table 2
(Continued)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Xanthandrus (Xanthandrus) plaumanni Fluke, 1937	XP32	Colombia, Cali, Cerro Las Brisas, 1970 m. 20. VIII.2004. Leg.: C. Prieto	EF127307	–
Paragini				
Paragus (Pandasyopthalmus) haemorrhous Meigen, 1822	S48	Spain, Alicante, 2000. Leg.: S. Rojo	AY174470	AY476866
Paragus (Paragus) pecchiolii Rondani, 1857	S71	Montenegro, Durmitor, 26.VI.2000.	AY476844	AY476864
Paragus (Paragus) bicolor (Fabricius, 1794)	S108	Greece, Lesbos island, IV.2001 Leg.: S. Rojo & C. Pérez	AY476857	AY476873
Paragus (Serratoparagus) cremulatus Thomson, 1869	S62	Malaysia, Sabah, Danum Valley, VIII.1999	AY476862	AY476880
Syrphini				
Allograpta (Allograpta) calopus (Loew, 1858)	XP39	South Africa, Western Cape, Constantia 34°092′24″ S 18°25′43′ E. 260 m. 28.IX/06. X.2004. Leg.: M.E. Irwin, F. Parker & M. Hauser	EF127311	EF127390
Allograpta (Allograpta) fasciata Curran, 1932	S490	Costa Rica, PN Tapanti, 1600 m, 12.I.2005 Leg.: C. Pérez-Bañón	EF127366	EF127445
Allograpta (Allograpta) obliqua (Say, 1823)	XP38	USA, Utah, Garfield Co., Alvoy Wash. 7 km S Escalante. 37°42.5′N 111°37.8′W. 1990 m. 29.VI.2002. Leg.: M.E. Irwin & F. Parker	EF127310	EF127389
Allograpta (Allograpta) fuscotibialis (Macquart, 1842)	XP37	South Africa, Western Cape, Constantia. 34°092′24″ S 18°25′43′ E. 260 m. 28.IX/ 06.X.2004. Leg.: M.E. Irwin, F. Parker & M. Hauser	EF127309	EF127388
Allograpta (Fazia) centropogonis Nishida, 2003	S492	Costa Rica, PN Tapanti, Estacion La Esperanza, 2600 m, 13.I.2005. Leg.: A. Martinez	EF127367	EF127447
Allograpta (Fazia) sp. 1	XP25	Colombia, Cali, Cerro San Antonio 2180 m. 20.VII.2004. Leg.: C. Prieto.	EF127300	EF127379
Allograpta (Fazia) sp. 2	S491	Costa Rica, PN Tapanti, 1600 M, 12.I.2005. Leg.: m. Zumbado	–	EF127446
Allograpta (Allograpta) exotica (Wiedemann, 1830)	XP35	USA, New Mexico, Chaves Sagebrush Valley Road at Squa Canyon road. 32° 57′N 104° 50′W. 1/10.V.2004. Leg.: M.E. Irwin & F. Parker	EF127308	EF127387
Asarkina (Asarkina) ericetorum (Fabricius, 1781)	S222	Kenya, Kakamega forest, 5.XII.1995, 0°17. 13′N 34°56.32′E, Leg.: Earthwatch Team 6	EF127353	EF127434
Asarkina (Asarkina) fulva Hull, 1941	XP51	Madagascar, Fianarantsoa Prov. Ranomafana N.P., Talatakely region, near the river. 19.XI.2004. Leg.: X. Mengual.	–	EF127397
Chrysotoxum bicinctum (Linnaeus, 1758)	G139	Finland, Ab: Korppoo, 1997. Leg.: A. Haarto	EF127370	–
Chrysotoxum intermedium Meigen, 1822	S17	Spain, Alicante, 1999. Leg.: S. Rojo	EF127327	EF127408
Dasysyrphus albostriatus (Fallén, 1817)	S565	The Netherlands, Leiden, Meijendel dune area, 5.IX.2005. Leg.: excursion participants	EF127323	EF127402

Table 2
(Continued)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Dasysyrphus creper (Snow, 1895)	S359	USA, Arizona, San Doval, La Cueva, 2002. Leg.: M. Hauser	EF127368	EF127448
Dasysyrphus hilaris (Zetterstedt, 1843)	Y7	Finland, N: Vantaa, Keimola, 05.VI.2003. Leg.: G. Ståhls	EF127362	EF127442
Dasysyrphus lotus (Williston, 1887)	XP23	Colombia, Cali, Cerro San Antonio. 2200 m. 25.VIII.2004. Leg.: C. Prieto	EF127298	EF127377
Didea fuscipes Loew, 1863	XP26	USA, MO: Carter Co. Van Burer, 4 mi, SE. Big Spring Campground. 15.IV.2004. Leg. J. & W. van Steenis.	EF127301	EF127380
Didea intermedia Loew, 1862	S90	Finland	EF127336	EF127418
Dideoides coquilletti (van der Goot, 1964)	XP8	Korea, Gangweon-do, Weonju-si. Maeji-ri, Yonsei Univ. Campus. 4.X.1999. Leg.: C.H. Park.	EF127293	EF127373
Dideopsis aegrota (Fabricius, 1805)	S92	Australia. Leg.: J. Skevington	EF127333	EF127414
Epistrophe melanostoma (Zetterstedt, 1843)	S60	Finland, N: Keimola, 10.VI.2000. Leg.: G. Ståhls	EF127324	EF127405
Epistrophe nitidicollis (Meigen, 1822)	S61	Finland, Liesjärvi, 11.VI.2000. Leg.: G. Ståhls	EF127325	EF127406
Epistrophella euchroma (Kowarz, 1885)	S559	Czech Republic, Bohemia PLA distr. Chrudim Hermanuv mestec, park, 3.VI.2005. Leg.: L. Mazanek	EF127315	EF501964
Episyrphus (Episyrphus) balteatus (De Geer, 1776)	G77	Finland, Ta: Valkeakoski, 10.VIII.1997. Leg.: G. Ståhls	EF127335	EF127416
Episyrphus (Episyrphus) stuckenbergi (Doesburg, 1957)	XP52	Madagascar, Fianarantsoa Prov. Road from Valbio to Ranomafana City. 22.XI.2004. Leg.: X. Mengual.	EF127319	EF127398
Eriozona syrphoides (Fallén, 1817)	Y184	Russia, Gornyi Altai, Turotshakskii r-kordon obogo, 950 m, 30.VI.2003. Leg.: Krolatscheva D	EF127358	EF127439
Eupeodes (Lapposyrphus) lapponicus (Zetterstedt, 1838)	S65	Czech Republic, Olomouc, Svaty Kopecek, 13.V.2000. Leg.: J. Mazánková	DQ158897	EF127403
Eupeodes (Macrosyrphus) confrater (Wiedemann, 1830)	Y101	Korea, Gyeongsangbuk-do, Yeongju Sunheung-myeon, 8.VI.2002. Leg.: D.S. Choi	EF127355	EF127436
Eupeodes (Metasyrphus) fumipennis (Thomson, 1869)	XP46	Canada, BC: Vancouver Island. Nanaimo; Morrel Sanct. 49°08'49' N 123°58'31' W, 140 m. 5.V.2005. Leg.: W. van Steenis.	EF127313	EF127392
Eupeodes (Metasyrphus) lucasi (Marcos-Garcia & Laska, 1983)	L13	Spain, Alicante, Leg.: S. Rojo	EF127337	EF127419
Fagisyrphus cinctus (Fallén, 1817)	S512	Czech Republic, Jizerské Mountains, Rybí peat-bog, sq. 5158, 850 m, Malaise trap. 5/20.VIII.2003. Leg.: Preisler	EF127371	EF127450
Leucozona (Ischyrosyrphus) glaucia (Linnaeus, 1758)	XP5	Spain, Pyrenees, Aran Valley, nr. Arties, 1500 m, 1.VIII.2003. Leg.: G. Ståhls	EF127292	EF127372
Leucozona (Leucozona) lucorum (Linnaeus, 1758)	S139	Italy, South Tirol, Val Venosta, VII.2001. Leg.: G. Ståhls	EF127346	EF501965

Table 2
(Continued)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Megasyrphus erraticus (Linnaeus, 1758)	Y183	Finland, Ab: Karislojo, Karkalinniemi, V.2004. Leg.: G. Ståhls	EF127357	EF127438
Megasyrphus laxus (Osten Sacken, 1875)	XP27	Canada, AB. Jasper NP. Valley o/t Five Lakes. 117°98'E 52°48'N. 27.VIII.2004. Leg. W. van Steenis.	EF127302	EF127381
Melangyna (Melangyna) lasiophthalma (Zetterstedt, 1843)	Y5	Finland, N: Mäntsälän Mustametsä, 10.V.2003. Leg.: G. Ståhls	EF127361	EF501966
Melangyna (Melangyna) subfasciata (Curran, 1925)	XP28	Canada, Kluane. Whitehorse Airport. 135°05'E 60°45'N. 4.VIII.2004. Leg. W. van Steenis	EF127303	EF127382
Meligramma triangulifera (Zetterstedt, 1843)	S560	Czech Republic, Jizerské Mountains, Rybí loucky-peat-bog, sq. 5158, 850 m (malaise trap with alcohol), 5/20.VIII.2003. Leg.: Preisler	EF127316	EF501967
Meligramma guttata (Fallén, 1817)	Y478	Finland, Ab. Mietoinen, Perkko, 6733:222, 21.VII.2004. Leg.: A. Haaarto	EF501960	EF501968
Meliscaeva auricollis (Meigen, 1822)	S123	Greece, Lesbos island, IV.2001. Leg.: S. Rojo & C. Pérez	EF127341	EF127423
Meliscaeva cinctella (Zetterstedt, 1843)	S557	Czech Republic, Bohemia, PLA Jezerske mountains, Korenov, 12.VI.2005. Leg.: L. Mazanek	EF501961	EF501969
Ocyptamus (Hermesomyia) wulpianus (Lynch Arribalzaga, 1891)	Y121	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash; 24°27.25'S 65°17.83'W. 1278 m, 27.X/14.XI.2003. Leg.: M.E. Irwin & F.D. Parker.	EF127356	EF127437
Ocyptamus (Ocyptamus) antiphates (Walker, 1849)	XP29	USA, FL: Monroe Co. Everglades NP: Mtazek Pond. 25°08.4'N 080°55.5'W. 1.I.2004. Leg.: W. van Steenis	EF127304	EF127383
Ocyptamus (Ocyptamus) funebris Macquart, 1834	S487	Costa Rica, Heredia, INBioparque, 15/21.I.2005, Malaise trap. Leg.: G. Ståhls and M. Zumbado	EF127364	EF127443
Ocyptamus (Ocyptamus) fuscipennis (Say, 1823)	XP15	USA, Florida. Johns CO. Anastasia isl. 29°43'N 81°15' W. 24.V.2002.	EF127294	EF501970
Ocyptamus (Ocyptamus) sp.	S143	Costa Rica, Volcan Arenal area, VIII.2001. Leg.: G. Ståhls	EF127345	EF127427
Ocyptamus (Orphnabaccha) sp.	XP24	Colombia, Cali, Cerro San Antonio. 2180 m. 20.VII.2004. Leg.: C. Prieto	EF127299	EF127378
Ocyptamus lineatus (Macquart, 1846)	XP30	USA, Florida, Monroe. Big Pink Key: Long Beach. 24°38.503'N 081°19,953'W 04.I.2004. Leg. Stuke	EF127305	EF127384
Ocyptamus melanorrhinus (Philippi, 1865)	Y215	Chile, Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos; Malaise in stable dunes. 58 m, 31°50.96'S 71°29.60'W. 28.XII.2003/8.I.2004. Leg.: M.E. Irwin	EF127360	EF127441
Parasyrphus lineolus (Zetterstedt, 1843)	S137	Italy, South Tirol, Val Venosta, VII.2001. Leg.: G. Ståhls.	EF127342	EF127424

Table 2
(Continued)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Pseudodoros (Dioprosopa) clavatus (Fabricius, 1794)	S84	Cuba, La Habana, II.2001. Leg.: M.A. Marcos-García	EF127332	EF127413
Salpingogaster (Eosalpingogaster) conopida (Philippi, 1865)	Y214	Chile, Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos; Malaise in stable dunes, 58 m, 31°50.96'S 71°29.60'W. 28.XII.2003/8.I.2004. Leg.: M.E. Irwin	EF127359	EF127440
Scaeva (Scaeva) pyrastri (Linnaeus, 1758)	S57	Spain, Alicante, 1999	EF127329	EF127410
Scaeva (Semiscaeva) selenitica (Meigen, 1822)	S69	Czech Republic, distr. Ostrava, Polanecký les, 3.IV.2000. Leg.: T. Kuras.	AY603764	EF127404
Scaeva opinius (Walker, 1852)	Y100	Korea, Gaeweon-do, Hongcheon-gun Nae-myeon, 6.VI.2000. Leg.: D.S. Choi	EF127354	EF127435
Simosyrphus aegyptius (Wiedemann, 1830)	XP48	Madagascar, Majunga Prov., Ampijoroa (Andranofasika) Nat. Park, hand net in deciduous forest. 46 M. 16°19.16'S 46°48.80'E E MG25-23. 9/20.XI.2003. Leg.: M.E. Irwin, F. Parker & m. Hauser	EF127312	EF127391
Simosyrphus scutellaris (Fabricius, 1805)	S157	Hong Kong, Park, 7.X.2001. Leg.: D. Iliff	AY603768	EF127429
Sphaerophoria (Sphaerophoria) loewi Zetterstedt, 1843	S273	Sweden, Upplands-Bro, 15.VI.2002. Leg.: H. Bartsch	EF127318	EF127396
Sphaerophoria (Sphaerophoria) macrogaster (Thomson, 1869)	XP44	Australia, Jimbour Qld. 11.IX.2003. Leg. L.W. Smith. Det. L.W. Smith	–	EF501971
Sphaerophoria (Sphaerophoria) rueppellii (Wiedemann, 1830)	S12	Spain, Alicante, 1999	EF127328	EF127409
Sphaerophoria (Sphaerophoria) scripta (Linnaeus, 1758)	G229	Finland, Loppi, 4.IX.1994, Leg.: G. Ståhls	AY261708	AY261755
Syrphus opinator Osten Sacken, 1877	XP34	Canada, BC: Vancouver Island. Nanaimo; Buttertub Marsh. 63 m, 49°10′25′ N 123°58′03′ W. 5.V.2005. Leg. W. van Steenis.	EF501962	EF127386
Syrphus vitripennis Meigen, 1822	S53	Greece, Lesbos island, IV.2001. Leg.: S. Rojo & C. Perez	AY212797	AY261728
Xanthogramma flavipes (Loew, 1863)	XP31	USA, NE: Cass Co. Louisville, Platte River SP. 19.V.2005. Leg.: W. van Steenis.	EF127306	EF127385
Xanthogramma stackelbergi Violovitsh, 1975	XP10	Finland, 667:10, Al: Nåtö, Malaise trap nr. biol station, 30.VI/6.VII.2003, Leg.: G. Ståhls	EF127295	–
Toxomerini				
Toxomerus aeolus (Hull,1942)	XP20	Costa Rica, PN Tapantí. 1600 m, 12.I.2005. Leg.: X. Mengual	–	EF127376
Toxomerus CR-3 Thompson, *in litt*	XP18	Costa Rica, PN Tapantí. 1600 m 12.I.2005. Leg.: F.C. Thompson	EF127297	EF127375
Toxomerus marginatus (Say, 1823)	S64	USA, New York, Geneva, VII.1999. Leg.: M. Schmaedick	AY261705	AY261752
Toxomerus pictus (Macquart, 1842)	S146	Costa Rica, Monte Verde, nr biol station, VIII.2001. Leg.: G. Ståhls	EF127344	EF127426

Table 2
(Continued)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S
Toxomerus virgulatus (Macquart, 1850)	S79	Brazil, 2000	EF127330	EF127411
Toxomerus watsoni (Curran, 1930)	S145	Costa Rica, Monte Verde, forest nr biol station, VIII.2001. Leg.: G. Ståhls	EF127343	EF127425
Pipizini				
Pipiza sp.		Finland, Nousiainen	AY174459	AY261741
Pipizella viduata (Linnaeus, 1758)	S169	Sweden, Björnlunda	AY261695	AY261742
Trichopsomyia flavitarsis (Meigen, 1822)		Sweden, Uppland	AY212798	AY261729
Outgroup				
Volucella pellucens (Linnaeus, 1758)		Germany, Wörlitz	AY261689	AY261735

DNA manipulation

DNA was extracted from one to three legs or other parts of single individuals of either dry, pinned or ethanol preserved specimens using the NucleoSpin Tissue DNA Extraction kit (Machery-Nagel, Düren, Germany) following manufacturer's protocols and resuspended in 50 μL ultra-pure water. Male genitalia were conserved for the purpose of morphological studies and remnants of specimens are preserved as DNA voucher specimens, deposited at Finnish Museum of Natural History (MZH) and labeled as listed in Table 2. All sequences were submitted to GenBank, see Table 2 for accession numbers.

Polymerase chain reaction (PCR) amplifications for both gene fragments were carried out in 25 μL reactions containing 1–3 μL DNA extract, 1 μL of each primer (at 10 pmol/mL), 0.25 μL of Taq DNA polymerase (5 U/mL), 2 μL 2.5 mM MgCl2, 2.5 μL 10 × Buffer II (Applied Biosystems, Foster City, CA, USA) and 4 μL 200 mM dNTP (GeneAmp) and ultra-pure water. Thermocycler conditions were initial denaturing at 95 °C 2 min, 29 cycles of 30 s denaturing at 94 °C, 30 s annealing at 49 °C, 2 min extension at 72 °C, followed by a final extension of 8 min at 72 °C. The universally conserved primers used for amplifying and sequencing the *COI* and *28S* fragments are listed in Table 3. Generally, the *COI* fragment was amplified using the forward primer C1-S-1718 (alias Beet) and the reverse primer TL2-N-3014 (alias Pat). The homologous *COI* sequence fragment could also be obtained by using primer combinations C1-S-1718 + C1-N-2735 (alias Inger) and C1-J-2183 (alias Jerry) + TL2-N-3014 using the above PCR and sequencing conditions (see Table 3). The D2-3 region of the nuclear *28S rRNA* gene was amplified with the primers (Table 3) and PCR profiles described in Belshaw and Quicke (1997) and Campbell et al. (1993) (see also Laurenne et al., 2006). PCR products were purified using the GFX PCR Purification Kit (Amersham Biotech, Little Chalfont, UK). Amplified PCR was checked for size and products (bands) running 4 μL on a 1% agarose gel and then sequenced (with the PCR primers) in both directions using the Big Dye Terminator Cycle Sequencing Kit versus 1.1 (Applied Biosystems) at one-fourth of the recommended volumes on an ABI PRISM 377 (Applied Biosystems) sequencer. The sequences were inspected and edited for base-calling errors and assembled using Sequence Navigator™ (version 1.01, Applied Biosystems).

Phylogenetic analysis

The analysis used 102 terminal taxa. The full data set included three data partitions, two for the mitochondrial

Table 3
Primers used for amplifying and sequencing the COI and 28S fragments.

	Primer	Sequence	Source
COI	C1-J-2183 (Jerry)	5′-CAACATTTATTTTGATTTTTTGG-3′	Simon et al. (1994)
	C1-S-1718 (Beet)	5′-GGAGGATTTGGAATTGATTAGTTCC-3′	Simon et al. (1994)
	TL2-N-3014 (Pat)	5′-TCCAATGCACTAATCTGCCATATTA-3′	Simon et al. (1994)
	C1-N-2735 (Inger)	5′-AAAATGTTGAGGGAAAAAATGTTA-3′	Lunt et al. (1996)
28S	28Sforward (F2)	5′-AGAGAGAGAGTTCAAGAGTACGTG-3′	Belshaw et al. (2001)
	28Sreverse (3DR)	5′-TAGTTCACCATCTTTCGGGTC-3′	Belshaw et al. (2001)

COI gene and one for the nuclear D2-3 *28S rRNA* gene region. The *28S* sequences were not aligned prior to analysis.

Direct optimization

The combined molecular data were analyzed using direct optimization (optimization alignment), a method described by Wheeler (1996) and implemented in the computer program POY (Gladstein and Wheeler, 1996–2000). POY was also used for calculation of Bremer support (Bremer, 1988, 1994) values.

Direct optimization searches for the shortest tree using unaligned sequences as input (which may be of unequal length) (Wheeler, 1996; Schulmeister et al., 2002; Wheeler et al., 2006). The optimization algorithm incorporates indels as events in the procedure in addition to base transformations. This allows searching for the shortest tree, the one that best explains the observed data, without the intermediate step of producing a multiple alignment (Aagesen, 2005). Direct optimization provides heuristics to determine the cost of optimizing the unaligned sequences on a tree and, furthermore, incorporates heuristic search strategies known from other phylogenetic tree search programs when searching for the optimal tree, which itself is an NP-complete problem (De Laet and Wheeler, 2003; Wheeler et al., 2006). With this approach, direct optimization intends to overcome some of the drawbacks of the two-step approach, multiple sequence alignment followed by phylogenetic analysis, which is commonly used in phylogenetic analysis. The method has been applied in several recent studies (e.g., Frost et al., 2001; Giribet et al., 2001; Sanchis et al., 2001; Meier and Wiegmann, 2002; Ståhls et al., 2003; Bybee et al., 2004; Laurenne et al., 2006).

The parsimony analyses were run using a parallelized version of the program POY version 3.0.11 on a 19-node Beowulf cluster with 2.4 GHz processors employing Scyld unix and parallel virtual machine (PVM) software at the Finnish Museum of Natural History, Helsinki, Finland. The following string of commands was used:

```
-norandomizeoutgroup -holdmaxtrees 25
-maxtrees 5 -nodiscrepancies -fitchtrees
-replicates 100 -buildsperreplicate 5
-stopat 10 -minstop 15 -seed -1 -slop 2
```

```
-checkslop 5 -drifttbr -numdrifttbr 5
-treefuse -fuselimit 25 -impliedalignment
-indices -noleading.
```
The analyses were performed using equal weights [gap cost = 1, change cost = 1] (see Frost et al., 2001 and Grant and Kluge, 2003 for a discussion). The trees in parenthetical notation were converted into a strict consensus tree with the program JACK2HEN (available at http://www.cladistics.com).

Results

Data

Representatives of 17 genera currently classified into Syrphinae are lacking in our analysis, and most of these are very rare, monotypical or with few species described (see Table 1). Ninety-eight species were finally analyzed as ingroup, representing 40 of 57 genera (48 of 81 subgenera) of the four recognized tribes of Syrphinae, and several species of the same genus were analyzed when it was possible. Representatives of three of five genera of the tribe Pipizini were also included (see Table 2).

The mitochondrial *COI* data set comprised 1128 nucleotide characters for 78 ingroup taxa included in phylogenetic analysis and, a partial *COI* sequence (between 638 and 972 nucleotides) was obtained for 15 ingroup taxa. A total of 446 nucleotide sites were parsimony informative. *COI* of only five taxa [*Asarkina fulva* (XP51), *Toxomerus aeolus* (XP20), *Rohdendorfia dimorpha* (S562), *Allograpta* (*Fazia*) sp. 2 (S491) and *Sphaerophoria macrogaster* (XP44)] could not be amplified. The mean AT content of the *COI* sequences was 71.81%. The uncorrected pairwise sequence divergences for the *COI* gene between the outgroup *Volucella pellucens* and all ingroup taxa ranged from 10.55 to 21.88% (mean 12.22%). The highest intergeneric uncorrected pairwise divergence among ingroup taxa was 15.28% between *Baccha elongata* (Y242) and *Ocyptamus wulpianus* (Y121), and the lowest values were 4.08% between *Spazigaster ambulans* (S158) and *Syrphocheilosia claviventris* (G327). Between congeneric species, uncorrected pairwise distances varied from
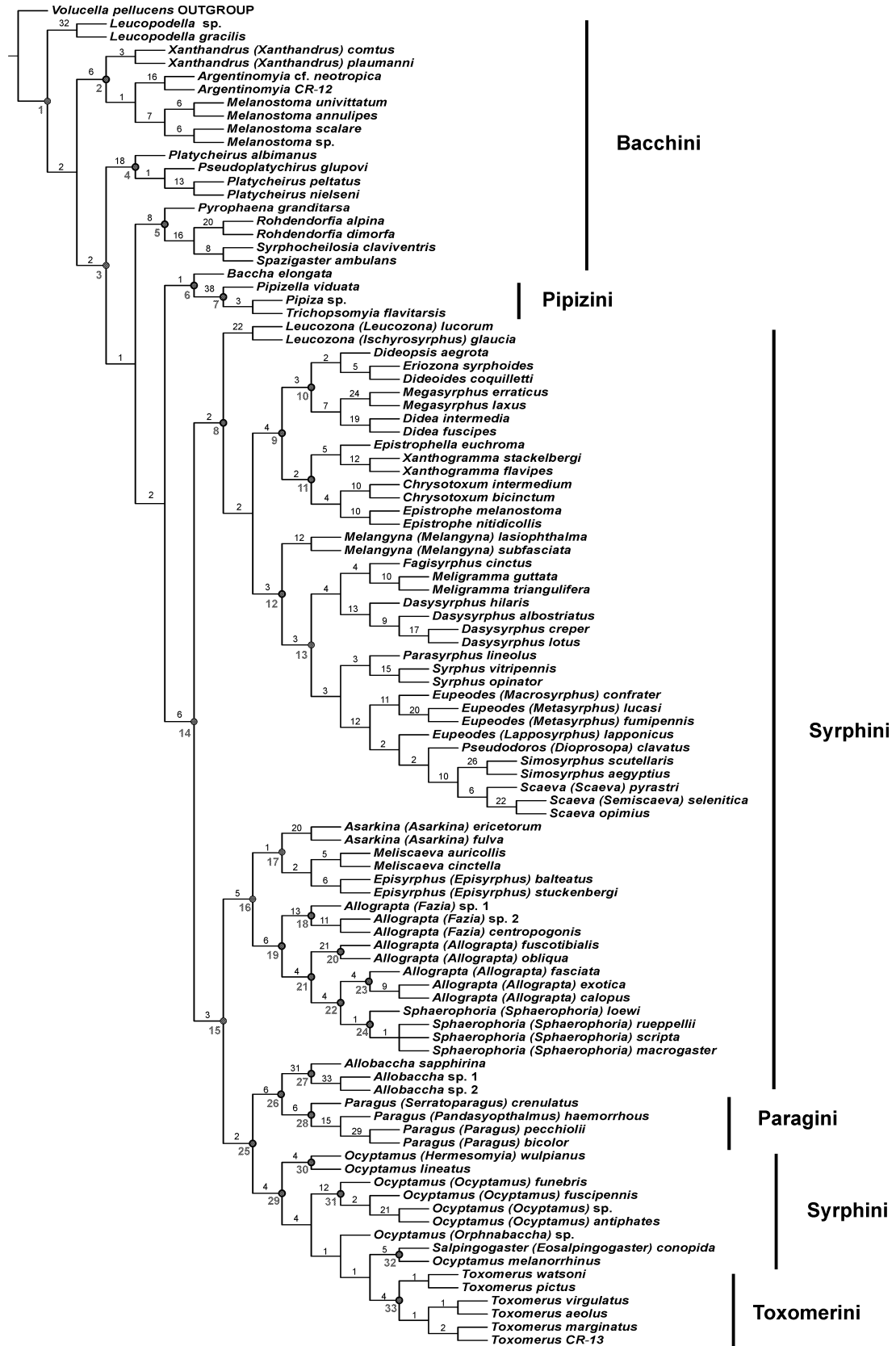
Fig. 1. Most parsimonious tree inferred from sequences of COI and 28S (length = 6603 steps). Current tribal classification is indicated on the tree. Bremer support values are indicated above branches. Number nodes are below branches.

0.15% between *Simosyrphus aegyptius* (XP48) and *Simosyrphus scutellaris* (S157) to 13.59%, between *Ocyptamus wulpianus* (Y121) and *Ocyptamus fuscipennis* (XP15). The obtained ribosomal D2–3 region of *28S rRNA* gene was sequenced for 95 ingroup taxa and comprised 573–601 nucleotides sites. *Chrysotoxum bicinctum* (G139), *Xanthogramma stackelbergi* (XP10) and *Xanthandrus plaumanni* (XP32) could not be amplified.

Phylogenetic analysis

The parsimony analysis using equal weighting values (1 : 1) resulted in one most parsimonious tree (length = 6603 steps), shown in Fig. 1. During the course of the study, DNA sequences of particular taxa were added to the matrix when these became available for molecular work. Thereby the parsimony analysis was repeated multiple times with an ever-growing taxon set (17 analyses in total). During this endeavor, the placements of Pipizini, *Baccha*, *Leucopodella* and *Pyrophaena* were unstable. Certain parts of the topology remained stable in succeeding analyses, as the clade with most of Syrphini and the topology of the clade with syrphines and New World genera (nodes 14, 8 and 15). Nodes are labeled with reference numbers to easily locate particular clades.

Pipizini was resolved as the sister group of the genus *Baccha* in the present analysis.

Xanthandrus, *Argentinomyia* and *Melanostoma* form a separate clade (node 2). The tribe Melanostomini *sensu* Hull (1949a,b) comprises all these genera plus the members of the other two resolved clades (nodes 4 and 5), which include *Platycheirus*, *Syrphocheilosia*, *Rohdendorfia* and *Pyrophaena* (*Spazigaster* was considered Bacchini by Hull). The genus *Baccha*, the type genus of the tribe Bacchini, appears alone as the sister group of the tribe Pipizini (node 6).

Node 8 was recovered in all analyses, and comprises two-thirds of all taxa that traditionally were placed in the tribe Syrphini, with the exception of some genera that were resolved in other clades of the tree (nodes 16, 27 and 29). Several clades appear inside Syrphini and genus *Leucozona* is resolved as the sister group. One clade relates *Eriozona*, *Didea*, *Dideopsis*, *Dideoides* and *Megasyrphus*. Genera *Chrysotoxum* and *Epistrophe* are resolved in the same clade of *Epistrophella* and *Xanthogramma*. In the other main group (node 11), *Melangyna*, *Fagisyrphus*, *Meligramma* and *Dasysyrphus* are members of a clade related to *Syrphus Parasyrphus*, *Eupeodes*, *Pseudodoros*, *Simosyrphus* and *Scaeva*.

Node 15 delimitates a clade formed by the tribes Toxomerini and Paragini with some genera traditionally included in Syrphini, i.e., *Asarkina*, *Episyrphus*, *Meliscaeva*, *Allograpta*, *Sphaerophoria* and *Ocyptamus*, plus two genera traditionally placed in Bacchini, *Allobaccha* and *Salpingogaster* (Shannon, 1921, 1922, 1923;

Hull, 1949a,b; Goffe, 1952; Wirth et al., 1965; Shatalkin, 1975). This is the first time that these relationships are reported whether using morphological or molecular characters. Our results consistently resolved a clade never suggested before, formed by the monophyletic tribe Toxomerini and other New World genera as *Ocyptamus* and *Salpingogaster* (*Eosalpingogaster*) (node 29). The tribe Paragini was resolved as monophyletic, and related to the genus *Allobaccha* (node 26), this clade being the sister group of the previous. On the other hand, *Asarkina* + *Episyrphus* + *Meliscaeva* are members of a clade (node 17) always recovered in prior analyses, here placed as the sister group of *Allograpta* + *Sphaerophoria* (node 19). Representatives of only two subgenera of *Allograpta* (*Allograpta* s.s. and *Fazia*) could be included in the present study. Both subgenera are resolved as related with *Sphaerophoria*.

Discussion

We discuss our results following the present classification of Syrphinae using tribes (in alphabetical order).

Tribe Bacchini

The tribe Bacchini comprises 13 genera with world wide distribution, and 18 subgenera are recognized (see Table 1). In the present analysis, representatives of 11 genera (11 subgenera) were included.

Different authors have either combined the tribes Melanostomini and Bacchini or treated them as separate, and the taxonomic concept of the tribes has varied among authors. Williston (1887) divided Melanostomini and Bacchini based on adult morphological characters. Hull (1949a) recognized the tribe Bacchini formed by *Baccha* (a complex group of species from different genera with many synonyms under the name *Baccha* as subgenera), *Rhinoprosopa*, *Salpingogaster* and *Rhinobaccha*. Genera *Melanostoma*, *Xanthandrus*, *Tuberculanostoma* and *Platycheirus* were the members of Melanostomini for Hull (1949a), and close to them there was *Rohdendorfia*. *Argentinomyia* had an inconsistent position; Hull discussed a placement allied to *Paragus* or close to *Chrysotoxum*. Goffe (1952) put Bacchini as a subtribe under Sphaerophorini and did the same with Melanostomini, under the tribe Stenosyrphini. Vockeroth (1969) discussed the tribe Bacchini as being a traditional artificial aggregation of forms of diverse origins that have independently developed a petiolate abdomen, together with other forms with parallel-sided abdomens. Hence, he suggested that to transfer some genera from Bacchini to Syrphini would result in a remaining natural group for Bacchini. He also discussed a classification with a union of the two tribes or perhaps a division of Bacchini into several tribes, as

for him this tribe was a non-natural group. A brief scheme since the work of Wirth et al. (1965) is given in Rotheray and Gilbert (1989), who considered *Baccha*, *Sphaerophoria*, *Platycheirus* and *Pyrophaena* as members of Bacchini, while Melanostomini was formed only by *Melanostoma* and *Xanthandrus*. Vockeroth (1969) followed Wirth et al. (1965) considering Bacchini as a monogeneric tribe, and Melanostomini comprised the other genera listed above. Dusek and Laska (1967) included all of them under Melanostomini, but presently the classification of the World Catalogues includes all of them under the name Bacchini.

Our results resolved Bacchini in five clades. Genus *Leucopodella* appears resolved alone. In previous analyses, this genus was resolved in the same clade with *Xanthandrus*, *Argentinomyia* and *Melanostoma*. One group is formed by *Xanthandrus*, *Argentinomyia* and *Melanostoma* (node 2). This group was represented in the larval analyses of Rotheray and Gilbert (1989, 1999) by *Melanostoma* and *Xanthandrus*, which, in their analysis, were isolated from the other genera of the "traditional" Bacchini by the tribe Syrphini. These authors suggested a tribe Melanostomini with *Melanostoma* and *Xanthandrus* as Palaearctic members.

The third group inside Bacchini is *Platycheirus*, which is resolved in node 4 with *Pseudoplatycheirus*. These genera were resolved as the sister group of the next clade in most of the prior analyses. The fourth clade of Bacchini supported by molecular evidence (node 5) is formed by genera *Pyrophaena*, *Rohdendorfia*, *Syrphocheilosia* and *Spazigaster*. Genus *Pyrophaena*, like *Syrphocheilosia*, *Pseudoplatycheirus*, *Spazigaster* and *Rohdendorfia*, were treated as subgenera of *Platycheirus* by some authors (Hull, 1949a; Vockeroth and Thompson, 1987; Thompson and Vockeroth, 1989; Thompson and Rotheray, 1998; Thompson, 2006) and others treated it as a separate genus (Williston, 1887; Shannon, 1921, 1922, 1923; Goffe, 1952; Wirth et al., 1965; Dusek and Laska, 1967; Shatalkin, 1975; Rotheray and Gilbert, 1989, 1999). Molecular evidence places *Pyrophaena* close to the other traditional subgenera of *Platycheirus* except *Pseudoplatycheirus*, a hypothesis supported also by larval characters (Rotheray and Gilbert, 1999). Shatalkin (1975) also mentioned some differences in the lobes of the surstyli comparing *Pyrophaena* with *Platycheirus*. *Pseudoplatycheirus* and *Platycheirus* were resolved as the sister groups, but differ in some morphological characters as pilosity of the eyes and dichoptic males.

Our results place *Baccha* in an isolated position (node 6), as the sister group of the tribe Pipizini. We used *Baccha elongata* (Fabricius), type species of the genus, in the analyses. Characters from larvae (Rotheray and Gilbert, 1989, 1999) suggested a closer relationship between *Baccha*, *Allograpta* and *Sphaero-*

phoria that is not supported by molecular characters. Present results support a monogeneric tribe for *Baccha*, as suggested already by Wirth et al. (1965) and Vockeroth (1969).

The relationships here reported for traditional Bacchini were discussed by Shatalkin (1975) using characters of the male genitalia. Shatalkin suggested two subtribes for Melanostomini (Melanostominia and Platycheirina) and placed *Baccha* and related genera in another tribe, the Bacchini. *Leucopodella*, *Melanostoma*, *Tuberculanostoma* and *Xanthandrus* were the members of Melanostominia, and five genera, *Platycheirus*, *Pseudoplatycheirus*, *Pyrophaena*, *Rohdendorfia* and *Spathiogaster* (= *Spazigaster*), composed the subtribe Platycheirina. Our results are remarkably similar to those proposed by Shatalkin.

Tribe Paragini

Paragini, with the single genus *Paragus*, is a compact and distinctive group (as suggested by Verrall, 1901) occurring in all continents other than South America and Antarctica. Shannon (1921, 1922, 1923), Wirth et al. (1965), Dusek and Laska (1967) and other authors recognize this tribe as a natural group, based on morphological characters of the adults and some exclusive features of the male genitalia. Goffe (1952) recognized *Paragus* as a subtribe under Syrphini, indicating a relationship between these two groups. Dusek and Laska (1967) did not comment on the sister group of *Paragus* but mentioned that the genera *Didea* and *Paragus* share some characters of the adult morphology and male genitalia and they placed Paragini as one of the first branches of Syrphinae, commonly called basal clades. Shatalkin (1975) said that Paragini was a tribe aberrant in relation to all other tribes of the subfamily based on characters of the male genitalia. Using larval characters, Rotheray and Gilbert (1989) resolved Paragini as the sister group of Pipizini, supporting the conclusion made by Verrall (1901) and placing *Paragus* again as a "basal" clade in the evolution of the subfamily. Later on, *Paragus* was placed in a derived position close to *Scaeva* and *Eupeodes*, taxa that are high specialized aphid-feeder (Rotheray and Gilbert, 1999).

Although there are recent studies about the intrageneric classification of *Paragus* (Kassebeer, 1999a,b, 2001; Rojo et al., 2006; Vujic et al., 2008), the placement of this tribe in the subfamily Syrphinae is unresolved as previous results disagree. Molecular evidence resolved Paragini as monophyletic (node 28) and placed it as the sister group of *Allobaccha* (node 26), a position never suggested before. Interestingly, the relationship of Paragini and Syrphini suggested by Goffe (1952) is supported by our results. However, Paragini represents a large radiation (more than 100 species described) and

more taxa must be included in the analysis to stabilize its phylogenetic position.

Tribe Syrphini: part 1

Syrphini are well spread over the world and this tribe comprises 42 genera, classified into 59 different subgenera (see Table 1). In the present analysis, 27 genera representing 33 subgenera are included. We divided this tribe into two groups for discussion: part 1, includes the members of Syrphini resolved in node 8, and part 2, genera of Syrphini resolved above node 15.

Our results suggest two major groups for Syrphini *sensu stricto* (nodes 9 and 12) and genus *Leucozona*, with *Ischyrosyrphus* as subgenus, as the sister group of them (node 8). In node 9, two clades appear in the results grouping *Dideoides, Eriozona, Dideopsis, Megasyrphus* and *Didea* (node 10). In the other clade (node 11), *Epistrophella* and *Xanthogramma* were resolved related with *Chrysotoxum* and *Epistrophe*. Genus *Melangyna* was resolved as the sister group of two other clades of Syrphini genera (see node 12). One of these clades is formed by genera *Fagisyrphus, Meligramma* and *Dasysyrphus*. Related with them, in the node 13, appears another clade where *Parasyrphus, Syrphus, Eupeodes* (subgenera *Macrosyrphus, Metasyrphus* and *Lapposyrphus*), *Pseudodoros, Simosyrphus* and *Scaeva* are the members.

Dusek and Laska (1967) considered *Ischyrosyrphus* as a separate genus, but Hippa (1968) suggested a close relationship of *Eriozona* and *Leucozona*, and placed *Ischyrosyrphus* under *Leucozona*. Vockeroth (1969) remarked that the closest relative of *Ischyrosyrphus* is undoubtedly *Leucozona*. In our studies, *Ischyrosyrphus* was always recovered as the sister group to *Leucozona*, confirming the close relationship between them. Uncorrected pairwise distance between *L. lucorum* (S139) and *L. (Ischyrosyrphus) glaucia* (XP5) is 7.01%.

Node 10 is formed by genera *Megasyrphus, Didea, Dideoides, Eriozona* and *Dideopsis. Megasyrphus* was erected as a new genus by Dusek and Laska (1967). As indicated by these authors and Vockeroth (1969), *Megasyrphus* resembles *Didea* with similarities in body shape and abdominal pattern, while male genitalia characters are similar to *Eriozona*. In the late 1980s, Rotheray and Gilbert (1989) suggested a closer relationship to *Didea* and proposed to synonymize *Megasyrphus* under *Didea*. Vockeroth (1992) did not accept the synonymy due to adult morphological differences. Thompson and Rotheray (1998) placed *Megasyrphus* as a subgenus of *Eriozona* in the Manual of Palaeractic Diptera in his identification based on adult morphology. The present results support a sister relationship of *Didea* and *Megasyrphus*, in congruence with larval characters. Uncorrected pairwise divergence between the two included species of *Didea* was 3.87% and 2.84% for *Megasyrphus*.

Between both genera, uncorrected pairwise distances varied from 7% (*D. intermedia* and *M. laxus*) and 7.48% (*D. fuscipes* and *M. laxus*). *Eriozona* was resolved as the sister group of *Dideoides*, a placement not suggested earlier, and related with *Dideopsis*.

In the late 1960s, *Chrysotoxum* was considered a monogeneric tribe by Vockeroth (1969), but later he placed it into Syrphini (Vockeroth, 1992). The present results show *Chrysotoxum* as part of the clade of *Xanthogramma* + *Epistrophe* (node 11), thus supporting Vockeroth.

Epistrophe is a very diverse genus in adult morphology. Although the adults are similar to *Syrphus*, they have completely different larval morphology. The cladistic analyses of Rotheray and Gilbert (1989) placed *Epistrophe* with *Epistrophella*, and *Meligramma* together with *Parasyrphus* or with *Xanthogramma* and *Doros* (Rotheray and Gilbert, 1999). Fluke (1950) transferred species from *Epistrophe* to *Stenosyrphus* (junior synonym of *Melangyna*) and placed *Epistrophe* as subgenus of *Syrphus*. Wirth et al. (1965) recognized *Epistrophe* as a separate genus from *Stenosyrphus*. Dusek and Laska (1967) followed Wirth et al. (1965) and created a new genus for *Syrphus euchromus* Kowarz, 1885, *Epistrophella*. Vockeroth (1969) indicated the unusual variation in thoracic and abdominal markings of *Epistrophe* and suggested to use the two subgenera: *Epistrophe* s.s. and *Epistrophella*. The analyses of larval morphology guided Rotheray and Gilbert to synonymize *Epistrophella* under *Meligramma*.

Our results suggest that *Epistrophella* is close to *Xanthogramma*, in agreement with larval evidence (Rotheray and Gilbert, 1999), close to the clade of *Epistrophe* (node 11) but not placed in the same clade with *Meligramma*. Present analyses also indicate that *Allograpta* is not related with *Epistrophe* as suggested by Hull (1949a) who could not find any valid distinctions except upon the abdominal pattern, and the relationship between *Meligramma* and *Epistrophe* is not close as larval evidence suggests.

The position of *Xanthogramma* as the sister group of *Epistrophella* is not consistent with larval evidence, that placed *Xanthogramma* as the sister group of all the rest of Syrphini (Rotheray and Gilbert, 1989) or as the sister group of the genus *Doros* (Rotheray and Gilbert, 1999). Unfortunately, *Doros* was not available for this study to test this relationship.

Fagisyrphus, Meligramma and *Dasysyrphus* have always placed close to *Syrphus*, sometimes as the sister groups. The four species of *Dasysyrphus* used in the analysis are resolved together, although the genus shows a great variation in male genitalia and larval characters. *Meligramma* was reduced to a subgenus of *Melangyna* by Vockeroth (1969) and World Catalogues followed him, but larval characters did not support a sister group relationship between them, a result our present results

support. Thus, molecules and larval evidence support results of Dusek and Laska (1967) in giving *Meligramma* full generic status.

Torp (1984, 1994) followed Dusek and Laska (1967) and treated *Fagisyrphus* in a separate genus, but Rotheray and Gilbert (1989) proposed to synonymize *Fagisyrphus* under *Melangyna* based on shared larval characters, they did not used this synonymy in the later analysis of 1999. Our results support Dusek and Laska (1967) resolving *Fagisyrphus* as sister to *Meligramma*. In our analyses *Melangyna* (node 12) was resolved separately from *Meligramma* and *Fagisyrphus* (node 13), contradicting the larval evidence (Rotheray and Gilbert, 1989).

Parasyrphus was described by Matsumura and Adachi in (1917) as subgenus of *Syrphus*. In the late 1960s, Vockeroth (1969) included *Parasyrphus* in his "unrecognized genera" and commented that Dusek and Laska (1967) used the name *Mesosyrphus* for the genus that he called *Phalacrodira*. Years later, *Mesosyrphus sensu* Dusek and Laska (1967) was synonymized as a junior synonym of *Melangyna* and *Phalacrodira* as a junior synonym of *Parasyrphus* by Vockeroth (1973b). *Mesosyrphus* based on *Mesosyrphus constrictus* Matsumura (1917) was considered synonym of *Melangyna*. Vockeroth (1969) suggested a close relationship between *Phalacrodira* (= *Parasyrphus*) and *Melangyna* that the analyses using molecular characters do not support. Rotheray and Gilbert (1989) concluded that *Parasyrphus* was the sister group of *Epistrophe*, *Epistrophella* and *Meligramma*, but 10 years later (Rotheray and Gilbert, 1999) the position of *Parasyrphus* was completely changed and it appeared between *Fagisyrphus* and the group formed by *Meliscaeva*, *Episyrphus* and *Betasyrphus*. Current results of our analyses placed *Syrphus* as the sister group of *Parasyrphus*. These are new results for the placements of these genera.

Vockeroth (1969) synonymized *Metasyrphus* with *Eupeodes* on the bases of similarity of male genitalia, wing microtrichia and almost indistinguishable females. At the same time, he placed *Lapposyrphus* Dusek and Laska, (1967) as a subgenus of *Eupeodes*. Our results support *Eupeodes (Macrosyrphus)* as related with *Eupeodes*. Present results reveal *Lapposyrphus* as a separate genus, placed in the same clade as *Eupeodes*. Thus, *Lapposyrphus* is suggested as good genus and it appears as the sister group of *Pseudodoros* + *Simosyrphus* + *Scaeva*. The relationship of *Scaeva* with *Simosyrphus* and *Ischiodon* has been recently published (Laska et al., 2006) but based on larval characters. In this paper the authors synonymized *Ischiodon* with *Simosyrphus*. Rotheray and Gilbert (1999) using larval characters also revealed a group formed by *Eupeodes*, *Scaeva* and *Ischiodon*. The two species of *Simosyrphus* used in the present analysis

belonged to *Ischiodon* before the synonymization made by Laska et al. (2006).

Pseudodoros is a genus comprising four species (Kassebeer, 2000), divided in two subgenera, *Dioprosopa* (that occurs in Neotropical and Nearctic regions) and *Pseudodoros* (in Palaearctic and Afrotropical regions). No previous cladistic hypotheses about its phylogenetic placement exist. Our results placed *Pseudodoros clavatus* into Syrphini as the sister group of *Scaeva* + *Simosyrphus*.

Tribe Syrphini: part 2

In this part of the discussion, genera of Syrphini resolved above node 15 are treated. These genera are grouped in two clades from nodes 16 and 25.

Node 16 is the base for two clades: (*Asarkina* + *Episyrphus* + *Meliscaeva*) and (*Allograpta* + *Sphaerophoria*). The relationship between *Episyrphus* and *Meliscaeva* was reported from larval characters by Rotheray and Gilbert (1989, 1999). Goeldlin de Tiefenau (1974) considered *Meliscaeva* and *Episyrphus* synonyms based on larval characters. Dusek and Laska (1967) and Hippa (1968) agreed in that the placement of *Episyrphus* should be close to *Megasyrphus* and *Eriozona*, but Hippa added that *Episyrphus* resembles the genus *Allograpta* and included them (*Episyrphus*, *Megasyrphus* and *Allograpta*) in a suprageneric group based on characters of the male genitalia. Vockeroth (1969) affirmed that *Episyrphus* "is almost certainly closely related to *Meliscaeva*, the only other genus consistently with discrete black sclerotized dots along the posterior wing margin". Later on, Ghorpade (1981) described a new species, *Episyrphus meliscaevoides* (= *E. stuckenbergi* Thompson, 2006), from Madagascar and pointed out that this new species shows morphological characters intermediate between the closely related genera *Episyrphus* and *Meliscaeva*. Our results placed this taxon as sister to *E. balteatus*.

Larval characters and adult morphology related above genera with *Allograpta*, a hypothesis also supported by our results which place them as the sister group of *Allograpta* + *Sphaerophoria* (node 19). Shatalkin (1975) created a tribe called Dideini formed by *Didea*, *Eriozona*, *Megasyrphus*, *Asarkina*, *Episyrphus* and *Meliscaeva*. For him, the first three genera undoubtedly constituted a natural group, and *Episyrphus* and *Meliscaeva* were distinct and closely related.

Goffe (1952) created a tribe called Sphaerophorini, which was divided into two subtribes, Bacchina and Sphaerophorina, indicating the close relationship of both genera groups. In a larval study by Rotheray and Gilbert (1989), and with the absence of *Allograpta*, *Baccha* was placed as the sister group of *Sphaerophoria*. Ten years later, Rotheray and Gilbert (1999) revealed a clade formed by *Baccha* as the sister

group of *Allograpta* and *Sphaerophoria*. Our results do not support the relation of *Baccha* with *Allograpta* + *Sphaerophoria*.

Molecular evidence resolved genus *Sphaerophoria* into *Allograpta* (see node 24). The subgenus *Allograpta* s.s. is divided in two clades (nodes 20 and 23), indicating a sister relationship of a group of species and genus *Sphaerophoria* (node 22). Present results resolved subgenus *Fazia* in another branch (node 18) with high Bremer support forming an independent clade from *Allograpta* s.s. + *Sphaerophoria*, which could question the validity of the subgeneric rank.

The relationship between *Allograpta* and *Sphaerophoria* is intriguing but not surprising, as some authors have previously presented some data that support this relationship. Vockeroth (1969) commented that *Allograpta* and *Ocyptamus* (his *Orphnabaccha*) "are the most varied in the tribe Syrphini". He listed four morphological characters (p. 128) to distinguish *Allograpta* from all other genera except *Sphaerophoria* and *Exallandra*. Shatalkin (1975) concluded that *Allograpta* and *Sphaerophoria* are closely connected with the tribe Bacchini. Shatalkin thought that this similarity has arisen convergently due to the location of *Allograpta* in the southern hemisphere and *Sphaerophoria* in the Holarctic region (with some species in the Oriental region).

Node 25 defines two clades: tribe Paragini with *Allobaccha*, and, on the other hand, genera *Ocyptamus*, *Salpingogaster* and *Toxomerus*. *Allobaccha* was established as a subgenus of *Baccha* by Curran (1928) and Hull (1949b) followed his consideration. Shatalkin (1975) associated *Allobaccha* with *Baccha* and with the species of his tribe Dideini (genera *Didea*, *Eriozona*, *Megasyrphus*, *Asarkina*, *Episyrphus* and *Meliscaeva*) on the basis of characters of the male genitalia. Smith and Vockeroth, 1980) included *Allobaccha* into the tribe Bacchini, but later Thompson and Vockeroth (1989) placed this genus in the tribe Syrphini. Molecular evidence of this study agrees in part with the results of Shatalkin, indicating a relationship (node 15) of *Allobaccha* and a part of the Shatalkin's Dideini (*Asarkina*, *Episyrphus* and *Meliscaeva*), but both have other sister groups.

The included representatives of the genera *Ocyptamus*, *Salpingogaster* and the tribe *Toxomerini* were resolved together at node 29. The species of these genera occur mainly in the Neotropical region, with some species extending their distribution into the Nearctic region. In 1969, Vockeroth pointed out that the Netropical Syrphini are composed almost entirely of one medium-sized genus and another very large genus, both extremely diverse, and both divided by previous workers into a number of genera. These two genera are *Allograpta* and *Orphnabaccha* (= *Ocyptamus*). He created two new genera, *Pseudoscaeva* and *Hermesomyia*, but Thompson et al. (1976) treats these as synonyms or subgenera of *Ocyptamus*.

Ocyptamus is a very large genus, endemic to the New World, and has over 300 species in the Neotropical and 22 in the Nearctic region (Thompson, 1999; Rotheray et al., 2000). Although Vockeroth (1969) stated that no well-defined subgroups could be established, Thompson and Zumbado (2000) noted the putative existence of some subgenera, all of which are not represented in this study due to the difficulty of obtaining specimens. *Ocyptamus wulpianus* has different larval feeding mode than those of the *O. funebris* clade (node 31), which are mainly aphidophagous. *O. wulpianus* (= *Hermesomyia bacchiformis*) is a predator of insect larvae in bromeliads (Rotheray et al., 2000) and is resolved as sister of *O. lineatus* (node 30), with unknown larval feeding mode. These taxa are placed as the sister group of the remaining species of *Ocyptamus*, *Salpingogaster* and the tribe Toxomerini.

The placement of the single included species of *Salpingogaster* (*Eosalpingogaster*) is a novelty (node 32) as it has previously been placed in the tribe Bacchini by earlier authors. In the present study it appears as the sister group of one species of *Ocyptamus*, *O. melanorrhinus*, forming together the sister group of Toxomerini. *Eosalpingogaster* mainly feeds on scale insects (Dactylopiidae) and Coccidae (Rojo et al., 2003). Shatalkin (1975) found many data that indicated the close connection between *Salpingogaster* and *Ocyptamus*, but both genera remained in Bacchini.

Tribe Toxomerini

Toxomerini was resolved as a monophyletic group within *Ocyptamus* (node 33). This monogeneric tribe has about 150 described species (Metz and Thompson, 2001) and it is the tribe of Syrphinae with the most restricted distribution, occurring only in the New World. *Allograpta* and *Ocyptamus* comprise morphologically diagnosable groups that could be divided into subgenera (Thompson, pers. comm.), but more species of *Toxomerus* need to be studied to suggest a subdivision of this genus. Shatalkin (1975) examined Toxomerini and suggested a connection between this tribe and the genus *Ocyptamus*. Vockeroth (1969) did not find any characters in the male genitalia to suggest that *Toxomerus* is a natural group distinct from *Mesograpta* (= *Toxomerus* Thompson et al., 1976) and recommended the inclusion of several genera erected by Enderlein (1938) in *Toxomerus*. The analyses of molecular characters support the relation that Shatalkin suggested using characters of the male genitalia.

Conclusions

In comparison with the current tribal classification, only Paragini and Toxomerini were in the present study

recovered as monophyletic tribes in congruence with present arrangements. Node 14 (Syrphini + Paragini + Toxomerini) has always been recovered in our analyses, being consistent through the 17 analyses. Whether Syrphini comprises all taxa from node 14, or is best divided into multiple tribes, awaits further study. Our results did not recover Bacchini as a single monophyletic clade, rather a classification into three tribes is suggested. The close relationship between the taxa within these particular groups was proposed by Shatalkin (1975) giving the names Melanostomina and Platycheirina, within Melanostomini, and Bacchini for genus *Baccha*.

Among particular results we found that *Epistrophella* was not recovered as a subgenus of *Epistrophe*, *Chrysotoxum* was resolved as part of Syrphini s.s., and *Meligramma* and *Fagisyrphus* were not directly related with *Melangyna*. The traditional placement of *Lapposyrphus* as a subgenus of *Eupeodes* was not found, the taxon was resolved as a separate lineage and sister group of *Scaeva*, *Simosyrphus* and *Pseudodoros*. The placement of *Pseudodoros* is unexpected, but few estimates of its phylogenetic affinities exist. *Megasyrphus* was resolved as sister to *Didea*, and not close to *Eriozona* s.s., supporting results of larval evidence by Rotheray and Gilbert (1999). Based on the present data, the rank of these taxa could be subgeneric or generic. A phylogenetic placement of *Eriozona* s.s. as sister to *Dideoides* was not suggested earlier. Also the placement of *Xanthogramma* was not previously suggested.

Allobaccha is sister group of Paragini, a position never reported before for *Allobaccha*. *Asarkina*, *Episyrphus* and *Meliscaeva* are related with *Allograpta*, and not with traditional Syrphini. *Allograpta* and *Sphaerophoria* are closely related based on separate studies on adult morphology, larvae and molecules, but following our results, the genus *Allograpta* is paraphyletic without *Sphaerophoria*.

Our most interesting finding is the monophyletic clade comprising the included representatives of the genera *Ocyptamus*, *Salpingogaster* (*Eosalpingogaster*) and *Toxomerus* occurring only in the New World. *Ocyptamus* taxa fall into several lineages, and future studies will aim to increase the taxon sampling of this diverse lineage for an improved estimate of relationships and classification. Whether *Toxomerus* and *Ocyptamus* are members of the same tribe or eventually as a result of a more extensive taxon and character sampling of these speciose genera will be resolved as monophyletic units awaits further study. Multiple genera comprise species with distributions extending into the New World, e.g., *Allograpta*, *Didea*, *Scaeva*, *Eriozona*, and *Xanthandrus*, to name a few, but few genera are distributed exclusively in the Neotropical region, such as *Argentinomyia*, *Notosyrphus* or *Talahua*.

Based on the current results we hesitate to make changes in Syrphinae classification, we rather stress the necessity of a combined analysis of available morphological and molecular characters, to test if the phylogenetic affinities shown in the present results will remain unchallenged.

References

Aagesen, L., 2005. Direct optimization, affine gap costs, and node stability. Mol. Phylogenet. Evol. 36, 641–653.

Arevalo, E., Zhu, Y., Carpenter, J.M., Strassmann, J.E., 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. BMC Evol. Biol. 4, 8.

Belshaw, R., Quicke, D.L.J., 1997. A molecular phylogeny of the Aphidiinae (Hymenoptera: Braconidae). Mol. Phylogenet. Evol. 7, 281–293.

Belshaw, R., Lopez-Vaamonde, C., Degerli, N., Quicke, D.L.J., 2001. Paraphyletic taxa and taxonomic chaining: evaluating the classification of braconine wasps (Hymenoptera: Braconidae) using 28S, D2–3 rDNA sequences and morphological characters. Biol. J. Linn. Soc. Lond. 73, 411–424.

Brammer, C.A., von Dohlen, C.D., 2007. Evolutionary history of Stratiomyidae (Insecta: Diptera): The molecular phylogeny of a diverse family of flies. Mol. Phylogenet. Evol. 43, 660–673.

Bremer, K., 1988. The limits of amino acid sequence data in angiosperms phylogenetic reconstruction. Evolution 42, 795–803.

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

Bybee, S.M., Taylor, S.D., Nelson, C.R., Whiting, M.F., 2004. A phylogeny of robber flies (Diptera: Asilidae) at the subfamilial level: molecular evidence. Mol. Phylogenet. Evol. 30, 789–797.

Campbell, B.C., Steffen-Campbell, J.D., Werren, J.H., 1993. Phylogeny of *Nasonia* species complex (Hymenoptera, Pteromalidae) inferred from an internal described spacer (ITS2) and 28S rDNA sequences. Insect Mol. Biol. 2, 225–237.

Caterino, M.S., Reed, R., Kuo, M., Sperling, F.A.H., 2001. A partioned likelihood analysis of swallowtail butterfly phylogeny. Syst. Biol. 50, 106–127.

Cheng, X., Lu, J., Huang, C., Zhou, H., Dai, Z., Zhang, G., 2000. Determination of phylogenetic position of Pipizini (Diptera: Syrphidae): based on molecular, biological and morphological data. Sci. China C 42, 146–156.

Curran, C.H., 1928. The Syrphidae of the Malay Peninsula. J. Fed. Malay St. Mus. 14, 141–324.

De Laet, J., Wheeler, W.C., 2003. POY, Version 3.0.11 (Wheeler, W.C., Gladstein, D.S., De Laet, J., May 6, 2003). Command line documentation.

Dusek, J., Laska, P., 1967. Versuchzum Aufbau eines naturlichen Systems mitteleuropaischer Arten der Unterfamilie Syrphinae (Diptera). Acta Sci. Nat. Brno 1, 349–390.

Enderlein, G., 1938. Beitrag zur Kenntnis der Syrphiden. Sber. Ges. Naturf. Freunde Berl. 1937, 192–237.

Fabricius, J.C., 1805. Systema Antliatorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Carolum Reichard, Brunsvigae (=Brunswick).

Fluke, C.L., 1950. The male genitalia of Syrphus, Epistrophe and related genera (Diptera, Syrphidae). Trans. Wis. Acad. Sci. Arts. Lett. 40, 115–148.

Fluke, C.L., 1956. Catalogue of the family Syrphidae in the Neotropical region. Rev. Bras. Entomol. 6, 193–268.

Frost, D.R., Rodrigues, M.T., Grant, T., Titus, T.A., 2001. Phylogenetics of the lizard genus Tropidurus (Squamata: Tropiduridae: Tropidurinae): Direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. Mol. Phylogenet. Evol. 21, 352–371.

Ghorpade, K.D., 1981. An anomalous new Episyrphus (Diptera: Syrphidae) from Madagascar. Colemania 1, 89–94.

Giribet, G., Edgecombe, G.D., Wheeler, W.C., 2001. Arthropod phylogeny based on eight molecular loci and morphology. Nature 413, 157–161.

Gladstein, D.S., Wheeler, W.C., 1996–2000. POY: phylogeny reconstruction via direct optimization of DNA data. Available at ftp.amnh.org/pub/molecular/poy

Goeldlin de Tiefenau, P., 1974. Contribution à l'étude systématique et écologique des Syrphidae (Dipt.) de la Suisse occidentale. Bull. Soc. Entomol. Suisse 47, 151–251.

Goffe, E.R., 1952. An outline of a revised classificaton of the Syrphidae (Diptera) on phylogenetic lines. Trans. Soc. Br. Entomol. 11, 97–124.

Grant, T., Kluge, A.G., 2003. Data exploration in phylogenetic inference: scientific, heuristic, or neither. Cladistics 19, 379–418.

Hippa, H., 1968. A generic revision of the genus Syrphus and allied genera (Diptera, Syrphidae) in the Palearctic region, with descriptions of the male genitalia. Acta Entomol. Fenn. 25, 1–94.

Hull, F.M., 1949a. The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. Trans. Zool. Soc. Lond. 26, 257–408.

Hull, F.M., 1949b. The genus Baccha from the New World. Entomol. Am. 27, 89–291.

Kassebeer, C.F., 1999a. Die Gattung Paragus Latreille, 1804 (Diptera, Syrphidae) in der Elfenbeinküste. Dipteron 2, 31–44.

Kassebeer, C.F., 1999b. Die Gattung Paragus Latreille, 1804 (Diptera, Syrphidae) auf Madagaskar, den Komoren und den Maskarenen. Dipteron 2, 75–92.

Kassebeer, C.F., 2000. Zur Gattung Pseudodoros Becker, 1903 (Diptera, Syrphidae). Dipteron 3, 73–92.

Kassebeer, C.F., 2001. Eine neue Paragus Latreille, 1804 (Diptera, Syrphidae) aus Äthiopien. Dipteron 4, 33–36.

Laska, P., Pérez-Bañón, C., Mazánek, L., Rojo, S., Ståhls, G., Marcos-García, M.A., Bicik, V., Dusek, J., 2006. Taxonomy of the genera Scaeva, Simosyrphus and Ischiodon (Diptera: Syrphidae):

Descriptions of immature stages and status of taxa. Eur. J. Entomol. 103, 637–655.

Laurenne, N.M., Broad, G.R., Quicke, D.L.J., 2006. Direct optimization and multiple alignment of 28S, D2–D3 rDNA sequences: problems with indels on the way to a molecular phylogeny of the cryptine ichneumon wasps (Insecta: Hymenoptera). Cladistics 22, 442–473.

Lunt, D.H., Zhang, D.X., Szymura, J.M., Hewitt, G.M., 1996. The insect cytochrome oxidase I gene: evolutionary patterns and conserved primers for phylogenetic studies. Insect Mol. Biol. 5, 153–165.

Matsumura, S., Adachi, J., 1917. Synopsis of the economic Syrphidae of Japan (Part III). Entomol. Mag. Kyoto 3, 14–46.

Meier, R., Wiegmann, B.M., 2002. A phylogenetic analysis of Coelopidae (Diptera) based on morphological and DNA sequence data. Mol. Phylogenet. Evol. 25, 393–407.

Mengual, X., Ståhls, G., Vujic, A., Marcos-Garcia, M.A., 2006. Integrative taxonomy of Iberian Merodon species (Diptera, Syrphidae). Zootaxa 1377, 1–26.

Metz, M.A., Thompson, F.C., 2001. A revision of the larger species of Toxomerus (Diptera: Syrphidae) with description of a new species. Stud. Dipt. 8, 225–256.

Mogi, M., Chan, K.L., 1996. Predatory habits of dipteran larvae inhabiting Nepenthes pitchers. Raffles Bull. Zool. 44, 233–245.

Newman, E., 1834. Attempted division of British insects into natural orders. Entomol. Mag. 2, 379–431.

Nishida, K., Rotheray, G.E., Thompson, F.C., 2002. First non-predaceous syrphinae flower fly (Diptera: Syrphidae): a new leaf-mining Allograpta from Costa Rica. Stud. Dipt. 9, 421–436.

Rojo, S., Gilbert, F., Marcos-Garcia, M.A., Nieto, J.M., Mier, M.P., 2003. A World Review of Predatory Hoverflies (Diptera, Syrphidae: Syrphinae) and their Prey. CIBIO Ediciones, Alicante.

Rojo, S., Ståhls, G., Perez-Bañon, C., Marcos-Garcia, M.A., 2006. Testing molecular barcodes: Invariant mitochondrial DNA sequences vs the larval and adult morphology of West Palaearctic Pandasyopthalmus species (Diptera: Syrphidae: Paragini). Eur. J. Entomol. 103, 443–458.

Rotheray, G.E., 1993. Colour Guide to Hoverfly Larvae (Diptera, Syrphidae) in Britain and Europe. Dipterists Digest no. 9. Derek Whiteley, Sheffield, UK.

Rotheray, G.E., 2003. The predatory larvae of two Nepenthosyrphus species living in pitcher plants (Diptera, Syrphidae). Stud. Dipt. 10, 219–226.

Rotheray, G.E., Gilbert, F., 1989. The phylogeny and systematics of European predacious Syrphidae (Diptera) based on larval and puparial stages. Zool. J. Linn. Soc. 95, 29–70.

Rotheray, G.E., Gilbert, F., 1999. Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages. Zool. J. Linn. Soc. 127, 1–112.

Rotheray, G.E., Zumbado, M., Hancock, E.G., Thompson, F.C., 2000. Remarkable aquatic predators in the genus Ocyptamus (Diptera, Syrphidae). Stud. Dipt. 7, 385–389.

Sanchis, A., Michelena, J.M., Latorre, A., Quicke, D.L.J., Gärdenfors, U., Belshaw, R., 2001. The phylogenetic analysis of variable-length sequence data: elongation factor-1α introns in European populations of the parasitoid wasp genus Pauesia (Hymenoptera: Braconidae: Aphidiinae). Mol. Biol. Evol. 18, 1117–1131.

Schulmeister, S., Wheeler, W.C., Carpenter, J.M., 2002. Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. Cladistics 18, 455–484.

Shannon, R.C., 1921. A reclassification of the subfamilies and genera of North American Syrphidae (Diptera). Bull. Brooklyn Entomol. Soc. 16, 65–72.

Shannon, R.C., 1922. A reclassification of the subfamilies and genera of North American Syrphidae (Diptera). Conclusions. Bull. Brooklyn Entomol. Soc. 17, 30–42.

Shannon, R.C., 1923. A reclassification of the subfamilies and genera of North American Syrphidae (Diptera). Appendix. Bull. Brooklyn Entomol. Soc. 18, 17–21.

Shatalkin, A.I., 1975. A taxonomic analysis of the hover flies (Diptera, Syrphidae). I. Entomol. Rev. Wash. 54, 117–125.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H., Flook, P., 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene-sequences and a compilation of conserved polymerase chain-reaction primers. Ann. Entomol. Soc. Am. 87, 651–701.

Smith, K.V.G., Vockeroth, J.R., 1980. Family Syrphidae. In: Crosskey, R.W. (Ed.), Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, pp. 488–510.

Sorensen, J.T., Campbell, B.C., Gill, R.J., Steffen-Campbell, J.D., 1995. Non-monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropterodea Hemiptera (s.1.) and a proposal for new monophyletic suborders. Pan-Pacific Entomol. 71, 31–60.

Ståhls, G., 2006. Placement of Cacoceria and phylogenetic relationships of the xylotine genera of the tribe Milesiini (Diptera, Syrphidae: Eristalinae) based on molecular characters. Zootaxa 1171, 17–29.

Ståhls, G., Nyblom, K., 2000. Phylogenetic analysis of the genus Cheilosia (Diptera, Syrphidae) using mitochondrial COI sequence data. Mol. Phylogenet. Evol. 15, 235–241.

Ståhls, G., Hippa, H., Rotheray, G., Muona, J., Gilbert, F., 2003. Phylogeny of Syrphidae (Diptera) inferred from combined analysis of molecular and morphological characters. Syst. Entomol. 28, 433–450.

Ståhls, G., Vujic, A., Stuke, J.H., Doczkal, D., Muona, J., 2004. Phylogeny of the genus Cheilosia and the tribe Rhingiini (Diptera, Syrphidae) based on molecular and morphological characters. Cladistics 4, 1–17.

Thompson, F.C., 1969. A new genus of microdontine flies (Diptera: Syrphidae) with notes on the placement of the subfamily. Psyche 76, 74–85.

Thompson, F.C., 1972. A contribution to a generic revision of the Neotropical Milesiinae (Diptera: Syrphidae). Arq. Zool. 23, 73–215.

Thompson, F.C., 1999. Key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical Region including descriptions of new genera and species and a glossary of taxonomic terms. Contr. Entomol. Int. 3, 319–378.

Thompson, F.C. (Ed.), 2006. Biosystematic Database of World Diptera, Version 7.5. Available from http://www.diptera.org/biosys.htm (accessed 15 February 2007).

Thompson, F.C., Rotheray, G.E., 1998. Family Syrphidae. In: Papp, L., Darvas, B. (Eds.), Manual of Palaearctic Diptera, Vol. 3. Science Herald, Budapest, pp. 81–139.

Thompson, F.C., Vockeroth, J.R., 1989. Family Syrphidae. In: Evenhuis, N.L. (Ed.), Catalog of the Diptera of the Australasian and Oceanian Regions. Special Publication 86, Bishop Museum, Honolulu, pp. 437–458.

Thompson, F.C., Zumbado, M., 2000. Flower flies of the subgenus Ocyptamus (Mimocalla Hull) (Diptera: Syrphidae). Proc. Entomol. Soc. Wash. 102, 773–793.

Thompson, F.C., Vockeroth, J.R., Sedman, Y.S., 1976. A catalogue of the Diptera of the Americas south of the United States. Chap. 46: Family Syrphidae. Museum of Zoology of the University of Sao Paulo, Sao Paulo, Brazil.

Torp, E., 1984. De danske svirrefluer (Diptera: Syrphidae): Kendetegn, levevis og udebrelse. Danmarks Dyreliv, bind 1. Fauna Bøger, Copenhagen, Denmark.

Torp, E., 1994. Danmarks Svirrefluer (Diptera: Syrphidae). Danmarks Dyreliv, Bind 6. Apollo Books, Stenstrup, Denmark.

Verrall, G.H., 1901. British Flies, VIII. Platypezidae, Pipunculidae and Syrphidae of Great Britain. Gurney & Jackson, London.

Vockeroth, J.R., 1969. A revision of the genera of the Syrphini (Diptera, Syrphidae). Mem. Entomol. Soc. Can. 62, 1–176.

Vockeroth, J.R., 1973a. Three additional synonyms of Allograpta (Diptera: Syrphidae). Can. Entomol. 105, 1101–1104.

Vockeroth, J.R., 1973b. The identity of some genera of Syrphini (Diptera: Syrphidae) described by Matsumura. Can. Entomol. 105, 1175–1179.

Vockeroth, J.R., 1986. Nomenclatural notes on Nearctic Eupeodes (including Metasyrphus) and Dasysyrphus (Diptera: Syrphidae). Can. Entomol. 118, 199–204.

Vockeroth, J.R., 1992. The flower flies of the Subfamily Syrphinae of Canada, Alaska, and Greenland (Diptera: Syrphidae). The Insects and Arachnids of Canada, Part 18. Centre for Land and Biological Resources Research, Ottawa.

Vockeroth, J.R., Thompson, F.C., 1987. Family Syrphidae. In: McAlpine, J.F. (Ed.), Manual of Nearctic Diptera, Vol. 2. Agriculture Canada, Canadian. Government Publishing Centre, Hull, Quebec.

Vujic, A., Ståhls, G., Rojo, S., Radenkovic, S., Simic, S., 2008. Systematics and phylogeny of the tribe Paragini (Diptera: Syrphidae) based on molecular and morphological characters. Zool. J. Linn. Soc. 152, 507–536.

Wheeler, W.C., 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics 12, 1–9.

Wheeler, W.C., Aagesen, L., Arango, C.P., Faivovich, J., Grant, T., D'Haese, C., Janies, D., Smith, W.L., Varon, A., Giribet, G., 2006. Dynamic Homology and Phylogenetic Systematics. A Unified Approach Using POY. AMNH, New York.

Williston, S.W., 1887. Synopsis of the North American Syrphidae. Bull. US Nat. Mus. 31.

Winterton, S.L., Wiegmann, B.M., Schlinger, E.I., 2007. Phylogeny and Bayesian divergence time estimations of small-headed flies (Diptera: Acroceridae) using multiple molecular markers. Mol. Phylogenet. Evol. 43, 808–832.

Wirth, W.W., Sedman, Y.S., Weems, H.V., 1965. Family Syrphidae. In: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H., Coulson, J.R. (Eds.), A Catalog of the Diptera of America North of Mexico. Agricultural Research Service, United States Department of Agriculture, Washington, DC, pp. 557–625.