Phylogenetic relationships of the bacchine flower flies (Diptera: Syrphidae) based on molecular characters, with a description of a new species of *Melanostoma* (Schiner, 1860)

Ximo Mengual

Zoologisches Forschungsmuseum Alexander Koenig,
Adenauerallee 160, 53113 Bonn, Germany
x.mengual@leibniz-zfmk.de

Abstract

The phylogenetic relationships among the genera of the tribe Bacchini *sensu lato* (i.e., Syrphinae with simple, unsegmented aedeagus) were inferred using molecular evidence. The mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI) and the nuclear ribosomal 28S and 18S rRNA genes for 54 bacchine taxa were analyzed using Bayesian inference and Maximum Likelihood. Among the analyzed taxa there is a new species of *Melanostoma* (Schiner) from Cameroon, *Melanostoma janeceki* Mengual, **sp. nov.**, which is described in full. This new species has a complete metasternum without excavation, a characteristic that is not present in other species of *Melanostoma*, usually with an excavated metasternum, but it is the diagnostic character of the genus *Afrostoma* Skevington, Thompson & Vockeroth. Based on the phylogenetic placement of *Melanostoma janeceki* Mengual, **sp. nov.** the taxonomic status of *Afrostoma* as a genus is discussed and a new generic classification of Bacchini **stat. rev.** and Melanostomini **stat. rev.** is presented in the light of the inferred phylogeny. Results did not recover Bacchini *sensu lato* monophyletic, but into two groups as follows: *Melanostoma* and related genera, and *Baccha*, *Platycheirus* and related genera. *Pseudoplatycheirus* van Doesburg is considered **junior synonym** of *Platycheirus* Le Peletier & Audinet-Serville, and *Afrostoma* Skevington, Thompson & Vockeroth as **junior synonym** of *Melanostoma*. *Pyrophæna* Schiner and *Eocheilosia* Hull **comb. nov.** are ranked as valid genera, and consequently, the genus *Platycheirus* is divided into four subgenera: *Platycheirus* (*Carposcalis*) (Enderlein), *Platycheirus* (*Pachysphyria*) (Enderlein), *Platycheirus* (*Platycheirus*), and *Platycheirus* (*Tuberculanostoma*) (Fluke) **comb. nov.**

Keywords

Afrostoma – bacchine – Bacchini – melanostomine – Melanostomini – new synonym

Introduction

Commonly known as flower flies or hoverflies, syrphids (Diptera: Syrphidae) are distributed worldwide, absent only in remote oceanic islands and Antarctica (Thompson & Rotheray, 1998). While adults feed on pollen and nectar, larvae have a large array of natural histories (Ureña & Hanson, 2010; Rotheray & Gilbert, 2011; Pérez-Lachaud et al., 2014; Fleischmann et al., 2016). Syrphid species have been used as bioindicators (Sommaggio, 1999; Tscharnkte et al., 2005; Ricarte et al., 2011; Sommaggio & Burgio, 2014), and they contribute to very important ecosystem services, such as pollination, biological control of pests or decomposition of organic matter (Lardé, 1989; Schmidt et al., 2004; Bergh & Short, 2008; Bugg et al., 2008; Ssymank & Kearns, 2009; Morales & Wolff, 2010; Martínez-Falcón et al., 2012; Nelson et al., 2012; Inouye et al., 2015).

The family is currently divided into four subfamilies, namely Microdontinae, Eristalinae, Pipizinae, and Syrphinae (Mengual et al., 2015), although some authors prefer to consider the microdontines as a different family (Thompson, 1969; Speight, 1987, 2018). Phylogenetically, Pipizinae and Syrphinae form a clade (Ståhls et al., 2003; Hippa & Ståhls, 2005; Mengual et al., 2015; Young et al., 2016a) whose members have primarily predatory larvae (Rotheray, 1993; Rojo et al., 2003; Downes et al., 2017). However, some Syrphinae species have become phytophagous secondarily (Nishida et al., 2002; Weng & Rotheray, 2008; Reemer & Rotheray, 2009; Zuijen & Nishida, 2011; Dumbardon-Martial, 2016). Vockeroth (1969) divided the subfamily Syrphinae into six tribes, namely Bacchini, Melanostomini, Paragini, Toxomerini, Chrysotoxini and Syrphini. Later, Vockeroth (1992) rearranged his tribal system with the currently accepted four tribes: Bacchini, Paragini, Toxomerini, and Syrphini. This current tribal classification of

Syrphinae needs a revision based on recent molecular studies, where Bacchini and Syrphini were never resolved as monophyletic (Mengual et al., 2008a, 2012, 2015; Mengual & Thompson, 2011; Mengual, 2015; Young et al., 2016a; Pauli et al., 2018).

Classically, Bacchini is defined as Syrphinae taxa with the aedeagus of the male genitalia rather simple, undivided (Vockeroth, 1969, 1992), and face and scutellum entirely black. The coloration of the face and scutellum is no longer a defining characteristic for Bacchini as there are Bacchini species with pale parts of the face (Vockeroth, 1990; Thompson, 1999) and Syrphini species with face and scutellum entirely black (Vockeroth, 1969, 1990; Huo, 2014). The tribe Bacchini *sensu lato*, hereafter the members of Syrphinae with a simple aedeagus, has undergone several modifications in its definition, mostly due to the concept of the genus *Baccha* Fabricius, 1805, which ended up to an extremely diverse tribe (Vockeroth, 1969). Bigot (1883) was the first to use a name to refer a suprageneric group, Bacchidae. Since Williston (1885) separated them into Melanostominae and Bacchinae, in almost every case where the author distinguished between Melanostomini (also wrongly written as Melanostomatini; see Sabrosky, 1999) and Bacchini, the latter included several genera and species of Syrphini placed under *Baccha* (Williston, 1885; Hull, 1949; Wirth et al., 1965; Vockeroth, 1969; Shatalkin, 1975). Thompson et al. (1976) made a major rearrangement redefining the genus *Ocyptamus* Macquart, 1834 and placing it within Syrphini, which helped in the current definition of Bacchini, but the current concept of Bacchini *sensu lato* is based mostly on Vockeroth (1992) and Thompson (1999).

Although the members of Bacchini were accepted without major controversy, generic definitions have been unclear and the systematic status of some supraspecific taxa was unstable (Thompson & Rotheray, 1998; Mengual

et al., 2008a; Láska et al., 2013; Young et al., 2016a). Young et al. (2016b) gave a precise background on how the genera *Platycheirus* Le Peletier & Audinet-Serville, 1828 and *Melanostoma* Schiner, 1860 have been defined historically. Nowadays the genus *Melanostoma* only includes species with an excavated metasternum (Andersson, 1970), and the metasternum with an anterior excavation is established as the diagnostic character to separate this genus from the other bacchines (Andersson, 1970; Barkalov, 2009). The latest member to be part of Bacchini *sensu lato* was described by Thompson & Skevington (2014), the monotypic genus *Afrostoma* Skevington, Thompson & Vockeroth, 2014. Besides the description of their new genus, Thompson & Skevington (2014) also provided an excellent outline of the tribe Bacchini *sensu lato* since its origin and gave a synopsis for each genus. Thompson & Skevington (2014) used DNA barcodes (Hebert et al., 2003a, b) to place their new genus *Afrostoma* in a phylogenetic context and stated some diagnostic characteristics, i.e., lack of male secondary characters in legs (as in *Melanostoma*, but usually present in many *Platycheirus* species), metasternum without basolateral excavation (as in *Platycheirus*, but the diagnostic character for *Melanostoma*), antennal pits confluent, and male genitalia without synapomorphies of *Platycheirus*. At first glance, *Afrostoma* looks like a *Melanostoma* without metasternal excavation and male genitalia of *Melanostoma* species (Fluke, 1957) are overall very similar to those of *Afrostoma*. Male genitalia characters are rather distinct between *Afrostoma* and *Platycheirus*, the two genera close to *Melanostoma* with metasternum not excavated: i.e., *Platycheirus* has surstyli with a long, slightly curved lateral lobe, and a short, stout basomedial lobe (surstyli elongate and simple in *Afrostoma*, with a small tubercle instead of a basomedial lobe); *Platycheirus* has postgonites usually slender

with a hook-like process (postgonites massive, solid, irregular in shape in *Afrostoma*), and the distiphallus in *Platycheirus* is slightly expanded at apex (distiphallus notched in *Afrostoma*) (Fluke, 1957; Thompson & Skevington, 2014; Young et al., 2016b).

Recent phylogenetic studies have resolved the tribe Bacchini *sensu lato* into two or three different clades, grouping genera related to *Melanostoma* in one clade, and genera related to *Platycheirus* in another (Mengual, 2015; Mengual et al., 2015; Young et al., 2016a), and sometimes, resolving the genus *Baccha* in its own evolutionary lineage (Rotheray & Gilbert, 1999; Ståhls et al., 2003; Mengual et al., 2008a). Only the phylogeny by Hippa & Ståhls (2005) based on morphological characters have inferred all these groups into a single clade. The proposed classification of Shatalkin (1975), with Melanostomini divided into *Platycheirina* and *Melanostomina* (see Thompson, 1972), reflects most of the present phylogenetic relationships among Bacchini. In this study, Shatalkin (1975) placed *Baccha* under Bacchini together with *Ocyptamus* (currently in Syrphini) and *Allobaccha* Curran, 1928 (currently also in Syrphini), and his Melanostomini was equivalent to the current Bacchini with the exclusion of *Baccha*.

The present author gathered molecular data during some years to study more closely the phylogenetic relationships among Bacchini *sensu lato*. To perform the analysis we used three molecular markers: almost the entire mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI), the D2–D3 region of the nuclear ribosomal 28S rRNA gene, and a small fragment of the nuclear ribosomal 18S rRNA gene. The aims of this study are twofold: (i) to infer the phylogenetic relationships of the tribe Bacchini *sensu lato* based on molecular characters and the largest taxon sampling up-to-date; and (ii) to describe a new species of *Melanostoma* from Cameroon without

metasternal excavation. Consequently, a new generic classification of Bacchini **stat. rev.** and Melanostomini **stat. rev.** is presented and some taxonomic actions are carried out: *Pseudoplatychirus* van Doesburg, 1955 is considered **junior synonym** of *Platycheirus* and *Afrostroma* as **junior synonym** of *Melanostoma*. *Pyrophæna* Schiner, 1860 and *Eocheilosia* Hull, 1949 **comb. nov.** are ranked as valid genera, and consequently, the genus *Platycheirus* is divided into four subgenera: *Platycheirus* (*Carposcalis*) (Enderlein, 1938), *Platycheirus* (*Pachysphyria*) (Enderlein, 1938), *Platycheirus* (*Platycheirus*), and *Platycheirus* (*Tuberculanostoma*) (Fluke, 1943) **comb. nov.**

Material and methods

Taxonomy

The new species of *Melanostoma* was collected during the field work done by Vlašánková et al. (2017) in the Mendong Buo area (6.592699°N, 10.189999°E; 2100–2200 m above sea level), ca. 5 km south-east of Big Babanki, in the Bamenda Highlands, North-West Province, Cameroon. This new species to science is refereed as *Melanostoma* sp. in Vlašánková et al. (2017). In the present study, the division between Bacchini *sensu stricto* and Melanostomini stated by Thompson & Skevington (2014) will be followed to discuss the results.

New species is described in full with terminology following Thompson (1999) and Cumming & Wood (2017). In the description of type labels, the contents of each label is enclosed within double quotation (" "), italics denote handwriting, and the individual lines of data are separated by a double forward slash (//). At the end of each record, between square brackets ([]) and separated by a comma, the number of specimens and sex, the holding institution, and the unique identifier or number are given. The abbreviations used

for collections follow the standard of the *Systema Dipterorum* (Thompson, 2013), and their equivalents are given below:

BMNH: The Natural History Museum, London, UK.

NBC: Naturalis Biodiversity Center, Leiden, The Netherlands.

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

All measurements are in millimeters and were taken using a reticule in a Leica M165 C microscope. Photographs were composed using the software Zerene Stacker 1.04 (Richland, Washington, USA), based on images of pinned specimens taken with a Canon EOS 7D mounted on a P-51 Cam-Lift (Dun Inc., VA, USA) and with the help of Adobe Lightroom (version 5.6). Body length was measured from the anterior oral margin to the posterior end of the abdomen, in lateral view. Wing length was measured from the wing tip to the basicosta.

Taxon sampling for molecular analyses

The selection of taxa for this study was based on Thompson & Skevington (2014) (see fig. 1). Members of all genera and subgenera of Bacchini and Melanostomini were included in the analysis, with the exception of *Afroxyanthandrus* Kassebeer, 2000 and *Xanthandrus* (*Androsyrphus*) Thompson, 1981 because there were no available specimens for the present molecular study. A total of 90 taxa were used in the analyses, including 54 bacchine and melanostomine taxa. Table 1 lists the species included in the analysis, the collection data and the GenBank accession numbers. Some new species to science, which will be described in following publications, were included as well and they are indicated in fig. 2 as 'sp.n.' plus the lab code in brackets.

Microdon mutabilis (Linnaeus, 1758) was constrained as outgroup as all previous phylogenies resolved Microdontinae as the sister

TABLE 1 Taxa used in the molecular analyses, including GenBank accession numbers. GenBank accession numbers of newly generated sequences (this study) are in boldface

Taxa	Locality information	Lab code	Accession No. COI	Accession No. 28S	Accession No. 18S
OUTGROUP					
<i>Microdon mutabilis</i> (Linnaeus, 1758)	UK: England, Cumbria, Whithorow, IV.2004. Leg.: S.M. Hewitt. Det.: M. Reemer.	MZH_Y149	EU431494	EU431463	EU431537
ERISTALINAE					
<i>Neoscia tenur</i> (Harris, 1780)	THE NETHERLANDS: De Wiechen, A'foort co., 199–521, 31.VII.2007. Leg.: M.P. van Zuijen. Det.: M.P. van Zuijen.	MZH_XP220	EU431489	EU431458	EU431526
<i>Eumerus ovatus</i> Loew, 1848	FRANCE: Dep. Bas-Rhin, Selestat, Foret de l'Ill, 184 m., 23.VI.2005. Leg.: M.P. van Zuijen & J. van Steenis.	MZH_Y463	EU431483	EU431452	EU431518
PIPIZINAE					
<i>Claussenia hispanica</i> (Strobl, 1909)	GREECE: Samos island, IV.2011. Leg.: A. Vujic. Det.: A. Vujic.	MZH_Y1452	HF542942	HF542912	KM224476
<i>Cryptopipiza notabila</i> (Violovitsh, 1985)	SWEDEN: Småland, Skärvete, Skirö, 23.VI.2010. Leg.: N. Johansson. Det.: G. Ståhls.	MZH_Y1330	KM224516	HF542914	KM224473
<i>Heringia heringi</i> (Zetterstedt, 1843)	GREECE: Lesvos, nr. Agiassos, 08.V.2007. Leg.: A. Vujic. Det.: A. Vujic.	MZH_Y984	HF542944	HF542915	KM224477
<i>Neonemodon intensica</i> (Curran, 1921)	CANADA: Quebec, Gatineau Co., Masham Twp., hilltop nr Duncan Lake, 21.VII.2001. Leg.: J. & A. Skevington.	MZH_Y1012	HF542948	HF542919	KM224479
<i>Pipiza quadrimaculata</i> (Panzer, 1804)	FINLAND: Ka, Joutseno, Riikanmaa, KKJ-Y 3591:6777, 05.VII.2007. Leg.: M.P. van Zuijen & W. & J. van Steenis. Det.: G. Ståhls.	MZH_XP218	EU431506	EU431474	EU431562
<i>Pipizella certa</i> Violovitsh, 1981	SWEDEN: Ds Skållerud, Ryrs naturreservat, RN 652492–9 130725–9, 29.VI.2006. Leg.: Nils Ryrholm. Det.: G. Ståhls.	MZH_XP119	KM224518	KM224501	KM224475
<i>Trichopsomyia lasiotibialis</i> Fluke, 1937	PERU: Madre de Dios, rio Tambopata, Sachavacayoc centre, 12°51'S 69°22'W, 4.IX.2009. Leg.: J. T. Smit.	MZH_Y1121	HF546068	HF546074	KM224484
<i>Triglyphus fulvicornis</i> Bigot, 1884	AUSTRALIA: Tasmani. Lake St. Clair NP, Shadow Lake circuit, AMG 55 429–5337, 850 m., 22.I.2006. Leg.: W. van Steenis.	MZH_XP113	EU431508	EU431476	EU431564
SYRPHINAE					
<i>Allograpta obliqua</i> (Say, 1823)	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. Det.: F.C. Thompson.	MZH_XP38	EF127310	EF127389	EU241833

TABLE 1 Taxa used in the molecular analyses, including GenBank accession numbers. GenBank accession (cont.)

Taxa	Locality information	Lab code	Accession No. COI	Accession No. 28S	Accession No. 18S
<i>Argentinomyia catabomba</i> (Williston, 1891)	COLOMBIA: Dpto Valle del Cauca. Cali, Cerro San Antonio, 2200 m., 03°29.137'N 76°33.596'W, 24.II.2006. Leg.: X. Mengual. Det.: X. Mengual.	ZFMK_XP132	MK751024	MK751054	MK751085
<i>Argentinomyia longicornis</i> (Walker, 1836)	COLOMBIA: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2175 m., 15.II.2006. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP95	KM270850	KM270819	KM270767
<i>Argentinomyia luculenta</i> (Fluke, 1945)	PERU: Cuzco. Est. Biol. Wayqecha, Trocha Oso near 2nd landslide, Malaise trap 6, WP 532, 13°11.07'S 71°35.075'W, 2806 m., 8–11.XII.2011. Leg.: Norrbom, Steck, Sutton & Nolasco. Det.: X. Mengual.	ZFMK_XM138	MK751025	MK751055	MK751086
<i>Argentinomyia neotropica</i> (Curran, 1937)	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. Det.: X. Mengual.	MZH_Y208	EF127363	EF501963	MK751087
<i>Argentinomyia</i> sp.	ECUADOR: Zamora-Chinchipe Prov., Cantón Zamora, Sector San Francisco, Páramo, 2600 m., 26.VII–11.VIII.2012, Malaise, 3°59.488'S 79°7.655'W. Leg.: X. Mengual. Det.: X. Mengual.	ZFMK_Do22	MK751026	MK751056	MK751088
<i>Argentinomyia</i> sp. nov.1	COSTA RICA: Páramo, Cerro de la Muerte, 14.I.2005. Leg.: F.C. Thompson. Det.: X. Mengual.	MZH_XP17	EF127296	EF127374	
<i>Argentinomyia</i> sp. nov.2	COSTA RICA: PN Tapantí, Estación La Esperanza, 2800 m, 13.I.2005. Det.: F.C. Thompson.	MZH_XP129	MK751027	MK751057	MK751089
<i>Baccha elongata</i> (Fabricius, 1775)	FINLAND: Ta, Vesijako, Malaise Trap. 2004. Leg.: J. Jakovlev. Det.: G. Ståhls.	MZH_Y242	EF127326	EF127407	EU431540
<i>Baccha maculata</i> Walker, 1852	MALAYSIA: Sabah (Borneo), Penampang Distr., Crocker Range, Ulu Kalangan, Dipterocarp tree, 5°51.383'N 116°18.484'E, 1350 m., 20.X.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	ZFMK_XM121	KM270856	KM270825	KM270773
<i>Chrysotoxum intermedium</i> Meigen, 1822	SPAIN: Alicante, Ibi, E.B. Torretes, 18.V.2007. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP154	EU431498	EU431466	EU431541

<i>Dasyrphus albostratus</i> (Fallén, 1817)	THE NETHERLANDS: Leiden, Meijendel dune area, 5.IX.2005. Leg.: excursion participants. Det.: G. Ståhl.	MZH_S565	EF127323	EF127402	EU431542
<i>Didea intermedia</i> Loew, 1854	FINLAND: Espoo, VII.2001. Leg.: G. Ståhl.	MZH_S90	EF127336	EF127418	EU431543
<i>Eocheilosia</i> aff. <i>harrisii</i> [previously <i>Platycheirus</i> (<i>Eocheilosia</i>)]	NEW ZEALAND: Waikato, N of Taupo, paintball camp, 576 m., 38°31.283'S 176°2.35'E, 14–16.XII.2017, Malaise trap, Beech forest. Leg.: Chalcid Team. Det.: X. Mengual.	ZFMK_AHE266	MK751043	MK751074	MK751107
<i>Eosalpingogaster conopida</i> (Philippi, 1865)	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.2003–8.1.2004. Leg.: M.E. Irwin. Det.: F.C. Thompson.	MZH_Y214	EF127359	EF127440	EU241850
<i>Episyrphus balteatus</i> (De Geer, 1776)	SPAIN: Alicante, P.N. Marjal Pego-Oliva, Muntanyeta Verda, 19.V.2007. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP153	EU241740	EU241788	EU241840
<i>Eriozona syrphoides</i> (Fallén, 1817)	RUSSIA: Gornyi Altai, Turotshakskii r-kordon obogo, 950 m., 30.VI.2003. Leg.: Krolatscheva. Det.: G. Ståhl.	MZH_Y184	EF127358	EF127439	EU431544
<i>Eupeodes corollae</i> (Fabricius, 1794)	SPAIN: Alicante, Aspe, Partida Tolomó, 07.II.2006. Leg.: P. Hurtado. Det.: X. Mengual.	MZH_XP141	EU431499	EU431467	EU431546
<i>Fazia centropogonis</i> (Nishida, 2003)	COSTA RICA: PN Tapanti, Estación La Esperanza, 2600 m., 13.I.2005. Det.: F.C. Thompson.	MZH_S492	EF127367	EF127447	EU241816
<i>Ischiodon aegyptius</i> (Wiedemann, 1830)	SOUTH AFRICA: Kwazulu Natal, Royal Natal N.P., trail to The Crack, walking back in the evening, gorge forest and adjacent grassland, 1600 m., 09.XII.2012, 28°41.072'S 28°56.245'E. Leg.: S. Rojo. Det.: X. Mengual	ZFMK_Do77	MF446529	MF446477	MF446434
<i>Leucopodella balboa</i> (Hull, 1947)	PANAMA: Fortuna Reserve, 1200 m., 8°41.76'N 82°13.2'W, 23.VIII.2012. Leg.: S. Bot. Det.: X. Mengual.	ZFMK_Do43	MK751028	MK751058	MK751090
<i>Leucopodella bigoti</i> (Austen, 1893)	PANAMA: Palo Seco Forest, 800 m., 8°46.8'N 82°11.4'W, 24.VIII.2012. Leg.: S. Bot. Det.: X. Mengual.	ZFMK_Do44	MK751029	MK751059	MK751091
<i>Leucopodella gracilis</i> (Williston, 1891)	COSTA RICA: Cartago, PN Tapanti, 1600 m., 12.I.2005. Leg.: S. Rojo. Det.: X. Mengual.	MZH_S488	EF127365	EF127444	EU431547
<i>Leucopodella</i> sp. (<i>gracilis</i> complex)	BRAZIL: 2000. Det.: X. Mengual.	MZH_S78	EF127331	EF127412	MK751092
<i>Leucopodella</i> sp. nov.1	ECUADOR: Zamora-Chinche Prov., Cantón Zamora, Podocarpus np, Estación Científica San Francisco, 1900 m., 3°58.382'S 79°4.864'W, 15.V.2011, Malaise trap. Leg.: B. Thormann. Det.: X. Mengual.	ZFMK_Do35	MK751030	MK751060	MK751093

TABLE 1 Taxa used in the molecular analyses, including GenBank accession numbers. GenBank accession (cont.)

Taxa	Locality information	Lab code	Accession No. COI	Accession No. 28S	Accession No. 18S
<i>Leucopodella</i> sp. nov.2	VENEZUELA: Lara, El Cercado, 10°07'N 69°14'W, 530 m., 1.I.2015. Leg.: E. Arcaya. Det.: X. Mengual.	ZFMK_D039 / ZFMK_D276	MK751031	MK751061	MK751094
<i>Leucopodella</i> sp. nov.3	COLOMBIA: Dpto Caldas, Manizales, Correg. Las Palomas, Reserva Natural Río Blanco. 18.II.2006, 2200–2500 m., 5°04'N 75°26.2'W. Leg.: C. Gutierrez. Det.: X. Mengual.	MZH_XP136	MK751032	MK751062	MK751095
<i>Leucopodella</i> sp. nov.4	COLOMBIA: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2200 m., 15.II.2006. Leg.: C. Gutiérrez. Det.: X. Mengual.	MZH_XP144	KM270870	KM270838	KM270792
<i>Leucopodella</i> sp. nov.5	PERU: Cuzco, Est. Biol. Wayqecha, Trocha Oso ner 2nd landslide, Malaise trap 6, WP 532, 13°11.07'S 71°35.075'W, 2806 m., 8–11.XII.2011. Leg.: Norrbom, Steck, Sutton & Nolasco. Det.: X. Mengual.	ZFMK_XM137	MK751033	MK751063	MK751096
<i>Leucozona (Leucozona) lucorum</i> (Linnaeus, 1758)	ITALY: South Tirol, Val Venosta, VII.2001. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_S139	EF127346	EF501965	EU431548
<i>Megasyrphus erraticus</i> (Linnaeus, 1758)	FINLAND: Ab, Karislojo, Karkalinniemi, V.2004. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_Y183	EF127357	EF127438	EU431545
<i>Melangyna (Melangyna) lasiophthalma</i> (Zetterstedt, 1843)	FINLAND: N, Mäntsälän Mustametsä, 10.V.2003. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_Y5	EF127361	EF501966	KM270796
<i>Melanostoma annulipes</i> (Macquart, 1842)	MADAGASCAR: Fianarantsoa Prov., road from Valbio to Ranomafana, 25.XI.2004. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP53	EF127320	EF127399	KM270798
<i>Melanostoma diffusum</i> Hull, 1941	MADAGASCAR: Fianarantsoa Prov., Ranomafana N.P., Sakaraoa region, 26.XI.2004. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP103		MK751064	MK751097
<i>Melanostoma janeceki</i> Mengual, sp. nov.	CAMEROON: North-West Prov., Bamenda Highlands, 5km SE Big Babanki, Mendong Buu area, 6°5.434'N 10°18.15'E, 2100–2200 m., XI.2012. Leg.: S. Janeček. Det.: X. Mengual.	ZFMK_D226	MK751034	MK751065	MK751098
<i>Melanostoma janeceki</i> Mengual, sp. nov.	CAMEROON: North-West Prov., Bamenda Highlands, 5km SE Big Babanki, Mendong Buu area, 6°5.434'N 10°18.15'E, 2100–2200 m., XI.2012. Leg.: S. Janeček. Det.: X. Mengual.	ZFMK_D227	MK751035	MK751066	MK751099

<i>Melanostoma janeceki</i> Mengual, sp. nov.	CAMEROON: North-West Prov., Bamenda Highlands, 5 km SE Big Babanki, Mendong Buo area, 6°54'34"N 10°18'15"E, 2100–2200 m., XI.2012. Leg.: S. Janeček. Det.: X. Mengual.	ZFMK_D228	MK758105	MK771146	MK771144
<i>Melanostoma mellinum</i> (Linnaeus, 1758)	GERMANY: 2015. Det.: X. Mengual.	ZFMK_D140	MK751036	MK751067	MK751100
<i>Melanostoma scalare</i> (Fabricius, 1794)	FINLAND: Ok, Kuhmo, Lentuankoski, 15.VIII.2006. Leg G. Ståhlh. Det.: G. Ståhlh.	MZH_Y441	EU431500	EU431468	EU431549
<i>Melanostoma polynesiot</i> Mengual & Ramage, 2018	FRENCH POLYNESIA: Tahiti, Tahiti iti – sentier vers le Mt Atara, 20.IX.2012 (fauchage), 17°47'375"S 149°14'899 W, 825 m. Leg.: T. Ramage. Det.: X. Mengual.	ZFMK_D269	MF446515	MF446466	MF446421
<i>Melanostoma quadripunctatum</i> (Skevington & Thompson, 2014) [previously <i>Afrostoma quadripunctatum</i>]	KENYA: Western Prov., Kakamega Forest, 00°14'13"N 34°51'87"E, 30.VIII–5.IX.2000, Malaise trap. Leg.: R. Copeland. Det.: F.C. Thompson. (USNM ENT 00036401)	SYCNC010–13	KF919067		
<i>Melanostoma sybarum</i> Hull, 1941	MADAGASCAR: Fianarantsoa Prov., Ranomafana N.P., Talatakely region, Valbio Center. 18.XI.2004. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP54	MK751037	MK751068	
<i>Melanostoma univittatum</i> (Wiedemann, 1824)	INDONESIA: Northern Sulawesi, Tumarates, Langowan [Lagoon]. 1°08'N 124°50'E, 13–20.VIII.2004. Leg.: M. Meray, M.F. & C. Dien. Det.: X. Mengual.	MZH_XP47	EF127314	EF127393	MK751101
<i>Meligranma guttata</i> (Fallén, 1817)	FINLAND: Ab, Miettinen, Perkkio, 6733:222, 21.VII.2004. Leg.: A. Haarto. Det.: G. Ståhlh.	MZH_Y478	EF501960	EF501968	KM270800
<i>Melisaeca cinctella</i> (Zetterstedt, 1843)	CZECH REPUBLIC: Bohemia, PLA Jezerske mountains, Korenov, 12.VI.2005. Leg.: L. Mazánek. Det.: L. Mazánek.	MZH_S557	EU241743	EU241791	EU241845
<i>Ocyptamus funebris</i> Macquart, 1834	COSTA RICA: San José, Heredia, INBioparque, 15–21.I.2005, Malaise trap. Det.: F.C. Thompson.	MZH_S487	EF127364	EF127443	EU409242
<i>Orphnabaccha calda</i> (Walker, 1852)	ECUADOR: Zamora-Chinchipe Prov., Cantón Zamora, Carretera Vieja, Point 1, 1500 m., 7.VIII.2012, 3°57'334"S 79°1'633"W. Leg.: X. Mengual. Det.: X. Mengual.	ZFMK_Do38	MK751038	MK751069	MK751102
<i>Paragus (Pandasyophthalmus) haemorrhous</i> Meigen, 1822	SPAIN: Alicante, 2000. Leg.: A. Vujić. Det.: A. Vujić.	MZH_S48	AY174470	AY476866	EU409259

TABLE 1 Taxa used in the molecular analyses, including GenBank accession numbers. GenBank accession (cont.)

Taxa	Locality information	Lab code	Accession No. COI	Accession No. 28S	Accession No. 18S
<i>Parasyrphus macularis</i> (Zetterstedt, 1843)	GERMANY: Nordrhein-Westfalen, NP Eiffel, 50°30.484'N 6°15.034'E, Gut Heistert, Perlenbachtal Aue, Kalterherberg, 533 m., 17.V.2012. Leg. A. Ssymank. Det. A. Ssymank.	ZFMK_Do17	MK751039	MK751070	MK751103
<i>Pelloloma nigrifacies</i> Vockeroth, 1973	SOUTH AFRICA: Woodcliffe, Naude's Nek, Maclear, Eastern Cape, 2500 m., 30°43.9'S 28°8.216'E, 09.II.2016. Leg.: A. Vujić. Det.: A. Ssymank.	ZFMK_D282	MK751040	MK751071	MK751104
<i>Platycheirus (Carposcalis) chalconotus</i> (Philippi, 1865)	COLOMBIA: Dpto Caldas, Villamaría, via al Nevado del Ruiz, Sector El 8, 3500 m., 19.II.2006. Leg.: C. Gutierrez. Det.: X. Mengual.	MZH_XP126	MK751041	MK751072	MK751105
<i>Platycheirus (Carposcalis) spinipes</i> Vockeroth, 1990	COLOMBIA: Dpto Caldas, Villamaría, via La Esperanza km 8, 2530 m., 19.II.2006. Leg.: C. Gutierrez. Det.: X. Mengual.	MZH_XP140	MK751042	MK751073	MK751106
<i>Platycheirus (Pachysphyria) coeruleus</i> (Williston, 1887)	USA: NE, Sioux Co., Harrison 6 mi. NNE, Gilbert Baker SWMA, 18.IV.2004. Leg.: J. & W. van Steenis. Det. W. van Steenis.	MZH_XP96	MK751044	MK751075	MK751108
<i>Platycheirus (Platycheirus) albianus</i> (Fabricius, 1781)	SWEDEN: 2000. Leg.: J. van Steenis. Det.: J. van Steenis.	MZH_E38	EF127351	EF127432	KM270805
<i>Platycheirus (Platycheirus) glupovi</i> (Barkalov, 2007) [previously <i>Pseudoplathycheirus glupovi</i>]	RUSSIA: Altai, Plateau Ukok, VII.2005. Leg.: A.V. Barkalov. Det.: A.V. Barkalov	MZH_S561	EF127317	EF127394	
<i>Platycheirus (Platycheirus) nielsenii</i> Vockeroth, 1990	SWEDEN: 2000. Leg.: J. van Steenis. Det.: J. van Steenis.	MZH_E36	EF127352	EF127433	KM270806
<i>Platycheirus (Platycheirus) peltatus</i> (Meigen, 1822)	FINLAND: Li, Ivalo. 76200:35219, 12.VII.2007. Leg.: G. Ståhl. Det.: G. Ståhl.	MZH_XP210	EU431501	EU431469	EU431550
<i>Platycheirus (Tuberculanostoma) sp. nov.</i> [previously <i>Tuberculanostoma</i>]	COLOMBIA: Dpto Caldas, Villamaría, via al Nevado del Ruiz, Sector El 8, 3500 m., 19.II.2006. Leg.: F.C. Thompson. Det.: X. Mengual.	MZH_XP73	MK751047	MK751078	MK751111
<i>Platycheirus (Tuberculanostoma) antennatum</i> (Fluke, 1943) [previously <i>Tuberculanostoma</i>]	COLOMBIA: 2008. Leg.: F.C. Thompson. Det.: X. Mengual.	ZFMK_MS3	MK751048	MK751079	MK751112

<i>Platycheirus (Tuberculanostoma)</i> <i>pectinis</i> (Fluke, 1943) [previously <i>Tuberculanostoma</i>]	PERU: Cuzco, Acjanaco, WP 540, 13°11.954'S 71°37.074'W, 3519 m., 9.XII.2011. Leg.: Norrbom, Steck, Sutton & Nolasco. Det.: X. Mengual.	ZFMK_XM223	MK751049	MK751080	MK751113
<i>Pyrophaena granditarsa</i> (Forster, 1771)	THE NETHERLANDS: Leiden, Kortenhof fen area, 5.IX. 2005, Leg.: J. van Steenis. Det.: G. Ståhls.	MZH_S563	EF127321	EF127400	EU431551
<i>Pyrophaena rosarum</i> (Fabricius, 1787)	GERMANY: Nordrhein-Westfalen, Nationalpark Eifel, Winterberg, 05–19.VIII.2012, Malaise, 405 m., 50°36.441'N 6°24.651'E. Leg.: J. Esser. Det.: X. Mengual. (ZFMK-TIS-2861)	ZFMK_D203	MK751045	MK751076	MK751109
<i>Rohdendorfia alpina</i> Sack, 1938	ITALY: Stelvio Pass. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_G344	EF127338	EF127420	EU431552
<i>Rohdendorfia bella</i> Mengual, 2019	INDIA: Jammu and Kashmir State, Ladakh, near Tso Moriri (lake), 32°54'N 78°18'E, 5333 m., 25–28.VIII.2010. Leg.: I. Abela-Hofbauerová. Det.: X. Mengual.	ZFMK_D268	MH282897	MH282902	MH282904
<i>Salpingogaster nigra</i> Schiner, 1868	COLOMBIA: Dpto Meta, PNN Sumapaz, Cabaña Las Mirilas, 710 m., 3°48'N 73°52'W, 29.V–19.VI.2004. Leg.: H. Vargas. Det.: X. Mengual.	MZH_XP77	EU241748	EU241796	EU241853
<i>Scaeva pyrastris</i> (Linnaeus, 1758)	SPAIN: Alicante, 1999. Det.: S. Rojo.	MZH_S57	EF127329	EF127410	EU431553
<i>Spazigaster ambulans</i> (Fabricius, 1798)	AUSTRIA: Imst. Leg.: J. van Steenis. Det.: J. van Steenis.	MZH_S158	EF127350	EF127431	KM270811
<i>Sphaerophoria scripta</i> (Linnaeus, 1758)	SPAIN: Alicante, Aspe, Partida Tolomó, 07.II.2006. Leg.: P. Hurtado. Det.: X. Mengual.	MZH_XP142	EU241752	EU241800	EU241860
<i>Syrphocheilosia claviventris</i> (Strobl, 1910)	ITALY: South Tirol, Stelvio Pass, 28.VII.1999. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_G327	EF127334	EF127415	KM270812
<i>Syrphus vitripennis</i> Meigen, 1822	GREECE: Lesbos island, IV.2001. Leg.: S. Rojo & C. Perez. Det.: S. Rojo.	MZH_S53	AY212797	AY261728	EU431554
<i>Talachua fervida</i> (Fluke, 1945)	COLOMBIA: Dpto Boyacá, SFF Iguaque, Lagunillas, 5°25'N 73°27'W, 3380 m., 28.VI–19.VII.2001. Leg.: P. Reina. Det.: X. Mengual.	MZH_XP76	MK751046	MK751077	MK751110
<i>Toxomerus marginatus</i> (Say, 1823)	USA: New York, Geneva, VII.1999. Leg.: M. Schmaedick. Det.: F.C. Thompson.	MZH_S64	AY261705	AY261752	EU431555
<i>Xanthandrus (Xanthandrus) agrolas</i> (Walker, 1849)	AUSTRALIA: Tasmania, Mt Field NP, Lake Belcher Track, AMG 55 468–5273, 1100 m., 21.I.2006. Leg.: W. van Steenis. Det.: X. Mengual.	MZH_XP110	MK751050	MK751081	MK751114
<i>Xanthandrus (Xanthandrus) bucephalus</i> (Wiedemann, 1830)	ECUADOR: Zamora-Chinchipe Prov., Cantón Zamora, Carretera Vieja, Point 2, 4°16'13"S 79°0.564'W, 27.VII.2012, 1230 m. Leg.: X. Mengual. Det.: X. Mengual.	ZFMK_Do73	MK751051	MK751082	MK751115

TABLE 1 Taxa used in the molecular analyses, including GenBank accession numbers. GenBank accession (cont.)

Taxa	Locality information	Lab code	Accession No. COI	Accession No. 28S	Accession No. 18S
<i>Xanthandrus (Xanthandrus) talamaui</i> (Meijere, 1924)	CHINA: Sichuan Prov., Ya'an, Baoxing, Dengchigou, christian church of priest Armand David. 30°22.534'N 102°49.733'E, 1600–1800 m., 13.VI.2014, sweeping. Leg.: J. Hájek, J. Růžička, M. Tkoč. Det.: X. Mengual.	ZFMK_D241	MK751052	MK751083	MK751116
<i>Xanthandrus (Xanthandrus) comtus</i> (Harris, 1780)	GREECE: Lesbos island, IV.2001. Leg.: S. Rojo & C. Pérez. Det.: G. Stähls.	MZH_S121	EF127340	EF127422	EU431556
<i>Xanthandrus (Xanthandrus) plaumanni</i> Fluke, 1937	COLOMBIA: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2200 m., 03°29.137'N 76°33.596'W, 24.II.2006. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP98	KM270876	KM270844	KM270813
<i>Xanthandrus (Xanthandrus) ruficorne</i> (Bigot, 1884)	AUSTRALIA: Tasmania, Mt. Field np, Lake Belcher Track, AMG 55 468–5273, 1100 m., 21.I.2006. Leg.: M.P. van Zuijen & W. van Steenis. Det.: W. van Steenis.	MZH_XP122	MK751053	MK751084	MK751117
<i>Xanthogramma pedissequum</i> (Harris, 1776)	GREECE: Lesbos island, IV.2001. Leg.: S. Rojo & C. Perez. Det.: S. Rojo.	MZH_S120	EF127339	EF127421	EU431557

FIGURE 2 Maximum-likelihood tree based on the combined dataset (COI, 28S, and 18S) using Garli v.2.1.17 and the structural alignment for 28S and 18S. Bootstrap support values (above) and Bayesian posterior probabilities (below) are depicted at the nodes (only >50 or >0.5, respectively). BS = Bootstrap support values; PP = Bayesian posterior probabilities.

group of (Eristalinae + (Pipizinae + Syrphinae)); the same argument is valid for the inclusion of all genera of Pipizini plus *Eumerus ovatus* Loew, 1848 and *Neoascia tenur* (Harris, 1780). Members of Bacchini and Melanostomini were resolved as sister taxa of the other tribes of Syrphinae in previous works. Thus, in order to have a general view of the subfamily Syrphinae and to avoid any bias in the results due to taxon sampling, several Syrphini genera were also included in the analysis (see table 1).

DNA extraction and sequencing

A large fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene, a fragment of the nuclear 18S rRNA gene (variable region V4), and the D2–D3 region of the nuclear 28S rRNA gene were used to performed the analyses. One to three legs, the entire abdomen or the entire specimen, either dry pinned or ethanol preserved, were typically used for DNA extraction. Extractions were carried out using the NucleoSpin Tissue DNA Extraction kit (Machery-Nagel, Düren, Germany) following manufacturer's instructions; samples were resuspended in 100 µl ultra-pure water. Remnants of specimens were preserved and labelled as DNA voucher specimens and deposited at the Zoological Museum of the Finnish Museum of Natural History [MZH] and at the Zoological Museum Alexander Koenig [ZFMK], as listed in table 1.

DNA primers and PCR amplification protocols for mitochondrial COI, and nuclear 28S and 18S rRNA genes were the same as described in Mengual et al. (2008b, 2015) and Rozo-Lopez & Mengual (2015). Amplified DNA was electrophoresed on 1.5% agarose gels for visual inspection of amplified products. PCR products were enzymatically treated with ExoSap-IT (USB, Cleveland, oh, USA) or were cleaned using the commercially available QIAquick PCR Purification Kit (QIAGEN®). Bi-directional sequencing reactions were carried

out by MacroGen© Inc. Chromatograms were edited for base-calling errors and assembled using Geneious 7.1.3 (Biomatters© Ltd).

Sequence alignment

The alignment of the protein-coding COI gene was done manually and it was not necessary to include gaps in this alignment. A total of 1,128 nucleotide characters were obtained for the COI data matrix. The 18S and 28S rRNA genes were aligned using the secondary structure of these genes, as explained by Kjer (1995) and implemented in Mengual et al. (2012, 2015) and Mengual (2015). The aligned small fragment of 18S used in this analysis had a total sequence length of 370 bp including gaps (ranging from 350 bp to 356 bp without gaps), and the D2–3 region of 28S a total of 658 bp including gaps (ranging from 562 bp to 589 bp without gaps). The final dataset had 2,156 bp.

Barcoding analysis

Thompson & Skevington (2014) used DNA barcodes of the Bacchini *sensu lato* genera to place *Afrostroma* into phylogenetic context. Although the utility of a fragment of a single gene for phylogenetic inference is questionable (see Doyle, 1992; Nichols, 2001; Hebert & Gregory, 2005, among others), the present author followed the analytical methodology used by Thompson & Skevington (2014), explained in Skevington & Thompson (2012), in order to incorporate the new species of *Melanostoma* without metasternal excavation to the same data matrix and to be able to compare the results of the barcoding analysis with the phylogenetic analysis based on three molecular markers. DNA sequences for the 5' end of the COI gene for the species analyzed by Thompson & Skevington (2014) were downloaded from GenBank and three sequences from the new *Melanostoma* species from Cameroon were added to the matrix (658 bp of the 5' end).

Bayesian inference using the Markov Chain Monte Carlo algorithm as implemented in MrBayes 3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was performed using a parallelized version of the software. Data were not divided into partitions following Thompson & Skevington (2014). The best model of evolution for the data was determined using jModelTest 2.1.5 (Darriba et al., 2012) under the Akaike Information Criterion (AIC). The model chosen was GTR+I+G. Four chains (three hot, one cold) were run simultaneously for 500,000 generations, which were sufficient to bring the convergence (average standard deviation) to a value <0.009 (Ronquist et al., 2005). Trees were sampled every 100 generations, the temperature was set to 0.2 and the number of runs to 6. The initial 1,250 trees (25%) were discarded as burn-in and Bayesian posterior probabilities (PP) were calculated using a 50% majority-rule consensus tree inferred from the data (fig. 1).

Phylogenetic analyses

The Maximum Likelihood analysis and the Bayesian inference were performed two times each, one without the COI barcode sequence of *Afrostroma quadripunctatum* Skevington & Thompson, 2014, and a second time with the inclusion of this short sequence (647 bp) to evaluate the phylogenetic position of this species even with only a partial sequence of one of the three sequenced genes. For the analytical runs the data set was divided in five partitions: first codon position of COI, second codon position of COI, third codon position of COI, 28S gene and 18S gene. The best evolutionary model that fit the data was chosen each partition using jModelTest 2.1.5 (Darriba et al., 2012) under the Akaike Information Criterion (AIC), as recommended by Posada and Buckley (2004). The model chosen for position 1 of COI was GTR+I+G, TIM1+I+G for position 2 and TIM3+I+G for position 3. The

model GTR+I+G was selected for 28S and the preferred model for 18S was TVM+I+G. The inclusion of the COI sequence of *Afrostroma quadripunctatum* did not change the model selection.

Data was analyzed under the recommended models using Garli v.2.1.17 (Zwickl, 2006, 2011) under Maximum Likelihood (ML) criterion. The author conducted 24 independent runs using scorethreshforterm = 0.05 and significanttopchange = 0.0001 settings and the automated stopping criterion, terminating the search when the ln score remained constant for 50,000 consecutive generations. The tree with the highest likelihood was retained and is presented here (fig. 2). Bootstrap support values (BS) were estimated from 500 replicates using the same independent models in Garli.

Bayesian inference (BI) using the Markov Chain Monte Carlo algorithm as implemented in MrBayes 3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was performed using a parallelized version of the software. Data were divided into the above five partitions and a separate GTR+I+G model for each partition was specified in the analysis where each partition has its own set of parameters. Priors were applied with default values. Six runs, with four chains each (one "cold" chain and three heated chains; temp = 0.2), were performed simultaneously for 20,000,000 generations, which were sufficient to bring the convergence (average standard deviation) to a value <0.007 (Ronquist et al., 2005), sampling trees every 2,500 generations. The program Tracer 1.7.1 (Rambaut et al., 2018) was used to check convergence and acceptable mixing. The initial 2,000 trees (25%) were discarded as burn-in and Bayesian posterior probabilities (PP) were calculated using a 50% majority-rule consensus tree inferred from the data (fig. 2).

Maximum Likelihood analysis and Bayesian inference were performed on the CIPRES

Science Gateway (Miller et al., 2010). All trees were drawn with the aid of FigTree v.1.4.4 (Rambaut, 2018), Adobe Illustrator® and Adobe Photoshop® CS5.

Results

Barcoding analysis

The Bayesian phylogram (fig. 1) based only on the DNA barcode region (the 5' end of the COI gene) compares favorably with the cladogram from Thompson & Skevington (2014, figure 2). The same groupings and the same inferred relationships were found in the present analysis with a minor nomenclatural change: *Platycheirus concinnus* (Snow, 1895) appears as *Platycheirus pictipes* (Bigot, 1884) following the synonymy proposed by Young et al. (2016b). The novelty in the present study is the placement of the new species without metasternal excavation, *Melanostoma janeceki* sp. nov., as sister-group of *Afrostroma quadripunctatum* [= *Melanostoma quadripunctatum* comb. nov. in fig. 1] with the highest Bayesian posterior probability. Note that *Afrostroma quadripunctatum* appears as *Afrostroma vockerothi* in the figure 2 of Thompson & Skevington (2014), and hereafter this species is referred as *Afrostroma quadripunctatum* or as *Melanostoma quadripunctatum* comb. nov. The group (*Melanostoma janeceki* sp. nov. + *Afrostroma quadripunctatum*) has a PP of 1, and the barcode similarity based on uncorrected pairwise distance between *Melanostoma janeceki* sp. nov. and *Afrostroma quadripunctatum* is 96.136% with the D226 and D228 specimens (25 nucleotide differences) and 96.059% with the D227 specimen (26 nucleotide differences).

The DNA barcodes for the three specimens of *Melanostoma janeceki* sp. nov. were almost identical. The only difference among the sequences of *Melanostoma janeceki* sp. nov. was an ambiguous call in one base (W for

specimen D227 and A for specimens D226 and D228).

Phylogenetic analyses

No topological differences were found when *Afrostroma quadripunctatum* [= *Melanostoma quadripunctatum* comb. nov. in fig. 2] was excluded from the analysis, and the same relationships among taxa were recovered with both dataset, with or without the DNA barcode sequence of *Afrostroma quadripunctatum*. The ML and BI analyses resulted in highly similar tree topologies and are summarized together. The ML tree including the *Afrostroma* barcode with the best likelihood score (−28846.913085) is presented in fig. 2 with the PP from the Bayesian analysis and the BS values from the ML analysis.

Although the taxonomic sampling effort was done to include all the diversity of the Bacchini *sensu lato*, it is worth to mention the other syrphine genera and pipizines were resolved in agreement with previous studies (Mengual et al., 2008a, 2012, 2015; Mengual, 2015; Young et al., 2016a; Mengual et al., 2018), with members of Pipizinae resolved as sister-group of Syrphinae. The subfamily Syrphinae was resolved monophyletic with genera grouped into three major clades. The first major clade comprises all the Syrphini genera, including the representatives of Toxomerini and Paragini. The second major clade comprises the genera *Leucopodella* Hull, 1949, *Pelloloma* Vockeroth, 1973, *Talahua* Fluke, 1945, *Xanthandrus* Verrall, 1901, *Argentinomyia* Lynch Arribalzaga, 1891, *Afrostroma* and *Melanostoma*. In this clade, *Leucopodella* species were placed as sister-group of two smaller clades: (*Pelloloma* + (*Talahua* + *Xanthandrus*)) and (*Argentinomyia* + *Melanostoma*), including *Afrostroma*. It is important to point out that the two studied species without metasternal excavation, i.e., *Melanostoma janeceki* sp. nov. and *Afrostroma quadripunctatum*, were resolved as sister taxa and

embedded among the species of the genus *Melanostoma*, which all have an excavation in the metasternum.

The third major clade as resolved in the present study has the representatives of the Bacchini, with *Baccha*, *Platycheirus* and all the other genera related to *Platycheirus*, i.e., *Tuberculanostoma*, *Pyrophaena*, *Syrphocheilosia* Stackelberg, 1964, *Spazigaster* Rondani, 1843, and *Rohdendorfia* Smirnov, 1924. Within this clade, *Baccha* was resolved as the sister-group of the other genera, *Tuberculanostoma* was placed embedded in the *Platycheirus* radiation, and (*Pyrophaena* + (*Rohdendorfia* + (*Syrphocheilosia* + *Spazigaster*))) were resolved as a clade sister to *Platycheirus*, including *Tuberculanostoma*.

***Melanostoma janeceki* Mengual, sp. nov.**

Melanostoma sp. in Vlašánková et al. (2017).
Figs. 3, 5C–E.

Differential diagnosis. Black, straight face with small, round facial tubercle; black thorax and abdomen black with terga 3–5 with two lateral, small yellow maculae on anterior margin (fig. 3). This species of *Melanostoma* with a complete metasternum (fig. 5C, D) is only known from Cameroon, and it is very similar to *Melanostoma quadripunctatum* (Skevington & Thompson, 2014) **comb. nov.**, known from Kenya and Uganda (fig. 5A, B). They differ by the COI gene sequence, sterna coloration in females (entirely yellow in *M. janeceki* sp. nov.; entirely black with two lateral yellow maculae on anterior margin of terga 2–5 in *M. quadripunctatum*; fig. 5E, F) and by the leg coloration: *M. janeceki* sp. nov. has pro- and mesofemora yellow in both sexes, and metafemora black except yellow on basal 1/4–1/3 in males or metafemora entirely yellow in females (fig. 3); and *M. quadripunctatum* males and females have all femora black with the very apex pale (fig. 5A).

Type locality. Cameroon: Northwest Province, Bamenda Highlands, ca. 5 km south-east of Big Babanki, Mendong Buo area, 6.592699°N, 10.189999°E, 2100–2200 m.

Description

Male: Head: Face straight with distinct facial tubercle, entirely black, pale pilose, sparsely grey pruinose except tubercle shiny; lunule black, shiny; frontal triangle black, sparsely grey pruinose, brownish pilose; eye contiguity long, longer than vertical triangle; ocellar triangle dark pilose; antenna brown, basoflagellomere darker apically; arista pilose, with pile shorter than the arista width at base; occiput black, silver grey pruinose, white pilose on ventral 1/2, brownish pilose on dorsal 1/2.

Thorax: Black except postalar callus slightly paler, brownish black; scutum shiny black, sparsely brownish pruinose, with short and long yellow pile with some darker pile; postpronotum white/grey pruinose, bare; scutellum black, yellow pilose with some darker pile intermixed, subscutellar fringe long, yellow. Pleuron black, pale pilose, sparsely pale pruinose; calypter yellow, yellow pilose; plumula yellow; halter pedicel and capitulum yellow; posterior spiracular fringes yellow; metasternum complete, bare. Scutum and pleuron with a golden iridescence. **Wing:** brownish, entirely microtrichose; alula broader than costal cell. **Legs:** pro- and mesofemora brown; pro- and mesotrochanter yellow; pro- and mesofemora yellow; pro- and mesotibia yellow with a medial black annulus; protarsi dark, probasitarsomere yellow basally; apical three mesotarsomeres black, basal two mesotarsomeres yellow; metacoxa black and metatrochanter yellow; metafemur black with basal 1/4–1/3 yellow and femoral-tibial joints yellow; metatibia black with basal 1/4–1/3 yellow; metatarsi black.

Abdomen: Parallel-sided, without lateral margin, entirely black except for the two lateral, small yellow maculae on anterior margin of

FIGURE 3 *Melanostoma janeceki* Mengual, sp. nov. A, male holotype (ZFMK-DIP-00015940), lateral view; B, female paratype (ZFMK-DIP-00015958), lateral view; C, male holotype, habitus; D, female paratype (ZFMK-DIP-00015958), habitus; E, male holotype, frontal view; F, female paratype (ZFMK-DIP-00015958), frontal view; G, male holotype, labels; H, female paratype (ZFMK-DIP-00015958), labels.

FIGURE 4 A–B: *Melanostoma* sp. from Cameroon (ZFMK-DIP-00015959) with complete metasternum. A, lateral view; B, habitus. C–H: *Platychirus solitarius* (van Doesburg, 1955) **comb. nov.** C, female holotype, lateral view; D, female holotype, habitus; E, female holotype, frontal view; F, female holotype, labels; G, female paratype, lateral view; H, female paratype, head, lateral view.

FIGURE 5 A–B: *Melanostoma quadripunctatum* (Skevington & Thompson, 2014) **comb. nov.**, male holotype. A, lateral view; B, habitus. C, *Melanostoma janeceki* Mengual, sp. nov., male holotype, ventral view. D, *Melanostoma janeceki* Mengual, sp. nov., male paratype (ZFMK-DIP-00015941), detail of metasternum (ms). E, *Melanostoma janeceki* Mengual, sp. nov., female paratype (ZFMK-DIP-00015957), ventral view. F, *Melanostoma quadripunctatum*, female (ZFMK-DIP-00015952), ventral view.

terga 3–4; tergum 5 has also two lateral, small yellow maculae but less evident. Terga dull black pruinose, with long yellow pile laterally and short black pile medially; sterna black except sterna 3–4 with a yellow fascia on posterior margin and sternum 5 with two lateral yellow maculae. *Male genitalia*: very similar

to male genitalia of *M. quadripunctatum* (Thompson & Skevington, 2014, figure 3).

Female: Similar to male except for normal sexual dimorphism and as follows: frons black with two lateral silver pruinose maculae on eye margin; pro- and mesolegs yellow except apical tarsomeres; metafemur yellow; terga

2–5 black with two lateral yellow maculae (those on tergum 2 elongated along lateral margin); sterna yellow.

Variation: No variation has been observed in the studied specimens, although some variability in the extension of the abdominal maculae and in the coloration of the legs at some extent might be possible.

Length (N = 3): Body, 9.17 mm (8.3–10.2 mm); wing, 7.9 mm (7.2–8.6 mm).

Geographical distribution. Species known from Cameroon.

Etymology. The new species is named after its collector, Dr. Štěpán Janeček. Species epithet to be treated as a noun in the genitive case.

Biology. See Vlašánková et al. (2017, as *Melanostoma* sp.) for its relationship with *Impatiens burtonii* var. *burtonii* Hook. f. (Balsaminaceae).

Material examined: Type material. *Holotype*, male, pinned with genitalia in microvial, deposited in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany, and labelled: “CAMEROON: North-West Prov., // Bamenda Highlands, 5 km SE Big // Babanki, Mendong Buo area, // 6.592699°N, 10.189999°E // 2100–2200 m., XI.2012. // Leg.: S. Janeček.” “DNA voucher specimen // ZFMK, Lab code // D226 // Bonn, Germany” “HOLOTYPE // *Melanostoma* // *janeceki* // Det. X. Mengual 2017” [red] “ZFMK DIP 00015940” [barcode]. *Paratypes*: 1♂, same data as holotype, DNA voucher ZFMK-D227 [ZFMK; ZFMK-DIP-00015941]; 1♀, same data as holotype, DNA voucher ZFMK-D228 [ZFMK; ZFMK-DIP-00015942]; 1♂, CAMEROON: North-West Prov., Mezan Division, Bafut-Ngemba Forest Reserve (35 km from Bamenda), in the way to the Lake (env. Chemin du Lac), 1500 m., 12.x.1970, L. Matile [ZFMK;

ZFMK-DIP-00015955]; 1♂, CAMEROON: North-West Prov., Mezan Division, Bafut-Ngemba, env. Maison Forest, 2000 m., 10.x.1970, L. Matile [MNHN; ZFMK-DIP-00015954]; 1♂, CAMEROON: North-West Prov., Mezan Division, Bafut-Ngemba, Vallée de la Haute Ngemba, 2100 m., 27.x.1975, Mission Cameroun C.N.R.S. RCP 318 [MNHN; ZFMK-DIP-00015956]; 1♀, CAMEROON: North-West Prov., Mezan Division, Bafut-Ngemba, Vallée de la Haute Ngemba, galerie, marigot avaut lac, 1800–1900 m., 30.x.1975, Mission Cameroun C.N.R.S. RCP 318 [MNHN; ZFMK-DIP-00015957]; 1♀, CAMEROON: North-West Prov., Mezan Division, Bafut-Ngemba, Vallée de la Haute Ngemba, prés Maison forestière, marigot, 2000 m., 25.x.1975, Mission Cameroun C.N.R.S. RCP 318 [ZFMK; ZFMK-DIP-00015957].

Material of *Melanostoma quadripunctatum* (Skevington & Thompson, 2014) comb. nov. KENYA: Kakamega Forest, 1585 m. [=5200 ft.], 18.xii.1970, E.E. Stubbs [4♂ 2♀, BMNH; 2♂ 1♀, ZFMK; ZFMK-DIP-00019927, ...00015944, ...00015945, ...00015947, ...00015950, ...00015951, ...00015943, ...00015946, ...00015952]; ..., 19.xii.1970, ... [1♀, BMNH; ZFMK-DIP-00015953]; ..., 20.xii.1970, ... [2♂, BMNH; ZFMK-DIP-00015948, ...00015949].

Remarks. Prior to this study, female specimens of *M. quadripunctatum* were unknown. They are very similar to females of *M. janeceki* sp. nov., but they can be distinguished by sternal and leg coloration as indicated in the diagnosis (fig. 5F).

Discussion

Inferred generic relationships

Pelloloma, *Talahua*, *Tuberculanostoma* and *Eocheilosia* have been included in a multi-gene phylogenetic analysis for the first time (see fig. 2). In its original description, Vockeroth (1973) placed the genus *Pelloloma* within the

Syrphini, but already mentioned the possibility that it could be placed among the Melanostomini. Kassebeer (2000a) explained using morphological characters the reason to move *Pelloloma* to Melanostomini. Present results (fig. 2) support the placement of this genus in the Melanostomini.

Fluke (1945) described a new *Melanostoma* subgenus, *Melanostoma* (*Talahua*), for the species *Melanostoma fervidum* Fluke, 1945, which is characterized by large male genitalia. Hull (1949) followed Fluke (1945) and considered *Talahua* as a *Melanostoma* subgenus, but Thompson et al. (1976) elevated *Talahua* to full generic status as it has a complete metasternum, not reduced as defined for *Melanostoma*. More recently, Thompson (1999) placed a second species in the genus *Talahua*, *Melanostoma palliatum* Fluke, 1975, which has normal-sized male genitalia. Hereafter, the size of the male genitalia was not diagnostic for *Talahua*, but only the character of metacoxa with a pile tuft postero-medially as stated in the identification key by Thompson (1999). Our analysis resolved *Talahua* and *Xanthandrus* as sister taxa and *Argentinomyia* as sister taxon of *Melanostoma* (fig. 2), supporting the decision of Thompson et al. (1976).

When Fluke (1943) described his new genus *Tuberculanostoma* from Ecuador, he stated the similarity with *Carposcalis* Enderlein, 1938 (at the time most *Carposcalis* species were treated as *Melanostoma*) based on the presence of curved bristles on the profemur. This similarity was also pointed out by Hull (1949). Fluke (1943) also mentioned some diagnostic characters, such as face produced forward into a snout and a prominent facial tubercle, and the preferential habitat in high elevations. Years later, van Doesburg (1955) described *Tuberculanostoma solitarium* van Doesburg, 1955 from the Karakorum Mountains (a mountain range spanning the borders of Pakistan, India, and China) (see fig. 4C–H). This species has a

produced face and a clear facial tubercle, but there are many differences from the Neotropical *Tuberculanostoma* as stated by Thompson & Skevington (2014). Results from Young et al. (2016b) using the 5' end of the COI gene resolved *Tuberculanostoma* embedded in *Platycheirus*, somehow related with the *stegnus* subgroup, referred as subgenus *Platycheirus* (*Carposcalis*) by other authors (see Vockeroth, 1990; Thompson & Skevington, 2014; Young et al., 2016b). Previously, Vockeroth (1990) suggested the possibility to include *Tuberculanostoma* in *Platycheirus* as an alternative placement. Present results (fig. 2) support the suggestion of Vockeroth (1990) and corroborate the results of Young et al. (2016b). Based on the current evidences, the genus *Platycheirus* comprises four subgenera: *Platycheirus* (*Carposcalis*), *Platycheirus* (*Pachysphyria*), *Platycheirus* (*Platycheirus*), and *Platycheirus* (*Tuberculanostoma*) **comb. nov.** Nevertheless, as stated by Young et al. (2016b), there is the possibility that other monophyletic species groups within the genus *Platycheirus* could be recognized as distinct in the future. The present results differ from the proposed subgeneric classification of Thompson & Skevington (2014) as *Pyrophaena* and *Eocheilosia* are supported as valid genera and *Pseudoplatycheirus* is recognized as a junior synonym of *Platycheirus* (**new synonym**). *Platycheirus* (*Pachysphyria*) is equivalent to the *Platycheirus ambiguus* species group *sensu* Vockeroth (1990), Nielsen (2004, 2014) and Young et al. (2016b). Based on molecular characters (Mengual et al., 2008; this study) and the morphological characters of the original descriptions, the *Pseudoplatycheirus* species are *Platycheirus* species with elongated antennae, dichoptic males, widened protarsi, profemur with long, strong, curly setae and projected face. Broadened protarsi, projected face and modified setae on the profemur are characteristics also found in other species groups within *Platycheirus*. All

known specimens of *Pseudoplatychirus* were collected at high elevations (van Doesburg, 1955; Zimina, 1958; Barkalov, 2007).

The present author has studied the holotype and paratype females of *Tuberculanostoma solitarium* deposited at NBC (fig. 4C–H) together with several Neotropical *Tuberculanostoma* species, and a few morphological differences are clear: frons broader than eye width in frontal view (much narrower than eye width in frontal view for the Neotropical species), frons and vertex with very long, erected pile (much shorter in Neotropical species), dorsal occiput without long, black bristles (dorsal occiput with 15–20 long, black bristles in Neotropical species), face with a patch of long pile on parafacia (Neotropical species without such pile patch), deep antero-apical tentorial pit in the inner side of the basoflagellomere (absence of tentorial pits in Neotropical species), procoxa medially broadened laterally (procoxa without modifications in Neotropical species), scutellum without bristles (scutellum with 1, usually 2 pairs of long, black bristles on posterior margin in Neotropical species), femora with dense, long pile postero-ventrally (femora with scattered pile in Neotropical species), wing marginal fringe short (wing marginal fringe longer in Neotropical species). The author of the present paper finds some morphological similarity between *Tuberculanostoma solitarium* and the species of *Pseudoplatychirus* such as projected face, somehow reduced eyes, and enlarged gena and ventral occiput. The two known species of *Pseudoplatychirus* resemble extremely morphologically modified species of the *Platycheirus manicatus* species group (see Nielsen & Barkalov, 2017). In the *P. manicatus* species group both sexes have the face slightly to strongly protruding below as in *Pseudoplatychirus*, and males of the *P. manicatus* species group are characterized by the two basal broadened tarsomeres

of the proleg, a character also present in the *Pseudoplatychirus* males. Unfortunately, only females of *Tuberculanostoma solitarium* are known and this sex does not have the mentioned broadened tarsomeres of the proleg. Either related to *Platycheirus* species with produced face or not, the species *Platycheirus solitarius* (van Doesburg, 1955) **comb. nov.** does not belong to *Platycheirus* (*Tuberculanostoma*) based on the morphological differences, and the shared morphological characters (produced face) might possibly be the result of adaptation to extreme conditions, in this case, very high elevations in the Andes and in the Karakorum Mountains. Perhaps, the only two known females of *Platycheirus solitarius* (collected conspecifically with the type series of *Pseudoplatychirus peteri* van Doesburg, 1955) belong to the same *Platycheirus* species group as the two species described as *Pseudoplatychirus*.

Hull (1949) described *Eocheilosia* as a subgenus of *Cheilosia* Meigen, 1822 (Eristalinae, Rhingiini) for the species *Cheilosia ronana* Miller, 1921. Thompson (1972) placed his new species *Platycheirus milleri* Thompson, 1972 [now known as *Eocheilosia huttoni* (Thompson in Thompson & Vockeroth, 1989)] in *Platycheirus*, although he pointed out that this taxon may deserve generic recognition. Thompson & Vockeroth (1989) and Thompson & Skevington (2014) considered *Eocheilosia* as subgenus of *Platycheirus*, and Thompson (2008) stated that *Eocheilosia* is used for those species of *Platycheirus* with unmodified male prolegs present in New Zealand. Present study (fig. 2) resolved *Eocheilosia* within a clade of genera previously placed under *Platycheirus* (Thompson & Rotheray, 1998), including *Rohdendorfia*, *Syrphocheilosia*, *Spazigaster*, and *Pyrophaena*. Previous DNA barcoding analyses (Thompson & Skevington, 2014; Young et al., 2016b; van Steenis et al., 2019) based on the 5' end of the COI gene also resolved *Eocheilosia*

notata (Bigot, 1884) [as *Platycheirus* (*Pseudo-platycheirus*) *notatus* in Young et al. (2016b, figure 6)] within this clade. Hence, molecular evidence supports the full generic status for *Eocheilosia* **comb. nov.**

Although there were no specimens available for the present study, the generic status of *Afroxanthandrus* is worth to comment. Kassebeer (2000b) described *Afroxanthandrus* as a new genus including *Xanthandrus congoensis* Curran, 1938 and his new species, *Afroxanthandrus longipilus* Kassebeer, 2000. Whittington (2003) listed the genus in his assessment of the Afrotropical syrphid fauna, but Mengual et al. (2008a) overlooked this taxon and did not include it in their classification. Later, Thompson & Skevington (2014) considered it as a subgenus of *Xanthandrus*, but did not officially propose it. Recently, Thompson (2019) considered *Afroxanthandrus* a junior synonym of *Xanthandrus*. The genus *Xanthandrus sensu* Thompson & Skevington (2014) is found in all biogeographic regions (Borges & Pamplona, 2002), with the typical subgenus present in the Neotropical, Nearctic, Palaearctic, Oriental and Australasian Regions, *Afro-xanthandrus* found in the Afrotropical Region, and the subgenus *Androsyrphus* known only from Jamaica. The main differences between *Afroxanthandrus* and *Xanthandrus* are: head of the female swollen medially (flat in *Xanthandrus*), scutum entirely pruinose and granulate (shiny without granulation in *Xanthandrus*), femora slightly thickened (not so in *Xanthandrus*), and male genitalia. *Xanthandrus* species have one-lobe, digitiform or pointed surstyli and small postgonites squarish or triangular in shape (see Dušek & Láska, 1967; Borges & Pamplona, 2003). On the other hand, *Afroxanthandrus congoensis* has small surstyli laterally displaced and enlarged postgonites rectangular in shape, with a quite distinct aedeagus (Kassebeer, 2000b). Based on male genitalia characters, the present author

tentatively considers *Afroxanthandrus* as a valid genus (table 2).

The other taxon not available for molecular work in the present study is also placed in *Xanthandrus*. Thompson (1981) erected a new subgenus, *Xanthandrus* (*Androsyrphus*), for a species with swollen metafemora and with ventral spines on meso- and metafemora from Jamaica. He agreed that some dipterists might give full generic rank to *Androsyrphus*, but he hesitated to do so in the Bacchini *sensu lato* based on a leg character as legs are very variable in this group. Further analysis of this taxon combining morphology and molecular markers might change Thompson's (1981) decision.

New generic diagnosis for Melanostoma

Generic concepts within Bacchini *sensu lato* have generally been difficult to define (Young et al., 2016b). Nowadays, there are published identification keys to sort out all the bacchine and melanostomine genera using morphological characters (Vockeroth & Thompson, 1987; Thompson & Rotheray, 1998; Thompson, 1999; Thompson et al., 2010; Láska et al., 2013; Thompson & Skevington, 2014). The importance of the metasternum shape during the history of syrphidology has been significant. The confusion between *Platycheirus* and *Melanostoma* was frequent until Andersson (1970) found the differences in the shape of the metasternum. Since then, a largely reduced, spearhead-shaped metasternum is a diagnostic character for the genus *Melanostoma* and *Platycheirus* species have an entire metasternum. Although the molecular data were limited, the lack of the basolateral excavation in the metasternum was a diagnostic character for Thompson & Skevington (2014) to erect a new genus, *Afrostroma*. Based on their own arguments, *Afrostroma* flies look very like *Melanostoma* species, endemic of the Afrotropical Region where the only other melanostomine is *Melanostoma*, with very similar

TABLE 2 New synthesis of generic and subgeneric names of Bacchini stat. rev. and Melanostomini stat. rev. (Syrphidae: Syrphinae)

Tribe	Genus	Subgenus	Author, year	Type species
Melanostomini	<i>Afroxanthandrus</i>		Kassebeer, 2000	<i>Afroxanthandrus congoensis</i> (Curran, 1938)
Melanostomini	<i>Argentinomyia</i>		Lynch Arribalzaga, 1891	<i>Argentinomyia testaceipes</i> Lynch Arribalzaga, 1891
Melanostomini	<i>Leucopodella</i>		Hull, 1949	<i>Leucopodella lanei</i> (Curran, 1936) = <i>Leucopodella bigoti</i> (Austen, 1893)
Melanostomini	<i>Melanostoma</i>		Schiner, 1860	<i>Melanostoma mellinum</i> (Linnaeus, 1758)
Melanostomini	<i>Pelloloma</i>		Vockeroth, 1973	<i>Pelloloma nigrifacies</i> Vockeroth, 1973
Melanostomini	<i>Talahua</i>		Fluke, 1945	<i>Talahua fervida</i> (Fluke, 1945)
Melanostomini	<i>Xanthandrus</i>	<i>Androsyrphus</i>	Thompson, 1981	<i>Xanthandrus</i> (<i>Androsyrphus</i>) <i>setifemoratus</i> Thompson, 1981
Melanostomini	<i>Xanthandrus</i>	<i>Xanthandrus</i>	Verrall, 1901	<i>Xanthandrus</i> (<i>Xanthandrus</i>) <i>comtus</i> (Harris, 1780)
Bacchini	<i>Baccha</i>		Fabricius, 1805	<i>Baccha elongata</i> (Fabricius, 1775)
Bacchini	<i>Eocheilosia</i>		Hull, 1949	<i>Eocheilosia ronana</i> (Miller, 1921)
Bacchini	<i>Platycheirus</i>	<i>Carposcalis</i>	Enderlein, 1937	<i>Platycheirus</i> (<i>Carposcalis</i>) <i>steg-nus</i> (Say, 1829)
Bacchini	<i>Platycheirus</i>	<i>Pachysphyria</i>	Enderlein, 1937	<i>Platycheirus</i> (<i>Pachysphyria</i>) <i>dexter</i> (Harris, 1780)
Bacchini	<i>Platycheirus</i>	<i>Platycheirus</i>	Lepeletier & Serville, 1828	<i>Platycheirus</i> (<i>Platycheirus</i>) <i>scutatus</i> (Meigen, 1822)
Bacchini	<i>Platycheirus</i>	<i>Tuberculanostoma</i>	Fluke, 1943	<i>Platycheirus</i> (<i>Tuberculanostoma</i>) <i>antennatus</i> (Fluke, 1943)
Bacchini	<i>Pyrophaena</i>		Schiner, 1860	<i>Pyrophaena rosarum</i> (Fabricius, 1787)
Bacchini	<i>Rohdendorfia</i>		Smirnov, 1924	<i>Rohdendorfia dimorpha</i> Smirnov, 1924
Bacchini	<i>Spazigaster</i>		Rondani, 1843	<i>Spazigaster apennini</i> Rondani, 1843 = <i>Spazigaster ambulans</i> (Fabricius, 1798)
Bacchini	<i>Syrphocheilosia</i>		Stackelberg, 1964	<i>Syrphocheilosia aterrima</i> Stackelberg, 1964 = <i>Syrphocheilosia claviventris</i> (Strobl, 1910)

* *Pseudoplatychirus* van Doesburg, 1955 is a junior synonym of *Platycheirus* Le Peletier & Audinet-Serville, 1828 and *Afrostroma* Skevington, Thompson & Vockeroth, 2014 is a junior synonym of *Melanostoma* Schiner, 1860.

male genitalia, and without male external secondary characters as all other *Melanostoma* species, but with an entire metasternum.

Two morphological characters were diagnostic to separate *Melanostoma* and *Platycheirus* species (Andersson, 1970; Barkalov, 2009; Haarto & Ståhls, 2014): the shape of the metasternum and the morphology of male genitalia, especially the shape of surstyli and postgonites. Most *Platycheirus* males have

modified protarsi, protibiae and/or with distinctive bristles or pile tufts on profemora, but they are so variable that cannot be used as diagnostic characters to define generic groups (Vockeroth, 1990; Young et al., 2016b). In a series of papers devoted to Bacchini *sensu lato*, Fluke (1937, 1943, 1945, 1957) studied in deep this group of genera and was the first author to study the male genitalia of these taxa (Fluke, 1957). When male genitalia

are compared, there are no evident differences between *Melanostoma* and *Afrostroma*. However, differences between these two taxa and *Platycheirus* are clear (see Fluke, 1957; Shatalkin, 1975; Vockeroth, 1990, 1992; Haarto & Ståhls, 2014; Thompson & Skevington, 2014; Young et al., 2016b). *Platycheirus* species have: bifid or bilobed surstyli with a long, slightly curved lateral lobe, and a short, stout basomedial lobe; and postgonites usually slender and recurved, sickle-shaped. On the other hand, *Melanostoma* species and *Afrostroma* have: simple, one-lobed, elongate surstyli with a small basomedial tubercle; and postgonites massive, irregular or squarish in shape. Thus, male genitalia characters do not distinguish between *Afrostroma* and *Melanostoma*.

The present COI cladogram (fig. 1) places the specimens of *Melanostoma janeceki* sp. nov. as sister group of *Afrostroma quadripunctatum*, and its topology is identical to the cladogram by Thompson & Skevington (2014), except for the inclusion of the new *Melanostoma* species described here. *Melanostoma janeceki* sp. nov. has an entire metasternum like *Afrostroma quadripunctatum* and the COI analysis corroborates their close relationship. But results from the multigene analysis presented here do not support the generic concept of *Afrostroma*, as *Afrostroma quadripunctatum* is embedded within the *Melanostoma* species (fig. 2), as sister group of *Melanostoma janeceki* sp. nov. Thus, the present author recognizes *Afrostroma* as a **junior synonym** of *Melanostoma*, which means that there is a group of *Melanostoma* species with the metasternum entire, not reduced.

Afrotropical species of *Melanostoma* are in urgent need of a taxonomic revision. There are few published identification keys (Bezzi, 1915; Curran, 1938; Dirickx, 2001) and none of them include all the described species. The same revisionary work is needed for the Oriental *Melanostoma* species (Lambeck & van Brink, 1973), and probably also in the other

biogeographical regions where this genus occurs. *Melanostoma* species have a limited number of structural characters enough variable to be used for distinguishing species, and some of them are chromatic (Dirickx, 2001). Male genitalia in this genus are remarkably homogeneous (Dirickx, 2001) and the intraspecific variability is high, plus there are several species described based only on one sex. Thus, it is very likely that the same taxon has been described two times under different names based on different sexes or very distinct specimens of the same species. Haarto & Ståhls (2014) showed that the DNA barcode, the 5' end of the COI gene, does not help to sort out species in *Melanostoma* alone and the sequencing of another molecular marker, i.e., the ITS2 as in Haarto & Ståhls (2014), is needed to characterize different species. In short, the taxonomy of Afrotropical *Melanostoma* has been never globally attempted, and most of the species where described before Andersson (1970) pointed out the shape of the metasternum as diagnostic for this genus. During this work, the author studied many *Melanostoma* specimens from different collections trying to understand the variability of this character, and found other morphologically distinct *Melanostoma* species with a complete metasternum (see fig. 4A, B). Consequently, there is a group of *Melanostoma* species in the Afrotropical Region without basolateral excavation in the metasternum as in *Platycheirus*, and the group has more members besides *Melanostoma quadripunctatum* **comb. nov.** and *Melanostoma janeceki* sp. nov. Nevertheless, the largely reduced, spearhead-shaped metasternum as defined by Andersson (1970) is still a valid a diagnostic character for the genus *Melanostoma* outside the Afrotropical Region.

Bacchines and melanostomines

Williston (1885) was the first author to recognize and name the two groups with simple,

unsegmented aedeagus as Bacchinae (including only *Baccha*) and Melonostominae (with *Pyrophaena*, *Platycheirus* and *Melanostoma*). Later, Williston (1887) reorganized his classification giving Melanostomini a tribe level and synonymizing *Ocyptamus* under *Baccha*. This classification was adopted by later authors (see Hull, 1949; Vockeroth, 1969) with small modifications until Vockeroth (1992), who lumped all the genera with simple, unsegmented aedeagus in Bacchini *sensu lato*. Before the step taken by Vockeroth (1992), Dušek & Láska (1967) grouped *Xanthandrus* with *Melanostoma*, and *Platycheirus* with *Rohdendorfia*, *Spazigaster*, and *Pachysphyria*, leaving the genus *Baccha* alone in their tribe Bacchini. Thompson (1972) also divided Melanostomini into two groups of genera based on male genitalia characters and the presence or absence of modified protibiae in males: the *Melanostoma* group and the *Platycheirus* group. In a similar line of thought, Shatalkin (1975) suggested two tribes, i.e., Melanostomini (subdivided into Melanostomina and Platycheirina) and Bacchini including *Baccha*, but also other Syrphini genera like *Allobaccha* and *Ocyptamus*; a group defined as “an artificial aggregation” by Vockeroth (1969). Later, Kassebeer (2000b) proposed a morphological synapomorphy for the melanostomine genera previously suggested by Fluke (1943), and considered Melanostomini monophyletic.

Male genitalia characters have been used to group these taxa. Thompson (1972) divided Melanostomini into the *Melanostoma* group (simple legs in males, with triangular or quadrate postgonites and elongate, usually not forked, surstyli) and the *Platycheirus* group (modified protibiae in males, sickle-shaped postgonites and forked surstyli). Later, Shatalkin (1975) used the same argument for his subtribes Melanostomina and Platycheirina within Melanostomini. Based on published literature (Fluke, 1957; Dušek & Láska, 1967; Thompson, 1972; Vockeroth, 1973, 1990,

1992; Shatalkin, 1975; Ôhara, 1980; Claussen, 1987; Dirickx, 2001; Borges & Pamplona, 2003; Barkalov, 2007; Barkalov & Nielsen, 2010; Haarto & Ståhls, 2014; Thompson & Skevington, 2014; Young et al., 2016b) sickle-shaped postgonites and forked or bilobed surstyli are present in all *Platycheirus* subgenera, although some *Carposcalis* species do not have sickle-shaped postgonites, but triangular postgonites like a scalene triangle with a broad base, or their surstyli are not evidently bilobed. The species *Platycheirus (Tuberculanostoma) antennatum* (Fluke, 1943) is also an exception. The two species described as *Pseudoplatychirus* also have bilobed surstyli and sickle-shaped postgonites, but smaller, more compressed.

Eocheilosia has globular surstyli and sickle-shaped postgonites, and *Syrphocheilosia claviventris* (Strobl, 1910) has one-lobed surstyli and elongate, one-lobed postgonites. *Spazigaster ambulans* (Fabricius, 1798) has sickle-shaped postgonites but one-lobed surstyli, while *Rohdendorfia* species have one-lobed, sickle-shaped surstyli curved ventrally, and bilobed postgonites with dorsal lobe hook-shaped (Mengual & Barkalov, 2019). *Pyrophaena rosarum* (Fabricius, 1787) has sickle-shaped postgonites but broad, elongate, one-lobed surstyli. *Pyrophaena granditarsa* (Forster, 1771) also has elongate, not bilobed surstyli with a small basomedial tubercle, but solid, triangular postgonites. *Pyrophaena rufigaster* (Vockeroth, 1990) has one-lobed surstyli and postgonites with three dorsal hook-shaped protuberances, very similar to *Platycheirus (Platycheirus) coracinus* Vockeroth, 1990, a member of the *Platycheirus pictipes* species group *sensu* Young et al. (2016b). Final placement of these species is unclear and is beyond the scope of this study.

Regarding the genus *Baccha*, *B. elongata* (Fabricius, 1775) have massive postgonites with two processes pointed postero-ventrally and elongate surstyli with a small basomedial

tubercle, which could be interpreted as bilobed surstyli.

Argentinomyia, *Leucopodella*, *Pelloloma*, *Melanostoma*, and *Xanthandrus* species have one-lobed, elongate surstyli and postgonites massive (solid), irregular, elongate, triangular or squarish in shape. Some *Argentinomyia* species present surstyli very variable in shape, but nothing like a bilobed surstylus. *Talahua fervida*, however, has strongly modified male genitalia with elongate postgonites and surstyli three to four times longer than wide.

Cytotaxonomy, although scarce, can be used as an alternative data source for these groupings. On this topic, *Leucopodella* has five chromosome pairs and *Argentinomyia* species have four or five chromosome pairs (Boyes & van Brink, 1964; Boyes et al., 1971, 1973). *Melanostoma*, *Xanthandrus*, *Platycheirus sensu stricto* and *Platycheirus (Carposcalis)* has four chromosome pairs, but different in structure (Boyes & van Brink, 1964; Boyes et al., 1971). On the other hand, *Baccha* species have three (*B. elongata* and *B. obscuripennis* Meigen, 1822) or four (*Baccha maculata* Walker, 1852) pairs of chromosomes. Boyes et al. (1971) pointed out that the karyotypes of *Carposcalis* and *Platycheirus* are very similar, but quite different from *Melanostoma* and *Xanthandrus*, and they suggested two distinct groups although all have $2n = 8$. Some exceptions occur, e.g., *Xanthandrus bucephalus* (Wiedeman, 1830) with $2n = 10$, as *Bacchini sensu lato* has high karyological variation.

Based on previous studies and the results presented here, the current concept of *Bacchini sensu lato* is not monophyletic. Syrphinae genera with simple, unsegmented aedeagus are divided into two groups as follows: *Melanostoma* and related genera, and *Baccha*, plus *Platycheirus* and related genera. Although Shatalkin (1975) stated that the male genitalia of *Baccha* is reminiscent to genitalia of *Melanostoma* and *Leucopodella*, the genus *Baccha*

has been resolved as sister group of *Platycheirus* and related genera based on the latest molecular analyses (Mengual, 2015; Mengual et al., 2015; Young et al., 2016a; this study). See table 2 for a list of genera and subgenera of *Bacchini stat. rev.* and *Melanostomini stat. rev.* and a new generic classification based on the present results.

Acknowledgements

I am very grateful to Štěpán Janeček and Anna Vlašánková for letting me study the material they collected in Cameroon and for a very fruitful collaboration. I thank Nigel Wyatt (BMNH), Ben Brugge and Pasquale Ciliberti (NBC), and Christophe Daugeron and Emmanuel Delfosse (MNHN) for letting me study material in their care. I am very indebted to all colleagues and collectors that made specimens available for so many years; without them this study would not have been possible. This research received support from the SYNTHESYS Project (<http://www.synthesys.info/>, grant FR-TAF-5931), which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Program.

References

- Andersson, H. (1970) Taxonomic notes on the genera *Platycheirus* and *Melanostoma* (Dipt., Syrphidae) with lectotype designations. *Entomol. Scand.*, 1, 236–240. doi:10.1163/187631270X00087
- Barkalov, A.V. & Nielsen, T.R. (2010) Revision of the genus *Rohdendorfia* Smirnov, 1924 (Diptera, Syrphidae). *Norw. J. Entomol.*, 57, 154–161. <http://www.entomologi.no/journals/nje/2010-2/pdf/nje-vol57-no2-barkalov-nielsen.pdf>
- Barkalov, A.V. (2007) A genus and a species of hover-flies, new for the Russian fauna (Diptera, Syrphidae). *Entomol. Rev.*, 87, 930–933. doi:10.1134/S0013873807070172

- Barkalov, A.V. (2009) Hover-flies of the genus *Melanostoma* closely related to *Melanostoma dubium* (Diptera, Syrphidae). *Entomol. Rev.*, 89, 1013–1017.
- Bergh, J.C. & Short, B.D. (2008) Ecological and life-history notes on syrphid predators of woolly apple aphid in Virginia, with emphasis on *Heringia calcarata*. *BioControl*, 53, 773–786. doi:10.1007/s10526-007-9114-0
- Bezzi, M. (1915) *The Syrphidae of the Ethiopian Region*. British Museum (N.H.), London.
- Bigot, J.M.F. (1883) Diptères nouveaux ou peu connus. 21e partie. XXXII. Syrphidi (1^{re} partie). *Ann. Soc. Entomol. Fr.*, Ser. 6, 3, 221–258.
- Borges, Z.M. & Pamplona, D.M. (2002) Revision of the Neotropical *Xanthandrus Verral* (Diptera, Syrphidae). *Rev. Bras. Entomol.*, 47, 155–167. doi:10.1590/S0085-56262003000200002
- Boyes, J.W., Boyes, B.C., van Brink, J.M. & Vockeroth, J.R. (1973) Cytotaxonomy of South American Syrphidae (Diptera: Syrphidae). *Genet.*, 44, 368–415. doi:10.1007/BF00161313
- Boyes, J.W., van Brink, J.M. & Boyes, B.C. (1971) *Chromosomes of Syrphinae (Diptera: Syrphidae)*. The Genetics Society of Canada, Ottawa, Canada.
- Boyes, J.W. & van Brink, J.M. (1964) Chromosomes of Syrphidae I. Variations in Karyotype. *Chromosoma*, 15, 579–590.
- Bugg, R.L., Colfer, R.G., Chaney, W.E., Smith, H.A. & Cannon, J. (2008) Flower flies (Syrphidae) and other biological control agents for aphids in vegetable crops. *UC ANR*, Publication 8285. <http://anrcatalog.ucanr.edu/pdf/8285.pdf>
- Claussen, C. (1987) *Syrphocheilosia claviventris* (Strobl, 1910) und *Cheilosia laeviseta* nom.n. (Diptera: Syrphidae), mit taxonomischen Anmerkungen und neuen Nachweisen aus den Alpen. *Entomol. Z.*, 97, 337–352.
- Cumming, J.M. & Wood, D.M. (2017) Adult morphology and terminology. In: A.H. Kirk-Spriggs & B.J. Sinclair (Eds) *Manual of Afrotropical Diptera. Volume 1*. Suricata 4, pp. 89–133. South African National Biodiversity Institute, Pretoria.
- Curran, C.H. (1938) Records and descriptions of African Syrphidae II (Diptera). *Am. Mus. Nov.*, 1010, 1–20. <http://hdl.handle.net/2246/2208>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods*, 9, 772. doi:10.1038/nmeth.2109
- Dirickx, H.G. (2001) Notes sur le genre *Melanostoma* Schiner, 1860 (Diptera, Syrphidae) à Madagascar et les îles voisines avec descriptions de cinq espèces nouvelles. *Rev. Suisse Zool.*, 108, 993–1029. doi:10.5962/bhl.part.80173
- Downes, M.F., Skevington, J.H. & Thompson, F.C. (2017) A new ant inquiline flower fly (Diptera: Syrphidae: Pipizinae) from Australia. *Aust. Entomol.*, 44, 29–38.
- Doyle, J.J. (1992) Gene trees and species trees: molecular systematics as one-character taxonomy. *Syst. Bot.*, 17, 144–163. <https://www.jstor.org/stable/2419070>
- Dumbardon-Martial, E. (2016) Pollen feeding in the larva of *Toxomerus pulchellus* (Diptera, Syrphidae). *Bull. Soc. Entomol. Fr.*, 121, 413–420. doi:10.1080/00222930802610576
- Dušek, J. & Láska, P. (1967) Versuch zum Aufbau eines natürlichen Systems mitteleuropäischer Arten der Unterfamilie Syrphinae (Diptera). *Acta Sc. Nat. Brno*, 1, 349–390.
- Fleischmann, A., Rivadavia, F., Gonella, P.M., Pérez-Bañón, C., Mengual, X. & Rojo, S. (2016) Where is my food? Brazilian flower fly steals prey from carnivorous sundews in a newly discovered plant-animal interaction. *PLoS ONE*, 11, e0153900. doi:10.1371/journal.pone.0153900
- Fluke, C.L. (1937) New South American Syrphidae (Diptera). *Am. Mus. Nov.*, 941, 1–14. <http://hdl.handle.net/2246/2182>
- Fluke, C.L. (1943) A new genus and new species of Syrphidae (Diptera) from Ecuador. *Ann. Entomol. Soc. Am.*, 36, 425–431. doi:10.1093/aesa/36.3.425
- Fluke, C.L. (1945) The Melanostomini of the Neotropical Region (Diptera, Syrphidae). *Am. Mus. Nov.*, 1272, 1–29. <http://hdl.handle.net/2246/3720>

- Fluke, C.L. (1957) A study of the male genitalia of the Melanostomini (Diptera-Syrphidae). *Trans. Wis. Acad. Sci. Arts Lett.*, 46, 261–279.
- Haarto, A. & Ståhls, G. (2014) When mtDNA COI is misleading: congruent signal of ITS2 molecular marker and morphology for North European *Melanostoma* Schiner, 1860 (Diptera, Syrphidae). *ZooKeys*, 431, 93–134. doi:10.3897/zookeys.431.7207
- Hebert, P.D.N., Cywinska, A., Ball, S.L. & J.R. de Waard (2003a) Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. B. Biol. Sci.*, 270, 313–321. doi:10.1098/rspb.2002.2218
- Hebert, P.D.N. & Gregory, T.R. (2005) The promise of DNA barcoding for taxonomy. *Syst. Biol.*, 54, 852–859. doi:10.1080/10635150500354886
- Hebert, P.D.N., Ratnasingham, S. & DeWaard, J.R. (2003b) Barcoding animal life: Cytochrome C oxidase subunit 1 divergences among closely related species. *Proc. R. Soc. Lond. B. Biol. Sci.*, 270, S96–S99. doi:10.1098/rsbl.2003.0025
- Hippa, H. & Ståhls, G. (2005) Morphological characters of adult Syrphidae: descriptions and phylogenetic utility. *Acta Zool. Fenn.*, 215, 1–72.
- Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian inference of phylogenetic trees. *Biometrics*, 17, 754–755. doi:10.1093/biometrics/17.8.754
- Hull, F.M. (1949) The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. *Trans. Zool. Soc. London*, 26, 257–408. doi:10.1111/j.1096-3642.1949.tb00224.x
- Huo, K-K. (2014) *Spazigasteroides* a new genus from China with a black face and scutellum in the Syrphini (Diptera: Syrphidae). *Zootaxa*, 3755, 230–240. doi:10.11646/zootaxa.3755.3.2
- Inouye, D., Larson, B.M.H., Ssymank, A. & Kevan, P.G. (2015) Flies and flowers III: Ecology of foraging and pollination. *J. Pollinat. Ecol.*, 16, 115–133.
- Kassebeer, C.F. (2000a) Revision der Gattung *Pelloloma* Vockeroth, 1973 (Diptera, Syrphidae), mit der Beschreibung neuer Arten aus Zentralafrika. *Dipteron*, 3, 159–166.
- Kassebeer, C.F. (2000b) *Afroanthandrus* gen. nov. (Diptera, Syrphidae), eine neue Gattung der Syrphinae aus Westafrika. *Dipteron*, 3, 149–158.
- Kjer, K.M. (1995) Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Mol. Phylogenet. Evol.*, 4, 314–330. doi:10.1006/mpev.1995.1028
- Lambeck, H.J.P. & van Brink, J.M. (1973) Contribution to the knowledge of the taxonomy, faunal composition and cytology of the syrphid flies (Diptera: Syrphidae) of Kashmir (India). I. Taxonomic account and faunal composition. *Genen. Phaenen.*, 16, 87–100.
- Lardé, G. (1989) Investigation on some factors affecting larval growth in a coffee-pulp bed. *Biol. Wastes*, 30, 11–19. doi:10.1016/0269-7483(89)90139-0
- Láska, P., Mazánek, L. & Bičík, V. (2013) Key to adults and larvae of the genera of European Syrphinae (Diptera, Syrphidae). *Čas. Slez. zemského muz.*, 62, 193–206. doi:10.2478/cszma-2013-0021
- Martínez-Falcón, A.P., Marcos-García, M.A., Moreno, C.E. & Rotheray, G.E. (2012) A critical role for *Copestylum* larvae (Diptera, Syrphidae) in the decomposition of cactus forests. *J. Arid Environ.*, 78, 41–48. doi:10.1016/j.jaridenv.2011.10.010
- Mengual, X., Ståhls, G., Láska, P., Mazánek, L. & Rojo, S. (2018) Molecular phylogenetics of the predatory lineage of flower flies *Eupeodes-Scaeva* (Diptera: Syrphidae), with the description of the Neotropical genus *Austroscaeva* gen. nov. *J. Zoo. Syst. Evol. Research*, 56, 148–169. doi:10.1111/jzs.12212
- Mengual, X., Ståhls, G. & Rojo, S. (2008a) 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. *Cladistics*, 24, 543–562. doi:10.1111/j.1096-0031.2008.00200.x
- Mengual, X., Ståhls, G. & Rojo, S. (2008b) Molecular phylogeny of *Allograpta* (Diptera, Syrphidae) reveals diversity of lineages and non-monophyly

- of phytophagous taxa. *Mol. Phylogenet. Evol.*, 49, 715–727. doi:10.1016/j.ympev.2008.09.011
- Mengual, X., Ståhls, G. & Rojo, S. (2012) Is the mega-diverse genus *Ocyptamus* (Diptera, Syrphidae) monophyletic? Evidence from molecular characters including the secondary structure of 28S rRNA. *Mol. Phylogenet. Evol.*, 62, 191–205. doi:10.1016/j.ympev.2011.09.014
- Mengual, X., Ståhls, G. & Rojo, S. (2015) Phylogenetic relationships and taxonomic ranking of pipizine flower flies (Diptera: Syrphidae) with implications for the evolution of aphidophagy. *Cladistics*, 31, 491–508. doi:10.1111/cla.12105
- Mengual, X. & Barkalov, A.V. (2019) Two new species of *Rohdendorfia* (Diptera: Syrphidae) from Central Asia. *Acta Entomol. Mus. Nat. Pragae*, 59, 325–336. doi:10.2478/aemnp-2019-0025
- Mengual, X. & Thompson, F.C. (2011) Carmine cochineal killers: the flower fly genus *Eosalingogaster* Hull (Diptera: Syrphidae) revised. *Syst. Entomol.*, 36, 713–731. doi:10.1111/j.1365-3113.2011.00588.x
- Mengual, X. (2015) The systematic position and phylogenetic relationships of *Asiobaccha* Vshivtsh (Diptera, Syrphidae). *J. Asia-Pac. Entomol.*, 18, 397–408. doi:10.1016/j.aspen.2015.03.010
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov 2010, pp. 1–8. New Orleans, LA.
- Miranda, G.F.G. & Moran, K. (2017) The female abdomen and genitalia of Syrphidae (Diptera). *Insect Syst. Evol.*, 48, 157–201. doi:10.1163/1876312X-48022153
- Morales, G.E. & Wolff, M. (2010) Insects associated with the composting process of solid urban waste separated at the source. *Rev. Bras. Entomol.*, 54, 645–653. doi:10.1590/S0085-56262010000400017
- Nelson, E.H., Hogg, B.N., Mills, N.J. & Daane, K.M. (2012) Syrphid flies suppress lettuce aphids. *BioControl*, 57, 819–826. doi:10.1007/s10526-012-9457-z
- Nichols, R. (2001) Gene trees and species trees are not the same. *Trends Ecol. Evol.*, 16, 358–364. doi:10.1016/S0169-5347(01)02203-0
- Nielsen, T.R. & Barkalov, A.V. (2017) A revision of and key to the Holarctic and Oriental *Platycheirus manicatus* group species (Diptera, Syrphidae). *Norw. J. Entomol.*, 64, 28–52.
- Nielsen, T.R. (2004) European species of the *Platycheirus ambiguus* group (Diptera, Syrphidae), with description of new species. *Volucella*, 7, 1–30.
- Nielsen, T.R. (2014) Synopsis of the *Platycheirus ambiguus* species group (Diptera, Syrphidae), with description of *Platycheirus arnei* sp. n. and a preliminary key to the species. *Norw. J. Entomol.*, 61, 57–75.
- Nishida, K., Rotheray, G. & Thompson, F.C. (2002) First non-predaceous syrphine flower-fly (Diptera: Syrphidae): a new leaf-mining *Allograpta* from Costa Rica. *Stud. Dipterol.*, 9, 421–436.
- Ôhara, K. (1980) The genus *Platycheirus* Lepeletier and Serville, 1828 (Diptera, Syrphidae) of Japan, with descriptions of three new species. *Esakia*, 15, 97–142. https://catalog.lib.kyushu-u.ac.jp/opac_download_md/2405/97.pdf
- Pauli, T., Burt, T., Meusemann, K., Bayless, K., Donath, A., Podsiadlowski, L., Mayer, C., Kozlov, A., Vasilakopoulos, A., Liu, S., Zhou, X., Yeates, D., Misof, B., Peters, R.S. & Mengual, X. (2018) New data, same story: phylogenomics does not support Syrphoidea (Diptera: Syrphidae, Pipunculidae). *Syst. Entomol.*, 43, 447–459. doi:10.1111/syen.12283
- Pérez-Lachaud, G., Jervis, M.A., Reemer, M. & Lachaud, J.-P. (2014) An unusual, but not unexpected, evolutionary step taken by syrphid flies: the first record of true primary parasitoidism of ants by Microdantinae. *Biol. J. Linn. Soc.*, 111, 462–472. doi:10.1111/bij.12220
- Posada, D. & Buckley, T. (2004) Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Syst. Biol.*, 53, 793–808. doi:10.1080/10635150490522304

- Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.*, 67, 901–904. doi:10.1093/sysbio/syy032
- Rambaut, A. (2018) FigTree v. 1.4.4: Tree Figure Drawing Tool. <http://tree.bio.ed.ac.uk/software/figtree/>
- Reemer, M. & Rotheray, G.E. (2009) Pollen feeding larvae in the presumed predatory syrphine genus *Toxomerus* Macquart (Diptera, Syrphidae). *J. Nat. Hist.*, 43, 939–949. doi:10.1080/00222930802610576
- Ricarte, A., Marcos-García, M.A. & Moreno, C.E. (2011) Assessing the effects of vegetation type on hoverfly (Diptera: Syrphidae) diversity in a Mediterranean landscape: implications for conservation. *J. Insect Conserv.*, 15, 865–877. doi:10.1007/s10841-011-9384-9
- Rojo, S., Gilbert, F., Marcos-García, M.A., Nieto, J.M. & Mier, M.P. (2003) *A World Review of Predatory Hoverflies (Diptera, Syrphidae: Syrphinae) and Their Prey*. Centro Iberoamericano de la Biodiversidad (CIBIO), Alicante.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574. doi:10.1093/bioinformatics/btgi180
- Ronquist, F., Huelsenbeck, J.P. & van der Mark, P. (2005) *MrBayes 3.1 Manual*. Retrieved from <http://mrbayes.csit.fsu.edu/manual.php/> (accessed 12 March 2019)
- Rotheray, G.E. (1993) *Colour Guide to Hoverfly Larvae (Diptera, Syrphidae) in Britain and Europe*. Dipterists Digest No. 9, UK.
- 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. doi:10.1111/j.1096-3642.1989.tb02222.x
- Rotheray, G.E. & Gilbert, F. (1999) Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages. *Zool. J. Linn. Soc.*, 127, 1–112. doi:10.1111/j.1096-3642.1999.tb01305.x
- Rotheray, G.E. & Gilbert, F. (2011) *The Natural History of Hoverflies*. Forrest Text, Ceredigion.
- Rozo-Lopez, P. & Mengual, X. (2015) Mosquito species (Diptera, Culicidae) in three ecosystems from the Colombian Andes: identification through DNA barcoding and adult morphology. *ZooKeys*, 513, 39–64. doi:10.3897/zookeys.513.9561
- Sabrosky, C.W. (1999) Family-group names in Diptera. An annotated catalog. *Myia*, 10, 1–576.
- Schmidt, M.H., Thewes, U., Thies, C. & Tscharnkte, T. (2004) Aphid suppression by natural enemies in mulched cereals. *Entomol. Exp. Appl.*, 113, 87–93. doi:10.1111/j.0013-8703.2004.00205.x
- Shatalkin, A.I. (1975) A taxonomic analysis of the hover flies (Diptera, Syrphidae). I. *Entomol. Rev.*, 54, 117–125 (Originally published in Russian in *Entomol. obozr.*, 54, 164–175).
- Skevington, J.H. & Thompson, F.C. (2012) Review of New World *Sericomyia* (Diptera: Syrphidae), including description of a new species. *Can. Entomol.*, 144, 1–32. doi:10.4039/tce.2012.24
- Sommaggio, D. (1999) Syrphidae: can they be used as environmental bioindicators. *Agric. Ecosyst. Environ.*, 74, 343–356. doi:10.1016/S0167-8809(99)00042-0
- Sommaggio, D. & Burgio, G. (2014) The use of Syrphidae as functional bioindicator to compare vineyards with different managements. *Bull. Insectol.*, 67, 147–156.
- Speight, M.C.D. (1987) External morphology of adult Syrphidae (Diptera). *Tijdschr. entomol.*, 130, 141–175.
- Speight, M.C.D. (2018) Species accounts of European Syrphidae, 2018. In: *Syrph the Net, the database of European Syrphidae (Diptera)*, vol. 103. Syrph the Net publications, Dublin.
- Ssymank, A. & Kearns, C. (2009) Flies-pollinators on two wings. In: A. Ssymank, A. Hamm & M. Vischer-Leopold (Eds) *Caring for Pollinators – Safeguarding Agro-Biodiversity and Wild Plant Diversity*, pp. 39–52. Bundesamt für Naturschutz, Bonn.
- Stähls, 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. doi:10.1046/j.1365-3113.2003.00225.x
- Thompson, F.C., Rotheray, G.E. & Zumbado, M. (2010) Family Syrphidae. In: B. Brown, A. Borkent, J.M. Cumming, D.M. Wood, N.E. Woodley & M.A. Zumbado (Eds) *Manual of Central American Diptera, Volume 2*, pp. 763–792. NRC Press, Ottawa.
- Thompson, F.C. & Rotheray, G.E. (1998) Family Syrphidae. In: L. Papp & B. Darvas (Eds) *Contributions to a Manual of Palaearctic Diptera, Volume 3*, pp. 81–139. Science Herald, Budapest.
- Thompson, F.C. & Skevington, J.H. (2014) Afro-tropical flower flies (Diptera: Syrphidae). A new genus and species from Kenya, with a review of the melanostomine group of genera. *Zootaxa*, 3847, 97–114. doi:10.11646/zootaxa.3847.1.5
- Thompson, F.C., Vockeroth, J.R. & Sedman, Y.S. (1976) Family Syrphidae. *A catalogue of the Diptera of the American South of the United States*, 46, 1–195. <https://repository.si.edu/handle/10088/17070>
- Thompson, F.C. & Vockeroth, J.R. (1989) Family Syrphidae. In: N.L. Evenhuis (Ed.) *Catalog of the Diptera of the Australasian and Oceanian Regions*, pp. 437–458. Bishop Museum Special Publication vol. 86, Hawaii.
- Thompson, F.C. (1969) A new genus of microdontine flies (Diptera: Syrphidae) with notes on the placement of the subfamily. *Psyche*, 76, 74–85. doi:10.1155/1969/62102
- Thompson, F.C. (1972) A new *Platycheirus* from New Zealand. First record of a melanostomine syrphid fly associated with ants. *N. Z. J. Sci.*, 15, 77–84. <https://repository.si.edu/handle/10088/17048>
- Thompson, F.C. (1999) A key to the genera of the flower flies of the Neotropical Region including the descriptions of genera and species and a glossary of taxonomic terms. *Contrib. Entomol. Int.*, 3, 319–378. <https://repository.si.edu/handle/10088/17492>
- Thompson, F.C. (2008) A conspectus of New Zealand flower flies (Diptera: Syrphidae) with the description of a new genus and species. *Zootaxa* 1716, 1–20. doi:10.5281/zenodo.181009
- Thompson, F.C. (2019) A new flower fly from the Afrotropics (Diptera: Syrphidae). *Entomol. Mon. Mag.* 155, 159–162. doi:10.31184/M00138908.1553.3967
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecol. Lett.*, 8, 857–874. doi:10.1111/j.1461-0248.2005.00782.x
- Ureña, O. & Hanson, P. (2010) A fly larva (Syrphidae: *Ocyptamus*) that preys on adult flies. *Rev. Biol. Trop.*, 58, 1157–1163. doi:10.15517/rbt.v58i4.5401
- van Doesburg, P.H. Sr. (1955) Report on the Syrphid Flies, collected by the “Fourth Dutch Karakorum Expedition, 1935”. *Beaufortia*, 5, 47–51. <https://www.repository.naturalis.nl/record/505205>
- van Steenis, J., Young, A.D., Ssymank, A.M., Wu (Bill), T.-H., Shiao, S.-F. & Skevington, J.H. (2019) The species of the genus *Platycheirus* Lepeletier & Serville, 1828 (Diptera, Syrphidae) from Taiwan, with a discussion on intersex specimens. *J. Asia-Pac. Entomol.*, 22, 281–295. doi:10.1016/j.aspen.2018.12.004
- Vlašánková, A., Padyšáková, E., Bartoš, M., Mengual, X., Janečková, P. & Janeček, Š. (2017) The nectar spur is not only a simple specialization for long-proboscid pollinators. *New Phytol.*, 215, 1574–1581. doi:10.1111/nph.14677
- Vockeroth, J.R. (1969) A revision of the genera of the Syrphini (Diptera, Syrphidae). *Mem. Ent. Soc. Can.*, 62, 1–176.
- Vockeroth, J.R. (1973) Some new or uncommon Syrphini (Diptera: Syrphidae) from Southern Africa. *Ann. Natal Mus.*, 21, 595–607. https://hdl.handle.net/10520/AJA03040798_646
- Vockeroth, J.R. (1990) Revision of the Nearctic species of *Platycheirus* (Diptera, Syrphidae). *Can. Entomol.*, 122, 659–766. doi:10.4039/Ent122659-7
- 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. <http://publications.gc.ca/pub?id=9.811395&sl=0>
- Vockeroth, J.R. & Thompson, F.C. (1987) 52. Syrphidae. In: J.F. McAlpine (Ed.) *Manual of Nearctic Diptera*, Volume 2, pp. 713–743. Agriculture Canada, Ottawa.
- Weng, J.L. & Rotheray, G.E. (2008) Another non-predaceous syrphine flower fly (Diptera: Syrphidae): pollen feeding in the larva of *Allograpta micrura*. *Stud. Dipterol.*, 15, 245–258.
- Williston, S.W. (1885) On classification of North American Diptera. *Bull. Brooklyn Entomol. Soc.*, 7, 129–139.
- Williston, S.W. (1887) Synopsis of the North American Syrphidae. *Bull. U.S. Nat. Mus.* (1886), 31, xxx + 1–335. doi:10.5479/si.03629236.31.i
- Wirth, W.W., Sedman, Y.S. & Weems, H.V. (1965) Family Syrphidae. In: A. Stone, C.W. Sabrosky, W.W. Wirth, R.H. Foote & J.R. Coulson (Eds) *A Catalog of the Diptera of America North of Mexico*, pp. 557–625. Agricultural Research Service, United States Department of Agriculture, Washington, DC.
- Young, A.D., Lemmon, A.R., Skevington, J.H., Mengual, X., Ståhls, G., Reemer, M., Jordaens, K., Kelso, S., Lemmon, E.M., Hauser, M., De Meyer, M., Misof, B. & Wiegmann, B.M. (2016a) Anchored enrichment dataset for true flies (order Diptera) reveals insights into the phylogeny of flower flies (family Syrphidae). *BMC Evol. Biol.*, 16, 143.
- Young, A.D., Marshall, S.A. & Skevington, J.H. (2016b) Revision of *Platycheirus* Lepeletier and Serville (Diptera: Syrphidae) in the Nearctic north of Mexico. *Zootaxa*, 4082, 1–317. doi:10.11646/zootaxa.4082.1.1
- Zimina, L.V. (1958) New genus of hover-flies (Diptera, Syrphidae) indigenous to the USSR. *Entomol. obozr.*, 37, 206–207. [In Russian]
- Zuijlen, M.P. & Nishida, K. (2011) Description of life history and immature stages of phytophagous flower fly, *Allograpta zumbadoi* Thompson (Diptera: Syrphidae: Syrphinae). *Stud. dipterol.*, 17, 37–51.
- Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the Maximum Likelihood criterion*. PhD Thesis, The University of Texas at Austin, USA. <http://hdl.handle.net/2152/2666>
- Zwickl, D.J. (2011) *GARLI (Genetic Algorithm for Rapid Likelihood Inference) version 2.01*. Retrieved from <https://code.google.com/archive/p/garli/downloads> (accessed 12 March 2019)

RECEIVED: 26 APRIL 2019 | REVISED AND ACCEPTED:
19 NOVEMBER 2019

EDITORS: F. RHEBERGEN & H. DE JONG