

Molecular phylogenetics of the predatory lineage of flower flies *Eupeodes-Scaeva* (Diptera: Syrphidae), with the description of the Neotropical genus *Austroscaeva* gen. nov.

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Abstract

Phylogenetic relationships among the genera and subgenera of the *Scaeva-Eupeodes* clade (Diptera: Syrphidae: Syrphinae) were analyzed based on molecular characters. Sequence data from three gene regions were analyzed using maximum likelihood and Bayesian inference: the mitochondrial protein-coding gene *cytochrome c oxidase subunit I* (COI) and the nuclear 28S and 18S ribosomal RNA genes. The genus *Paragus* (single representative of the tribe Paragini) was resolved as sister group of the monophyletic *Scaeva-Eupeodes* lineage. Inside this clade, a Neotropical radiation of genera was well supported comprising *Notosyrphus*, *Austroscaeva* gen. nov., and *Dioresoprosopa*. For the first time, the placement of *Doros*, *Pseudodoros*, and *Betasyrphus* was inferred using molecular data. Our results resolved the genus *Pseudodoros* as sister group of *Ischiodon*, corroborating the generic rank of *Ischiodon*, *Simosyrphus*, *Dioresoprosopa*, and *Pseudodoros*. The current subgeneric division of *Eupeodes* with three subgenera is not supported by our data. Present results and the study of adult morphological characters prompted us to erect a new genus, *Austroscaeva* gen. nov., which includes four Neotropical species, that is, *Austroscaeva melanostoma* (Macquart, 1842) comb. nov., *Austroscaeva occidentalis* (Shannon, 1927) comb. nov., *Austroscaeva patagoniensis* (Kassebeer, 1999) comb. nov., and *Austroscaeva penai* (Marnef in Dušek & Láska, 1985) comb. nov. We described and characterized *Austroscaeva* gen. nov., and provided the description of the male of *Scaeva patagoniensis* (=*Austroscaeva patagoniensis*) and *Scaeva penai* (=*Austroscaeva penai*), as well as an illustrated identification key for the *Austroscaeva* species. Moreover, we explained and stated that the correct name for *Syrphus lunatus* Wiedemann, 1830 is *Scaeva opimia* (Walker, 1852).

Resumen

Filogenia molecular del linaje de sírfidos depredadores *Eupeodes-Scaeva* (Diptera: Syrphidae), con la descripción del género Neotropical *Austroscaeva* gen. nov.

Las relaciones filogenéticas entre los géneros y subgéneros del clado *Scaeva-Eupeodes* (Diptera: Syrphidae: Syrphinae) se analizaron en base a caracteres moleculares. Para los análisis basados en máxima verosimilitud e inferencia bayesiana, se usaron las secuencias de tres regiones génicas: el gen mitocondrial codificador de la proteína *citocromo c oxidasa subunidad I* (COI) y los genes nucleares 28S y 18S de ARN ribosómico. El género *Paragus* (representante único de la tribu Paragini) se resolvió

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como un grupo hermano del linaje monofilético *Scaeava-Eupeodes*. Dentro de este clado, se resolvió una radiación neotropical de géneros bien soportada, incluyendo *Notosyrphus*, *Austroscaeava* gen. nov. y *Dioprosopa*. Por primera vez, la ubicación de *Doros*, *Pseudodoros* y *Betasyrphus* se infirió utilizando datos moleculares. Nuestros resultados resolvieron el género *Pseudodoros* como grupo hermano de *Ischiodon*, corroborando el rango genérico de *Ischiodon*, *Simosyrphus*, *Dioprosopa* y *Pseudodoros*. La división subgenérica actual de *Eupeodes* con tres subgéneros no es compatible con nuestros datos. Los resultados actuales y el estudio de los caracteres morfológicos adultos nos llevaron a erigir un nuevo género, *Austroscaeava* gen. nov., que incluye cuatro especies neotropicales, a saber, *Austroscaeava melanostoma* (Macquart, 1842) comb. nov., *Austroscaeava occidentalis* (Shannon, 1927) comb. nov., *Austroscaeava patagoniensis* (Kassebeer, 1999) comb. nov., y *Austroscaeava penai* (Marnef in Dušek & Láska, 1985) comb. nov. A su vez, se describió y se caracterizó el género *Austroscaeava* gen. nov., y se proporcionó por primera vez la descripción del macho de *Scaeava patagoniensis* (=*Austroscaeava patagoniensis*) y *Scaeava penai* (=*Austroscaeava penai*), así como una clave de identificación ilustrada para las especies de *Austroscaeava* gen. nov. Además, se explica que el nombre correcto para *Syrphus lunatus* Wiedemann, 1830 es *Scaeava opimia* (Walker, 1852).

KEY WORDS

hoverflies, molecular phylogeny, Neotropical Region, new genus, *Pseudodoros*, Syrphinae, systematics

1 | INTRODUCTION

The genus *Scaeava* Fabricius, 1805 includes medium to large species of flower flies (Diptera: Syrphidae, Syrphinae) with very clear wings, pilose eyes, oblique and often lunulate abdominal maculae, and usually with strongly swollen frons in male (Vockeroth, 1969). Adults are common in forests and grasslands, where they visit flowers of several plant families. The widespread species *Scaeava pyrastri* (Linnaeus, 1758) is highly mobile and migratory (Speight, 2016), and it has been used as a species model to study the genetic base of the antennal olfaction (Li et al., 2016). Larvae, on the other hand, are predators of aphids, psyllids, adelgids, scale insects (Hemiptera), and thrips (Thysanoptera) (see Rojo, Gilbert, Marcos-García, Nieto, & Mier, 2003 for a review). A total of 16 species of *Scaeava* are known (Dušek & Láska, 1985; Peck, 1988; Thompson, 2013), mostly from the Palaearctic region, while four taxa have been described from the Neotropics (Kassebeer, 1999). Five species reach the Oriental region, that is, *S. albomaculata* (Macquart, 1842), *S. latimaculata* (Brunetti, 1923), *S. opimia* (Walker, 1852), *S. pyrastri*, and *Scaeava selenitica* (Meigen, 1822) (Sengupta et al., 2016). One species, *S. pyrastri*, occurs in the Nearctic region along the West coast (from Alaska to New Mexico), and another, *S. selenitica*, was introduced into North Carolina although there is no indication that the species has become established (Thompson, 2013).

A revision of the Palaearctic species of the genus *Scaeava* was carried out firstly by Violovitsh (1975). Later, Kuznetzov (1985) again

reviewed the Palaearctic taxa of *Scaeava*, while Dušek and Láska (1985) did the same for all *Scaeava* species. In addition to improving the systematics of the genus, these two works created a bit of confusion as they did not refer to each other, and different species concepts were employed in the two papers (Speight, 2016). Based on morphological characters, Kuznetzov (1985) divided *Scaeava* into three subgenera, while Dušek and Láska (1985) characterized three species groups with phylogenetic significance within *Scaeava*. Unfortunately, the species groups of Dušek and Láska (1985) were not equivalent to the subgenera of Kuznetzov (1985). One of the *Scaeava* species groups of Dušek and Láska (1985) comprised the Neotropical taxa of this genus that were not treated in Kuznetsov's work.

The Neotropical species of *Scaeava* were reviewed by Kassebeer (1999), who described a new species and provided an identification key and diagnoses for all four species, that is, *S. melanostoma* (Macquart, 1842), *S. occidentalis* Shannon, 1927, *S. penai* Marnef in Dušek & Láska, 1985, and *S. patagoniensis* Kassebeer, 1999. These Neotropical taxa occur in the Andean region and differ remarkably from the Palaearctic species in some morphological characters, such as a more forward produced face and an almost straight vein R_{4+5} (Dušek & Láska, 1985; Kassebeer, 1999). Two of these species, *S. penai* and *S. patagoniensis*, are only known from females.

The systematics of *Scaeava* and its phylogenetic relationships have been addressed several times in combination with the genus *Eupeodes* Osten Sacken, 1877, and these studies are considerably uninformative

without the other genera that together form a distinct "natural group" (*sensu* Dušek & Láska, 1967, 1985). These genera, subgenera, or species groups related to *Scaeva* are *Eupeodes*, *Ischiodon* Sack, 1913, *Lapposyrphus* Dušek and Láska, 1967, *Macrosyrphus* Matsumura, 1917, *Metasyrphus* Matsumura, 1917 (a junior synonym of *Eupeodes*; see Vockeroth, 1986), and *Simosyrphus* Bigot, 1882. The ranking of each of them with regard to the others has changed many times based on the perception of previous authors, and difficulties to reach a consensus among taxonomists about their ranking and inter-relationships still prevail. The close relationship among these taxa has been reported several times based on preimaginal morphological characters (Láska et al., 2006; Rotheray, 1987; Rotheray & Gilbert, 1989, 1999), molecular characters (Mengual, 2015a; Mengual, Stähls, & Rojo, 2008a), or a combination of molecular and adult morphological characters (Mengual, Stähls, & Rojo, 2015).

On the other hand, three major contributions published in the 1960s in three consecutive years are the base of the current systematics of the tribe Syrphini (Syrphidae: Syrphinae), where all these taxa belong. Dušek and Láska (1967) tried to create a "natural system" for European genera of the subfamily Syrphinae, and one of their "natural groups" comprised *Scaeva* and *Eupeodes* (as *Metasyrphus*, as *Posthosyrphus* Enderlein, 1938, and as *Scaevosyrphus* Dušek & Láska, 1967; all three junior synonyms of *Eupeodes*). One year later, Hippa (1968) reviewed the Palaearctic genera related to *Syrphus* Fabricius, 1775 using male genitalia characters. Hippa 1968 divided *Scaeva* into two subgenera: *Scaeva* s. str., whose male genitalia were similar to *Eupeodes* (as *Posthosyrphus*), and his new subgenus *Beszella* Hippa, 1968 (a junior synonym of *Lapposyrphus*), with male genitalia similar to *Epistrophe* Walker, 1852 and comprising the single species *Scaeva lapponica* Zetterstedt, 1838.

Lastly, the revisionary work of Vockeroth (1969) had a much broader taxonomic scope, the Syrphini genera of the World. He pointed out the close taxonomic relationship between *Metasyrphus*, *Lapposyrphus*, *Eupeodes*, and *Scaeva*, and at some extent with *Noto-syrphus* Vockeroth, 1969. In his work, Vockeroth (1969) recognized two subgenera for *Metasyrphus*, namely *Lapposyrphus* and *Metasyrphus* s. str., comprising three different species groups (*corollae*, *confrater*, and *luniger* species groups). Moreover, Vockeroth (1969) mentioned the possibility to consider *Eupeodes* and *Metasyrphus* synonyms, a synonymy that the same Vockeroth published later (Vockeroth, 1986). With the establishment of *Metasyrphus* as a junior synonym of *Eupeodes*, Vockeroth (1986) only recognized two subgenera in *Eupeodes*: *Lapposyrphus* and *Eupeodes* s. str. (see Vockeroth, 1992). Earlier, Vockeroth (1973) synonymized *Macrosyrphus* (originally described as a subgenus of *Syrphus*) with *Metasyrphus*. The type species of *Macrosyrphus* belongs to the *confrater* group *sensu* Vockeroth (1969).

The concept of the genus *Eupeodes* changed again years later, when Thompson and Vockeroth (1989) considered *Macrosyrphus* and *Metasyrphus* as valid subgenera of *Eupeodes*, establishing a system of four subgenera that was also adopted by Thompson and Rotheray (1998). These subgenera, namely *Eupeodes*, *Macrosyrphus*, *Metasyrphus*, and *Lapposyrphus*, reflect the species grouping of Vockeroth

(1969). Thus, the current concept of *Eupeodes* follows Thompson and Vockeroth (1989). In this contemporary view, the subgenus *Eupeodes* comprises only the type species of the genus, *Eupeodes volucris* Osten Sacken, 1877, while the subgenus *Macrosyrphus* contains at least, or at best, three species (i.e., *Syrphus confrater* Wiedemann, 1830, *Syrphus horishanus* Matsumura, 1917, and *Syrphus okinawensis* Matsumura, 1916), but there are no detailed studies on this subgenus and its composition may vary in the future. The subgenus *Lapposyrphus* comprises only two species, *Syrphus aberrantis* Curran, 1925 and *Scaeva lapponica*, and all the other species belong to the subgenus *Metasyrphus* (Thompson, 2013).

The other two genera related with the *Scaeva* group, that is, *Ischiodon* and *Simosyrphus*, are rather small, but they have probably caused more confusion than any other group of very distinct species in Syrphinae (Vockeroth, 1969). *Ischiodon* has three species with quite distinct distributions: *I. aegyptius* (Wiedemann, 1830) is mainly present in Africa, *I. feae* (Bezzi, 1912) is endemic of the Cape Verde Islands, and *I. scutellaris* (Fabricius, 1805) occurs in the Oriental and Australasian regions. On the other side, *Simosyrphus* comprises a single species, *S. grandicornis* (Macquart, 1842), widely distributed throughout Oceania, New Zealand and Australia, reaching Hawaiian Islands (Mengual, 2015b). Both genera have been previously synonymized with one another several times, despite some important differences in the male genitalia (Vockeroth, 1969). Recently, Láska et al. (2006) synonymized *Ischiodon* under *Simosyrphus* based on larval and pupal morphology, supported by a molecular study of a very limited taxon sampling using only part of the gene *cytochrome c oxidase subunit 1* (COI).

In the same paper, Láska et al. (2006) rearranged the genus *Scaeva*, dividing it into two subgenera that corresponded to two of the species groups defined by Dušek and Láska (1985). Láska et al. (2006) used the subgenus names erected by Kuznetsov (1985), but these names were applied to completely different taxa: the subgenus *Semiscaeva* Kuznetsov, 1985 comprised the *selenitica* species group, and the subgenus *Scaeva* s. str. referred to the *pyrastri* species group. The third subgenus erected by Kuznetsov (1985), *Mecoscaeva* Kuznetsov, 1985, was synonymized under *Semiscaeva* (Láska et al., 2006). Both *Scaeva* subgenera were characterized by Dušek and Láska (1985) and Láska et al. (2006) using adult and immature morphological characters. Láska et al. (2006), however, did not studied the third species group defined by Dušek and Láska (1985) comprising the Neotropical species, but they mentioned that these Neotropical *Scaeva* species form a separate monophyletic group, probably sister group to all Palearctic *Scaeva* species and that these Neotropical taxa should be classified as a separate taxon.

More recently, Láska, Mazánek, and Bičík (2013) pointed out a neglected adult morphological character for the genera of the *Scaeva* group, the broad and undulating wing membrane posterior to veins dm-cu and M_1 . This character was already mentioned by Dušek and Láska (1985) together with the reduction in the wing microtrichia. Furthermore, Láska et al. (2013) stated that they kept *Semiscaeva* as subgenus of *Scaeva* for practical purposes but they would have preferred to consider it as a valid genus.

The aim of this study was to re-explore the phylogenetic relationships among the genera of the *Eupeodes-Scaeava* clade based on significantly increased taxon sampling within the *Eupeodes-Scaeava* clade as compared to Mengual et al. (2008a) and Mengual (2015a). Moreover, we provide the description of the male of *Scaeava penai* and *Scaeava patagoniensis*, and an identification key for the Neotropical species of *Scaeava*, improved with images and based on a translation from Kassebeer (1999). To perform this study, we analyzed the sequences of the mitochondrial gene *cytochrome c oxidase subunit I* (*COI*), a fragment of the nuclear *18S rRNA*, and the region D2–D3 of the nuclear *28S rRNA* genes. We used the secondary structure of the ribosomal genes *28S* and *18S* to align the obtained DNA sequences.

2 | MATERIAL AND METHODS

2.1 | Taxonomy

Males of *Scaeava penai* and *Scaeava patagoniensis* are described in full, with terminology following Thompson (1999) and Mengual (2012). The abbreviations used for collections follow the standard of the *Systema Dipterorum* (Thompson, 2013), and their equivalents are given below:

CAS: California Academy of Sciences, San Francisco, USA.

ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

At the end of each record, between square brackets ([]) and separated by commas, the number of specimens and sex, and the holding institution are given. 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.

2.2 | Taxon sampling

The taxon sampling covered as much taxonomic diversity as possible for the *Scaeava-Eupeodes* clade, as well as most genera and subgenera of the tribe Syrphini. Members of other tribes of Syrphinae were also included (Bacchini and Paragini). Table 1 lists the species included in the analysis, the collection data and the GenBank accession numbers. A total of 108 taxa were included in this study. We sequenced and analyzed for the first time 43 specimens representing 34 different species. Additionally, we obtained new sequences for 10 already sequenced voucher specimens of 10 different species (Table 1, GenBank accession numbers starting with MF; MF446421–MF446565). Members of the subfamily Eristalinae were

used as outgroups as the monophyly of Syrphinae is well supported (Hippa & Stähls, 2005; Mengual et al., 2015; Stähls, Hippa, Rotheray, Muona, & Gilbert, 2003; Young et al., 2016). We also included representatives of Pipizinae, that is, *Neocnemodon vitripennis* (Meigen, 1822) and *Pipiza quadrimaculata* (Panzer, 1804). *Merodon equestris* (Fabricius, 1794) (Syrphidae: Eristalinae) was constrained as outgroup. DNA sequences for the genera *Doros* Meigen, 1803, *Pseudodoros* Becker, 1903, *Notosyrphus*, and *Austroscaeava* gen. nov. were obtained for the first time for molecular phylogenetic study.

2.3 | Laboratory protocols

One to three legs, the entire abdomen or the entire specimen, either dry pinned or ethanol preserved, were used for DNA extraction. Extractions were carried out using the NucleoSpin Tissue DNA Extraction kit (Machery-Nagel, Düren, Germany) following the manufacturer's instructions; samples were resuspended in 50–100 µl ultra-pure water. Entire specimens or remnants of specimens were preserved and labeled as DNA voucher specimens for the purpose of morphological studies and deposited at the Zoological Museum of the Finnish Museum of Natural History [MZB], at the Colección Entomológica de la Universidad de Alicante [CEUA], 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, Stähls, and Rojo (2008b), Mengual et al. (2012). 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) and then sequenced (using the PCR primers) in both directions. The sequences were edited for base-calling errors and assembled using Geneious R7 (version 7.1.3, Biomatters Ltd.). All new sequences were submitted to GenBank (see Table 1 for accession numbers).

2.4 | Sequence alignment

The alignment of the protein-coding *COI* gene was done manually, and it was not necessary to include gaps in this alignment. The *COI* data matrix contained a total of 1,371 nucleotide characters. The alignment of *18S* and *28S rRNA* genes was done using the secondary structure of these genes, as explained by Kjer (1995) and implemented by Gillespie, Cannone, Gutell, and Cognato (2004), Gillespie, Johnston, Cannone, and Gutell (2006), Mengual (2015a) and Mengual et al. (2012, 2015). As a result, 650 bps were included in the analysis for the D2–D3 regions of *28S*, and 605 bp for *18S*, both numbers including gaps. A nexus file with the final alignment is provided as online Supporting Information (File S3), and two additional text files are also given in the Supporting Information with the original structural alignment for *28S* and *18S* before trimming (Files S4 and S5, respectively).

TABLE 1 Taxon sampling used in the molecular analysis, including GenBank accession numbers. All GenBank accession numbers starting with MF denote new sequences used for the first time in the present study

Species	Label information	DNA voucher code	COI	28S	18S
<i>Allograpta neotropica</i> Curran, 1936	Colombia: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2175 m., 15.ii.2006. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP59	EU241733	EU241780	EU241831
<i>Asiobaccha marissae</i> Mengual, 2016	Indonesia: SE Sulawesi, North Kolaka, Mekongga Mt., nr Tinukari, 1000 m., 03°38'23.244"S 121°08'56.76"E, 30.ix.2010. Leg.: R.B. Kimsey. Det.: X. Mengual.	ZFMK_XM127	KM270854	KM270823	KM270771
<i>Austroscaeva melanostoma</i> (Macquart, 1842)	Chile: Limari prov., Fray Jorge Natl. Park, 30.ix–4.x.1997. Leg.: M. E. Irwin & D.K. Yeates. Det.: G. Stähls.	MZH_S185	MF446558	MF446505	–
<i>Austroscaeva occidentalis</i> (Shannon, 1827)	Chile: Limari prov., Fray Jorge Natl. Park, 30.ix–4.x.1997. Leg.: M. E. Irwin & D.K. Yeates. Det.: G. Stähls.	MZH_S184	MF446559	MF446506	–
<i>Baccha elongata</i> (Fabricius, 1775)	Finland: Ta, Vesijako, vii.2004, malaise trap. Leg.: J. Jakovlev. Det.: G. Stähls.	MZH_Y242	EF127326	EF127407	EU431540
<i>Betasyrphus aff. adligatus</i>	South Africa: Botanical Royal Garden, Pitermaritzburg, 12.xii.2012. Leg.: S. Rojo. Det.: A. Ssymank.	ZFMK_D081	MF446532	MF446480	MF446436
<i>Betasyrphus intersectus</i> (Wiedemann, 1824)	South Africa: Drakensberg (Sentinel Peak), 8.xii.2012. Leg.: C. Pérez-Bañón & S. Rojo. Det.: A. Ssymank.	ZFMK_D079	MF446530	MF446478	MF446435
<i>Betasyrphus intersectus</i> (Wiedemann, 1824)	South Africa: Kwazulu-Natal, near Howick, meadow near exit 125 of N3 to Balgowan, 1280 m., 29°21'45.9"S 30°05'52.5"E, 18.x.2015. Leg. X. Mengual. Det.: X. Mengual.	ZFMK_D232	MF446539	MF446487	MF446443
<i>Betasyrphus keiseri</i> Ssymank, 2010	Madagascar: Fianarantsoa Prov., Ranomafana N.P., open area in front of ValBio, 19.xi.2004. Leg.: X. Mengual. Det.: A. Ssymank.	MZH_XP101	MF446549	–	MF446453
<i>Betasyrphus keiseri</i> Ssymank, 2010	Madagascar: Fianarantsoa Prov., Ranomafana N.P. Open area in front of Valbio, 21.xi.2004. Leg.: X. Mengual. Det.: A. Ssymank.	MZH_XP55	MF446548	MF446496	–
<i>Chrysotoxum caustum</i> (Harris, 1776)	Greece: Lesvos Island, Agiasos, 08.v.2007. Leg.: G. Stähls. Det.: G. Stähls.	MZH_XP166	KM270857	KM270826	KM270774
<i>Chrysotoxum continuum</i> Bezzi, 1915	Tanzania: Kilimanjaro N.P., Horombo to Mandara campament, 3200 m., 09.vi.2007. Leg.: A. Menargues. Det.: X. Mengual.	MZH_XP216	MF446553	MF446500	MF446457
<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>Dasysyrphus albostriatus</i> (Fallén, 1817)	The Netherlands: Leiden, Meijendel dune area, 5.ix.2005. Leg.: excursion participants. Det.: G. Stähls.	MZH_S565	EF127323	EF127402	EU431542
<i>Dasysyrphus creper</i> (Snow, 1895)	USA: Arizona, San Doval Co. Det.: L. Mazánek.	MZH_S359	EF127368	EF127448	MF446464
<i>Dasysyrphus hilaris</i> (Zetterstedt, 1843)	Finland: N: Vantaa, Keimola, 05.06.2003. Leg.: G. Stähls. Det.: G. Stähls.	MZH_Y7	MF446554	MF446501	MF446458
<i>Dasysyrphus lenensis</i> Bagatshanova, 1980	Germany: Nordrhein-Westfalen, TK: 5403, R 2521143, H 5596510, Döppeskuhl 2009, Malaise-Falle, Bachtal, Nebenbach des	ZFMK_D006	KM270861	KM270829	KM270777

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
	Fuhrtsbachtals, FFH DE-5403-301. NP Eifel, 18.v–01.vi.2009. Leg.: J. Esser. Det.: A. Ssymank.				
<i>Dasysyrphus lotus</i> (Williston, 1887)	Colombia: Cali, Cerro San Antonio, 2200 m, 25.viii.2004. Leg. C. Prieto. Det. F.C. Thompson.	MZH_XP23	EF127298	EF127377	MF446451
<i>Didea fuscipes</i> Loew, 1863	USA: New Mexico, San Doval Co., 4 km NW La Cueva FR 144, 9.vii–17.viii.2002, malaise trap. Leg. M. Hauser. Det.: G. Ståhls.	MZH_XP1	MF446545	MF446493	MF446449
<i>Didea intermedia</i> Loew, 1854	Finland: Espoo, vii.2001. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_S90	EF127336	EF127418	EU431543
<i>Dideoides coquillettii</i> (Goot, 1964)	South Korea: Gangwon-do, Weonju-si, Maeji-ri, Yonsei Univ. Campus, 4.x.1999. Leg.: C.H. Park. Det.: H.Y. Han & D.S. Choi.	MZH_XP8	EF127293	EF127373	KM270778
<i>Dideoides latus</i> (Coquillett, 1898)	South Korea: kangwon-do, Wonju, panbumyon, Seogok-ri. Mt. Paekun from Yongsu-gol, 5.vii.1998. Leg.: H.Y. Han, K.E. Ro & H.W. Byun. Det.: H.Y. Han & D.S. Choi.	MZH_XP7	MF446546	MF446494	MF446450
<i>Dideopsis aegrota</i> (Fabricius, 1805)	Australia: Queensland, Daintree National Park, Cafe Tribulation, 16°05'S 145°29'E, 4.vi.1997, rainforest opening. Leg.: J. & A. Skevington. J95#1241. Det.: J. Skevington.	MZH_S92	EF127333	EF127414	MF446463
<i>Dideopsis aegrota</i> (Fabricius, 1805)	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Kipandi Butterfly Park, 720 m., 5°52'20"N 116°14'53"E, 15.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	ZFMK_XM225	KM270862	KM270830	KM270779
<i>Dioprosopa clavata</i> (Fabricius, 1794)	Cuba: La Habana, ii.2001. Leg.: M.A. Marcos- García. Det.: G. Ståhls.	MZH_S84	EF127332	EF127413	MF446462
<i>Dioprosopa clavata</i> (Fabricius, 1794)	Mexico: Villa de Álvarez, Crta. Minatitlán, Colonia Burócratas, 23.viii.2006. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP116	KM270873	KM270841	KM270807
<i>Dioprosopa clavata</i> (Fabricius, 1794)	Peru: Valle del Cañete, Huaral trap, 17.04.2008. Leg.: S. Rojo. Det.: X. Mengual.	MZH_Y914	MF446555	MF446502	–
<i>Dioprosopa vockerothi</i> Kassebeer, 2000	Peru: Valle del Cañete, 4.iv.2008. Det.: X. Mengual.	MZH_Y915	MF446563	MF446514	–
<i>Dioprosopa vockerothi</i> Kassebeer, 2000	Peru: Dpto. Lima, Cañete, point 4, 04.iv.2008. AECID 013484–07. Leg. X. Mengual. Det.: X. Mengual.	ZFMK_D068	MF446531	MF446479	MF446433
<i>Doros destillatorius</i> Mik, 1885	France: Dpt. Haute-Garonne, Castelnau- Picampeau, 07–22.vi.2005. Leg.: J.P. Sarthou. Det.: J.P. Sarthou.	MZH_XP167	MF446551	MF446498	MF446455
<i>Doros profuges</i> (Harris, 1780)	France, Dpt. Haute-Garonne, Montégut- Bourjac, 10–25.vi.2004. Leg.: J.P. Sarthou. Det.: J.P. Sarthou.	MZH_XP168	MF446552	MF446499	MF446456
<i>Epistrophe eligans</i> (Harris, 1780)	The Netherlands: Limburg, Epen, Bovenste bos. 50°45'24.6"N 5°53'55.7"E, 19.v.2012. Leg. X. Mengual. Det. X. Mengual.	ZFMK_D010	MF446525	MF446473	MF446428
<i>Epistrophe melanostoma</i> (Zetterstedt, 1843)	Finland: N: Keimola, 10.vi.2000. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_S60	EF127324	EF127405	MF446461
<i>Epistrophe nitidicollis</i> (Meigen, 1822)	Finland: Liesjärvi, 11.vi.2000. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_S61	EF127325	EF127406	KM270780

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
<i>Epistrophella euchroma</i> (Kowarz, 1885)	Czech Republic: Bohemia, PLA distr., Chrudim Hermanuv mestec, park, 3.vi.2005. Leg.: L. Mazánek. Det.: L. Mazánek.	MZH_S559	EF127315	EF501964	KM270781
<i>Episyphus 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. Ståhls.	MZH_Y184	EF127358	EF127439	EU431544
<i>Eupeodes (Eupeodes) volucris</i> Osten Sacken, 1877	USA: NE, Cass Co., Louisville Platte River Sp., 19.v.2005. Leg. W. van Steenis. Det. W. van Steenis.	MZH_XP43	KM270868	KM270836	KM270787
<i>Eupeodes (Macrosyrphus) confrater</i> (Wiedemann, 1830)	South Korea: Gyeongsangbuk-do, Yeongju Sunheung-myeon, 8.vi.2002. Leg.: D.S. Choi. Det.: G. Ståhls.	MZH_Y101	EF127355	EF127436	KM270788
<i>Eupeodes (Metasyrphus) corollae</i> (Fabricius, 1794)	Spain: Alicante, Aspe, Partida Tolomó, 07.ii.2006. Leg.: P. Hurtado. Det.: X. Mengual.	MZH_XP141	EU431499	EU431467	EU431546
<i>Eupeodes (Metasyrphus) fumipennis</i> (Thomson, 1869)	Canada: BC, Vancouver Island, Nanaimo, Morrel Sanct., 49°08'49"N 123°58'31"W, 140 m., 05.v.2005. Leg. W. van Steenis. Det. W. van Steenis.	MZH_XP46	EF127313	EF127392	MF446452
<i>Eupeodes (Metasyrphus) latifasciatus</i> (Macquart, 1829)	Germany: Nordrhein-Westfalen, Bonn, ZFMK garden, 50°43'18.6"N 07°06'48.8"E, 67 m., 18.v.2013. Leg.: X. Mengual. Det.: X. Mengual.	ZFMK_D208 (ZFMK-TIS-22072_Diptera)	MF446536	MF446484	MF446440
<i>Eupeodes (Metasyrphus) lucasi</i> (Marcos-García & Láaska, 1983)	Spain, 2003. Leg. S. Rojo.	CEUA_L13	EF127337	EF127419	—
<i>Eupeodes (Metasyrphus) luniger</i> (Meigen, 1822)	Germany: Nordrhein-Westfalen, Monschau, Döppeskaul, 50°30'14.4"N 06°17'50.6"E, 560–580 m., 5.x.2009. Leg.: J. Esser. Det.: A. Ssymank.	ZFMK_D209 (ZFMK-TIS-2903_Diptera)	MF446537	MF446485	MF446441
<i>Eupeodes (Metasyrphus) nitens</i> (Zetterstedt, 1843)	Germany: Nordrhein-Westfalen. TK: 5404, R 2529538, H 5605439. Helingsberg 2009, Malaise-Falle, ehemaliger Sprengplatz, Dreisborner Hochfläche, ehem. Truppenübungsplatz Vogelsang. NP Eifel, 500 m., 29.vi-13.vii.2009. Leg. J. Esser. Det. A. Ssymank.	ZFMK_D013 (ZFMK-TIS-2898_Diptera)	MF446527	MF446475	MF446430
<i>Eupeodes (Metasyrphus) rojasi</i> Marnef, 1999	Venezuela: Lara, Lomas de Cubiro, 1710 m., 9°47'N 59°33'W, 31.iii.2015. Leg.: E. Arcaya, D. Medina, A. Arcaya, K. Arcaya, S. Matute. Det.: X. Mengual.	ZFMK_D275	MF446541	MF446489	MF446445
<i>Eupeodes (Metasyrphus) rojasi</i> Marnef, 1999	Chile: Limari prov., Fray Jorge Natl. Park, 30.ix-4.x.1997. Leg.: M. E. Irwin & D.K. Yeates. Det.: G. Ståhls.	MZH_S197	MF446560	MF446507	—
<i>Fagisyrphus cinctus</i> (Fallén, 1817)	Czech Republic: Bohemia, PLA Kokorinsko, Vojtechov, 14.v.2005. Leg.: L. Mazánek. Det.: L. Mazánek.	MZH_S558	KM270869	KM270837	KM270789
<i>Graptomyza longirostris</i> Wiedemann, 1820	Singapore: Dairy Farm N.P., 02.v.2012. Leg.: V. Gowda. Det.: X. Mengual.	ZFMK_D007	KM270878	KM270847	KM270816

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
<i>Ischiodon aegyptium</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°41'04.3"S 28°56'14.7"E. Leg.: S. Rojo. Det.: X. Mengual.	ZFMK_D077	MF446529	MF446477	MF446434
<i>Ischiodon aegyptium</i> (Wiedemann, 1830)	Algeria: Mostaganem Province, Mazagran, 35°54'N 0°43'E, 04.iii.2014, feeding on <i>Myzus persicae</i> in pepper plants. Det.: S. Rojo.	ZFMK_D190	MF446534	MF446482	MF446438
<i>Ischiodon scutellaris</i> (Fabricius, 1805)	French Polynesia: Bora Bora, Vairupe, 13.xi.2012, Malaise trap. Leg.: T. Ramage. Det.: X. Mengual.	ZFMK_D267	MF446540	MF446488	MF446444
<i>Ischiodon scutellaris</i> (Fabricius, 1805)	China: Hong Kong, Park, 7.x.2001. Leg.: D. Iliff. Det.: G. Stähls.	MZH_S157	AY603768	EF127429	KM270790
<i>Lapposyrphus lapponicus</i> (Zetterstedt, 1838)	Germany: Nordrhein-Westfalen, Euskirchen, Schleiden, Kermeter, 475 m., 50°36'05"N 06°26'55.7"E, 30.v.2011. Leg. J. Esser. Det. A. Ssymank.	ZFMK_D210 (ZFMK-TIS-2876_Diptera)	MF446538	MF446486	MF446442
<i>Lapposyrphus lapponicus</i> (Zetterstedt, 1838)	U.S.A.: New Mexico, San Doval Co., 4 km NW La Cueva, FR144, 35°54.25' N 106°40.10' W, 9–17.vii.2002, malaise trap. Leg.: M. Hauser.	MZH_S358	MF446564	MF446512	–
<i>Lapposyrphus lapponicus</i> (Zetterstedt, 1838)	Czech Republic: 13.v.2000. Leg.: L. Mazánek. Det.: L. Mazánek.	MZH_S65	DQ158897	DQ158897	KM270791
<i>Leucozona (Ischyrosyrphus) glauca</i> (Linnaeus, 1758)	Spain: Pyrenees, Aran Valley, nr Arties, 1500 m., 1.viii.2003. Leg. G. Stähls. Det.: G. Stähls.	MZH_XP5	EF127292	EF127372	KM270793
<i>Leucozona (Leucozona) inopinata</i> Doczkal, 2000	Germany: Nordrhein-Westfalen. TK: 54034, 50°30'51.1"N, 06°17'09.9"E; Fuhrtsbachtal, nahe Antoniusbrücke, Narzissen-Bärwurzwiese, Meum athamaticum in Vollblüte. NP Eifel, 537 m., 09.vi.2012. Leg. A. Ssymank. Det. A. Ssymank.	ZFMK_D004	MF446524	MF446472	MF446427
<i>Leucozona (Leucozona) lucorum</i> (Linnaeus, 1758)	Italy: South Tirol, Val Venosta, vii.2001. Leg.: G. Stähls. Det.: G. Stähls.	MZH_S139	EF127346	EF501965	EU431548
<i>Megasyrphus erraticus</i> (Linnaeus, 1758)	Finland: Ab: Karislojo, Karkalinniemi, v.2004. Leg.: G. Stähls. Det.: G. Stähls.	MZH_Y183	EF127357	EF127438	EU431545
<i>Megasyrphus laxus</i> (Hull, 1925)	Canada: AB, Jasper NP, Valley o-t Five Lakes, 117°98'E 52°48'N, 27.viii.2004. Leg. W. van Steenis. Det. W. van Steenis.	MZH_XP27	EF127302	EF127381	KM270794
<i>Melangyna (Austrosyrphus) collata</i> (Walker, 1852)	Australia: Victoria, Tarra Bulga NP, near Tarra Bulga Visitor Centre, AMG 55,462–5746, 26.i.2006. Leg.: W. van Steenis. Det.: W. van Steenis.	MZH_XP124	KM270871	KM270839	KM270795
<i>Melangyna (Austrosyrphus) viridiceps</i> (Macquart, 1847)	Australia: Victoria, Mt. Buffalo NP, The Horn top, AMG 55,479–5929, 1723 m., 29.i.2006. W. van Steenis. Det.: W. van Steenis.	MZH_XP123	MF446550	MF446497	MF446454

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
<i>Melangyna</i> (<i>Melangyna</i>) <i>lasiophthalma</i> (Zetterstedt, 1843)	Finland: N: Mäntsälän Mustametsä, 10.v.2003. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_Y5	EF127361	EF501966	KM270796
<i>Melangyna</i> (<i>Melangyna</i>) <i>subfasciata</i> (Curran, 1925)	Canada: Kluane, Whitehorse Airport, 135°05'E 60°45'N, 4.viii.2004. Leg.: W. van Steenis. Det.: W. van Steenis.	MZH_XP28	EF127303	EF127382	KM270797
<i>Melanostoma scalare</i> (Fabricius, 1794)	Finland: Ok: Kuhmo, Lentuankoski, 15.viii.2006. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_Y441	EU431500	EU431468	EU431549
<i>Meligramma guttata</i> (Fallén, 1817)	Finland: Ab: Mietoinen, Perkko, 6733:222, 21.vii.2004. Leg.: A. Haarto. Det.: G. Ståhls.	MZH_Y478	EF501960	EF501968	KM270800
<i>Meligramma</i> <i>triangulifera</i> (Zetterstedt, 1843)	Czech Republic: Jizerské Mountains, Rybí loucky-peat-bog, sq. 5158, 850 m, (malaise trap with alcohol), 5–20.viii.2003. Leg.: Preisler. Det.: G. Ståhls.	MZH_S560	EF127316	EF501967	KM270799
<i>Meliscaeva auricollis</i> (Meigen, 1822)	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Pérez. Det.: L. Mazánek.	MZH_S123	EF127341	EF127423	EU241844
<i>Merodon equestris</i> (Fabricius, 1805)	Finland: N, Askola, 12.i.2007. Leg. G. Ståhls. Det.: Ståhls.	MZH_Y690	EU431486	EU431455	EU431523
<i>Myolepta dubia</i> (Fabricius, 1850)	Germany: Nordrhein-Westfalen, NP Eifel, FO: 7757 R 2532921, H 5613552. Odenbachtal-Felskuppen, 320 m., 24.vi–08.vii.2010, Malaise. Leg.: J. Esser. Det. A. Ssymank.	ZFMK_D012	KM270877	KM270846	KM270815
<i>Neocnemodon</i> <i>vitripennis</i> (Meigen, 1822)	Finland: N: Sibbo, Hindsby, 26.v.2004. Leg.: G. Ståhls. Det.: G. Ståhls.	MZH_Y211	EU431503	KM270845	EU431559
<i>Notosyrphus</i> <i>goldbachi</i> (Fluke, 1950)	Argentina, Tucuman, San Javier, Hotel Sol, Ruta 340 – Km 23, 1250 m., 26°47'52" S 65°21'31" W, 01.xi.2008. Leg.: X. Mengual. Det.: X. Mengual.	MZH_Y916	MF446556	MF446503	MF446459
<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>Paragus</i> (<i>Afroparagus</i>) <i>caligneus</i> Ssymank & Mengual, 2014	Gabon: Ogooué-Ivindo, Ivindo NP, Makokou (518 m), 16–19.ix.2012. Am Ivindo nahe Station (Malaisetrap 4). Leg.: R. Peters. Det. X. Mengual.	ZFMK_D067	KJ158454	KJ158455	MF446432
<i>Paragus</i> (<i>Pandasophthalmus</i>) <i>haemorrhous</i> Meigen, 1822	Spain: Alicante, 2000. Leg.: A. Vujić. Det.: A. Vujić.	MZH_S48	AY174470	AY476866	EU409259
<i>Paragus</i> (<i>Paragus</i>) <i>bicolor</i> (Fabricius, 1794)	Tajikistan: Tigrovaya Balka Nature Reserve, 21.iv.2014. Leg.: A. Barkalov. Det.: A. Barkalov.	ZFMK_D168	MF446533	MF446481	MF446437
<i>Paragus</i> (<i>Paragus</i>) <i>pecciolii</i> Rondani, 1857	Montenegro: Durmitor, 26.vi.2000. Leg.: A. Vujić. Det.: A. Vujić.	MZH_S71	AY476844	AY476864	KM270803
<i>Paragus</i> (<i>Serratoparagus</i>) <i>crenulatus</i> Thomson, 1869	Malaysia: Sabah, Danum Valley, viii.1999. Det.: A. Vujić.	MZH_S62	AY476862	AY476880	KM270802

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
<i>Parasyrphus malinellus</i> (Collin, 1952)	Germany: Nordrhein-Westfalen, Monschau, Döppeskaul, 50°30'14.4"N 06°17'50.6"E, 560–580 m., 16.vi.2009. Leg.: J. Esser. Det.: A. Ssymank.	ZFMK_D207 (ZFMK-TIS-2914_Diptera)	MF446535	MF446483	MF446439
<i>Parasyrphus lineolus</i> (Zetterstedt, 184)	Italy: South Tirol, Val Venosta, vii.2001. Leg.: G. Stähls. Det.: L. Mazánek.	MZH_S137	EF127342	EF127424	KM270804
<i>Pipiza quadrimaculata</i> (Panzer, 1804)	Finland: Ka, Joutseno, Riikanmaa. KKJ-Y, 05.vii.2007. Leg.: M.P. van Zuijen & W. & J. van Steenis. Det.: G. Stähls.	MZH_XP218	EU431506	EU431474	EU431562
<i>Platycheirus albimanus</i> (Fabricius, 1781)	Sweden: 2000. Leg.: J. van Steenis. Det.: J. van Steenis.	MZH_E38	EF127351	EF127432	KM270805
<i>Pseudodoros nigricollis</i> Becker, 1903	Cyprus: Pafos, Polis Chrysochou, 14.xi.2015. Leg.: Ch. Makris; wing sheltered spot in reed bed of <i>Phragmites australis</i> close to coast line. Det.: A. van Eck.	ZFMK_D280	MF446543	MF446491	MF446447
<i>Pseudodoros nigricollis</i> Becker, 1903	Egypt: 3 km W of Siwa town, Siwa oasis, Fatnas spring and conservancy, Reed swamp, –42 m., 29°11'34.8" N 25°28'48" E, 13.v.2009. Leg.: K.-D.B. Dijkstra. Det.: G. Stähls.	MZH_Y912	MF446565	MF446513	MF446465
<i>Pseudodoros nigricollis</i> Becker, 1903	Tanzania: Kigoma region, 35–38 km W of Uvinza, Lower Malagarasi Basin, Igamba and Kasagwe, 05.18"S 30.06"E, 7.viii.2009. Leg.: K.-D.B. Dijkstra. Det.: G. Stähls.	MZH_Y1108	MF446557	MF446504	–
<i>Rohdendorfia alpina</i> Sack, 1938	Italy: Stelvio Pass. Leg.: G. Stähls. Det.: G. Stähls.	MZH_G344	EF127338	EF127420	EU431552
<i>Salpingogaster nigra</i> Schiner, 1868	Colombia: Dpto Meta, PNN Sumapaz, Cabaña Las Mirlas, 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 (Scaeva) albomaculata</i> (Macquart, 1842)	Greece: Lesvos island, iv.2001. Leg.: S. Rojo & C. Pérez. Det.: S. Rojo.	MZH_S105	AY603765	MF446510	–
<i>Scaeva (Scaeva) albomaculata</i> (Macquart, 1842)	Spain: Alicante, 1999. Leg.: S. Rojo. Det.: X. Mengual.	MZH_S57	EF127329	EF127410	EU431553
<i>Scaeva (Scaeva) caucasica</i> Kuznetzov, 1985	China: Gansu prov., Bayin, vii.2001. Leg.: J. Bancroft.	MZH_S190	MF446561	MF446508	–
<i>Scaeva (Scaeva) pyrastri</i> (Linnaeus, 1758)	Germany: Nordrhein-Westfalen, Watchberg–Bonn, Oberbachem, Werthovener Weg., FO: 7891, TK: 530842, 138 m, 27.vii.2012. Leg. A. Ssymank. Det. A. Ssymank.	ZFMK_D009	KM270874	KM270842	KM270809
<i>Scaeva (Semiscaeva) dignota</i> (Rondani, 1857)	Greece: Lesvos island, iv.2001. Leg.: S. Rojo & C. Pérez. Det.: S. Rojo.	MZH_S100	MF446562	MF446509	–
<i>Scaeva (Semiscaeva) komabensis</i> (Matsumura, 1918)	Japan: Nagano Prefecture, Ueda, Sugadaira Kogen, near SMRC, grassland, 1330 m., 05–19.vii.2014, 36°31'18"N 138°21'03"E, Malaise trap. Leg.: A. Blanke. Det. X. Mengual.	ZFMK_D279	MF446542	MF446490	MF446446
<i>Scaeva (Semiscaeva) komabensis</i> (Matsumura, 1918)	South Korea: Gaeweon-do, Hongcheon-gun Nae-myeon, 6.vi.2000. Leg.: D.S. Choi. Det.: X. Mengual.	MZH_Y100	EF127354	EF127435	MF446460

(Continues)

TABLE 1 (Continued)

Species	Label information	DNA voucher code	COI	28S	18S
<i>Scaeva (Semiscaeva) mecoptera</i> (Bigot, 1860)	France: Rhone-Alpes, RNN Gorges de L'Ardec, TM02, Dune de Guad, 27.v–08.vi.2015. Leg.: N. Bazin. Det.: M.C. Speight.	ZFMK_D281	MF446544	MF446492	MF446448
<i>Scaeva (Semiscaeva) mecoptera</i> (Bigot, 1860)	Spain: Alicante, 1999. Leg.: S. Rojo. Det.: S. Rojo.	MZH_S16	MF446547	MF446495	–
<i>Scaeva (Semiscaeva) selenitica</i> (Meigen, 1822)	Germany: Nordrhein-Westfalen. TK: 5304, R 2531820, H 5607402. MF Hellberg (Kermeter, südexponierter Waldrand, Grenze Buchenwald, totholzreicher Douglasien-Kahlschlag). NP Eifel, 475 m., 16–30.v.2011. Leg. J. Esser, Det. A. Ssymank.	ZFMK_D015	MF446528	MF446476	MF446431
<i>Scaeva (Semiscaeva) selenitica</i> (Meigen, 1822)	Czech Republic: distr. Ostrava, Polanecký les, 3.iv.2000. Leg.: T. Kuras. Det.: L. Mazánek.	MZH_S69	AY603764	EF127404	KM270808
<i>Simosyrphus grandicornis</i> (Macquart, 1842)	Australia: Brisbane, 5.x.2002. Leg.: H. Hippa. Det.: G. Stähls.	MZH_S288	AY603770	MF446511	–
<i>Simosyrphus grandicornis</i> (Macquart, 1842)	Australia: Victoria, Mt. Buffalo NP, Dicksons Falls, AMG 55 481–5929, 1440 m., 29.i.2006. Leg.: W. van Steenis. Det.: W. van Steenis.	MZH_XP125	KM270875	KM270843	KM270810
<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>Syrphus shorae</i> Fluke, 1950	Venezuela: Edo. Aragua. P.N. Henri Pittier, Portachuelo, 1152 m., 10°20.828'N 067°41.309'W, 26.i.2007. Leg.: X. Mengual. Det.: X. Mengual.	MZH_XP158	EU409136	EU409191	EU409252
<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>Xanthogramma citrofasciatum</i> (De Geer, 1776)	Germany: Nordrhein-Westfalen. TK: 5304, 50°37'53"N, 06°26'37"E; Heimbach-Hasenfeld, Parkplatz Büdenbach, trockene Böschung mit <i>Euphorbia cyparissias</i> . NP Eifel, 303 m., 19.v.2012. Leg. A. Ssymank. Det. A. Ssymank.	ZFMK_D002	MF446523	MF446471	MF446426
<i>Xanthogramma laetum</i> (Fabricius, 1794)	Germany: Nordrhein-Westfalen. TK: 5304, R 2531820, H 5607402. MF Hellberg (Kermeter, südexponierter Waldrand, Grenze Buchenwald, totholzreicher Douglasien-Kahlschlag). NP Eifel, 475 m., 16–30.v.2011. Leg. J. Esser. Det. A. Ssymank.	ZFMK_D011	MF446526	MF446474	MF446429
<i>Xanthogramma flavipes</i> (Loew, 1863)	USA: NE, Cass Co., Louisville, Platte River SP. 19.v.2005. Leg. W. van Steenis. Det. W. van Steenis.	MZH_XP31	EF127306	EF127385	KM270814
<i>Xanthogramma pedissequum</i> (Harris, 1776)	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Perez. Det.: S. Rojo.	MZH_S120	EF127339	EF127421	EU431557

2.5 | Phylogenetic analyses

For the combined dataset, maximum-likelihood (ML) analysis and Bayesian inference were performed to infer the phylogenetic relationships of the members of the *Scaeva-Eupeodes* clade. For both approaches, the dataset was divided into five partitions: first codon position of *COI*, second codon position of *COI*, and third codon position of *COI*, *28S* gene, and *18S* gene. We determined the best choice of model for each partition using jModelTest 2.1.1 (Darriba, Taboada, Doallo, & Posada, 2012) under the Akaike Information Criterion (AIC), as recommended by Posada and Buckley (2004). The model chosen for positions 1 and 2 of *COI* was GTR + I + G, and TrN + I + G for position 3. The model GTR + I + G was selected for *28S*, and the preferred model for *18S* gene was TVM + I + G. Data were analyzed under the recommended models using Garli v.2.01 (Zwickl, 2006, 2011). Forty-eight independent runs were conducted using scorethreshforterm = 0.05 and significanttopochange = 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 (Figure 1). Bootstrap support values (BS) were estimated from 1,000 replicates using the same independent models in Garli.

Phylogenetic estimation 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 (XSEDE in CIPRES Science Gateway). 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 <0.03 (Ronquist, Huelsenbeck, & van Mark, 2005), sampling trees every 2,500 generations. The program Tracer 1.5 (Drummond & Rambaut, 2007; Rambaut & Drummond, 2007) 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.

Analytical runs were performed on CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010). All trees were drawn with the aid of FigTree v.1.3.1 (Rambaut, 2009).

3 | RESULTS

3.1 | Phylogenetic analyses

The ML tree with the best likelihood score ($-31,292.223746$) is presented in Figure 1 (a .tre file, File S6, is provided as online Supporting Information). Although the taxonomic sampling was focused on the diversity within the *Eupeodes-Scaeva* clade and most Syrphini genera were included in our analyses, we would like to comment on the

topology for the other taxa. The two members of Pipizinae were resolved as sister group of Syrphinae, and members of the tribe Bachini were not recovered in a single clade, as in previous analyses (Mengual et al., 2015; Young et al., 2016). Most of the relationships among genera of Syrphinae are in agreement with previous analysis (Mengual, 2015a) with well-supported clades such as (*Eriozona* Schiner, 1860 + (*Didea* Macquart, 1838 + *Megasyrphus* Dušek & Láska, 1967)), (*Leucozona* Schiner, 1860 + (*Epistrophella* Dušek & Láska, 1967 + *Epistrophe*)), or the clade comprising the genera *Salpingogaster* Schiner, 1868, *Allograptia* Osten Sacken, 1875, *Sphaerophoria* Lepeletier & Serville, 1828, *Ocyptamus* Macquart, 1834, *Asiobaccha* Violovitsh, 1976, *Episyrrhus* Matsumura & Adachi, 1917, and *Meliscaeva* Frey, 1946.

Inside Syrphini, *Dideopsis* was resolved as the sister group of the remaining Syrphini + Paragini. Regarding the taxa tested in molecular phylogenetic analysis for the first time, *Doros* was placed as sister group of *Xanthogramma* Schiner, 1860, while *Notosyrphus* was recovered in a clade as sister group of *Dioprosopa* Hull, 1949 and *Austroscaeva* gen. nov., all with high support values (Figure 1). The genus *Pseudodoros* was resolved as sister group of *Ischiodon* with very high support (BS = 100).

The genus *Paragus* Latreille, 1804 was resolved as the sister group of the *Scaeva-Eupeodes* clade, wherein five clades received high support values: the genera *Betasyrphus* Matsumura, 1917, *Eupeodes*, and *Lapposyrphus*, the clade (*Notosyrphus* + (*Austroscaeva* + *Dioprosopa*)) and the clade comprising the two subgenera of *Scaeva*, *Simosyrphus*, *Pseudodoros*, and *Ischiodon*. Within the last clade, three groupings received very high support (BS = 100) and posterior probabilities with a value of 1, that is, *Scaeva* (*Semiscaeva*), *Scaeva* (*Scaeva*), and (*Simosyrphus* + (*Pseudodoros* + *Ischiodon*)).

The topology of the majority-rule consensus tree resulting from Bayesian inference compares favorably with the most likely tree, with some small differences (Fig. S2). The most remarkable difference between both approaches is the placement of *Betasyrphus* as the sister group of *Eupeodes*, being *Lapposyrphus* sister group of these two genera with a posterior probability of 0.70. Both topologies also disagree in the relationship between the two subgenera of *Scaeva*. Our ML analysis placed the subgenus *Scaeva* (*Scaeva*) as the sister group of *Simosyrphus* (*Pseudodoros* + *Ischiodon*) with very low support (BS = 51) and the subgenus *Scaeva* (*Semiscaeva*) as the sister group of this set of taxa, while in the Bayesian inference, *Scaeva* (*Scaeva*) and *Scaeva* (*Semiscaeva*) were resolved as sister groups with low probability (PP = 0.63) (Figure 1; Figs S1 and S2). These results imply that the two subgenera are valid clades (both subgenera have BS = 100 and PP = 1), but our molecular data were not sufficient to infer their relationship with confidence and high support values.

3.2 | Systematics

Our results based on molecular characters showed no doubt about the relationship of the Neotropical taxa of *Scaeva* and the other *Scaeva* species. The placement of *S. melanostoma* and *S. occidentalis* in a different clade from Palaearctic *Scaeva* species, with *Notosyrphus*

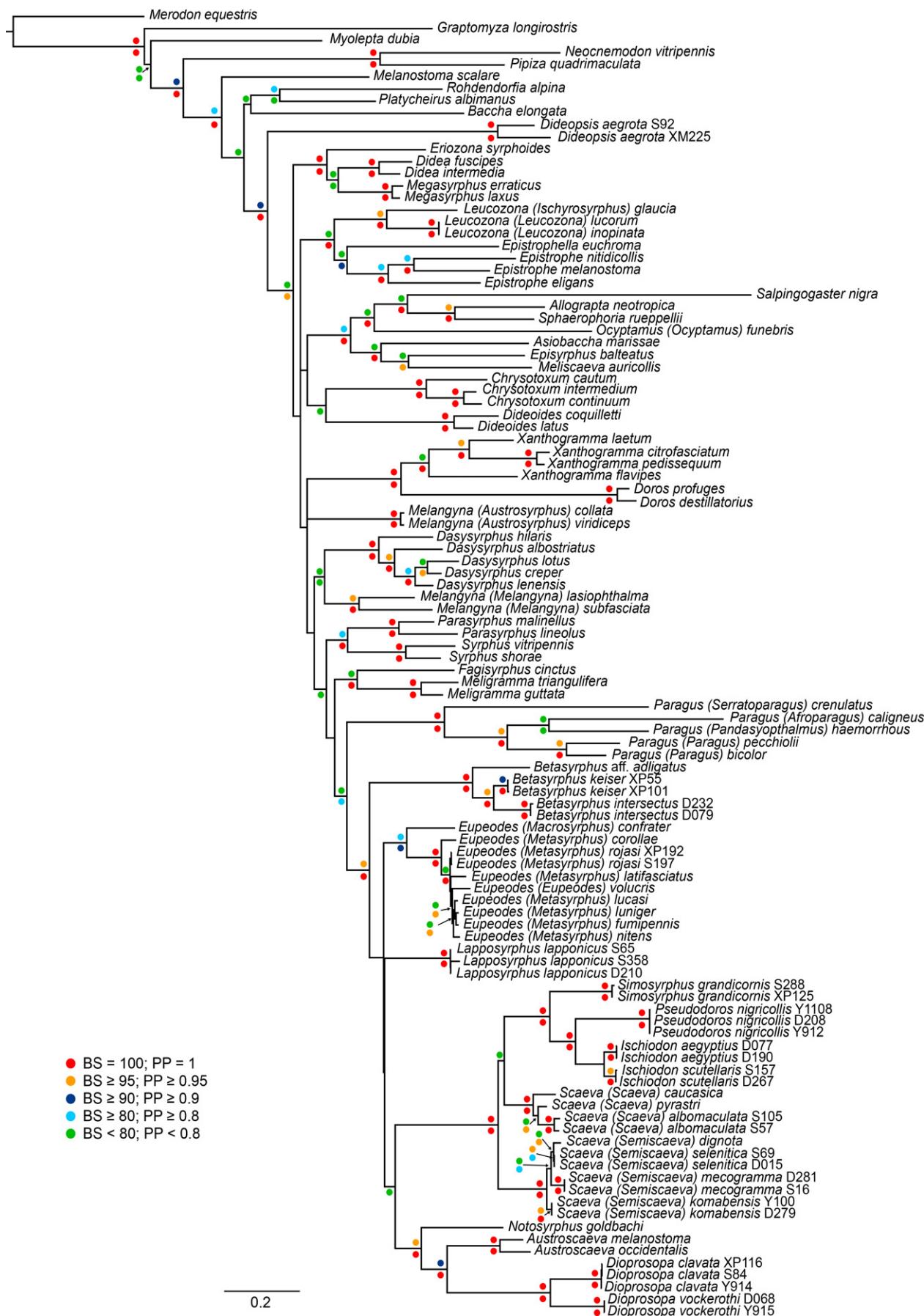


FIGURE 1 Maximum-likelihood tree ($\ln L = -31,292.223746$) based on the combined dataset (COI, 28S, and 18S) using Garli v.2.01.1067 and the structural alignment for 28S and 18S. Bootstrap support values (above) and Bayesian posterior probabilities (below) are depicted at the nodes (only >50 or >0.5, respectively). BS = Bootstrap support values; PP = Bayesian posterior probabilities

and *Dioprosopa*, provided robust support to the species group established by Dušek and Láska (1985), which together with the morphological differences mentioned by Dušek and Láska (1985) and Kassebeer (1999) prompted us to erect a new genus, *Austroscaeva* gen. nov., for this Neotropical species group.

3.2.1 | *Austroscaeva* Láska, Mazánek & Mengual gen. nov.

Figures 2–4

Type species

Syrphus melanostoma Macquart, 1842.

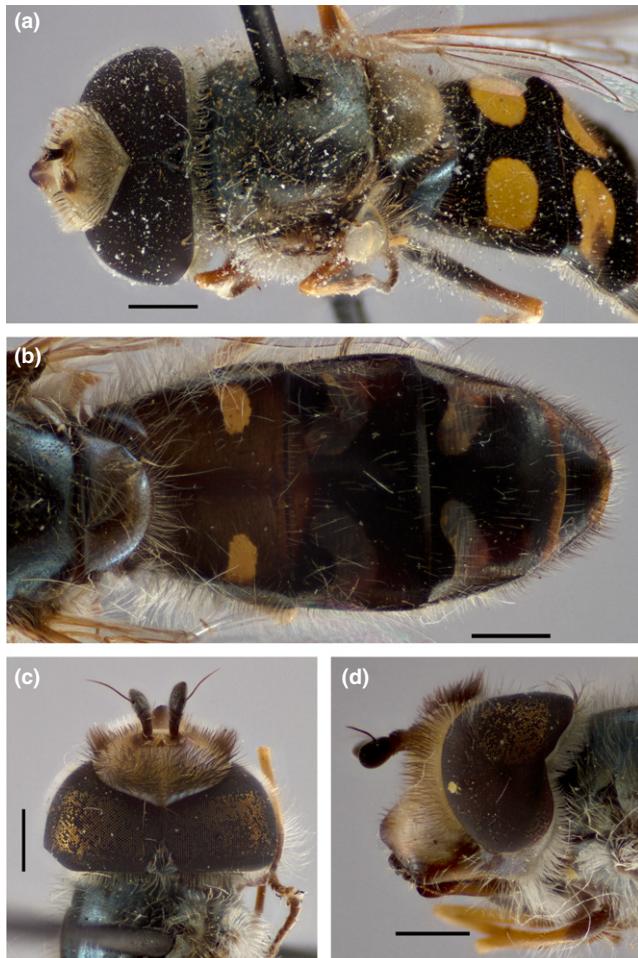


FIGURE 2 *Austroscaeva occidentalis* (Shannon), male ZFMK-DIP-00019580: (a) Head and thorax, dorsolateral view. *Austroscaeva melanostoma* (Macquart), male CNC DIPTERA #233009: (b) Abdomen, dorsal view. (c) Head, dorsal view. (d) Head, lateral view. Scales = 1 mm

Etymology

The name *Austroscaeva* is feminine and is a combination of *Austro*, meaning southern, and *Scaeva*, referring to the superficially similar genus *Scaeva*.

Included species

Austroscaeva melanostoma (Macquart, 1842) comb. nov., *Austroscaeva occidentalis* (Shannon, 1927) comb. nov., *Austroscaeva patagoniensis* (Kassebeer, 1999) comb. nov., and *Austroscaeva penai* (Marnef in Dušek & Láska, 1985) comb. nov.

Diagnosis

Very similar to the genus *Scaeva* (see diagnosis in Vockeroth, 1969: 70). Medium to large, moderately slender to robust species with very

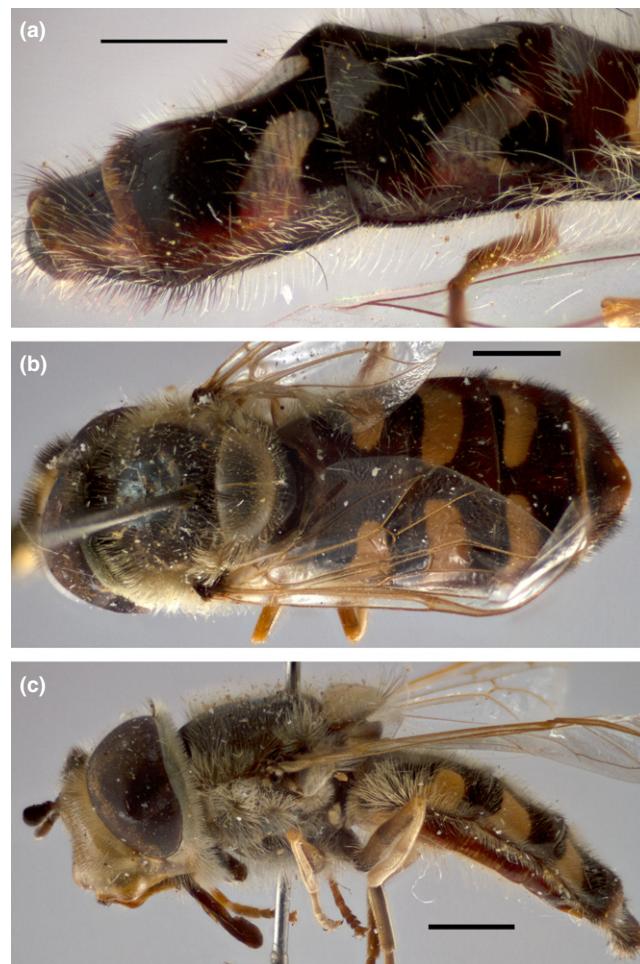


FIGURE 3 *Austroscaeva occidentalis* (Shannon), male ZFMK-DIP-00019580: (a) Abdomen, lateral view. Scale = 1 mm. *Austroscaeva penai* (Marnef), male ZFMK-DIP-00019582: (b) Abdomen, dorsal view. (c) Habitus, lateral view. Scales = 2 mm

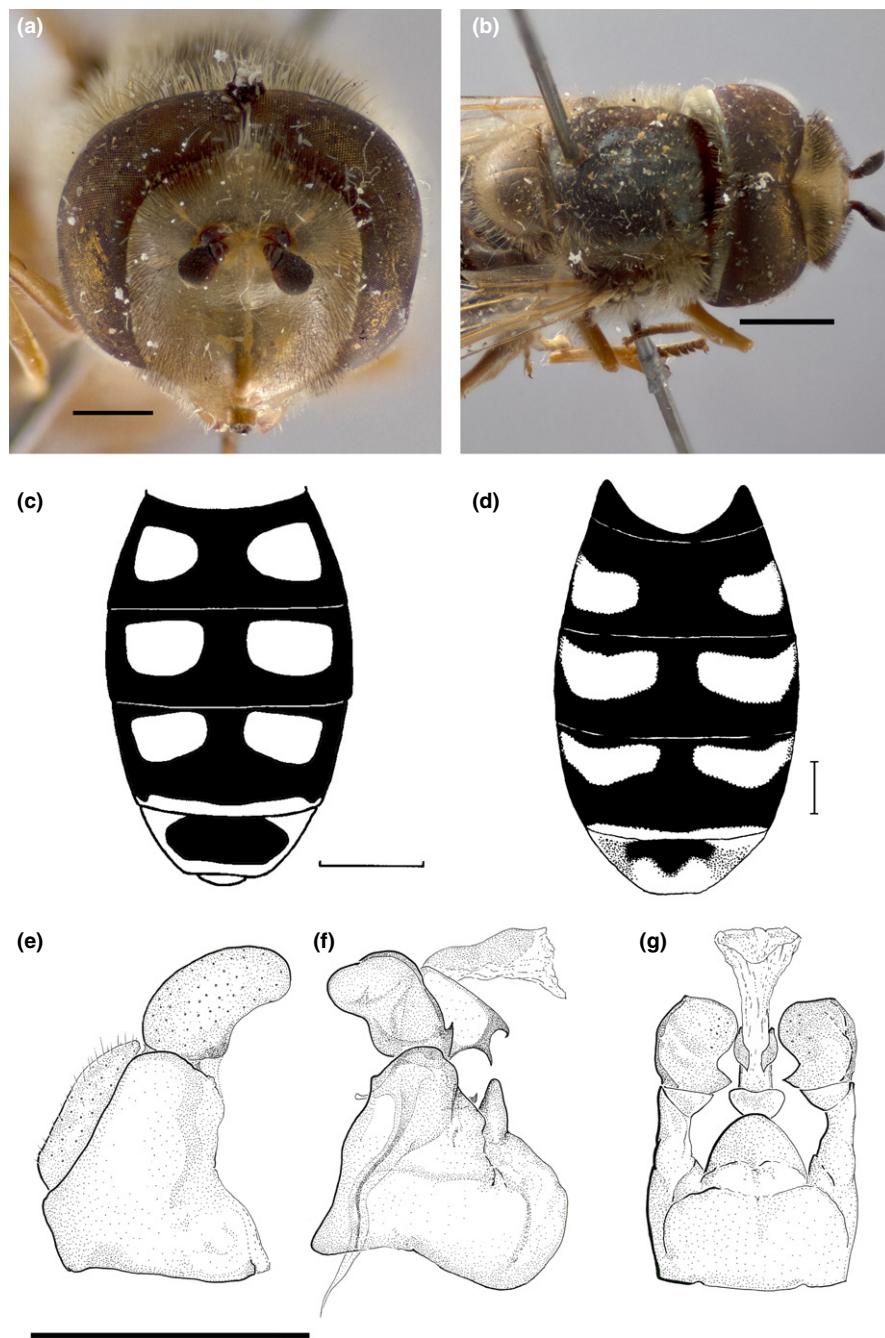


FIGURE 4 *Austroscaeva penai* (Marnef), male ZFMK-DIP-00019582: (a) Head, frontal view. (b) Head and thorax, dorsal view. Scales = 2 mm. *Austroscaeva patagoniensis* (Kassebeer), female (adapted from Kassebeer, 1999): (c) Abdomen, dorsal view. Scale = 1 mm. *Austroscaeva penai* (Marnef), male ZFMK-DIP-00019582: (d) Abdomen, dorsal view. Scale = 1 mm. (e) Male genitalia, epandrium, lateral view. (f) Male genitalia, hypandrium, lateral view (g) Male genitalia, hypandrium, ventral view. Scale = 1 mm

clear wings, pilose eyes, long pile on thorax and sometimes on abdomen as well, and oblique and often lunulate abdominal maculae.

Face produced forward; clypeus elongated. Front of male relatively broadened, strongly swollen (less in *A. occidentalis*). Dorsal 1/3–2/3 of eye of male with an extensive area of almost uniformly enlarged facets; eyes meeting anteriorly at an angle broader than 120°. Front of female only slightly swollen but broad. Face in both sexes moderately to strongly swollen. Mesonotum shining black, always pale pilose, without a clear lateral yellow vitta. Scutellum yellow, shiny medially or entirely pollinose, dull. Pleura black, densely pale pilose, subshining to moderately pollinose. Metasternum bare or pilose. Vein R_{4+5} nearly straight; basal section of vein R_{4+5} diverging from vein M, not running parallel as in *Scaeva* or *Lapposyrphus*; narrow and irregularly undulated

wing membrane posterior to veins dm-cu and M_1 . Microtrichia greatly reduced, absent from at least basal 1/2 of wing. Abdomen narrowly to broadly oval, flattened, strongly margined from tergum 2 to tergum 5. Terga 2–4 each with a pair of slightly to strongly oblique, narrow to broad, whitish-yellow to bright yellow maculae.

Karyology

The karyology of *Austroscaeva* gen. nov. is different from that of *Scaeva*. *Austroscaeva melanostoma* and *A. occidentalis* have five pairs of chromosomes plus an heteromorphic pair XY, with X short telocentric and Y very short telocentric (Boyes, Boyes, van Brink, & Vockeroth, 1973). On the other hand, *Scaeva albomaculata* (Macquart, 1842), *S. pyrastri*, and *S. selenitica* have four pairs of

chromosomes and a short heteromorphic pair XY (Boyes, van Bring, & Boyes, 1971; Boyes & van Brink, 1964).

Geographic distribution

Andean region (Argentina, Chile, Bolivia, Peru, Ecuador and Colombia) (see Kassebeer, 1999).

Natural history

Nothing is known about their larval biology or visited flowers. However, it is very likely that a U-shaped grasping organ (Rotheray, 1987) formed with the abdominal locomotory prominences of the larva is present also in these taxa. This structure is characteristic for the genera *Scaeva*, *Eupeodes*, *Ischiodon* (Rotheray & Gilbert, 1999), and *Dioprosopa* (Arcaya Sánchez, 2012).

Systematics

Austroscaeva gen. nov. comprises four species previously referred as the Neotropical *Scaeva* species group (Dušek & Láska, 1985; Kassebeer, 1999). Present molecular results place it as a sister group of *Dioprosopa* (BS = 90; PP = 1) in a clade with *Notosyrphus* (BS = 95; PP = 1) within the broader lineage *Scaeva-Eupeodes*. Láska et al. (2006) suggested that *Austroscaeva* gen. nov. might be sister to all Palaearctic *Scaeva*, *Ischiodon*, and *Simosyrphus* species according to the pattern of wing venation and other characters, a placement that agrees with our results in part.

Remarks

For more detailed information on species distribution and species descriptions, see Kassebeer (1999).

3.2.2 | *Austroscaeva patagoniensis* (Kassebeer, 1999) comb. nov.

Figures 4c and 5a–f

Description of the male

Robust, large species. Body length 13.5 mm; wing length 10 mm. Head (Figure 5d). Head width about 5 mm. Face very broad, rather produced in profile, entirely yellow, with black pile dorsally and laterally, pale pilose medially. Mouth edge mostly yellow. Gena yellow, pale pilose. Eye with pale pile. Area of enlarged facets distinct with marked border. Anterior angle of approximation of eyes wide, about 135°. Ocellar triangle equilateral. Pile on vertical triangle pale. Frontal triangle yellow, inflated, black pilose laterally and pale pilose in median line over antennae. Antenna brown; basoflagellomere dark, paler ventrally. Occiput densely whitish pollinose, with several rows of pale pile, rather broader than in, for example, *S. pyrastri*. Occiput dorsally with row of rather black cilia.

Thorax (Figure 5a,b). Black, postpronotum and anterior part of notopleuron pale, densely pale pilose, uniformly long. Pleuron black, yellow pilose and yellow microtrichose. Scutellum entirely yellow,

shiny medially, yellow microtrichose on lateral margin; scutellar fringe with long yellow pile. Metasternum bare. Plumula pale. Halter pale. Wing: microtrichia reduced as in other species of genus; alula bare. Vein R_{4+5} almost straight. Wing membrane beyond apical cross-veins rather narrow and irregularly undulated. Legs: entirely yellow, except coxae and trochanters black, and apical tarsomeres a bit darker, entirely pale pilose.

Abdomen (Figure 5a,b). Robust, about 6.8 mm long and broad (3.8 mm). Terga 3 and 4 circa two times broader than long (tergum 3 about 2 times broader; tergum 4 about 1.8 times broader). Tergum 1 shiny black, with blue iridescence. Terga 2–4 black, mate with black pollinosity, with two square yellow maculae not reaching the lateral margin (maculae on tergum 4 might reach lateral margin on antero-lateral corner of tergum), yellow pilose except some black pile on tergum 5 and genital segments. Maculae on terga 3 and 4 with anterior margin straight, but oblique. Tergum 4 with a yellow fascia on posterior margin. Tergum 5 mostly yellow with a medial dark macula. Sterna yellow, except a diffuse dark oval macula on sterna 2 and 3, yellow pilose. Male genitalia (Figure 5d–f): Rounded surstyli about as long as cerci. Hypandrium with a long, well-developed lingula (Figure 5e), longer than in male genitalia of *A. penai* (Figure 4f). Base of aedeagus (basiphallus) of the same shape as in other species of *Scaeva* with two teeth of similar size (Figure 5e). Distal part of aedeagus (distiphallus) cylindrical without basal bulge in lateral view. Superior lobe (postgonite) elongated with apical margin rounded. Superior lobe pointed dorsally, with anterodorsal corner triangular, and a remarkable tooth situated near distal margin of superior lobe (Figure 5e,f).

Material examined

CHILE: Coquimbo region, 5 miles N of Laguna Dam, 2438 m. (8000 ft.), 06.xii.1950, R. & M. Bacher [1♂, CAS, ZFMK-DIP-00022587].

Differential diagnosis

This species differs from *A. melanostoma* and *A. occidentalis* by having the orange-yellow mouth edge (black in *A. melanostoma* and *A. occidentalis*), frontal triangle black pilose with pale pilose medially (entirely black pilose in *A. melanostoma* and *A. occidentalis*), and a broader abdomen, with terga 3 and 4 two or more times broader than long (in *A. occidentalis* and *A. melanostoma* the abdomen is narrower, with terga 3 and 4 about 1.6–1.7 times broader than long). See differential diagnosis under *A. penai* for the differences between *A. patagoniensis* and *A. penai*.

3.2.3 | *Austroscaeva penai* (Marnef in Dušek & Láska, 1985) comb. nov.

Figures 3b,c and 4a,b,d–g

Description of the male

Robust, large species. Body length 15 mm; wing length 10.5 mm. Head (Figure 4a,b). Head width about 4.5 mm. Face very broad

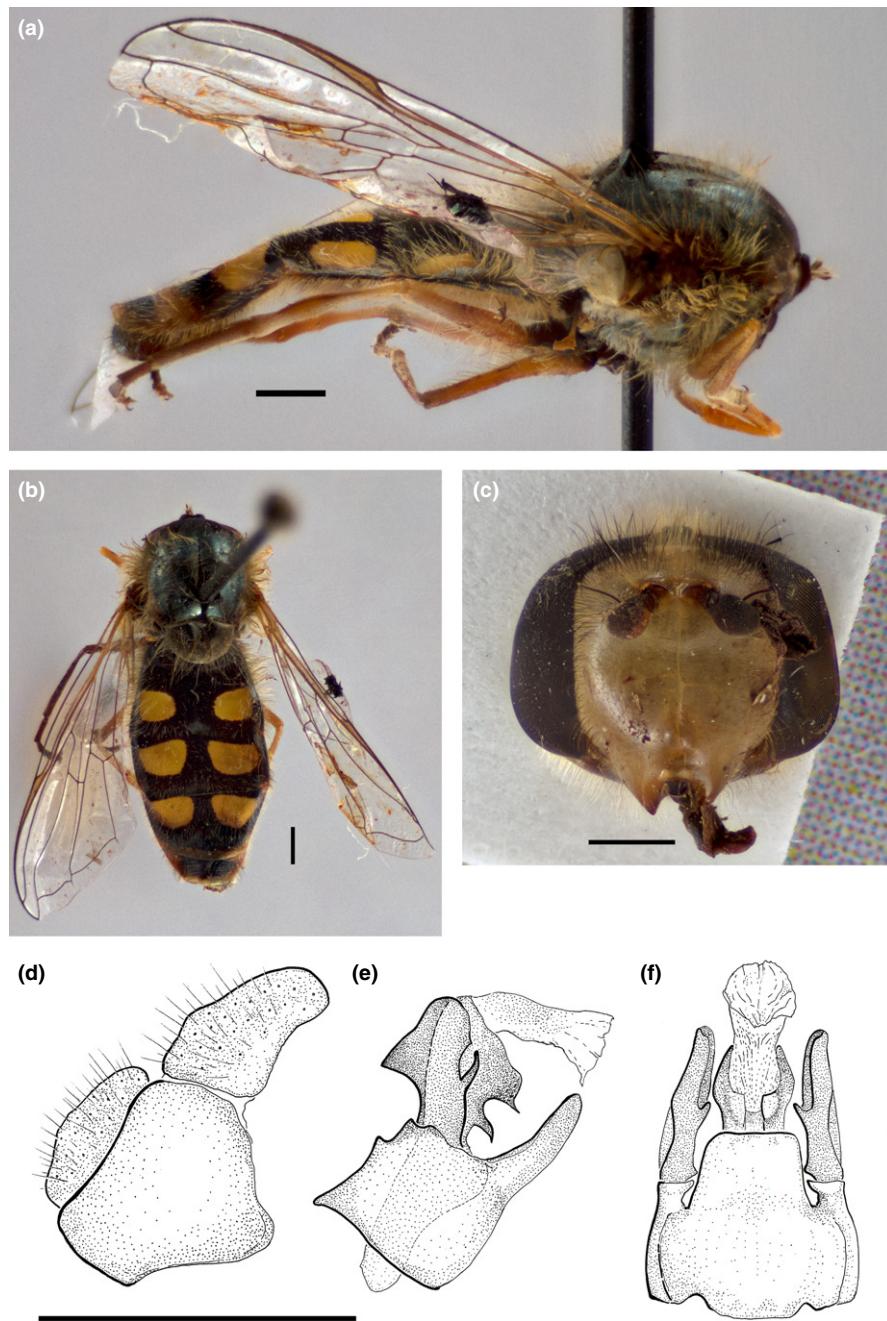


FIGURE 5 *Austroscaeva patagoniensis* (Kassebeer), male ZFMK-DIP-00022587: (a) Thorax and abdomen, lateral view. (b) Thorax and abdomen, dorsal view. Scales = 1 mm. (c) Head, frontal view. Scale = 1 mm. (d) Male genitalia, epandrium, lateral view. (e) Male genitalia, hypandrium, lateral view (f) Male genitalia, hypandrium, ventral view. Scale = 1 mm

occupying about 65% of head width, rather produced in profile, entirely yellow, with black pile dorsally and laterally, pale pilose ventrally. Mouth edge mostly yellow; clypeus very long (0.9 mm) and narrow (0.18 mm), broadened at base (0.25 mm). Gena yellow, pale pilose. Eye densely pilose, pile in dorsal part about 0.15 mm long. Area of enlarged facets distinct with marked border. Anterior angle of approximation of eyes wide, about 135°, posterior angle of approximation of eyes about 50°. Anterior ocellus about 0.75 mm distant from the apex of anterior angle of approximation of eyes. Pile on vertical triangle black on anterior 1/2, white on posterior 1/2. Occiput dorsally with row of rather black cilia. Frontal triangle yellow, inflated, with one brown macula at each antennal base, black pile laterally and pale pilose in median line over antennae. Antenna

brown; basoflagellomere dark, paler ventrally, 0.52 mm long and 0.5 mm wide; scape and pedicel 0.5 mm long together, arista 1 mm long. Occiput densely whitish pollinose, with several rows of pale pile, rather broader than in, for example, *S. pyrastri*.

Thorax (Figures 3b,c and 4b). Black, postpronotum and anterior part of notopleuron pale, densely pale pilose, uniformly long. Pleuron mostly black, except anterior anepisternum pale, posterior anepisternum pale on posterior 1/3, anepimeron yellow dorsally and posteriorly, katatergum yellow. Scutellum entirely yellow, black on anterolateral corners, pale pilose with some black pile on posterior margin; pile on disk 0.4–0.5 mm long, on posterior margin 0.75–0.85 mm long. Metasternum with several (about 15) long pale pile. Plumula pale. Halter pale. Wing: microtrichia reduced as in other

species of genus; alula bare. Vein R_{4+5} almost straight. Wing membrane beyond apical cross-veins rather narrow and irregularly undulated. Legs: coxae and trochanters black, femora pale except dark very basally (1/6 or less), entirely pale pilose, except several black setae on distal ends of tarsomeres.

Abdomen (Figures 3b,c and 4d). Robust, about 6.7 mm long and very broad (4.7 mm), equivalent 70% of the length of abdomen. Terga 3 and 4 more than two times broader than long (tergum 3 about 2.4 times broader; tergum 4 about 2.3 times broader). Terga 2–4 black with two yellow maculae reaching the lateral margin on anterolateral corner of tergum, yellow pilose except posterolateral corners of terga 2–5. Maculae on terga 3 and 4 with anterior margin slightly concave. Tergum 4 with a yellow fascia on posterior margin. Tergum 5 mostly yellow with a medial dark fascia. Sterna yellow, except a diffuse dark oval macula on sterna 2 and 3, yellow pilose. **Male genitalia** (Figure 4e–g): Like genitalia of other *Austroscaeva* species, most similar to *A. melanostoma* but a little larger. Epandrium broader than high (width about 0.75 mm, height about 0.5 mm). Rounded surstylos about as long as cerci. Hypandrium about as high as broad (0.53 mm) with angular distal lateral lobes in ventral view and with a well-developed lingula (Figure 4f). Base of aedeagus (basiphallus) not enlarged, of the same shape as in other species of *Scaeva* with two teeth of similar size (Figure 4f). Distal part of aedeagus (distiphallus) cylindrical without basal bulge in lateral view. Superior lobe (postgonite) about 0.3 mm high and 0.2 mm broad, forming rounded lobe dorsally in apical part (Figure 4f,g). Basal tooth on superior lobe small, almost inconspicuous; apical tooth distinct and broadly pointed, situated near distal margin of superior lobe.

Material examined

ARGENTINA: Neuquén, Cabecera E Lago Huechulafquen, 16.xii.1997, on *Phacelia* sp., G.G. Roitman & N.H. Montaldo [1♂, ZFMK, ZFMK-DIP-00019582].

Differential diagnosis

This species differs from *A. melanostoma* and *A. occidentalis* by having the orange-yellow mouth edge (black in *A. melanostoma* and *A. occidentalis*), metasternum pilose (metasternum bare in *A. melanostoma* and *A. occidentalis*), frontal triangle black pilose with pale pilose medially (entirely black pilose in *A. melanostoma* and *A. occidentalis*), and a broader abdomen, with terga 3 and 4 more than two times broader than long (in *A. occidentalis* and *A. melanostoma* the abdomen is narrower, with terga 3 and 4 about 1.6–1.7 times broader than long). From the male of the close species *A. patagoniensis*, this species differs as stated in the identification key by having more abundant pile on metasternum, male genitalia (Figures 4e–g and 5d–f), and by the abdominal pattern. Females of *A. penai* can easily be distinguished from females of *A. patagoniensis* by the frontal pilosity (pale pilose medially, black pilose laterally in *A. penai*, but uniformly black pilose in *A. patagoniensis*), mesonotal pilosity (uniformly long pile in *A. penai*, but long and very short pile in *A. patagoniensis*), and abdominal pattern (see Kassebeer, 1999).

3.2.4 | Identification key to the species of *Austroscaeva* gen. nov. (translated and adapted from Kassebeer, 1999)

1. Scutellum entirely dull, grey pollinose (Figure 1a). Male: eye angle about 120° (Figure 1a)..... *occidentalis* (Shannon)
 - Scutellum densely grey pollinose, dull, except shiny mesobasally in dorsal view (Figures 1b and 2b). Male: eye angle broader than 120° (Figures 2c and 4b) 2
 2. Mouth edge and gena black (Figure 2d). Maculae on terga 2–4 with transverse striae of very fine pale pollinosity, in oblique or lateral view (Figures 2b and 3a). Metasternum bare. Smaller species (8.3 to 13.7 mm) *melanostoma* (Macquart)
 - Mouth edge and gena predominantly orange-yellow (Figures 3c and 5c). Maculae on terga 2–4 without silvery gray pollinosity striae (Figures 3b,c and 5a). Metasternum usually pilose. Large species (12.1 to 15.3 mm) 3
 3. Maculae on terga 2–4 large, more less square with anterior margin almost straight and oblique, not reaching lateral margins (Figures 4c and 5b). Metasternum bare or only with a few long pile. Alula with a group of microtrichia basally. Female: frontal triangle uniformly black pilose (see Figures 2a,c,d); mesonotum with long and very short pile. Male: frons pale pilose medially, black pilose laterally (Figure 5c). Male genitalia as in Figures 5d–f.
 - *patagoniensis* (Kassebeer)
 - Maculae on terga 2–4 narrower, elongated, with anterior margin slightly concave, reaching the lateral margins on the anterolateral corner (Figures 3b and 4d). Metasternum with numerous long pile. Alula bare. Male and female: frons or frontal triangle pale pilose medially, black pilose laterally (Figure 4a,b). Female: mesonotum with uniformly long pile (Figure 3c). Male genitalia as in Figure 4e–g. *penai* (Marnef)

4 | DISCUSSION

The taxon sampling constricts our discussion on the tribal relationships within Syrphinae or on the placement of certain genera because this was not the major goal of our study. Nevertheless, present results agree with earlier phylogenetic molecular works on Syrphidae in general (Mengual, 2015a; Mengual et al., 2008a,b, 2015; Young et al., 2016) and indicate that the traditional systematic arrangement of Syrphinae (with current tribes Bacchini, Syrphini, Paragini, and Toxomerini) is in need of a revision. The tribe Bacchini was resolved in several clades and Paragini was placed within Syrphini, a result reported in the last phylogenetic analyses on Syrphidae (Mengual, 2015a; Mengual et al., 2008a, 2015; Young et al., 2016).

The phylogenetic relationships of the genus *Paragus* have always been controversial and unclear (Dušek & Láska, 1967; Shatalkin, 1975; Vujić, Stáhls, Rojo, Radenković, & Šimic, 2008). Mengual et al. (2008a) resolved it as sister group of *Allobaccha* Curran, 1928, but this placement was probably an artifact as a result of a long-branch attraction effect (Mengual, 2015a). Mengual et al. (2015), using

molecular and adult morphological characters, recovered *Paragus* as the sister group of the *Scaeva-Eupeodes* clade. The same result was obtained by Young et al. (2016) using anchored-hybrid enrichment data and in the present study. This position is in agreement with Rotheray and Gilbert (1999), who analyzed larval morphological characters. Based on the current evidence, *Paragus* is largely corroborated as the sister group of the *Scaeva-Eupeodes* clade.

Our results defined a *Scaeva-Eupeodes* clade with two major subclades. On one hand, the genera *Eupeodes* (including *Macrosyrphus*), *Lapposyrphus*, and *Betasyrphus*, but without clear relationships among them. On the other hand, the genera *Simosyrphus*, *Pseudodoros*, *Ischiodon*, *Scaeva*, *Notosyrphus*, *Austroscaeva* gen. nov., and *Dioprosopa*, with the last three genera forming a well-supported monophyletic group and the set of the other four genera resolved as a clade. Our data supported a new genus concept of *Eupeodes*, with only two subgenera, that is, *Eupeodes* s. str. and *Macrosyrphus*, which is the sister group of all the rest *Eupeodes* species. There was no evidence to support the subgenus *Metasyrphus*, as the single species of *Eupeodes* (*Eupeodes*) was resolved in the middle of the *Eupeodes* (*Metasyrphus*) species, and *Eupeodes* (*Metasyrphus*) *corollae* (Fabricius, 1794) was resolved as the sister group of the remaining species except *E. (Macrosyrphus) confrater*. The *Eupeodes* subdivision by Vockeroth (1969), with *Metasyrphus* and *Eupeodes*, is not supported. He mentioned three species groups within *Metasyrphus*: 1) the *corollae* group with only one species, *E. corollae*, that differs by the enlarged genitalia; 2) the *confrater* group, again with a single species and several undescribed ones, which refers to the subgenus *Macrosyrphus*; and 3) the *luniger* species groups, including all the other species of the genus. Vockeroth (1969) only kept in *Eupeodes* its type species, *E. volucris*. A later concept of *Eupeodes* by Vockeroth (1973, 1986) with *Macrosyrphus* and *Metasyrphus* as synonyms is very close to our results. Regarding *Macrosyrphus*, its position was quite well supported (BS = 89) with a PP = 0.93, but its ranking as a synonym of *Eupeodes*, as a subgenus or as a valid genus, seems only a subjective opinion.

Lapposyrphus is a separate taxon and a valid genus always recovered as an independent lineage from *Eupeodes* in previous molecular studies (Mengual, 2015a; Mengual et al., 2008a). It is most likely related to *Eupeodes* and *Betasyrphus*, although our analysis did not resolve its relationships among them (Figures 1 and S2). Another interesting data source to separate these taxa is their karyology. As in *Scaeva* and *Austroscaeva* gen. nov., the number of chromosomes of *Lapposyrphus* and *Eupeodes* (including *Metasyrphus*) is different (Boyes et al., 1971). *Lapposyrphus lapponicus* has five pairs of chromosomes plus a small XY pair, while *Eupeodes* species have four pairs plus XY (Boyes et al., 1971). It must be noted that *Syrphus aberrantis* placed under *Lapposyrphus* by Vockeroth (1969) has only four pairs of chromosomes as all the studied species of *Eupeodes*. The placement of *S. aberrantis* needs further studies to corroborate its generic affinities.

Vockeroth (1969), however, suggested that *Betasyrphus* was probably related to those genera with a well-developed lingula and a margined abdomen (*Syrphus*, *Epistrophe*, *Dasysyrphus* Enderlein, 1938, *Scaeva* and *Eupeodes*, as *Metasyrphus*). Rotheray and Gilbert (1999) resolved *Betasyrphus* as sister to *Episyphus* based on larval

morphological characters, but Mazánek, Láska, Bičík, Dušek, and Novotný (1999) pointed out the similarity of *Betasyrphus* puparia to those of *Scaeva* and *Eupeodes*. More recently, Young et al. (2016) recovered *Betasyrphus* as sister group of *Scaeva*. Our results placed *Betasyrphus* either as sister group of *Eupeodes* (PP = 0.90; Figure S2) or as sister group of the rest of the *Scaeva-Eupeodes* clade without support (Figure 1).

There is a Neotropical radiation within the *Scaeva-Eupeodes* clade. All the Neotropical taxa, except the Neotropical species *Eupeodes rojasii* Marnef (1999), were resolved in a well-supported clade (BS = 95) with a PP = 1 as (*Notosyrphus* + (*Dioprosopa* + *Austroscaeva*)). Vockeroth (1969) stated that *Notosyrphus* was certainly related to *Dasysyrphus*, although it shared the pilosity pattern of the katepisternum and the reduction in the wing microtrichia with *Scaeva*. Present results did not support a close relationship of *Notosyrphus* with *Dasysyrphus*, but with other Neotropical taxa of the *Scaeva-Eupeodes* clade.

Hull (1949) erected *Dioprosopa* as a new subgenus of *Baccha* Fabricius, 1805 for the species *Syrphus clavatus* Fabricius, 1794 based on the forward produced face. Thompson, Vockeroth, and Sedman (1976) synonymized *Dioprosopa* under *Pseudodoros*, although the distribution of *Dioprosopa* (New World) does not overlap with the geographic distribution of *Pseudodoros* (West Mediterranean, Iran, and Afrotropical region) (Dirickx, 1994; Gilasian, Vujić, Hauser, & Parhami-Araghi, 2017; Thompson, 2013; Van Eck & Makris, 2016). In his very detailed revisionary work, Kassebeer (2000) described a new species of *Dioprosopa* and explained and illustrated the differences between *Dioprosopa* and *Pseudodoros*. Mengual et al. (2008a) listed *Dioprosopa* as a subgenus of *Pseudodoros* and recovered *Dioprosopa* as sister group of (*Ischiodon* + *Scaeva*), but Mengual (2015) resolved *Dioprosopa* together with *Lapposyrphus* as sister group of the *Scaeva-Eupeodes* clade. Albeit some authors consider the separation of *Dioprosopa* and *Pseudodoros* an "excessive splitting" (Sinclair, Thompson, & Wyatt, 2016), the taxa are not closely related. Present results did confirm the validity of both as separate taxa with generic rank, and most importantly, the placement of *Pseudodoros* in our results helped to solve the problem between *Ischiodon* and *Simosyrphus*.

The genus *Ischiodon* was synonymized under *Simosyrphus* based on the similar larvae and puparia and the sister group relationship of these two taxa based on part of the COI gene (Láska et al., 2006). This close relationship of *Ischiodon* and *Simosyrphus* was also noted by Vockeroth (1969) and reported by Mengual (2015a). However, the addition of *Pseudodoros* in the molecular study revealed that both taxa are valid and corroborated the study of Kassebeer (2000), who considered *Pseudodoros* and *Dioprosopa* as separate genera. Thus, we resurrect the genus *Ischiodon* as a separate taxon from *Simosyrphus* with generic rank.

The three species groups of *Scaeva* as defined by Dušek and Láska (1985) were recovered in our analysis. Neotropical species were resolved as sister group of *Dioprosopa*, and a new genus, *Austroscaeva* gen. nov., has been erected for them. The other two species groups concur with the suggested *Scaeva* subgenera by Láska et al. (2013). Subgenera *Scaeva* s. str. and *Semiscaeva* were resolved with high support (BS = 100) and a PP = 1, but the relationship among these two

subgenera and the clade (*Simosyrphus* + (*Pseudodoros* + *Ischiodon*)) was not. ML tree (Figure 1) did resolve *Scaeava* s. str. as the sister group of (*Simosyrphus* + (*Pseudodoros* + *Ischiodon*)) (BS = 51), in the same way as Mengual et al. (2008a) and Mengual (2015a), but the Bayesian inference placed *Scaeava* s. str. and *Semiscaeva* as sister group (PP = 0.63). The support is too low to make conclusions, and both placements seem plausible with the current evidence. Among the studied *Scaeava* species, the placement of *S. mecogramma* (Bigot, 1860) must be further discussed. Vockeroth (1969) did not study this species, and most of the previous identification keys to genera did not key properly out this taxon (Speight, 2016). This is a very peculiar *Scaeava* species with yellow fascia on abdominal terga 3 and 4, instead of the typical oblique and often lunulate abdominal maculae; so distinct from other *Scaeava* species that even Kuznetsov (1985) erected a subgenus only for it. Speight (2016) argued that *S. mecogramma* shared only one character with the other *Scaeava* species, the postero-lateral continuity between the dorsal and ventral pile patches on the katepisternum, but this character also occurs in other genera, such as *Dasysyrphus*. In his argumentation, Speight (2016) doubted about the generic affinity of *S. mecogramma* and proposed a closer relationship of this species with *Betasyrphus*. Dušek and Láska (1985) and Láska et al. (2013) included *S. mecogramma* in the subgenus *Semiscaeva* (equivalent to the *selenitica* species group) and our results agreed with this placement.

During our study, we found two species names to refer to the same taxon, that is, *Scaeava lunata* (Wiedemann, 1830) and *Scaeava opimia* (Walker, 1852). There are two valid and different species originally described as *Syrphus lunatus*: *Syrphus lunatus* Fabricius, 1794 [currently *Eumerus lunatus* (Fabricius, 1794)], and *Syrphus lunatus* Wiedemann, 1830 [currently *Scaeava opimia* (Walker, 1852)]. Following the articles 57.2 and 60.2, a junior primary homonym is permanently invalid and has to be replaced by the oldest valid synonym if available, with its own authorship and date. In such case, *Syrphus lunatus* Wiedemann, 1830 is invalid, and its synonym *Syrphus opimus* Walker, 1852 must be used for this valid taxon as *Scaeava opimia* (Walker, 1852) (Dušek & Láska, 1985; Thompson, 2013).

As a novelty based on molecular characters, and outside the *Scaeava-Eupeodes* clade, our results recovered the genus *Doros* as sister group of *Xanthogramma*. Both genera resemble morphologically, and this relationship has been already suggested based on larval morphological characters (Rotheray & Gilbert, 1999) and on adult and genital characters (Dušek & Láska, 1967; Shatalkin, 1975). *Olbiosyrphus* Mik, 1897 was erected for *Syrphus laetus* Fabricius, 1794 (= *Xanthogramma laetum*) based on the presence of pile on eyes. Present results did not support the separation between *Xanthogramma* and *Olbiosyrphus* but agreed with Vockeroth (1969) who synonymized *Olbiosyrphus* under *Xanthogramma*.

5 | CONCLUSION

The relationships of the *Scaeava-Eupeodes* clade of genera were studied, and the monophyly of all the genera was well supported, except

for *Scaeava* and *Eupeodes* (*Macrosyrphus*) as part of *Eupeodes*. The two proposed subgenera of *Scaeava* by Láska et al. (2006), that is, *Scaeava* and *Semiscaeva*, were resolved as monophyletic groups with high support but not necessarily as sister groups. *Scaeava* subgenera were placed together with the clade (*Simosyrphus* + (*Pseudodoros* + *Ischiodon*)) in the same well-supported group, although the relationships between the *Scaeava* subgenera and this clade of genera were resolved with very low support.

Subgeneric division of *Eupeodes* should include only two taxa, *Eupeodes* s. str. and *Macrosyrphus*. *Betasyrphus*, *Lapposyrphus*, and *Eupeodes* were resolved as related, and our analysis resulted in two other very well-supported clades, that is, all Neotropical genera in one hand, and *Scaeava*, *Simosyrphus*, *Pseudodoros*, and *Ischiodon* on the other hand. Based on adult morphological characters and the present molecular results, a new genus was erected for the Neotropical species previously placed within *Scaeava*, namely *Austroscaeava* gen. nov. Despite the well-supported monophyly of each genus, the relationships among the genera belonging to the *Scaeava-Eupeodes* clade need further study as the support values for some nodes were very low. At the same time, we hope that immature stages of *Austroscaeava* gen. nov. become available to study their morphology and the biology of these Neotropical species, resulting in a better understanding of their phylogenetic relationships.

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SUPPORTING INFORMATION

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