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The systematic position and phylogenetic relationships of *Asiobaccha* Violovitsh (Diptera, Syrphidae)

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ABSTRACT

The placement and phylogenetic relationships of *Asiobaccha* were explored using molecular evidence. The mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI) and the nuclear 28S and 18S ribosomal RNA genes were analysed using parsimony, Bayesian inference and Maximum Likelihood. Two alignments approaches were used for rRNA genes: a multiple sequence alignment software, MAFFT, and their secondary structure. The present results do not place *Asiobaccha* close to *Baccha* or *Allobaccha*, which are placed in different evolutionary lineages, but close to *Episyrphus* and *Meliscaeva*. The relationship among these three genera is not fully resolved. Morphological characters are discussed and *Asiobaccha* stat. rev. is proposed as a valid genus.

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Introduction

Flower flies (Diptera: Syrphidae) comprise over 6000 described species (Thompson, 2013) with fascinating and diverse natural histories (Rotheray and Gilbert, 2011). These excellent mimics of aculeate Hymenoptera feed on pollen and nectar as adults and are important pollinators in natural ecosystems and crops (Pérez-Bañón et al., 2003; Ssymank et al., 2008; Ssymank and Kearns, 2009). Larval stages of this family exhibit a very diverse array of feeding modes with complex morphological and behavioural adaptations, such as predation, phytophagy, mycophagy and saprophagy (the famous rat-tailed maggots) (Rotheray and Gilbert, 1999; Rotheray et al., 2000; Nishida et al., 2003; Weng and Rotheray, 2008; Reemer and Rotheray, 2009; Ureña and Hanson, 2010).

Among the subfamily Syrphinae, the genus *Baccha* Fabricius, 1805 is easy to recognise in the Holarctic Region by its dark coloration, small size and very elongate, wasp-waisted abdomen. The notion of the genus *Baccha* has changed enormously since its original description. The concept of previous authors was a large, diverse group of flies mostly with petiolate abdomen, partially yellow face, and bare metasternum with worldwide distribution. Nowadays, *Baccha* is restricted a small group of species with simple unsegmented aedeagus (Thompson, 1981). Many species originally described as *Baccha* belong to several genera, such as *Ocyptamus* Macquart, 1834, *Pseudodoros* Becker, 1903, *Eosalpingogaster* Hull, 1949, *Leucopodella* Hull, 1949, *Toxomerus* Macquart, 1855, *Meliscaeva* Frey, 1946, *Allobaccha* Curran, 1928, *Asiobaccha* Violovitsh, 1976, *Spheginobaccha* Meijere, 1908, and *Baccha* (Thompson, 1981, 2013). But even more genera were mixed and/or confused with *Baccha* as some researchers modified the concept of this genus. If this did not create enough confusion, earlier authors started to describe new taxa using the word "baccha" in their new names, i.e. *Rhinobaccha* Meijere, 1908, *Bacchiopsis* Matsumura, 1916 (jun. syn. of *Doros* Meigen, 1803), *Pelecinobaccha* Shannon, 1927, *Atylobaccha* Hull, 1949, *Aulacibaccha* Hull, 1949, or *Orphnabaccha* Hull, 1949 (the last four are synonymised under *Ocyptamus*).

Baccha belongs to the tribe Bacchini, but the limits and contents of the tribe Bacchini, as part of Syrphinae, have been always questioned (see discussion in Mengual et al., 2008a). Vockeroth (1969) considered this tribe an artificial aggregation of forms with petiolate abdomen. It seems possible that only the genus *Baccha* s. str. might form Bacchini (Mengual et al., 2008a). Other genera with petiolate abdomen, e.g. *Allobaccha*, *Asiobaccha*, and *Ocyptamus*, belong to the tribe Syrphini.

Asiobaccha Violovitsh, 1976 comprises seven species distributed in the Oriental, Australian and Oceanian Zoogeographic Regions (Thompson, 2013), extending into the Sino-Japanese Region (sensu Holt et al., 2013). Violovitsh (1976) proposed *Asiobaccha* as a new subgenus of *Baccha* for the species *Baccha nubilipennis* Austen, 1893. He used the postmetacoxal bridge to separate both subgenera, *Asiobaccha* and *Baccha* s. str. *Baccha* species have a well-sclerotised postmetacoxal bridge, which means metaepisterna are elongated behind metacoxae and connected medially, while *Asiobaccha* has an incomplete postmetacoxal bridge, presenting a membrane behind metacoxae and sternite 1 reduced.

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

Taxon	Lab code	Label information	Accession no COI	Accession no 28S	Accession no 18S
Allobaccha sapphirina (Wiedemann, 1830)	MZH_S87	Thailand: Chiang Mai, iv.2001. Leg.: D. Quicke & N. Laurenne. Det.: F.C. Thompson.	EF127349	EF127430	EU409230
Allobaccha sp.1	ZFMK_XM141	Vietnam: PN Tam Dao, Malaise trap, 15-23.vi.2011. Leg.: S.W. Lingafelter. Det.: X. Mengual.	KM270848	KM270817	KM270764
Allobaccha sp.2	ZFMK_XM228	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Kiulu (bamboo forest), 570 m., 5°52′34″N 116°15′00″E, malaise, 18-24.x.2011. Leg.: S. Gaimari & M. Hauser. Det.: X. Mengual.	KM270849	KM270818	KM270765
Allobaccha sp.3	MZH_S150	Tanzania: Amani Hills, 2001. Det.: G. Ståhls.	EF127347	EF127428	KM270766
Allobaccha sp.4	MZH_XP177	East Timor: Maliana, road verge in town. 8°58′51″S 125°13′08″E, 200 m., 11.xii.2005. Leg.: M.P. van Zuijen. Det.: X. Mengual.	EU409120	EU409175	EU409229
Antillus ascitus Vockeroth, 1969	MZH_XP33	Dominican Republic: Pedernales Prov., PN Sierra de Baoruco las Abejas. 18°09.011′N 71° 37.342′W, 1150 m., 18.vi.2005. Leg.: N.E. Woodley. Det.: F.C. Thompson.	EU241713	EU241761	EU241810
Allograpta neotropica Curran, 1936	MZH_XP59	Colombia: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2175 m., 15.ii.2006. Leg.: X. Mengual. Det.: X. Mengual.	EU241733	EU241780	EU241831
Allograpta obliqua (Say, 1823)	MZH_XP38	USA: Utah, Garfield Co., Alvoy Wash. 7 km S Escalante. 37°42.5′N 111°37.8′W. 1990 m. 29.vi.2002. Leg.: M.E. Irwin & F. Parker. Det.: F.C. Thompson.	EF127310	EF127389	EU241833
Argentinomyia longicornis (Walker, 1836)	MZH_XP95	Colombia: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2175 m., 15.ii.2006. Leg.: X. Mengual. Det.: X. Mengual.	KM270850	KM270819	KM270767
Asarkina sp.1	ZFMK_XM218	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Kipandi Butterfly Park, 720 m., 5°52′20″N 116°14′53″E, 14-24.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270851	KM270820	KM270768
Asarkina ericetorum (Fabricius, 1781)	MZH_S222	Kenya: Kakamega forest, 5.xii.1995, 0°17.13′N 34°56.32′E. Leg.: Earthwatch Team 6. Det.: G. Ståhls.	EF127353	EF127434	EU241837
Asarkina fulva Hull, 1941	MZH_XP100	Madagascar: Fianarantsoa Prov., Ranomafana N.P., Talatakely region, 22.xi.2004. Leg.: X. Mengual. Det.: X. Mengual.	EU241738	EU241785	EU241838
Asarkina sp. 2	ZFMK_XM126	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.	KM270852	KM270821	KM270769
Asarkina sp. 3	MZH_XP99	Madagascar: Fianarantsoa Prov., Ranomafana N.P., Talatakely region, 27.xi.2004. Leg.: X. Mengual. Det.: X. Mengual.	EU241739	EU241786	EU241839
Asiobaccha 88-16 Thompson, in litt.	CNC_JSM218	Australia: Sanford Valley, Cedar Creek, 15.iv.2000. Leg.: M. Mathieson, J. & A. Skevington. Det.: X. Mengual.	KM270853	KM270822	KM270770
Asiobaccha n.sp.	ZFMK_XM127	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.	KM270854	KM270823	KM270771
Asiobaccha virtuosa (Curran, 1928)	ZFMK_XM224	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Gunung Alab, 1660 m., 5°48′47″N 116°20′16″E, 14.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270855	KM270824	KM270772
Baccha elongata (Fabricius, 1775)	MZH_Y242	Finland: Ta, Vesijako, vii.2004, malaise trap. Leg.: J. Jakovlev. Det.: G. Ståhls.	EF127326	EF127407	EU431540
Baccha sp.	ZFMK_XM121	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Ulu Kalanggan, Diptero-carp tree, 5°51′23″N 116°18′29″E, 1350 m., 20.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270856	KM270825	KM270773
Chrysotoxum cautum (Harris, 1776)	MZH_XP166	Greece: Lesvos Island, Agiasos, 08.v.2007. Leg.: G. Ståhls. Det.: G. Ståhls.	KM270857	KM270826	KM270774
Chrysotoxum intermedium (Meigen, 1822)	MZH_XP154	Spain: Alicante, Ibi, E.B. Torretes, 18.v.2007. Leg.: X. Mengual. Det.: X. Mengual.	EU431498	EU431466	EU431541
Citrogramma currani Ghorpadé, 2012	ZFMK_XM128	Vietnam: Cao Bang Prov., Phia Oac Mt. road, 1422 m., 22°33.972′N 105°52.238′E, general daytime collecting, 24.v-5.vi.2011. Leg.: S. Lingafelter, E. Jendek, E. Vives, P. Hong Thai. Det.: X. Mengual.	KM270858	–	–
Citrogramma fascipleurum (Curran, 1931)	ZFMK_XM120	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Long Gong Kugan, 1630 m., 5°49′44″N 116°19′37″E, 22.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270859	KM270827	KM270775
Claraplumula latifacies Shannon, 1927	ZFMK_XM139	Colombia: Antioquia, Belmira, Paramo Belmira, 3241 m., Jana arbusto, 06°38′43.9″S 75°40′10″W, 8.i.2011. Leg.: A.L. Montoya. Det.: F.C. Thompson.	KM270860	KM270828	KM270776
Dasysyrphus albostriatus (Fallén, 1817)	MZH_S565	The Netherlands: Leiden, Meijendel dune area, 5.ix.2005. Leg.: excursion participants. Det.: G. Ståhls.	EF127323	EF127402	EU431542
Dasysyrphus lenensis Bagatshanova, 1980	ZFMK_D006	Germany: Nordrhein-Westfalen. TK: 5403, R 2521143, H 5596510. Döppeskaul 2009, Malaise-Falle, Bachtal, Nebenbach des Fuhrtsbachtals, FFH DE-5403-301. NP Eifel, 18.v-01.vi.2009. Leg.: J. Esser. Det.: A. Ssymank.	KM270861	KM270829	KM270777
Didea intermedia Loew, 1854	MZH_S90	Finland. Det.: G. Ståhls.	EF127336	EF127418	EU431543
Dideoides coquilletti (van der Goot, 1964)	MZH_XP8	South Korea: Gangweon-do, Weonju-si, Maeji-ri, Yonsei Univ. Campus, 4.x.1999. Leg.: C.H. Park. Det.: H.Y. Han & D.S. Choi.	EF127293	EF127373	KM270778
Dideopsis aegrota (Fabricius, 1805)	ZFMK_XM225	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.	KM270862	KM270830	KM270779
Eosalpingogaster conopida (Philippi, 1865)	MZH_Y214	Chile: Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos, malaise in stable dunes, 58 m., 31°50.96′S, 71°29.60′W, 28.xii.2003-8.i.2004. Leg.: M.E. Irwin. Det.: F.C. Thompson.	EF127359	EF127440	EU241850
Eosalpingogaster umbra Mengual & Thompson, 2011	MZH_Y1035	Venezuela: Lara, P.N. Cerro Saroche, Sector Batatal. 700 m. 15-19.vii.2008. Trampa amarilla. Leg.: E. Arcaya. Det.: X. Mengual.	HQ845759	HQ845762	HQ845767
Epistrophe nitidicollis (Meigen, 1822)	MZH_S61	Finland: Liesjärvi, 11.vi.2000. Leg.: G. Ståhls. Det.: G. Ståhls.	EF127325	EF127406	KM270780
Epistrophella euchroma (Kowarz, 1885)	MZH_S559	Czech Republic: Bohemia, PLA distr., Chrudim Hermanuv mestec, park, 3.vi.2005. Leg.: L. Mazanek. Det.: L. Mazanek.	EF127315	EF501964	KM270781
Episyrphus balteatus (De Geer, 1776)	MZH_XP153	Spain: Alicante, P.N. Marjal Pego-Oliva, Muntanyeta Verda. 19.v.2007. Leg.: X. Mengual. Det.: X. Mengual.	EU241740	EU241788	EU241840

Table 1 (*continued*)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S	Accession no 18S
Episyrphus divertens (Walker, 1856)	ZFMK_XM123	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.	KM270863	KM270831	KM270782
Episyrphus stuckenbergi (Doesburg, 1957)	MZH_XP52	Madagascar: Fianarantsoa Prov., road from Valbio to Ranomafana city, 22.xi.2004. Leg.: X. Mengual. Det.: X. Mengual.	EF127319	EF127398	EU241841
Episyrphus obligatus (Curran, 1931)	ZFMK_XM140	Vietnam: Cao Bang Prov., Phia Oac, near Phja-Den, 22°32.4′N 105°52.0′E, 948 m., canopy Malaise trap, 26.v-6.vi.2011. Leg.: S. Lingafelter. Det.: X. Mengual.	KM270864	KM270832	KM270783
Episyrphus sp.	ZFMK_XM227	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Gunung Alab, 1660 m., 14.x.2011, 5°48′47″N 116°20′16″E. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270865	KM270833	KM270784
Episyrphus viridaureus (Wiedemann, 1824)	ZFMK_XM119	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Long Gong Kugan, 1630 m., 5°49′44″N 116°19′37″E, 22.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270866	KM270834	KM270785
Episyrphus viridaureus (Wiedemann, 1824)	ZFMK_XM125	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Long Gong Kugan, 1630 m., 5°49′44″N 116°19′37″E, 22.x.2011. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270867	KM270835	KM270786
Episyrphus viridaureus (Wiedemann, 1824)	MZH_XP173	East Timor: Maliana, road verge in town. 8°58′51″S 125°13′08″E, 200 m., 11.xii.2005. Leg.: M.P. van Zuijen. Det.: X. Mengual.	EU241741	EU241789	EU241842
Eriozona syrphoides (Fallén, 1817)	MZH_Y184	Russia: Gornyi Altai, Turotshakskii r-kordon obogo, 950 m, 30.vi.2003. Leg. Krolatscheva. Det.: G. Ståhls.	EF127358	EF127439	EU431544
Eupeodes (*Eupeodes*) *volucris* Osten Sacken, 1877	MZH_XP43	USA: NE, Cass Co., Louisville Platte River Sp., 19.v.2005. Leg. W. van Steenis. Det. W. van Steenis.	KM270868	KM270836	KM270787
Eupeodes (*Macrosyrphus*) *confrater* (Wiedemann, 1830)	MZH_Y101	South Korea: Gyeongsangbuk-do, Yeongju Sunheung-myeon, 8.vi.2002. Leg.: D.S. Choi. Det.: G. Ståhls.	EF127355	EF127436	KM270788
Eupeodes (*Metasyrphus*) *corollae* (Fabricius, 1794)	MZH_XP141	Spain: Alicante, Aspe, Partida Tolomó, 07.ii.2006. Leg.: P. Hurtado. Det.: X. Mengual.	EU431499	EU431467	EU431546
Exallandra cinctifacies (Speiser, 1910)	MZH_XP148	Kenya: Aberdares Nat. Park., 31.xii-14.i.2006, Malaise trap. Det.: F.C. Thompson.	EU241742	EU241790	EU241843
Fagisyrphus cinctus (Fallén, 1817)	MZH_S558	Czech Republic: Bohemia, PLA Kokorinsko, Vojtechov, 14.v.2005. Leg.: L. Mazanek. Det.: L. Mazanek.	KM270869	KM270837	KM270789
Fazia aff. *centropogonis* (Nishida, 2003)	MZH_XP151	Costa Rica: INBio code: 3430.	EU241715	EU241763	EU241812
Fazia micrura (Osten Sacken, 1877)	MZH_XP183	Venezuela: Aragua, P.N. Henri Pittier, Portachuelo, 1152 m., 26.i.2007, 10° 20.828′N 067° 41.309′W. Leg.: X. Mengual. Det.: X. Mengual.	EU241723	EU241771	EU241821
Ischiodon scutellaris (Fabricius, 1805)	MZH_S157	China: Hong Kong, Park, 7.x.2001. Leg.: D. Iliff. Det.: G. Ståhls.	AY603768	EF127429	KM270790
Lapposyrphus lapponicus (Zetterstedt, 1838)	MZH_S65	Czech Republic: 13.v.2000. Leg.: L. Mazanek. Det.: L. Mazanek.	DQ158897	DQ158897	KM270791
Leucopodella delicatula (Hull, 1943)	MZH_XP144	Colombia: Dpto Valle del Cauca, Cali, Cerro San Antonio, 2200 m., 15.ii.2006. Leg.: C. Gutiérrez. Det.: X. Mengual.	KM270870	KM270838	KM270792
Leucozona (*Ischyrosyrphus*) *glaucia* (Linnaeus, 1758)	MZH_XP5	Spain: Pyrenees, Aran Valley, nr Arties, 1500 m., 1.viii.2003. Leg. G. Ståhls. Det.: G. Ståhls.	EF127292	EF127372	KM270793
Leucozona (*Leucozona*) *lucorum* (Linnaeus, 1758)	MZH_S139	Italy: South Tirol, Val Venosta, vii.2001. Leg.: G. Ståhls. Det.: G. Ståhls.	EF127346	EF501965	EU431548
Megasyrphus laxus (Hull, 1925)	MZH_XP27	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.	EF127302	EF127381	KM270794
Melangyna (*Austrosyrphus*) *collatus* (Walker, 1852)	MZH_XP124	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.	KM270871	KM270839	KM270795
Melangyna (*Melangyna*) *lasiophthalma* (Zetterstedt, 1843)	MZH_Y5	Finland: N, Mäntsälän Mustametsä, 10.v.2003. Leg.: G. Ståhls. Det.: G. Ståhls.	EF127361	EF501966	KM270796
Melangyna (*Melangyna*) *subfasciata* (Curran, 1925)	MZH_XP28	Canada: Kluane, Whitehorse Airport, 135°05′E 60°45′N, 4.viii.2004. Leg.: W. van Steenis. Det.: W. van Steenis.	EF127303	EF127382	KM270797
Melanostoma annulipes (Macquart, 1842)	MZH_XP53	Madagascar: Fianarantsoa Prov., road from Valbio to Ranomafana, 25.xi.2004. Leg.: X. Mengual. Det.: X. Mengual.	EF127320	EF127399	KM270798
Melanostoma scalare (Fabricius, 1794)	MZH_Y441	Finland: Ok, Kuhmo, Lentuankoski, 15.viii.2006. Leg.: G. Ståhls. Det.: G. Ståhls.	EU431500	EU431468	EU431549
Meligramma triangulifera (Zetterstedt, 1843)	MZH_S560	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.	EF127316	EF501967	KM270799
Meligramma guttata (Fallén, 1817)	MZH_Y478	Finland: Ab, Mietoinen, Perkko, 6733:222, 21.vii.2004. Leg.: A. Haarto. Det.: G. Ståhls.	EF501960	EF501968	KM270800
Meliscaeva auricollis (Meigen, 1822)	MZH_S123	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Pérez. Det.: L. Mazanek.	EF127341	EF127423	EU241844
Meliscaeva cinctella (Zetterstedt, 1843)	MZH_S557	Czech Republic: Bohemia, PLA Jezerske mountains, Korenov, 12.vi.2005. Leg.: L. Mazanek. Det.: L. Mazanek.	EU241743	EU241791	EU241845
Meliscaeva sp.	ZFMK_XM226	Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Gunung Alab, 1660 m., 17.x.2011, 5°48′47″N 116°20′16″E, light. Leg.: M. Hauser & S. Gaimari. Det.: X. Mengual.	KM270872	KM270840	KM270801
Neocnemodon larusi (Vujić, 1999)	MZH_Y473	Finland: Ab, Karjalohja, Karkalinniemi, 66.81°N 24.8°E, 10.v.2006. Leg.: G. Ståhls. Det.: G. Ståhls.	EU431504	EU431472	EU431560
Neocnemodon vitripennis (Meigen, 1822)	MZH_Y211	Finland: N, Sibbo, Hindsby, 26.v.2004. Leg.: G. Ståhls. Det.: G. Ståhls.	EU431503	KM270845	EU431559
Ocyptamus (*Orphnabaccha*) *coeruleus* (Williston, 1891)	MZH_XP89	Colombia: Dpto. Cauca, Corrg. El Tambo, 20 De Julio, 2900 m., 6-8.iii.2006. Leg.: C. Prieto. Det.: X. Mengual.	EU409138	EU409193	EU409254
Ocyptamus (*Ocyptamus*) *funebris* Macquart, 1834	MZH_S487	Costa Rica: San José, Heredia, INBioparque, 15-21.i.2005, malaise trap. Det.: F.C. Thompson.	EF127364	EF127443	EU409242

(*continued on next page*)

Table 1 (*continued*)

Taxon	Lab code	Label information	Accession no COI	Accession no 28S	Accession no 18S
Ocyptamus (*Ocyptamus*) *melanorrhinus* (Philippi, 1865)	MZH_Y215	Chile: Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos, malaise in stable dunes, 28.xii.2003-8.i.2004; 58 m., 31°50.96′S 71°29.60′W. Leg.: M.E. Irwin. Det.: F.C. Thompson.	EF127360	EF127441	EU409248
Ocyptamus (*Hermesomyia*) *wulpianus* (Lynch Arribalzaga, 1891)	MZH_Y121	Argentina: Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash, 24°27.25′S 65°17.83′W, 1278 m., 27.x-14.xi.2003. Leg.: M.E. Irwin, F.D. Parker. Det.: F.C. Thompson.	EF127356	EF127437	EU241849
Ocyptamus (*Pipunculosyrphus*) *tiarella* (Hull, 1944)	MZH_XP176	Venezuela: Aragua, P.N. Henri Pittier, Portachuelo, 1152 m., 26.i.2007. 10°20.828′N 067°41.309′W. Leg.: A. Martínez. Det.: X. Mengual.	EU241744	EU241792	EU241846
Paragus (*Paragus*) *bicolor* (Fabricius, 1794)	MZH_S108	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Pérez. Det.: A. Vujić.	AY476857	AY476873	–
Paragus (*Serratoparagus*) *crenulatus* Thomson, 1869	MZH_S62	Malaysia: Sabah, Danum Valley, viii.1999. Det.: A. Vujić.	AY476862	AY476880	KM270802
Paragus (*Pandasyopthalmus*) *haemorrhous* Meigen, 1822	MZH_S48	Spain: Alicante, 2000. Leg.: A. Vujić. Det.: A. Vujić.	AY174470	AY476866	EU409259
Paragus (*Paragus*) *pecchiolii* Rondani, 1857	MZH_S71	Montenegro: Durmitor, 26.vi.2000. Leg.: A. Vujić. Det.: A. Vujić.	AY476844	AY476864	KM270803
Parasyrphus lineolus (Zetterstedt)	MZH_S137	Italy: South Tirol, Val Venosta, vii.2001. Leg.: G. Ståhls. Det.: L. Mazanek.	EF127342	EF127424	KM270804
Pipiza quadrimaculata (Panzer, 1804)	MZH_XP218	Finland: Ka, Joutseno, Riikanmaa. KKJ-Y coord.: 3591:6777, 05.vii.2007. Leg.: M.P. van Zuijen & W. & J. van Steenis. Det.: G. Ståhls.	EU431506	EU431474	EU431562
Pipizella viduata (Linnaeus, 1758)	MZH_XP121	Sweden: Ha Veinge motor-banan. RN 62718 13327, 17.VIII.2006. Leg.: N. Ryrholm	EU431507	EU431475	EU431563
Platycheirus albimanus (Fabricius, 1781)	MZH_E38	Sweden: 2000. Leg.: J. van Steenis. Det.: J. van Steenis	EF127351	EF127432	KM270805
Platycheirus nielseni Vockeroth, 1990	MZH_E36	Sweden: 2000. Leg.: J. van Steenis. Det.: J. van Steenis	EF127352	EF127433	KM270806
Pseudodoros (*Dioprosopa*) *clavatus* (Fabricius, 1794)	MZH_XP116	Mexico: Villa de Álvarez, Crta. Minatitlán, Colonia Burócratas, 23.viii.2006. Leg.: X. Mengual. Det.: X. Mengual.	KM270873	KM270841	KM270807
Rhinoprosopa lucifer Hull, 1943	MZH_XP79	Costa Rica, PN Tapantí, Site 2, 1500 m., 11.i.2005. G. Ståhls. Det.: X. Mengual.	EU241729	EU241776	EU241827
Rohdendorfia alpina Sack, 1938	MZH_G344	Italy: Stelvio Pass. Leg.: G. Ståhls. Det.: G. Ståhls.	EF127338	EF127420	EU431552
Salpingogaster cornuta Hull, 1944	MZH_XP78	Colombia: Dpto. Cauca, Corrg. El Tambo, 20 De Julio. 2900 m., 6-8.iii.2006. Leg.: C. Prieto. Det.: X. Mengual.	EU241746	EU241794	EU241851
Salpingogaster nigra Schiner, 1868	MZH_XP77	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.	EU241748	EU241796	EU241853
Salpingogaster pygophora Schiner, 1868	MZH_XP169	Venezuela: Edo. Aragua, P.N. Henri Pittier, Portachuelo, 1152 m., 10°20.828′N 067°41.309′W, 26.i.2007. Leg.: G. Ståhls. Det.: X. Mengual.	EU241749	EU241797	EU241854
Scaeva selenitica (Meigen, 1822)	MZH_S69	Czech Republic: distr. Ostrava, Polanecký les, 3.iv.2000. Leg.: T. Kuras. Det.: L. Mazanek.	AY603764	EF127404	KM270808
Scaeva pyrastri (Linnaeus, 1758)	ZFMK_D009	Germany: Nordrhein-Westfalen, Watchberg/Bonn, Oberbachem, Werthovener Weg,. FO: 7891 D, TK: 530842, 138 m, 27.vii.2012. Leg. A. Ssymank. Det. A. Ssymank.	KM270874	KM270842	KM270809
Simosyrphus grandicornis (Macquart, 1842)	MZH_XP125	Australia: Victoria, Mt. Buffalo NP, Dicksons Falls, AMG 55 481-5929, 1440 m., 29.i.2006. Leg.: W. van Steenis. Det.: W. van Steenis.	KM270875	KM270843	KM270810
Spazigaster ambulans (Fabricius, 1798)	MZH_S158	Austria: Imst. Leg.: J. van Steenis. Det.: J. van Steenis.	EF127350	EF127431	KM270811
Sphaerophoria loewi Zetterstedt, 1843	MZH_S273	Sweden: Upplands-Bro, 15.vi.2002. Leg.: H. Bartsch. Det.: G. Ståhls.	EF127318	EF127396	EU241856
Sphaerophoria rueppellii (Wiedemann, 1830)	MZH_S12	Spain: Alicante, 1999. Leg.: S. Rojo. Det.: S. Rojo.	EF127328	EF127409	EU241859
Sphaerophoria scripta (Linnaeus, 1758)	MZH_XP142	Spain: Alicante, Aspe. Partida Tolomó, 07.ii.2006. Leg.: P. Hurtado. Det.: X. Mengual.	EU241752	EU241800	EU241860
Syrphocheilosia claviventris (Strobl, 1910)	MZH_G327	Italy: South Tirol, Stelvio Pass, 28.vii.1999. Leg.: G. Ståhls. Det.: G. Ståhls.	EF127334	EF127415	KM270812
Syrphus shorae Fluke, 1950	MZH_XP158	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.	EU409136	EU409191	EU409252
Syrphus vitripennis Meigen, 1822	MZH_S53	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Perez. Det.: S. Rojo.	AY212797	AY261728	EU431554
Tiquicia zumbadoi (Thompson, 2003)	MZH_XP203	Costa Rica: San José Prov., Parque Nacional Chirripó, Llano Bonito, refugio, 2550 m., near *Centropogonis ferrugineus* plants, 09°27′08″N 083°32′20″W, 20.iv.2005. Leg.: Kenji Nishida. Det.: F.C. Thompson.	EU241714	EU241762	EU241811
Toxomerus apegiensis (Harbach, 1974)	MZH_XP184	Suriname: Distr. Brokopondo, Brownsberg National Park. Mazaroni Trail. 04°56′45″N 55°10′59″W, 04.iii.2006. Leg.: M. Reemer. Det.: M. Reemer.	EU409144	EU409199	EU409261
Toxomerus politus (Say, 1823)	MZH_XP82	Costa Rica: PN Tapantí, 1600 m., 12.i.2005. Leg.: X. Mengual. Det.: F.C. Thompson.	EU241755	EU241803	EU241863
Toxomerus watsoni (Curran, 1930)	MZH_XP188	Suriname: Distr. Para, Colareek (nr. Zanderij), 05°27′58″N 55°13′47″W, 23.iii.2006. Leg.: M. Reemer. Det.: M. Reemer.	EU409174	EU409228	EU409292
Xanthandrus plaumanni Fluke, 1937	MZH_XP98	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.	KM270876	KM270844	KM270813
Xanthogramma flavipes (Loew, 1863)	MZH_XP31	USA: NE: Cass Co., Louisville, Platte River SP. 19.v.2005. Leg. W. van Steenis. Det. W. van Steenis.	EF127306	EF127385	KM270814
Xanthogramma pedissequum (Harris, 1776)	MZH_S120	Greece: Lesbos island, iv.2001. Leg.: S. Rojo & C. Perez. Det.: S. Rojo.	EF127339	EF127421	EU431557
Outgroup					
Merodon equestris (Fabricius, 1794)	MZH_Y690	Finland: N, Askola, 12.i.2007. Leg. G. Ståhls. Det.: Ståhls.	EU431486	EU431455	EU431523
Myolepta dubia (Fabricius, 1805)	ZFMK_D012	Germany: Nordrhein-Westfalen, NP Eifel, FO: 7757R 2532921, H 5613552. Odenbachtal-Felskuppen, 320 m., 24.vi-08.vii.2010, Malaise-Falle. Leg.: J. Esser. Det. A. Ssymank.	KM270877	KM270846	KM270815
Graptomyza longirostris Wiedemann, 1820	ZFMK_D007	Rep. Singapore: Dairy Farm N.P., 02.v.2012. Leg.: V. Gowda. Det.: X. Menguasl.	KM270878	KM270847	KM270816

Since Violovitsh (1976), *Asiobaccha* species have been considered as *Baccha* (Huang, 1992; Thapa, 2000; Mitra et al., 2008; Ahmad and Nasim, 2009), as a subgenus of *Allobaccha* or as *Allobaccha* (Kapoor et al., 1979; Muraleedharan and Radhakrishnan, 1986; Peck, 1988; Cheng and Huang, 1997; Han and Choi, 2001; Huo et al., 2007; Huang and Cheng, 2012), or as a subgenus of *Episyrphus* Matsumura & Adachi, 1917 (Thompson and Vockeroth, 1989; Thompson and Rotheray, 1998; Carver et al., 2003; Mengual et al., 2008a). The systematics of this taxon was so unclear that Knutson et al. (1975) listed *Asiobaccha* species under the subgenera *Allobaccha* and *Baccha* as part of the genus *Baccha*. At the same time, *Allobaccha* has been recognised as a subgenus of *Baccha* or as a valid genus.

Some other authors expressed their doubts about where to place the species of *Asiobaccha*. Ichige (2009) in an excellent introduction explained the difficulty to separate *Baccha*, *Asiobaccha* and *Allobaccha*. He showed his doubts about placing *Asiobaccha nubilipennis* under *Episyrphus* and stated that the genitalia of *A. nubilipennis* are very different from other Bacchini taxa. Dirickx (2010) said that the bare postpronotum and the presence of some hairs in the anterior anepisternum seem decisive to classify this species among *Allobaccha*.

This current controversy about *Asiobaccha* affinities and placement prompted the author to make the present analysis. The aim of this study is double, firstly to study the phylogenetic relationships of *Asiobaccha* using molecular characters, i.e. the mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI), the D2-3 region of the nuclear ribosomal 28S rRNA gene and a small fragment of the nuclear ribosomal 18S rRNA gene; secondly, to examine the placement of this taxon among Syrphidae. To accomplish with these objectives several methodologies were used and compared, as well as two different alignment approaches for rRNA genes: the secondary structure of rRNA genes and the alignment provided by MAFFT. The use of COI in phylogenetics is common and wide among different animal groups (e.g. Wiegmann et al., 2011; Dimitrov et al., 2013; Schwentner et al., 2013; Cadahía et al., 2014), and 28S and 18S markers have been proved to be useful for phylogeny reconstruction (Hedin and Bond, 2006; Mallatt and Giribet, 2006; Gao et al., 2008; Krabberød et al., 2011), especially when their secondary structure is taken into account (Gillespie et al., 2005; Subbotin et al., 2007; Marvaldi et al., 2009; Murienne et al., 2010).

Material and methods

Taxon sampling

Taxa included in the analyses were based on previous molecular studies on Syrphidae (Ståhls et al., 2003; Mengual et al., 2008a,b, 2012, 2015). Table 1 lists the species included in the analysis, the collection data and the GenBank accession numbers. From a total of 107 included taxa, 31 individuals were analysed for the first time in the present study. Species of Syrphinae were sampled as ingroup as monophyly of this subfamily is well known (Skevington and Yeates, 2000; Ståhls et al., 2003; Hippa and Ståhls, 2005; Mengual et al., 2015). Three species of the subfamily Eristalinae were included as outgroup, namely *Merodon equestris* (Fabricius, 1794) (member of Merodontini), *Myolepta dubia* (Fabricius, 1805) (tribe Brachyopini) and *Graptomyza longirostris* Wiedemann, 1820 (tribe Volucellini). *Merodon equestris* was constrained as outgroup based on previous studies because Merodontini is always resolved as one of the first splits among Eristalinae. Members of the subfamily Pipizinae were also included.

Three species of *Asiobaccha* were sampled; two of them are undescribed taxa new to science (Mengual unpubl. data). Several specimens of the genera *Allobaccha*, *Baccha*, *Episyrphus* and *Meliscaeva* were included, as well as representative members of all tribes within Syrphinae and major syrphine clades based on results from Mengual et al. (2008a). A total of 100 syrphine taxa were studied as ingroup. DNA sequences for the genera *Citrogramma* Vockeroth, 1969 and *Claraplumula* Shannon, 1927 were obtained for the first time for molecular study.

Laboratory protocols

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 the manufacturer's instructions; samples were resuspended in 100 μl ultra-pure water.

Entire specimens or remnants of specimens were preserved and labelled as DNA voucher specimens for the purpose of morphological studies 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, 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 R6 (version 6.1.6, Biomatters Ltd.). All new sequences were submitted to GenBank (see Table 1 for accession numbers).

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 1371 nucleotide characters. The alignment of 18S and 28S rRNA genes was done in two different ways. Firstly, both genes were aligned using the E-INS-I strategy implemented in MAFFT (Katoh et al., 2005, 2009). The E-INS-I strategy is optimised for a small-scale alignment and recommended for sequences with multiple conserved domains and long gaps, such as rRNA genes (Katoh et al., 2009). This strategy implements iterative refinement methods (Katoh et al., 2005; Katoh and Standley, 2013) and shows one of the highest accuracy scores in currently available sequence alignment programmes (Katoh, 2013). The other considered strategy, Q-INS-I, was not used because its advantage for relatively conserved RNAs, such as SSU and LSU rRNA, is small as the extra computational time is spent on the comparison of no overlapping fragmentary sequences, which have no reasonable solutions (Katoh, 2013; Katoh and Standley, 2013). The small fragment of 18S used in this analysis had a total of 607 bp including gaps, and the D2-3 region of 28S a total of 643 bp including gaps (Appendix A of the Supporting information).

Secondly, 18S and 28S rRNA genes were aligned using the secondary structure of these genes, as explained by Kjer (1995) and implemented by Gillespie et al. (2004, 2006) and Mengual et al. (2012). Small regions of ambiguous alignment, named Regions of Expansion and Contraction (REC) by Kjer et al. (2009), were not excluded from the phylogeny inference analysis because the author wanted to compare the exact same sequence using MAFFT and secondary structure alignment. Moreover, Dixon and Hillis (1993) stated that stems and loops of the 28S rRNA gene contain phylogenetic information, obtaining the best results when the complete data set is used. As a result 622 bp were included in the analysis for the D2-3 region of 28S, and 610 bp for 18S, both numbers including gaps (Appendices B and C of the Supporting information).

Phylogenetic analyses

For the two data sets, i.e. a data set with the alignment provided by MAFFT and another data set with the 18S and 28S genes aligned using the secondary structure of these rRNA genes, different methodologies were applied to infer the phylogenetic relationships of *Asiobaccha*. Data sets may be extremely sensitive to parameters or models, although

there is no justification for pluralism in phylogenetic systematics (Giribet et al., 2002). The reason for this approach was to compare the results between the two alignments independently of the methodology used to analyse the data. Analytical runs were performed on the Topaz cluster at the National Museum of Natural History, Smithsonian Institution, Washington DC. All trees were drawn with the aid of FigTree v.1.3.1 (Rambaut, 2009).

Maximum Likelihood analysis

For Maximum Likelihood analysis and for Bayesian inference, the data set 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 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 TIM3 + I + G, TPM1uf + I + G for position 2 and TPM3uf + G for position 3. There was a little variation in the chosen model for 28S between the different alignments. The model TIM3 + G was selected for 28S using the MAFFT alignment, but the preferred model for the same gene using the secondary structure for the alignment was TIM3 + I + G. The selected model for 18S did not change among the different alignments, TVM + I + G.

Data was analysed under the recommended models using Garli v.2.01.1067 (Zwickl, 2006, 2011). The author conducted 30 independent runs (3 runs with the command searchreps = 10) 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 (Appendix D of the Supporting information). The tree with the highest likelihood was retained and is presented here. Bootstrap support values (BS) were estimated from 1000 replicates using the same independent models in Garli.

Bayesian inference

Phylogenetic estimation using the Markov Chain Monte Carlo algorithm as implemented in MrBayes 3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was performed using a parallelised version of the software. Data were divided into the above five partitions and a separate GTR + I + G model for each partition, except for position 3 of COI (GTR + G), 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 2500 generations. The programme Tracer 1.5 (Drummond and Rambaut, 2007; Rambaut and Drummond, 2007) was used to check convergence and acceptable mixing. The initial 2000 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.

Parsimony analysis

Parsimony analysis was executed in the computer programme TNT version 1.1 (Goloboff et al., 2003, 2008) and gaps were treated as missing data. The parsimony analysis was done using New Technology search commands. The author used default values for Sectorial Search, Tree fusing and Drift algorithms, but Ratchet parameters were changed to stop perturbation phase after 25 substitutions. Bremer support values (BR) (Bremer, 1988, 1994) were calculated as well as Jackknife support values (JK) (Farris et al., 1996), which were calculated on 1000 replicates with a 36% character removal probability using the same parameters for New Technologies. Bootstrap support values (BT) were also estimated from 1000 replicates using the same parameters.

Results

Maximum Likelihood analysis

The likelihood score for the best ML tree using the MAFFT alignment (Fig. E.1) was −38,677.586440, and for the best ML tree using the secondary structure alignment (Fig. 1) was −38,872.392069. Both topologies agree in the majority of the clades, except for the placement of *Asarkina* Macquart, 1834 and the relationships among *Asiobaccha*, *Episyrphus* and *Meliscaeva*. In the case of *Asarkina*, the analysis with the alignment obtained with MAFFT for rRNA genes resolves it as the sister group of a big clade including the radiation of *Allograpta*–*Sphaerophoria*, *Salpingogaster* Schiner, 1868, *Citrogramma* and *Ocyptamus* + *Toxomerus* + *Eosalpingogaster*. Using the structural alignment for rRNA genes, *Asarkina* was recovered as sister group of *Asiobaccha*, *Episyrphus* and *Meliscaeva*, which is the sister group of the previous clade.

The most remarkable difference between both analyses is the placement of *Asiobaccha*. Although not very well-supported in any case, *Asiobaccha* was resolved as sister group of *Episyrphus* or as sister group of *Episyrphus* + *Meliscaeva* using MAFFT or structural alignment respectively.

Bayesian inference

The topologies of the majority rule consensus trees resulting from Bayesian inference compare favourably with the most likely trees, with the basic difference of the polytomy within the clade Syrphini + Paragini. Differences between Bayesian trees using the MAFFT alignment (Fig. E.2) and the secondary structure alignment (Fig. E.3) are small, and the placement of *Baccha* and *Allobaccha* is identical in both topologies. The clade with *Asiobaccha*, *Episyrphus* and *Meliscaeva* was well supported (PP = 0.99 using MAFFT alignment, and PP = 1 using secondary structure of rRNA genes), as well as each of the three genera. As it was resolved for Maximum Likelihood analyses, *Asiobaccha* was recovered as sister group of *Episyrphus* using the MAFFT alignment (Fig. E.2) and as sister group of *Episyrphus* + *Meliscaeva* when the secondary structure was used for the alignment of rRNA genes (Fig. E.3), although with much higher support value in the second case (PP = 0.96 versus PP = 0.63).

Parsimony analysis

Parsimony analysis of the data set using the MAFFT alignment for 28S and 18S rRNA genes resulted in two equally parsimonious trees with 8452 steps, CI = 0.203 and RI = 0.489 (strict consensus shown in Fig. E.4). Using secondary structure alignment, two equally parsimonious trees of 8509 steps (CI = 0.203, RI = 0.487) were obtained using TNT (strict consensus shown in Fig. 2). Both cladograms resolved clades in a different placement compared with ML and Bayesian analyses, but *Asiobaccha* was resolved as sister group of *Meliscaeva* + *Episyrphus* with very low support (always below 50 for JK and BT).

The main difference with Bayesian and ML topologies is the placement of *Allobaccha* as sister group of Paragini within Syrphinae, but in general lines, parsimony topologies are very similar to the most parsimonious tree by Mengual et al. (2008a).

Discussion

Overall, the present results agree with earlier molecular works on Syrphidae (Mengual et al., 2008a,b, 2012, 2015) and point out that the current tribal classification of Syrphinae needs a revision. Pipizines were recovered as sister group of the subfamily Syrphinae, and only

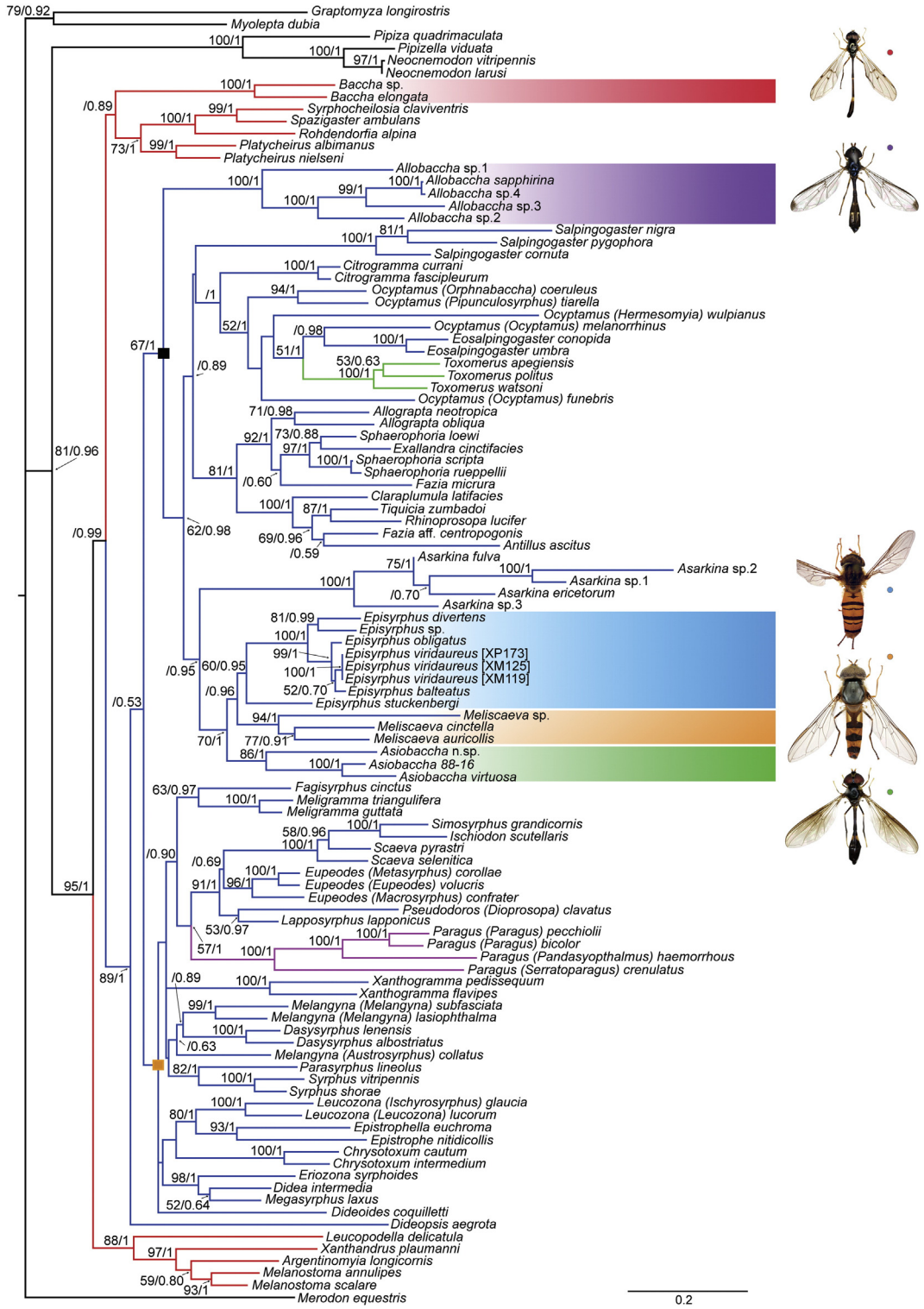

Fig. 1. Maximum Likelihood tree (ln $L = -38{,}872.392069$) based on the combined dataset using Garli v.2.01.1067 and the structural alignment for 28S and 18S. Bootstrap support values (left) and Bayesian posterior probabilities (right) are depicted above the nodes (>50%). Syrphinae tribes are indicated using coloured branches: Bacchini = red; Paragini = pink; Syrphini = blue; and Toxomerini = green. Black and orange squares denote the two major groups within Syrphini. Images: red = *Baccha maculata* Walker, 1852; violet = *Allobaccha apicalis* (Loew, 1858); orange = *Meliscaeva cinctella* (Zetterstedt, 1843); green = *Asiobaccha nubilipennis*; and blue = *Episyrphus balteatus* (De Geer, 1776). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the monogeneric tribes Toxomerini and Paragini were recovered monophyletic. The other two tribes within Syrphinae, Bacchini and Syrphini were resolved as non-monophyletic in two major clades with moderate support, also in agreement with previous morphological and molecular studies. In the author's opinion, new morphological characters should be used to define tribes in agreement with molecular evidence, but this is beyond the objective and resolution of the present paper.

In the tribe Bacchini, genus *Baccha* was placed with low or moderate support as sister group of *Platycheirus* Lepeletier & Serville, 1828 and related genera, i.e. *Rohdendorfia* Smirnov, 1924, *Syrphocheilosia* Stackelberg,

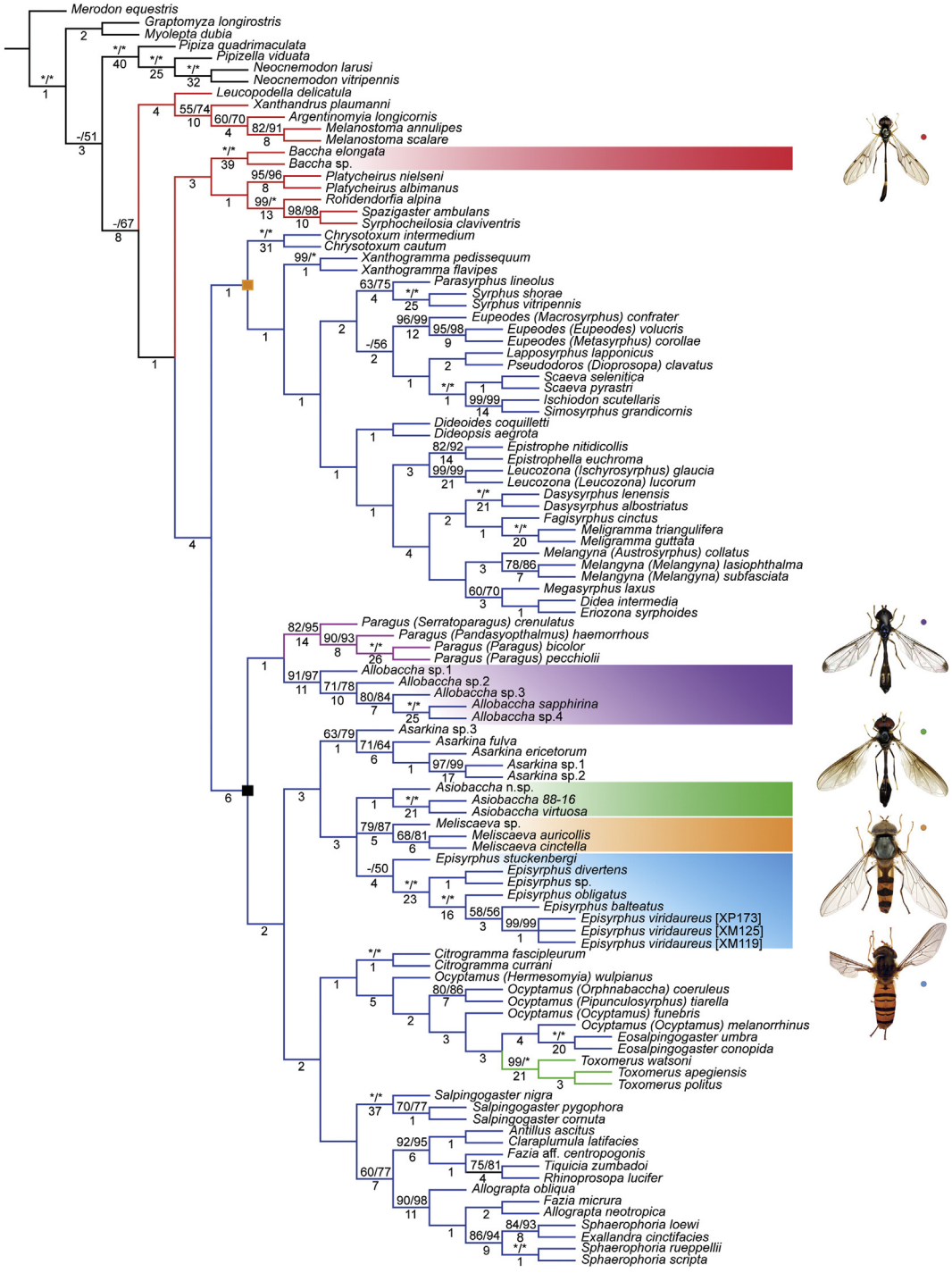

Fig. 2. Strict consensus tree of 2 equally parsimonious trees based on the combined dataset using the structural alignment for 28S and 18S (length = 8509 steps). Bremer support values are indicated below nodes; Bootstrap (left) and Jackknife (right) resampling values are above each node (>50%). An asterisk (*) denotes a value of 100. Syrphinae tribes are indicated using coloured branches: Bacchini = red; Paragini = pink; Syrphini = blue; and Toxomerini = green. Black and orange squares denote the two major groups within Syrphini. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1964 and *Spazigaster* Rondani, 1843. The other bacchine clade comprises *Leucopodella*, *Melanostoma* Schiner, 1860, *Argentinomyia* Lynch Arribalzaga, 1891 and *Xanthandrus* Verrall, 1901, and only Bayesian and Likelihood analyses showed a moderate support for this group.

Syrphini was resolved in a similar way as in the analysis by Mengual et al. (2008a) in all three analyses, with one major group including mostly Holarctic taxa (Syrphini sensu stricto, denoted by an orange square in Figs. 1 and 2), and another major group with a large Neotropical radiation plus some Oriental taxa and the genus *Sphaerophoria* Lepeletier & Serville, 1828 (indicated by a black square in Figs. 1 and 2). The tribe Paragini was resolved among taxa of the first clade except in parsimony analysis (see Fig. 2), but this topology did not receive high statistical support in any analysis. Toxomerini was always placed among members of the second clade embedded among members of the genus *Ocyptamus*. Genus *Allobaccha* was recovered in the second major Syrphini grouping as sister group of the remaining taxa with relative high support values, except in parsimony analysis where *Allobaccha* was recovered in a similar placement but with Paragini with lower support (Fig. 2).

The results resolved *Asiobaccha*, *Episyrphus* and *Meliscaeva* in a clade, not always well-supported but recovered in all the different analyses, independent of the methodology used to infer the phylogeny. In all analyses, the three mentioned genera were recovered monophyletic and *Asiobaccha* was resolved as sister group of *Episyrphus* + *Meliscaeva*, with the exception of the Bayesian and Maximum Likelihood analyses using the MAFFT alignment. In these two cases, *Meliscaeva* was recovered as the sister group of *Asiobaccha* + *Episyrphus*.

For the first time, *Citrogramma* and *Claraplumula* species were available for DNA sequencing. In the case of *Citrogramma*, two species were included in this study and they were recovered together as sister group of *Toxomerus* + *Eosalpingogaster* + *Ocyptamus* sensu lato (including all putative *Ocyptamus* subgenera). This topology is present in all three analyses but statistically supported in Bayesian analyses only. With a strong superficial resemblance to *Xanthogramma* Schiner, 1860, *Citrogramma* was included by Mengual et al. (2009) as related to *Allograpta*, and this placement is an unexpected novelty.

Genus *Claraplumula* was placed with very high support values in the clade of genera that were previously considered subgenera of *Allograpta*, i.e. *Antillus* Vockeroth, 1969, *Rhinoprosopa* Hull, 1942, *Tiquicia* Thompson, 2012 and part of *Fazia* Shannon, 1927. The placement of *Claraplumula* supports the decision of elevating it to genus rank (Thompson, 2012). Its placement is in agreement with previous molecular analyses suggesting the division of *Allograpta* sensu Vockeroth (1973) into several genera (Mengual et al., 2008a,b, 2012). Although current division into valid genera makes more sense than the previous *Allograpta* genus concept, *Fazia* is still resolved as non-monophyletic. Several lineages of phytophagous taxa within the *Allograpta* radiation were supported by Mengual et al. (2008b). One of these lineages includes all known taxa whose larvae are leaf-miners and stem-borers, and *Claraplumula* is resolved in this clade. Nothing is known about the biology of the immature stages of *Claraplumula*, but they might have a feeding mode related to phytophagy.

Phylogenetic relationships of Asiobaccha

In the past, *Asiobaccha* has been related to three different genera, i.e. *Baccha*, *Allobaccha* and *Episyrphus*. In the present analyses *Baccha*, *Allobaccha* and *Asiobaccha* are placed in remotely related clades. The tribe Bacchini is resolved in almost all analyses divided into two major clades and *Baccha* as sister group of *Platycheirus* and related genera. Shatalkin (1975) using male genitalia characters already suggested the subtribes Melanostominia and Platycheirina within Melanostomini. Earlier, Wirth et al. (1965) separated the tribes Bacchini and Melanostomatini, although most of their Bacchini taxa are currently placed into Syrphini.

Allobaccha is resolved as sister group of the clade within Syrphini with mostly Neotropical and Oriental taxa, not related to Syrphini sensu stricto. This position is recovered in both Bayesian and ML inferences but not in the parsimony analyses. Shatalkin (1975) stated that *Allobaccha* and *Baccha* were related with the species of his tribe Dideini (genera *Didea* Macquart, 1834, *Eriozona* Schiner, 1860, *Megasyrphus* Dušek & Láska, 1967, *Asarkina*, *Episyrphus* and *Meliscaeva*) on the basis of characters of the male genitalia. The present results agree partly with Shatalkin's opinion as two genera groups were recovered for his Dideini but not closely related, i.e. one group with *Didea*, *Eriozona* and *Megasyrphus*, and another clade with *Asarkina*, *Episyrphus* and *Meliscaeva*. In the present analysis, *Allobaccha* is placed in a close relationship with the second group.

Parsimony cladograms show *Allobaccha* as sister group of *Paragus* Latreille, 1804, the same placement as in the parsimony analysis by Mengual et al. (2008a). Morphologically both genera have nothing in common and *Paragus* is a quite distinctive group. The position for *Paragus* recovered by Bayesian and ML trees as sister group of the *Scaeva* clade, including *Scaeva* Fabricius, 1805 and *Eupeodes* Osten Sacken, 1877 and related genera, is not new. Rotheray and Gilbert (1999) suggested this relationship based on larval morphological characters, such as setae accompanying ventral sensilla of metathorax. Here, I hypothesise that *Allobaccha* and *Paragus* are resolved together in the parsimony analyses probably because a long-branch attraction effect (Felsenstein, 1978; Bergsten, 2005) but only found when parsimony is chosen as optimality criterion with the present dataset (but see Kück et al., 2012).

Asiobaccha is certainly related to *Episyrphus* and *Meliscaeva*. In all the present analyses, these three taxa are placed as sister group of *Asarkina*, in agreement with results by Mengual et al. (2008a). Larval morphological characters used by Rotheray and Gilbert (1989, 1999) also suggest a close relationship between *Episyrphus* and *Meliscaeva*, as well as male genitalia characters do (Shatalkin, 1975). Consequently and based on the present results, *Asiobaccha* is not closely related to *Baccha* or *Allobaccha*, neither is *Baccha* to *Allobaccha*.

An interesting result is the very low support for *Asiobaccha* n.sp. [ZFMK_XM127] as sister group of the remaining *Asiobaccha* species. A similar situation is found with *Episyrphus stuckenbergi* (Doesburg, 1957) as related to the other studied species of *Episyrphus*. Both taxa are morphologically distinct from other species of their genera.

Monophyly of *Episyrphus* supported in all analyses under different alignments and methodologies. *Episyrphus stuckenbergi* is always recovered as the sister group of the remaining included species of *Episyrphus*, which are grouped in two clades. One of these clades is formed by *Episyrphus divertens* (Walker, 1856) and a possible new species to science (ZFMK_XM227). The other clade consists of *Episyrphus balteatus* (De Geer, 1776), *Episyrphus obligatus* (Curran, 1931) and *Episyrphus viridaureus* (Wiedemann, 1824). Several specimens of *E. viridaureus* were included in the analyses as this species has a broad distribution ranging from New Caledonia to Malayan Peninsula (Knutson et al., 1975; Thompson and Vockeroth, 1989), and Java is its type locality (Wiedemann, 1824).

Wright and Skevington (2013) explained precisely the taxonomic problems of *Episyrphus* in the Oriental and Australasian Regions and the reasons to keep a conservative approach to cite Australian specimens as *E. viridaureus*. In an elegant experiment, Wright and Skevington (2013) reared larvae at different temperatures and concluded that some of the morphological characters may depend on the development temperature. Interestingly, all five specimens from Australia sequenced by Wright and Skevington (2013) share the same COI sequence, 647 bp of the Folmer fragment used for DNA barcoding. Specimens from Borneo and East Timor included in the present analyses share the same sequences for COI, 28S and 18S, and they show 10 nucleotide substitutions when compared with the Australian specimens. These changes represent only a 1.7% uncorrected pairwise distance between Australian and non-Australian individuals.

Taxonomic status of Asiobaccha

Data from the alignment using fast Fourier transform (MAFFT) programme and from the alignment based on the secondary structure of 28S and 18S infer different relationships for *Asiobaccha*, *Episyrphus* and *Meliscaeva*, but support values for these relationships are not very high with the exception of the Bayesian posterior probabilities. These three genera were recovered as three distinct lineages within a single monophyletic group, here called '*Episyrphus* clade'.

The first work suggesting a close relationship between *Asiobaccha* and *Episyrphus* was the identification key by Thompson and Rotheray (1998). In this work, there is no explanation or argumentation about considering *Asiobaccha* as a subgenus of *Episyrphus*, but it is easy to guess that a crucial morphological character to associate *Asiobaccha*, *Episyrphus* and *Meliscaeva* is "a series of minute closely spaced black maculae [dots] on posterior margin of the wing", plus the "anterior anepisternum with pile at least posterodorsally". Previously, Vockeroth (1969) admitted that *Episyrphus* and *Meliscaeva* are closely related because both genera have "discrete black sclerotized dots along the posterior wing margin". Interestingly, there is another Syrphini genus with these sclerotised maculae on posterior wing margin, *Fagisyrphus* Dušek

& Láska, 1967. In the present analyses, *Fagisyrphus* is always found as sister group of *Meligramma* Frey, 1946, the same phylogenetic position as reported by previous molecular results (Mengual et al., 2008a).

Another character shared by *Asiobaccha*, *Episyrphus* and *Meliscaeva* is the presence of some pile on anterior anepisternum, at least posterodorsally. There are some other Syrphini taxa with the anterior anepisternum pilose, such as *Parasyrphus* Matsumura, 1917, *Toxomerus*, *Hermesomyia* Vockeroth, 1969, *Orphnabaccha* Hull, 1949 and *Pseudoscaeva* Vockeroth, 1969, the last three currently considered putative subgenera of *Ocyptamus*. Consequently, the combination of pilose anterior anepisternum and sclerotised maculae on posterior wing margin seems to define the '*Episyrphus* clade', with *Asiobaccha*, *Episyrphus* and *Meliscaeva*.

Table 2 shows the morphological characters that have been scored and considered to be of good diagnostic value to define the studied Syrphini genera. *Asiobaccha* is easily distinguished from other petiolate genera, namely *Allobaccha* and *Baccha*, by the presence of black, sclerotised dots on posterior wing margin and by a pilose anterior anepisternum. Although some *Allobaccha* species may present some hairs in the anterior part of the anterior anepisternum, *Asiobaccha* species have pile on the posterodorsal and dorsomedial sections of the anterior anepisternum. On the other hand, *Baccha* has a complete postmetacoxal bridge (incomplete for *Allobaccha* and *Asiobaccha*) and simple, unsegmented aedeagus, a characteristic of the tribe Bacchini.

It seems that there is no single diagnostic morphological feature to distinguish all the studied genera listed in Table 2, but some combinations of them work very well. Morphological diagnostic characteristics for *Episyrphus* are proepimeron pilose, mesonotal collar absent, anatergum pilose, metasternum pilose, and metaepisternum pilose ventrad to spiracle. *Meliscaeva* is diagnosed by proepimeron pilose, mesonotal collar absent, anatergum pilose, metasternum bare, and metaepisternum bare ventrad to spiracle. In the case of *Asiobaccha*, morphological diagnostic characteristics are proepimeron bare, mesonotal collar present or absent, anatergum microtrichose (not pilose), metasternum bare, and metaepisternum pilose ventrad to spiracle.

The pilosity of the metasternum is very commonly used to define taxa, as well as the pilosity of the metaepisternum. It seems clear that the morphological characters that are variable among *Asiobaccha*, *Episyrphus* and *Meliscaeva* are diagnostic at genus level. Consequently, *Asiobaccha* stat. rev. should be considered a valid genus based on morphological and molecular evidence.

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Table 2
Morphological characters considered to be of good diagnostic value to define the studied Syrphinae genera.

Character statement	*Episyrphus*	*Meliscaeva*	*Asiobaccha*	*Allobaccha*	*Baccha*	*Fagisyrphus*
Head						
Eye pilosity	Bare	Bare	Bare	Bare	Bare	Bare
Thorax						
Proepimeron pilosity	Pilose	Pilose	Bare	Pilose	Bare	Pilose
Postpronotum pilosity	Bare	Bare	Bare	Bare/pilose	Bare	Bare
Anterior anepisternum pilosity	Pilose	Pilose	Pilose	Pilose/bare	Bare	Bare
Pile on anterior anepisternum	Posterodorsally and anteriorly	Posterodorsally and anteriorly	Dorsomedially, posterodorsally	Usually anteriorly	–	–
Mesonotoal fringe, collar	Absent	Absent	Absent/present	Absent/present	Absent	Absent
Anatergum pilosity	Pilose	Pilose	Microtrichose	Bare/pilose	Bare	Pilose
Metasternum pilosity	Pilose	Bare	Bare	Bare	Bare	Bare
Metaepisternum pilosity, ventrad to spiracle	Pilose	Bare	Pilose	Pilose	Bare/pilose in some Oriental species	Bare
Posmetacoxal bridge	Incomplete	Incomplete	Incomplete	Incomplete	Complete	Incomplete
Subscutellar fringe	Present, dense	Present, dense	Absent/present in a few species	Absent/present	Absent	Present, sparse
Wing						
Black, sclerotised dots on posterior wing margin	Present	Present	Present	Absent	Absent	Present
Alula shape	Broad	Broad	Absent/linear/triangular/broad	Broad/triangular	Absent/linear/narrow	Broad
Plumula	Present	Present	Absent/present	Absent/present	Absent	Present
Abdomen						
Abdomen shape	Parallel-sided to slightly oval, or constricted basally	Parallel-sided to slightly oval	Petiolate	Petiolate	Petiolate	Parallel-sided to slightly oval
Abdominal margin	Absent	Absent	Absent	Absent	Absent	Absent
Male genitalia						
Aedeagus	Segmented	Segmented	Segmented	Segmented	Unsegmented	Segmented

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