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2023-10-10

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Ståhls, G, Rotheray, G & Thompson, F C 2023, Exploring the intra-tribal relationships of Volucellini (Diptera Syrphidae) using molecular and morphological characters. in Contributions to Dipterology in honour of F. Christian Thompson. vol. 23, Studia Dipterologica Supplement, AMPYX VERLAG, Halle, pp. 237-244.

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# Exploring the intra-tribal relationships of Volucellini (Diptera: Syrphidae) using molecular and morphological characters

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## Abstract

The tribe Volucellini (Diptera: Syrphidae: Eristalinae) comprises four genera, *Copestylum* MACQUART, 1846, *Graptomyza* WIEDEMANN, 1820, *Ornidia* LEPELETIER & SERVILLE, 1828 and *Volucella* GEOFFREY, 1762. The monophyly of the tribe was never refuted, but the generic relationships have remained contradictory. This study addresses the intratribal generic relationships using a combined analysis of molecular (mitochondrial COI and nuclear 28S rDNA sequences) and morphological characters of adult and immature stages. Results of the Maximum Likelihood (ML) analysis for the combined molecular and morphological data were congruent with one of the previously proposed hypotheses presented by THOMPSON in 1972. The ML analysis of combined data supports the phylogenetic relationships among the genera as *Graptomyza* + (*Volucella* + (*Copestylum* + *Ornidia*)), with the included members of genera *Copestylum* and *Ornidia* resolved in a polytomy.

**Key words:** Volucellini, DNA, mtDNA COI, 28S rDNA, morphology

## Introduction

The family Syrphidae (Diptera) presently comprises over 6200 described species (PAPE & EVENHUIS 2019). Syrphid flies are almost worldwide in distribution and are most speciose in the New World tropics. The tribe Volucellini is one of the nine tribes presently recognized in the subfamily Eristalinae (MORAN et al. 2022), one of the four subfamilies of Syrphidae. Volucellini, as traditionally defined (THOMPSON 1972), comprise the genera *Copestylum* MACQUART 1846, *Graptomyza* WIEDEMANN, 1820, *Ornidia* LEPELETIER & SERVILLE, 1828, *Tachinosyrphus* HULL, 1936 and *Volucella* GEOFFREY, 1762. THOMPSON (1991) placed the monotypic genus *Tachinosyrphus* as a subgenus of *Copestylum*.

The cumulative distribution of the tribe includes all zoogeographical regions except Antarctica, but individual genera are more restricted. *Copestylum* and *Ornidia* are endemic to the New World, *Volucella* is known from the Oriental and Holarctic regions (THOMPSON 1972), while *Graptomyza* is the most widespread genus, known from the Afrotropical, Oriental, Palaearctic (only Eastern part) and Australasian regions (WHITTINGTON 1994). *Ornidia obesa* (FABRICIUS, 1775) has been introduced by human activity into the Old World tropics and the Pacific (THOMPSON 1991; WHITTINGTON & ROTHERAY 1997; RAMAGE et al. 2018), and *Copestylum melleum* (JAENNICKE, 1867) has been introduced and is established in the Canary Islands (ROMIG & HAUSER 2004). Although *Graptomyza* and *Copestylum* in particular are still poorly understood, the species richness of these four genera is remarkably disparate: *Ornidia* has five species (THOMPSON 1991; DA SILVA CARVALHO FILHO & ESPOSITO 2009); *Volucella* 42 species, *Graptomyza* has 83 species (WHITTINGTON 1992); and *Copestylum* comprises more than 400 species (ROTHERAY et al. 2009).

The members of the tribe Volucellini are readily distinguished from other eristaline tribes by the possession of a straight or recessive wing vein  $M_1$  in combination with a plumose antennal arista (THOMPSON 1972). Concerning the larval characters, the tribe is distinguished by the division of the anal segment into anterior and posterior sections, with the anterior section bearing two pairs of fleshy projections or lappets (three pairs in most other eristaline tribes). Additionally, the head skeleton has reduced mandibles that do not protrude as a pair of hooks from the oral cavity (mouth hooks are large and well developed in other eristaline tribes with two pairs of lappets) (THOMPSON et al. 2010). Larval feeding modes include saprophagy in a wide variety of decaying vegetable matter, and entomophagy in nests of aculeate Hymenoptera in several *Volucella* species (WHITTINGTON 1994; THOMPSON & ROTHERAY 1998; ROTHERAY et al. 2005, 2007; ROTHERAY 2009; THOMPSON et al. 2010).

Within the Volucellini, *Graptomyza* is perhaps the most morphologically distinctive genus within the adult stage, having dichoptic males and the scutellum with a well-developed, setose depression (WHITTINGTON 1992). Adult and larval stages of *Volucella*, *Copestylum* and *Ornidia* are not so morphologically distinct. Adults of *Volucella* have the thorax with the anterior anepisternum pilose, whereas this sclerite is bare in the majority of *Copestylum* and *Ornidia* species.

#### *Diagnoses of the tribe Volucellini*

**Adult** (adapted from THOMPSON 1972: 104, some terminology following Thompson 1999)

**Head:** Face pilose, usually distinctly tuberculate, rarely straight; oral margin notched anteriorly; facial grooves elongate, long, almost extending to antennal bases; facial stripes differentiated; antennal pits confluent; ocellar triangle small, distinctly anterior to posterior margin of eye; eye pilose; holoptic except dichoptic in *Graptomyza* and *Copestylum* (*Megametopon*) (GIGLIO-TOS); antenna short, shorter than face, with scape and pedicel always very short; arista usually plumose, rarely sparsely pilose, bare only in *Copestylum* (*Tachinosyrphus*).

**Thorax:** Usually with distinct bristles; anterior anepisternum pilose; anterior anepimeron pilose; metasternum pilose and underdeveloped; meron with pilose area anteroventral to spiracle. **Legs:** Simple, without spines or basoventral spinose area on hind femur. **Wing:** crossvein  $r-m$  clearly basal, always located basal to middle of cell  $M$ ; radial sector with microbristles; vein  $M_1$  (apical crossvein) straight or recessive, never progressive.

**Abdomen:** Short, oval or suboval, never elongate, emarginate or petiolate.

**Larva** (adapted from ROTHERAY et al. 2005)

Length 4–30 mm. Anterior and posterior ends truncate or tapered; subcylindrical to dorso-ventrally flattened in cross-section; mouth lacking protruding mouth-hooks; anterior spiracles usually present; anal segment divided into anterior and posterior sections with the anterior section bearing two pairs of fleshy projections or lappets, the posterior section with one pair of lappets, and the base of the antero-dorsal pair of the lappets on the anterior section, bearing a short projection and an apical sensillum; mesothoracic prolegs with crochets present; prolegs and crochets usually present on first six abdominal segments, crochets usually in straight transverse rows, rarely in curved rows; anal segment short or long; larva saprophagous in a wide variety of wet, decaying organic substance.

#### *Phylogenetic relationships*

HULL (1949) was the first to classify the volucellines, and in his synopsis of syrphid flies he treated the taxon as the subfamily Volucellinae including two tribes, the Volucellini (*Volucella* [including *Copestylum*], *Megametopon*, and *Tachinosyrphus*) and the Graptomyzini (*Graptomyza*). THOMPSON (1972) presented Hennigian argumentation scheme

analyses based on morphological characteristics mainly of the adult stage of Volucellini, and he found two possible phylogenetic arrangements of the Volucellini genera: i) Volucellini = (*Graptomyza* + *Volucella*) + (*Ornidia* + (*Copestylum* + *Tachinosyrphus*)); or ii) Volucellini = *Graptomyza* + (*Volucella* + (*Ornidia* + (*Copestylum* + *Tachinosyrphus*))) (see also THOMPSON & WHITEHEAD 1986; THOMPSON 1991). WHITTINGTON (1992) using a slightly different morphological character set presented the relationships as: Volucellini = *Graptomyza* + (*Copestylum* + (*Ornidia* + *Volucella*)). Thus, these hypotheses agree only on the placement of the genus *Graptomyza* as sister to the other Volucellini taxa.

The study of STÅHLS et al. (2003) explored the phylogenetic relationships within the Syrphidae using both morphological and molecular characters. They used parsimony analysis under optimization alignment for the combined data under various weighting schemes, and included three *Volucella* and one *Graptomyza* species. The *Volucella* species (with immature stages with different feeding modes) were resolved as a well-supported monophyletic group, while *Graptomyza* was placed as sister group to the non-volucelline taxon *Alipumilio avispa* VOCKEROTH, 1964, albeit with low support. HIPPA & STÅHLS (2005) in their study of the phylogenetic utility of adult morphological characters of Syrphidae also included the mentioned Volucellini taxa. Their parsimony analysis resolved the included taxa of *Graptomyza* and *Volucella* as a clade. YOUNG et al. (2016) included representatives of *Graptomyza* and *Copestylum* in their Maximum Likelihood analysis using anchored enrichment sequence data for 343 selected genetic loci, and the monophyly of Volucellini was supported (100% bootstrap support). MORAN et al. (2022) in their eight-gene phylogeny recovered a well-supported Volucellini (only including representatives of *Graptomyza* and *Copestylum*), and discussed elevating the ranks of tribes Ceriodini, Merodontini and Volucellini as recovered in the phylogenetic tree to subfamilial level.

Hence, the phylogenetic relationships of Volucellini, including representatives of all genera, are still in demand. Here, we specifically explore the relationships among the Volucellini genera using a fair representation of the taxonomic diversity of the tribe and DNA sequence data of two gene regions frequently employed in syrphid molecular phylogenetic studies (e.g., STÅHLS et al. 2004; MENGUAL et al. 2008, 2015; VUJIĆ et al. 2008, 2020). These data were analysed under Maximum Likelihood, and in combination with newly generated morphological characters of adult and early stages and including multiple outgroup eristaline taxa.

## Material and Methods

### *Taxon sampling*

The present study includes 17 species of *Copestylum*, five species of *Volucella*, four of *Graptomyza*, and two species of *Ornidia* (28 taxa in total; Table 1). Representatives of all eristaline tribes were included as outgroups (13 taxa in total), and *Eumerus erythrocerus* LOEW, 1858 (Eristalinae: Merodontini) was used to root the trees. The total number of species was 41. Species new to science awaiting description are denoted with abbreviations (e.g. CR-29 refers to species number 29 from Costa Rica), and were identified as such by F. C. THOMPSON (Tables 1 & 3).

### *Molecular data*

Adult specimens were used for DNA extraction, and the remains of specimens were preserved and labelled as DNA voucher specimens and deposited in the entomological collections of the Finnish Museum of Natural History Luomus [institutional acronym MZH] (Table 1). DNA was extracted from 1–3 legs of either dry, pinned or ethanol preserved

specimens using the Nucleospin Tissue DNA Extraction kit (Macherey-Nagel, Düren, Germany) following manufacturer's protocols and resuspended in 50 µl of ultrapure water. A large fragment of the mitochondrial cytochrome *c* oxidase subunit I (hereafter COI) and the D2–3 expansion region of the nuclear ribosomal 28S rRNA gene were sequenced. PCR primers and amplification protocols for mitochondrial COI, and nuclear 28SrRNA genes were the same as in MENGUAL et al. (2008, 2015). Amplified DNA was electrophoresed on 1.5% agarose gels and purified for sequencing with the GFX PCR Purification Kit (Amersham Biotech, Little Chalfont, UK). Sanger sequencing was outsourced to the sequencing service laboratory at FIMM, Biomedicum, University of Helsinki. The sequences were edited for base-calling errors and assembled using Sequence Navigator™ version 1.01 (Applied Biosystems, Waltham, Massachusetts, USA) or Sequencher version 5.1 (GeneCodes, Ann Arbor, Michigan, USA).

### *Morphological data*

Morphological characters were obtained across the entire body of the adult and final larval instar or puparial stage. F.C. THOMPSON generated a data matrix of 56 characters (23 binary, 33 multistate) of the adult fly (Matrices 1 & 2; Ståhls 2022). The adult characters were scored for ingroup and outgroup taxa mainly by F. C. THOMPSON; a few were also scored by G. STÅHLS. The specimens used for scoring for the adult morphological dataset are partly deposited in the United States National Museum collection (Washington, USA; Table 2), and some specimens used for molecular analysis were also used for character scoring. G.E. ROTHERAY generated and scored a data matrix of 41 early-stage characters (22 binary, 19 multistate; appendices 3 and 4). The immature samples used for scoring larval characters are deposited in the National Museums of Scotland collection (Edinburgh, UK). Morphological terminology follows THOMPSON (1999) for adults and ROTHERAY & GILBERT (1999) for early stages.

### *Phylogenetic analyses*

The 28S rRNA sequences were aligned with MAFFT version 7 (KATO & STANDLEY 2013) using the E-INS-i algorithm (KATO et al. 2005). The gap-free COI sequences were manually trimmed to have the same 5'-end start point, and likewise truncated in the 3'-end. Maximum likelihood analyses of DNA data and combined dataset analyses were executed on the IQ-tree (MINH et al. 2020) web server using IQ-TREE multicore version 1.6.12 (<http://iqtree.cibiv.univie.ac.at>) (TRIFINOPOULOS et al. 2016). ModelFinder (KALYAANAMOORTHY et al. 2017) as implemented in IQ-tree was used to identify the most optimal evolutionary models. Branch support was estimated using ultrafast bootstrap (HOANG et al. 2017). Consensus trees, with branch support values shown at nodes, were visualized and rooted in MEGA version X (KUMAR et al. 2018).

## **Results**

### *Morphological data*

The morphology matrix totalled 97 parsimony informative characters. See Appendices 1 and 2 for character descriptions, and Ståhls (2022) for character matrices.

### *Molecular data*

The mitochondrial COI dataset comprised 1128 nucleotide characters (partially incomplete sequences for two ingroup species). The mean A+T-content of the COI sequences was 71.1%. For the sequenced D2–3 fragment of 28S rRNA gene we obtained 560–590 nucleotides (lacking for two ingroup species), and the aligned matrix comprised 631 nucleotide sites. Thus, the aligned molecular dataset comprised 1759 nucleotide sites in total.

### *Phylogenetic analyses*

The best-fit evolutionary model (under both AIC and BIC criterion) for molecular data was GTR+F+I+G4, and the best-fit model for morphological data was MK+FQ+ASC+G4. The log likelihood for the best tree of the combined of the morphology tree was -1,861.9396 (Fig. 1), the log likelihood for the best tree of the molecular data was -15,949.1115 (Fig. 2) and for the combined data -18,543.228 (Fig. 3). Consensus trees are shown with bootstrap values indicated at the nodes (Figs 1–3).

### *Phylogenetic relationships*

Results of the ML analysis for the molecular data only (Fig. 2) and combined molecular and morphological data (Fig. 3) were congruent with the second of the argumentation schemes suggested by THOMPSON (1972), namely Volucellini = *Graptomyza* + (*Volucella* + (*Copestylum* + *Ornidia*)). In the separate analysis of the morphological data the relationships among the volucelline genera were not satisfactorily resolved, with the members of *Volucella* and *Copestylum* found in several clusters. However we stress that among the volucellines, the larvae and puparia of *Ornidia* are similar to those of *Copestylum*, and most similar to those of the *Copestylum scutellata* group *sensu* FLUKE (1951) (ROTHERAY et al. 2005).

*Graptomyza* was resolved as sister to the rest of the Volucellini in the preferred tree from the combined analysis (Fig. 3) with high support. *Graptomyza robusticornis* VAN DOESBURG, 1957 from Madagascar was resolved as sister taxon to *G. longirostris* WIEDEMANN, 1820 from Malaysia in all topologies with high support, and not placed as sister taxon to the two *Graptomyza* species from East Africa.

*Volucella inflata* (FABRICIUS, 1794) was sister to the rest of the *Volucella* species (Figs 2–3), a position we have found previously (STÅHLS et al. 2003). This species is apparently unusual among *Volucella* in having a saprophagous larva in tree sap exudations (ROTHERAY 1999). Only seven other *Volucella* species have been reared but they are all associated with nests of social aculeates (Hymenoptera), where they have mixed saprophagous and zoophagous feeding modes although one species, *Volucella inanis* (LINNAEUS, 1758), is a strict zoophage (RUPP 1989).

The included representatives of *Copestylum* were resolved in three clades in the combined analysis (Fig. 3). Our results from the combined dataset are not conclusive about the relationship of *Copestylum* and *Ornidia*.

### **Discussion**

For a genus of its size, second largest within the Volucellini and the most widely distributed, *Graptomyza* is biologically poorly known. Rearing data apparently exist for less than ten species. WHITTINGTON (1994) described the puparium of an Australian species, *Graptomyza mitis* CURRAN & BRYAN, 1926 and the puparia of two Afrotropical taxa, *G. signata* and *G. triangulifera* (BIGOT, 1883). *Graptomyza signata* has been reared from tomato and unidentified rotting fruit, and *Graptomyza triangulifera* (BIGOT, 1883) from unidentified seed pods (WHITTINGTON 1994). He also indicated that an unidentified Australasian *Graptomyza* species close to *G. flavicollis* FERGUSON, 1926 was reared from fallen fruit of *Castanospermum australe* (Leguminosae) (WHITTINGTON 1994). KRIVOSHEINA & KRIVOSHEINA (1996) reared and described the larva and puparium of the Palaearctic *Graptomyza alabeta* SÉGUY, 1948. The larva was found in wet decaying sap under bark of fallen trees of *Maackia amurensis* Rupr. (Leguminosae) and *Phellodendron sachalinensis* Rupr. (Rutaceae). More recently, ARACIL et al. (2019) described the immature stages of the

Afrotropical species *Graptomyza signata* (WALKER, 1860) reared from an *Aloe*-like plant. An Australasian species *G. brevis* WIEDEMANN, 1820, that we examined in the Smithsonian Institution, was reared from decaying tomato fruits. Thus, decaying tree sap and decaying fruits comprise the recorded larval feeding habits in this genus.

We included only a limited representation of the known species diversity of *Copestylum*, hence the intrageneric relationships are only briefly discussed. Within this genus, several authors have recognized different species groups (THOMPSON 2006; ROTHERAY et al. 2007; RICARTE et al. 2015), and there are many generic names synonymized under *Copestylum* that deserve attention and further evaluation. Although the clades resolved in *Copestylum* are broadly congruent with adult morphology and biology, some inconsistencies exist. For example, combined analysis placed *C. varians* (BIGOT, 1875) + *C. emeralda* (HULL, 1944) as basal within *Copestylum* (Fig. 3) whereas the molecular only analysis has this taxon placed two nodes up from the base (Fig 2). *Copestylum varians* is a member of a small group referred to as the *chalybescens* species group by THOMPSON (pers. comm.). Although most species are distinctive on adult characters, both adult and larval morphology is relatively simple and generalised with respect to other *Copestylum* (ROTHERAY et al. 2009). In Syrphidae, relatively simple, generalised morphology is either associated with secondary losses, or with early-branching taxa (ROTHERAY & GILBERT 1999).

The clade in Fig. 3 including *Copestylum emeralda*, taxa of the *variens* species group and species of the *vagum* species group (RICARTE et al. 2015) corresponds mainly to species from closed, forest habitats or forest fringes where breeding occurs in pockets of decay in a wide range of living and dead plants and plant parts (ROTHERAY et al. 2007). The clade from *Copestylum macquarti* to *Ornidia therezinhae* includes *C. elizabethae* HANCOCK & ROTHERAY, 2007, *C. macquarti* CURRAN, 1926 and the *Ornidia* species, which can be found in many habitats, while other species are characteristic of open, xeric habitats where breeding occurs in decaying agaves and cacti (ROTHERAY et al. 2009). *Ornidia* species were consistently resolved related to *Copestylum scutellata* (MACQUART, 1842) and other *Copestylum* species (Fig 3). *Copestylum scutellata* is a member of a large and distinctive species group within *Copestylum*, which is recognisable from various characters such as a scutellum with large, socketed spines (FLUKE 1951). This species group appears to have radiated in open, high-altitude habitats where they breed in decaying cacti (ROTHERAY et al. 2009). The *scutellata* species group shares adult and larval characters with *Ornidia*, such as an inflated postpronotum and a facial tubercle extending laterally to the facial grooves in the adult, and similarities in the posterior breathing tube of the larvae (ROTHERAY et al. 2005).

Within *Ornidia*, *O. obesa* is particularly common and widespread in comparison with the other four species. SACK (1921) recorded the larva of *O. obesa* from rotting fruits of apple, citrus and breadfruit, and from dung from cesspits. This species can be of concern to public health through carrying harmful bacteria when frequenting latrines (GREENBERG 1971; THOMPSON 1991). Myiasis by *O. obesa* in humans has been reported multiple times in the literature (for a review see PÉREZ-BAÑÓN et al. 2020). In Costa Rica, larvae of *O. obesa* have been reported in flesh wounds in livestock (F. C. THOMPSON, pers. comm.), and in Brazil, MARTINS et al. (2010) reported it from pig carcasses. On the other hand, *O. obesa* can be a useful species as a natural recycler of organic wastes and as a source of protein for domestic animals (LARDÉ 1989). Many unpublished rearing records exist in collections. Nearly all of them are synanthropic and involve a wide variety of decaying materials, particularly dung and decaying vegetable matter. MORALES & WOLFF (2010) stated that in Colombia, *O. obesa* is present throughout every stage of composting and is among the most abundant species in

this process. Non-synanthropic breeding sites for *O. obesa* include exudations of tree sap (ROTHERAY et al. 2005). *Ornidia major* CURRAN, 1930 has been reared from fallen fruits of palm trees (Palmaceae) and from exuding tree sap, while *Ornidia whiteheadi* THOMPSON, 1991 has been reared from larvae refuse dumps in ant nests of *Atta* FABRICIUS, 1805 (Formicidae) (ROTHERAY et al. 2005). Immature stages of *Ornidia therezinhae* CARVALHO FILHO & ESPOSITO, 2009 remain unknown.

Although our data set has low taxon sampling, it is still comparable to most multi-locus phylogenetic studies in species diversity and definitely larger than most phylogenomic data sets. Our results report an unsatisfactorily resolved relationship between *Copestylum* and *Ornidia*, sometimes in a polytomy or with *Ornidia* embedded in the radiation of *Copestylum*. As the taxon sampling in the present study is not comprehensive concerning the highly speciose genus *Copestylum*, we hypothesize a change of rank of genus *Ornidia* as subgenus of *Copestylum*, but we refrain from taking any systematic action herein. Future studies with increased taxon sampling will help establish relationships within *Copestylum* and *Graptomyza*, and additionally corroborate the placement of *Ornidia*.

### Acknowledgements

We thank Andrew WHITTINGTON for species identification of the *Graptomyza* specimens from Madagascar and Malaysia. We are indebted to the Instituto Nacional de Biodiversidad (INBio, Costa Rica) for logistical support over several years.

### Literature

- ARACIL, A., PÉREZ-BAÑÓN, C., MENGUAL, X., RADENKOVIĆ, S., STAHL, G., VUJIĆ, A. & ROJO, S. (2019): New information about the pre-imaginal morphology of genus *Graptomyza* (Diptera, Syrphidae, Volucellini): description of third-instar larva and re-description of puparium of *G. signata* (WALKER, 1860). – *African Invertebrates* **60**: 15–30. <https://doi.org/10.3897/afrinvertebr.60.31521>
- DA SILVA CARVALHO FILHO, F. S. & ESPOSITO, M. C. (2009): A review of the flower fly genus *Ornidia* Lepeletier & Serville (Diptera: Syrphidae) with the description of a new species from Brazil. – *Zootaxa* **2014**: 59–64. <https://doi.org/10.11646/zootaxa.2014.1.6>
- FLUKE, C. L. (1951): Syrphid flies related to *Volucella scutellata* Macquart. – *American Museum Novitates* **1503**: 1–83.
- GREENBERG, B. (1971): Fly-organism associations with systematic list of fly species. – Pp. 192–478. – In: GREENBERG, B. (ed): *Flies and Disease. Volume 1. Ecology, Classification and Biotic Associations*: xii + 856 pp., Princeton: Princeton University Press. <https://doi.org/10.1515/9780691196763>
- HIPPA, H. & STAHL, G. (2005): Morphological characters of adult Syrphidae: descriptions and phylogenetic utility. – *Acta Zoologica Fennica* **215**: 1–72.
- HOANG, D. P., CHERNOMOR, O., VON HAESLER, A., MINH, B. Q. & VINH, L. S. (2012): UFBoot2: Improving the ultrafast bootstrap approximation. – *Molecular Biology and Evolution* **35**: 518–522. <https://doi.org/10.1093/molbev/msx281>
- HULL, F. M. (1949): The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. – *Transactions of the Zoological Society, London* **26**: 257–408.
- KALYAANAMOORTHY, S., MINH, B. Q., WONG, T. K. F., VON HAESLER, A. & JERMIIN, L. S. (2017): ModelFinder: Fast model selection for accurate phylogenetic estimates. – *Nature Methods* **14**: 587–589. <https://doi.org/10.1038/nmeth.4285>
- KATO, K., KUMA, K., TOH, H. & MIYATA, T. (2005): MAFFT version 5: improvement in accuracy of multiple sequence alignment. – *Nucleic Acids Research* **33**: 511–518. DOI: <https://doi.org/10.1093/nar/gki198>

- KATOH, K. & STANDLEY, D. M. (2013): MAFFT Multiple Sequence Alignment Software Version 7: improvements in performance and usability. – *Molecular Biology and Evolution* **30**(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- KRIVOSHEINA, M. G. & KRIVOSHEINA, N. P. (1996): Biology and immature stages of *Graptomyza alabeta* Séguy (Diptera, Syrphidae). – *International Journal of Dipterology Research* **7**(4): 276–270.
- KUMAR, S., STECHER, G., LI, M., KNYAZ, C. & TAMURA, K. (2018): MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. – *Molecular Biology and Evolution* **35**: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- LARDÉ, G. (1989): Investigation on some factors affecting larval growth in a coffee-pulp bed. – *Biological Wastes* **30**: 11–19.
- MARTINS, E., NEVES J. A., MORETTI, C., GODOY, W.A.C. & THYSSEN, P. J. (2010): Breeding of *Ornidia obesa* (Diptera: Syrphidae: Eristalinae) on Pig Carcasses in Brazil. – *Journal of Medical Entomology* **47**(4): 690–694. <https://doi.org/10.1603/ME09254>.
- MENGUAL, X., STÅHLS, G. & ROJO, S. (2008): First phylogeny of predatory hoverflies (Diptera, Syrphidae, Syphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the current tribal classification. – *Cladistics* **24**: 543–562. <https://doi.org/10.1111/j.1096-0031.2008.00200.x>
- MENGUAL, X., STÅHLS, G. & ROJO, S. (2015): Phylogenetic relationships and taxonomic ranking of pipizine flower flies (Diptera: Syrphidae) with implications for the evolution of aphidophagy. – *Cladistics* **31**: 491–408. <https://doi.org/10.1111/cla.12105>
- MINH, B. Q., SCHMIDT, H. A., CHERNOMOR, O., SCHREMPF, D., WOODHAMS, M. D., VON HAESLER, A. & LANFEAR, R. (2020): IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. – *Molecular Biology and Evolution* **37**: 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- MORALES, G. E. & WOLFF, M. (2010): Insects associated with the composting process of solid urban waste separated at the source. – *Revista Brasileira Entomologica* **54**: 645–653. <https://doi.org/10.1590/S0085-56262010000400017>
- MORAN, K. M., SKEVINGTON, J. H., KELSO, S., MENGUAL, X., JORDAENS, K., YOUNG, A. D., STÅHLS, G., MUTIN, V., BOT, S., VAN ZUIJEN, M., ICHIGE, K., VAN STEENIS, J., HAUSER, M. & VAN STEENIS, W. (2021): A multigene phylogeny of the eristaline flower flies (Diptera: Syrphidae), with emphasis on the subtribe Criorhinina. – *Zoological Journal of the Linnean Society* **194**: 120–135. <https://doi.org/10.1093/zoolinnean/zlab006>
- PAPE, T. & EVENHUIS, N. (2019): *Systema Dipteriorum*. The biosystematic database of world Diptera, v. 2.1, <http://diptera.org> [accessed 10.06.2021].
- PÉREZ BAÑÓN, C., ROJAS, C., VARGAS, M., MENGUAL, X. & ROJO, S. (2020): A world review of reported myiasis caused by flower flies (Diptera: Syrphidae), including the first case of human myiasis from *Palpada scutellaris* (Fabricius, 1805). – *Parasitology Research* **119**: 815–840. <https://doi.org/10.1007/s00436-020-06616-4>.
- RAMAGE, T., SYLVAIN, C., & MENGUAL, X. (2018): Flower flies (Diptera, Syrphidae) of French Polynesia, with the description of two new species. – *European Journal of Taxonomy* **448**: 1–37. <https://doi.org/10.5852/ejt.2018.448>
- RICARTE, A., MARCOS-GARCÍA, M. Á., HANCOCK, E. G. & ROTHERAY, G. E. (2015): Neotropical *Copestylum* Macquart (Diptera: Syrphidae) Breeding in Fruits and Flowers, Including 7 New Species. – *PLoS ONE* **10**(11): e0142441. <https://doi.org/10.1371/journal.pone.0142441>
- ROMIG, T. & HAUSER, M. (2004): *Copestylum melleum* (Jaenicke, 1867) (Diptera, Syrphidae) is an established neozoon on the Canary Islands. – *Volucella* **7**: 185–191.
- ROTHERAY, G. E. (1999): Descriptions and a key to the larval and puparial stages of north-west European *Volucella* (Diptera, Syrphidae). – *Studia dipterologica* **6**: 103–116.

- ROTHERAY, G. & GILBERT, F. (1999): Phylogeny of Palaearctic Syrphidae (Diptera): Evidence from larval stages. – *Zoological Journal of the Linnean Society* **127**: 1–112. <https://doi.org/10.1111/j.1096-3642.1999.tb01305.x>
- ROTHERAY, G. E., HANCOCK, E. G., MARCOS-GARCÍA, M. A. & ZUMBADO, M. (2005): Early stages and breeding sites of three species of Neotropical *Ornidia* (Diptera, Syrphidae). – *Studia dipterologica* **12**: 419–427.
- ROTHERAY, G. E., HANCOCK, E. G. & MARCOS-GARCÍA, M. A. (2007): Neotropical *Copestylum* (Diptera, Syrphidae) breeding in bromeliads (Bromeliaceae) including 22 new species. – *Zoological Journal of the Linnean Society* **150**: 267–317. <https://doi.org/10.1111/j.1096-3642.2007.00288.x>
- ROTHERAY, G. E. (2009): Neotropical *Copestylum* (Diptera, Syrphidae) breeding in Agavaceae and Cactaceae including seven new species. – *Zoological Journal of the Linnean Society* **156**: 697–749.
- SACK, P. (1921): Dr. L. Zürchers Dipteren-Ausbeute aus Paraguay: Syrphiden. – *Archive für Naturgeschichte* **87**: 127–149.
- STÅHLS, G., HIPPA, H., ROTHERAY, G., MUONA, J. & GILBERT, F. (2003): Phylogeny of Syrphidae (Diptera) inferred from combined analysis of molecular and morphological characters. – *Systematic Entomology* **28**: 433–450. <https://doi.org/10.1006/mpev.2000.0787>
- Ståhls, Gunilla (2022), “Datamatrices for Volucellini study”, Mendeley Data, V1, doi: 10.17632/n37t43zxxwg.1
- THOMPSON, F. C. (1972): A contribution to a generic revision of the Neotropical Milesinae (Diptera: Syrphidae). – *Arquivos de Zoologia* **23**: 73–215. <https://doi.org/10.11606/issn.2176-7793.v23i2p73-215>
- THOMPSON, F. C. (1991): The flower fly genus *Ornidia* (Diptera, Syrphidae). – *Proceedings of the Entomological Society of Washington* **93**: 248–261.
- THOMPSON, F. C. (1999): A key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical Region including descriptions of new genera and new species and a glossary of taxonomic terms. – *Contributions Entomology International* **3**: 322–378.
- THOMPSON, F. C. (2006): First Neotropical Syrphidae identification workshop. 21<sup>st</sup>–27<sup>th</sup> of February, 2006. Manuscript. (Universidad del Valle, Cali, Colombia).
- THOMPSON, F. C. & ROTHERAY, G. E. (1998): Family Syrphidae. – Pp. 81–139. – In: PAPP, L. & DARVAS, B. (eds): *Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance)*. Higher Brachycera **3**: 880 pp.; Budapest: Science Herald.
- THOMPSON, F. C., ROTHERAY, G. E., ZUMBADO M. A. (2010): Syrphidae. – Pp. 763–792. – In: BROWN, B. V., BORKENT, A., CUMMING, J. M., WOOD, D. M., WOODLEY, N. E. & ZUMBADO, M. A. (eds): *Manual of Central American Diptera* **2**: 728 pp. NRC, Ottawa, ON, Canada.
- VOCKEROTH, J. R. & THOMPSON, F. C. (1987): Syrphidae. – Pp. 713–743 – In: MCALPINE, J. F., PETERSON, B. V., SHEWELL, G. E., TESKEY, H. J., VOCKEROTH, J. R. & WOOD, D. M. (eds.): *Manual of the Nearctic Diptera. Volume 2. Research Branch, Agriculture Canada, Monograph* **28**: vi + 675–1332; Ottawa: Canadian Government Publishing Centre..
- VUJIĆ, A., STÅHLS, G., ROJO, S., RADENKOVIĆ, S. & ŠIMIĆ, S. (2008): Systematics and phylogeny of the tribe Paragini (Diptera: Syrphidae) based on molecular and morphological characters. – *Zoological Journal of the Linnean Society* **152**: 507–536. <https://doi.org/10.1111/j.1096-3642.2007.00353.x>
- VUJIĆ, A., LIKOV, L., RADENKOVIĆ, S. KOČIŠ TUBIĆ, N., DJAN, M., ŠEBIĆ, A., PÉREZ-BAÑÓN, C., BARKALOV, A., HAYAT, R., ROJO, S., ANDRIĆ, A. & STÅHLS, G. (2020) Revision of

the *Merodon serrulatus* group (Diptera, Syrphidae). ZooKeys **909**: 79–158.

<https://doi.org/10.3897/zookeys.909.46838>

WHITTINGTON, A. E. (1992): Revision of the Afrotropical species of *Graptomyza* Wiedemann (Diptera: Syrphidae). – *Annals of the Natal Museum* **33**(1): 209–269.

WHITTINGTON, A. E. (1994): Descriptions of the puparia of three *Graptomyza* species (Diptera: Syrphidae). – *Tropical Zoology* **7**(1): 57–65

WHITTINGTON, A. E. & ROTHERAY, G. E. (1997): Afrotropical distribution and larval description of *Ornidia obesa* (FABRICIUS, 1775) (Diptera; Syrphidae). – *Journal of African Zoology* **111**: 365–372.

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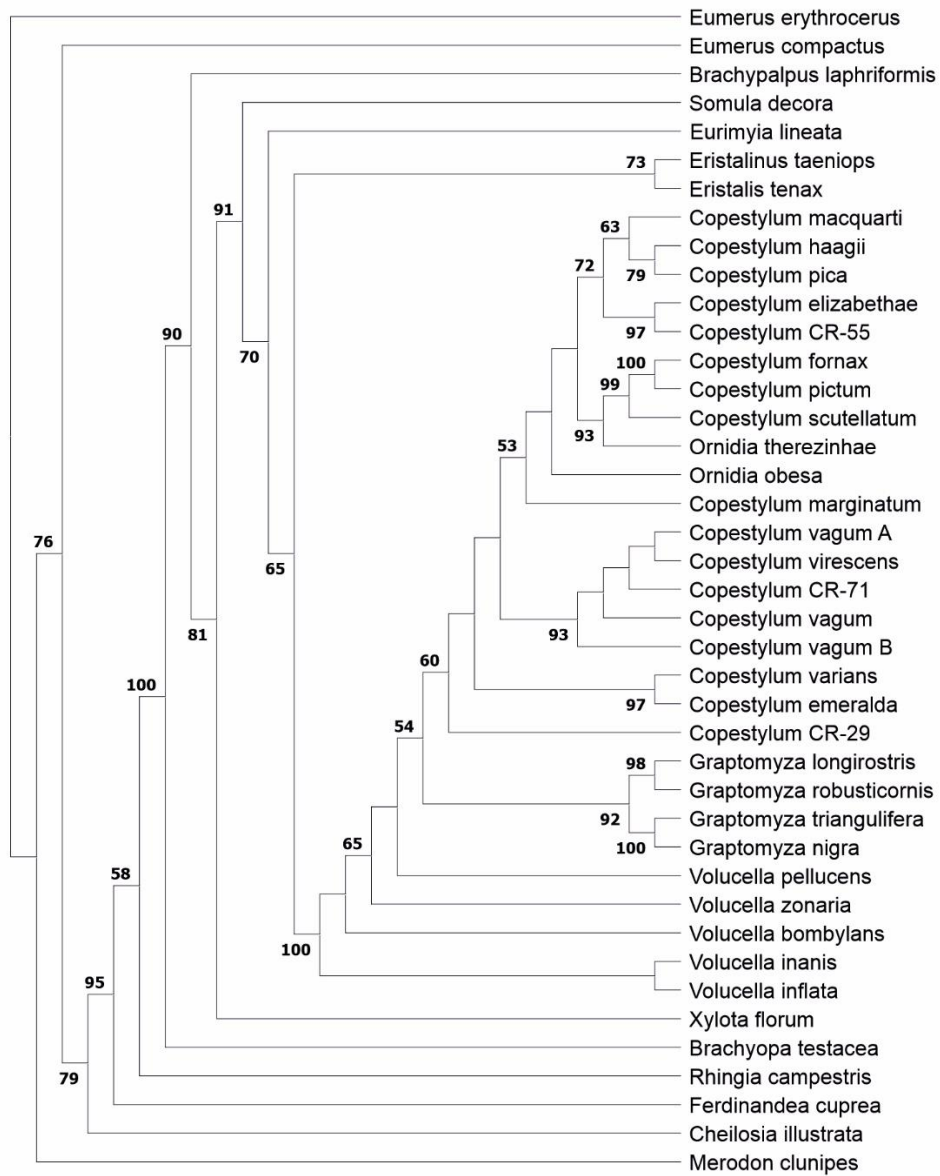
<sup>2</sup> National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, UK. Email: grahamrotheray@googlemail.com

F. Christian THOMPSON<sup>3</sup>

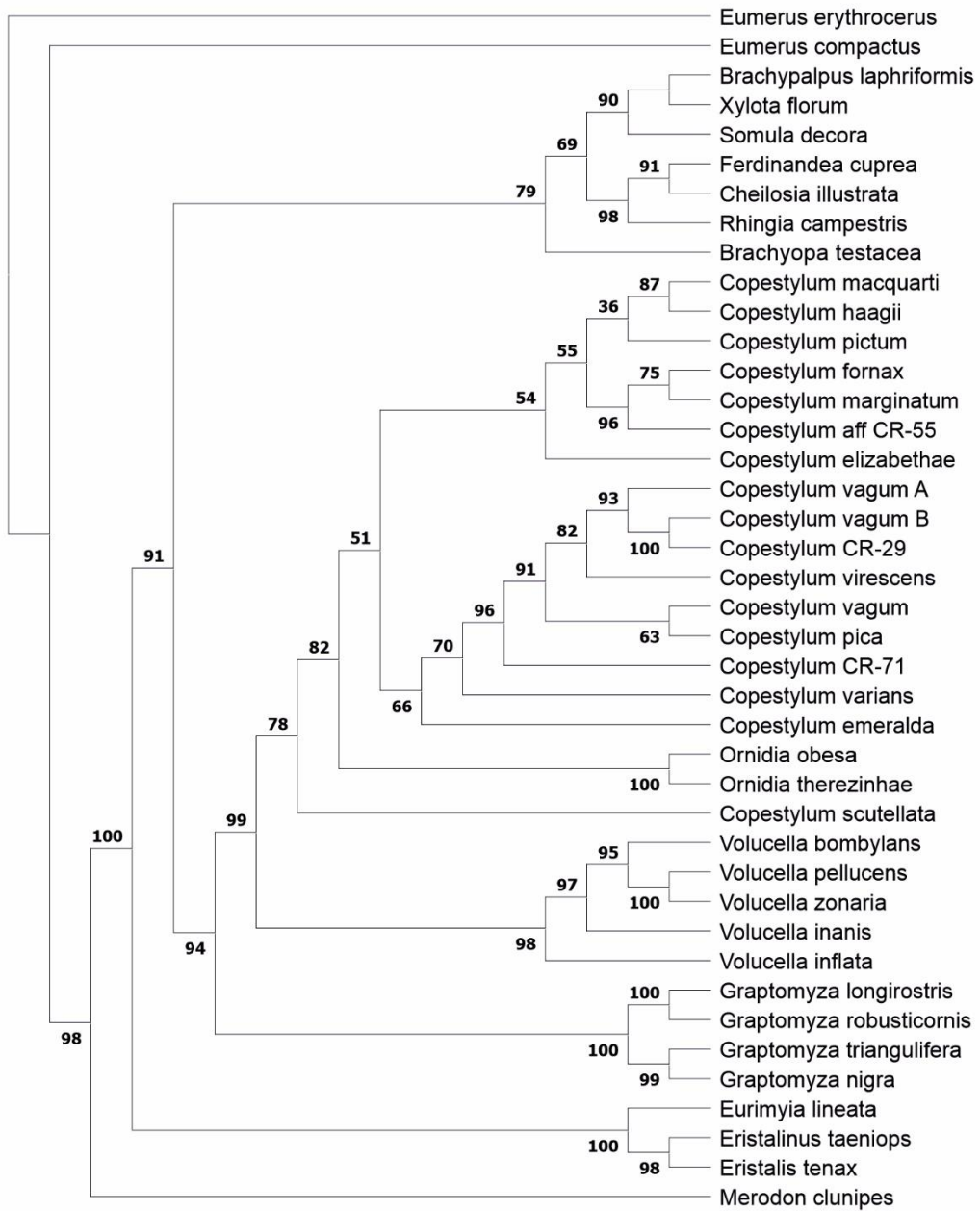
<sup>3</sup> National Museum of Natural History, Department of Entomology, Smithsonian Institution, 10th Street & Constitution Avenue NW, Washington, D.C., 20560-0169, USA. Deceased.

**Figure captions**

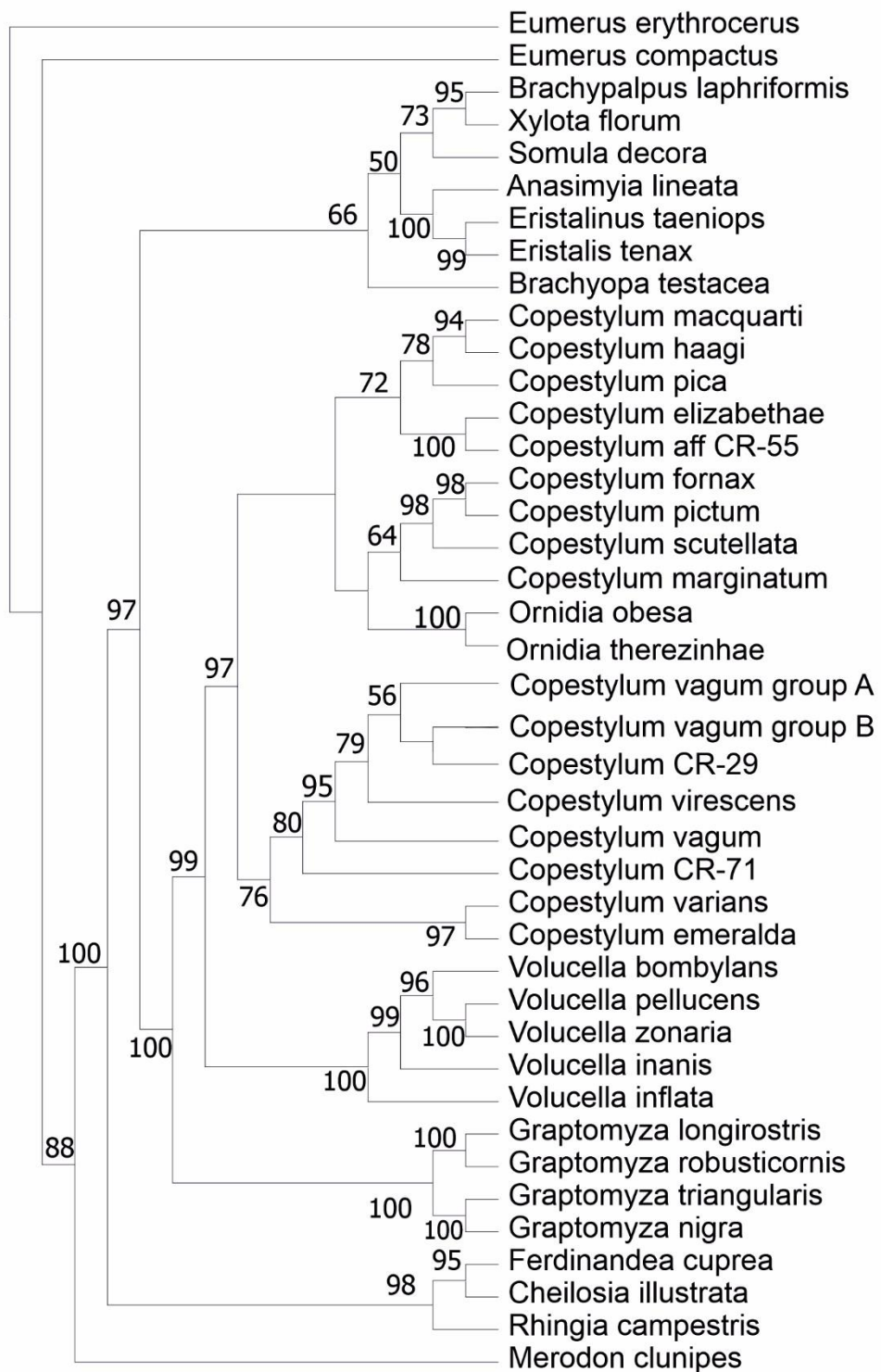
**Fig. 1:** Maximum likelihood tree for morphological data. Ultrafast bootstrap values >50% indicated at each node.



**Fig. 2:** Maximum likelihood tree for molecular data. Ultrafast bootstrap values >50% indicated at each node.



**Fig. 3:** Maximum likelihood analysis of combined data. Ultrafast bootstrap values >50% indicated at each node.



**Table 1.** Specimens used for molecular and morphological study.

**Table 2.** Specimens used for morphological study.

**Appendix 1.** Descriptions of characters and character states of the imagoes.

01. Body length: small <8 mm long (0); large >8 mm long (1); very large > 10 mm (2).
02. Body colouration: not obvious for mimicry or crypsis (0); mimicry (1); or crypsis (metallic, shining) (2).
03. Shape of head from above: about 2x as wide as long (0); more than 2x as wide as long (1).
04. Distribution of hairs on arista: without hairs or with short hairs (0); plumose (1).
05. Length of third antennal segment: about as long as broad (0); elongate, up to 2x as long as broad (1); elongate, more than 2x as long as broad (2).
06. Shape of third antennal segment: oval (0); elongate and parallel sided (1); elongate and broader at base (2).
07. Distance between eyes at level of antenna: about the same (0); < 2x apart at lower eye margin (1); > 2x apart at lower eye margin (2).
08. Length of eye contiguity in male: eyes not meeting (0); length of eye contiguity less than length of ocellar triangle (1); length of eye contiguity 1–3x length of ocellar triangle (2); length of eye contiguity >3x length of ocellar triangle (3).
09. Density of eye pilosity: sparse (0); dense (1); missing (2)
10. Distribution of eye pilosity: band down centre of eyes (0); reaching lower margin (1); inapplicable (?).
11. Length of eye pilosity: equal or smoothly changing (0); mixed long and short (1); inapplicable (?).
12. Colour of eye pilosity: unicolorous (0); striped (1); inapplicable (?).
13. Position of facial tubercle: absent (0); below centre of face (1); at centre of face (2).
14. Shape of face between antennae and tubercle: curved in lateral view (0); almost straight in lateral view (1).
15. Dusting of sides of face: with light dusting (0); heavy dusting (1); bare (no dusting) (2).
16. Pruinosity of sides of face: absent / not applicable (0); pruinose patch/stripe (1); covered in pruinosity (2); bare (3).
17. Sides of face, shape: concave (0); straight, at same level (1); inflated (2); convex (tubercles) (3).
18. Anterior view of sides of face: not tapering (0); tapering smoothly from tentorium (1); tapering sharply from cheeks (2).
19. Vittae on face: absent (0); present (1).
20. Colour of facial pilosity: unicolorous (0); mixed (1); absent (2).
21. Postpronotum size: rounded (0); very rounded (1); flattened (2).
22. Notopleuron, number of bulges: absent (0); one (1); two (2).
23. Notopleuron: size of outer bulge raised but not bulging (0); bulging outward like a bubble projecting clear of dorsum (1); absent / not applicable (?).
24. Thoracic bristles: absent (0); present (1).
25. Prescutellar bristles: absent (0); present (1).
26. Length of pile on scutum compared with width of front tibia: shorter (0); longer (1).
27. Composition of pile on scutum: uniform (0); mixed length (1).
28. Constitution of vittae on dorsum: absent (0); pruinosity (1); integumental colour (2); setae (3).
29. Pilosity of anterior anepisternum: pruinose (0); pilose (1); bare (2).
30. Pilosity of posterior anepimeron: pruinose (0); pilose (1); bare (2).
31. Surface of scutellum: without depression (0); with complete depression (1); with depression at apex (2); with concentration of punctures at apex (3).
32. Length of pile on scutellum compared with width of front tibia: shorter (0); longer (1).

33. Composition of pile on scutellum: uniform (0); mixed length (1).
34. Density of pile on scutellum: not densely pilose (0); densely pilose (1).
35. Bristles around scutellum margin: absent (0); complete (1); missing at apex (2).
36. Tubercles supporting apical bristles: small (0); large (1).
37. Colour of scutellum in relation to dorsum of thorax: concolorous (0); not concolorous (1).
38. Posterior apex of middle tibiae: setae not longer than rest (0); setae longer than rest (1) bristles (2).
39. Colour of leg pilosity: unicolorous (0); mixed (1).
40. Density of leg pilosity: not densely pilose (0); densely pilose (1).
41. Size of middle femora: not swollen (0); swollen (1).
42. Extension of CuA<sub>1</sub> beyond apical cross vein: present (0); absent (1).
43. Extension of M<sub>2</sub> beyond apical cross vein: present (0); absent (1).
44. Closure of R<sub>1</sub> (marginal cell): open (0); closed without a bulge (1); closed with a slight bulge (2); closed with a large bulge (3).
45. Shape of upper marginal cross vein M<sub>1</sub>: recessive (0); not recessive (1).
46. Microtrichia on wing: covered entirely (0); bare (1); bare at base (2); base and centre bare (3).
47. Appearances of wings: no marks (0); marks (1); infuscated (2).
48. Position of brown marks: one main mark at centre (0); at apex (1); several marks (2);
49. Shape of abdomen from above: subrectangular (0); somewhat wider than long (1); much wider than long (2); quadrate (3).
50. Width of abdominal segments compared to thorax: as wide as thorax (0); wider than thorax (1); much wider than thorax (2).
51. Point of maximum width laterally of abdominal segments: no projecting point (0); anterior shoulders of tergite 2 (1); posterior apex of tergite 2 (2).
52. Colour pattern of tergite 2: no markings (0); pair of spots (1); pale band (2).
53. Curvature of tergite 4: not down curved (0); slightly down curved (1); much down curved (2).
54. Length of tergite 4 in relation to tergite 3: tergite 4 shorter (0); tergite 4 same length or longer (1).
55. Relative length of pilosity on dorsum of tergite 3 as compared with tergite 4: same length (0); tergite 4 with longer pilosity (1).
56. Pilosity of tergite 4: equal length (0); unequal length (1).

## Appendix 2. Description of immature characters and character states.

01. Projection supporting antennomaxillary organs: the antennomaxillary organs are mounted on projections that vary in length and shape. A short, rounded dome, like a ball cut in half (0); a longer, straight sided cylindrical projection, like a tube (1) or, as (1) but stepped with a wider basal and a narrower apical stage (2).
02. Two staged supporting projection: the apical section may be a single structure (0) or, it is bifurcated (1), if inapplicable coded as unknown (?).
03. Sclerotization of the mandibular lobes: The mandibular lobes are a pair of food-gathering organs next to the mouth, and are a unique apomorphy for the Eristalinae sensu stricto. They are placed where the fleshy pseudocephalon has fused with the mandibular sclerite, and they have variation in degree of sclerotization (ROTHERAY & GILBERT 1999). The mandibular lobes may be fleshy (0); black and heavily sclerotized (1) or they may be brown and less heavily sclerotized (2).
04. Position of the mandibular lobes: The position of the mandibular lobes varies in relation to the cavity in front of the mouth. The mandibular lobes may be external to this cavity (0); partially inside (1) or completely inside (2).
05. Vestiture of the dorsal lip: The dorsal lip is another unique apomorphy of the Eristalinae. It is situated between the mouth and the base of the projections bearing antennomaxillary organs and appears as a transverse strip, which may be bare (0) or have setae (1).
06. Protruding mouth hook: The apex of the larval mandible is a mouth hook, which partially protrudes from the mouth (0), is large and almost completely protruding (1) or is reduced and non-protruding (2).
07. Size of the lateral lips: The lateral lips are a unique apomorphy of the Syrphidae and are a pair of dome-shaped, fleshy, food gathering organs on either side of the mouth cavity. By landmark sensilla, they are part of the prothorax (ROTHERAY & GILBERT 1999) and they vary in size and development. They may be slight and little projecting (0), larger and more defined (1) or, well-developed and clearly distinguished (2).
08. Basal vestiture of the lateral lips: The base of the lateral lips coated in various types of setae. Setae may be short (0), elongate and cylindrical in cross-section (1) or, long and flattened (2).
09. Apical vestiture of the lateral lips: The apex of the lateral lips coated in setae that are short (0) or long (1).
10. Vestiture of the anterior fold: Apically, the prothorax curves down to the base of the antennomaxillary organs. This part of the prothorax is well-developed in the Eristalinae and is the anterior fold. It may lack sclerotized setae or spicules (0) or, it may be coated in transverse rows of spicules (1).
11. Size of spicules on anterior fold: The spicules of the anterior fold may be even sized (0) or, variable in size (1), inapplicable coded as unknown (?).
12. Distribution of spicules on anterior fold: The spicules of the anterior fold may occur broadly over the anterior fold (0) or, they may occur in a narrow, transverse band (1), inapplicable coded as unknown (?).
13. Presence of spicules on the dorsum of the prothorax: The dorsum of the prothorax has three, longitudinal lines indented into the integument that are unique to the Syrphidae (ROTHERAY & GILBERT 1999). Between these lines spicules may be absent (0) or, they may be present (1).
14. Presence of anterior spiracles: On the posterolateral margins of the prothorax a pair of anterior spiracles may (0) or, may not be present (1).
15. Number of spiracular openings: The anterior spiracles may have 1 or 2 spiracular openings (0) or, 3 or more openings (1).

16. Length of anterior spiracles: The length of an anterior spiracle may be as long as basally broad (0) or, it may be longer than broad (1).
17. Presence of spicules on the anterodorsal margin of the mesothorax: The anterodorsal margin of the mesothorax may lack transverse rows of spicules (0) or, such spicules may be present (1).
18. Presence of spicules on the lateral margins of the mesothorax: The lateral margins of the mesothorax may lack spicules (0) or, such spicules may be present (1).
19. Number of spicules on the lateral margins of the mesothorax: The number of spicules per group may be up to 10 (0) or, more than 10 (1), if inapplicable coded as unknown (?).
20. Presence of spicules on the anterodorsal margin of the metathorax: The anterodorsal margin of the mesothorax may lack spicules (0) or, spicules may be present (1).
21. Presence of spicules on the lateral margins of the mesothorax: The lateral margins of the mesothorax may lack spicules (0) or, spicules may be present (1).
22. Size of mesothoracic prolegs: The ventral aspect of the mesothorax may have prolegs i.e. a pair of crochet-rimmed projections with a planta or indented apex. This indentation represents a muscle attachment point, which contracts the proleg. Mesothoracic prolegs may be absent (0); weakly developed (1) or, strongly developed (2).
23. Presence of spicules on the ventral aspect of the metathorax: Spicules may be absent (0); spicules may be aggregated into two groups (1) or, a transverse row of spicules may be present (2).
24. Vestiture of the thorax: Vestiture in the form of setae may coat the thorax and may be short (0) or long (1).
25. Shape of thorax: The outline shape of the thorax may be truncate (0); broadening to apex (1) or, tapering to apex (2).
26. Number of sensilla on ventral aspect of the abdomen: The number of sensilla varies from 2 pairs (0) to 3 pairs (1) per segment.
27. Abdominal locomotory organs: Paired locomotory organs occur on segments 1–6/7 and may appear as simple, raised domes lacking crochets (0), prolegs and crochets (1) or, suckers i.e. centrally indented structures with a distinctly raised rim (2).
28. Presence of prolegs or suckers on abdominal segments: Prolegs and suckers may not be present on the first 7 abdominal segments (0) or, they may be present (1).
29. Number of crochet rows: Crochets may not be organised into rows (0), form 2 rows (1), or, form 3 or more rows (2), if inapplicable coded as unknown (?).
30. Organisation of crochet rows on prolegs: Crochet rows may be aggregated into a group (0); form straight, transverse rows (1) or, form curved rows (2), if inapplicable coded as unknown (?).
31. Numbers of crochets in the primary row: Crochets in the anterior or first row are usually larger than any behind. The number of crochets in the primary row may be up to 5 (0) or, more than 6 (1), if inapplicable coded as unknown (?).
32. Presence of crochets on prolegs: Crochets may be absent on posterior prolegs, segments 5/6–7 (0) or, they may be present on these segments (1), if inapplicable coded as unknown (?).
33. Spicules between or posterior to prolegs: In addition to crochets, spicules may be present between or behind the prolegs (1) or, spicules may be absent (0), if inapplicable coded as unknown (?).
34. Number of lappets on the anal segment: The anal segment usually has tapering, fleshy projections or lappets on the dorsal and/or lateral margins. The anal segment may have 4 pairs (0) or 3 pairs (1) of lappets.

35. Number of sections of the anal segment: The dorsal and lateral margins of the anal segment have more or less continuous indented, transverse lines dividing it into tapering sections. There may be two (0) or three (1) sections.
36. Size of lappets: The posterior, and usually most dorsal, first pair of lappets may be longer than the middle or second pair (0) or, the middle pair may be longer (1), or these pairs of lappets may be equal in length (2).
37. Sensilla on first pair of lappets: In addition to the apical sensilla, an isolated sensilla may be present on the lower lateral margin of the first pair of lappets (1) or, such sensilla may be absent (0).
38. Size of the anal segment: In relation to the length of abdominal segment 6, the anal segment may be slightly longer (0), shorter (1) or, much longer (2).
39. Cross sectional body shape: In cross section the body shape varies from being subcylindrical (slightly wider than deep) (0), to slightly (1) or greatly (2) dorsoventrally flattened or, cylindrical (as wide as deep) (3).
40. Setae on ventrolateral abdominal margin: The lower side of the abdomen may have setae forming a line (1) or such a line of setae may be absent (0).
41. Length of the posterior respiratory process (prp): An almost unique apomorphy of larval Syrphidae is the fusion of the paired posterior spiracles to form a variably long, bulbous to stick-like projection, the prp, on the anal segment. The length of the prp may be about the same as body width (0), shorter (1), slightly longer (2) or much longer (3) than body width.
42. Width of thoracic vestiture: narrow (0), broad (1).

Lab codes	Species	Locality data (FMNH Luomus specimen ID URI's included if available)	COIa + COIb	28S
MZH_Stahls_Y2261	<i>Eumerus erythrocerus</i> Loew	South Africa, Kwazulu-Natal, Royal Natal National Park, The Crack path, 28°40'58,7"S 28°56'33,1"E, 22.ii.2016, G. Ståhls leg.  <a href="http://id.luomus.fi/GM.15475">http://id.luomus.fi/GM.15475</a>	OP712679	OP730906
MZH_Stahls_Y1732	<i>Eumerus compactus</i> van Doesburg	South Africa, Kwazulu-Natal, Royal Natal National Park, The Crack, 9.xii.2012, A. Vujic leg.	OP712678	NS
MZH_Stahls_Y1247	<i>Merodon clunipes</i> Sack	Greece, Samos island, Kosmadei, 37°45'41N 26°39'38E, 568 m, 12.VI.2010, S.Rojo, G.Ståhls & A.Vujić leg.	MH521920, HE653244	HE797749
MZH_Stahls_Y258	<i>Rhingia campestris</i> Meigen	Finland 669:40, N: Sibbo, Hindsby, 60°21'05"N 25°11'50"E, 26.V.2004, G. Ståhls leg.	EU431491	AY261744
MZH_Stahls_Y1354	<i>Cheilosia illustrata</i> (Harris)	Finland, Kb: Ilomantsi, Mekrijärvi Res. Station, 62°46'03"N 30°59'10"E , 8.VII.2010, G. Ståhls & E. Rättel leg.	MH521946, MH495987	MH426728
MZH_Stahls_Y190	<i>Ferdinanda cuprea</i> (Scopoli)	Finland, Ta: Lammi, Evo, 61°13'12"N 25°09'01"E, 15.VI.2004, G. Ståhls leg.  <a href="http://id.luomus.fi/GJ.2215">http://id.luomus.fi/GJ.2215</a>	MH521924, EU431486	EU431455
MZH_Stahls_Y1854	<i>Brachyopa testacea</i> (Fallén)	Russia, Altay, Teletskoe lake area, 51°47'29.502N 87°19'06.11E, 23-25.VI.2013, G. Ståhls leg.	KM224508	KM224492
MZH_Stahls_Y389	<i>Xylota florum</i> (Fabricius)	Finland, Terjärv, 26.VII.2006, G. Ståhls leg.  <a href="http://id.luomus.fi/GJ.2376">http://id.luomus.fi/GJ.2376</a>	OP712682	OP730911
MZH_Stahls_Y679	<i>Eristalis tenax</i> (L.)	Greece, Lesvos, nr Sikaminia, 11.V.2007, G. Ståhls leg	MH521922, MH549217	MH430044
MZH_Stahls_Y1824	<i>Eristalinus taeniops</i> (Wiedemann)	South Africa, Bergville (Hillside Farm), 6.XII.2012, C. Pérez-Bañón & S. Rojo leg.	OP712683	OP730909

MZH_Stahls_Y337	<i>Eurimyia lineata</i> (Fabricius)	Canada, British Columbia, Vancouver island, Nanaimo, Buttertub Marsh, N 49°10'25" W 123°58'03", 5.V.2005, alt. 63 m, W. van Steenis leg.  <a href="http://id.luomus.fi/GJ.2248">http://id.luomus.fi/GJ.2248</a>	OP712680	OP730907
MZH_Stahls_Y1788	<i>Brachypalpus laphriformis</i> (Fallén)	Finland, U: Helsinki, Santahamina, 3.VII.2012, S. Kerppola leg.	MH521919 MH495995	MH543335
MZH_Stahls_Y468	<i>Somula decora</i> Macquart	USA, Northampton Co., NC, 5.V.2005, B. Kondratieff, R. Zuellig, & R.F. Kirchner leg.  <a href="http://id.luomus.fi/GJ.2454">http://id.luomus.fi/GJ.2454</a>	OP712681	OP730908
MZH_Stahls_Y224	<i>Graptomyza robusticornis</i> van Doesburg  ( <i>robusticornis</i> species group)	Madagascar, Fianarantsoa Prov., Ranomafana NP, Talatahely región, O.A, 02.XII.2004, X. Mengual leg.  <a href="http://id.luomus.fi/GJ.2244">http://id.luomus.fi/GJ.2244</a>	EU431484	EU431453
MZH_Stahls_Y2574	<i>Graptomyza triangulifera</i> (Bigot) ( <i>varia</i> species group)	Uganda, Western Region, Kasese District, Rwenzori Mountains N.P., 00°20'58.63" N 30°01'46.56" E, 1740 m., 5.xii.2018, G. Ståhls leg.	OP712697	OP730925
MZH_Stahls_Y2575	<i>Graptomyza nigra</i> Bezzi  ( <i>aurea</i> species group)	Uganda, Western Region, Kasese District, Rwenzori Mountains N.P., along Mahoma Trail, 00°21'28.85" N 30°01'0.84" E, 2100 m., 4.xii.2018, G. Ståhls leg.	OP712698	OP730926
MZH_Stahls_G422	<i>Graptomyza longirostris</i> Wiedemann	Malaysia, Poring, VIII.1999	KM270878	KM270847
MZH_Stahls_Y470	<i>Copestylum haagii</i> (Williston)	USA, New Mexico, Chaves Sagebrush Valley road at Squa Canyon road, 32.57°N, 105.50°W, 1-10.V.2004, ME Erwin leg.	OP712691	OP730918
MZH_Stahls_S299	<i>Copestylum fornax</i> (Townsend)	USA, Arizona, Cochise Co. Portal, 31°53.26N, 100°10.25W, 12.VII-17.VII.2002, malaise trap, M. Hauser leg.	OP712686	OP730912
MZH_Stahls_Y118	<i>Copestylum maquarti</i> (Curran) species group	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash; 1278 m, 24°27.25' S, 65°17.83' W, 27.X-14.XI.2003; ME Irwin, FD Parker leg.	OP712684	NA

MZH_Stahls_Y494	<i>Copestylum marginatum</i> (Say)	Mexico, Hidalgo, Metztitlan, 26.09.2005, P266, A. Paola Martinez leg.	NS	NS
MZH_Stahls_Y2794	<i>Copestylum</i> Thompson aff CR-55	Venezuela, Lara state, P.N. Yacambú, sector “El Blanquito”, roadside, 29.01.2007, G. Ståhls leg.	OP712695	OP730923
MZH_Stahls_Y81	<i>Copestylum</i> Thompson CR-29	Costa Rica, Heredia, INBio parque, 14.II.2003, F. C. Thompson leg.	OP712687	OP730914
MZH_Stahls_Y507	<i>Copestylum elizabethae</i> Hancock & Rotheray, 2007	Trinidad, Morne Blue, 1-15.VII.2006, larva ex bromeliad	OP712694	OP730921
MZH_Stahls_Y120	<i>Copestylum pictum</i> (Wiedemann)	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash; 1278 m, 27.X/14.XI.2003; ME Irwin, FD Parker; 24°27.25' S, 65°17.83' W	OP712689	OP730916
MZH_Stahls_Y119	<i>Copestylum pica</i> (Schiner)	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash; 1278 m, 27.X/14.XI.2003; ME Irwin, FD Parker; 24°27.25' S, 65°17.83' W	OP712693	OP730920
MZH_Stahls_Y124	<i>Copestylum scutellatum</i> (Macquart)	Chile, Regio IV, Limari Prov., Fray Jorge Nat'l Park, malaise in picnic area; 12/31.XII.2003; 250 m; M.E. Irwin, 30°38.38' S, 71° 39.00' W	OP712690	OP730917
MZH_Stahls_Y2793 (Y357 XM-2008)	<i>Copestylum virescens</i> (Williston) ( <i>vagum</i> -group)	Colombia, Dpto Caldas, Manizales, Corrg. Las Palomas, Reserva Natural Río Blanco, 18-II-2006, 2200-2500 m, 5°04'N 75°26.2'W, X. Mengual leg.	EU431481	EU431450
MZH_Stahls_Y481	<i>Copestylum vagum</i> (Wiedemann)	Colombia, Dpto. Cauca, Corrg. El Tambo, 20 De Julio, 2900 m, 6-8/III/2006, C. Prieto leg.	OP712692	OP730919
MZH_Stahls_S239	<i>Copestylum</i> sp. ( <i>vagum</i> species group A)	Costa Rica, Heredia, INBio parque, 14.II.2003, F. C. Thompson leg.	NS	NS
MZH_Stahls_S240	<i>Copestylum</i> sp. ( <i>vagum</i> species group B)	Costa Rica, Heredia, INBio parque, 14.II.2003, F. C. Thompson leg.	NS	NS
MZH_Stahls_Y080	<i>Copestylum varians</i> (Bigot)	Costa Rica, Heredia, INBio parque, 14.II.2003, F. C. Thompson leg.	partial, NS	OP730913
MZH_Stahls_Y2792	<i>Copestylum</i> sp. CR-71 (BOLD BIN:ABY2393)	Colombia, Dpto Caldas, Manizales. Corrg. Las Palomas, Reserva Natural Río Blanco. 18-II-2006. 2200-2500 m. 5°04'N 75°26.2'W, X. Mengual leg.	NS	OP730922
MZH_Stahls_Y2798	<i>Copestylum emeralda</i> (Hull)	Peru, Dpto Junín, Chanchamayo Prov., Distrito San Ramón, near La Merced, Fundo Génova, Selva, point	NS	OP730927

		#4, 24.iii.2008, 1053 m., 11°05'44"S 75°21'19"W. Project AECID A/013484/07.		
MZH_Stahls_Y502	<i>Ornidia obesa</i> (Fabricius)	Venezuela, Aragua state, Monumento Natural Pico Codazzi, 2185 m, N10° 24.387' W067° 18.559', 25.01.2007, G. Ståhls leg.	OP712688	OP730915
MZH_Stahls_Y2022	<i>Ornidia therezinhae</i> Da Silva Carvalho-Filho & Esposito	Brazil, Minas Gerais state, 10.XII.2013, Mirian N. Morales leg.	OP712696	OP730924
GJAA.1415	<i>Volucella bombylans</i> (L.)	Finland, Enontekiö, Vuontisjärvi 15.VII.2020, G. Ståhls leg. <a href="http://id.luomus.fi/GJAA.1415">http://id.luomus.fi/GJAA.1415</a>	OP712685	OP730910
MZH_Stahls_G388	<i>Volucella inflata</i> (Fabricius)	Germany, Sachsen-Anhalt, 17.3.1999, F. Dziock leg.	AY261688	AY261734
MZH_Stahls_S585	<i>Volucella inanis</i> (L.)	Finland, N: Helsinki, VIII.2006, G. Ståhls leg.	AY261690	AY261736
MZH_Stahls_Y1974	<i>Volucella pellucens</i> (L.)	Russia, Primorsk region, near Gorno-Taezhnoye biol. stat., 43°41'43"N 132°09'50", 4.IX.2014, G. Ståhls & E. Rättel leg	MH521923, MH495996	MH445921
MZH_Stahls_S262	<i>Volucella zonaria</i> (Poda)	Greece, Lesvos, Vatoussa, 5.5.2001, S. Rojo & C. Perez-Banon leg.	EU431493	EU431462

NA= Not Available, NS=Not Submitted.

In Uganda, collecting permits were obtained from the Uganda Wildlife Authority (UWA/COD/96/05) and the Uganda National Council for Science and Technology (UNCST) (NS642). None of the collected species occur on red lists or are considered to be endangered/threatened, neither is any ranked in IUCN lists or protected by CITES.

The “Guidance document on the scope of application and core obligations of Regulation (EU) No 511/2014 of the European Parliament and of the Council on the compliance measures for users from the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilisation in the Union (2021/C 13/01)”, the “Paragraph 2.3.3.1. Research and development” states: “Identification of a genetic resource is also to be considered to precede utilization. Taxonomic identification of biological or genetic material, by morphological or molecular analysis, including through the use of DNA sequencing, is not considered to constitute utilization in the meaning of the EU ABS Regulation, as it does not involve the discovery of specific genetic and/or biochemical functionality. There is no difference whether the taxonomic identification points to a previously named entity or an unnamed entity. Taxonomic studies, where they do not look into genetic properties (functionality), are thus not within scope of the EU ABS Regulation.”

Taxon	Sex	Country	Locality	Specimen code
<i>Cheilosia illustrata</i> (Harris)	male	Germany		USNM ENT 00037131
<i>Rhingia campestris</i> Meigen	male	Netherlands		USNM ENT 00037134
<i>Ferdinandea cuprea</i> (Scopoli)	male	Germany		USNM ENT 00037129
<i>Xylota florum</i> (Fabricius)	male	Denmark		USNM ENT 00037135
<i>Eristalis tenax</i> (L.)	male	USA	Maryland	USNM ENT 00037132
<i>Eurimyia lineata</i> (Fabricius)	male	Denmark		USNM ENT 00037136
<i>Graptomyza longirostris</i> Wiedemann	male	Philippines		USNM ENT 00037126
<i>Copestylum</i> Thompson CR-29	male	Costa Rica		USNM ENT 00075305
<i>Copestylum maquarti</i> (Curran)	male	Mexico		USNM ENT 00037143
<i>Copestylum haagii</i> (Williston)	male	USA	Texas	USNM ENT 00037141
<i>Copestylum fornax</i> (Townsend)	male	USA	Arizona	USNM ENT 00037140
<i>Copestylum marginatum</i> (Say)	male	USA	California	USNM ENT 00037142
<i>Copestylum pictum</i> (Wiedemann)	male	Ecquador		USNM ENT 00037144
<i>Copestylum pica</i> (Schiner)	male	Costa Rica		INBIOCRI002133870
<i>Copestylum scutellatum</i> (Macquart)	male	Chile		USNM ENT 00037139
<i>Copestylum vagum</i> (Wiedemann)	male	Costa Rica		INBIOCRI001116203
<i>Copestylum varians</i> (Bigot)	male	Costa Rica		INBIOCRI001888082
<i>Ornidia obesa</i> (Fabricius)	male	Dominica		USNM ENT 00037124
<i>Volucella bombylans</i> (L.)	male	USA	Maryland	USNM ENT 00019365
<i>Volucella inflata</i> (Fabricius)	male	France		USNM ENT 00037149
<i>Volucella inanis</i> (L.)	male	Czech Republic		USNM ENT 00037145
<i>Volucella pellucens</i> (L.)	male	Poland		USNM ENT 00037146
<i>Volucella zonaria</i> (Poda)	male	Hungary		USNM ENT 00037147