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A conspectus of the flower fly genus *Allograpta* (Diptera: Syrphidae) with description of a new subgenus and species

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Abstract

A new subgenus [*Allograpta* (***Costarica*** Mengual & Thompson), type *Allograpta zumbadoi* Thompson], and one new species [*Allograpta* (*Costarica*) ***nishida*** Mengual & Thompson; type-locality: Costa Rica, type-depository: Instituto Nacional de Biodiversidad de Costa Rica] of flower flies (Diptera: Syrphidae) are described from the Neotropical biotic region. A checklist of the world species of *Allograpta* including synonyms is provided, and a key to and diagnoses of the subgenera are also supplied. The phylogenetic relationships among *Allograpta* species, representing all hitherto detected morphological diversity of the genus, and related genera were studied under parsimony based on morphological characters.

Key words: *Costarica*, identification key, Syrphinae, taxonomy

Introduction

Allograpta flower flies are common in all areas except the extreme north and south and most of the Palaearctic Region. These flies are pollinators and show considerable variation in morphological characters, such as color pattern and head shape. The immatures of most species are predators of hemipteran pests (see Rojo *et al.* 2003 for review of published prey records). Recent studies have revealed that some species are secondarily leaf-miners (Nishida *et al.* 2002), stem-borers (Zuijen & Nishida 2009) or pollen-feeders (Weng & Rotheray 2009). This major and important shift in biology from predation to phytophagy has highlighted the need for a reassessment of the genus *Allograpta*. This is the first review of the current classification of the group including a new name for the group of stem-boring species. All subgenera and species groups are morphologically diagnosed, and all names of included species in each subgenus or comparable grouping are given, as well as a key to subgeneric taxa. In order to provide a basis for further studies, morphological characters of *Allograpta* species and related genera, representing all known morphological diversity, were studied to explore their phylogenetic information content.

Other reports on the genus are in process. Mengual *et al*. (2008b) examined DNA sequence data and the immature stages will be analyzed. Then a phylogenetic assessment based on the combined dataset may provide resolution upon which to base a new and improved classification.

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History of the classification of *Allograpta* and related groups

Allograpta was established for the Nearctic species, *Scaeva obliqua* Say, as Osten Sacken felt that this species "... cannot well be placed in any of the existing genera of this group" (Osten Sacken 1875: 63). He noted differences from *Sphaerophoria* (small genitalia), *Toxomerus* [as *Mesograpta*] (male vertical triangle and mesonotal coloration) and while he said that "... it might be placed among the species of *Syrphus* with a linear abdomen," he noted that "*Scaeva obliqua* possesses in the structure of the eyes of the male, and in the peculiar markings of its abdomen, sufficient characters of its own." His name, *Allograpta*, "... is given in allusion to the peculiar coloration of the typical species." He provisionally placed *Scaeva emarginata* Say [now *Epistrophella* Dušek & Laská (1967) or *Epistrophe* (*Epistrophella*) Vockeroth (1969, 1992)] in *Allograpta* and suggested "... more than one *Syrphus* from Mexico and the West Indies belongs to the same group; as for instance *S. delineatus* Macq., but, of course, it is impossible to judge from descriptions alone." Later Osten Sacken (1877: 331) described a second species from California [*Allograpta fracta* Osten Sacken]. The peculiar characters that Osten Sacken mentioned for this genus, the male eye structure (dorsal ommatidia about twice as large as ventral ones) and the combination of oblique lateral and straight medial vittae on 4th and 5th terga are no longer considered significant as these characters vary considerably among species within the currently defined concept of *Allograpta*.

Williston was the first specialist on New World flower flies, with his PhD thesis being a revision of the North American species (Williston 1887). His concept of *Allograpta* (Williston 1882: 310, 1887: 96, 1888: 50, 1896: 87, 1908: 255) was the same as Osten Sacken's. However, in his last key (1908: 255) he noted that the group was "feebly characterized." Bigot (1883: 256) likewise considered the group as dubiously distinct.

Lynch Arribalzaga (1892: 58) recognized the genus and included the first Neotropical representative (*hortensis* Philippi).

While Shannon (1922; 1923) made major improvements in the classification of New World flower flies, his concept of *Allograpta* remained the same as Osten Sacken's and Williston's. He used the character of a premarginal sulcus on the abdomen (emarginate abdomen) in his first couplet to the key to genera of Syrphinae to separate the tribe Melanostomini from the tribe Syrphini. However he noted that *Allograpta* and about half the species of *Syrphus* also lacked the premarginal sulcus on the abdomen. Later when Shannon (1927: 2) described *Claraplumula* and *Fazia*, he separated these two genera along with *Scaeva* and *Syrphus* from *Allograpta* by the well-developed calypter and plumula.

Curran (1925b: 19, couplet 17) seems to be the first to have used the abdominal premarginal sulcus character to separate various Syrphini genera. *Allograpta* was grouped with those without a premarginal sulcus on the abdomen, but otherwise his definition of *Allograpta* remained the same as previous definitions (also Curran 1934: 255). Nevertheless, Curran greatly expanded the number of species included in *Allograpta* from 3 to 13, providing a key to them in 1932.

Fluke, in a series of papers (1931, 1933, 1935), addressed the classification of a number of syrphine genera, but did not mention *Allograpta*. In his 1935 paper, he introduced the character of the pilosity of the metasternum, whether bare or pilose. In 1942, Fluke revised the Neotropical Syrphini, dealing with *Allograpta* and its related groups for the first time. He separated *Allograpta* (current definition) from other genera by its pilose metasternum and lack of a premarginal sulcus on the abdomen. He recognized *Allograpta*, *Claraplumula* and *Epistrophe*, with subgenus *Fazia*, although "*Epistrophe*, *Fazia* and *Allograpta* are scarcely separable." This classification was reasonable except that Fluke included some species of *Ocyptamus* in his *Epistrophe*. He also noted that "A careful study of the genitalia of the males of *Allograpta*, *Fazia*, *Claraplumula* and *Epistrophe* shows the close relationship of these groups." Later he published his work on the male genitalia (Fluke 1950), where he restricted the taxonomic concept of *Epistrophe*, recognized *Allograpta*, *Claraplumula*, and *Fazia*, but left a few species of *Allograpta* in *Stenosyrphus* (*Episyrphus* and *Metepistrophe*).

In 1938, Enderlein published contributions to the knowledge of Syrphidae, which unfortunately was more of obfuscation than enlightenment. For the *Allograpta* group, he recognized *Fazia*, which he placed in the

Syrphini. *Allograpta* and his new genus *Chasmia* were placed in the Toxomerini. His *Chasmia* is a synonym of *Allograpta,* but he included one species (*quadricincta*) of *Toxomerus* in it. In *Allograpta*, he included a species of *Dasysyrphus* (*munzoi = Dasyrphus pauxillus*) and two species of *Ocyptamus* (*delimbata* and *schoenemanni*). His *Fazia* included only species of *Allograpta*, *sensu stricto*.

Frey (1946) in his revision of the syrphine genera followed previous workers in using the presence or absence of the premarginal sulcus of the abdomen to separate the genera related to *Epistrophe*. However, he separated *Epistrophe* and other genera from the *Allograpta* related groups by the lack of bright sharply defined yellow maculae on the pleuron. Then he divided the genera related to *Allograpta* first on the basis of facial shape as expressed as the shape of the oral opening (short and oval versus long and narrow). Finally *Sphaerophoria* was separated on its traditional characters of enlarged male genitalia. What is clear is that Frey apparently did not know the type of *Allograpta* as he would have realized that its facial shape is the same as his new genus, *Miogramma*. Under *Allograpta*, Frey merely wrote that the abdominal pattern well characterizes the genus. Under his *Miogramma,* he included a long discussion of how the group differs from *Epistrophe, Sphaerophoria, Xanthogramma, Obliosyrphus, Ischiodon, Meligramma* et alia, but no mention of *Allograpta*. Likewise, *Microsphaerophoria* was contrasted with *Sphaerophoria,* not *Allograpta*.

Hull (1949a), in his review of New World *Baccha,* included a key to the genera and subgenera related to *Baccha*. He separated *Allograpta* and *Epistrophe* from *Baccha* on the basis of the pilose metasternum and separated *Rhinoprosopa* from *Baccha* on the basis of its facial shape and widely separated antennal pits. However, his major work on the classification of flower flies (1949b) treated *Allograpta* and related groups as subgenera of *Epistrophe*. Unfortunately his concept of *Epistrophe* is "ein mischmash" [as Meigen (1822: 382) wrote of Fabricius' *Eristalis*]. Hull divided the syrphine genera first on whether there was a premarginal sulcus on the abdomen and then whether the metasternum was bare or pilose (Hull 1949b: 281, couplets 2–4). Then, after excluding *Afrosyrphus* and *Paragus* on antennal length, he was left with his *Epistrophe* and *Sphaerophoria* (1949b: 282. couplets 25–29). *Sphaerophoria* was separated by its traditional characters, especially enlarged male genitalia. Under *Epistrophe* he recognized as subgenera: 1) *Epistrophe* [= *Epistrophe sensu stricto*]; 2) *Allograpta* [= *Allograpta sensu stricto*], 3) *Fazia* [= *Fazia*, in part], 4) *Metallograpta* [= *Fazia*, in part], 5) *Metepistrophe* [= *Fazia*, in part], 6) *Chasmia* [= *Fazia*, in part], 7) *Claraplumula* [= *Claraplumula*], 8) *Allograptina* [= *Argentinomyia*], 9) *Phalacrodira* [= *Parasyrphus*] and he did not recognize the available names *Euryepistrophe, Heterepistrophe* and *Episyrphus*. He separated these subgenera mainly on facial shape, abdominal pattern and shape. *Allograpta* was separated from *Epistrophe* on abdominal pattern as he explained "I cannot see any valid distinctions in the genotype except upon the abdominal pattern for this group." Then he named *Metallograpta* for those *Allograpta* species with a projecting face; and *Metepistrophe* for those "species of *Epistrophe* in which the epistoma juts forward." He separated this new subgenus from *Fazia* based on abdominal shape (oval in *Fazia,* elongate in *Metepistrophe*).

Bankowska (1962), when revising the Palaearctic species of *Sphaerophoria*, re-examined the relationships of *Syrphus javanus* Wiedemann, a species placed in *Sphaerophoria* by some earlier authors. She concluded that *javanus* could not be placed in *Sphaerophoria, Xanthogramma* or *Ischiodon*. So, being unaware of *Allograpta* and the work of Frey (1946), she erected a new genus for *javanus*, *Helenomyia,* which became a junior objective synonym of *Miogramma* Frey and a subjective synonym of *Allograpta*. Apparently Shiraki (1963) also recognized the distinctiveness of *javanus* as he placed a synonym (*nakamurae* Matsumura) of it in *Paraxanthogramma*, but never formally published a description of the genus. The name was subsequently used in a work on the biological control of aphids in Taiwan by Tao & Chiu (1971).

Vockeroth (1969, 1973) was responsible for the current concept of *Allograpta*. His 1969 paper included 55 *Allograpta* species representing almost all biogeographic regions and he was the first to recognize that Old World species belonged to the New World genus. Additionally, he discussed the zoogeography of the taxon. He based his concept of *Allograpta* on the male genitalia ["Despite the great variation in many characters the male terminalia are very distinctive and separate the genus sharply from all others"]. While Vockeroth did not explicitly define *Allograpta* in terms of male genitalic characters, the key characters were 1) the superior lobes

fused to the hypandrium (in most syrphines these are articulating) and 2) basal part of the aedeagus enlarged and with dense black denticles (figs. 11–16).

Identification

The Nearctic species were treated by Vockeroth (1992). The last key to the Neotropical species of *Allograpta* is by Fluke (1942), but is inadequate as he mixed the species of *Allograpta* and *Ocyptamus* among his "*Epistrophe*" and did not include *Rhinoproposa*. *Rhinoprosopa* was treated as part of the genus *Baccha* by Hull (1949a: 101, couplets 3–5). Frey (1946: 166) provided a key to the Old World species of *Allograpta* as his *Miogramma*.

Format

Terminology follows Thompson (1999b). The classification followed here is that of the BioSystematic Database of World Diptera (Evenhuis *et al*. 2008) and follows from that of Vockeroth (1969) and the various regional Diptera catalogs (Knutson *et al*. 1975; Peck 1988; Smith & Vockeroth 1981; Thompson *et al*. 1976; Thompson & Vockeroth 1989. Also see older catalogs such as Harris 1835; Osten Sacken 1878; Aldrich 1905; Kertész 1910; Fluke 1956–7). We recognize that some alternatives to this classification scheme can be considered following recently published results of Mengual *et al*. (2008a, b), but these are based only on molecular characters and other proposals are forthcoming. So, for uniformity and universality, we here accept the traditional classification of flower flies. The format for and abbreviations found in the generic synonymies follow the BioSystematic Database of World Diptera (BDWD, Thompson 1999a). The acronyms used for collections likewise follow BDWD standards and their equivalents are given in the acknowledgments. In the species lists, the use of an asterisk (*) means that material of the species was examined and two asterisks (**) means type material of the name was examined. The species are listed alphabetically by biotic regions. For each species we provide the valid epithet, the author, year and page number of the original description followed by the original genus in parenthesis and the distribution. If synonyms exist, they are given in brackets after the distribution.

Phylogeny

Recent improvements in laboratory techniques have made it feasible to employ an increasingly higher number of genes for the study the phylogenetic relationships of various insect groups (Bybee *et al*. 2004; Brammer & von Dohlen 2007; Kutty *et al*. 2007; Schuh *et al*. 2009). The first phylogeny of the predatory flower flies (subfamily Syrphinae) based on molecular characters was published (Mengual *et al*. 2008a). It was the first time that the genus *Allograpta* was included in a molecular study. The results of the study brought light on the relationships among Syrphinae genera and discussed the current division of the subfamily in 4 tribes. Based on new interrelationships of *Allograpta* and related taxa found in this article, a molecular study further exploring these placements was recently published by Mengual *et al*. (2008b).

Morphological characters have used for inferring Syrphidae phylogenies. Rotheray and Gilbert (1989, 1999) scored larval characters for the Palaearctic genera of Syrphidae and presented the first cladistic analysis of the group. Hippa and Ståhls (2005) presented a list of morphological characters with phylogenetic information and their results reported the monophyly of the family and the tribe Pipizini as the sister group of subfamily Syrphinae. Morphological characters have also combined with molecular characters to improve resolution and accuracy. The first combined phylogeny for the family Syrphidae was published by Ståhls *et al*. (2003), also other authors used DNA and morphological characters for trying to solve systematics of groups within Syrphidae (see Cheng *et al*. 2000; Ståhls *et al*. 2004; Milankov *et al*. 2005, 2007; Masetti *et al*. 2006; Vujić *et al.* 2008).

TABLE 1. Diagnostic characters of *Allograpta* and related flower flies.

The following is a list of the morphological characters that seem to vary among the distinctive groups related to and included in the genus *Allograpta*. Although some of these characters are invariant for the included taxa, they will be useful when the syrphines as a whole are analyzed. Characters 7, 8 and 26 separate studied taxa from *Chrysotoxum*; characters 13 and 27 separate them from *Ocyptamus*; character 24 separate them from *Salpingogaster* and *Lapposyrphus* and 3 from *Leucopodella*.

0. Face [length], frontal view:
    1. short, less than half eye height.
    2. medium, about as long as eye height.
    3. long, more than eye height.
1. Face [width], frontal view:
    1. narrow, about 1/4 as wide as head.
    2. medium, about 1/3 as wide as head.
    3. broad, 1/2 or more as wide as head.
2. Face [shape / production], lateral view:
    1. straight, not produced anteriorly; oral apex in line with antennal bases (oral opening about 2 times as long as broad) (fig. 8).
    2. produced anteriorly; oral apex distinctly more prominent than antennal bases (oral opening 3 or more times longer than broad) (figs. 7, 9 and 10).
3. Facial tubercle:
    1. absent (fig. 9).
    2. distinct.
4. Facial tubercle [shape]:
    1. indistinct or not differentiated dorsally (fig. 8).
    2. distinct both dorsally and ventrally (fig. 6).
    3. indistinct or not differentiated ventrally (fig. 3).
5. Eye [male]:
    1. holoptic.
    2. narrowly dichoptic, separated by less than ocellar triangle width.
    3. broadly dichoptic, separated by more than ocellar width.
6. Antennal pits:
    1. confluent (fig. 17).
    2. distinctly separated (fig. 18).
    3. broadly separated (fig. 19).
7. Antenna [length]:
    1. short, shorter than facial length.
    2. long, longer than facial length.
8. Scape [length]:
    1. short, as long as broad or shorter.
    2. long, longer than broad.
9. Basoflagellomere [shape / length]:
    1. oval, as long as broad.
    2. suboval, longer than broad, but not more than 1.5 times as long as broad.
    3. elongate, more than 1.5 times as long as broad.
10. Scutum:
    1. concolorous laterally and medially.
    2. with bright pale (usually yellow) coloration laterally, at least from postpronotum to transverse suture.
11. Anepisternum, anterior flattened portion:
    1. bare.
    2. with a single row of pile.
    3. entirely pilose.

TABLE 1. (continued)

12. Scutellum [subscutellar fringe]:
    1. with complete row of pile on ventral surface.
    2. with pile restricted laterally, with median ventral surface bare.
    3. completely bare ventrally.
13. Metaepisternum:
    1. bare.
    2. with tuft or row of pile ventrad to spiracle.
14. Metasternum:
    1. bare.
    2. pilose.
15. Calypter:
    1. bare.
    2. ventral lobe pilose on dorsal surface.
16. Plumula:
    1. absent or greatly reduced, shorter than subalare (see fig. 130 in Matsuda 1970: 310).
    2. short, as long as subalare.
    3. long, about 2 times as long as subalare.
17. Metacoxa:
    1. with pile posteromedially.
    2. bare posteriorly.
18. Wing:
    1. microtrichose.
    2. bare basomedially, on basal 1/3 or less.
    3. bare on basal 2/3 or more.
19. Wing [pattern]:
    1. hyaline, without maculae.
    2. fasciate, with medial dark fascia.
    3. with apical dark macula (fig. 6).
    4. with anterior margin dark.
20. Wing [posterior margin]:
    1. simple.
    2. with minute, discrete, black sclerotized puncta.
21. Vein M1 [curvature]:
    1. oblique, slightly sinuate (figs. 1–6).
    2. perpendicular, straight or nearly so (see fig. 11 in Vockertoh 1969: 146).
22. Vein M1 [terminal position]:
    1. joining vein R4+5 basal to termination of vein R2+3.
    2. joining vein R4+5 approximately at level of termination of vein R2+3.
    3. joining vein R4+5 apically to termination of vein R2+3.
23. Alula [size]:
    1. as broad as or broader than cell BM.
    2. narrower than cell BM, but broader than cell C.
    3. as broad as or narrower than cell C.
    4. absent.
24. Vein R4+5 apically [curvature]:
    1. straight or nearly so.
    2. sinuate, with a shallow loop into cell R4+5.
    3. strongly sinuate, with a large loop into cell R4+5.
25. Abdomen [shape]:
    1. oval, broader than thorax.
    2. elongate with parallel sides, as wide as thorax.
    3. petiolate, basally constricted, apically expanded, always narrower than thorax at constricted area.

TABLE 1. (continued)

26. Abdomen [shape, cross-section]:
    1. flattened.
    2. distinctly convex as in *Chrysotoxum*.
27. Abdomen [length]:
    1. short, less than two times as long as thorax (including scutellum).
    2. elongate, two times as long as thorax, but less than three times.
    3. greatly elongate, three or more times as long as thorax.
28. Abdominal margins:
    1. without distinct premarginal sulcus or only weak one on 5th tergum.
    2. with distinct premarginal sulcus from 2nd tergum to 5th tergum.
29. 5th tergum [shape]:
    1. narrow, about two times as broad as long.
    2. broad, about as broad as long.
30. Male genitalia [size]:
    1. small, with epandrium half as wide as abdomen or less.
    2. large, with epandrium about as wide as abdomen.
31. Male genitalia [epandrium postero-apically to cerci]:
    1. open, sides of epandrium broadly separated (see fig. 86b in Vockeroth 1969: 165).
    2. adjacent, sides of epandrium approximate but with distinct gap between them (see fig. 2a in Carver and Thompson 2003: 38; also see fig. 68 in Doesburg and Doesburg, 1977: 67).
    3. closed, with epandrium completely surrounding cerci and without a distinct edge separating the sides (see fig. 87e in Vockeroth 1969: 166).
32. Male genitalia [superior lobe]:
    1. fused basally with hypandrium.
    2. free and articulated with hypandrium.
33. Male gentialia [aedeagus]:
    1. basal aedeagus simple, not swollen nor with denticules.
    2. basal aedeagus swollen apically and with black denticules.
    3. basal aedeagus complex, without black denticules.

In the present study, a basic matrix of adult morphological characters (Table 1) is given for exemplar species (Table 2). The presumably related groups to *Allograpta* and the here diagnosed subgroup of *Allograpta* were included in the analysis. *Syrphus ribesii* (Linnaeus 1758) was chosen as the outgroup based on the results of Mengual *et al*. (2008a), and representatives of *Episyrphus*, *Meliscaeva*, *Anu*, *Citrogramma*, *Exallandra*, *Giluwea*, *Sphaerophoria* and *Eosphaerophoria* were studied with representatives of the subgenera of *Allograpta*.

Whether these are useful characters for cladistic analysis depends on a more rigorous examination of their distribution among all syrphine flies and related outgroup taxa and their true homology. As this examination has not been completed, these attributes are only presented as potential sources of useful characters for future phylogenetic analyses.

Allograpta Osten Sacken

Description (adapted from Vockeroth 1969: 126). Head: Face variable in structure, yellow, with or without medial black vitta; oral opening variable; frons normal, not swollen; antenna short, less than head width; scape about as long as broad, pedicel broader than long; basoflagellomere oval to slightly elongate, not more than 1.6 times as long as broad; arista basal, bare; eye bare; male usually holoptic (only 2 New Zealand species narrowly dichoptic), ommatidia uniform.

Thorax: Postpronotum bare, yellow; scutum usually yellow laterally to transverse suture or beyond; postalar callus yellow; scutellum at least partially yellow, with distinct ventral pile fringe; anepisternum bare on anterior flattened portion; katepisternum without anterodorsal pile tuft, with dorsal and ventral pile areas separated or narrowly joined posteriorly, otherwise broadly separated anteriorly; metasternum variable; metathoracic pleuron bare; calypter bare, plumula variable. Legs: simple; metacoxa without pile tuft on posteroventral apical angle. Wing: variable; vein R4+5 straight; vein M1 (apical crossvein) processive, slightly sinuate; posterior margin without black sclerotized puncta; alula variable.

Abdomen: variable; terga without marginal sulcus. Male genitalia: typical syrphine form; cercus elongate oval; surstyle elongate oval to triangular; lingula absent; aedeagus two-segmented, with apical segment flared apically, basal segment oval to elongate, with minute dark dense appressed spicules apically (except *Antillus*); superior lobe fused to hypandrium, usually triangular.

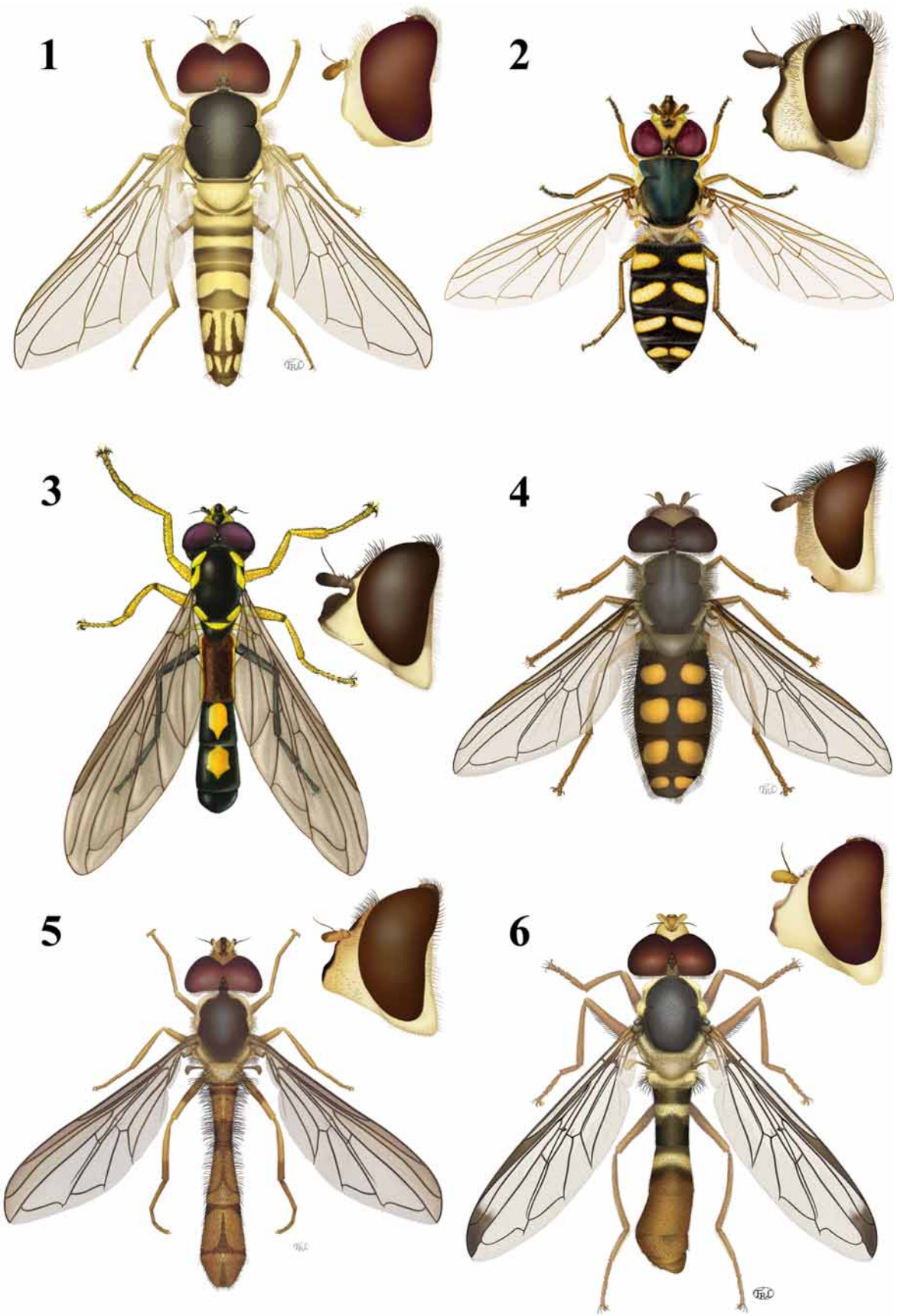
Etymology: *Allograpta* is derived from "*allo*" from the Greek meaning "another kind or strange" (Brown 1956: 80) and "*grapta*" also from the Greek meaning "marked" (Brown 1956: 379). Thus *Allograpta* means another kind of marking, clearly referring to the unique abdominal color pattern of the type species.

Allograpta is recognized among the syrphines (subfamily Syrphinae, tribe Syrphini) by a combination of characters: 1) eye bare; 2) anterior anepisternum bare; 3) calypter bare; 4) abdomen without premarginal sulcus; 5) metacoxa bare posteromedially; and 6) metathoracic pleuron bare.

TABLE 2. Taxa (specimens) scored for the matrix.

The specimens used to score the taxa for the attribute matrix are as follows. All specimens, unless otherwise noted, are preserved in the USNM.

Allograpta (*Allograpta*) *alamacula* Carver Australia (Holotype, ANIC)
Allograpta (*Allograpta*) *javana* (Wiedemann) India (USNM ENT 00036027)
Allograpta (*Allograpta*) *obliqua* (Say) USA: Texas (USNM ENT 00036016)
Allograpta (*Allograpta*) *ventralis* (Miller) New Zealand (USNM ENT 00035389)
Allograpta (*Antillus*) *ascita* (Vockeroth) Dominican Republic (USNM ENT 00036015)
Allograpta (*Claraplumula*) *latifacies* (Shannon) Peru (Holotype, USNM)
Allograpta (*Costarica*) *nishida* Thompson Costa Rica (Holotype, INBIOCRI003724240)
Allograpta (*Costarica*) *zumbadoi* Thompson Costa Rica (Paratype, INBIOCRI002472871)
Allograpta (*Fazia*) *centropogonis* Nishida Costa Rica (Paratype, INBIOCRI002538891)
Allograpta (*Fazia*) *decemmaculata* (Rondani) Chile (Holotype of *bullaephora* Shannon, USNM)
Allograpta (*Rhinoprosopa*) *aenea* (Hull) Dominican Republic (USNM ENT 00036014)
Allograpta (*Rhinoprosopa*) *flavophylla* (Hull) Costa Rica (INBIOCRI003788089)
Anu una Thompson New Zealand (Holotype, NZAC)
Citrogramma henryi Ghorphade Sri Lanka (Holotype, USNM)
Eosphaerophoria n. sp. Vietnam (USNM ENT 00036031)
Episyrphus balteatus (De Geer) Ireland (USNM ENT 00036026)
Exallandra cinctifacies (Speiser) Kenya (USNM ENT 00035918)
Giluwea flavomacula Vockeroth New Guinea (Paratype, USNM ENT 00035915)
Meliscaeva cinctella (Zetterstedt) Denmark (USNM ENT 00029694)
Sphaerophoria (*Loveridgeana*) *beattiei* (van Doesburg & van Doesburg) Saint Helena (Paratype, USNM ENT 00114661)
Sphaerophoria (*Sphaerophoria*) *novaeangliae* Johnson USA: New Hampshire (USNM ENT 00036030)
Sphaerophoria (*Sphaerophoria*) *scripta* (Linnaeus) Germany (USNM ENT 00036029)
Syrphus ribesii (Linnaeus) Norway (USNM ENT 00036028)

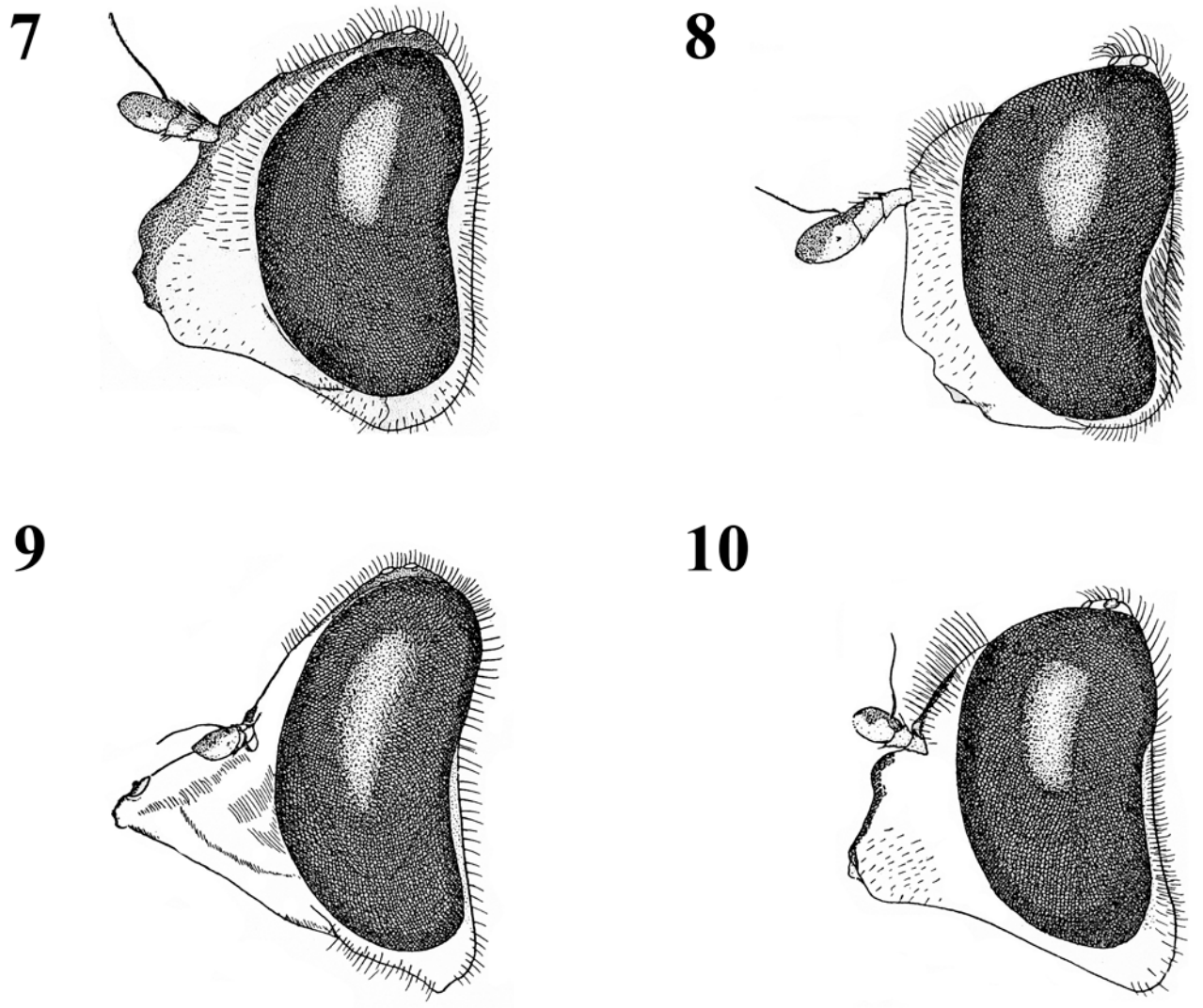


FIGURES 1–6. Habitus, dorsal view, with lateral view of head. 1. *Allograpta* (*Allograpta*) *obliqua* (Say); 2. *Allograpta* (*Fazia*) *centropogonis* Nishida; 3. *Allograpta* (*Costarica*) *zumbadoi* Thompson; 4. *Allograpta* (*Claraplumula*) *latifacies* (Shannon); 5. *Allograpta* (*Rhinoprosopa*) *aenea* (Hull); 6. *Allograpta* (*Antillus*) *ascitus* (Vockeroth).

The only genera likely to be confused with *Allograpta* are *Sphaerophoria* and *Exallandra* and the confusion is only with the typic subgenus. The other subgenera are readily distinguished from these genera by their facial shape (anteriorly extended) and automorphic characters (apical wing maculae, petiolate abdomen). Vockeroth (1969: 133) pointed out the difficulty of distinguishing *Sphaerophoria* [and *Exallandra*] females from those of *Allograpta*, "specifically if the latter lack the oblique tergite markings commonly found in that genus." *Allograpta (sensu stricto)* has a complete subscutellar fringe, which is well developed and at least moderately dense, whereas *Sphaerophoria* and *Exallandra* have a reduced or no subscutellar fringe.

Distribution. *Allograpta* is found in all Biotic Regions, but is absent from most of the Palaearctic Region and northern areas of the Nearctic (see fig. 22). The genus is absent from the western Palaearctic and occurs only along the southeastern edge of the region (from southern Far Eastern Russia, south to China). Only the typic subgenus is known from outside the Neotropical Region. The greatest diversity is found in the Neotropics, but there is a small radiation also in New Zealand. The species counts for the various regions are Palaearctic (2), Nearctic (4), Neotropical (52), Afrotropical (12), Oriental (10), Australian (33) and Oceania (10).

Allograpta species are structurally rather uniform throughout the World except in the Neotropics and New Zealand. The structural diversity is documented in the Neotropics by a number of subgeneric groups, but the diversity in New Zealand is not.



FIGURES 7–10. Heads, lateral view. 7. *Allograpta* (*Fazia*) *colombia* Curran; 8. *Allograpta* (*Allograpta*) *obliqua* (Say); 9. *Allograpta* (*Rhinoprosopa*) *flavophylla* (Hull); 10. *Allograpta* (*Rhinoprosopa*) *aenea* (Hull).

TABLE 3. Character state matrix for studied taxa.

Taxa	Characters																	
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Allograpta (*Allograpta*) *alamacula*	1	2	1	2	2	1	1	1	1	1	2	1	3	1	1	1	1	2
Allograpta (*Allograpta*) *javana*	1	2	1	2	2	1	2	1	1	1	2	1	1	1	2	1	3	2
Allograpta (*Allograpta*) *obliqua*	1	1	1	2	1	1	2	1	1	2	2	1	1	1	2	1	3	2
Allograpta (*Allograpta*) *ventralis*	1	2	1	2	2	3	1	1	1	1	2	1	3	1	2	1	1	2
Allograpta (*Antillus*) *ascita*	1	2	2	2	2	1	1	1	1	1	2	1	3	1	1	1	1	2
Allograpta (*Claraplumula*) *latifacies*	1	3	1	2	1	1	3	1	1	1	1	1	1	1	2	1	3	2
Allograpta (*Costarica*) *nishida*	1	2	2	2	3	1	3	1	1	1	2	1	3	1	1	1	1	2
Allograpta (*Costarica*) *zumbadoi*	1	2	2	2	3	1	3	1	1	1	2	1	3	1	1	1	1	2
Allograpta (*Fazia*) *centropogonis*	2	3	2	2	2	1	3	1	1	1	2	1	1	1	2	1	3	2
Allograpta (*Fazia*) *decemmaculata*	2	3	2	2	2	1	3	1	1	1	2	1	1	1	2	1	3	2
Allograpta (*Rhinoprosopa*) *aenea*	1	1	2	2	2	1	3	1	1	1	2	1	3	1	1	1	1	2
Allograpta (*Rhinoprosopa*) *flavophylla*	1	1	2	1	1	1	3	1	1	1	2	1	3	1	1	1	1	2
Anu una	1	2	1	2	2	1	1	1	1	1	2	1	2	1	1	1	2	2
Citrogramma henryi	2	2	1	2	1	1	2	1	1	2	2	1	1	1	2	1	2	2
Eosphaerophoria n. sp.	1	1	1	2	2	3	1	1	1	1	2	1	2	1	1	1	1	2
Episyrphus balteatus	1	2	1	2	2	1	1	1	1	1	1	2	1	1	2	1	3	2
Exallandra cinctifacies	1	2	1	2	2	1	1	1	1	1	2	1	2	1	2	1	2	2
Giluwea flavomacula	1	2	2	2	2	3	2	1	1	1	2	1	1	1	1	1	1	2
Meliscaeva cinctella	2	2	1	2	2	1	1	1	1	1	1	3	1	1	1	1	3	2
Sphaerophoria (*Loveridgeana*) *beattiei*	1	1	1	2	1	3	1	1	1	1	2	1	3	1	2	1	2	2
Sphaerophoria (*Sphaerophoria*) *novaeangliae*	1	2	1	2	2	1	1	1	1	1	2	1	2	1	2	1	1	2
Sphaerophoria (*Sphaerophoria*) *scripta*	1	2	1	2	2	1	1	1	1	2	2	1	2	1	2	1	3	2
Syrphus ribesii	2	2	1	2	2	1	1	1	1	2	1	1	1	1	1	2	3	1

continued.

Taxa	Characters																
	18	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
Allograpta (*Allograpta*) *alamacula*	2	3	1	1	2	1	1	2	1	2	1	1	1	2	1	2
Allograpta (*Allograpta*) *javana*	2	1	1	1	3	1	1	2	1	2	1	1	1	1	1	2
Allograpta (*Allograpta*) *obliqua*	3	1	1	1	2	1	1	2	1	2	1	1	1	1	1	2
Allograpta (*Allograpta*) *ventralis*	2	1	1	1	2	3	1	3	1	2	1	1	1	1	1	2
Allograpta (*Antillus*) *ascita*	3	3	1	1	2	1	1	2	1	2	1	1	2	1	1	3
Allograpta (*Claraplumula*) *latifacies*	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Allograpta (*Costarica*) *nishida*	1	1	1	1	1	2	1	2	1	2	1	2	1	1	1	2
Allograpta (*Costarica*) *zumbadoi*	1	1	1	1	1	2	1	2	1	2	1	2	1	1	1	2
Allograpta (*Fazia*) *centropogonis*	2	1	1	1	2	1	1	2	1	1	1	1	1	1	1	2
Allograpta (*Fazia*) *decemmaculata*	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2
Allograpta (*Rhinoprosopa*) *aenea*	1	1	1	1	2	3	1	3	1	3	1	2	1	1	1	2
Allograpta (*Rhinoprosopa*) *flavophylla*	1	1	1	1	2	3	1	3	1	3	1	2	1	1	1	2
Anu una	2	1	1	1	3	2	1	2	1	1	1	1	1	1	2	1

Taxa	Characters															
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Episyrphus balteatus	2	1	2	1	3	1	1	2	1	1	1	1	1	1	2	1
Exallandra cinctifacies	2	1	1	1	3	1	1	2	1	1	1	1	1	1	2	1
Giluwea flavomacula	1	1	1	1	3	3	1	2	1	1	1	1	1	1	2	1
Meliscaeva cinctella	2	1	2	1	3	1	1	2	1	1	1	1	1	1	2	1
Sphaerophoria (*Loveridgeana*) *beattiei*	1	1	1	1	3	2	1	2	1	2	1	2	2	2	2	1
Sphaerophoria (*Sphaerophoria*) *novaeangliae*	2	1	1	1	3	2	1	2	1	2	1	1	2	1	2	1
Sphaerophoria (*Sphaerophoria*) *scripta*	2	1	1	1	3	1	1	2	1	3	1	2	2	3	2	1
Syrphus ribesii	2	1	1	1	2	1	1	1	1	1	2	1	1	1	2	1

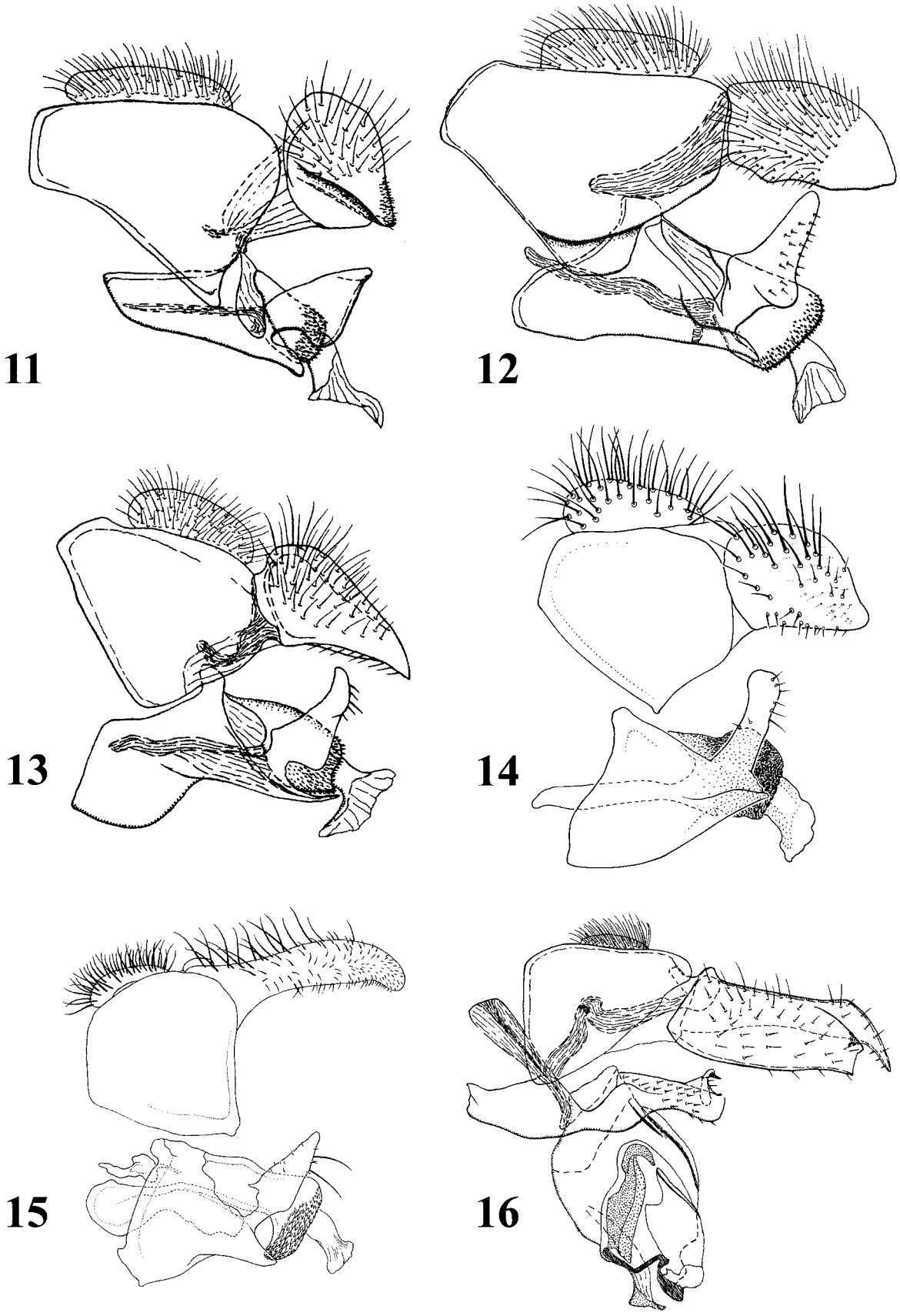
Key to the subgenera and species groups of *Allograpta*

1. Metasternum pilose; plumula present and well developed 6
- Metasternum bare; plumula absent or very short 2
2. Wing extensively bare basally; antennal pits confluent 4
- Wing completely microtrichose; antennal pits separate. Alula narrow, narrower than cell BM 3
3. Face with abrupt tubercle; abdomen parallel-sided (fig. 3) ..... *Costarica*
- Face with indistinct or no tubercle (fig. 9–10); abdomen petiolate (fig. 5) ..... *Rhinoprosopa*
4. Alula narrow, as wide as costal cell; male broadly dichoptic; wing without distinct apical macula ..... *Allograpta*, *ventralis* group
- Alula broad, broader than costal cell, as broad or broader than cell BM; male holoptic; wing with distinct apical brown macula 5
5. Face produced anteriorly; oral apex distinctly more prominent than antennal bases; oral opening 3.5 times longer than broad (fig. 6); large flies, 13 mm or greater ..... *Antillus*
- Face straight, not produced anteriorly; oral apex distinctly less prominent than antennal bases; oral opening only about 2 times as long as broad; small flies, 6 mm or less ..... *Allograpta*, *alamacula* group
6. Face produced forward; oral apex distinctly more prominent than antennal bases; oral opening 3 or more times longer than broad; facial tubercle high, distinctly differentiated (fig. 7) ..... *Fazia*
- Face straight, not produced forward; oral apex distinctly less prominent than antennal bases; oral opening only about 2 times as long as broad; facial tubercle usually low (except *armillata*), not differentiated dorsally (figs. 1, 8) 7
7. Abdomen oval, with 4 pairs of large round maculae (fig. 4); large flies, 13 mm ..... *Claraplumula*
- Abdomen elongate, tapering, usually with fasciae and/or vittae (fig. 1); smaller flies, usually 10 mm or less ..... *Allograpta*, *obliqua* group

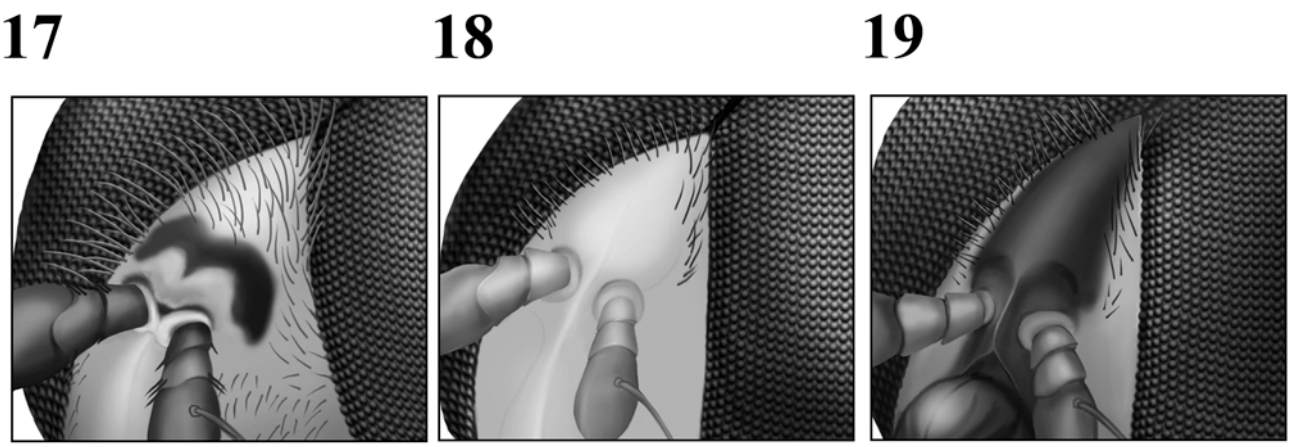
Subgenus *Allograpta* Osten Sacken

Allograpta Osten Sacken 1875: 49. Type-species, *Scaeva obliqua* Say (monotypy).
Neoscaeva Frey 1946: 170. Type-species, *Syrphus aeruginosifrons* Schiner (original designation).
Microsphaerophoria Frey 1946: 168. Type-species, *plaumanni* Frey (original designation).
Miogramma Frey 1946: 165. Type-species, *Syrphus javanus* Wiedemann (original designation).
Helenomyia Bankowska 1962: 311. Type-species, *Syrphus javanus* Wiedemann (original designation).
Paraxanthogramma Tao & Chiu 1971: 74 *nomen nudum* based on *Syrphus javanus* Wiedemann as *nakamurae* Matsumura.

Diagnosis. Face straight, with low indistinct tubercle of variable size; oral opening about 1.5 to 2 times as long as wide, with oral apex at level of antennal base; antennal pits confluent; plumula well developed or absent; subscutellar fringe distinct or absent; wing partially bare basomedially, with or without apical dark macula; alula broad, about 1.5 times as broad as cell BM; metasternum pilose or bare; abdomen elongate, parallel to slightly petiolate.



FIGURES 11–16. Male genitalia, lateral view. 11. *Allograpta* (*Allograpta*) *obliqua* (Say); 12. *Allograpta* (*Claraplumula*) *latifacies* (Shannon); 13. *Allograpta* (*Rhinoprosopa*) *aenea* (Hull); 14. *Allograpta* (*Costarica*) *zumbadoi* Thompson; 15. *Allograpta* (*Fazia*) *centropogonis* Nishida; 16. *Allograpta* (*Antillus*) *ascitus* (Vockeroth).



FIGURES 17–19. Heads, oblique anterodorsal view of antennal pits. 17. *Syrphus ribesii* Linnaeus; 18. *Allograpta (Allograpta) obliqua* (Say); 19. *Allograpta (Costarica) zumbadoi* Thompson.

***Allograpta obliqua* species group**

Diagnosis. Face straight, with low indistinct tubercle; oral opening about 1.5 times as long as wide, with oral apex at level of antennal base; antennal pits confluent; plumula well developed; subscutellar fringe distinct; wing partially bare basomedially, without apical dark macula; alula broad, about 1.5 times as broad as cell BM; metasternum pilose; abdomen elongate.

Included species. AFROTROPICAL: ***borbonica*** Kassebeer 2000: 46 (*Allograpta*) Reunion; ****calopoides*** Curran 1938: 9 (*Syrphus*) Kenya, Ethiopia, Tanzania, Uganda, Congo; ****calopus*** Loew 1858: 379 (*Syrphus*) Sudan, Ethiopia, Kenya, Namibia, Nigeria [=*abyssinica* Frey 1946: 168 (*Miogramma*)]; ****fuscotibialis*** Macquart 1842: 155 (*Syrphus*) South Africa [=*rotundicornis* Loew 1858: 379 (*Syrphus*)]; ***hypoxantha*** Bezzi 1923: 343 (*Syrphus*) Kenya, Madagascar, Tanzania, Uganda, Congo [=*calinus* Curran 1938: 10 (*Syrphus*)]; ***nasuta*** Macquart 1842: 156 (*Syrphus*) western Africa, Diego Garcia, Mauritius, Reunion, Madagascar [=*pfeifferi* Bigot 1884: 89 (*Syrphus*)]; ***nigra*** Keiser 1971: 225 (*Epistrophe*) Madagascar; ***nummularia*** Bezzi 1920: 137 (*Syrphus*) Tanzania, Kenya; ***phaeoptera*** Bezzi 1920: 139 (*Xanthogramma*) Tanzania; ***rediviva*** Bezzi 1915: 34 (*Syrphus*) South Africa; ***rufifacies*** Keiser 1971: 225 (*Epistrophe*) Madagascar; ***tenella*** Keiser 1971: 227 (*Epistrophe*) Madagascar; ****varipes*** Curran 1927b: 55 (*Epistrophe*) Congo, Uganda.

AUSTRALIAN: *****atkinsoni*** Miller 1921: 311 (*Platycheirus*) New Zealand; ****australensis*** Schiner 1868: 347 (*Melithreptus*) Australia (NSW, Qld.); ***buruensis*** Meijere 1929: 383 (*Allograpta*) Indonesia (Buru); ****distincta*** Kertesz 1899: 177 (*Melithreptus*), New Guinea to Fiji & Solomons; ****flavofaciens*** Miller 1921: 302 (*Syrphus*) New Zealand; ****hirsutifera*** Hull 1949d: 727 (*Epistrophe*) New Zealand; ****hudsoni*** Miller 1921: 302 (*Syrphus*) New Zealand; ***pallida*** Bigot 1884: 93 (*Syrphus*) Australia; ****pseudoropalus*** Miller 1921: 293 (*Paragus*) New Zealand; ****ropalus*** Walker 1849: 593 (*Syrphus*) New Zealand.

NEARCTIC: *****exotica*** Wiedemann 1830: 136 (*Syrphus*) Oregon to North Carolina, s. to Argentina, Hawaii (introduced) [=*quadrigemina* Thomson 1869: 500 (*Syrphus*), =*fracta* Osten Sacken 1877: 331 (*Allograpta*), =*bilineata* Enderlein 1938a: 220 (*Allograpta*), =*duplofasciata* Enderlein 1938a: 217 (*Allograpta*)]; ****obliqua*** Say 1823: 89 (*Scaeva*) Washington to Quebec, s. to Argentina; Hawaii (introduced) [=*securiferus* Macquart 1842: 100 (*Syrphus*), =*baccides* Walker 1849: 594 (*Syrphus*), =*dimemsus* Walker 1852: 235 (*Syrphus*), =*signatus* Wulp 1867: 144 (*Syrphus*), =*dejongi* Doesburg 1958: 44 (*Allograpta*)]; ****radiata*** Bigot (see below) Florida.

NEOTROPICAL: *****aeruginosifrons*** Schiner 1868: 352 (*Syrphus*) Brazil; ***annulipes*** Macquart 1850: 464 (*Paragus*) Colombia, Ecuador, Peru, Brazil, Bolivia [=*scutellata* Sack 1941: 99 (*Allograpta*), =*geminata* Fluke 1942: 16 (*Allograpta*)]; ****aperta*** Fluke 1942: 19 (*Allograpta*) Surinam, Guyana [=*notata* Doesburg

1966: 64 (*Allograpta*)]; ****bilineella*** Enderlein 1938a: 219 (*Allograpta*) Colombia; ****browni*** Fluke 1942: 17 (*Allograpta*) Ecuador; ****exotica*** Wiedemann (see above); ****falcata*** Fluke 1942: 16 (*Allograpta*) Colombia, Venezuela, Ecuador, Peru; ****hastata*** Fluke 1942: 17 (*Allograpta*) Peru, Brazil; ***hortensis*** Philippi 1865: 746 (*Syrphus*) Peru, Chile, Argentina [=*bimaculata* Enderlein 1938a: 223 (*Allograpta*)]; ****insularis*** Thompson 1981: 28 (*Allograpta*) Puerto Rico; ****limbata*** Fabricius 1805: 251 (*Scaeva*) West Indies, Brazil [=*fuscisquama* Curran 1927a: 4 (*Allograpta*)]; ****neotropica*** Curran 1936: 14 (*Allograpta*) Colombia, Ecuador, Brazil, Argentina); ***obliqua*** Say (see above); ****piurana*** Shannon 1927: 9 (*Allograpta*) Peru, Chile [=*chilensis* Sack 1941: 98 (*Allograpta*), =*harlequina* Hull 1949c: 76 (*Allograpta*)]; ****pulchra*** Shannon 1927: 25 (*Allograpta*) Chile; Easter Island [=*bifasciata* Enderlein 1938a: 221 (*Allograpta*)]; ***radiata*** Bigot 1857: 338 (*Syrphus*) Florida, West Indies, intr. Hawaii (not established) [=*venusta* Curran 1927a: 5 (*Allograpta*), =*cubana* Curran 1932: 3 (*Allograpta*)]; ***robinsoniana*** Enderlein 1938b: 664 (*Allograpta*) Juan Fernandez Island; ***splendens*** Thomson 1869: 501 (*Syrphus*) Galápagos; ****tectiforma*** Fluke 1942: 18 (*Allograpta*) Ecuador; ****teligera*** Fluke 1942: 18 (*Allograpta*) Ecuador, Brazil; ****trilimbata*** Bigot 1889: 253 (*Sphaerophoria*) Mexico.

OCEANIAN: ***amphoterum*** Bezzi 1928: 74 (*Xanthogramma*) Rarotonga, Fiji; ****citronella*** Shiraki 1963: 136 (*Epistrophe*) Caroline Is.: Palau & Ponape; ***distincta*** Kertesz (see above); ****longulus*** Shiraki 1963: 139 (*Epistrophe*) Guam; ***nigripilosa*** Hull 1944a: 52 (*Xanthogramma*) Society Is.; ****neofasciata*** Thompson 1989: 441 Marianas Is. [=*fasciata* Shiraki 1963: 139 (*Epistrophe*); ***obliqua*** Say (see above, introduced Hawaii); ***radiata*** Bigot 1857: 338 (see above, intr. Hawaii (not established) ****septemvittata*** Shiraki 1963: 138 (*Epistrophe*) Mariana Is.

ORIENTAL: ****dravida*** Ghorpade 1994: 7 (*Allograpta*) India; ***javana*** Wiedemann 1824: 34 (*Syrphus*) India to Japan, s. Indonesia [= *nakamurae* Matsumura 1918: 9 (*Xanthogramma*)]; ***kinabalensis*** Curran 1931: 350 (*Syrphus*) Borneo; ***maculipleura*** Brunetti 1913: 162 (*Syrphus*) India, Myanmar [=*bouvieri* Herve-Bazin 1923: 26 (*Xanthogramma*)]; ***medanensis*** Meijere 1914: 166 (*Sphaerophoria*) Sumatra; ***obscuricornis*** Meijere 1914: 165 (*Sphaerophoria*) Java; ***philippina*** Frey 1946: 167 (*Miogramma*) Phillipines; ***purpureicollis*** Frey 1946: 167 (*Miogramma*) Sumatra; ***robinsoni*** Curran 1928: 208 (*Syrphus*) Malaya [=*nigrotibialis* Curran 1928: 241 (*Sphaerophoria*)].

PALAEARCTIC: ***javana*** Wiedemann (see above) Japan; ***maritima*** Mutin 1986: 829 (*Allograpta*) Russian Far East.

Allograpta alamacula species group

Diagnosis. Face straight, with large tubercle; oral opening about 2 times as long as wide, with oral apex at level of antennal base; antennal pits confluent; plumula absent; subscutellar pile fringe absent; wing broadly bare basomedially, with apical dark macula; alula broad, as broad as cell BM; metasternum bare; abdomen elongate.

Included species. AUSTRALIAN: ****alamacula*** Carver 2003: 37 (*Allograpta*) Australia (Queensland).

Carver (Carver & Thompson 2003) reared her species from maggots preying on whiteflies (*Aleurocanthus t-signatus* (Aleyrodidae)). Also see Carver and Thompson (2003: 38, figs. 1 and 2) for black and white habitus and male genitalia.

Allograpta ventralis species group

Diagnosis. Face straight, with large low tubercle; oral opening about 2 times as long as wide, with oral apex at level of antennal base; antennal pits confluent; plumula absent; subscutellar pile fringe absent; wing broadly bare basomedially, without apical dark macula; alula narrow, about 1/2 as broad as cell BM; metasternum bare or with 2–3 very short pile; abdomen elongate or slightly petiolate.

Included species. AUSTRALIAN: ****dorsalis*** Miller 1924: 284 (*Ocyptamus*) New Zealand; ****ventralis*** Miller 1921: 296 (*Sphaerophoria*) New Zealand.

The biology of *ventralis* was described by Bowie (2001) and the species are typical *Allograpta* predators which feed on mealybugs (*Balanococcus cordylinidis* (Pseudococcidae)). See also Thompson (2008: 4, fig. 4) for colour habitus.

Subgenus *Antillus* Vockeroth

Antillus Vockeroth 1969: 130. Type-species, *ascitus* Vockeroth (original designation).

Diagnosis. Face greatly produced anteriorly, with low small tubercle; oral opening about 3.5 times as long as wide, with oral apex greatly extended beyond level of antennal base; antennal pits confluent; plumula absent; subscutellar pile fringe absent; wing broadly bare basomedially, with apical dark macula; alula broad, much broader than cell BM; metasternum bare; abdomen elongate.

Included species. NEOTROPICAL: ****ascita*** Vockeroth 1969: 130 (*Antillus*) Hispaniola.

Subgenus *Claraplumula* Shannon

Claraplumula Shannon 1927: 8. Type-species, *latifacies* Shannon (original designation).

Diagnosis. Face straight, with tubercle; oral opening about twice as long as wide, with oral apex at level of antennal base; antennal pits broadly separated; plumula well developed, long; subscutellar pile fringe abundant, dense; wing extensively microtrichose, only narrowly bare basally, without apical dark macula; alula broad, about 1.5 times as broad as cell BM; metasternum pilose; abdomen oval.

Included species. NEOTROPICAL: ****latifacies*** Shannon 1927: 8 (*Claraplumula*) Ecuador, Peru.

Subgenus *Fazia* Shannon

Fazia Shannon 1927: 25. Type-species, *bullaephora* Shannon (original designation) = *decemmaculata* (Rondani).
Chasmia Enderlein 1938a: 213 (preoccupied by Enderlein 1922). Type-species, *hians* Enderlein (original designation).
Metepistrophe Hull 1949b: 293 (as subgenus of *Epistrophe*). Type-species, *Epistrophe altissima* Fluke (original designation). Misidentified type-species. Originally named type was *Epistrophe remigis* Fluke, but Fluke (1951) noted that the specimen used by Hull was mislabelled by him and was actually *altissima* Fluke. Hence, under Article 70.3 of the International Code of Zoological Nomenclature (ICZN 1999), we hereby fixed the type species of *Metepistrophe* Hull to the taxonomical species, *altissima* Fluke.
Metallograpta Hull 1949b: 293 (as subgenus of *Epistrophe*). Type-species, *Allograpta colombia* Curran (original designation).

Diagnosis. Face moderately to greatly produced anteriorly, with distinct tubercle; oral opening about 5 times as long as wide, with oral apex greatly extended beyond level of antennal base; antennal pits separate; plumula well developed; subscutellar pile fringe distinct, one or two rows of long pili; wing broadly bare basomedially, without apical dark macula; alula broad, about 1.5 times as broad as cell BM; metasternum pilose; abdomen broadly to narrowly elongate.

Included species. NEARCTIC: ****micrura*** Osten Sacken 1877: 330 (*Sphaerophoria*) NE: British Columbia, south to California, Texas & Mexico [=*picticauda* Bigot 1884: 102 (*Sphaerophoria*), =*trifasciata* Enderlein 1938a: 218 (*Allograpta*), =*transversa* Hull 1943a: 32 (*Sphaerophoria*)].

NEOTROPICAL: ****alta* Curran 1936: 15 (*Allograpta*) Colombia, Ecuador [=*flavomaculata* Hull 1937b: 169 (*Allograpta*)]; ****altissima*** Fluke 1942: 10 (*Epistrophe*) Ecuador; ****argentipila*** Fluke 1942: 13

(*Epistrophe*) Ecuador, Peru, Argentina; ****centropogonis*** Nishida in Nishida *et al*. 2002: 423 (*Allograpta*) Costa Rica; ****colombia*** Curran 1925a: 349 (*Allograpta*) Colombia, Ecuador, Brazil, Argentina; ****decemmaculata*** Rondani 1863: 12 (*Syrphus*) Chile, Ecuador [=*bullaephora* Shannon 1927: 25 (*Fazia*)]; ****eupeltata*** Bigot 1884: 91 (*Syrphus*) Mexico [=*mexicana* Enderlein 1938a: 212 (*Fazia*)]; ****fasciata*** Curran 1932: 4 (*Allograpta*) Ecuador, Peru [=*bisinterrupta* Enderlein 1938a: 210 (*Fazia*)]; ****fascifrons*** Macquart 1846: 265 (*Syrphus*) Colombia, Ecuador [=*armillata* Fluke 1942: 12 (*Epistrophe*)]; ****flukei*** Curran 1936: 13 (*Allograpta*) Cuba; ****funeralia*** Hull 1944b: 27 (*Epistrophe*) NT: Jamaica; ****hians*** Enderlein 1938a: 213 (*Chasmia*) Mexico; ****imitator*** Curran 1925a: 351 (*Epistrophe*) Colombia, Ecuador, Bolivia; ****luna*** Fluke 1942: 8 (*Epistrophe*) Ecuador; ****macquarti*** Blanchard 1852: 411 (*Syrphus*) Chile, Argentina [=*australis* Shannon 1927: 26 (*Fazia*)]; ***mu*** Bigot 1884: 105 (*Mesograpta*) Mexico; ****nasigera*** Enderlein 1938a: 212 (*Fazia*) Colombia; ****plaumanni*** Frey 1946: 168 (*Microsphaerophoria*) Brazil; ****remigis*** Fluke 1942: 9 (*Epistrophe*) Ecuador; ****roburoris*** Fluke 1942: 11 (*Epistrophe*) Ecuador, Argentina; ****rostrata*** Bigot 1884: 102 (*Sphaerophoria*) Mexico [=*nasuta* Enderlein 1938a: 214 (*Chasmia*), =*rhina* Thompson in Thompson *et al*. 1976: 37 (*Allograpta*)]; ****saussurii*** Giglio-Tos 1892: 2 (*Syrphus*) Mexico; ****similis*** Curran 1925a: 350 (*Allograpta*) Colombia, Brazil, Argentina; ****strigifacies*** Enderlein 1938a: 211 (*Fazia*) Brazil [=*hermosa* Hull 1941: 48 (*Allograpta*), =*brunneola* Frey 1946: 170 (*Neoscaeva*)]; ****syrphica*** Giglio-Tos 1892: 2 (*Sphaerophoria*) Mexico; ****willistoni*** Giglio-Tos 1893: 31 (*Sphaerophoria*) Mexico [=*forreri* Giglio-Tos 1893: 32 (*Sphaerophoria*)].

Subgenus *Rhinoprosopa* Hull

Oligorhina Hull 1937a: 30 (preoccupied by Fairmaire & Germain 1863). Type-species, *aenea* Hull (original designation).
Rhinoprosopa Hull 1942: 23 (new name for *Oligorhina* Hull).

Diagnosis. Face greatly produced anteriorly, with low indistinct tubercle or no tubercle; oral opening about 5.5 times as long as wide, with oral apex greatly extended beyond level of antennal base; antennal pits distinctly separated; plumula absent; subscutellar pile fringe absent; wing microtrichose, without apical dark macula; alula absent or narrow, less than 1/2 as wide as cell BM; metasternum bare; abdomen narrowly to strongly petiolate.

Included species. NEOTROPICAL: ****aenea*** Hull 1937a: 31 (*Oligorhina*) Hispaniola; ****flavophylla*** Hull 1943b: 139 (*Rhinoprosopa*) Peru; ****lucifera*** Hull 1943c: 216 (*Rhinoprosopa*) Ecuador; ****nasuta*** Bigot 1884: 103 (*Sphaerophoria*) Mexico [=*nasuta* Bigot 1888: 253 (*Sphaerophoria*)]; ****sycorax*** Hull 1947: 239 (*Rhinoprosopa*) Costa Rica, Colombia, Venezuela.

Subgenus *Costarica* Mengual & Thompson, subgen. nov.

Type-species: *Allograpta zumbadoi* Thompson

Diagnosis. Face greatly produced anteriorly, with no tubercle but distinctly concave beneath antenna creating an appearance of a tubercle; oral opening about 5 times as long as wide, with oral apex greatly extended beyond level of antennal base; antennal pits distinctly separated; plumula absent; subscutellar fringe absent; wing microtrichose, without apical dark macula; metasternum bare; abdomen narrowly petiolate or elongate.

Included species. NEOTROPICAL: ****nishida*** Mengual & Thompson, sp. nov. Costa Rica; ****zumbadoi*** Thompson 2000: 34 (*Allograpta*) Costa Rica.

Costarica is readily distinguished from all other *Allograpta* groups by the distinctive facial shape and by the dense thick appressed pile on 1st and 2nd terga in the males. These characters are unique among flower flies.

The life history of the type species, *zumbadoi*, has been worked out by Zuijen and Nishida (2009). The larval stages are stem-borers in *Centropogon* (Campanulaceae). The plant genus ranges from Mexico to Peru and contains some 230 species, but so far these flies are only known from the higher elevations in Costa Rica.

Etymology. The name *Costarica* is the name of the country which is the home for the two included species and is to be treated as feminine.

Key to the species of *Allograpta (Costarica)*

1. Male & female with medial yellow macula on 3rd & 4th terga; female 2nd tergum entirely yellow; pro and mesofemora extensively yellow; katepisternum, postalar callus yellow ..... *zumbadoi*
- Male & female with basal arcuate yellow fasciae on 3rd & 4th terga; female 2nd tergum black with submedial fasciate yellow macula; pro and mesofemora extensively black; katepisternum, postalar callus brownish-black .... *nishida*

***Allograpta* (*Costarica*) *nishida* Mengual & Thompson, sp. nov.**
Figures 20 and 21.

Male. Head: Face black medially, narrowly yellow laterally, short yellow pilose laterally; gena yellow, yellow pilose; lunule black; frontal triangle black except very narrowly yellow laterally, black pollinose and pilose; eye contiguity long, as long as vertical triangle; vertical triangle black, black pollinose and pilose; occiput yellow on ventral 1/3 and black on dorsal 2/3, white pollinose and yellow pilose on ventral 2/3, black pollinose and pilose on dorsal 1/3. Antenna brownish black except pale yellowish orange basoventral 1/3 of basoflagellomere, black pilose; arista black.

Thorax: Black except yellow posterior notopleuron, narrowly along base of scutellum, posterior 1/3 of anepisternum; yellow pilose except black pilose on dorsolaterally to wing base; calypter black; halter black except yellow capitulum. Legs: brownish black except yellow femoral apices and basal 1/3 of tibiae, black pilose except a few yellow pili on bases of femora. Wing: hyaline except costal and subcostal darker brownish, microtrichose.

Abdomen: Elongate, slightly narrower than thorax, shiny brownish black except for basal arcuate yellow fasciae on 3rd–4th terga and yellow lateral 1/3 of 1st tergum, black pilose except long lateral white pile and with dense thick brownish-black pile at dorsomedial part on 1st and 2nd terga (fig. 20a); sterna dark; 1st sternum long white pilose; 2nd sternum short white pilose; 3rd–5th sterna appressed black pilose. Male genitalia as figured (fig. 21).

Female. Similar to male except for normal sexual dimorphism and: frons black except yellow laterally on ventral 2/3, dull, yellow pilose; 2nd tergum with arcuate yellow fascia narrowly divided medially. Abdomen mainly shiny, dull black pollinose on most of 2nd terga except apical margin and yellow fasciae, black pollinose areas on 3rd thru 5th terga restricted to medial area posterior to yellow fasciae (see fig. 20b).

Types. Holotype: Male from Costa Rica, Limon: Parque Internacional La Amistad, sendero Circular, 2406 m, LS 340258 577465, 20 June - 5 July 2003, D. Rubi, net collected, #74159 (1 ♂ INB0003724240 INBIO), deposited in Instituto Nacional de Biodiversidad, Santo Domingo. Paratypes: COSTA RICA. Cartago: Genesis II, 2360 m, LN 188600 545900, 9 June 1994, M. M. Chavarria, #3157 (1 ♀ INBIOCRI002014790 USNM); Puntarenas, Parque Internacional La Amistad, Cerro Hoffman, Sendero hacia, 2160 m, LS 337931 575490, 30 June–5 July 2003, D. Rubi, net collected, #74163, (1 ♀ INB0003724104, USNM)

Length. Male (1): body, 11.3 mm; wing, 10.0 mm. Female (2): body, 11.5–13.0 (12.3) mm; wing, 10.1–11.8 (10.9) mm.

Etymology. This species is named after Kenji Nishida in recognition of his discoveries on the diverse life histories of *Allograpta* species in Costa Rica. The name is to be treated as a noun in apposition.

Allograpta nishida is readily distinguished from *zumbadoi* as outlined in the key.

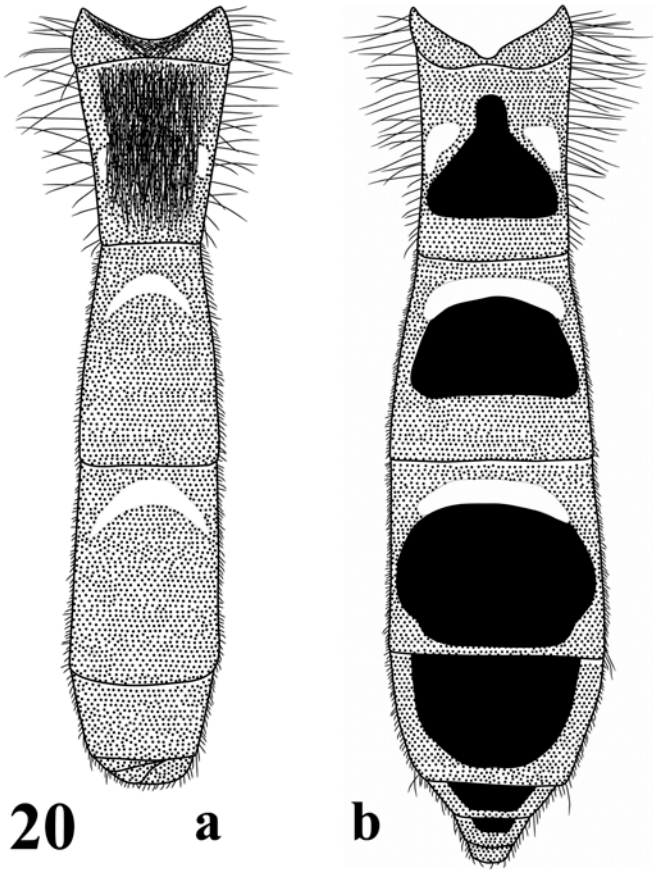


FIGURE 20. Abdomen of *Allograpta (Costarica) nishida* sp. nov., dorsal view: a, male; b, female.

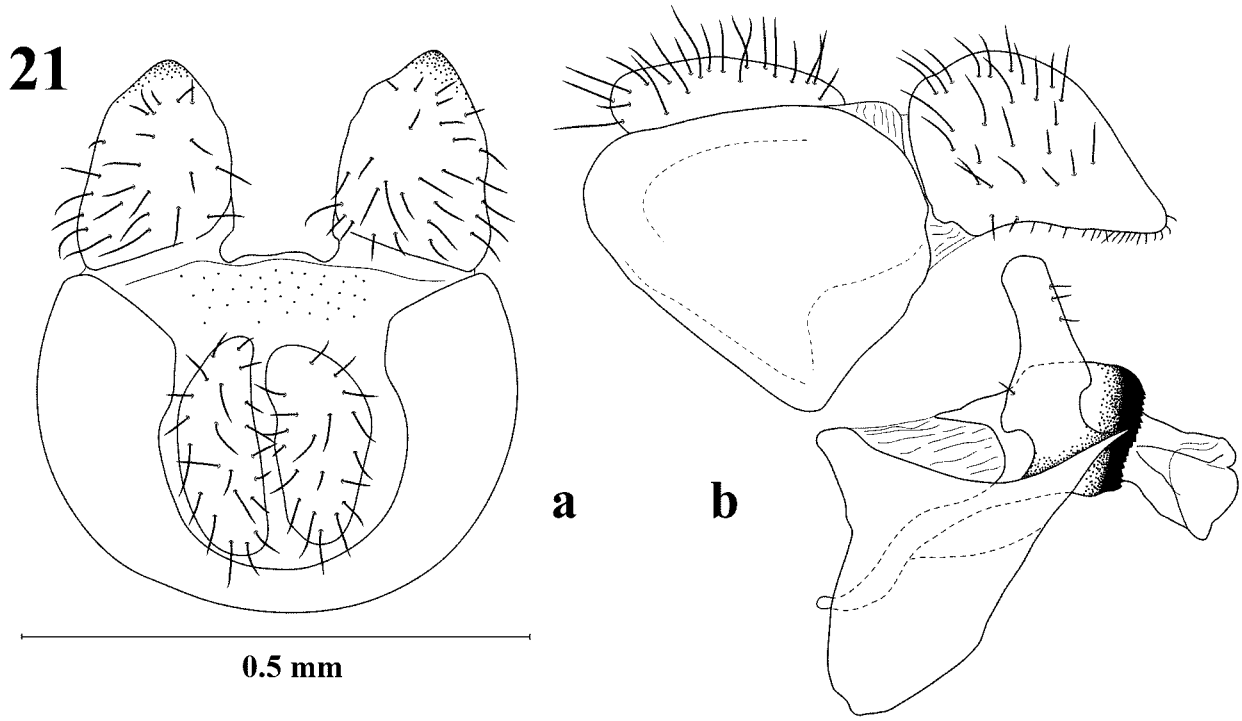


FIGURE 21. Male genitalia of *Allograpta (Costarica) nishida* sp. nov.: a, dorsal view; b, lateral view.

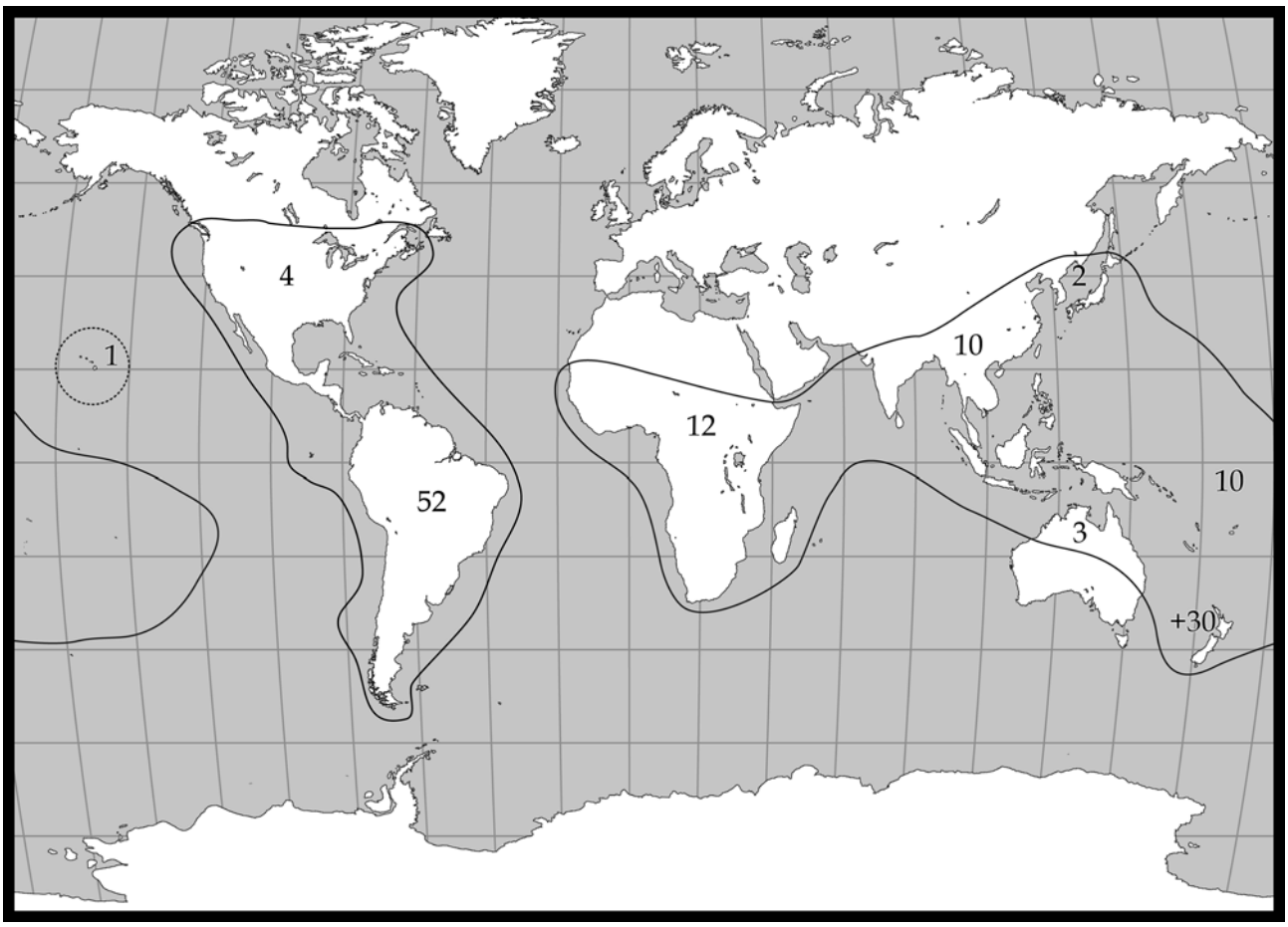


FIGURE 22. World distribution of the genus *Allograpta*, modified from Vockeroth (1969).

Phylogenetic analysis

A total of 22 ingroup taxa and 34 morphological characters were analyzed (see Tables 1 and 2). Parsimony was chosen as the optimality criterion for this study. The data matrix of morphological characters was analyzed in TNT (Goloboff *et al*. 2008) using the command ie (*implicit enumeration)* for an exact search. The analysis resulted in 5 equally parsimonious trees of 91 steps of length (C.I. = 0.42, R.I. = 0.65) (figs. 25-29). The strict consensus tree is shown in figure 23. Figure 24 represents the agreement subtree, with the largest subset of taxa for which the relationships among them are invariant across all parsimonious trees. Figures were edited in Winclada (Nixon 2002). Bootstraping and Jackknife values were obtained with 1000 replications in TNT.

In the strict consensus tree, only 8 nodes were resolved with different support values. Two species of *Sphaerophoria, S. (Loveridgeana) beattiei* and *S. (Sphaerophoria) novaeangliae*, were resolved together in the strict consensus tree with low bootstrap and jackknife values, but more importantly *S. scripta* was never recovered with these 2 species of the same genus in any of the 5 equally parsimonious trees. Vockeroth (1969) indicated that the terminalia of *S. novaeangliae* and *S. loewii* do differ rather markedly from those of the other species. Previous molecular analyses (Mengual *et al*. 2008b) resolved *S. loewii* as the sister-taxon of *Exallandra cinctifacies*. Present results placed *S. novaeangliae* with the subgenus *Loveridgeana*, a fact that highlights the morphological differences between these two species of *Sphaerophoria* and the rest of the same subgenus.

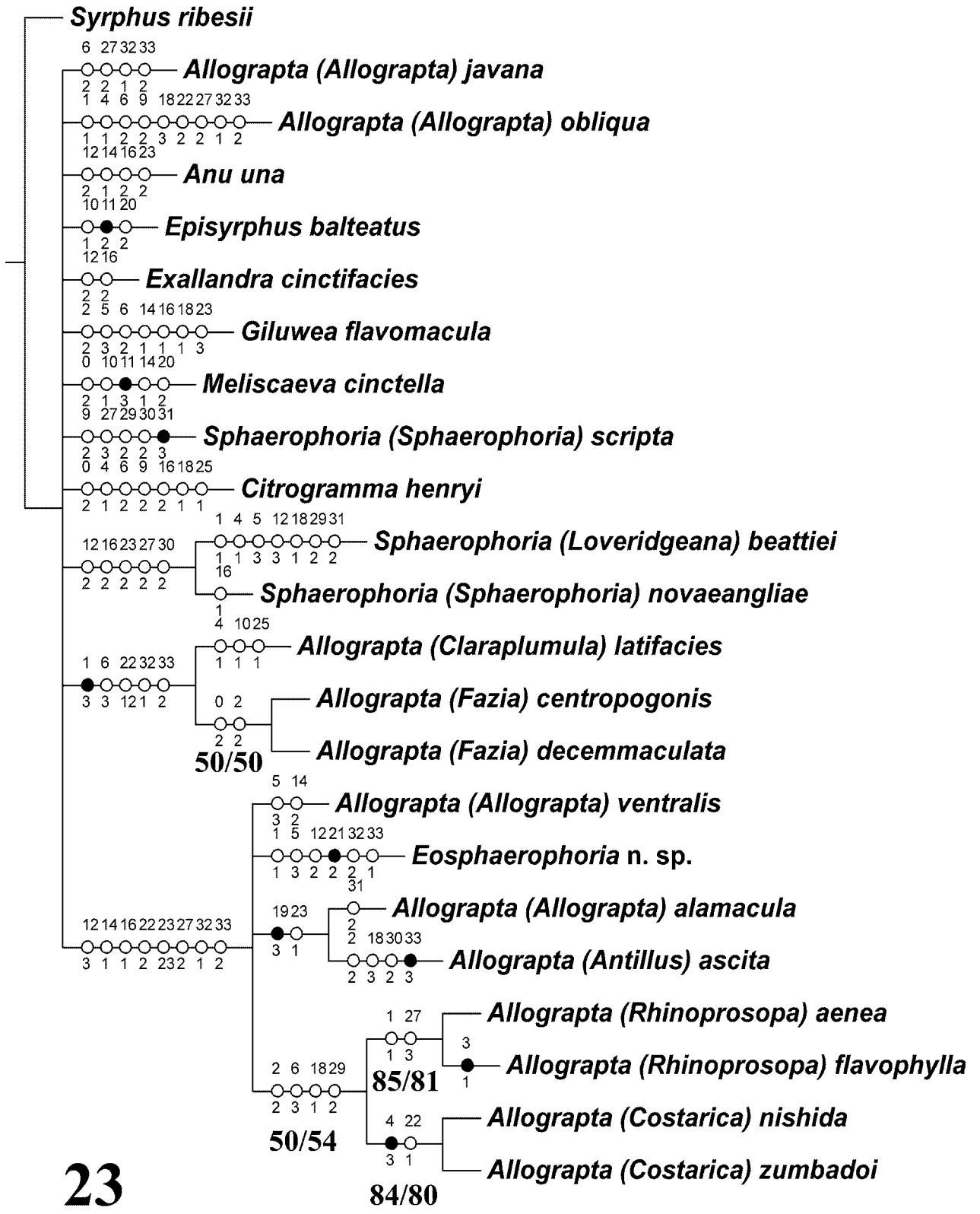
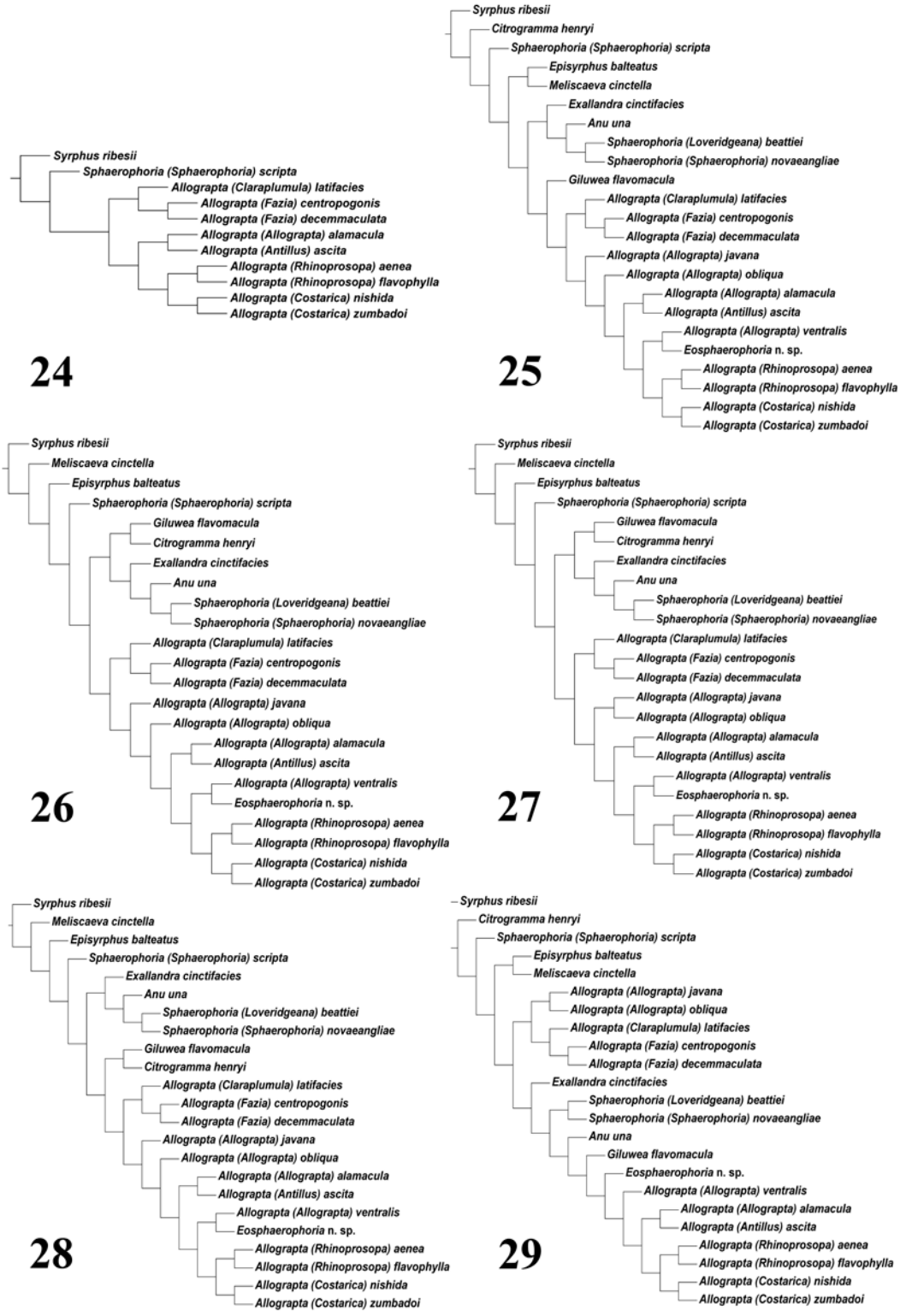


FIGURE 23. Strict consensus tree of five most parsimonious trees based on morphological characters using parsimony. Bootstrap and Jackknife support values above 50% are indicated below branches (Boostrap/Jackknife).



FIGURES 24–29. Cladograms of *Allograpta* relationships. 24. Agreement subtree; 25–29. The individual most parsimonious trees resulted from the analysis of morphological characters.

The genus *Allograpta* was resolved into several species groups in the strict consensus tree. The species of *Allograpta* sensu stricto, *A. obliqua* and *A. javana*, were placed in the basal polytomy in the consensus tree, but looking at the 5 equally parsimonious trees, in the majority of the cases they form a clade with the rest of *Allograpta* species including *Eosphaerophoria*.

Two groups of *Allograpta* species are found in the strict consensus tree: one group with the species of the subgenus *Fazia* with the subgenus *Claraplumula*, and a second group with *A. (Allograpta) ventralis*, *A. (Allograpta) alamacula*, the representatives of the subgenera *Costarica*, *Antillus* and *Rhinoprosopa*, and the genus *Eosphaerophoria*. Subgenera *Costarica* and *Rhinoprosopa* were recovered in the strict consensus tree and related. The placement of *A. alamacula* with *A. (Antillus) ascita* probably is due to the presence of a dark macula in the wing. These results show that inclusion of more taxa and/or additional morphological characters are necessary to increase the topological resolution and clade support values. Although the monophyly of the genus *Allograpta* is questionable based on our results, some groups were consistently recovered (see fig. 24). The combination of morphological and molecular data is vital for a better supported hypothesis of the phylogenetic relationships among the included genera and to generate a stable classification.

Acknowledgments

This work is the first of many planned on the syrphine clade that includes *Allograpta*. Future papers will address the phylogeny of the group based on morphology and DNA characters (Mengual *et al.* in prep.) as well as a revision of the Neotropical species (Ruiz *et al*., in prep.). The order of authorship is merely chronological by age; the junior authors in age contributed the new insights and inspiration for the paper and the senior the history and "wisdom!"

The color habitus drawings [figs. 1, 4–6] were provided by Taina Litwak except that of *A. (Costarica) zumbadoi* [fig. 3], which was drawn by Jennifer Fairman and reproduced from Thompson et alia (2000) and *A. (Fazia) centropogonis* [fig. 2], which was drawn by Leonardo Donzo and reproduced from Nishida et alia (2002). The black and white line drawings were from Hull (1949b) [figs. 7–10], Thompson *et al.* (2000) [fig. 14], Carver & Thompson (2003) [fig. 15] and Vockeroth (1969 [figs. 11–13], 1973 [fig. 16]), Taina Litwak (new) [figs. 17-19] and Ximo Mengual (new) [figs. 20-21]. The distribution map [fig. 22] was produced by Charyn Michel.

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