BIOTAXONOMY OF TEPHRITOIDEA
Isr. J. Entomol. Vol. 35-36, 2005/6, pp. 9-34

Morphology and Phylogenetic Relationships of Species Groups of the Genus *Hexachaeta* Loew (Diptera: Tephritidae: Trypetinae)

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ABSTRACT

A revision is made of the supra-specific classification and relationships of the American genus *Hexachaeta* Loew. Two subgenera and four species groups are recognized: *Hexachaeta sensu stricto* including two species groups: 1) the *eximia* group, comprising *H. barbiellinii barbiellinii* Lima, *H. barbiellinii itatiaiensis* Lima et Leite, *H. dinia* (Walker), *H. enderleini* Lima, *H. eximia* (Wiedemann), *H. seabrai* Lima, *H. venezuelana* Lima, *H. zeteki* Lima, and two undescribed species; and 2) the *colombiana* group, comprising *H. colombiana* Lima, *H. bifurcata* Hernández-Ortiz, *H. nigriventris* Hernández-Ortiz, *H. leptofasciata* Hernández-Ortiz, and *H. ecuatoriana* Hernández-Ortiz. *Costamyia*, new subgenus, also including two species groups: 1) the *amabilis* group, comprising *H. amabilis* (Loew), *H. homalura* Hendel, *H. obscura* Hendel, *H. shannoni* Lima, *H. juliorosalesi* Hernández-Ortiz, and two undescribed species; and 2) the *socialis* group comprising *H. aex* (Walker), *H. bondari* Lima et Leite, *H. cronia* (Walker), *H. fallax* Lima, *H. major* (Macquart), *H. monostigma* Hendel, *H. nigripes* Hering, *H. oblita* Lima, *H. parva* Lima, *H. socialis* (Wiedemann), *H. valida* Lima, and four undescribed species. A cladistic analysis of the genus is presented, and the phylogenetic relationships of the subgenera and species groups are discussed.

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INTRODUCTION

The Tephritidae or true "fruit flies" are one of the largest families of Diptera. They are of major economic importance world-wide (Foote, 1967a), because the larvae of most species are phytophagous, breeding in fruits, seeds, flowers, leaves, roots and stems of a wide variety of plants, including many agricultural crops (Christenson & Foote, 1960). This family is represented by about 4,350 described species and the greatest diversity is in the tropics (Norrbom *et al.*, 1999a).

In continental America there are approximately 935 tephritid species in about one hundred genera (Hernández-Ortiz, 1996). With almost 200 known species, *Anastrepha* Schiner is both the most diverse and best studied Neotropical genus. Other indigenous genera of this region, including *Hexachaeta*, have been poorly studied (Norrbom *et al.*, 1999b).

The genus *Hexachaeta* Loew comprises about 28 valid species, although additional species remain undescribed (Hernández-Ortiz, in preparation). It is almost exclusively distributed in the Neotropical Region, from southern Texas (USA) to Argentina, but is absent from Chile.

Most of the taxonomic work on this genus was done by Lima (1935, 1953a, 1953b, 1954; Lima and Leite, 1952), who also described the extraordinary morphological variation among the species, but the interspecific relationships have not been clearly documented.

The aim of this study was to explore the phylogenetic relationships, and to diagnose the species groups, within *Hexachaeta*, based on adult morphology.

Taxonomic position of *Hexachaeta*

Korneyev (1999) recognized in the Tephritidae six subfamilies: Phytalmiinae, Tachiniscinae, Blepharoneurinae, Dacinae, Tephritinae and Trypetinae. The Trypetinae are represented in America by the tribes Adramini (including Euphrantini, *sensu* Korneyev, 1994), Toxotrypanini, Trypetini, and Carpomyini (Foote *et al*., 1993).

Hexachaeta is currently placed in the Trypetinae, but its tribal affinities are uncertain. Previous studies (Foote, 1967a; 1980) tentatively assigned *Hexachaeta* Loew to the tribe Acanthonevrini together with numerous Old World genera and the American genera *Blepharoneura* Loew, *Ceratodacus* Hendel, *Pyrgotoides* Curran and *Ischyropteron* Bigot, based on the presence of a plumose arista and/or six scutellar bristles. Currently the genera *Blepharoneura* and *Ceratodacus* are placed in the subfamily Blepharoneurinae (Norrbom and Condon, 1999); *Pyrgotoides* in the Tephritinae, and *Ischyropteron* in the Tachiniscinae (Korneyev, 1999), and the relationships of *Hexachaeta* remain unresolved.

Hexachaeta differs from the Acanthonevrini, which are widely distributed in the tropical regions of Asia, Africa and Australia, by the complete fusion of the aculeus tip, the presence of small denticles on the spermathecal surface, and by the lack of tactile subapical setae on the aculeus tip, refuting the hypothesis that it belongs in that tribe (Hancock, 1986; Korneyev, 1994, 1999).

Studies on the phylogeny of several tephritid genera based on ribosomal (16S) DNA sequences (Han & McPheron, 1997) indicated that *Hexachaeta* (represented by *H. amabilis*) has a close relationship with members of the Toxotrypanini (*sensu* Foote *et al*., 1993), which includes only the Neotropical genera, *Anastrepha* Schiner and *Toxotrypana* Gerstaecker, suggesting that *Hexachaeta* is the sister group of that tribe. The *Molynocoelia* group (*Molynocoelia* Giglio-Tos, *Pseudophorellia* Lima, *Alujamyia* Norrbom) may also belong in this group (Norrbom, 2006, this volume).

Taxonomic studies of *Hexachaeta*

The first species of *Hexachaeta* were described in other genera, e.g., *Trypeta eximia* Wiedemann (1830: 477) and *Trypeta socialis* Wiedemann (1830: 491) based on material from Surinam and Brazil, respectively. Additional species were described by Walker (1837, 1849) and Macquart (1847). Later, in the North American Diptera Monographs, Loew (1873) described *Trypeta amabilis* and carried out a morphological analysis of *T. eximia* Wiedemann. He also proposed the new genus *Hexachaeta* : "I did so on account of the great resemblance in the plastic characters of *T. eximia* with *T. amabilis*, with *T. socialis* Wied., and with several other South American species. These species form a very well-defined group, for which I choose the name of *Hexachaeta*, and which deserves to be considered as a separate genus."

Loew´s diagnosis is based on the description of *T. eximia,* including the head shape and its parts, coloration of thorax and scutellum, number and position of setae, spines on the legs, as well as the wing pattern and setulae on the wing veins.

At the begining of the 20th century other taxa were added to this genus, including *H. homalura, H. monostigma*, and *H. amabilis* var. *obscura*, described by Hendel (1914b), and *H. nigripes* Hering (1938).

The first revision of the genus was made by Lima (1935), who presented taxonomic descriptions and a key to 11 species, which were separated into two groups, one of which was further subdivided. Following these groupings, Lima published additional partial revisions describing *H. bondari*, *H. shannoni, H. colombiana, H. venezuelana, H. seabrai, H. zeteki, H. parva, H. oblita, H. fallax* and *H. valida* (Lima & Leite, 1952; Lima 1953a, 1953b, 1954).

Lima (1935) divided *Hexachaeta* into species groups based on wing pattern characters, size of the ocellar seta, and the position of crossvein R-M. He briefly diagnosed these groups as follows:

Group 1: Apical dark fascia of wing forming an arc with the posterior concavity isolated from other dark markings (=subapical plus anterior apical bands); ocellar seta rudimentary; distance between crossveins R-M and DM-Cu one and half times as long as R-M. This group included *H. amabilis* and *H. obscura*, with *H. shannoni* (Lima 1953a) added subsequently.

Group 2: Dark areas of apical part of wing forming two slender apical fascia (= anterior and posterior apical bands). This group was separated into two divisions. The first division, characterized by two inverted triangular hyaline areas in cell r_1, comprises two subgroups: One subgroup was diagnosed by the ocellar seta well developed; vein Cu_1 setulose dorsally; distance between crossveins R-M and DM-Cu at most twice as long as R-M, or R-M located at the middle of discal cell. In this group Lima (1935) included: *H. eximia*, *H. enderleini*, *H. aegiphilae*, *H. barbiellinii* and *H. dinia*. Later *H. seabrai*, *H. venezuelana*, *H. zeteki* and *H. colombiana* were added (Lima, 1953b). The other subgroup was characterized by ocellar seta rudimentary, piliform; distance between crossveins R-M and DM-Cu more than twice as long as R-M. Only *H. homalura* was placed in this subgroup.

The second division was diagnosed by having only one inverted triangular hyaline mark in cell r_1*;* ocellar seta rudimentary, piliform; vein Cu_1 bare; distance between crossveins R-M and DM-Cu more than twice as long as DM-Cu, and crossvein R-M located at middle of discal cell. The species placed here were *H. aex, H. monostigma, H. socialis* and *H. cronia*. In later revision of this group Lima (1954) also included *H. major, H. parva, H. oblita, H. fallax*, *H. valida* and *H. nigripes*.

Although Lima studied most species of *Hexachaeta*, the groups he recognized were ambiguous, because the characters were not consistently employed. In addition, some important features of the male and female terminalia were not used in this analysis. The present analysis of all these characters in a phylogenetic framework demonstrates that Lima's groups are not monophyletic.

MATERIALS AND METHODS

Examined specimens

About 600 specimens of 32 species of *Hexachaeta* were examined from many regions of the Neotropics. Specimens were observed using a Zeiss-Stemi SV6 microscope provided with a camera lucida for illustrations. The number of specimens analyzed for phylogeny varied, but when enough material was available, five specimens of each sex served to detect possible intraspecific variability. Characters of the terminalia of both sexes were observed by dissecting the abdomen and heating it in a solution of NaOH (10%) according to Gurney *et al.* (1964). In some cases permanent slides in Canadian Balsam were made, but most samples were preserved in glycerin in microvials.

Taxonomic terminology employed in this revision follows McAlpine (1981) for general terms, White *et al.* (1999) for specific tephritid terminology, and Foote (1981) for the wing pattern.

The collections that loaned material for this study and their acronyms are as follows:

AMNH — American Museum of Natural History, New York, USA
ANSP — Academy of Natural Sciences of Philadelphia, Philadelphia, USA
BMNH — The Natural History Museum (formerly, British Museum of Natural History), London, UK
CAS — California Academy of Sciences, California, USA
CMNH — Carnegie Museum of Natural History, Pittsburgh, USA
CNC — Canadian National Collection, Ottawa, Canada
CUIC — Cornell University Insect Collections, Ithaca, USA
DEI — Deutsches Entomologisches Institut, Eberswalde, Germany
FML — Fundación Miguel Lillo, Universidad de Tucumán, Tucumán, Argentina
FMNH — Field Museum of Natural History, Chicago, USA
FSCA — Florida State Collection of Arthropods, Gainesville, USA
IBUNAM — Instituto de Biología, Universidad Nacional Autónoma de México, D.F., México
IEXA — Instituto de Ecología A.C., Xalapa, México
INBIO — Instituto Nacional de Biodiversidad, Heredia, Costa Rica
INPA — Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, USA
MIZA — Museo de Insectos de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
MNHN — Museum Nacional d'Histoire Naturelle, Paris, France
MSU — Michigan State University, Michigan, USA. NMW — Naturhistorisches Museum Wien, Vienna, Austria
SMN — Staatlisches Museum für Naturkunde, Stuttgart, Germany
SMTD — Staatlisches Museum für Tierkunde, Dresden, Germany

TAMU — Texas A & M University Insect Collection, Texas, USA
TAUI — Tel-Aviv University Insect Collection, Tel-Aviv, Israel
UCD — University of California, Davis, USA. USNM — National Museum of Natural History, Washington D.C., USA
USP — Universidade de São Paulo, São Paulo, Brazil
USU — Utah State University Entomological Museum, Logan, USA
UVC — Universidad del Valle, Cali, Colombia
ZMB — Zoologisches Museum of Humboldt University, Berlin, Germany

Cladistic analysis

To explore phylogenetic relationships among species, a data matrix was prepared comprising 34 taxa and 47 characters. These were coded using *Anastrepha* (*A. leptozona* Hendel and *A. obliqua* (Macquart)) as outgroup (Table 1, Appendix 1). This outgroup was chosen based on the genetically-based results of Han and McPheron (1997) which indicate that *Hexachaeta* is the sister group of the Toxotrypanini, a monophyletic group containing two Neotropical genera, *Anastrepha* Schiner and *Toxotrypana* Gerstaecker (*sensu* Foote *et al.*, 1993).

The ingroup comprised 32 taxa, including six species recently described (Hernández-Ortiz, 1999, 2002) and eight undescribed species found in this study. *Hexachaeta aex, H. bondari,* and *H. major* were not included because they were not represented in the examined material. *Hexachaeta guatemalensis* was also excluded because it is considered to be a new synonym of *H. zeteki* (Hernández-Ortiz, in preparation).

A phylogenetic analysis was carried out using parsimony by the computer package NONA 2.0 (Goloboff, 1993). Search options were: hold maximum number of trees 1000, and mult* 100, followed by branch swapping max*. All characters were weighted equally, and those characters with multiple states were treated as nonadditive (7, 26, 37, 43). The resulting trees were subsequently subjected to WinClada (Nixon, 1999) for character optimization.

TAXONOMY AND SYSTEMATICS

Genus *Hexachaeta* Loew, 1873

Hexachaeta Loew 1873: 219. Type species: *Trypeta eximia* Wiedemann (designated by Coquillett 1910: 552); Wulp 1899: 402 (key and discussion of 6 species); Hendel 1914a: 82 (in key and descriptions); Hendel 1914b: 23 (taxonomy, discussion of South American species); Bates 1933: 50 (description); Lima 1933: 382 (taxonomy); Curran 1934: 287 (in key to American genera); Lima 1935a: 235 (revision); Hering 1938: 414 (description); Hering 1941: 123 (key, discussion of known species); Aczél 1949: 192 (in Neotropical catalog); Aczél 1951: 123 (in supplement to the Neotropical catalog); Lima & Leite 1952: 297 (key to species, descriptions); Aczél 1953: 104 (in key, Acanthonevrini genera); Lima 1953a: 153 (key and descriptions of species of "*amabilis* group"); Lima 1953b: 557 (key and descriptions of species of "*eximia* group*"*); Lima 1954: 281 (key and descriptions to species of "*socialis* group"); Foote 1964: 317, 320-324 (revision of Walker types); Foote 1967a: 26 (in Neotropical catalog, error as *Hetschkomyia*); Foote 1967b: 1327 (records of North American species); Silva *et al*. 1968: 584 (in catalog of hosts in Brazil); Foote *et al*. 1993: 50, 205 (in key to Nearctic genera, discussion of North American species); Norrbom *et al.*

1999b: 158 (catalog); Hernández-Ortiz 1999: 631 (revision of species of the *colombiana* group); Norrbom *et al.* 1999a: 305 (discussion of phylogenetic relationships); Hernández-Ortiz 2002: 129 (new species of the *amabilis* group).

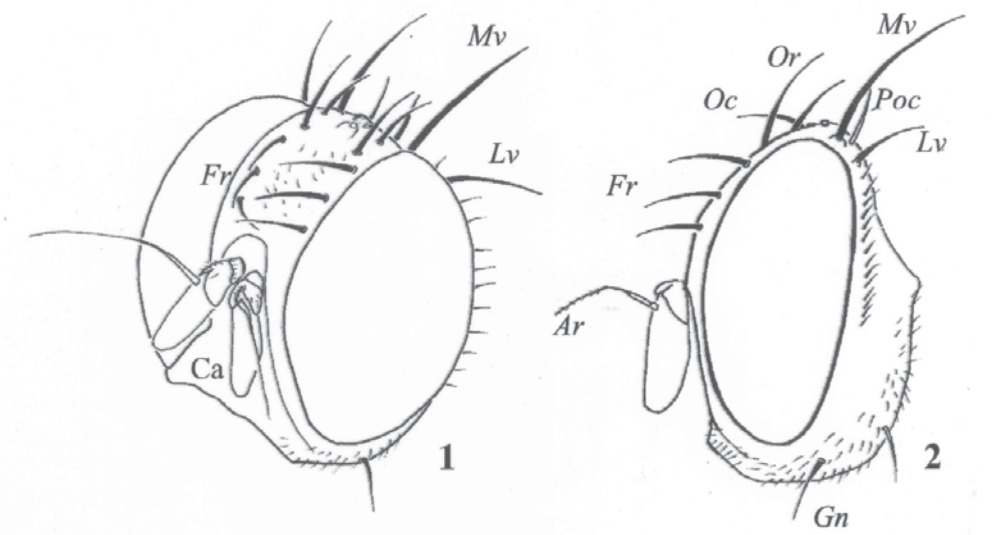
Neohexachaeta Lima 1953b: 566. Type species - *Neohexachaeta guatemalensis* Lima (by original designation); Foote 1967a: 31 (in Neotropical catalog); Foote 1980: 31 (synonymy).

Redescription

Head (Figs. 1 and 2). Yellow with some parts of frons reddish, covered by short and sparse setulae; facial carina weak or undifferentiated; frons with three frontals and two orbital setae; ocellar seta weak (in some cases undifferentiated) or well developed; postocellar seta black or yellow; first flagellomere shorter than face; arista finely and sparsely pilose, sometimes bare on basal two thirds.

Thorax (Figs. 3-7). Mesonotum usually yellow or reddish brown, sometimes with black marks on presutural and postsutural regions, or just at posterior margin of scutum; chaetotaxy (setae black): 1 postpronotal, 1 presutural supra-alar, 1 postsutural supra-alar, 1 postalar, 1 intra-alar, 1 acrostichal, 1 dorsocentral, and 3 scutellars. Dorsocentral seta placed near level of postalar (*eximia* group), or near midpoint between postsutural supra-alar and postalar (*colombiana* group, Fig. 4).

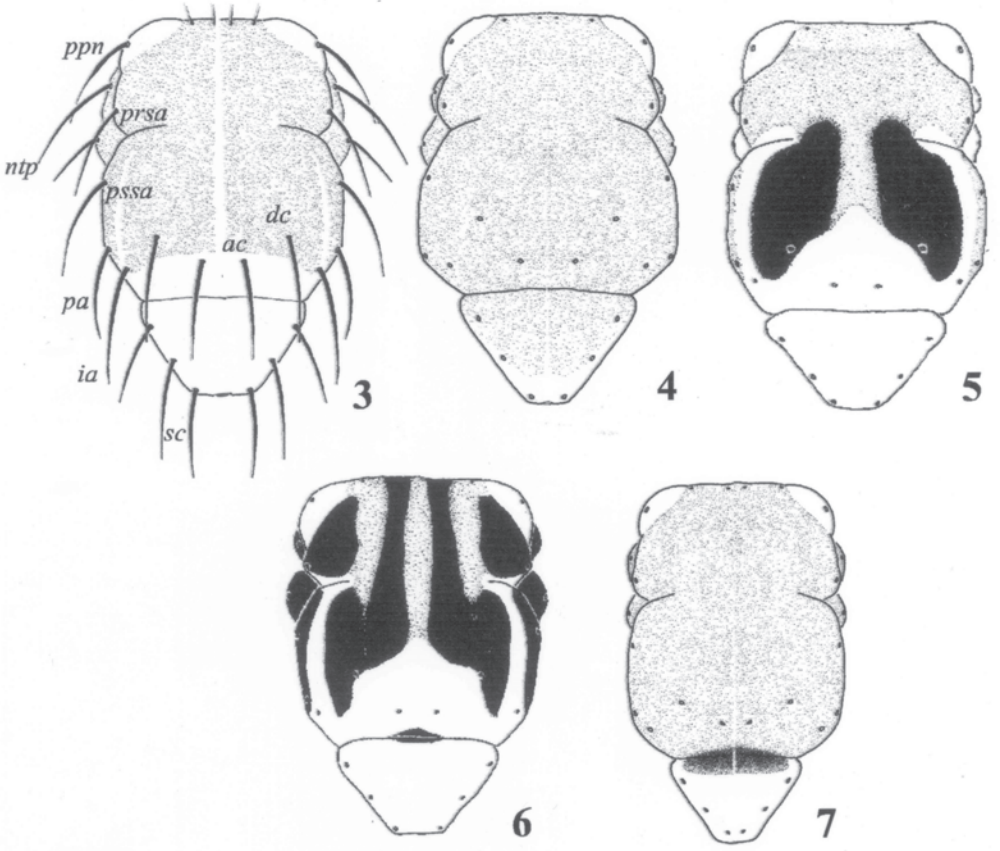
Scutellum reddish yellow similar to scutum, or bright whitish and/or with dark marks basally; disc setulose or bare; subapical pair of scutellar setae sometimes reduced, or extra pair present in aberrant specimens (e.g., holotype of *Neohexachaeta guatemalensis*); mediotergite usually reddish yellow or with black lateral marks. Pleural sclerites and legs usually yellow in species of the subgenus *Hexachaeta*, and with black marks on anepisternum, anepimeron and katepisternum in many species of the subgenus *Costamyia.* Male forefemur robust and wider than in females.



Figs. 1-2. Morphology of head of *Hexachaeta* species. 1. Anterolateral view of *H. obscura*. 2. Lateral view of *H. seabrai*. Abbreviations: Ar: arista; Ca: facial carina; Fr: frontal setae; Gn: genal seta; Mv: medial vertical seta; Oc: ocellar seta; Or: orbital seta; Lv: lateral vertical seta; Poc: postocellar seta.

Wing (Figs. 8-10). Dorsal setulae on vein Cu present or absent; crossvein R-M at or distal to level of apex of vein R_1; vein R_{4+5} with dorsal setulae extended at least to crossvein R-M; posteroapical lobe of cell bcu elongated, approximately one half or less as long as main part of cell. Wing pattern with broad brownish dark marks or bands usually interconnected: sub-basal, discal, subapical, anterior apical (always present and 2-6 times as wide as costal vein), and posterior apical (absent in some species of the *amabilis* group). Radial cells with one or two usually triangular hyaline spots distal to apex of vein R_1; proximal hyaline spot, if present, reaching to or beyond vein R_{4+5}; distal hyaline spot either triangular or extended to posterior margin of wing; discal cell usually with hyaline spots on basal and/or distal portion, sometimes entirely blackish.

Abdomen. Tergites usually yellow with black bands, but sometimes entirely yellow or blackish.



Figs. 3-7. Mesonotal pattern and chaetotaxy of *Hexachaeta* species. 3. *H. seabrai.* 4. *H. colombiana.* 5. *H. juliorosalesi.* 6. *H. obscura.* 7. *H. valida*. Abbreviations of setae: ac: acrostichal; prsa: presutural supra-alar; dc: dorsocentral; ia: intra-alar; ntp: notopleural; pa: postalar; ppn: postpronotal; pssa: posterior supra-alar; sc: scutellars.

Male terminalia (Figs. 19-22). Epandrium well developed and spherical; hypandrium sclerotized and stout in distal portion; lateral surstylus long and sometimes strongly curved posteriorly in lateral view, extreme apex usually with fold and often hook shaped dorsally or ventrally in lateral view; medial surstylus nearly half to almost as long as lateral surstylus, with one or two prensisetae developed; glans elongated or stout, sometimes with broad sclerotized areas internally.

Female terminalia (Figs. 23-30). Oviscape short (at most as long as tergites 5-6 combined) or longer than abdomen; three spherical spermathecae present, covered by small denticles. Aculeus dorsoventrally compressed; tip with conspicuous modifications, often with lateral margins serrated or with lateral projections; extreme apex simple or bilobed.

Key to subgenera and species groups of *Hexachaeta*

1. Ocellar seta well developed (at least as long and thick as postocellar) (Fig. 2); base of vein Cu setulose dorsally (Fig. 8); scutellum disc setulose; medial surstylus nearly half as long as lateral surstylus, with two prensisetae; apex of aculeus usually not bilobed .... ***Hexachaeta, sensu stricto*** **2**
-. Ocellar seta undifferentiated or very weak (Fig. 1); vein Cu without dorsal setulae (Fig. 9); scutellum disc without setulae; medial surstylus nearly as long as lateral surstylus and with only one prensiseta well developed; apex of aculeus bilobed .... ***Costamyia*****, new subgenus 3**
2. Proctiger without ventro-basal sclerite; wing: discal and subapical bands always connected in or anterior to discal cell; apical third of discal cell mainly brownish black, or occasionally only with small slender isolated hyaline spot; distal hyaline mark in cell r_1 at most extended to vein M; basal third of discal cell with isolated round hyaline spot (Figs. 17, 18) .... ***eximia*** **group**
-. Proctiger with ventro-basal sclerite; wing: discal and subapical bands separated along discal cell or occasionally weakly connected on vein Cu_1; distal hyaline triangular mark in cell r_1 extended into discal cell, or reaching posterior margin of wing; basal and apical thirds of discal cell broadly hyaline (Figs. 15, 16) ..... ***colombiana*** **group**
3. Distance between crossveins R-M and DM-Cu distinctly longer than crossvein DM-Cu; crossvein R-M almost at level of apex of vein R_1; cell r_1 only with distal hyaline triangular mark present; posterior apical band present (Figs. 13, 14); aculeus at least three times as long as wide ..... ***socialis*** **group**
-. Distance between crossveins R-M and DM-Cu shorter, equal or slightly longer than crossvein DM-Cu; crossvein R-M distal to level of apex of vein R_1; cell r_1 with two hyaline marks; posterior apical band usually absent (except in *H.* sp. n. B and *H. homalura*) (Figs. 11, 12); aculeus at most twice as long as wide (Fig. 23) ..... ***amabilis*** **group**

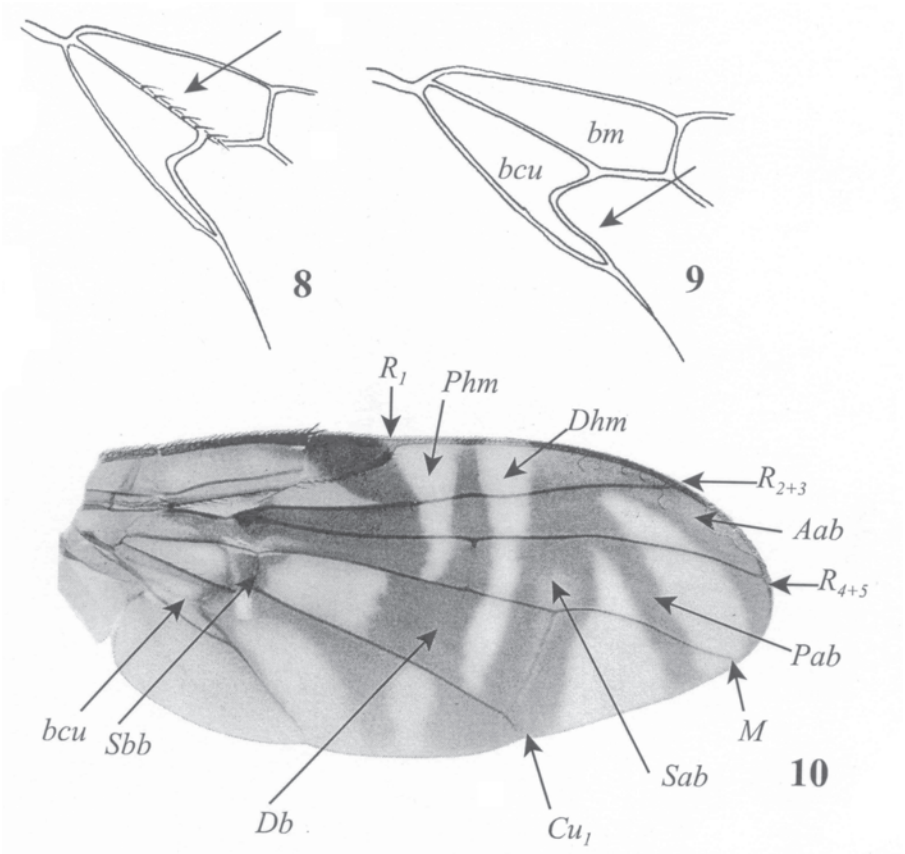
DIAGNOSIS OF SUBGENERA AND SPECIES GROUPS OF *HEXACHAETA*

Subgenus *Hexachaeta* sensu stricto

Type species: *Trypeta eximia* Wiedemann, by designation of Coquillett 1910:552.

Diagnosis

Ocellar seta well developed (at least as long as postocellar); scutellum disc setulose; base of vein



Figs. 8-10. Morphology and terminology of the wing. 8. Dorsal setulae on base of vein Cu (arrow). 9. Posteroapical lobe of cell bcu (arrow). 10. Wing pattern of *H. colombiana*. Abbreviations: Aab: anterior apical band; Cu_1: cubital vein 1; Db: discal band; Dhm: distal hyaline mark; M: medial vein; Pab: posterior apical band; Phm: proximal hyaline mark; Sab: subapical band; Sbb: subbasal band. R_1, R_{2+3}, R_{4+5}: Radial veins.

Cu_1 (along cell bcu) with dorsal setulae; distance between crossveins R-M and DM-Cu always shorter than length of crossvein DM-Cu; crossvein R-M distal to level of apex of vein R_1; lateral surstylus strongly curved posteriorly, wider basally than at apex in lateral view, with hook-like dorsoapical fold. Male: medial surstylus half as long as lateral surstylus, with two apical prensisetae developed; glans usually elongated and slender, weakly sclerotized. Female: aculeus tip usually short, with lateral margin not serrated and extreme apex not bilobed (except in *H. bifurcata*).

Included groups

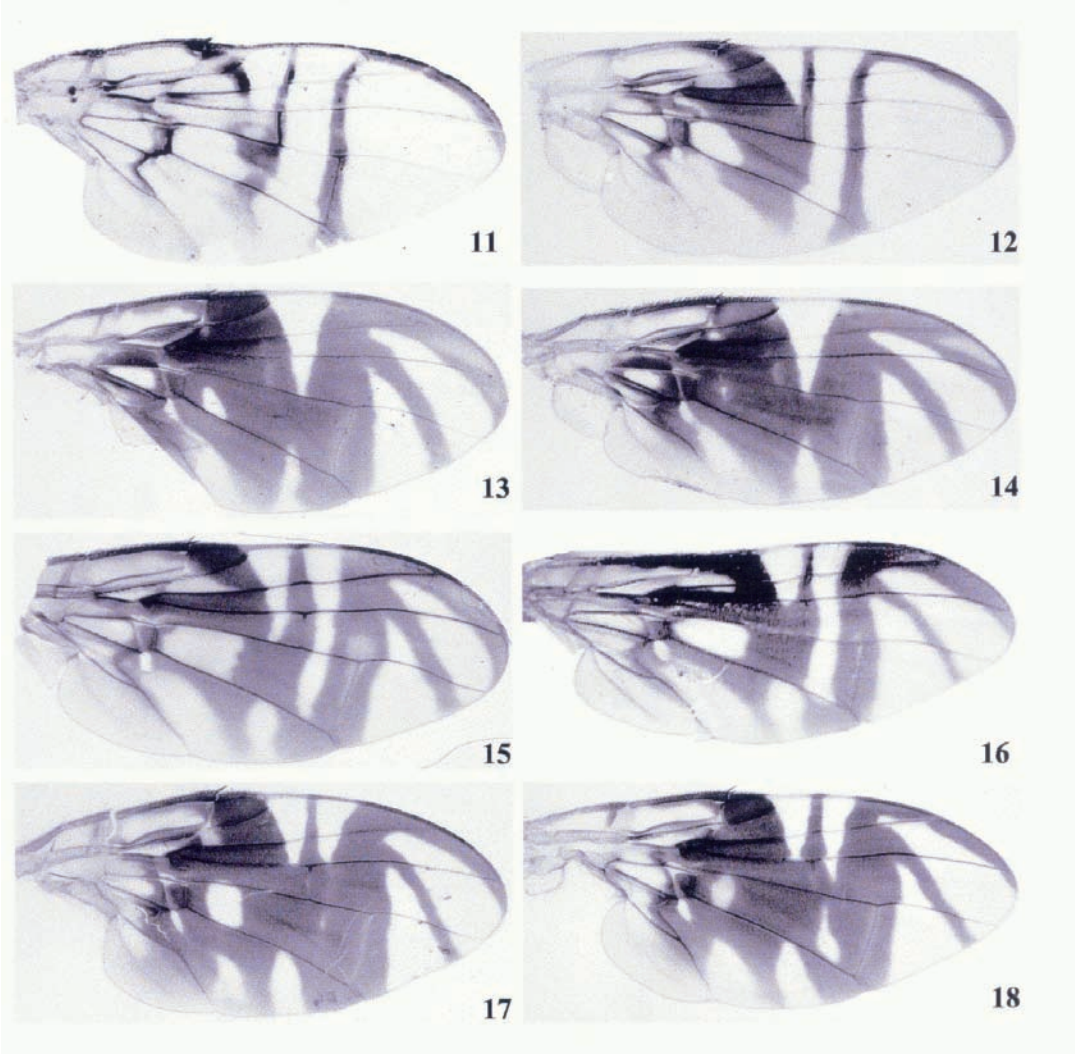
The *eximia* and *colombiana* species groups.

The *eximia* species group

Diagnosis

Postocellar seta yellow or blackish; mesonotum with presutural and postsutural region usually yellow or reddish without any black marks; posterior margin of scutum and scutellum

pale yellow, together forming a rhomboidal area, but in some species scutum and scutellum more or less uniformly colored, lacking such distinctive area; dorsocentral seta close to level of postalar seta. Wing pattern with broad brown or blackish spots or bands covering most of wing surface; proximal and distal hyaline triangular spots in radial cells present; discal and subapical bands connected in or anterior to discal cell; anterior and posterior apical bands present and usually slender (except in *H. dinia*); abdominal tergites yellow or with dark brownish bands. Wings with posteroapical lobe of cell bcu slightly shorter than half length of main part of cell. Male: proctiger membranous, without basal sclerite. Female: aculeus short and usually without large lateral projections, or sometimes with only one moderate projection; lateral margins of aculeus tip nonserrated, and extreme apex not bilobed.



Figs. 11-18. Typical wing patterns of *Hexachaeta* species. 11. *H. shannoni.* 12. *H. amabilis*. 13. *H. fallax*. 14. *H. parva.* 15. *H. colombiana*. 16. *H. nigriventris.* 17. *H. eximia*. 18. *H. enderleini*.

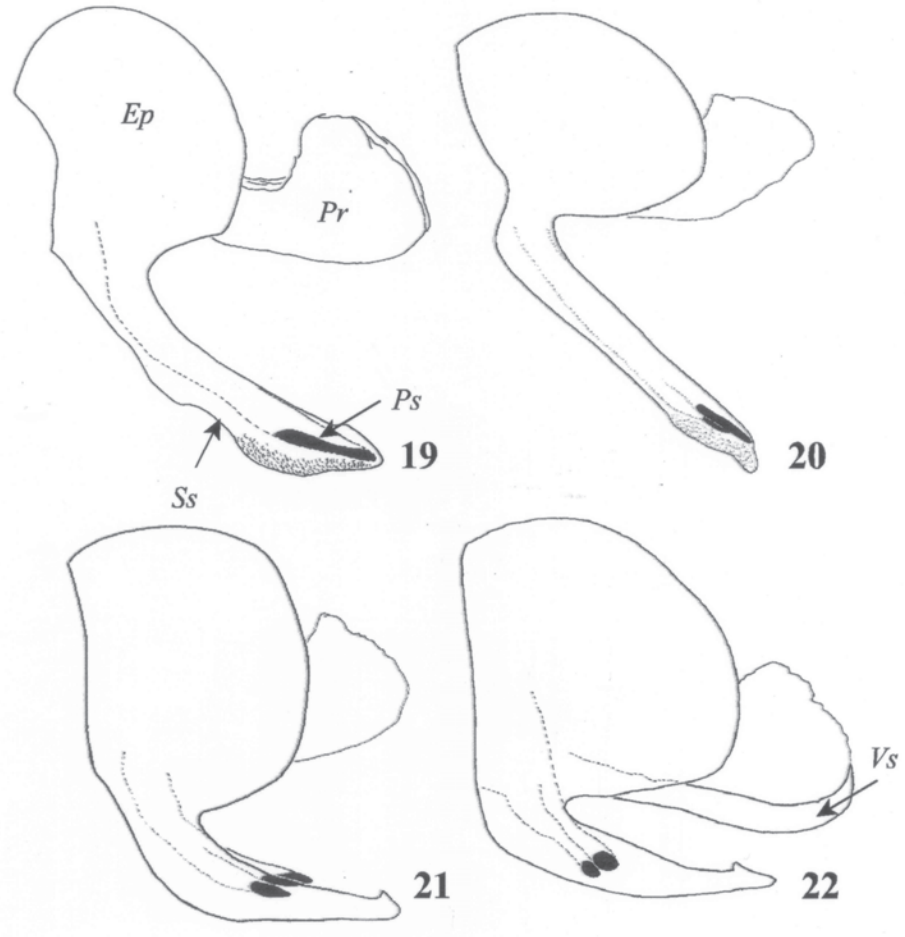
Included species

H. barbiellinii barbiellinii Lima, *H. barbiellinii itatiaiensis* Lima et Leite, *H. dinia* (Walker), *H. enderleini* Lima, *H. eximia* (Wiedemann), *H. seabrai* Lima, *H. venezuelana* Lima, *H. zeteki* Lima, *Hexachaeta* sp. G, *Hexachaeta* sp. H.

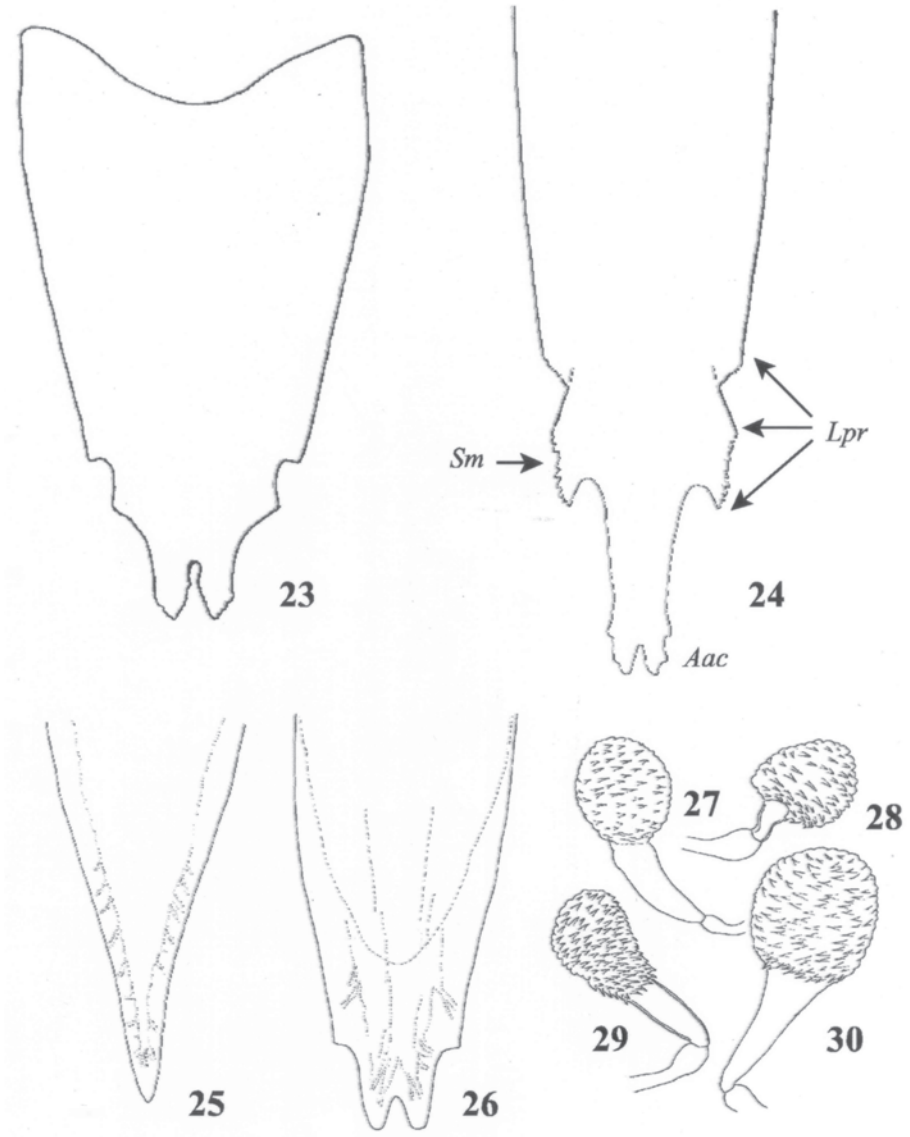
The *colombiana* species group

Diagnosis

Postocellar seta black or reddish brown; scutum yellow or reddish without any black mark on posterior margin; scutellum usually concolorous with scutum; mediotergite and subscutellum reddish; dorsocentral seta near midpoint between postsutural supra-alar and postalar setae; pleuron and legs yellow. Wing pattern with bands slender and two hyaline marks



Figs. 19-22. Male terminalia of *Hexachaeta* species. 19. *H. obscura* (*amabilis* group). 20. *H. oblita* (*socialis* group). 21. *H. enderleini* (*eximia* group). 22. *H. ecuatoriana* (*colombiana* group). Abbreviations: Ep: epandrium; Pr: proctiger; Ps: prensisetae; Ss: lateral surstylus; Vs: ventral sclerite.



Figs. 23-30. Female terminalia of *Hexachaeta* species. 23-26. Ventral view of the aculeus: 23. *H. amabilis* (entire aculeus). 24. *H. oblita* (aculeus tip). 25. *H. venezuelana* (aculeus tip). 26. *H. bifurcata* (aculeus tip). 27-30. Spermathecae: 27. *H. eximia*. 28. *H. homalura*. 29. *H. amabilis*. 30. *H. socialis*. Abbreviations: Aac: apex of the aculeus; Lpr: lateral projections; Sm: serrated margin.

present in radial cells; proximal hyaline mark triangular; distal hyaline mark extended into discal cell or reaching posterior margin of wing; posteroapical lobe of cell bcu usually slightly less than half as long as main part of cell; anterior apical band at most three times as wide as costal vein; posterior apical band present; discal and subapical bands usually not connected but sometimes touching on vein Cu_1; basal third of discal cell with broad hyaline spot; cell bm

broadly hyaline. Abdominal tergites variable, usually yellow but sometimes completely black as in *H. nigriventris*. Male: proctiger with basal sclerite present. Female: aculeus short, approximately 0.4-0.7 times as long as oviscape; aculeus tip with lateral margin nonserrated, sometimes with one lateral projection, apex not bilobed except in *H. bifurcata*.

Included species

H. colombiana Lima, *H. bifurcata* Hernández-Ortiz, *H. nigriventris* Hernández-Ortiz, *H. leptofasciata* Hernández-Ortiz, and *H. ecuatoriana* Hernández-Ortiz.

Subgenus *Costamyia* Hernández-Ortiz, new subgenus

Type species: *Hexachaeta amabilis* var. *obscura* Hendel, 1914b.

Diagnosis

Ocellar seta extremely weak or undifferentiated; scutum reddish, sometimes with black markings at least on posterior margin; lateral black marks on subscutellum usually present; scutellum dorsally whitish; setulae on scutellum disc absent; vein Cu_1 dorsally bare throughout its length. Male: medial surstylus as long as lateral surstylus, or sometimes slightly longer, with only one prensiseta well developed; glans stout and heavily sclerotized. Female: aculeus strong and broad, usually strongly modified, with 1-3 lateral projections, and lateral margin frequently serrated; aculeus tip bilobed.

Etymology

This subgenus is named in memory of A. da Costa Lima in recognition of his contribution to the taxonomic knowledge of the genus. It consists of his name, Costa, and the Greek noun, “myia”, meaning “fly”.

Included groups

The *amabilis* and *socialis* species groups.

The *amabilis* species group

Diagnosis

Postocellar seta black or dark brown; mesonotum usually with pattern of black spots or stripes at least on postsutural region (except in *H. shannoni* and *H. homalura*); dorsocentral seta near midpoint between postsutural supra-alar and postalar setae (except in *H. homalura*); pleuron usually with blackish marks, but sometimes completely yellow; distance between crossveins R-M and DM-Cu shorter than crossvein DM-Cu; crossvein R-M distal to level of apex of vein R_1. Wing pattern brownish black, with two hyaline marks in cell r_1; proximal hyaline mark triangular, and distal mark reaching posterior margin of wing or anterior margin of discal cell; discal and subapical bands frequently unconnected or joined just in discal cell; anterior apical band slender (two or three times as wide as costal vein); posterior apical band usually absent (present in *H. homalura* and *Hexachaeta* sp. B). Male: Lateral surstylus elongated, conspicuously curved posteriorly, and uniformly wide, except its apical part swollen in lateral view. Female: Oviscape broad and short, nearly as long as last two or three tergites combined; aculeus broad (approximately twice as long as wide at widest portion); lateral margin of aculeus tip usually with two projections but sometimes just one or none.

Included species

H. amabilis (Loew), *H. homalura* Hendel, *H. obscura* Hendel, *H. shannoni* Lima, *H. juliorosalesi* Hernández-Ortiz, *Hexachaeta* sp. A, *Hexachaeta* sp. B.

The *socialis* species group

Diagnosis

Distance between crossveins R-M and DM-Cu longer than crossvein DM-Cu; wing pattern dark brown or blackish; cell r_1 only with distal hyaline triangular mark present; proximal hyaline mark in radial cells absent; anterior and posterior apical bands present; subapical band broad and connected to discal band. Male: epandrium globose; lateral surstylus very long and slender beginning at base, apex with ventrally directed, hook-like fold in ventral view. Female: aculeus usually more than four times as long as wide, always bilobed at apex; aculeus tip sagittate, serrated on lateral margin and with large lateral projections (usually two or three pairs).

Included species

H. aex (Walker), *H. bondari* Lima et Leite, *H. cronia* (Walker), *H. fallax* Lima, *H. major* (Macquart), *H. monostigma* Hendel, *H. nigripes* Hering, *H. oblita* Lima, *H. parva* Lima, *H. socialis* (Wiedemann), *H. valida* Lima, *Hexachaeta* sp. C, *Hexachaeta* sp. D, *Hexachaeta* sp. E, and *Hexachaeta* sp. F.

PHYLOGENETIC RELATIONSHIPS OF *HEXACHAETA*

Outgroup

Two species of *Anastrepha* (Toxotrypanini) were used as an outgroup in the phylogenetic analysis. Although *Hexachaeta* shows no evident synapomorphies with Toxotrypanini, no characters contradict the hypothesis that together they form a monophyletic group. The general wing pattern of *Hexachaeta* (especially of the *colombiana* group) is similar to that of many *Anastrepha* species. A bicolored abdomen is a character widely distributed in *Hexachaeta* species, but suspected to be homoplastic. It is shared by most species of *Toxotrypana* and at least some species of the *Anastrepha serpentina*, *cryptostrepha*, *schausi*, *punctata*, *grandis* and *daciformis* species groups.

Full development of the ocellar seta in *Hexachaeta* was considered as an apomorphic state for the analysis, but its polarity is uncertain in the tribe (Norrbom *et al.* 1999a), because this seta is reduced in *Toxotrypana* and almost all *Anastrepha* species, except *A. tripunctata* Wulp, in which the ocellar seta is well developed. Synapomorphies of *Anastrepha* include the apex of vein M anteriorly curved, and the well developed hook-like scales on the eversible membrane (characters 20.1 and 40.1, respectively), both absent in all species of *Hexachaeta*.

Ingroup

Although the possible relationships of *Hexachaeta* with other taxa were not explored in the present analysis, some possible synapomorphies were discovered that could indicate its monophyly (employing *Anastrepha* as the outgroup). These are: facial carina weak or indistinct (1.1); and the presence of three pairs of scutellar setae (4.1). However, the polarity of the latter character is uncertain in a broad sense for the Tephritidae (Norrbom, 1994b), because 3 pairs of scutellars are present in most Tachiniscinae (including the Ortalotrypetini), many Phytalmiinae

and all Blepharoneurinae (*sensu* Korneyev, 1999). Nevertheless, this state is doubtfully plesiomorphic for the Trypetinae or Toxotrypanini, being extremely rare in these taxa. The following wing pattern characters, which are very similar in all species and are possible synapomorphies, could also support the monophyly of *Hexachaeta*: a distal hyaline triangular spot in cell r_1, extended at least from costal margin to vein R_1, sometimes reaching the posterior margin of wing; the connection of the subapical and anterior apical band in cell r_1; and the presence of a dark marking along crossvein BM-Cu.

Cladograms (Figs. 31 and 32)

In the first analysis all characters were considered and the multistate characters (7, 26, 37, and 43; Table 1 and Appendix 1) were treated as non-additive. Results of this analysis yielded 176 trees with a length of 122 steps (ci: 0.42; ri: 0.83). Topology of all trees was basically the

Table 1
Matrix of character state distributions in *Hexachaeta* species

Taxa / Characters	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444 1234567
A. leptozona	0000000000	0000000001	0000000000	0000000001	0000000
A. obliqua	0000001001	0000000001	0000000000	0000011001	0001010
H. amabilis	1001?12011	011110??00	1000121110	0001102010	1101011
H. homalura	1001001001	1100000000	1000110101	0101101010	???????
H. juliorosalesi	1011011001	0100000000	1000110111	0101111010	1101011
H. obscura	1000012001	0111101100	1000121110	1001??????0	1101011
H. shannoni	1001000001	0100100000	1000121110	0001??????0	1101011
H. sp. A	1001?12011	0111101100	1000111110	?001102010	1101011
H. sp. B	1011011000	0100000000	1000110101	0100111010	1101011
H. cronia	1001000100	1100000000	0011000001	0111111000	???????
H. fallax	1001002011	1111101100	0011000001	1101113000	1110011
H. monostigma	1001002011	1111101100	0011000101	1101112100	1110011
H. nigripes	1001002011	1111111110	0011000101	1101113000	1110011
H. oblita	1001002011	1111101100	0011000001	0101113000	1110011
H. parva	1001002011	1111101100	0011000001	1101101000	1100011
H. socialis	1001002101	1111101100	0011000001	0101112000	???????
H. valida	1001002011	0111101100	0011000001	0101112000	1110011
H. sp. C	1001002011	1111101100	0011000001	0101113000	1100011
H. sp. D	1001000101	1100100100	0011000001	0101101000	111?011
H. sp. E	1001002011	1111100100	0011000001	0101111000	111?011
H. sp. F	1001002011	1111101100	0011000001	0101112100	1110011
H. dinia	1111000100	0000000000	0100110001	0110000100	0021000
H. enderleini	1111000100	0000000000	0100110101	0101001100	0021000
H. eximia	1111000101	0000000000	0100110101	0101000100	0021000
H. seabrai	1101001001	0000000000	0100110101	0101000100	0021000
H. venezuelana	1111001001	0000000000	0100110101	0101000000	???????
H. zeteki	1111000000	0000000000	0100110101	0101???100	0021000
H. sp. G	1111001000	0000000000	0100110101	0100001000	00210?0
H. sp. H	1111001001	0000000000	0100110101	0101001000	0021000
H. bifurcata	1101000100	1000000000	1100121000	0001101000	0121100
H. colombiana	1101000100	1000000000	1100121000	0000000100	0021100
H. ecuatoriana	1101000100	1000000000	1100121000	0010001000	0021100
H. leptofasciata	1111000100	1000000000	1100121100	0000001000	???????
H. nigriventris	11?1000100	1000000000	1100111000	0011001000	???????

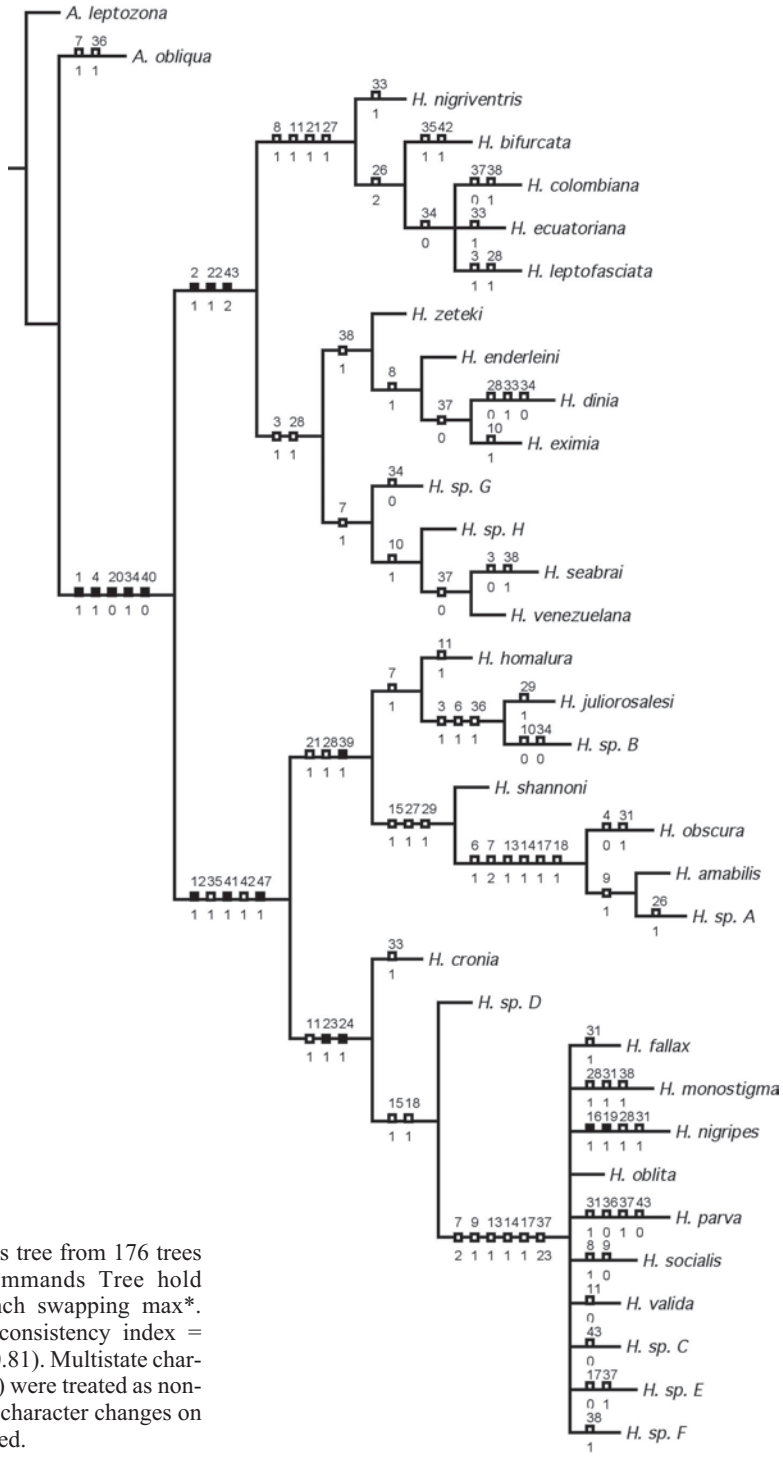


Fig. 31. Strict consensus tree from 176 trees resulting from the commands Tree hold 1000, mult* 100, branch swapping max*. Length of 129 steps (consistency index = 0.39, retention index = 0.81). Multistate characters (7, 26, 37, and 43) were treated as non-additive. Unambiguous character changes on the branches are indicated.

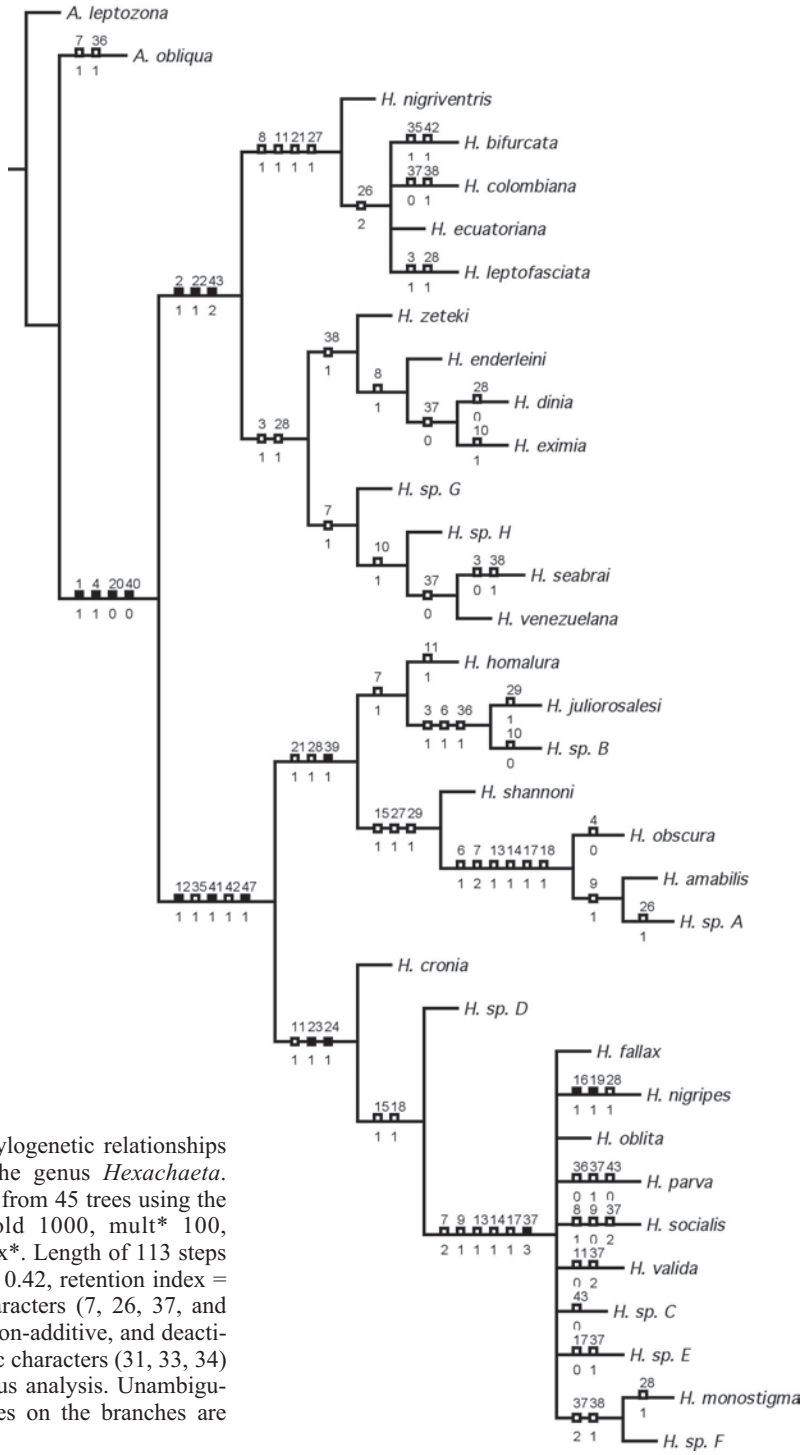


Fig. 32. Possible phylogenetic relationships among species of the genus *Hexachaeta*. Strict consensus tree from 45 trees using the commands Tree hold 1000, mult* 100, branch swapping max*. Length of 113 steps (consistency index = 0.42, retention index = 0.84). Multistate characters (7, 26, 37, and 43) were treated as non-additive, and deactivation of homoplastic characters (31, 33, 34) resulted from previous analysis. Unambiguous character changes on the branches are indicated.

same for all clades, except in the subclade denominated here as the *socialis* species group. The strict consensus tree resulting from this analysis had a length of 129 steps (ci: 0.39; ri: 0.81) (Fig. 31). From this tree it was clear that several characters, such as the hyaline spot at basal third of discal cell (31), color of apical third of discal cell (33) and the coloration of abdominal tergites (34), are highly homoplastic.

Further analysis using the same command options, but with the deactivation of homoplastic characters (31, 33, 34), yielded 45 trees with a length of 109 steps (ci: 0.44, ri: 0.85). In this case, the strict consensus tree had a length of 113 steps (ci: 0.42; ri: 0.84), and it was selected to represent the hypothesis of the phylogenetic relationships of the genus *Hexachaeta* (Fig. 32).

On the basis of this cladogram, *Hexachaeta* species form two monophyletic lineages recognized here as two subgenera, *Hexachaeta sensu stricto*, and *Costamyia*, new subgenus. Each of these subgenera is composed of two subclades: *Hexachaeta sensu stricto* is composed of the *colombiana* and *eximia* species groups, and *Costamyia* is composed of the *amabilis* and *socialis* species groups.

The monophyly of the subgenus *Hexachaeta* is substantiated based on the following synapomorphies: ocellar seta well developed, at least as long as postocellar seta (2.1); dorsal setulae on base of vein Cu_1 present (22.1); and the apex of lateral surstylus curved dorsally in lateral view (43.2). There are also two symplesiomorphies for this clade: absence of black spots on mediotergite (10.0), and base of lateral surstylus broader than distal part in lateral view (46.0).

The *colombiana* species group is recognized in this study as a monophyletic group by some possible synapomorphies, (although they are homoplastic and have also evolved in other species groups): coloration of scutellum similar to the rest of scutum (8.1), dorsocentral seta aligned near mid-distance between postsutural supra-alar and postalar setae (11.1); posteroapical lobe of cell bcu less than half as long as main part of cell (21.1); and distal hyaline spot in cell r_1 usually reaching posterior margin of wing or at least posterior margin of discal cell (27.1). The *colombiana* group could also be recognized by at least one autapomorphic character, namely the basal sclerite of the proctiger (45.1), which is present in all known males of this group and is a unique character within *Hexachaeta*; but males of *H. leptofasciata* and *H. nigriventris* are unknown.

The monophyly of the *eximia* species group is substantiated by two synapomorphies: postocellar seta yellow or reddish (3.1) although it is blackish in *H. seabrai*; and the anterior apical band very slender, at most three times as wide as costal vein (28.1), but wider in *H. dinia*.

The species of the subgenus *Costamyia* are inferred to be related based on the following synapomorphies: setulae on scutellum disc absent (12.1); medial surstylus nearly as long as lateral surstylus (41.1); and the glans broad and robust, strongly sclerotized (47.1). Two other synapomorphies are the extreme apex of the aculeus tip bilobed (35.1); and only one prensiseta developed (42.1), although both are shared with *H. bifurcata* (*colombiana* group) and are interpreted here as homoplasy.

The *amabilis* group was briefly characterized by Lima (1935; 1953a) based on the wing pattern of three species (*amabilis*, *obscura*, and *shannoni*). However, as a result of the current analysis, *H. homalura, H. juliorosalesi*, and two undescribed species are also included. The monophyly of the group is supported by the unusually broad aculeus that is at most twice as long as wide (39.1), which is a clear synapomorphy. Other synapomorphies of this group are the posteroapical lobe of cell bcu less than half as long as main part of cell (21.1; shared with species of the *colombiana* group), and the extremely slender apical band (28.1; also present in

the *eximia* group). A unique character within the genus is the absence of the posterior apical band (29.1) at least in five of the seven species of the *amabilis* group *(H. amabilis*, *H. obscura*, *H. shannoni*, *H. juliorosalesi*, and *H*. sp. A).

The monophyly of the *socialis* group is substantiated by two autapomorphies: distance between crossveins R-M and DM-Cu greater than length of crossvein DM-Cu (23.1); and crossvein R-M at level of apex of vein R_1 (24.1). In addition, the following two apomorphies support the monophyly of this group: the alignment of the dorsocentral seta near mid-distance between postsutural supra-alar and postalar setae (11.1); and the apex of lateral surstylus with apicoventral fold in lateral view (43.1), which is present only in species of this group, although it is absent in *H. parva* and *H.* sp. C.

Distribution

To explain the biogeographic origin of American Tephritidae and in particular *Hexachaeta*, it is necessary to define the limits between the Nearctic and Neotropical Regions. The "Mexican Transition Zone" (MTZ) is defined as the territory of complex overlapping areas occupied by fauna of Neotropical and Nearctic origin, with the northern limits variously reaching some regions of the south, southwest, and southeast of the United States, throughout Mexico and a part of Central America to around the Great Lakes of Nicaragua (Halffter, 1976).

In this sense, the current distribution of the tribe Toxotrypanini suggests a Neotropical origin on the basis of the Neotropical dispersal pattern described by Halffter (1976), which includes taxa broadly distributed in South America, mainly throughout the tropical lowlands, having a limited penetration into some southern and southeastern regions of the USA. The apparently closely related genera, *Anastrepha*, *Toxotrypana* and *Hexachaeta*, reveal a higher species diversity in South America (Norrbom *et al.*, 1999a), where most of the species are closely associated with humid tropical environments. In the MTZ, these genera are distributed throughout the coastal plains, especially along the Gulf of Mexico, extending into southern USA with representatives in Texas and Florida.

Of the 36 *Hexachaeta* species recognized in this study, most are restricted to South America, 13 are reported from the area between Mexico and Costa Rica, and only three have also been recorded from the USA, all from the Rio Grande Valley in Texas (Foote et al., 1993). Central American species that extend as far as the northern limit of the MTZ are: *H. bifurcata* and

Table 2
Known host plants for species of the genus *Hexachaeta*

Species	Host	Common name	References
H. barbiellinii	?	"pau de tamanco"	Lima & Leite, 1952
H. eximia (as *H. aegiphilae*)	*Aegiphila cuspidata* (Verbenaceae)	?	Lima, 1935
H. bondari	*Sorocea* sp. (Moraceae)	"jequitiá de leite"	Silva *et al.*, 1968
	Helicostylis poeppigiana (Moraceae)	"amora preta"	Silva *et al.*, 1968
H. cronia	*Helicostylis poeppigiana* (Moraceae)	"amora preta"	Silva *et al.*, 1968
H. fallax	? (Moraceae)	"mulberry twigs"	Baker *et al*., 1944
H. valida	*Sorocea affinis* (Moraceae)	?	Present study
Hexachaeta sp. F	*Trophis mexicana* (Moraceae)	?	Present study
	Pseudolmedia oxyphyllaria (Moraceae)	"ojoche"	Present study

H. colombiana (*colombiana* group); *H. seabrai* and *H. zeteki* (*eximia* group); *H. amabilis* and sp. A (*amabilis* group); and *H. fallax*, *H. oblita*, *H. valida*, *H. parva*, *H*. sp. C, *H*. sp. D, *H*. sp. F (*socialis* group), although some of these species also extend their distribution to South America.

Host plants

Unfortunately, information about the host plants of *Hexachaeta* species is scarce (Table 2). A few species have been reported as being frugivorous, while some species have been recorded to breed in twigs or seeds, mostly on plants of the family Moraceae, and one on Verbenaceae. Moraceous fruits are known to be infested by other American tephritid taxa such as some species of the genus *Anastrepha*, mainly of the *robusta* and *fraterculus* groups (Norrbom, 1985). *Eutreta* Loew (Tephritinae) includes gall-forming species on plants of the family Verbenaceae (Foote *et al.*, 1993). The known host plants for the species of the *socialis* group, such as *H. bondari*, *H. cronia*, *H. fallax*, *H. valida* and *H. sp. M*, are in the family Moraceae. However, the only identified host plant for a species of the *eximia* group (*H. eximia*) belongs to the family Verbenaceae, and *H. barbiellinii* has been recorded breeding on unidentified fruits, commonly known in Brazil as "pau de tamanco" (Lima and Leite, 1952). The host plants for species of the *colombiana* and *amabilis* groups remain unknown.

ACKNOWLEDGMENTS

I thank the following colleagues and institutions who kindly loaned numerous specimens of *Hexachaeta* deposited in their respective collections: Julian Stark (AMNH), Nigel Wyatt and John Chainey (BMNH), Chen W. Young (CMNH), J.M. Cumming (CNC), Richard Hoebeke (CUIC), J. Ziegler (DEI), Guillermo Claps (FML), Philip P. Parrillo (FMNH), Gary J. Steck and P.E. Skelley (FSCA), H. Brailovsky (IBUNAM), Manuel Zumbado (INBIO), José A. Rafael (INPA), Ruth Contreras-Lichtenberg (NMW), Hans-Peter Tschorsnig (SMN), Uwe Kallweit (SMTD), E.G. Riley and R.A. Wharton (TAMU), Amnon Freidberg (TAUI), S.L. Heydon (UCD), Carlos Julio Rosales (MIZA), Allen L. Norrbom (USNM), Cleide Costa and Francisca do Val (USP), Wilford J. Hanson (USU), Nancy Carrejo (UVC), H. Shumann (ZMB).

I am especially grateful to Amnon Freidberg and colleagues, of Tel Aviv University, for all facilities provided during the First International Tephritidologist Meeting held in Israel. This chapter was prepared thanks to generous financial support by Tel Aviv University and the Instituto de Ecologia A.C. I also thank Allen Norrbom (USDA) and two anonymous referees for their useful comments and suggestions in the early stages of the manuscript.

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APPENDIX 1

Morphological characters used in cladistic analysis within the genus *Hexachaeta*

The plesiomorphic character states are coded by 0. Multistate characters (7, 26, 37, 43) were treated as nonadditive.

Head

1. Facial carina: 0) well developed; 1) weak or indistinct.
2. Ocellar seta: 0) very reduced, weak or absent; 1) well developed (at least as long and stout as postocellar).
3. Postocellar seta: 0) black or dark brown; 1) yellow or reddish.

Thorax

4. Number of scutellar setae: 0) two pairs; 1) three pairs.
5. Presutural region: 0) uniformly yellow or reddish; 1) with black spots behind postpronotum and/or submedial and sublateral stripes.
6. Postsutural region (anterior to dorsocentral seta): 0) uniformly yellow or reddish; 1) with black spots or stripes.
7. Posterior margin of scutum: 0) yellow or reddish (similar to the rest of the scutum); 1) bright white; 2) with blackish spots mainly along scuto-scutellar suture.
8. Scutellum coloration: 0) different to the rest of scutum (usually bright white); 1) similar to the rest of scutum.
9. Black spot on base of scutellum: 0) absent; 1) present.
10. Black spots on mediotergite: 0) absent; 1) present.
11. Alignment of dorsocentral seta: 0) close to level of postalar seta; 1) near mid-distance between postsutural supra-alar and postalar setae.
12. Setulae on scutellum disc: 0) present; 1) absent.
13. Anepisternum: 0) yellow; 1) partly or completely black.
14. Anepimeron: 0) yellow; 1) partly or completely black.
15. Katepisternum: 0) yellow; 1) partly or completely black.

Legs

16. Forefemur: 0) yellow; 1) partly or completely black
17. Midfemur: 0) yellow; 1) partly or completely black.
18. Hindfemur: 0) yellow; 1) partly or completely black.
19. Forecoxa: 0) yellow; 1) partly or completely black.

Wing

20. Apex of vein vein M: 0) straight; 1) anteriorly curved.
21. Posteroapical lobe of cell bcu: 0) At least half as long as main part of cell; 1) less than half as long as main part of cell.
22. Setulae on base of vein Cu dorsally: 0) absent; 1) present.
23. Distance between crossveins R-M and DM-Cu: 0) less than length of DM-Cu; 1) more than length of DM-Cu.
24. Location of crossvein R-M: 0) distal to level of apex of vein R_1; 1) at level of apex of vein R_1.
25. Number of hyaline spots in cell r_1: 0) one; 1) two.
26. Proximal hyaline spot in cell r_1: 0) absent; 1) present, extending at most to vein R_{4+5}; 2) present, extending to vein M or beyond.

27. Distal hyaline spot in cell r_1: 0) extending at most to vein M; 1) extending to posterior margin of wing.
28. Anterior apical band: 0) broad (nearly five times as wide as costal vein); 1) slender (at most three times as wide as costal vein).
29. Posterior apical band: 0) present; 1) absent.
30. Connection of discal and subapical bands: 0) absent; 1) present at discal cell or anterior to it.
31. Hyaline spot at basal third of discal cell: 0) present; 1) absent.
32. Apical third of discal cell: 0) broadly hyaline; 1) mostly dark brownish.
33. Black spots in second costal cell: 0) absent; 1) present.

Abdomen

34. Abdominal tergites: 0) completely yellow; 1) with black stripes or spots.
35. Extreme apex of aculeus: 0) simple; 1) bilobed.
36. Lateral margins of aculeus tip: 0) non-serrated; 1) finely serrated.
37. Lateral projections of aculeus tip: 0) absent; 1) one pair; 2) two pairs; 3) three pairs.
38. Length of oviscape: 0) at most half as long as abdomen; 1) at least two thirds as long as abdomen.
39. Aculeus length: 0) at least three times greatest width; 1) at most twice greatest width.
40. Sclerotized scales of eversible membrane: 0) reduced, forming small plates; 1) dorsobasal scales well developed, hooklike.
41. Length of medial surstylus: 0) nearly half as long as lateral surstylus; 1) nearly as long as lateral surstylus.
42. Number of prensisetae: 0) two; 1) one.
43. Apex of lateral surstylus in lateral view: 0) straight on both sides; 1) expanded ventrally; 2) expanded dorsally.
44. Lateral surstylus: 0) straight throughout length; 1) gradually curved posteriorly.
45. Basal sclerite of proctiger: 0) absent; 1) present.
46. Base of lateral surstylus in lateral view: 0) distinctly broader than distal part; 1) nearly as broad as distal part.
47. Glans: 0) elongated and slender, weakly sclerotized; 1) broad and robust, strongly sclerotized.

APPENDIX 2

List of recognized taxa and classification of the genus *Hexachaeta*

* Taxa not included in the phylogenetic analysis

Genus *Hexachaeta* Loew, 1873
- Subgenus *Hexachaeta* Loew, 1873, new status
- *eximia* group
- **Hexachaeta barbiellinii* Lima, 1935
  - *Hexachaeta barbiellinii barbiellinii* Lima, 1935
  - *Hexachaeta barbiellinii itatiaiensis* Lima and Leite, 1952
- *Hexachaeta dinia* (Walker, 1849)

Hexachaeta enderleini Lima, 1935
Hexachaeta eximia (Wiedemann, 1830)
= *Tephritis luctuosa* Macquart, 1835
= *Tephritis fasciventris* Macquart, 1851
= *Trypeta lutescens* Walker, 1858
= *Trypeta sinica* Walker, 1858
= *Hexachaeta aegiphilae* Lima, 1935
Hexachaeta seabrai Lima, 1953b
Hexachaeta venezuelana Lima, 1953b
Hexachaeta zeteki Lima, 1953b
**Hexachaeta guatemalensis* (Lima, 1953b)
Hexachaeta sp. G
Hexachaeta sp. H

colombiana group
Hexachaeta colombiana Lima, 1953b
Hexachaeta bifurcata Hernández-Ortiz, 1999
Hexachaeta nigriventris Hernández-Ortiz, 1999
Hexachaeta leptofasciata Hernández-Ortiz, 1999
Hexachaeta ecuatoriana Hernández-Ortiz, 1999

Costamyia Hernández-Ortiz, new subgenus

amabilis group
Hexachaeta amabilis (Loew, 1873)
= *Hexachaeta amabilis* var. *oculata* Hendel, 1914
= *Hexachaeta amabilis* form *decolorata* Lindner, 1928
Hexachaeta homalura Hendel, 1914
Hexachaeta juliorosalesi Hernández-Ortiz, 2002
Hexachaeta obscura Hendel, 1914
Hexachaeta shannoni Lima, 1953a
Hexachaeta sp. A
Hexachaeta sp. B

socialis group
**Hexachaeta aex* (Walker, 1849)
= *Tephritis quinquefasciata* Walker, 1837
**Hexachaeta bondari* Lima and Leite, 1952
Hexachaeta cronia (Walker, 1849)
Hexachaeta cronia cronia (Walker, 1849)
Hexachaeta cronia spitzi Lima and Leite, 1952
Hexachaeta fallax Lima, 1954
**Hexachaeta major* (Macquart, 1847)
Hexachaeta monostigma Hendel, 1914
Hexachaeta nigripes Hering, 1938
Hexachaeta oblita Lima, 1954

Hexachaeta parva Lima, 1954
Hexachaeta socialis (Wiedemann, 1830)
Hexachaeta valida Lima, 1954
Hexachaeta sp. C
Hexachaeta sp. D
Hexachaeta sp. E
Hexachaeta sp. F