

ABSTRACT

Title of dissertation: STUDIES ON THE PHYLOGENETIC RELATIONSHIPS
OF THE SUPERFAMILY OPOMYZOIDEA WITH AN
ASSESSMENT OF THE PHYLOGENETIC UTILITY OF
THE INTERNAL FEMALE REPRODUCTIVE TRACT
AND A GENERIC REVISION OF *AULACIGASTER*
MACQUART (DIPTERA, CYCLORRHAPHA).

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Department of Entomology

This work is directed at defining and elucidating some of the basic problems in the phylogenetic classification of the Opomyzoidea. (chapter 1).

In chapter 2, I present a quantitative phylogenetic analysis of the Asteioinea (Opomyzoidea). The ingroup and outgroup samples accommodate differing hypothesis of relationships by authors since Hennig. A total of 49 exemplar species and 123 morphological characters are analyzed under six combinations of character coding and weighting methods. The results support the monophyly of the Opomyzoidea and

Asteioinea *sensu* J. F. McAlpine (1989), with the exception that the Odiniidae is separated from the Opomyzoidea by several outgroup nodes. The outgroup consistently nearest the Opomyzoidea is the family Chyromyidae (Sphaeroceroidea). Within Asteioinea, Asteidae + Xenasteidae are consistently grouped with Aulacigastridae, and Neminidae + Neurochaetidae + Periscelididae are consistently grouped together. The position of the Teratomyzidae is uncertain. The genera *Stenomicro*, *Cyamops* and *Planinasus* consistently grouped with the Periscelididae. The sister-group of *Aulacigaster* is an undescribed genus from Malaysia, and I propose to expand the definition of the Aulacigastridae to include that taxon.

In chapter 3, I revise the World species of the genus *Aulacigaster* Macquart, now numbering 42. New species are described for the Neotropical (28 spp) and Oriental (1 sp) regions, and the genus is divided into six species groups, of which five are new. Keys to species, diagnoses, detailed distributional data, notes on the biology and illustrations are provided to assist species identification. Based on a quantitative phylogenetic analysis, I provide evidence for the monophyly of the *Aulacigaster*, and the included species groups

In chapter 4, I describe the internal female reproductive tract of six species of Opomyzidae, representing three of the four known genera of the family, which I compare with the female tract of other opomyzoid families. The following structures of the female genital tract may prove informative within the context of phylogenetic analyses of the

Opomyzoidea: the presence/ absence of multiple chambers in the ventral receptacle; the degree of sclerotization and shape of the ventral receptacle; and the presence of a ring-shaped sclerotization on the wall of the vagina, posterior to the ventral receptacle.

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OF *AULACIGASTER* MACQUART (DIPTERA, CYCLORRHAPHA)

by

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Dissertation Submitted to the Faculty of the Graduate school of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor in Philosophy
2003

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PREFACE

This dissertation should not be considered a scientific publication for the purposes of zoological nomenclature.

ACKNOWLEDGEMENTS

This dissertation would not have been accomplished without the help and assistance of several people. First and foremost, I would like to thank my advisors, Drs. Charles Mitter and Wayne N. Mathis. Their patience, support and continuous guidance made it possible for me to believe that I could finish this work.

My committee members, Dr. Jeffrey Shultz, Dr. Charles Delwiche and Dr. David Hawthorne, who also served as my professors in different disciplines, helped me to broaden my knowledge in different areas of entomology, besides providing assistance and encouragement throughout my studies. I Especially thank Chuck and Jeff for their invaluable insights, during our Wednesday seminar discussion sessions. I would also like to thank Dr. Marion Kotrba, a friend, colleague and a mentor throughout this work. Marion gave me invaluable information on the female genital tract of acalyprates, besides taking such good care of me during my visit to Berlin.

This research and most of the fieldwork was generously funded by a grant from the Partnerships for Enhancing Expertise in Taxonomy program (PEET), National Science Foundation (PEET 952-1773). I am grateful to PEET for the opportunity to learn and practice taxonomy and for allowing me to open further the fascinating world of Diptera or true flies. Some of the fieldwork in Brazil was funded by the FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), which I also acknowledge and thank. The Department of Entomology provided me with graduate teaching assistantships that also helped me gain experience in the classroom. The Department of Entomology helped finance the latter stages of this dissertation.

To my colleagues and their institutions listed below that loaned specimens, I

express my sincere thanks: Dr. Jon K. Gelhaus and Mr. Donald F. Azuma (Academy of Natural Sciences of Philadelphia, Pennsylvania, USA); Dr. Jeffrey M. Cumming (Canadian National Collection, Ottawa, Ontario, Canada); Drs. Frank Menzel and Joachim Ziegler (Deutsches Entomologisches Institut, Eberswalde, Germany); Dr. Márcia Souto Couri (Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil); Dr. Francisca do Val (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil); Dr. Amnon Freidberg (Tel Aviv University, Tel Aviv, Israel); Dr. Luciane Marinoni (Universidade Federal do Paraná, Curitiba Paraná, Brazil); Dr. T.A. Wheeler (University of Guelph, Guelph, Canada).

I am indebted to Dr. Hugo de Souza Lopez, Dr. Amnon Freidberg and Rita Tibana for graciously providing me with their encouragement as well as their preliminary but valuable notes and ideas on various taxonomic aspects of *Aulacigaster*. They had earlier started research projects on this family. I also would like to thank Dr. Sonja Scheffer and my colleague Isaac Winkler, for teaching me DNA analysis techniques.

I thank my parents, Carlos and Lidia Chaves, and my sister Vanessa Chaves, for their continuous encouragement, and for their constant, unwavering support of me. I thank my son, Johann Baptista, for giving me a reason to persevere, and my friends Miriam, Neil, Jennifer, Catherine and Matthew, for providing invaluable support in times of difficulty. I'm especially thankful to Jeffrey Felsher, for providing practical and moral assistance during the last two years of my work. Without his help, this dissertation might never have been completed.

TABLE OF CONTENTS

Chapter 1 : General introduction.....	1
Chapter 2 :A quantitative phylogenetic analysis of the Asteioinea (Diptera, Opomyzoidea).....	5
Abstract.....	5
Introduction.....	6
Past and present classifications of Opomyzoidea.....	7
The Asteioinea: composition and phylogenetic relationships.....	9
The families of Asteioinea: composition and phylogenetic relationships.....	9
Methods.....	12
Results and discussion.....	17
Morphology and character coding.....	17
Head coloration, vestiture and morphology.....	18
Head appendages (antennae and mouthparts).....	32
Thorax.....	36
Male abdomen and terminalia.....	49
Female abdomen and terminalia.....	61
Phylogenetic analysis.....	62
Opomyzoidea: Monophyly and composition.....	65
Asteioinea: monophyly and internal phylogenetic structure.....	67
Character performance and previous phylogenies.....	70
Figures.....	97
Chapter 3 : A revision of the Genus <i>Aulacigaster</i> Macquart (Diptera: Aulacigastridae)	124
Abstract.....	124
The Family Aulacigastridae: historic and taxonomic background.....	125
The Genus <i>Aulacigaster</i> Macquart: historic and taxonomic background.....	126
Methods.....	128

Results and discussion	132
Taxonomy	132
Genus <i>Aulacigaster</i> Macquart.....	132
Implicit Attributes.....	135
Neotropical species.....	136
Key to the Neotropical species of <i>Aulacigaster</i> Macquart	136
The <i>bromeliae</i> group.....	144
<i>Aulacigaster bromeliae</i> , new species.....	146
<i>Aulacigaster korneyev</i> , new species	150
<i>Aulacigaster lopezi</i> , new species	152
<i>Aulacigaster serrana</i> , new species	154
<i>Aulacigaster tibanae</i> , new species.....	157
<i>Aulacigaster vespertina</i> , new species	159
The <i>ecuadoriensis</i> group.....	161
<i>Aulacigaster ecuadoriensis</i> (Hennig)	162
<i>Aulacigaster melanoleuca</i> (Hennig).....	165
<i>Aulacigaster stenoptera</i> , new species.....	167
<i>Aulacigaster</i> sp.a., undescribed species.....	169
The <i>femorata</i> group.....	170
<i>Aulacigaster bella</i> , new species.....	172
<i>Aulacigaster irwini</i> , new species	174
<i>Aulacigaster femorata</i> , new species	176
<i>Aulacigaster lobata</i> , new species.....	180
<i>Aulacigaster peruana</i> , new species.....	182
<i>Aulacigaster peruana</i> , new species.....	182
<i>Aulacigaster</i> sp.b, undescribed species.....	184
<i>Aulacigaster</i> sp.c. undescribed species.....	185
<i>Aulacigaster</i> sp. h., undescribed species.....	187
The <i>grimaldii</i> group	188
<i>Aulacigaster grimaldii</i> , new species.....	188

The <i>minuta</i> group.....	192
<i>Aulacigaster appendiculata</i> , new species.....	193
<i>Aulacigaster costaricana</i> , new species.....	195
<i>Aulacigaster gaimarii</i> , new species.....	197
<i>Aulacigaster minuta</i> (Hennig).....	200
<i>Aulacigaster nigratarsa</i> , new species.....	202
The <i>plesiomorphica</i> group.....	204
<i>Aulacigaster albifacies</i> , new species.....	206
<i>Aulacigaster belize</i> , new species.....	209
<i>Aulacigaster bifasciata</i> , new species.....	211
<i>Aulacigaster conspicua</i> , new species.....	213
<i>Aulacigaster erika</i> , new species.....	216
<i>Aulacigaster kenna</i> , new species.....	218
<i>Aulacigaster plesiomorphica</i> (Hennig).....	220
<i>Aulacigaster proxima</i> , new species.....	222
<i>Aulacigaster rufifemur</i> , new species.....	225
<i>Aulacigaster trifasciata</i> , new species.....	227
<i>Aulacigaster</i> sp. d., undescribed species.....	230
The <i>leucopeza</i> group.....	231
<i>Aulacigaster colombiana</i> , new species.....	232
<i>Aulacigaster spangleri</i> , new species.....	234
<i>Aulacigaster</i> sp.e, undescribed species.....	237
Afrotropical species.....	239
Key to the Afrotropical species of <i>Aulacigaster</i>	239
<i>Aulacigaster africana</i> Barraclough.....	240
<i>Aulacigaster borbonica</i> Hilger and Kassebeer.....	241
<i>Aulacigaster perata</i> Barraclough.....	243
Nearctic species.....	244
<i>Aulacigaster neoleucopeza</i> Mathis and Freidberg.....	245
<i>Aulacigaster mcalpinei</i> Mathis and Freidberg.....	249

<i>Aulacigaster sabroskyi</i> Mathis and Freidberg	252
Palaearctic species	254
<i>Aulacigaster afghanorum</i> Papp.....	256
<i>Aulacigaster falcata</i> Papp.....	258
<i>Aulacigaster leucopeza</i> (Meigen,)	260
Oriental species.....	263
Key to the Oriental species of <i>Aulacigaster</i> Macquart.....	263
<i>Aulacigaster india</i> , new species.....	264
<i>Aulacigaster</i> sp.f, undescribed species	266
<i>Aulacigaster</i> sp. g, undescribed species.....	268
Morphology and character coding	269
Morphology of the head, and head appendages.....	271
Thorax morphology	274
Male abdomen and terminalia.....	276
Phylogenetic analysis.....	278
Figures.....	287

Chapter 4 : The internal female reproductive tract of opomyzoidea (Diptera, Schizophora)	329
Abstract.....	329
Introduction.....	329
Methods.....	330
Results.....	331
Superfamily Opomyzoidea	331
Internal female reproductive tract of Clusiidae, general description.....	337
Internal female reproductive tract of Anthomyzidae, general description	339
Suprafamily Asteioinea.....	341
Internal female reproductive tract of Aulacigastridae, general description.....	341
Internal female reproductive tract of Periscelididae, general description.....	343
Periscelidinae	345
Stenomicroinae	345

Internal female reproductive tract of Asteiidae	347
Superfamily Diopsoidea.....	348
<i>Incertae sedis</i>	349
Internal female reproductive tract of Odiniidae, general description	349
Discussion.....	351
Literature cited.....	353
Chapter 1:.....	353
Chapter 2:.....	354
Chapter 3:.....	360
Chapter 4:.....	365

LIST OF TABLES

Table 2.1.–Composition of the "Opomyzoidea" according to different authors.	72
Table 2.2.–Composition of the "Asteioidea" according to different authors.	73
Table 2.3.–Species used in the phylogenetic analysis, their distribution, and classification according to J. F. McAlpine (1989).	74
Table 2.4.–Summary of the results of six analyses performed with combinations of heuristic search settings, character ordering and weighting schemes.	76
Table 2.5.–List of characters.	77
Table 2.6.–List of apomorphies for the internal branches of cladogram in Fig. 111.	85
Table 2.7.–List of apomorphies for the terminal taxa in cladogram of Fig. 111.	92
Table 3.1.– List of characters	283
Table 3.2.– Summary of the results of four analyses performed with combinations of character ordering and weighting schemes.	286

LIST OF FIGURES:

FIGURE 2.1.- Cladogram showing the phylogenetic relationships among the families of Opomyzoidea (left) and among the superfamilies of Acalyptratae (right) according to J. F. McAlpine (1989).	97
FIGURE 2.2.- Diagrammatic representation of different definitions of the families Periscolididae and Aulacigastridae.	98
FIGURES 2.4-2.8.-Digital photographs of the dorsal aspect of the head and thorax of acalyptrates.	99
FIGURES 2.6-2.12.-Digital photographs of the anterior aspect of the head of aulacigastrids (Opomyzoidea).	100
FIGURES 2.13-2.17.-Digital photographs of the anterior aspect of the heads of acalyptrates.	101
FIGURES 2.18-2.23.-Digital photographs of the lateral aspect of the head of acalyptrates. Digital photographs of the lateral aspect of the head of acalyptrates.	102
FIGURES 2.30-2.33.-Schematic representation of the anterior aspect of the head of acalyptrates.	103
FIGURE 2.34 a-d.-Schematic representation of the anterior aspect of ocellar tubercle and ocellar setae, corresponding to characters 23-25. FIGURE 35 a-d. Schematic representation of the arrangement of supracervical setae on cervical region, corresponding to character 36. FIGURE 36. Frons of <i>Anomalochaeta guttipennis</i> , anterior aspect.	104
FIGURES 2.35-2.41.-Digital photographs of the lateral aspect of the antenna of opomyzoids.	105
FIGURES 2.42-2.45.-Digital photographs of the lateral aspect of the antenna of acalyptrates. FIGURE 45. Lateral aspect of the clypeus of <i>Geomyza</i> sp. (Opomyzoidea).	106
FIGURES 2.46-2.48.-Illustrations of the lateral aspect of the antenna of opomyzoids.	107

FIGURES 2.49-2.52.-Illustrations of the mesonotum of opomyzoids	108
FIGURES 2.53-2.68.-Schematic representation of the postnotum of opomyzoids.	109
FIGURE 2.69.- Digital photograph of the anepisternum of <i>Cyamops neotropicus</i> (Stenomicroinae, Opomyzoidea).	110
FIGURES 2.70-2.73.-Digital photographs of the wing of opomyzoids.	111
FIGURES 2.74-2.76.-Digital photographs of the wing of acalyptrates.	112
FIGURES 2.77-2.78. Digital photographs of the wing of acalyptrates.	113
FIGURES 2.81-2.85.-Illustrations of the male abdomen of opomyzoids	114
FIGURE 2.86.-Illustration of the ventral aspect of posterior portion of abdomen of <i>Periscelis annulata</i> (Periscelidinae).	115
FIGURES 2.87-2.90. Male terminalia of <i>Aulacigaster</i> (Opomyzoidea).	116
FIGURES 2.91-2.94.-Illustrations of the male terminalia of <i>Stenomicroa</i> sp, undescribed species (Opomyzoidea).	117
FIGURES 2.95-2.97.-Male terminalia of <i>Cyamops nebulosus</i> Melander (Opomyzoidea).	118
FIGURES 2.98-2.100.-Illustrations of the male terminalia of acalyptrates. 98-100. <i>Planinasus</i> sp. (Opomyzoidea).	119
FIGURES 2.102-2.106.-Digital photographs of the male terminalia of acalyptrates.	120
FIGURES 2.107-2.108.-Illustrations of the lateral aspect of the female abdomen of periscelidids (Opomyzoidea).	121
FIGURE 2.109. Strict consensus cladogram of four trees obtained with ordered characters, Goloboff weighting.	122
FIGURE 2.110. <i>Strict</i> consensus cladogram of 18 trees obtained after analysis employing ordered characters, successive weighting.	123

FIGURES 3.1-3.5.-Digital photographs of <i>Aulacigaster bromeliae</i> , new species (The <i>bromeliae</i> group, Neotropical region).	287
FIGURES 3.6-3.10.-Illustrations of <i>Aulacigaster bromeliae</i> , new species (The <i>bromeliae</i> group, Neotropical region).	288
FIGURES 3.11-3.14.-Digital photographs of <i>Aulacigaster korneyev</i> , new species (The <i>bromeliae</i> group, Neotropical region).	289
FIGURES 3.15-3.17.-Digital photographs of <i>Aulacigaster tibanae</i> , new species (The <i>bromeliae</i> group, Neotropical region).	290
FIGURES 3.18-3.21.-Digital photographs of <i>Aulacigaster vespertina</i> , new species (The <i>bromeliae</i> group, Neotropical region).	291
FIGURES 3.22-3.25.-Illustrations of the epandrium and internal genitalic structures (male) of aulacigastrids (The <i>bromeliae</i> group, Neotropical region).	292
FIGURES 3.26-3.28.-Illustrations of <i>Aulacigaster ecuadoriensis</i> (Hennig) (The <i>ecuadoriensis</i> group, Neotropical region).	293
FIGURES 3.29-3.31.-Digital photographs of <i>Aulacigaster ecuadoriensis</i> (Hennig) (The <i>ecuadoriensis</i> group, Neotropical region).	294
FIGURES 3.32-3.34.- Illustrations of <i>Aulacigaster melanoleuca</i> (Hennig) (The <i>ecuadoriensis</i> group, Neotropical region).	295
FIGURES 3.35-3.38.- Digital photographs of <i>Aulacigaster melanoleuca</i> (Hennig) (The <i>ecuadoriensis</i> group, Neotropical region).	296
FIGURES 3.39-3.41.- Illustrations of <i>Aulacigaster stenoptera</i> , new species (The <i>ecuadoriensis</i> group, Neotropical region).	297
FIGURES 3.42-3.46.- Digital photographs of <i>Aulacigaster bella</i> , new species (The <i>femorata</i> group, Neotropical region).	298
FIGURES 3.47-3.48.–Illustrations of <i>Aulacigaster bella</i> , new species (The <i>femorata</i> group, Neotropical region).	299
FIGURES 3.49-3.50.–Digital photographs of <i>Aulacigaster irwini</i> , new species	300

(The <i>femorata</i> group, Neotropical region).	
FIGURES 3.51-3.52.—Illustrations of <i>Aulacigaster irwini</i> , new species (The <i>femorata</i> group, Neotropical region).	301
FIGURES 3.53-3.58.—Illustrations of <i>Aulacigaster femorata</i> , new species (The <i>femorata</i> group, Neotropical region).	302
FIGURES 3.59-3.62.—Digital photographs of aulacigastrids (The <i>femorata</i> group, Neotropical region).	303
FIGURES 3.63-3.65.—Illustrations of the male terminalia of aulacigastrids (The <i>femorata</i> group, Neotropical region).	304
FIGURES 3.66-3.68.— Digital photographs of <i>Aulacigaster lobata</i> , new species (The <i>femorata</i> group, Neotropical region).	305
FIGURES 3.69-3.70.— Digital photographs of <i>Aulacigaster peruana</i> new species (The <i>femorata</i> group, Neotropical region).	306
FIGURES 3.71-3.72.—Illustrations of <i>Aulacigaster peruana</i> new species (The <i>femorata</i> group, Neotropical region).	307
FIGURES 3.73-3.75.— Digital photographs of <i>Aulacigaster Grimaldi</i> , new species (The <i>grimaldii</i> group, Neotropical region).	308
FIGURES 3.76-3.80.— Illustrations of <i>Aulacigaster Grimaldi</i> , new species (The <i>grimaldii</i> group, Neotropical region).	309
FIGURES 3.81-3.85.—Digital photographs of aulacigastrids (The <i>minuta</i> group, Neotropical region).	310
FIGURES 3.86-3.89.—Digital photographs of aulacigastrids (The <i>minuta</i> group, Neotropical region).	311
FIGURE 3.90.—Illustration of the epandrium and internal genitalic structures (male), of <i>Aulacigaster minuta</i> (Hennig) (The <i>minuta</i> group, Neotropical region).	312
FIGURES 3.91-3.94.—Illustrations of the terminalia and internal genitalic structures (male) of aulacigastrids (The <i>plesiomorphica</i> group, Neotropical region), lateral aspect.	313

FIGURES 3.95-3.103.-Digital photographs of aulacigastrids (The <i>plesiomorphica</i> group, Neotropical region).	314
FIGURES 3.104-3.109.-Illustrations of aulacigastrids (The <i>plesiomorphica</i> group, Neotropical region).	315
FIGURES 3.110-3.113. Digital photographs of aulacigastrids (The <i>plesiomorphica</i> group, Neotropical region).	316
FIGURES 3.114-3.116.- Illustrations of <i>Aulacigaster rufifemur</i> , new species (The <i>plesiomorphica</i> group, Neotropical region).	317
FIGURES 3.117-3.121.- Digital photographs of aulacigastrids (The <i>plesiomorphica</i> group, Neotropical region).	318
FIGURES 3.122-3.125.- Digital photographs of <i>Aulacigaster trifasciata</i> , new species (The <i>plesiomorphica</i> group, Neotropical region).	319
FIGURES 3.126-3.127.- Illustrations of <i>Aulacigaster trifasciata</i> , new species (The <i>plesiomorphica</i> group, Neotropical region).	320
FIGURES 3.128-3.133.-Digital photographs of aulacigastrids (The <i>leucopeza</i> group, Neotropical region).	321
FIGURES 3.134-3.135.-Digital photographs of <i>Aulacigaster</i> sp. (undescribed species, Afrotropical region).	322
FIGURES 3.136-3.140.-Digital photographs of aulacigastrids (The <i>leucopeza</i> group, Nearctic region).	323
FIGURES 3.141-3.146.-Digital photographs of aulacigastrids (The <i>leucopeza</i> group, Oriental region).	324
FIGURE 3.147.- Illustration of the epandrium and internal genitalic structures (male) of <i>Aulacigaster indiana</i> , new species (The <i>leucopeza</i> group, Oriental region).	325
FIGURES 3.148-3.154.-Digital photographs of aulacigastrids (The <i>leucopeza</i> group, Palearctic region).	326

FIGURE 3.155.-One of six cladograms generated using ordered characters, and successive weighting approach to character weighting 327

FIGURE 3.156.-One of the six cladograms generated using ordered characters, successive weighting approach to character weighting. 328

LIST OF ABBREVIATIONS USED IN THE FIGURES

- 1st fl: 1st flagellomere
- a dc s: anterior dorsocentral seta
- a ntpl s: anterior notopleural seta
- a scl s: anterior scutelar seta
- acr s: acrostical seta
- abd: abdomen
- acr s: acrostical setae
- anepst s: anepisternal seta
- ari: arista
- b scl s: basal scutelar seta
- bs: basisternum
- bas notch: basal notch
- ce: cerci
- ch: cheek
- clyp: clypeus
- ep: epandrium
- pv s: pseudovibrissal seta
- fac: face
- fac s: facial seta
- fl: flagellomere
- fr: frons
- frob s: fronto-orbital seta

frob pl: fronto-orbital plate
fs: furcasternum
gr amp: greater ampulla
hy: hypandrium
hy brid: hypandrial bridge
i vt s: inner vertical seta
if s: intrafrontal seta
katepist s: katepisternal seta
lat oc s: lateral ocellar seta
memb reg: membranous region
ntpl cal: notopleural calosity
poc s: post-ocellar seta
o vt s: outer vertical seta
oc s: ocellar seta
p ntpl s: posterior notopleural seta
p dc s: posterior dorsocentral seta
pal: palpus
pe: pedicel
pe cav: pedicelar cavity
pc: posteranium
per s: peristomal seta
pg: postgonite
pg arm: arm of postgonite
pg proj: projection of postgonite

ph: phallus
ph apod: phallapodeme
postscut: postscutellum
pg arm: postgonite arm
poc s: post-ocellar seta
pprn: postpronotum
pprn s: postpronotal seta
ptil fiss: ptilinal fissure
pv s: pseudovibrissal seta
s cerv s: supra-cervical setae
sc: scape
scut:scutum
scute: scutellum
spc: supracervical region
st: sternite
subscut: subscutellum
subscut memb: subscutellar membrane
sur: surstylus
sut: fronto-genal suture
syn: syntergite
sur: surstylus
vt: vertex
Wing:
A1: branch of anal vein

bm: basal medial cell

cup: posterior cubital cell

CuA1,CuA2: anterior branches of cubitus

dc, dm: discal medial cell

cm-cu: discal medial-cubital crossvein

h break: humeral break

M: branch of media

R1: anterior branch of radius

R2+3, R4+5: posterior branches of radius

r-m: radial-medial crossvein

Sc: Subcostal vein

Chapter 1 : GENERAL INTRODUCTION

The Diptera is among the more species rich, anatomically varied and ecologically diverse orders of insects (Yeates and Wiegmann 1999). It contains approximately 93,000 described species, but about 125,000 species have been estimated to exist in the entire order (Yeates and Wiegmann 1999).

The living species of Diptera have been classified into at least 130 families distributed into two suborders, the “Nematocera” (a paraphyletic group) and the Brachycera. Within the Brachycera, the following divisions are generally considered monophyletic: the Muscomorpha, the Eremoneura, the Cyclorrhapha and the Schizophora. The Schizophora is further subdivided into two major groups, the Acalyptratae and the Calyptratae.

The Acalyptratae contain 20% of the described species of Diptera, but almost half of the families (Yeates and Wiegmann 1999). The families Tephritidae, Lauxaniidae, Agromyzidae, Chloropidae, Drosophilidae and Ephydriidae together contain more than 50% of Acalyptratae species diversity.

The Acalyptratae have often been considered to be a paraphyletic group (Hennig 1958, Griffiths 1972). J. F. McAlpine (1989) and, less strongly, Hennig (1971), favored a monophyletic Acalyptratae as sister-group to Calyptratae.

Hennig pioneered the phylogenetic classification of the acalyptrates (1958, 1965, 1969, 1971, 1973). He subdivided the group into 12 superfamilies, and dealt

with generic composition of various families. His phylogenetic hypotheses have been scrutinized by Griffiths (1972), J. F. McAlpine (1989) and D. K. McAlpine (various contributions, of which Colless and McAlpine 1991 is the most updated and comprehensive).

Griffiths (1972) divided the acalyptrates into five superfamilies¹ but did not resolve the relationships among these. He inserted the rank prefamily between superfamily and family in his system, and classified most of the acalyptrates, along with the calyptrates, in his superfamily Muscoidea. He broke down the Muscoidea into the prefamilies Tanypezoinea, Micropezoinea, Australimyzoinea, Diopsionea, Sciomyzoinea, Anthomyzoinea, Agromyzoinea, Tephritoinea and Calyptratae.

J. F. McAlpine's (1989) phylogenetic arrangement, which will be used as a reference point in this dissertation, yielded two main Acalyptratae assemblages (Fig. 2.1): a clade including the superfamilies Nerioidea, Diopsoidea, Conopoidea, and Tephritoidea, and a clade comprising Lauxanioidea, Sciomyzoidea, Opomyzoidea, Carnoidea, Sphaeroceroidea, and Ephydroidea. He inserted the rank suprafamily between superfamily and family in his system. Therefore, J. F. McAlpine's "suprafamily" corresponds to Griffiths' "prefamily." J. F. McAlpine's fully resolved cladograms have been most recently used as a reference point (Wiegmann and Yeates 1997), but his work was criticized for containing misleading character and character state assignments (see for example D. K. McAlpine 1997:168). Among the

10 Acalyptratae superfamilies recognized by him, only the Neriioidea, Conopoidea, Sciomyzoidea and Ephydroidea have been consistently present in competing classifications.

The phylogenetic relationships of the Acalyptratae are amongst the most difficult issues in the classification of Diptera. The group is very diverse and poorly collected, and as a result new taxa are continuously being added from all zoogeographic regions (J. F. McAlpine 1989). Apparent homoplasy in most character systems makes assignment of synapomorphies within Acalyptratae in qualitative analyses contradictory (Yeates and Wiegmann 1999). As with other groups of Diptera, the monophyly of many superfamilies and families remains uncertain. Competing hypotheses of classification (Hennig 1971; Griffiths 1972; J. F. McAlpine 1989; Coless and McAlpine 1991) reflect, among other things, selective character sampling, and differing phylogenetic methods and approaches to taxon selection (Yeates 1995; Yeates and Wiegmann 1999).

Only a few modern analyses of dipteran phylogeny employ quantitative cladistic techniques (Grimaldi 1990; Courtney 1991; Oosterbroek and Courtney 1991, 1995; Pape 1992; Wiegmann, Mitter and Thompson 1993; Yeates 1995; Friedrich and Tautz 1997). Most works on the phylogenetic classification of acalyptrates are qualitative in approach. Following Hennig's methodology, many modern authors choose characters based on their subjective reliability, polarize their

characters prior to the analysis, and construct ground-plans for higher taxa, thereby generating cladograms without data conflict (see D. K. McAlpine 1988; Roháček 1987, 1994, 1998; Brake 2000), which openly contrasts with the high amount of homoplasy in dipteran morphological characters.

This dissertation is directed at defining and elucidating some of the basic problems in current Acalyptratae classification. Building on the revision and phylogenetic analysis of the family Aulacigastridae envisioned in the original PEET proposal (Chapter 3), it extends to a comprehensive analysis of the problematic superfamily Opomyzoidea (Chapter 2), and evaluates a previously-unexploited character system of potentially broad utility across the acalyptrates (Chapter 4).

Chapter 2 :A QUANTITATIVE PHYLOGENETIC ANALYSIS OF THE ASTEIOINEA (DIPTERA, OPOMYZOIDEA)

ABSTRACT

The Asteioinea, a widely distributed and poorly known group of acalyptrate Diptera (Opomyzoidea), exhibit wide morphological variation and significant homoplasy. Consequently, its taxonomy, composition and internal phylogenetic relationships have been in a state of flux. In this chapter I carry out a quantitative phylogenetic analysis of the group, adopting the view of J. F. McAlpine (1989) as the basic working hypothesis to be tested. The ingroup sample includes at least one representative of each Asteioinea family, and outgroups include exemplars of the families Anthomyzidae, Opomyzidae, Clusiidae, Odiniidae, Carnidae, Chyromyidae, Somatiidae, and Ulidiidae. A total of 49 exemplar species and 123 morphological characters are analyzed under six combinations of character coding and weighting methods. The results of these analyses collectively support the following: the Opomyzoidea *sensu* J. F. McAlpine (1989) generally grouped together, with the exception that the Odiniidae are invariably separated from the remaining opomyzoids by several outgroup nodes. The outgroup consistently nearest the Opomyzoidea, on my rooting, is the family Chyromyidae (superfamily Sphaeroceroidea). Within Asteioinea, Asteidae + Xenasteidae are consistently grouped with Aulacigastridae, and Neminidae + Neurochaetidae + Periscelididae are consistently grouped together. The genera *Stenomicro*, *Cyamops* and *Planinasus* consistently grouped with the Periscelididae. The sister-group of *Aulacigaster* is an undescribed genus from Malaysia, and I propose to expand the definition of the

Aulacigastridae to include that taxon. These findings must be regarded as provisional because of the weak support found for the analysis. The high amount of character conflict in the data calls for further studies employing different sources of characters.

INTRODUCTION

When Hennig published his first comprehensive phylogenetic classification of the Schizophora, he left several acalyptrate families unplaced in the section "families with unclear affinities" (Hennig 1958). Some of these families, together with groups that have been discovered more recently, belong in the superfamily Opomyzoidea according to the "Manual of Nearctic Diptera" (J. F. McAlpine 1989). Between Hennig's first attempt to organize these families into a coherent phylogenetic system and the publication of J. F. McAlpine's fully resolved cladogram, competing hypotheses of classification were proposed (Hennig 1971; Griffiths 1972; Colless and D. K. McAlpine 1991).

This chapter is directed at elucidating the phylogenetic relationships of a relatively rare and poorly known group of opomyzoid families, the Asteioinea (J. F. McAlpine 1989). The suprafamily contains six families and about 35 extant genera. The biology, behavior and distribution of most asteioid taxa are poorly known. The composition of Asteioinea, the limits of some of its included families, and its position with respect to the remaining Opomyzoidea, have been strongly debated. In this paper I lay out the unresolved problems in the phylogeny of Asteioinea and Opomyzoidea, construct a morphological data matrix based on re-evaluation of previously proposed synapomorphies as well as new observations, and carry out the

first quantitative phylogenetic analysis directed at resolving the composition, internal relationships, and placement of Asteioinea.

Past and present classifications of Opomyzoidea

Recent authors classify acalyptrates into ten or eleven superfamilies that are generally consistent with Hennig's classification (1971, 1973). Two superfamilies, the Opomyzoidea and Carnoidea, considered to be sister-groups by J. F. McAlpine (1989) (Fig. 2.1), are especially problematic. For example, the opomyzoid family Acartophthalmidae was recently included in the Carnoidea, as the sister-group of the Chloropidae *plus* Milichiidae (Brake 2000); and the families Cryptochaetidae (Wheeler 1994) and Risidae (Freidberg *et al.* 1998) were recently excluded from the Carnoidea.

As defined by J. F. McAlpine, the Opomyzoidea includes 13 families (Table 2.1, Fig. 2.1) grouped into four suprafamilies, the Clusioinea (Clusiidae and Acartophthalmidae), Agromyzoinea (Agromyzidae, Fergusoninidae and Odiniidae), Opomyzoinea (Opomyzidae and Anthomyzidae) and Asteioinea (Asteiidae, Aulacigastridae, Xenasteiidae, Teratomyzidae, Neurochaetidae and Periscelididae).

Hennig (1971, 1973) grouped the core of the Opomyzoidea under the name “Anthomyzoidea.” It included the Acartophthalmidae, Anthomyzidae, Asteiidae, Aulacigastridae, Clusiidae, Opomyzidae, Periscelididae, Teratomyzidae, and Chyromyidae. Hennig (*op.cit.*) classified the remaining opomyzoid families, *sensu* J. F. McAlpine (1989), in a separate superfamily, the Agromyzoidea (Odiniidae and Agromyzidae), and left the Fergusoninidae unplaced. The Xenasteiidae and

Neurochaetidae were described after Hennig.

In a series of contributions (D. K. McAlpine 1978, 1983, 1991, 1997) of which the most comprehensive was Colless and D. K. McAlpine (1991), D. K. McAlpine defined the Opomyzoidea as containing the families Acarthophtalmidae, Agromyzidae, Clusiidae, Fergusoninidae, Odiniidae, Opomyzidae, Xenasteiidae and Carnidae (Table 2.1). The remaining Opomyzoidea *sensu* J. F. McAlpine (1989) were classified in the superfamily Asteioidea. D. K. McAlpine also tentatively added the Afrotropical family Marginidae to the Opomyzoidea (1991). Colless and McAlpine (1991) followed J. F. McAlpine (1989) in classifying the Chyromyidae in the superfamily Sphaeroceroidea.

Griffiths divided the Schizophora into five superfamilies, the Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyboidea and Muscoidea. The Muscoidea contained the prefamily Calyptratae as well as several acalyptrate "prefamilies," including the Anthomyzoinea, which included the following families currently in the Opomyzoidea (J. F. McAlpine 1989): the Aulacigastridae, Anthomyzidae, Asteiidae and Opomyzidae. It also included the Chyromyidae, Heleomyzidae, Trixoscelididae, Rhinotoridae, and Sphaeroceridae (currently in the superfamily Sphaeroceroidea, J. F. McAlpine). Griffiths transferred the Periscelididae and Teratomyzidae to the superfamily "Nothyboidea," which also included the families Psilidae and Nothybidae, currently classified in the superfamily Diopsoidea (J. F. McAlpine 1989).

The Asteioinea: composition and phylogenetic relationships

Hennig (1971) divided the “Anthomyzoidea” into two groups: the Periscelidea, containing the Periscelididae, Aulacigastridae, Asteiidae, and Teratomyzidae; and the Anthomyzidea, containing the Acartophthalmidae, Clusiidae, Anthomyzidae, Opomyzidae and Chyromyidae. Griffiths (1972), however, excluded the Acartophthalmidae, Clusiidae, Periscelididae and Teratomyzidae from his “Anthomyzoinea,” and remarked that the Asteiidae also might belong elsewhere. J. F. McAlpine’s cladogram (1989; see also Fig. 2.1) clusters Periscelididae, Aulacigastridae, Asteiidae and Teratomyzidae, as well as the Xenasteiidae (Hardy 1980) and Neurochaetidae (D. K. McAlpine 1978) within the Opomyzoidea. These families make up his suprafamily “Asteioinea,” which is the sister-group of his “Opomyzoinea,” consisting of Opomyzidae and Anthomyzidae. Roháček (1998), like Griffiths (1972), questioned the placement of Periscelididae within Asteioinea, based on characters of the male terminalia.

Colless and D. K. McAlpine (1991) classified, under the superfamily Asteioidea, the families Anthomyzidae, Aulacigastridae, Asteiidae, Neurochaetidae, Periscelididae, and Teratomyzidae.

The families of Asteioinea: composition and phylogenetic relationships

The monophyly of the individual families of Asteioinea is generally well

accepted, except for Aulacigastridae and Periscelididae, between which genera have been repeatedly switched (Hennig 1971; J. F. McAlpine 1989; D. K. McAlpine 1983). J. F. McAlpine (1989) speculated that Periscelididae, Aulacigastridae and possibly Neurochaetidae might eventually constitute a single family. Grimaldi and Mathis (1993) suggested a sister-group relationship between Periscelididae and Neurochaetidae.

The characterization of Aulacigastridae also differs widely among authors (Hennig 1971; D. K. McAlpine 1983; J. F. McAlpine 1989), and up to five genera have been assigned to it, in addition to the type genus, *Aulacigaster* Macquart (Fig. 2.2). The Aulacigastridae *sensu stricto* is monotypic, and is distributed worldwide. A broader definition for the Aulacigastridae, first advanced by Hennig (1958, 1965, 1969, 1971), includes the cosmopolitan genera *Cyamops* Melander and *Stenomicra* Coquillett, the Neotropical *Planinasus* Cresson, and a fossil species from the Baltic amber, *ProtoAulacigaster electra* Hennig. Griffiths (1972, with the exclusion of *Stenomicra*), Teskey (1987) and J. F. McAlpine (1989)² followed this definition. D. K. McAlpine proposed a rather different characterization. He transferred *Stenomicra*, *Cyamops* (1978) and *Planinasus* (1983) from Aulacigastridae to Periscelididae, excluded *ProtoAulacigaster electra* from the family, and described two new genera: *Ningulus* (Afrotropical) and *Nemo* (Australian). In 1994, Freidberg described the family Neminidae for *Ningulus*, *Nemo*, and his new Afrotropical genus, *Nemula*.

Freidberg's work resulted in a monotypic Aulacigastridae. This characterization was most recently adopted by Mathis and Freidberg (1994), Papp (1997), and slightly modified by Roháček (1998), who tentatively transferred the genus *Echidnocephalodes* Sabrosky from the Anthomyzidae to the Aulacigastridae. Most recently Evenhuis (1994a,b) listed *ProtoAulacigaster electra* in *Aulacigaster*.

The family Periscelididae *sensu stricto* comprises five genera, the widely distributed *Periscelis* Loew and the Neotropical genera *Marbenia* Malloch, *Neoscutops* Malloch, *Scutops* Coquillett and *Parascutops* Mathis and Papp. The monophyly of this group is well supported (Hennig 1971; Mathis and Papp 1992; Grimaldi and Mathis 1993). D. K. McAlpine (1983) transferred the aulacigastrid genera *Stenomicro*, *Cyamops* (1978) and *Planinasus* to Periscelididae (1983), a characterization that has been followed by recent workers (Colless and McAlpine 1991, Mathis and Papp 1992; Baptista and Mathis, 1994, 1996, 2000). Griffiths (1972) considered *Diopsosoma* Malloch and the small Neotropical genus *Somatia* Schinner as belonging to the Periscelididae. However, Mathis and Papp (1992) and Grimaldi and Mathis (1993) questioned the placement of *Diopsosoma* in this family. Mathis (1993) considered *Somatia* as closely related to the Psilidae (Diopsoinea), while D. K. McAlpine (1997) treated Somatiidae (monotypic) as *incertae sedis*.

There is some controversy in the literature regarding the composition of the Asteiidae. The family comprises 11 genera. Hennig (1971) included the chamaemyiid genera *Paraleucops* Malloch and *Gayomyia* Malloch, as well as the psilid genus *Schizostomyia*, in the family. This classification was accepted by J. F.

McAlpine (1989).

METHODS

Descriptive terminology.—The terms used to describe the external morphology follow J. F. McAlpine (1981) with modifications noted below. Setae posterior to the pseudovibrissal seta are called peristomal setae. The nomenclature for structures of the male terminalia follows Cumming *et al.* (1995). Throughout the discussion, I will use the group names "Opomyzoidea" and "Asteioinea" as defined by J. F. McAlpine (1989).

Taxon sampling and tree rooting.—The central goal of this study was to assess the monophyly, composition, internal phylogeny, and phylogenetic position of the Asteioinea, by testing the working hypothesis of J. F. McAlpine (1989) against alternative proposals. The set of exemplar species (Yeates 1995) selected for this purpose (Table 2.3) comprises several elements. First, a putative ingroup sample was constructed that included at least one representative of each Asteioinea family. Sampling was especially dense within the Aulacigastridae and Periscelididae.

Putative outgroups (see below) were chosen initially on the basis of J. F. McAlpine's hypothesis (1989) of a sister group relationship between Asteioinea and Opomyzoinea. Five genera of the latter, representing both families, Anthomyzidae and Opomyzidae, were sampled. Three exemplars of Clusiidae and two of Odiniidae,

representing the other two opomyzoid superfamilies (Clusioinea and Agromyzoinea, respectively) were also included.

To this list were then added exemplars placed mostly in other acalyprate superfamilies by J. F. McAlpine (1989), which however have been postulated by various authors to lie close to or within the ingroup families. These were as follows:

1. *Somatia* was included to test Griffiths' (1972) postulate that the Somatiidae, placed next to Psilidae in the Diopsoidea by J. F. McAlpine (1989), are instead closely

related to Periscelididae. 2. Representatives of Chyromyidae, placed in

Sphaeroceroidea by J. F. McAlpine (1989), were included to test Griffiths (1972)

suggestion that they are instead closely related to the Aulacigastridae. 3.

Representatives of Carnidae, placed in Carnoidea, regarded as the sister group to

Opomyzoidea (J. F. McAlpine 1989), were included to test Colless and McAlpine's

(1991) postulate that the Carnidae are closely related to the opomyzoid families. 4. A

representative of the family Marginidae, tentatively placed in the Opomyzoidea by

D. K. McAlpine (1991), was included to test its placement in the superfamily. 5.

Echidnocephalodes barbatus Sabrosky, usually placed in Anthomyzidae, was

included to test Roháček's (1998) hypothesis that it is closely related to the

Aulacigastridae. 6. *Psila rosae* Fabricius was included to test Griffiths' (1972)

hypothesis that the families Teratomyzidae and Periscelididae are more closely

related to Psilidae than to the opomyzoid families. 7. I also included one species of

the superfamily Tephritoidea (Ulidiidae) as the only taxon that assuredly belongs

outside the Opomyzoidea.

I have included in the matrix a few taxa for which several characters are unknown, hoping that the gain in taxon sampling will increase rather than decrease accuracy of the analysis, as recent methodological studies suggest (e.g. Wiens 1998). These taxa include *Ningulus simatus* McAlpine (Neminidae) and the fossil species of the genus *Cyamops*. In addition, because the Marginidae are a very rare family with species known only by their holotypes, I have used D. K. McAlpine's description (1991) of the male postabdomen of *Margo aperta* to code some of the characters of the male terminalia of *M. clausa*. The latter species is only known from the female holotypes.

A limitation of this and all other studies of acalyprate phylogeny at present is that monophyly has not been securely established for essentially any broader grouping that subsumes Asteioinea. Thus, there is no way to anchor the trees with certainty. In keeping with the adoption of J. F. McAlpine's (1989) schema as a working hypothesis, trees were rooted so as to render Opomyzoidea *sensu* J. F. McAlpine monophyletic as nearly as possible. In this circumstance, it is possible to strongly *negate* the monophyly of Opomyzoidea or Asteioinea as defined by J. F. McAlpine, by showing that no rooting of a strongly supported tree for the present data set would render these monophyletic. However, a finding *consistent* with monophyly for either or both – i.e., most-parsimonious trees in which all the putative ingroups join all the putative outgroups through a single branch - would be more provisional, until one could conclusively dismiss paraphyly of the putative ingroups with respect to the outgroups (see Farris 1972).

Character sampling.—New and traditional morphological characters were combined in a quantitative phylogenetic analysis. I endeavored to include all characters that seemed independent and informative at the superfamily and family levels, without regard to their perceived levels of homoplasy. This contrasts with frequent practice in Diptera systematics (see for example D. K. McAlpine 1978:274), but accords with standard recent practice in numerical phylogenetics (see Wiens 1997).

Character coding.—Characters were coded for the analysis as either binary (68%) or qualitative multistate (32%). Multistate characters were ordered (see Table 2.5), minimizing the amount of apparent morphological change between states (similarity criterion), whenever a plausible transformation series was apparent. Otherwise, characters were left unordered. Analyses with all characters unordered were also performed, for the purpose of comparison.

Tree search.—All analyses were performed using PAUP 4.0 (Swofford 2000).

I analyzed the data set under the parsimony criterion, using unweighted parsimony, successive weighting (Farris 1969) by Farris' rescaled consistency index (Farris 1988), and the related "implied weights" criterion of Goloboff (1993; options: K=3). Successive weighting utilizes the set of trees found after unweighted analysis as a starting point to calculate character weights: highest weight is given to those characters which have the least amount of homoplasy in the initial set of trees. This is an iterative process and the weight of each character normally stabilizes following the third pass through the data. Search under Goloboff implied weights, on the other

hand, does not require an initial set of trees in order to calculate character weights. Another difference between the two methods of character weighting lies in the function used to calculate the weights themselves. Successive weighting employs either the consistency index or a function thereof, the rescaled consistency index. As discussed by Goloboff (1991, 1993) these do not necessarily give higher weights to less homoplasious characters: if a multistate and a binary character are in conflict on a tree, one extra step will lower the consistency index less for the multistate character than for the binary character. Goloboff's (1993) measure of character fit corrects for such differential weighting and employs an arbitrary constant, the constant of concavity (K), reflecting the degree of weighting against homoplasy. When $K=0$, Goloboff's function downweights homoplasious characters as heavily as the rescaled consistency index. The degree of concavity that should be used, and whether the same K can be used for different numbers of taxa, remain to be investigated (Goloboff 1993). Implied weights analysis often produces results that are more resolved and in better accord with intuitive evaluation of character data than standard unweighted parsimony, particularly for difficult phylogenetic problems (Goloboff 1997).

Tree search was heuristic, using tree-bisection-reconnection branch swapping with 100 random taxon addition sequences. Confidence for unweighted analyses was measured using the same heuristic search settings, and 100 bootstrap replicates.

Due to the poor fit of the data, I performed a series of searches changing some of the heuristic search settings in PAUP 4.0b4a (Swofford 2000). For this

particular data set, the use of PAUP's "steepest descent" option during branch swapping yielded the largest number of most-parsimonious trees (Table 2.4). Under this option, a round of swapping is not abandoned until all minimum trees from the previous round have been evaluated. For unordered characters, for example, PAUP found 4419 MP trees in the unweighted analysis when the "steepest descent" was in effect. When the "steepest descent" was turned off, only 110 MPRs were found. On the other hand, the number of trees obtained under Goloboff implied weights (Goloboff 1993, 1997) did not differ when "steepest descent" was in effect.

The data matrix contained 49 exemplar species and 124 morphological characters. Of the 122 characters included, 107 were parsimony-informative. Two characters (38 and 117) were excluded prior to the analysis (see character discussion, morphology section below).

RESULTS AND DISCUSSION

Morphology and character coding

In this section I describe the morphological variation observed and the characters extracted from it. The character codings are summarized in [Table 2.5](#).

Capital letters following the character numbers indicate characters proposed by previous authors, as follows: D = David McAlpine; F = Frank McAlpine; G = Griffiths, H = Hennig. Discussions of phylogenetic distribution of character states refer to the 'best estimate' phylogeny (see below) shown in Fig.2.112. The

consistency index on that tree for each character (multistate characters treated as ordered when possible) is given in parentheses after the character number.

Head coloration, vestiture and morphology

(Figs. 2.3-2.36)

The primary parts of the head capsule are the compound eyes, the frons and the clypeus medially, and the cheek laterally. The frons is divided into a dorsal postfrons ("frons") and a ventral prae frons ("face") (Fig. 2.28). The back of the head is the postcranium, including the occiput above and the postgenae below. Hennig (1958, 1971) made extensive use of characters from the head, such as sclerotization of the frons and face, and head chaetotaxy.

1. (0.66). In the outgroup taxa, the occipital region is nearly flat to slightly concave (1) (Figs. 2.7-2.8), being obviously concave medially, therefore leaving the supracervical region relatively exposed and easy to see (2) in most opomyzoid families (Figs. 2.5-2.6), but not in the Odiniidae. In the Neminidae, Neurochaetidae and Periscelididae, however, the occipital region is entirely concave, following the anterior curvature of the thorax (3). In these cases, the supracervical region remains concealed by the anterior portion of the thorax in dried specimens (Figs. 2.3-2.4). State 2 is synapomorphic for the Opomyzoidea, including Marginidae, and state 3 is synapomorphic for Neminidae + (Neurochaetidae + Periscelididae). States 2 and 3 occur in the Xenasteiidae (Asteioinea).

2. (0.66). The vertex, a relatively indefinite area on the upper portion of the head (J. F. McAlpine 1981), is usually straight between the compound eyes (1) (as in

Figs. 2.9-2.10, 2.12), but is sometimes excavated. This excavation may be semilunate (3), an autapomorphy for the species of *Aulacigaster* that occur on bromeliads (Fig. 2.11), or approximately V-shaped (2), a state independently acquired in *A.ecuadoriensis* (Fig. 2.28) and *Echidnocephalodes barbatus* (incertae sedis).

3. (0.12). The transition area between the vertex and the posterior occipital sclerite is either angulate (1) (as in Figs. 2.22-2.23), or forming a sharp ridge on the top of the head (2) (as in Figs. 2.4, 2.20). A sharp vertex is plesiomorphic for the Opomyzoidea and Asteioinea. An angulate vertex is a synapomorphy for *Echidnocephalodes barbatus* (incertae sedis) + undescribed Malaysian genus + *Aulacigaster*. This character is variable within some families (i.e., Odiniidae and Teratomyzidae) and proved highly homoplasious in this analysis.

4. (1.0). A microtomentose area adjacent to the compound eye is usually absent (1). The presence (2) of this band is a synapomorphy for the Periscelidinae (Mathis 1992). This band, however, is absent in some species of the family, as in *Parascutops*.

5. (0.22). The frontal margins of the eye usually diverge towards the top of the head, making the frons wider posteriorly (1) (as in Fig. 2.31). The margins are however sub-parallel (2) in the Clusiidae (Fig. 2.30), Asteiidae, and some *Cyamops* (Fig. 2.15), *Stenomicro* (Fig. 2.14) and *Planinasus* (Fig. 2.25) analyzed by me. In Marginidae (D.K. McAlpine 1992:170, Fig. 2) and Neurochaetidae, as well as in some species of *Cyamops* and *Aulacigaster* (Fig. 2.11), the frontal margins of the

eyes conspicuously converge posteriorly (3), an autapomorphic condition. It is sometimes difficult to distinguish between states of this character.

6. (0.33). F. The ommatidia of the anteroventral portion of the eye in acalyptrates are generally of the same size as the remaining ommatidia (1) (as in Fig. 2.17). The anteroventral ommatidia are enlarged, encroaching on the facial region to various degrees (2) in most families of Opomyzoidea (as in Figs. 2.13- 2.16), but not in *Traginops* (Odiniidae), Marginidae, and other non-opomyzoid taxa. J. F. McAlpine (1989:1460) considered the enlargement of the anteroventral ommatidia as a synapomorphy for the Opomyzidae + Anthomyzidae, and the encroachment of the anteroventral margin of the eye on the face (correlated with more extreme enlargement of ommatidia) as autapomorphic for the Asteioinea. In my observation, however, the degree to which the eye encroaches on the facial is highly variable among the taxa herein studied. State 2 is synapomorphic for the Chyromyidae + Opomyzoidea, but a reversal has to be postulated for *Margo* (Marginidae).

7. (1.0). The face of the male is narrower than the female face (2) in most species of *Cyamops*. However, some Australian (*C. micronesicus*) and Oriental (*C. femoratus*) species are not dimorphic in this respect. According with this analysis, face dimorphism is a derived feature within the genus.

8. (0.26). H. In the Schizophora, the frons lies between the ocellar tubercle above and the ptilinal fissure below (Fig. 2.28). It is divided into a median mesofrons and paired, lateral fronto-orbital plates (J. F. McAlpine 1981). Sclerotized areas of the frons are flat and homogeneous, whereas weakly sclerotized areas tend to look

"sunken," "convex" or wrinkled, depending on the degree of desclerotization and the extent of the area affected. A flat, completely sclerotized frons (1) (as in Figs. 2.9-2.10, 2.12) is part of the ground-plan of the Opomyzoidea. The frons is slightly less sclerotized and depressed centrally (2) in the Chyromyidae (Fig. 2.31) studied by me, as well as in *Chaetoclusia bakeri* Coquillett (Clusiidae), a state independently acquired by these groups. The frons is weakly sclerotized, and broadly concave between the ocellar tubercle and the ptilinal fissure (3), in some *Cyamops* (Fig. 2.15), *Stenomicro* (Fig. 2.14), and bromeliad-inhabiting species of *Aulacigaster* (Fig. 2.11). Many taxa studied by me have the frons depressed from the ptilinal suture to close to the apex of the ocellar triangle, between the fronto-orbital plates and the ocellar tubercle (4) (as in Fig. 2.36). State 4 proved to be synapomorphic for Clusiidae + Anthomyzidae + Opomyzidae, and for the Neurochaetidae. The weakly sclerotized area of the frons is strongly narrowed in Carnidae (Fig. 2.32) and *Traginops*, due to the enlargement of the ocellar plate (5). According to Hennig, the frons is completely sclerotized in the ground plan of the Schizophora (1971: 15). Hennig (1971:16) suggested that the weakening of the median portion of the frons is a synapomorphy uniting Opomyzidae, Chyromyidae, and Clusiidae. However, I have coded the state present in Chyromyiidae as distinct from that displayed by the other two families.

9. (0.5). The anterior portion of the frons, or lower frons, is concolorous with the remaining frons in most taxa. In some groups, however, this region is usually light colored (ranging from pale yellow to orange) compared with the dark brown coloration of the remainder of the frons (2-3). The lower 1/4-1/3 of the frons is

yellow (3) in *Asteia amoena* Meigen (Asteiidae), *Gymnochiromyia concolor* (Malloch)(Chyromyidae) and the undescribed genus from Malaysia (Fig. 2.12). My analysis indicates this state to be a synapomorphy uniting for the latter genus with *Aulacigaster*. Having the lower portion of the frons orange is synapomorphic for the *leucopez*a group (Fig. 2.29) of *Aulacigaster*. A reduction in the orange area of the frons occurs in the Neotropical species.

10. (1.0). A forward projection of the ocellar plate (2) is unique to *Traginops* (Odiniidae; J. F. McAlpine 1987:865, Fig. 72.2). The ocellar plate is slightly convex in *Paratraginops* (Odiniidae), suggesting a sister-group relationship between these two genera.

11. (0.5). The parafacial-genal suture is differentiated (1) (as in Figs. 2.24, 2.26) in all groups studied here, with the exception of *Stenomicro*a (Fig. 2.20) and Teratomyzidae (Fig. 2.21), where it cannot be discerned (2).

12. (0.8). H.F. G. Sclerotized areas of the face have a homogeneous surface, whereas weakly sclerotized areas tend to look "sunken," "excavated" or wrinkled, depending on the degree of desclerotization and the extent of the affected area. The face is homogeneously sclerotized (1) in most Asteioinea (as in Figs. 2.9-2.15, 2.18-2.21), a synapomorphy for this group according to my analysis. The face is weakly sclerotized medially when compared with the lateral portion (2) in the outgroup taxa Clusiidae, Opomyzidae (Fig. 2.16) and Anthomyzidae, and in the asteioid taxa Asteiidae and Xenasteiidae. The face is relatively weakly sclerotized and sunken parallel to the parafacial-genal suture (3) in *Pterocalla ocellata* Fabricius (Ulidiidae),

Somatiidae, Psilidae (Fig. 2.17), Odiniidae and Marginidae. In these forms, the midline of the face is strongly sclerotized. Having the entire mesofacial plate very weakly sclerotized and depressed (4) is a synapomorphy for Chyromyidae (Griffiths 1972). This state is also present in some Anthomyzidae not included in this analysis (ex. *Aschnomyia albicosta* (Walker)). In Carnidae, the face has deep facial grooves that house the antennae (5) (Fig. 2.32), a state difficult to homologize with the others. Henning's main morphological distinction between the "Periscelidea" and "Anthomyzidea" (see above) was the degree of sclerotization of the face. According to Hennig (1971), the face is uniformly sclerotized in the former group, versus centrally membranous in the latter. J. F. McAlpine (1989:1456) regarded the weak sclerotization of the face along the vertical midline as belonging to the ground plan of the Opomyzoidea, and apomorphic with regard to the ground plan of the Acalyptratae.

13. (0.5). F. The face is convex and visible from lateral view (2) (Figs. 2.18-2.21) in all Asteioinea that have a completely sclerotized face, except in *Echidnocephalodes barbatus* (incertae sedis). I have coded the exemplars that display states 2-5 of character 12 as "inapplicable" for this character. According with J. F. McAlpine (1989:1463), a convex face is a synapomorphy for the Asteioinea, consistent with the ACCTRAN optimization of this character on the cladogram in Fig. 2.112. The lower face is projected and/or inflexed to various degrees within the suprafamily, but a further separation of this character into distinct states describing the various shapes would render it nearly uninformative in this analysis.

14. (0.33). Most taxa analyzed in this study have the face shiny to dull and microtomentose (1). However, a narrow to broad microtomentose band on the face seems to have arisen independently (2) in the *leucopeza* group of *Aulacigaster*, the undescribed genus from Malaysia (Fig. 2.12), and *Asteia amoena* and other species of *Asteia* (Asteiidae).

15. (0.16). D. The lateral borders of the peribuccal cavity are formed by ventrolateral extensions of the mesofacial plate (1) in the ground plan of the Opomyzoidea. In contrast, the ventrolateral extensions of the mesofacialia are retracted inside the oral cavity, with the parafacial-genal region bordering the peribuccal region directly, in *Planinasus* (Fig. 2.26), some Periscelididae *sensu stricto* (Fig. 2.24), *Neurochaeta inversa* McAlpine (Neurochaetidae), Anthomyzidae, Carnidae (Fig. 2.32), and the new taxon from Malaysia (2). This character is inapplicable for *Stenomicro* and Teratomyzidae because, in these genera, the parafacial-genal suture is reduced (see character 11). D. K. McAlpine (1978) proposed that this character separates Anthomyzidae and Aulacigastridae from Periscelididae and Neurochaetidae. In my opinion, it is a highly homoplasious character whose states are difficult to tell apart in some cases. In the present analysis, it failed to support any major group within the Opomyzoidea.

Head chaetotaxy.—The head setae are the inner and outer vertical, on the vertex, the postocellar seta, behind the ocellar tubercle, the fronto-orbital setae, on the fronto-orbital plate, the interfrontal setae, on the frons (Figs. 2.25-2.28), and the supracervical setae, on the back of the head (Figs. 2.35).

16. (0.2). The inner vertical seta is present (2) (as in Figs. 2.25, 2.28) in most acalyptrates. It is missing (1) in extant species of the genus *Cyamops* (Fig. 2.15), in Xenasteiidae, *Nemula* (Neminidae) (Freidberg 1994:475, Fig. 1), some Asteiidae not used in this analysis (*Bahamia* and *Sigaloessa*), some species of *Aulacigaster* (Fig. 2.11) and Teratomyzidae. In *Somatia* both inner and outer vertical setae are missing (Fig. 2.33). Freidberg (1994) considered the vertical seta present in *Nemula* to be the inner vertical seta, but I consider it to be the outer vertical seta. This character failed to support any major group in my analysis.

17. (0.5). The inner vertical seta is erect on the vertex (1) (as in Figs. 2.25, 2.28) of most acalyptrates. It is proclinate (2) in the fossil species of the genus *Cyamops* and in some *Stenomicra* (subgenus *Podocera*) (Fig. 2.20).

18. (1.0). The region between the ocellar tubercle and the apex of the vertex is usually devoid of setae (1) except for the postocellar setae. A series of divergent, relatively well developed setae occurs on this region (2) in *Traginops* and *Odinia*, and is widespread in the Odiniidae (J. F. McAlpine 1987:865, Fig. 72.2).

19. (0.16). H.F. (see also character 21). The postocellar seta is absent (1) (as in Figs. 2.25, 2.27) in several opomyzoid taxa. It is present (2) in most acalyptrates (as in Fig. 2.13). A very thin, hair- like postocellar is present in some specimens of *Chaetoclusia bakeri* (Clusiidae), which I have coded as polymorphic for this character. Hennig (1958, 1969, 1971) and J.F.McAlpine (1989) considered the absence of this seta as a synapomorphy uniting *Aulacigaster*, *Stenomicra* and *Cyamops*, but according to my analysis, the postocellar seta has been lost

independently in the Aulacigastridae and Stenomicroinae (Periscelididae). This character failed to support any major group in my analysis.

20. (0.25). A postocellar seta can occur in two distinct regions of the vertex: (1) on the anterior portion of the head, immediately behind the ocellar tubercle, as in Clusiidae (Fig. 2.30), Periscelididae (Fig. 2.19), Odiniidae, some Opomyzidae not included in this analysis, and Neminidae; or (2), behind the apex of the vertex, on the back of the head (as in Fig. 2.6), the common condition. In *Psila rosae* (Psilidae), the postocellar seta is on top of the angulate vertex, and I have coded the character as ambiguous for this species. This character failed to support any major group in this analysis.

21. (0.20). F.G. The postocellar seta can be hair-like (1) (as in Fig. 2.6), or robust (2) (as in Fig. 2.13). According to J. F. McAlpine (1989: Fig. 116.5) the reduction of the postocellar seta is a synapomorphy for the Asteioinea, consistent with the DELTRAN optimization of this character on the cladogram in Fig. 2.112. Reduced postocellars are common in the Opomyzoidea and also occur in Somatiidae and *Pterocalla* (Ulidiidae). Griffiths (1972) wrongly attributed the possession of long, divergent postocellars to *Stenomicroa*. Some species of this genus have a single tiny, hair-like pair of setae posterior to the apex of the vertex.

22. (0.22). D. G. The postocellar setae can be: (1) convergent, as in Anthomyzidae, Chyromyidae, Xenasteiidae, *Auster* sp (Teratomyzidae), and Somatiidae; (2) parallel, as in some Neurochaetidae, Neminidae, *Echidnocephalodes barbatus* (incertae sedis) and *Meoneura flaviceps* (Carnidae); or divergent (3), as in

the other groups analyzed by me. In the exemplars of Asteiidae, I was unable to decide whether the postverticals are parallel or slightly divergent, so I coded the character as ambiguous. Colless and D.K. McAlpine (1991) considered the presence of parallel to divergent postocellars as diagnostic for the Opomyzoidea, and Griffiths (1972) considered it a synapomorphy for the Anthomyzoinea. In this analysis, parallel-sided postocellars were inferred to be synapomorphic for the Asteioidea excluding Teratomyzidae, but the feature is highly variable within this group.

23.(0.1). A pair of setae at the sides of the ocellar tubercle, behind the anterior ocellus (2) (as in Figs. 2.34a-b), is synapomorphic for Periscelididae plus Neurochaetidae in my analysis. This condition has apparently evolved independently in *Teratomyza*, Odiniidae, some Anthomyzidae, *Echidnocephalodes barbatus* (incertae sedis), Carnidae (Fig. 3.32) and *Somatia* (Fig. 3.33). It concurs with a pair of setulae inside the ocellar tubercle in some periscelidids and teratomyzids. I homologized the latter pair of setae with the ocellar setae of other taxa, and considered the seta outside the ocellar tubercle as a separate character. The usual interpretation, when both setae occur in the ocellar region, considers the stronger seta as the “true” postocellar. This character failed to support any major group.

24. (0.1). H. The ocellar seta, located inside the ocellar tubercle (Figs. 2.34a-d) behind the anterior ocellus, is absent (1) in *Stenomicro*, extant species of *Cyamops* and *Planinasus*, some Neurochaetidae, some Anthomyzidae, *Echidnocephalodes*

barbatus (incertae sedis), and some Carnidae. Within *Aulacigaster*, some species also lack the seta. The ocellar seta is present (2) (Figs. 2.30-2.32, 2.34) in most taxa analyzed in this study. In my analysis the absence of the ocellar seta is synapomorphic for Periscelididae plus Neurochaetidae. I was unable to decide if the ocellar seta is present in the Odiniidae, as several setae are present on the ocellus. The reduction of the ocellar seta is one of the synapomorphies of Hennig's Aulacigastridae (1958, 1963) (including *Cyamops*, *Stenomicra* and *Planinasus*) that was not supported by my analysis.

25. (0.37). I have coded the ocellar seta as reduced when it is hair-like in appearance (1) (see Figs. 2.34a-b), as in Asteiidae, some *Aulacigaster* and the fossil species of *Cyamops*. All other degrees of development of this seta were coded as well developed (2). A strong ocellar seta is present in the ground-plan of the Opomyzoidea and Asteioinea, and its reduction is a synapomorphy for *Aulacigaster*.

26. (0.37). The fronto-orbital setae vary in number from one to six (Figs. 2.16, 2.24-2.33). Only one long fronto-orbital (1) occurs in the Opomyzidae (Fig. 2.16), Asteiidae (close to the lower ocellus), Periscelididae *sensu stricto*, and Teratomyzidae (about halfway between the ocellar tubercle and the ptilinal suture, Fig. 2.21). Most asteioids have two fronto-orbital setae (2). The lower pair can be reclinate (some *Stenomicra*), inclinate (*Planinasus*, *Cyamops*, *Aulacigaster*, the undescribed genus from Malaysia), proclinate (*Nemo*) or slightly laterocline (*Nemula*). Taxa that have three fronto-orbital setae (3) (Fig. 2.30) always have the mid-seta reclinate, and the lower seta inclinate (*Clusia*, *Gymnochyromyia*, *Odinia*,

Traginops) or reclinate (*Anthomyza*). Four fronto-orbital setae (4) occur in the Neurochaetidae (*Neurotexis* and *Neurocytta*), and the second lower seta is internal to the others. In *Neurochaeta*, only 3 fronto-orbital setae occur, but the lowermost seta is internal to the others. It would be reasonable to assume that this seta is homologous with the second lower seta of other Neurochaetidae. Six short fronto-orbital setae (5) occur in *Ningulus simatus* (Neminidae). In *Somatia*, two rows of setae are present on what seems to be the fronto-orbital plate, the external row having about 10 weak setulae starting from the ptilinal suture (8). Two well-developed setae occur on the posterior portion of the frons in *Psila rosae* (Psilidae), preceded by several short setae (7). According to Hennig (1971:5), "the fronto-orbital setae have been independently reduced in several groups of Acalyptratae... In several families the number of fronto-orbital setae is higher in fossil specimens of the Baltic amber than in recent families." The fronto-orbital setae are difficult to homologize based on position and orientation, and for that reason, I only considered the number of setae. This character failed to support any major group.

27. (1.0). The uppermost fronto-orbital seta is usually reclinate in the groups studied here (1) (as in Figs. 2.30, 2.31), but a latero-clinate condition is synapomorphic for Carnidae (2) (Fig. 2.23; Brake 2000).

28. (0.6). When only two fronto-orbital setae occur on the frons, they are either vertically (1), diagonally (2), or transversely aligned (3). The lower seta is internal to the upper seta (2) in some species of *Nemo* (*N. corticeus* McAlpine and *N. centriseta* McAlpine) and in some *Cyamops* (Fig. 2.15). The posterior seta is slightly

internal to the lower seta (3) in some *Aulacigaster*, some *Stenomicroa*, and *Planinasus* (4) (Fig. 2.25). State 1 is present in the ground-plan of the Opomyzoidea and Asteioinea. This character failed to support any major group.

29. (0.2). The intrafrontal seta is usually absent (1). It is convergently present (2) in the Clusiidae (subfamily Clusiodinae and in *Clusia*; Fig. 2.30), in *Planinasus* (Fig. 2.25), Neminidae, and Carnidae (Fig. 2.32).

30. (1.0). When present, the intrafrontal setae may be proclinate (1) (as in Figs. 2.30, 2.32), a condition found in the Carnidae, Clusiidae, and Neminidae, or parallel and reclinate (2), characteristic of *Planinasus* (Fig. 2.25).

31. (0.2).F.G. The pseudovibrissa is absent (1) in the Opomyzidae (Fig. 2.16), Periscelididae *sensu stricto* (Fig. 2.13), *Planinasus* (Fig. 2.25), *Psila* (Figs. 2.17, 2.23) and *Pterocalla* (Ulidiidae) (Fig. 2.29). The pseudovibrissa is present (2) in most groups studied by me, although developed to different degrees. It is usually stronger than the peristomal setae and is often erect or directed posteriorly. D. K. McAlpine (1997:177) mentioned the presence of a "well differentiated cheek bristle (perhaps even to be identified as a vibrissa)" as evidence for the separation of the Somatiidae from the Diopsoidea. Although the presence of a "vibrissa" was advanced as an autapomorphy for the Anthomyzoinea of Griffiths (1972) and the Opomyzoidea of J. F. McAlpine (1989: Fig. 116.5), it was judged plesiomorphic for Opomyzoidea and Asteioinea in the present analysis.

32. (0.28). Each side of the face is marked by a suture that runs dorsally from the anterior tentorial pit toward the base of the antenna (as in Figs. 2.24-2.29). These

grooves are the frontogenal sutures, and the median facial plate (prae-frons, mesofacialia) lies between them. The "peristomal setae" occur internal to or at the frontogenal suture, forming a row that goes from the pseudovibrissa (when differentiated) to the posterior portion of the cheek (1). This row is reduced in the Clusiidae, reaching the middle of the cheek at most. The peristomal setae are not differentiated from other cheek setae (2) in the Opomyzidae, Chyromyidae and some Periscelididae. The cheek is bare (3) in *Planinasus* (Fig. 2.26), Somatiidae and Psilidae. In Teratomyzidae (Fig. 2.21) and *Stenomicro* (Fig. 2.20), the frontogenal suture is absent. For this reason, I was unable to decide whether the pseudovibrissa and the peristomal setae are present in these taxa. This character failed to support any major group in my analysis.

33. (1.0). An additional row of weakly developed peristomal setae, located between the margin of the peribuccal region and the peristomal row of setae, is unique to the undescribed genus from Malaysia (2).

34. (0.5). The median portion of the face (mesofacialia) is usually devoid of setae (1). In the Periscelididae *sensu stricto* and *Planinasus*, however, several long and well-developed setae are present on this region (2) (Figs. 2.13, 2.24, 2.25-2.26). This feature was independently acquired by these two groups, according to my analysis.

35. (0.14). The supracervical region may be devoid of setae (1), as in the Neminidae, most Periscelididae, and Aulacigastridae; or it may be setose (2), the state present in the ground-plan of the Opomyzoidea and Asteioinea. In my analysis,

state 1 was inferred to be synapomorphic for the Aulacigastridae, and for Neminidae + (Periscelididae + Neurochaetidae), with supracervical setae re-appearing secondarily in the Neurochaetidae.

36. (0.3). When present, the supracervical setae (Figs. 2.35 a-d) may occur in a single group (1), in two groups (2), in a pair of diagonally converging rows (3) or in a double row of basal setae (4). This character was left uncoded for several taxa because it is sometimes not possible to see the arrangement of the supracervical setae without dissecting the head. It failed to support any major group in this analysis.

Head appendages (antennae and mouthparts)

(Figs. 2.37-2.48)

Hennig (1958, 1971) and D. K. McAlpine (1979, 1983) gave high weight to the shape of certain antennal segments in their phylogenies. Although Frey (1921) made an extensive study of the mouthparts of Diptera Schizophora, mouthpart characters have been seldom used in acalyptrate systematics above the family level (but see Grimaldi 1990; Brake 2000). Traditional Diptera taxonomy has used numerical terminology for the first three segments of the cyclorrhaphous antenna (first, second, third). D. K. McAlpine (2000) has extended this system to include the apical segments that together form the arista, segments 4, 5 and 6. Another nomenclatural system calls the first two antennal segments "scape" and "pedicel." The third segment corresponds to three flagellomeres. The 1st flagellomere is enlarged, and the apical segments are reduced and closely associated, forming the arista (Fig. 2.47) (J. F. McAlpine 1981). The study of Stuckenberg (1999) indicates

that the postpedicel, in certain advanced brachycerans, was probably derived from several of the basal flagellomeres present in the brachyceran ground-plan, which fused to form the large, complex structure comparable with that of the Cyclorrhapha. I have however adopted the terminology in "Manual of Nearctic Diptera" (J. F. McAlpine, 1981),” because its use is more widespread among dipterists.

37. (0.5). H. D. In most groups studied by me, the pedicel articulates with the 1st flagellomere by means of a membrane that inserts into a basal cavity of the 1st flagellomere (1) (Fig. 2.44). Another type of articulation is present in the Perisclididae and Neurochaetidae, apparently synapomorphic for these two families: the 1st flagellomere is constricted basally into a basal notch that is inserted deeply into a central cavity of the pedicel (2) (Fig. 2.48). Hennig (1971, Figs 2-16, 2.22-2.29) depicted this character for some species, but discussed only the orientation of the 1st flagellomere in relation to the pedicel, i.e., whether the antenna is "porrect" or "geniculate.” D. K. McAlpine (1978) was the first to correctly describe this character. State 2 denotes the presence of a cap-like pedicel, and D. K. McAlpine used both features to support a definition of Perisclididae to include *Stenomicro*, *Planinasus* and *Cyamops*. Subsequent authors (Roháček 1998; J. F. McAlpine 1989), however, questioned D. K. McAlpine's conclusion, because a cap-like pedicel is widespread in acalyptrates.

38. The antenna is porrect (1) in most Opomyzoidea. It is geniculate (2) in the asteioid taxa Perisclididae, *Stenomicro*, *Planinasus* and *Cyamops*, and in the outgroup taxa *Somatia* and *Psila*. In some families, such as Anthomyzidae and

Asteiidae, intermediate states between porrect and geniculate antennae exist. This character was excluded from the analysis because, in practice, it is nearly impossible to separate into discrete states.

39. (1.0). F. The arista is basal and dorsal on the 1st flagellomere (1) (Figs. 2.37-2.42, 2.44) in most taxa I have studied. This condition is part of the ground-plan of the Opomyzoidea and Asteioinea. The arista is sub-apical and dorsal (2) in *Clusia lateralis* Haliday (Fig. 2.43)(Clusiidae) and *Margo clausa* McAlpine (Marginidae) (D.K. McAlpine 1992:170, Figs. 1-2), and apical (3) in *Chaetoclusia* and *Sobaracephala* (Clusiidae). J. F. McAlpine (1989) considered the basal dorsal insertion of the arista as a synapomorphy for the Opomyzoidea, excluding the Clusioinea (Clusiidae plus Acartophthalmidae).

40. (0.5). D. The arista often is 2-3-segmented, with the two basal-most segments short and annulate, and the apical segment long (1) (Figs. 2.42-2.44). The basal segmentation of the arista is inconspicuous or absent in *Aulacigaster* (Figs. 2.37-2.39), the undescribed genus from Malaysia, and *Stenomicro* (2). D. K. McAlpine (2000) described the arista segmentation for several taxa and commented on its possible phylogenetic significance.

41. (0.5). The arista axis may be straight (1) (Figs. 2.42-2.44), the common condition, or zigzagged, as in *Aulacigaster* and *Asteia* (2) (Figs. 2.37-2.39, 2.41).

42. (0.25). The arista may be bare (1), pubescent (2) (Figs. 2.37-2.41, 2.44), or bipectinate (3) (Figs. 2.37-2.41, 2.44). The arista was considered bare when no hairs or rays were observed on the arista axis. Only a few taxa present this (derived)

condition. A pubescent arista has rays arising from the dorsal, lateral and ventral sides of the arista axis. This condition is part of the ground-plan of the Opomyzoidea and Asteioinea. A bipectinate arista has rays alternating on the dorsal and ventral axis of the arista, and is synapomorphic for the Aulacigastridae, and for Periscelididae + Neurochaetidae. *Xenasteia shalam* (Xenasteiidae) has the apical half of the arista bare, and the basal half with short pectinations. I have assigned state 1 to this species.

43. (0.33). The arista may have short (1) (Figs. 2.38-2.39) or long rays (2) (Figs. 2.37, 2.40-2.41). Long dorsal and short ventral rays (3) occur in the arista of *Geomyza* and *Amigdalops* (Opomyzidae). State 1 is part of the ground-plan of the Opomyzoidea and Asteioinea. It also occurs in some *Aulacigaster*, Asteiidae, and some non-opomyzoid taxa. This character failed to support any major groups.

44. (1.0). The antennae lie close together below the ptilinal fissure (1) (as in Fig. 2.28). Species of *Planinasus* and *Diopsosoma* have the antennae separate from each other by a distance that is larger than the length of the pedicel (2) (Fig. 2.25). This feature is also present in *Neoscutops* (Periscelididae). Intermediate degrees of separation between the antennae occur in several groups. My attempts to separate this variation into discrete states turned into a very subjective endeavor, however, as I sampled through the exemplar specimens. For example, teratomyzids, *Chaetoclusia* (Clusiidae) and *Margo* (Marginidae) (D.K. McAlpine 1992:170, Fig. 2) have the antennae separated by a distance that equals the length of the pedicel, and the posterior portion of the ptilinal suture is relatively straight lined. I decided to code

the state present in *Planinasus* and *Diopsosoma*, quite distinctive, against all other shapes.

45. (1.0). The clypeus of males and females is equally developed in most groups studied (1). It is reduced, and closely connected with the oral cavity (2), in males of *Cyamops* with the exception of *C. micronesicus* (Australia) and *C. femoratus* (Oriental).

46. (1.0). The palpus is present (1) and assumes various shapes in the groups studied. It is very reduced or absent (2) in Teratomyzidae, a synapomorphy for the family.

47. (0.5). The palpus is most often long and slender (1) (as in Fig. 2.45). When modified, it may be teardrop-shaped as in *Aulacigaster* (Fig. 2.27), some Periscelididae and Neurochaetidae (2) or spatulate (3), as in *Clusia* and several other clusiid genera.

Thorax

(Figs. 2.53-2.61)

The dipteran thorax is dominated by the mesothorax, which accommodates the muscles of the single pair of wings. The prothorax and metathorax are greatly reduced. In comparison with the head capsule and appendages, the morphology of the thorax has not been extensively used in opomyzoid taxonomy (but see J. F. McAlpine 1989).

48. (0.16). The dipteran prothorax comprises the pronotum, -pleuron and -sternum. The proesternum is the principal sternal sclerite. It may be divided into an

anterior presternum and a posterior basisternum (see Figs 2.57- 2.58). The basisternum lies between the insertions of the coxae. A large basisternum that is wider than long (1) (as in Figs 2.57-2.58) occurs in the asteioid taxa Xenasteiidae, Asteiidae, Aulacigastridae the undescribed genus from Malaysia, and Stenomicrinae, and in the outgroup taxa Anthomyzidae, Clusiidae, and Somatiidae. A narrow basisternum (2) (Figs 2.59-2.60) is assigned to the ground plan of Opomyzoidea in my analysis, and is present in many ingroup and outgroup taxa.

According to Speight (1969) the basisternum can occur in three shapes. When the area between the coxae is mostly sclerotized, but the sclerite lies free between the membranes, it is basiliform. A reduced form of the basiliform basisternum occupies only a small portion of the area between the forecoxae, which is largely membranous. When the basisternum is well sclerotized and extended to join the propleuron, it is said to have a precoxal bridge. In this work I did not investigate the presence/absence of a precoxal bridge. There are many ways by which a precoxal bridge can be formed, and an accurate evaluation requires full dissection of the specimen. Given that many taxa I studied are rare in collections, I decided not to study this particular feature.

49. (0.66). F. A basisternum devoid of setae (1) (as in Figs 2.57-2.59) occurs in most groups being considered. A setose basisternum is present in Opomyzidae (2) (Fig. 2.60). In the Clusiidae and *Neurocytta prisca* McAlpine (Neurochaetidae), setae are typically located at the margin of the sclerite (3). J. F. McAlpine (1989)

mentioned the presence of setae on the basisternum as an autapomorphy for the Clusiidae and for the Opomyzidae, consistent with the results of this analysis.

50. (0.16). The basisternum is joined posteriorly to the furcasternum, which is defined by a V-shaped suture between the katapisterna (1); the furcasternal suture is ill defined laterally (2) in some *Stenomicro* (Fig. 2.57) and in Carnidae, being often missing (3) in the Schizophora. State 2 appears to be synapomorphic for Aulacigastridae, and is also present in *Stenomicro*, Neminidae, and *Pterocalla* (Ulidiidae). I was unable to evaluate this character for many taxa, as this would have required dissection of the mid-leg.

51. F. (0.33). The mesonotum includes the entire dorsum of the mesothorax. Its three basic components are prescutum, scutum and scutellum. It also includes the postnotum posteriorly. The greater ampulla corresponds to a basal swelling of the pleural wing process (a mediodorsal margin of the anepimeron that articulates with the wing). It is usually absent (1) in acalyptrates, but is present (2) in the Perisclididae (Fig. 2.61), Aulacigastridae, and Psilidae (Fig. 2.23). It is also a constant character among calyptrates. Throughout the Schizophora, the occurrence of a greater ampulla is almost always associated with a deeply seamed, geniculate pedicel (J. F. McAlpine 1989:1464). J. F. McAlpine (1989) based the monophyly of Perisclididae *plus* Aulacigastridae on the presence of a greater ampulla. According to my analysis, however, the greater ampulla has originated independently in the Aulacigastridae and Perisclididae.

52. (0.16). F. The notopleuron is flat (1) in many Clusiidae, *Parascutops* (Periscelididae), Chyromyidae, some Neminidae, Somatiidae, Psilidae, Xenasteiidae, and the undescribed genus from Malaysia. Typically, it bears a narrow to large posterior callosity (2) (as in Fig. 2.50). The posterior notopleural seta lies on top of this prominence.

53. (0.33). F. The upper posterior margin of the anepisternum forms a raised ridge (2) (as in Fig. 2.61) in all opomyzoid taxa with the exception of species of Odiniidae I have studied. J. F. McAlpine (1989:1456) considered state 2 to be a synapomorphy for the Opomyzoidea, consistent with the results of this study.

54. (0.33). F. The postnotum (Figs. 2.53-2.56) includes all the parts behind and below the scutellum. In the groups I have studied, the sclerite behind the scutellum (mediotergite) connects with the scutellum through a membranous region, the subscutellar membrane. The mediotergite is often convex on its dorsal portion, forming a subscutellum (2) (Figs. 2.53-2.56), although in some groups it is very weakly developed (Clusiidae). In Odiniidae, when the subscutellum is present, it is very narrow and only slightly convex. A similar condition is found in Carnidae. The subscutellum is absent (1) in Somatiidae, *Psila* (Psilidae), *Traginops* (Odiniidae) and *Nemula* (Neminidae). According to J. F. McAlpine (1989), the subscutellum is absent in the ground plan of Opomyzoidea, a conclusion in conflict with my results.

55. (0.25). D. The region of the mediotergite that lies ventral to the subscutellum is either flat or convex, and is called the postscutellum. It is narrow, almost inconspicuous (1), in *Teratomyza* (Teratomyzidae), Xenasteiidae, some

Neurochaetidae and *Echidnocephalodes barbatus* (incertae sedis). In all other taxa, it shows various degrees of development (2) (Figs. 2.53-2.56). The development of the subscutellum at the expense of the postscutellum is probably correlated with the dorsoventral compression of the thorax in neurochaetids (D. K. McAlpine 1988).

Thorax chaetotaxy (Figs. 2.49-52). The following setae are important in the taxonomy of the group herein considered: the acrostical row of setae, on the median portion of the mesonotum; the dorsocentral row of setae, external to the acrostical row; the scutellar setae, on the scutellum; the postpronotal seta, the anepisternal setae and the katepisternal setae, on the pleural region.

56. (0.14). The postero-dorsal portion of the anepisternum may be bare (1) or have one or more setae (2) (Figs. 2.49, 2.61). When setae are present, they are inserted on the raised ridge of the anepisternum (character 53). Posterior anepisternal setae occur in some species of *Cyamops* (contra Mathis and Papp 1992:367). This character is quite variable among genera of the surperfamily.

57. (0.16). In the groups I have studied, the upper portion of the katepisternum has one (1) or two (2) setae (Fig. 2.49). The presence of the anterior seta is a synapomorphy uniting the Marginidae with the Asteioinea, but reversals occur in the Periscelididae and Neminidae. Two outgroup taxa, the Anthomyzidae and the Odiniidae, also show state 2.

58. (1.0). The posterior katepisternal seta is absent (1) only in *Somatia* and *Psila*, a synapomorphy for these two taxa. It is present (2) in all other groups I have analyzed.

59. (1.0). The anterior notopleural seta is absent (1) only in *Somatia* and *Psila*, a synapomorphy for these two taxa. It is present (2) in all other groups analyzed by me.

60. (1.0). The posterior notopleural seta is absent (1) only in *Nemula longarista* Freidberg (Neminidae). It is present (2) in all other groups I have analyzed.

61. (0.14). The postpronotal seta is weakly developed or absent (1) in many Asteioinea (J. F. McAlpine 1989) with the exception of some Periscelididae and Neurochaetidae (Fig. 2.51). It is typically present and well developed (2).

62. (0.2). A presutural dorsocentral seta is usually absent (1) (as in Figs. 2.49-52) in the groups herein considered. It is present (2) in some Chyromyidae, Teratomyzidae, Odiniidae and Opomyzidae included in the analysis, as well as in *Meoneura flaviceps* (Carnidae). This character failed to support any major group within the Opomyzoidea.

63. (0.18). The acrostical rows of setulae are present on the median portion of the scutum, between the dorsocentral setae. The acrostical setulae may be reduced in number to absent (1), as in Asteiidae, Teratomyzidae, and Neminidae (Fig. 2.52). When present, they may be arranged in well-defined rows (2) (as in Fig. 2.50), as in most Asteioinea and in Carnidae, or randomly scattered on the scutum (3), as in some Clusiidae, Chyromyidae, Neurochaetidae (as in Fig. 2.51), Odiniidae, *Parascutops* (Periscelididae), Xenasteiidae, the undescribed genus from Malaysia, and Marginidae.

64. (0.33). When the acrostical setulae are arranged in rows on the scutum, they may occur in a single row (1), one pair of rows (2), 2 pairs of rows (3), or three pairs of rows (4). State 2 is characterizes the ground-plan of the Opomyzoidea. Reduction of the number of acrostical rows of setae is a synapomorphy for the asteioid clade containing *Aulacigaster*, *Echidnocephalodes barbatus* (incertae sedis), the Malaysian genus, Asteiidae and Xenasteiidae, with reversals within *Aulacigaster*. Within Periscelididae, states 2 and 3 also occur.

65. (0.11). One (1) or two (2) postsutural dorsocentral setae may be present on the scutum. Two dorsocentral setae are present in the ground-plan of Opomyzoidea. The absence of the anterior seta is a synapomorphy for the Asteioinea under ACCTRAN optimization, with reversals in Aulacigastridae, Periscelididae and isolated taxa within the suprafamily. This character is highly variable within acalyptrates.

66. (0.16). The basal scutellar seta is typically absent (1) in Asteiidae, *Stenomicroa*, *Planinasus*, Teratomyzidae, *Neurocytta prisca* (Neurochaetidae), and *Psila rosae* (Psilidae). It is present (2) in all other groups I studied. This seta is apomorphically lacking in *C. imitatus* and *C. nigeriensis*. It is minute in *Asteia crassifacies* and in other species of *Asteia* (Asteiidae).

67. (0.5). The apical scutellar seta is often posteroclinate (1), forming an angle larger than 90 degrees with the dorsum of the scutellum. It is erect (2), forming an angle of 90 degrees or less with the dorsum of the scutellum, in Neminidae (Freidberg 1994:476, Figs7, 8, 9) and *Neurocytta prisca* (Neurochaetidae).

68. (0.13). The apical pair of scutellar setae may be subparallel (1), the common condition; convergent (2), as in Carnidae, *Psila* (Psilidae), Chyromyidae and Odiniidae; or divergent (3), as in Neminidae (Freidberg 1994:476, Figs 7, 8, 9). This character is quite variable even among species of the same genus.

Wing (Figs. 2.62-2.78).—Characters from the wing have often been used in the taxonomy of acalyptrates, as well as in keys to families. Three of the seven synapomorphies that support the Opomyzoidea are from the wing (J.F. McAlpine, 1989:1455, Fig. 116.5). Some wing characters probably evolve together. For example, the tendency for the shortening of the veins costa and A1 in the Cyclorrhapha is correlated with the passive role the posterior portion of the wing plays during flight (Hennig 1971:19), a general trend in the evolution of the dipteran wing called costalization (Hennig 1973).

69. (0.08). F. The wing of acalyptrates is often patterned (1) (as in Figs. 2.64a, 2.70-72, 2.77-2.78). When the wing is completely translucent, it is said to be hyaline (2) (as in Figs 2.74-2.76). J. F. McAlpine (1989) considered the presence of a dark pattern on the wing as an autapomorphy for the Opomyzoidea. According to my analysis, a hyaline wing belongs to the ground plan of Opomyzoidea and Asteioinea. The intensity and coverage of the dark pattern on the wing varies greatly within the group.

70. (0.33). The costa, or costal vein, is devoid of spines (1) (as in Figs 2.70-2.78) in most taxa I have analyzed, but it has well-differentiated spines (2) in some

Aulacigastridae (Fig. 2.64), Neurochaetidae and in the undescribed genus from Malaysia (Fig. 2.66).

71. (0.22). The costa is usually long in acalyptrates, reaching vein M1 (1) (as in Figs. 2.64-2.65, 72, 2.75-78). It goes slightly beyond vein R4+5 (2) in *Neurochaeta stuckenbergi* (Neurochaetidae). The costal vein is shorter, reaching only vein R4+5 (3), in the Carnidae (Fig. 2.74), Periscelididae *sensu stricto* (Fig. 2.70), Teratomyzidae (Fig. 2.73), and Xenasteiidae (Papp 1998:306, Fig. 26.2). All three states are present in the Neurochaetidae.

72. (0.4). D.H.F. In Schizophora, two breaks in the costa, the humeral and the subcostal break, have apparently arisen independently several times (J. F. McAlpine 1989). The subcostal break occurs where the subcosta joins the costa, and can be present either as a weakness in the sclerotization of the costa (2) (as in Figs. 2.62-2.65, 2.67-69), the common condition, or as an interruption thereof (3), as in Carnidae (Fig. 2.74), some Neurochaetidae and some Teratomyzidae. State 2 belongs to the ground-plan of the Opomyzoidea and Asteioinea. It is not always easy to differentiate between a weakness in the costa and a true interruption. According to Hennig (1937, 1971) the costal break may be an adaptation for folding the wing in the puparium. The presence of a costal break was considered a synapomorphy for the Opomyzoidea (J. F. McAlpine 1989:1455, Fig. 116.5). Griffiths (1972) considered the absence of a costal break as an indication that the Asteiidae might belong outside his Anthomyzinea. Mathis and Papp (1992:367) implied that *Planinasus* has no costal break, but my observations indicate that a weakening of the costa just before

the apex of R1 is present in this genus. D. K. McAlpine (1991) suggested that the lack of a subcostal break is one synapomorphy uniting the Marginidae with Clusiidae and/or or Opomyzidae. I have coded the condition in Clusiidae as state 2.

73. (0.4). The humeral break lies just distal to the humeral crossvein. It is present as a weakness in the sclerotization of the costa (2) in *Planinasus*, Xenasteiidae (Papp 1998:306, Fig. 26.2), *Pterocalla* (Ulidiidae) and the undescribed genus from Malaysia.

74. (1.0). Vein R1 is usually bare of setae (1) but in *Chaetoclusia bakeri* (Clusiidae) it has a dorsal row of setae (2)

75. (0.18). Vein R2+3 may approach the costa halfway to the wing apex (1), as in Neminidae (Freidberg 1994:476, Figs. 10-12); on its apical two third (2); or at the apex of the wing (3), as in most outgroup taxa. The last two states are equally common and variable within some families (ex. Aulacigastridae). A short vein R2+3 (state 2) is a synapomorphy uniting *Margo clausa* with Asteioinea, according to my analysis.

76. (0.33). Vein R1 sometimes bears a short preapical kink (2). In some Aulacigastridae, this kink is better developed and reaches the costal vein. Roháček (1998) described this character as unique to Anthomyzidae and Opomyzidae, but it occurs in Agromyzidae (Agromyzinae), *Aulacigaster* and the undescribed genus from Malaysia. According to my results, it is a synapomorphy for Anthomyzidae plus Opomyzidae, and for *Aulacigaster*. Within the latter, the *femorata* group has secondarily lost the apical kink on vein R1 (see Fig. 2.65).

77. (0.2). F. The subcostal vein reaches the costa (2) in the Clusiidae, Chyromyidae, Somatiidae, *Pterocalla* (Ulidiidae) and Marginidae. It is incomplete (1) in all other taxa I have analyzed (as in Figs 2.62-2.63). Although I have treated the subcosta as incomplete in *Traginops* (Odiniidae) and *Psila rosae* (Psilidae), it reaches the costal vein as a fold in these groups. An "abbreviated" subcosta is a putative synapomorphy for the Opomyzoidea families excluding the Clusioinea (J.F. McAlpine 1989, Fig. 116.5). The optimization of this character yields an ambiguous state assignment at the base of the Opomyzoidea.

78. (0.5). When incomplete, the subcostal vein either fuses apically with vein R1 (1) (as in Figs 2.62-2.66), as in Anthomyzidae, Aulacigastridae and the undescribed genus from Malaysia; or, it lies free in the subcostal cell (2) (as in Fig. 2.67), the common condition.

79. (0.14). Crossvein bm-cu is usually present (2) (as in Figs 2.71, 2.73, 2.74-78), being absent (1) in *Aulacigaster* (Fig. 2.64) and the undescribed genus from Malaysia (Fig. 2.66), some Neurochaetidae, and some *Stenomicro*, some Australian and Oceanic species of *Cyamops* and *Nemula longarista* (Neminidae) (Freidberg 1994:476, Fig. 10), Asteiidae and Xenasteiidae (Papp 1998:306, Fig. 26.2).

80. (0.5). Crossvein bm-cu can be complete (1) or incomplete anteriorly, a state independently acquired in Opomyzidae and some Neminidae (D.K. McAlpine 1983:67, Figs. 14,15) (2)

81. (1.0). Crossvein r-m, typically present, joins vein R4+5 with vein M1 (1). It is absent in *Xenasteia palauensis* Hardy (Xenasteiidae), an autapomorphy for this species.

82. (0.5). Crossvein r-m, when present, can be complete (1) or incomplete (2), a state independently acquired in the undescribed genus from Malaysia and *Aulacigaster plesiomorphica*.

83. (0.4). Crossvein r-m occurs in three distinct locations: well below the middle (1) (as in Figs. 2.64, 2.66, 75), near the middle (2) (as in Figs. 2.70-2.71, 2.76), or well above the middle of cell dm (3) (as in Fig. 2.78). State 2 is the most widespread among the groups I studied. State 1 is a synapomorphy for the Asteiidae, Xenasteiidae, Aulacigastridae and the undescribed genus from Malaysia. I have coded this character as "?" for *Xenasteia shalam* because, in this species, cell dc is not delimited posteriorly. State 1 also occurs in the Marginidae and *Psila rosae* (Psilidae). State 3 occurs in Neminidae (Freidberg 1994:476, Figs. 10-12), *Traginops* (Odiniidae) and *Pterocalla* (Ulidiidae). I was unable to decide what state is present in *Echidnocephalodes barbatus* (incertae sedis). Here, the wing is long and crossveins are crowded into the anterior half of the wing, r-m being slightly below the middle of the discal cell.

84. (0.22). In acalyptrates, CuA2 joins A1 enclosing CuP and forming a closed posterior cubital cell (cell cup). Vein CuA2 can be absent (1) (as in Figs. 2.70, 2.72, 2.74), leaving the cell cup open; or present, closing the cell cup (2) (as in Figs. 2.64, 2.65), the common condition. An open cell cup can be found in

Echidnocephalodes barbatus (incertae sedis), Asteiidae, Carnidae, many Periscelididae, some Neurochaetidae and some Teratomyzidae, and in Xenasteiidae (Papp 1998:307, Fig. 26.9).

85. (1.0). The anal cell (cup) is relatively squarely closed in most schizophorous Muscomorpha (1) but it has an angular point (2) in many Ulidiidae and in the Tephritidae (as in Fig. 2.78).

86. (0.5). Cell dm can either be flat (1) or have a crease or fold along its midline (2) (as in Fig. 2.70). State 2 is often correlated to a weakening of the anterior end of cell bm-cu, and was mentioned by Mathis and Papp (1992) as a synapomorphy for the Periscelididae. This state is also present in Odiniidae. In *Stenomicro*, *Cyamops* and *Planinasus* the fold is less conspicuous than in other Periscelididae.

87. (0.37). D. H. Vein A1 is very reduced in species of the families Asteiidae, *Geomyza tripunctata* Fallén and other Opomyzidae, some Neurochaetidae and in Xenasteiidae (1) (Papp 1998:306, Fig. 26.2). It is abbreviated, reaching only about halfway to the wing margin (2) (as in Figs. 2.64a, 2.66, 2.71) in most opomyzoid taxa and outgroups. A longer vein A1 that reaches the wing margin as a fold (3) is present in the Odiniidae, and some Clusiidae not included in this analysis (i.e. *Tetrameringia* and *Sobarocephala*). Vein A1 is long, reaching the wing margin (4), in Teratomyzidae (Fig. 2.73) and *Pterocalla* (Ulidiidae) (Fig. 2.78). Hennig (1971) based the monophyly of the Anthomyzoidea on the reduction of vein A1. D. K. McAlpine (1991) suggested that the reduction of vein A1 is one synapomorphy

uniting the Marginidae with Clusiidae and/or or Opomyzidae. In this study, a short vein A1 is present in several outgroup taxa and is judged plesiomorphic for the Opomyzoidea.

Legs. Characters from the legs have been seldom used in the higher taxonomy of acalyptrates.

88. (0.2). F. In the groups herein analyzed, the femora may be slender (1), the common condition, or robust (2), a feature unique to the Periscelididae *sensu stricto*, Neurochaetidae, and isolated outgroup taxa. J. F. McAlpine (1989:1455) grouped the Neurochaetidae, Periscelididae and Aulacigastridae based solely on state 2 of this character. In my observation, however, *Aulacigaster*, *Stenomicra*, *Cyamops* and *Planinasus* do not have as robust a femur as do Neurochaetidae, Periscelididae *sensu stricto*, *Diopsosoma prima* (Periscelididae) and *Carnus hemapterus* Nitzsch (Carnidae).

89. (1.0). A ctenidial spine is usually not differentiated (1). In some Opomyzidae, it is apparently present, but not the strongest femoral seta (2). It is differentiated and stronger than all other femoral setae in the Anthomyzidae, a synapomorphy for this family (3).

Male abdomen and terminalia

(Figs. 2.81-2.106)

For convenience, the abdomen is divided into the preabdomen, consisting of segments 1-5, and the postabdomen, starting at segment 6 (Fig. 2.81). The segments

of the preabdomen are not affected by the formation of the male genitalia. Griffiths (1972), and to a lesser extent J. F. McAlpine (1989), utilized characters of the male abdomen in their phylogenies.

90. (1.0). The abdomen of acalyptrates usually has tergites and sternites well sclerotized (1). A weakly sclerotized abdomen (2) occurs in *Asteia* (Asteiidae).

91. (0.66). In acalyptrates, the sternites are usually narrower than the tergites, leaving a membranous area on the ventral side of the abdomen (1) as in Figs. 2.82, 2.85. The sternites are very reduced, about one-eighth the width of the respective tergites, in *Somatia* (Somatiidae) (2) (Hennig 1958:622, Fig. 235). Large sternites that occupy most of the ventral portion of the abdomen (3) are present in the undescribed genus from Malaysia and Neurochaetidae (D.K. McAlpine 1978:287, Fig. 21).

92. (0.5). F. The abdominal spiracles 1-5 usually lie in the abdominal membrane (1). They are located at the margin of the tergite or on the tergite (2) in the Asteiidae (Sabrosky 1987:91, Fig. 78.9), Xenasteiidae (Papp 1998:307, Fig. 26.10) and many Teratomyzidae. J. F. McAlpine (1989, Fig. 116.5) considered this condition synapomorphic for the apical Asteioinea. In my analysis, it is a synapomorphy for Asteiidae *plus* Xenasteiidae, with an independent origin in *Teratomyza*.

93. (1.0). Tergite five is usually present and well sclerotized (1). The reduction of this tergite is an autapomorphy for the Neminidae (D.K. McAlpine

1983:72, Fig. 24) (2). This family also shows reduction in all tergites posterior to tergite five.

94. (1.0). When present, tergite five is most often free from sternite five (1). It is fused with sternite five, forming a complete ring (2), in some Chyromyidae.

95. (0.33). Tergite six is missing (1) in the Neminidae, among the ingroup taxa. All Opomyzidae and Tephritoidea also lack this tergite. Tergite six is usually present in the abdomen of male acalyptrates (2) (as in Figs. 2.81, 2.84).

96. (0.33). When present, tergite six may be free from the pregenital segment (1) (as in Fig. 2.84), a more generalized condition, or fused with the pregenital segment (2), a feature independently acquired by *Aulacigaster*, Xenasteiidae (Papp 1998: 306, Figs. 26.3-4) and Carnidae.

97. (0.33). F. G. Tergite six, when free, is as long as tergite 5 in *Psila rosae* (Psilidae) and Teratomyzidae (1), and slightly reduced in relation to tergite 5 (2) in most taxa herein studied. A further reduced tergite 6 is found in *Gymnochiromyia concolor* and some Chyromyidae, Anthomyzidae (Roháček 1998:270, Fig. 22.15) and Odiniidae (3). Griffiths (1972:191) ascribed a somewhat shortened 6th tergite (2/3 the length of 5th tergum) to the ground plan of the Anthomyzoinea, and J. F. McAlpine (1989:1456) considered this to be a plesiomorphic feature for Opomyzoidea, a view compatible with the results of this analysis.

98. (1.0). When present and free, tergite 6 may be symmetrical (1) or asymmetrical (2). Only *Neurocytta prisca* (Neurochaetidae) has state 2 of this character.

99. (1.0). Sternite 6 is usually present in acalyptrates (2) (as in Figs. 2.82, 2.85-2.86), but is often reduced in size and asymmetrical (see below). A complete reduction of sternite 6 (1) occurs in the Chyromyidae (Chyromyia). In *Chyromyia flava*, sternite 5 is the last sternite before the genital segment.

100. (0.2). F. G. Sternite 6 is large and rectangular (1) in the Teratomyzidae and Periscelididae *sensu stricto* (Fig. 2.86) among the ingroup taxa, *Echidnocephalodes barbatus* (*incertae sedis*) and *Psila*, among the outgroup taxa. It is reduced and asymmetrical, displaced towards the left side (2), in the ground plan of the Opomyzoidea and the Asteioinea. Some *Stenomicro* have sternite 6 secondarily symmetrical, and joined with the pregenital segment on both sides, forming a complete ring. Sternite 6 assumes many different shapes in the families herein considered, being often fused with sternites 7 and 8. I have not coded the various degrees of reduction/modification of this sternite or sternite complex into discrete states, because it would render the character nearly uninformative above the family level (almost every terminal taxon would be assigned a different state). J. F. McAlpine (1989:1503) considered the reduction of sternite 6 as a synapomorphy for a group of superfamilies containing the Lauxanioidea, Sciomyzoidea, Opomyzoidea, Carnoidea, Sphaeroceroidea, and Ephydroidea. According to Griffiths (1972:127), a symmetric sternite 6 is part of the ground plan of all schizophoran superfamilies with the exception of the Muscoidea.

101. (1.0). The pregenital sclerite is usually considered to result from the fusion of sternites 7 and 8, which have shifted dorsally as a result of circumversion.

It is usually free from the epandrium (1) but is partly fused with this sclerite (2) in the Chyromyidae (J. F. McAlpine 1987:986, Fig. 91.6,) and *Psila rosae* (Psilidae). It is reduced and closely associated with the epandrium (3) in *Pterocalla* (Ulidiidae).

102. (0.2). F. G. The pregenital segment extends ventrally on both sides of the abdomen, usually less than or at most as far as the previous tergite (1); in some taxa, it is elongate on both sides, enclosing the abdominal spiracle (2). This is the case for Periscelididae (Fig. 2.86), Teratomyzidae, *Echidnocephalodes barbatus* (incertae sedis), Psilidae, *Meoneura flaviceps* Collin (Carnidae) and some species of *Somatia* (Somatiidae).

Male terminalia (Figs. 2.81-2.106).—The homology between the structures of dipteran male genitalia has been a matter of controversy, and different hypotheses of character transformation for the male genitalic structures have been proposed. I follow the hypothesis of Cumming *et. al.* (1995) because it has been a trend among recent authors to follow their nomenclature, and because they have produced illustrations that I can understand. Regardless of which working hypothesis of character transformation I adopt, it is difficult to consistently recognize some of the genitalic structures in acalyprates, as they often become highly modified and further fused with other structures. Griffiths (1972) based most of his conclusions on characters of the male terminalia, and his phylogenetic system has been criticized for employing characters that are rather plastic, and therefore not appropriate for making phylogenetic inferences (Hennig 1971; D. K. McAlpine 1978; J. F. McAlpine 1989)

The apical portion of the male abdomen is rotated 360 degrees (circumverted). The anus and genital structures are restored to their original positions but the main internal ducts of the genital system, the nervous system and the tracheal system are twisted around the hindgut. In the Muscomorpha, the first 180 degrees of rotation occur in the vicinity of segment 8. Dragging of the sternites 6 and 7 into the left side is sometimes apparent (although Griffiths 1972, places the rotation between segment 8 and 9, and regards sternite 8 to be in the dorsal position). Sternite 7 and segment 8 become somewhat fused into a single syntergosternite that occupies a more or less dorsal position. The final rotation occurs between segments 8 and 9. Where the symmetry of segments 6 and 7 is observable, it is probably due to reversal (J. F. McAlpine 1989; but see Griffiths 1972).

103. (1.0). The epandrium is a saddle shaped sclerite that articulates ventrally with the internal male terminalia (Figs. 2.83, 2.835, 2.86-2.88). It is absent (1) in *Neurochaeta inversa* (Neurochaetidae) (D.K.McAlpine 1978:287, Figs. 20-21), an autapomorphy for this species. A fully developed epandrium is usually present in acalyptrates (2).

104. (1.0). The epandrium forms a ring around the genital segment in *Somatia* (2), a feature unique to this group.

105. (0.33) In the Muscoidea, the epandrium is usually closely associated with a pair of lateral appendages, the surstyli. The surstyli are (1) freely articulated with the epandrium (Figs. 2.83, 2.94) in the ground plan of the Opomyzoidea, but fusion with the latter has occurred many times within the group. The surstylus is only

partially fused with the epandrium (2) in the Chyromyidae, but completely so (3) (as in Figs. 2.87-2.88) in several groups I have analyzed. The surstylus is fused with an inner sheath of the epandrium (4) in the bromeliad species of *Aulacigaster* (see chapter 2 above). This character is usually constant within opomyzoid families, but varies within Agromyzidae. According to one hypothesis for genitalic evolution, the surstylus functions as an aid to overcome morphological or behavioral female resistance. However, a study by Eberhard (2001) in Sepsidae suggests that the male surstyli evolved to function as courtship devices. Males of *Microsepsis eberhardi* and *M. armillata* use their genitalic surstyli to rhythmically squeeze the female's abdomen with stereotyped movements during copulation.

106. (0.5). The hypandrium is the main sclerite of the male internal terminalia. It is often U-shaped or some variation thereof, and its lateral arms articulate ventrally with the epandrium. Within the Opomyzoidea, the hypandrium assumes diverse forms. The anterior portion is often well sclerotized (1) (Figs. 2.97, 2.97, 2.98-2.99, 2.102, 2.106), but it is poorly sclerotized (2) in the Opomyzidae and Aulacigastridae (as in Fig. 2.89).

107. (1.0). The lateral arm of the hypandrium is elongate (2) in *Traginops irroratus* Coquillett (Odiniidae) (J. F. McAlpine 1987:865, Fig. 72.4) and, to a lesser extent, in other Odiniidae and some Agromyzidae (Spencer 1987:874, Fig. 73.15).

108. (1.0). The hypandrium is often open posteriorly (as in Figs. 2.96-2.97, 2.99). The lateral hypandrial arm either ends at the point of articulation with the epandrium or it extends posteriorly, forming a complex with the pregonite (1). When

the hypandrium is closed posteriorly, forming a ring around the base of the aedeagus, it is sometimes said to have a hypandrial bridge (2) (as in Figs. 2.89, 2.90, 2.105). A closed hypandrium is present in the Clusiidae (Soós 1987:856, Fig. 70.8), the undescribed genus from Malaysia, Anthomyzidae (Roháček 1998:270, Fig. 22.19), Opomyzidae (Vockeroth 1987:884, Fig. 74.10) and Aulacigastridae. It also occurs in other acalyptrate families, sometimes receiving other names. J. F. McAlpine (1989:1456) considered the absence of a hypandrial bridge synapomorphic for the Opomyzoidea, and the presence of a hypandrial bridge as a secondary acquisition.

109. (0.5). The hypandrial bridge may occur dorsal to the base of the aedeagus (1) (as in Fig. 2.89), or posterior to it (2) (as in Fig. 2.105). The first state occurs in the Clusiidae (Soós 1987:856, Fig. 70.8), the undescribed genus from Malaysia and Anthomyzidae (Roháček 1998:270, Fig. 22.19), and is morphologically similar to the hypandrial bridge that occurs in some Carnoidea. The hypandrial bridge characteristic of Opomyzidae and Aulacigastridae (Fig. 2.89), however, is distinct. It is formed by a dorsal expansion of the hypandrial arm that is closely connected to the basiphallus and the subepandrial sclerite dorsal to the base of the aedeagus. Roháček (1998) and J. F. McAlpine (1989:1455, Fig. 116.5) mentioned a connection between the hypandrial bridge and the phallapodeme in the Anthomyzidae and Opomyzidae that would be synapomorphic for both families. I do not see the condition present in the Anthomyzidae as morphologically similar to that present in the Opomyzidae.

110. (0.5). The pregonite is located anterior to the postgonite, connected to the lateral arm of the hypandrium (as in Figs. 2.89-2.90). The phallus lies internal to the hypandrium and connects laterally to the postgonite. The pregonite is plate-like and partly fused with the posterior internal portion of the hypandrial arm (1) in *Planinasus* (Fig. 2.99). It is fused with the postero lateral portion of the hypandrial arm (2) in most taxa I have analyzed (as in Figs. 2.87-2.93, 2.95-2.97, 2.102, 2.105).

111. (0.5). The pregonite bears an anterior apodeme (2) in *Aulacigaster* and in *Geomyza tripunctata* (Opomyzidae) (Vockeroth 1987: 884, Fig. 74.10), apparently due to independent evolution.

112. (1.0). The posterior arm of the hypandrium and fused pregonite are usually free from the base of the phallus (1), but they may extend posteriorly and bear a close connection with the phallus ventrally (2). This state is present in the Xenasteiidae. The posterior arm of the hypandrium is further attached to the bases of the phallus forming a closed ring (3) in *Stenomicroa*.

113. (0.5). The phallapodeme lies dorsal to the anterior portion of the hypandrium and connects with the phallus postero ventrally. The phallapodeme can be free, a condition referred to as cuneiform (1), or it can be connected to or extensively fused with the median internal surface of the hypandrium anteriorly (2). It can become further fused with the hypandrium to form a pouch- or sac-like structure (3), or become totally fused with the hypandrium and no longer recognizable (4). The first condition is the most common in acalyptrates, as well as in the Asteioinea. The second condition is present in Opomyzidae (Vockeroth 1987:

884, Fig. 74.10), Odiniidae (J.F.McAlpine 1987:865, Fig. 72.4), and *Auster*. The third condition is present in the Periscelididae *senus stricto* (Fig. 2.101), Psilidae (Fig. 2.101), Somatiidae. State 4 is present in *Teratomyza*.

114. (0.33). G. The posterior portion of the phallapodeme attaches to the base of the phallus. It is rod-like and simple (1) in many groups herein considered; it is bifurcate (2) in several families. In *Aulacigaster* (Fig. 2.99), it projects ventrally on both sides, shielding the aedeagus (3). This condition, first mentioned by Griffiths (1972:212), is synapomorphic for the genus. A similar shape is present in some *Stenomicro* (Fig. 2.91) and *Cyamops nebulosus* Melander (Fig. 2.96). In *Psila* (2.106), the aedeagal apodeme is broad, ill defined and excavated posteriorly (4), a condition unique to this genus. In *Echidnocephalodes barbatus* (incertae sedis) the posterior portion of the phallapodeme expands dorsally both sides, anchoring the hypandrial arms (5).

115. (0.33). The ejaculatory apodeme is usually present in acalyptrates (1) (as in Fig. 2.101). It is very reduced to absent (2), apparently by independent derivation, in the families Psilidae, Neminidae and Odiniidae. The ejaculatory apodeme serves for insertion of the muscles that act on the sperm pump.

116. (0.63). The phallus is the male's median phallic organ, and is closely associated with a dorsal apodeme (phallapodeme), which provides an attachment basis for abdominal muscles associated with exertion of the aedeagus and ejaculation. It assumes various forms within the group herein considered. Flies of the family Periscelididae have a long ribbon-like distiphallus (1) (Fig. 2.101). A similar

condition is found in *Somatia* and *Psila* (Fig. 2.106). The distiphallus is membranous and long, and branched distally in the Clusiidae (2) (Soós 1987:856, Fig. 70.8, 70.9). A ribbon-like distiphallus that is long and coiled is found in *P. ocellata* (Fig. 2.102) and all Tephritoidea (3). The distiphallus is relatively membranous and bears two internal rod-like sclerites, being minutely haired and resembling a brush apically in the Aulacigastridae and the undescribed genus from Malaysia (4) (Fig. 2.105). Although the aedeagus of *Echidnocephalodes barbatus* (*incertae sedis*) has a somewhat different shape, I have coded it as having this state because it also bears the internal rod-like sclerites. In Carnidae, the aedeagus is relatively membranous, wide, and hairy (5) (Sabrosky 1987:911, Figs. 80.7, 80.8). It is short and membranous (6) in Xenasteiidae, *Stenomicroa*, Odiniidae, and *Planinasus*. In the Neminidae, the distiphallus is extremely developed, asymmetrically curved, and often bears spines and thorns (7) (Freidberg 1994:477, Fig. 14). It is short to medium sized and bears complex apical sclerotization in Asteiidae, *Cyamops* (Fig. 2.95-2.96), Chyromyidae (J.F.McAlpine 1987:986, Figs. 91.6, 91.7), and Opomyzidae (8) (Vockeroth 1987:884, Fig. 74.10, 74.11).

117. I have homologized the “ventrally oriented, slender process at the ventral margin of the epandrium between the surstylus and the cerci” of Mathis and Papp (1992:371, Fig. 2), which occurs in *Periscelis* and *Parascutpos* (Periscelididae), with the subepandrial sclerite of other taxa. Although it is slightly modified to have a ventral process in some *Periscelis* (Fig. 2.101) and in *P. maculipennis*, this structure occurs in the same place as the subepandrial sclerite

(*processus longi*) of *Planinasus* (Fig. 2.99) and Psilidae (Fig. 2.106). In some *Periscelis*, it bears no ventral process and can be partly to completely fused with the anterior arm of the hypandrium.

118. (0.5). The subepandrial sclerite occurs primitively as a single plate that joins the posterior arms of the hypandrium with the inner margins of the surstyli laterally, and with the cerci posteriorly. Commonly it is divided throughout the order. In the Eremoneura, the subepandrial sclerite is modified laterally into two slender processes that extend to the outer apical margins of epandrium, or to the surstyli (Cumming *et al.*, 1995). In this condition, the subepandrial sclerite is often referred to as the *processus longi*. The subepandrial sclerite is absent (1) in the periscelidid genus *Neoscutops*, *Somatia*, and *Pterocalla*. In *Pterocalla*, the cerci are fused apically and bear close connection with an internal process of the surstylus. The subepandrial sclerite is present (2) (Figs. 2.99, 2.102-2.106) in all other groups, although mostly unsclerotized in *Cyamops* (Fig. 2.106).

119. (0.28). The subepandrial sclerite is a single, narrow plate connecting the hypandrial bridge (or the posterior portion of the hypandrium and fused pregonites, when a hypandrial bridge is absent) with the cerci posteriorly, and with the surstylus ventrally (1) in many Opomyzoidea (as in Figs. 2.89, 2.90). Such a plate is present in flies that have a closed or nearly closed hypandrium. In *Stenomicra*, the subepandrial sclerite is divided into 4 plates. I have interpreted this condition as a further modification of, and homologous to, state 1. A pair of sclerites connects the posterior arms of the hypandrium with the surstylus (2) in *Psila* (contra Griffiths

1972:124) (Fig. 2.106) and *Planinasus* (Fig. 2.99), and also in *Cyamops* (Fig. 2.96), where it is very weakly sclerotized. I have interpreted the "ventrally oriented process articulated with cercus and surstylus" of Mathis and Papp (1992:371) that occurs in *Periscelis* and *Parascutops*, as homologous to these sclerites (see character 17) (Fig. 2.101). A large plate postero-dorsal to the base of the aedeagus connects the posterior portion of the hypandrial arm with the cerci posteriorly and the surstylus ventrally in *Leiomyza*, *Teratomyza*, *Nemula longarista* (Neminidae), Xenasteiidae, Odiniidae, and Chyromyidae (3).

Female abdomen and terminalia

(Figs. 2.)

120.(1.0). The abdominal tergite 5 (female) is usually large and rectangular (1). It is modified, reduced (2) in the Neminidae (D.K. McAlpine 1983:67, Fig. 18).

121. (1.0). Segment 6 (female abdomen) is either present (1), the common condition, or absent (2), which is the case in *Gymnochiromyia concolor* (Chyromyidae).

122. (1.0). Sternite 6 (female abdomen) is most often free from tergite 6 (1). Fusion of sternite 6 with tergite 6 (2), forming a ring, is synapomorphic for the genus *Cyamops* (Fig. 2.107).

123. (0.4). F. Sternite 7 (female abdomen) is most often free from tergite 7 (1). It is fused with tergite 7, forming a ring (2), in some species of *Cyamops* (Fig. 2.107) though not in the Australian species, and in *Stenomicro*, Periscelididae *sensu stricto* (Fig. 2.108), and Somatiidae (Hennig 1958:623, Fig. 241). In Teratomyzidae,

Auster (AU) and *Pous* (AU) have tergite and sternite separate, whereas *Teratomyza* and *Camur* have the tergite and sternite fused. J. F. McAlpine (1989) used this character to support the monophyly of Periscelididae *plus* Aulacigastridae.

124. (0.5). H. F. The spermathecae vary in number from two to four in the groups herein concerned, with the exception of the Psilidae, which lack sclerotized spermathecae. Two spermathecae are present in most outgroup taxa (but not in *Pterocalla ocellata*, Ulidiidae), and most ingroup taxa. The Aulacigastridae and Periscelidinae (Periscelididae) have 3 spermathecae. Within *Cyamops* (Periscelididae) 2-4 spermathecae occur. J. F. McAlpine (1989: 1456) considered the presence of two spermathecae to be an autapomorphy for several subgroups within the Opomyzoidea; this assumes that three spermathecae is the plesiomorphic state and that the appearance of a spermatheca *de novo* is unlikely. According to my analysis, two spermathecae is the plesiomorphic state for the Opomyzoidea, and the re-appearance of one spermatheca must be postulated for the opomyzoid taxa mentioned above. Multiple spermathecae in Diptera are thought to have evolved within the context of cryptic female choice and enable females to better control the paternity of their offspring (Ward 1993). The spermathecae are more or less spherical or cylindrical, usually well sclerotized receptacles in which the spermatozoa are stored and from which the spermatozoa are released onto the eggs, as they are passed from the oviduct.

Phylogenetic analysis

The optimal trees resulting under the six combinations of character coding and

weighting methods are shown in Figures 2.9-2.10 and characterized in [Table 2.4](#)

The degree of phylogeny resolution varies considerably among analyses, and shows two trends. First, resolution was generally higher when phylogenetic orderings among character states were taken into account. For example, under unweighted parsimony, treating characters as unordered resulted in 4119 most parsimonious (MP) trees, the strict consensus of which resolved only 16 groups of 47 possible, all at the level of family, genus, or below. Inclusion of character orderings reduced the number of MP trees to 110, resolving 36 groups at a wide range of levels (Fig. 3.109-3.111). For a given type of character weighting, the additional groups resolved by character state orderings are generally not in conflict with those supported by unordered characters, suggesting that the orderings reflect additional phylogenetic signal; several exceptions to this generalization are discussed below.

Second, resolution was increased, for a given type of character coding, by weighting against homoplasious characters. For example, for ordered characters, unweighted parsimony resolved 36 groups (110 optimal trees), while successive weighting (18 optimal trees) and Goloboff weighting (4 optimal trees) both resolved 44 groups. With exceptions to be noted, the additional groups resolved by increased weighting against homoplasious characters are generally compatible with those supported by unweighted parsimony, suggesting that such weighting, like character ordering, amplifies phylogenetic signal in this data set. These two effects on phylogeny resolution appear non-independent and possibly interchangeable: the degree of increase in resolution with character ordering seems to vary inversely with

the degree of weighting against homoplasious characters. It is dramatic for unweighted parsimony, modest for successive weighting, and non-existent under Goloboff weighting.

The major features of the phylogeny collectively supported by these analyses are as follows. At the lowest level, all of the genera and families represented by more than one exemplar are recovered. At the highest level, the Opomyzoidea *sensu* J. F. McAlpine (1989) are generally monophyletic (but see below), with the exception that the Odiniidae are invariably separated from the remaining opomyzoids by several outgroup nodes. The outgroup consistently nearest the Opomyzoidea, on my rooting, is Sphaeroceroidea. Within Opomyzoidea, the two supra-families represented by multiple families, Opomyzoinea and Asteioinea, are generally recovered (but see below), and Opomyzoinea are consistently grouped with Asteioinea *plus* Marginidae.

Two departures from the foregoing generalizations, each unique to a single analysis, deserve mention. When characters are ordered but unweighted, the Carnidae fall within the Asteioinea, as sister group to the Neminidae (Fig. 3.111). In all other analyses, they are placed outside the Opomyzoidea, either as sister group to the Diopsoidea (Figs. 3.109-3.110) or as sister-group to the Chyromyidae + Opomyzoidea (Fig. 3.110). When implied weighting is applied to unordered characters, the Anthomyzidae become the sister group to Aulacigastridae (Fig. 3.109); in all other analyses, they fall outside the Asteioinea.

Within Asteioinea, Asteidae + Xenasteidae are consistently grouped with

Aulacigastridae and *Echidnocephalodes barbatus*, and Neminidae + Neurochaetidae + Periscelididae are consistently grouped together, except when character weights are equal (Figs. 3.11). The Teratomyzidae is consistently basal to the remaining asteioid families, except when characters are unordered, in which case the family is the sister-group of (Neminidae + (Neurochaetidae + Periscelididae)). Neither placement for the family is consistent with other proposals. J. F. McAlpine (1989) grouped the Teratomyzidae with the Asteiidae + Xenasteiidae, whereas Griffiths (1972) grouped them with the Periscelididae, Psilidae, and Nothybidae in the superfamily "Nothyboidea," far removed from the opomyzoid families of J. F. McAlpine (1989).

In my analyses, both character state ordering and weighting against apparent homoplasy (i.e., disagreement with other characters) appeared to enhance phylogenetic signal, providing increased tree resolution that was generally compatible with groupings supported without such ordering or weighting. I therefore place most credence in, and center my discussion on, the (identical) trees found using both character ordering and successive or implied weighting (Fig 3.112).

Opomyzoidea: Monophyly and composition

The Opomyzoidea *sensu* J.F. McAlpine (1989) were not strictly monophyletic in my analyses, in that the Odiniidae, representing the Agromyzoinea of that author, were consistently placed among the outgroup superfamilies. However, the remaining Opomyzoidea in my taxon sample, with exceptions as noted, invariably formed a group excluding the other superfamilies represented. This modified concept of

Opomyzoidea is supported by two unambiguous (albeit homoplasious) synapomorphies, both present in Marginidae but not in Odiniidae. These are a concave rather than flat occipital region (character 1, state 2; Figs. 2.5, 2.6), and the presence of a raised ridge on the anepisternum (character 53, state 2; Fig. 2.61).

Exclusion of the Odiniidae from Opomyzoidea, though contrary to J. F. McAlpine, is consistent with other proposals. Hennig (1971) placed the Odiniidae in his Agromyzoidea (Agromyzidae + Anthomyzidae), while Griffiths (1972) classified Odiniidae in the prefamily Tephritoinea, superfamily Muscoidea, a placement consistent with one rooting of my cladograms (Figs. 2.112). The inclusion of Marginidae among the Opomyzoidea conforms to a tentative proposal by D.K. McAlpine (1991; see Table 2.1). The presence of the anterior katepisternal seta (character 57, state 1; Fig. 2.49) and vein R2+3 short (character 75, state 2; Fig. 64a) support a sister-group relationship between the Marginidae and the Asteioinea (Fig.2.112).

Neither of the other proposed emendations to Opomyzoidea that I tested were upheld by my analysis. My trees favor the placement of the aberrant genus *Somatia* next to Psilidae (Diopsoidea) (Fig.2.112), well outside Opomyzoidea (J. F. McAlpine 1989), as opposed to the alliance with Periscelididae postulated by Griffiths (1972). The synapomorphies for Periscelididae and *Somatia* cited by Griffiths (1972:122), which lie mostly in the male and female postabdomen and terminalia, were not corroborated by the present analysis. However, my results should not be taken as the final statement on the phylogenetic position of this enigmatic genus. These flies are

bee mimics, with very autapomorphic external morphology. The male terminalia are also highly divergent, making the sclerites difficult to homologize with those of other acalyptrates. What I can say with some assurance is that *Somatia* lacks the apparent synapomorphies for both the Opomyzoidea and the Asteioinea (see below), and should therefore be classified outside these groups unless future evidence overrules those characters. Regarding Chyromyidae (Fig.2.112), my analysis finds no support for the close relationship to several opomyzoid taxa proposed by Hennig 1971; see Table 2.1) or the sister-group relationship with Aulacigastridae proposed by Griffiths (1972). This family, like *Somatia*, lacks the apparent synapomorphies of both Opomyzoidea and Asteoinea. However, Chyromyidae was invariably the sister group to Opomyzoidea as a whole in my trees, leaving a close relationship of this family (or Sphaeroceroidea as a whole, other families of which were not sampled) to Opomyzoidea quite plausible. The Chyromyidae have the antero-ventral ommatidia of the eye enlarged (character 6, state 1; as in Fig. 2.15a-b), a synapomorphy with the Opomyzoidea. The Carnoidea had been postulated to be closely related to Opomyzoidea by several authors including J. F. McAlpine (1989), who grouped these families citing the shared presence of two spermathecae (character 122, state 2) and a pilose basisternum (character 49, state 1). These synapomorphies were not supported by my analysis, which grouped Carnidae with the diopsoid families Somatiidae and Psilidae instead.

Asteioinea: monophyly and internal phylogenetic structure

The Asteioinea in my taxon sample, with exceptions as noted, invariably

formed a group excluding the other opomyzoid taxa. The clade is supported by two unambiguous (albeit homoplasious) synapomorphies (Fig. 3.112; Table 3.6). These are a face completely sclerotized (character 12, state 1; as in Fig. 2.13-2.15a-b) and the absence of posterior anepisternal setae.

Although monophyly of Asteioinea is supported by my analysis, the two main clades (Fig. 3.112) into which these families divide contrast sharply with the groupings proposed by J. F. McAlpine (Fig. 2.1). In my results, the Asteiidae, Xenasteiidae, Aulacigastridae and *Echidnocephalodes barbatus* are grouped together by four unambiguous (albeit homoplasious) synapomorphies: the presence of a wide basisternum (character 48, state 1; Figs. 2.57, 2.58); a reduced number of acrostical setulae (character 64, state 1; Fig. 2.3); the position of crossvein r-m, well below middle of discal cell (character 83, state 1; Figs. 2.6a, 2.65a); and the fusion of the surstylus with the epandrium (character 105, state 3; Figs. 2.88). Within this clade, a sister group relationship between families Asteiidae and Xenasteiidae, advocated by several previous authors (Hardy 1980; J.F.McAlpine 1989), is supported by four unambiguous synapomorphies (Fig. 3.112; Table 3.6), including secondary de-sclerotization of the midline of the face (character 12, state 2) and an extreme reduction in the length of vein A1 (character 2, state 1). Species of Asteiidae and Xenasteiidae (like some *Stenomicro* and some Neminidae) are small compared to other Asteioinea, and share other features often found in small flies, such as reductions in the wing venation and body chaetotaxy, and de-sclerotization of body parts.

My analysis also corroborates the suggestion of Roháček (1998) that *Echidnocephalodes barbatus* lies close to Aulacigastridae. This species has a completely sclerotized face, consistent with placement in Asteoinea (Fig. 3.112; Table 3.6). One unambiguous, non-homoplasious synapomorphy with the Aulacigastridae is the shape of the aedeagus (character 116, state 4; Fig. 2.105).

Monophyly for the genus *Aulacigaster* is strongly supported (bootstrap = 94%), as is its sister group relationship to an undescribed taxon from Malaysia (bootstrap = 90%). I propose the inclusion of the Malaysian taxon, to be described as a new genus in a subsequent publication, in the family Aulacigastridae. Aulacigastridae thus defined is supported by eight unambiguous (albeit homoplasious) synapomorphies (Fig. 3.112; Table 3.6).

The second major clade of Asteoinea in my analyses consists of Neminidae + (Periscelididae + Neurochaetidae). This grouping is supported by one unambiguous synapomorphy: the occipital region is entirely concave, following anterior curvature of the thorax (character 1, state 3; Figs. 2.3-2.4). This state appears to have arisen independently in *Xenasteia palauensis*, but is otherwise absent in all other Asteoinea and outgroup taxa examined. This is the first proposal of a synapomorphy linking Neminidae with other families of Asteoinea.

Corroborating a proposal by Grimaldi and Mathis (1993), the Periscelididae *sensu* D. K. McAlpine (1983) were recovered as the sister-group of the Neurochaetidae. The two families share one non-homoplasious synapomorphy, the type of articulation between the pedicel and the 1st flagellomere (character 37, state

2). Two other (homoplasious) synapomorphies, the presence of a weak ocellar seta (character 24, state 1), and the reduction of the palpus (character 47, state 2; Fig. 2.48), also support this pairing. The separation of Periscelididae from Aulacigastridae conflicts with J. F. McAlpine's (1989) suggestion that these two families, and possibly Neurochaetidae, form a monophyletic group. McAlpine based this conclusion primarily on the presence of robust femora; my interpretation of this feature (see character 88, in the morphology section, for a different interpretation of this character) is very different from that of McAlpine.

The Periscelididae (Fig.2.112) in my analysis include *Diopsosoma* and are supported by 5 unambiguous (albeit homoplasious) synapomorphies (Fig. 3.112; Table 3.6), including the presence of a greater ampulla (character, 1 state 2; Fig. 2.61). This character was used by J.F.McAlpine (1989) to unite Periscelididae with Aulacigastridae. In my analyses, however, the greater ampulla is inferred to have arisen twice within Opomyzoidea and independently in one outgroup as well (Psilidae; Fig. 2.23).

Character performance and previous phylogenies

An inescapable feature of the present study is that support for most groupings is limited by extensive homoplasy. For this reason, most of the conclusions reached here must be regarded as provisional. Previous studies of these flies may have arrived at seemingly more reliable groupings because they contained hidden assumptions about character evolution, employed tacit *a priori* character selection or weighting, and scored higher taxa using hypothetical ground-plans. This study, in

contrast, attempted to use all available characters that vary among families, and weighted characters only objectively and *a posteriori*, on the basis of their agreement with other characters. Almost 2/3 of the characters included in this analysis had a consistency index (CI) of 0.5 or less. Only 22% of the characters were free of apparent homoplasy, and of these seemingly reliable characters, very few (0.08%) supported groupings above the family level. Therefore, a well supported phylogeny of the Opomyzoidea, based on morphological characters that are all "reliable" or non-homoplasious is not likely to happen in the near future, unless one purposely ignores a great deal of evidence. As pointed by others (Yeates & Wiegmann 1999) definitive resolution of acalyprate phylogeny will undoubtedly require exploration of new character systems, including DNA sequences.

Table 2.1.—Composition of the "Opomyzoidea" according to different authors. The original name of the superfamily (or prefamily) is given below the author's name. The families considered to belong in the "Opomyzoidea," according to each author, are marked with an "X." A "*" indicates that the family was not described at the time. Literature references as follows: Hennig (1971), Griffiths (1972), J. F. McAlpine (1989) and Colless and D. K. McAlpine (1991).

Author Group name	Hennig (Anthomyzoidea)	Griffiths (Anthomyzoinea)	J. F. McAlpine (Opomyzoidea)	Colless and D. K. McAlpine (Opomyzoidea)
<hr/>				
\Family				
Acartophthalmidae	X		X	X
Agromyzidae			X	X
Asteiidae	X	X	X	
Anthomyzidae	X	X	X	
Aulacigastridae	X ¹	X ²	X ¹	
Carnidae				X
Chyromyidae	X	X		
Clusiidae	X		X	X
Fergusonidae			X	X
Heleomyzidae		X		
Neurochaetidae	*	*	X	
Oдиниidae			X	X
Opomyzidae	X	X	X	X
Periscelididae	X		X	
Rhinotoridae		X		
Sphaeroceridae		X		
Teratomyzidae	X		X	
Tricoscelididae		X		
Xenasteiidae	*	*		X

¹ Includes Cyamops, Stenomicro and Planinasus. ² Includes Cyamops and Planinasus.

Table 2.2.–Composition of the "Asteioidea" according to different authors. The families considered to belong in the "Asteioidea," according to each author, are marked with an "X." The original name of the superfamily (or prefamily) is given below the author's name. The families considered to belong in the "Opomyzoidea," according to each author, are marked with an "X." A "*" indicates that the family was not described at the time. Hennig (1971), Griffiths (1972), J. F. McAlpine (1989) and Colless and D. K. McAlpine (1991).

Author Group name /Family	Hennig (Periscelidea, Anthomyzoidea)	J. F. McAlpine (Asteioinea, Opomyzoidea)	Colless and D. K. McAlpine (Asteioidea)
Asteiidae	X	X	
Anthomyzidae			X
Aulacigastridae	X ¹	X ¹	X ³
Neurochaetidae		X	X
Periscelididae	X	X	X
Teratomyzidae	X	X	X
Xenasteiidae		X	

¹ Includes Cyamops, Stenomicroa and Planinasus. ³Includes Ningulus and Nemo.

Table 2.3.—Species used in the phylogenetic analysis, their distribution, and classification according to J. F. McAlpine (1989). The distribution of the family to which the species belongs is also given. Abbreviations: AT = Afrotropical region; AU = Australian region; Ne = Nearctic region; NT = Neotropical region; OR = Oriental region; PA = Palearctic region.

Family	Species	Classification (J. F. McAlpine)	Distribution (Family)	Distribution (species)			
Asteiidae	<i>Asteia amoena</i>	Opomyzoidea (Asteioinea)	Worldwide	PA			
	<i>Leiomyza curvinervis</i>			NE			
Aulacigastridae	<i>Aulacigaster mcalpinei</i>		PA, NE, NT, AT	NE			
	<i>A. leucopeza</i>			PA			
	<i>A. bromeliae</i>			NT			
	<i>A. minuta</i>			NT			
	<i>A. plesiomorphica</i>			NT			
	<i>A. equadoriensis</i>			NT			
	<i>A. femorata</i>			NT			
Periscelididae	<i>Periscelis flinti</i>		Worldwide	NT			
	<i>Parascutops maculipennis</i>			NT			
	<i>Planinasus ambiguous</i>			NT			
	<i>P. venezuelensis</i>			NT			
	<i>Stenomicra sp.a,</i> <i>undescribed species</i>			NT			
	<i>Stenomicra sp.b,</i> <i>undescribed species</i>			NT			
	<i>Cyamops micronesicus</i>			OC			
	<i>Cyamops nebulosus</i>			NE			
	<i>C. americanus</i>			NT			
	<i>Cyamops sp. (fossil)</i>			Baltic Amber			
	Neminidae			<i>Nemo corticeus</i>			AU, OC, AT
				<i>Ningulus simatus</i>			AT
				<i>Nemula longarista</i>			OR
Neurochaetidae	<i>Neurochaeta inversa</i>		AU, AT	AU			
	<i>Neurocytta prisca</i>			AT			
	<i>Neurotaxis charis</i>			AT			
Xenasteiidae	<i>Xenasteia palauensis</i>						
	<i>Xenasteia shalam</i>						

Table 2.3.—(continuation)

Family	Species	Superfamily (Suprafamily)	Family distribution	Species distribution
Anthomyzidae	<i>Anthomyza gracilis</i>	Opomyzoidea (Opomyzoinea)	Worldwide	PA, NE
	<i>Mumetopia terminalis</i>			
Opomyzidae	<i>Anomalochaeta</i>		PA, NE, AT	PA, NE
	<i>guttipennis</i>			PA
	<i>Geomyza tripunctata</i>			PA
	<i>Opomyza florum</i>			
Clusiidae	<i>Chaetoclusia bakeri</i>	(Clusioinea)	Worldwide	NT
	<i>Clusia lateralis</i>			NE
	<i>Clusiodes atra</i>			NE
Marginidae	<i>Margo clausa</i>		AT	AT
Odiniidae	<i>Odinia</i> sp.	(Agromyzoinea)	Worldwide	NE
	<i>Traginops irroratus</i>			NE
Unplaced	Gen. sp. Malaysia	Opomyzoidea ?	Malaysia	Malaysia
	<i>Diopsosoma prima</i>		NT	NT
	<i>Echidnocephalodes</i>		PA	PA
	<i>barbatus</i>			
Chyromyidae	<i>Chyromya flava</i>	Sphaeroceroidea	AT NE PA OR	PA NE
	<i>Gymnochiromyia concolor</i>			NE
Carnidae	<i>Carnus hemapterus</i>	Carnoidea	PA, NE	PA NE
	<i>Meoneura flaviceps</i>			
Ulidiidae	<i>Pterocalla ocellata</i>	Tephritoidea	Worldwide	NT
Psilidae	<i>Psila rosae</i>	Diopsoidea	AT NE PA OR	PA
Somatiidae	<i>Somatia aestiva</i>		NT	NT

Table 2.4.—Summary of the results of six analyses performed with combinations of heuristic search settings, character ordering and weighting schemes. The numbers on top refer to the analysis, 1-6.

Reference	1	2	3	4	5	6
Characters ordered	Y	N	Y	Y	N	N
Trees held			25	25	25	25
Steepest			Y	Y	Y	Y
Successive weighting	N	N	N	Y	N	Y
Cladograms	4	4	110	18	4419	37
Islands	1	1	13	9	41	21
G-fit	-67.4	-67.83	—	—	—	—
Steps	544	543-544	539	129.28	531	130.69
CI	0.32	0.32	0.32	0.5	0.33	0.57
RI	0.63	0.63	0.65	0.77	0.65	0.78

Table 2.5.–List of characters.

Head coloration, investiture and morphology:

1. Shape of occipital region: 1. nearly flat to slightly concave; 2. with posterior occipital sclerite obviously concave; 3. concave, following anterior curvature of thorax.
2. Shape of vertex, between compound eyes: 1. straight; 2. excavated, V-shaped ; 3. excavated, U-shaped.
3. Articulation between vertex and occipital sclerite: 1. angulated ; 2. a sharp ridge.
4. Microtomentose band on occiput, adjacent to the posterior margin of compound eye: 1. absent; 2. present.
5. Frontal margin of the eyes: 1. closer together at lower edge of frons; 2. subparallel; 3. converging towards apex.
6. Anteroventral ommatidia (relative size): 1. same size as remaining ommatidia; 2. larger than remaining ommatidia.
7. Anteroventral ommatidia (sexual dimorphism): 1. encroaching on facial to the same extent in both sexes; 2. encroaching more extensively on male than on female facial.
8. Sclerotization of mesofrons: 1. homogeneously sclerotized; 2. depressed, concave on midline; 3. slightly depressed between ptilinal fissure and lower ocellus; 4. depressed between fronto-orbital plates; 5. depressed between fronto-orbital plates and the large ocellar plate.
9. Coloration of lower frons: 1. concolorous with the rest of the frons; 2. pale yellow along anterior margin; 3. yellow on lower 1/3-2/3; 4. orange on lower 1/3-2/3.
10. Shape of ocellar plate: 1. not projected forward; 2. projected forward.
11. Presence of parafacial-genal suture: 1. differentiated; 2. not differentiated.
12. Sclerotization of face: 1. homogeneous; 2. weak on midline; 3. weak laterally, midline well sclerotized; 4. weak throughout; 5. face with two grooves to house the antennae, sunk in the middle.
13. Shape of face (when sclerotized): 1. nearly flat, not visible from lateral view; 2. convex, bowed, visible from lateral view.

14. Microtomentum coverage of face: 1. not forming a microtomentose band; 2. forming a microtomentose band at vibrissal angle.
15. Lateral borders of the peri-buccal cavity: 1. formed by ventro lateral extensions of the mesofacial plate, distinct from the parafacial-genal region; 2. formed by the parafacial-genal region, the ventro lateral extensions of the mesofacialia retracted inside the oral cavity.
16. Presence of inner vertical seta: 1. absent; 2. present.
17. Inclination of inner vertical seta: 1. erect; 2. proclinate.
18. Row of divergent setae from ocellus to vertex: 1. absent; 2. present.
19. Presence of postocellar seta: 1. absent; 2. present.
20. Position of postocellar seta: 1. right behind ocellar triangle, anterior to apex of vertex; 2. posterior to apex of vertex.
21. Development of postocellar seta: 1. reduced, hair-like; 2. well-developed.
22. Orientation of postocellar seta: 1. convergent; 2. parallel; 3. divergent.
23. Presence of lateral ocellar seta: 1. absent; 2. present.
24. Presence of ocellar seta: 1. absent; 2. present.
25. Development of ocellar seta: 1. reduced; 2. well-developed.
26. Number of fronto-orbital setae: 1. 1; 2. 2; 3. 3; 4. 4; 5. 5; 6. 6, very reduced; 7. 2 well developed, 7-10 weak setae; 8. about 10, reduced.
27. Inclination of upper fronto-orbital seta: 1. latero-clinate; 2. reclinate.
28. Relative position of fronto-orbital setae: 1. vertically aligned; 2. almost transversely aligned, anterior seta more internal; 3. transversely aligned; 4. almost transversely aligned, posterior seta more internal. USERTYPE (CSTREE) = (2, (3 4) 1).
29. Presence of intrafrontal setae: 1. absent; 2. present.

- 30. Orientation of intrafrontal setae: 1. convergent and directed anteriorly; 2. parallel and reclinate.
- 31. Presence of pseudovibrissa: 1. absent; 2. present.
- 32. Peristomal vestiture: 1. with a well-differentiated row of setae; 2. setose but without a differentiated row of setae; 3. bare of setae.
- 33. Additional row of peristomal setae: 1. absent; 2. present.
- 34. Presence of mesofacial setae: 1. absent; 2. present.
- 35. Presence of supracervical setae: 1. absent; 2. present.

Head appendages:

- 36. Arrangement of supracervical setae: 1. in a single tuft; 2. in two distinct tufts; 4. in a row of basal setae.
- 37. Articulation of pedicel with 1st flagellomere1. 1. pedicel with a median membrane fitting into a cavity on the 1st flagellomere; 2. pedicel with a median hole into which basal projection of the 1st flagellomere fits.
- 38. Shape of pedicel: 1. without a dorsal seam; 2. with a conspicuous, but not strongly pronounced dorsal seam; 3. with pronounced dorsal seam.
- 39. Position of arista on 1st flagellomere: 1. dorsal basal; 2. lateral subapical; 3. dorsal subapical; 4. apical.
- 40. Presence of basal segmentation of the arista: 1. absent; 2. present.
- 41. Shape of arista: 1. appearing straight; 2. appearing zigzagged.
- 42. Apical flagellomere: 1. bare; 2. with many dorsal, ventral, and lateral rays (pubescent); 3. with alternate, long to short rays (bipectinate).
USERTYPE (CSTREE) = (1,3)2.
- 43. Rays of arista: 1. long; 2. short; 3. dorsal rays long, ventral rays short.
- 44. Relative position of antennae: 1. approximate; 2. separated from each other by a distance longer than length of pedicel.
- 45. Sexual dimorphism of clypeus: 1. absent; 2. clypeus reduced in the male, somewhat retracted into the oral cavity.

46. Presence of palpus: 1. present, well developed; 2. very reduced or absent.
47. Shape of palpus: 1. finger-like; 2. tear-drop; 3. spatulate.
- Thorax:
48. Shape of basisternum: 1. large, wider than long; 2. reduced, longer than wide.
49. Vestiture of basisternum: 1. basisternum bare; 2. basisternum setose; 3. basisternum with marginal region setose.
50. Fusion between furcasternum and propleuron: 1. furcasternum separated from propleuron by a conspicuous suture; 2. furcasternum indistinctly separated laterally from propleuron; 3. furcasternum fused with propleuron, suture not present.
Ordered.
51. Presence of greater ampulla: 1. absent; 2. present.
52. Shape of notopleuron: 1. flat posteriorly; 2. bearing a posterior callosity.
53. Shape of anepisternum: 1. with upper posterior margin somewhat receded but flat; 2. with a raised ridge along upper posterior margin.
54. Presence of subscutellum: 1. absent ; 2. present.
55. Presence of postscutellum: 1. inconspicuous; 2. present.
56. Presence of posterior anepisternal setae: 1. absent; 2. present.
57. Presence of anterior katepisternal seta: 1. absent; 2. present.
58. Presence of posterior katepisternal seta: 1. absent; 2. present.
59. Presence of anterior notopleural seta: 1. absent; 2. present.
60. Presence of posterior notopleural seta: 1. absent; 2. present.
61. Presence of postpronotal seta: 1. weakly developed or absent; 2. well developed.
62. Presence of presutural dorsocentral seta: 1. weak or lacking; 2. well-developed.
63. Arrangement of acrostical setulae: 1. scattered, mostly absent; 2. arranged in well-defined rows; 3. not arranged in rows.

Ordered.

64. Number of rows of acrostical setulae: 1. 1; 2. 2; 3. 4; 4. 6.

Ordered.

65. Presence of anterior dorsocentral seta: 1. absent; 2. present.

66. Basal scutellar seta: 1. absent; 2. present.

67. Inclination of apical pair of scutellar setae: 1. posteroclinate; 2. erect.

68. Orientation of apical pair of scutellar setae: 1. subparallel; 2. convergent; 3. divergent.

69. Coloration of wing: 1. with a dark pattern; 2. hyaline.

70. Spines of costal vein: 1. not well-differentiated; 2. well-differentiated spines.

71. Length of costal vein: 1. extending to vein M; 2. extending only to vein R4+5.

72. Presence of a subcostal break: 1. absent; 2. present as a weakness; 3. present.

73. Presence of humeral break: 1. absent; 2. present as a weakness.

74. Presence of setae on vein R1: 1. absent; 2. present.

75. Length of vein R2+3: 1. approaching costa halfway to wing apex; 2. approaching costa on its apical two third; 3. approaching costa at wing apex.

Ordered.

76. Presence of apical kink on vein R1: 1. absent; 2. present.

77. Sc vein: 1. incomplete, not reaching costa; 2. complete to costa.

78. vein Sc (whether fused with vein R1): 1. partly fused to vein R1; 2. free from vein R1.

79. Presence of crossvein bm-cu: 1. absent; 2. present.

80. Crossvein bm-cu (whether complete): 1. complete; 2. incomplete anteriorly.

81. Presence of crossvein r-m: 1. absent; 2. present.

82. Crossvein r-m (whether complete): 1. complete; 2. complete as a fold on posterior half; 3. incomplete posteriorly.
83. Position of crossvein r-m: 1. well below middle of discal cell; 2. around the middle of discal cell; 3. well beyond the middle of discal cell.
84. Presence of vein CuA2: 1. absent; 2. present.
85. Shape of CuA2: 1. squarely closed; 2. with an angular point posteriorly.
86. Presence of a fold on cell dm: 1. absent; 2. present, running along entire length of cell dm.
87. Presence of vein A1: 1. very reduced, apparently absent; 2. short, not attaining wing margin; 3. reaching close to wing margin as a fold; 4. long, reaching close to wing margin.
Ordered.
88. Shape of femora: 1. slender; 2. robust.
89. Presence of ctenidial spine: 1. not differentiated; 2. apparently present, but not the strongest seta on femur; 3. well differentiated.
Ordered.

Male abdomen and terminalia:

90. Sclerotization of abdominal sclerites: 1. strong; 2. weak.
91. Sternites on preabdomen: 1. narrower than tergites; 2. as wide as tergites; 3. reduced, ca 1/8 the width of tergites; 4. as wide as tergites.
92. Position of abdominal spiracles 1-5: 1. in membrane; 2. on the margin of tergites.
93. Sclerotization of tergite 5: 1. well sclerotized; 2. weakly sclerotized, difficult to discern.
94. Shape of tergite 5: 1. free from sternite five; 2. fused with sternite five, forming a complete ring.
95. Presence of tergite 6: 1. absent; 2. present.
96. Tergite 6 (whether independent from pregenital segment): 1. free from pregenital segment; 2. fused with pregenital segment.

97. Length of tergite 6: 1. as long as tergite 5; 2. approximately 2/3 length of tergite 5; 3. approximately 1/5 to 1/10 the length of tergite 5.
Ordered.
98. Symmetry of tergite 6: 1. symmetrical; 2. asymmetrical.
99. Presence of sternite 6: 1. absent; 2. present.
100. Symmetry of sternite 6: 1. symmetrical; 2. displaced towards the left side.
101. Pregenital sclerite (whether free): 1. free from epandrium; 2. fused with epandrium; 3. closely associated with epandrium.
USERTYPE (CSTREE) = ((3)1)2;
102. Width of pregenital sclerite: 1. as wide as tergite 5; 2. wider than tergite 5, extended both sides enclosing spiracle.
103. Presence of epandrium: 1. present; 2. absent.
104. Shape of epandrium: 1. not forming a ring around genital segment; 2. forming a complete ring around genital segment.
105. Surstylus (articulation with epandrium): 1. articulated with the epandrium; 2. partly fused with epandrium; 3. completely fused with epandrium; 4. fused to an internal sheaf of the epandrium.
106. Sclerotization of anterior portion of hypandrium: 1. well sclerotized; 2. weakly sclerotized.
107. Length of lateral arm of hypandrium: 1. not elongate; 2. elongate, well-sclerotized.
108. Presence of a hypandrial bridge: 1. absent; 2. present.
109. Position of hypandrial bridge: 1. dorsal to base of aedeagus; 2. posterior to base of aedeagus.
110. Position of postgonite: 1. articulated to partly fused with posterior portion of hypandrial arm; 2. fused to posterior-lateral portion of hypandrial arm.
111. Presence of anterior apodeme of pregonite: 1. absent; 2. present.

112. Posterior portion pregonite: 1. free from basis of aedeagus ; 2. closely connected with the basis of the aedeagus ventrally; 3. closely connected with the basis of aedeagus anteriorly, forming a closed ring.
113. Phallapodeme : 1. free (cuneiform); 2. linked with hypandrium anteriorly; 3. extensively fused with hypandrium anteriorly; 4. partly fused with hypandrium lateral and anteriorly; 5. completely fused with the hypandrium.
114. Shape of posterior portion of phallapodeme: 1. rod-like; 2. bifurcate; 3. saddle-shaped; 4. excavated medially; 5. expanded and forming dorsal processes that are fused with hypandrial arms.
115. Presence of ejaculatory apodeme: 1. present; 2. strongly reduced to absent.
116. Shape of aedeagus: 1. ribbon-like; 2. sclerotized, elongate, slender, tapering towards apex ; 3. long, coiled; 4. membranous, bearing internal rod-like sclerites; 5. mostly membranous, hairy, coiled; 6. short, membranous, wide; 7. long, densely spinulose; 8. strong, bearing complex sclerotization apically.
117. Presence of ventrally oriented process articulated with cercus and surstylus: 1. absent; 2. present.
118. Presence of subepandrial sclerite: 1. absent; 2. present.
119. Shape of subepandrial sclerite: 1. single, opposite to phallapodeme; 2. paired, opposite to posterior arm of hypandrium; 3. a large, posterior dorsal plate (arising posterior dorsally to base of aedeagus).

Female abdomen and terminalia

120. Shape of abdominal tergite 5: 1. normal; 2. modified.
121. Presence of segment 6 (female abdomen): 1. present; 2. absent.
122. Sternite 6 (whether free): 1. free from tergite 6; 2. fused with tergite 6 forming a ring.
123. Sternite 7 (whether free): 1. free from tergite 7; 2. fused with tergite 7 forming a ring; 3. fused with tergite 7 and posterior sclerites forming an oviscape.
124. Number of spermathecae: 1. 1; 2. 2; 3. 3; 4. 4.

Table 2.6.– List of apomorphies for the internal branches of cladogram in Fig. 111. Characters optimized using Accelerated transformation (ACCTRAN). Single arrows denote ambiguous changes, arrows denote unambiguous changes.

Branch	Character	CI	Change
node_96 --> node_94	48	0.167	1 ==> 2
	68	0.133	1 --> 2
	69	0.083	1 ==> 2
	83	0.400	3 ==> 2
	87	0.375	3 ==> 2
node_94 --> node_90	6	0.333	1 ==> 2
	64	0.333	3 --> 2
	77	0.200	1 --> 2
	114	0.333	2 ==> 1
node_90 --> node_88	116	0.636	1 --> 8
	1	0.667	1 ==> 2
node_88 --> node_56	53	0.333	1 ==> 2
	68	0.133	2 --> 1
node_56 --> node_53	8	0.267	1 --> 4
	12	0.800	3 ==> 2
	48	0.167	2 --> 1
	108	0.500	1 ==> 2
	116	0.636	8 --> 2
node_53 --> node_50	26	0.375	3 --> 1
	63	0.182	3 ==> 2
	76	0.333	1 ==> 2
	77	0.200	2 --> 1
	89	1.000	1 ==> 2
	97	0.333	2 --> 3
node_53 --> node_52	3	0.125	2 ==> 1
	15	0.167	1 ==> 2
	22	0.222	3 ==> 1
	56	0.143	2 ==> 1
	57	0.167	1 ==> 2
	64	0.333	2 --> 1
	78	0.500	2 ==> 1
	89	1.000	2 ==> 3
	31	0.200	2 ==> 1
	32	0.286	1 --> 2
node_53 --> node_52	48	0.167	1 --> 2
	49	0.667	1 ==> 2
	62	0.200	1 ==> 2
	64	0.333	2 --> 3
	69	0.083	2 ==> 1
	80	0.500	1 ==> 2
	95	0.333	2 --> 1

	105	0.333	1	==>	3
	109	0.500	2	-->	1
	113	0.500	1	-->	2
	116	0.636	2	-->	8
node_52 --> node_51	64	0.333	3	==>	4
	106	0.500	1	==>	2
node_56 --> node_55	5	0.222	1	==>	2
	20	0.250	2	==>	1
	29	0.200	1	-->	2
	39	1.000	1	==>	3
	47	0.500	1	==>	3
	49	0.667	1	==>	3
node_55 --> node_54	21	0.200	2	==>	1
	52	0.167	2	==>	1
	69	0.083	2	==>	1
node_88 --> node_87	13	0.500	1	-->	2
	21	0.200	2	-->	1
	26	0.375	3	-->	2
	57	0.167	1	==>	2
	75	0.182	3	==>	2
	84	0.222	3	-->	1
node_87 --> node_86	12	0.800	3	==>	1
	56	0.143	2	==>	1
	61	0.143	2	-->	1
	63	0.182	3	==>	2
	65	0.111	2	-->	1
	77	0.200	2	-->	1
node_86 --> node_84	22	0.222	3	==>	2
	114	0.333	1	==>	2
node_84 --> node_68	26	0.375	2	-->	3
	48	0.167	2	==>	1
	64	0.333	2	==>	1
	79	0.143	2	-->	1
	83	0.400	2	==>	1
	105	0.333	1	==>	3
node_68 --> node_64	3	0.125	2	==>	1
	15	0.167	1	-->	2
	40	0.500	2	-->	1
	42	0.250	2	-->	1
	69	0.083	2	==>	1
	75	0.182	2	-->	3
	76	0.333	1	==>	2
	116	0.636	8	==>	4
node_64 --> node_63	19	0.167	2	==>	1
	26	0.375	3	-->	2
	35	0.143	2	==>	1
	47	0.500	1	==>	2

	51	0.333	1	==>	2
	56	0.143	1	==>	2
	70	0.333	1	==>	2
	78	0.500	2	==>	1
	84	0.222	1	-->	3
	108	0.500	1	==>	2
node_63 --> node_62	15	0.167	2	-->	1
	25	0.250	2	==>	1
	41	0.500	1	==>	2
	42	0.250	1	==>	3
	50	0.167	1	==>	3
	65	0.111	1	==>	2
	75	0.182	3	-->	2
	96	0.333	1	==>	2
	106	0.500	1	==>	2
	109	0.500	2	==>	1
	111	0.500	1	==>	2
	114	0.333	2	==>	3
	124	0.500	2	==>	3
node_62 --> node_59	9	0.500	1	==>	2
node_58 --> node_57	70	0.333	2	==>	1
node_62 --> node_61	9	0.500	2	-->	3
	28	0.600	1	==>	4
	69	0.083	1	==>	2
node_61 --> node_60	9	0.500	3	-->	4
	14	0.333	1	==>	2
	64	0.333	1	==>	2
	75	0.182	2	==>	3
node_68 --> node_67	12	0.800	1	==>	2
	22	0.222	2	-->	1
	87	0.375	2	==>	1
	92	0.500	1	==>	2
	119	0.286	1	==>	3
node_67 --> node_65	5	0.222	1	==>	2
	25	0.250	2	==>	1
	26	0.375	3	-->	1
	66	0.167	2	==>	1
	72	0.400	2	==>	1
node_67 --> node_66	16	0.200	2	==>	1
	36	0.300	1	-->	2
	52	0.167	2	==>	1
	55	0.250	2	==>	1
	63	0.182	2	==>	3
	68	0.133	1	==>	2
	71	0.222	1	==>	2
	73	0.400	1	==>	2
	96	0.333	1	-->	2

	112	1.000	1	==>	2
	116	0.636	8	==>	6
node_84 --> node_83	1	0.667	2	==>	3
	35	0.143	2	-->	1
	84	0.222	1	-->	3
node_83 --> node_80	8	0.267	1	-->	3
	23	0.100	1	-->	2
	24	0.100	2	==>	1
	28	0.600	1	-->	4
	30	1.000	1	-->	2
	37	1.000	1	==>	2
	42	0.250	2	-->	3
	43	0.333	2	-->	1
	47	0.500	1	==>	2
	61	0.143	1	-->	2
	88	0.200	1	-->	2
node_80 --> node_77	22	0.222	2	==>	3
	25	0.250	2	-->	1
	31	0.200	2	-->	1
	51	0.333	1	==>	2
	65	0.111	1	-->	2
	69	0.083	2	==>	1
	86	0.500	1	==>	2
	119	0.286	1	==>	2
	123	0.400	1	==>	2
node_77 --> node_69	20	0.250	2	==>	1
	21	0.200	1	==>	2
	26	0.375	2	==>	1
	34	0.500	1	==>	2
	64	0.333	2	-->	3
	71	0.222	1	==>	2
	72	0.400	2	==>	1
	75	0.182	2	==>	1
	84	0.222	3	-->	1
	100	0.200	2	==>	1
	102	0.200	1	==>	2
	105	0.333	1	==>	3
	113	0.500	1	==>	4
	116	0.636	8	==>	1
	124	0.500	2	==>	3
node_77 --> node_76	5	0.222	1	-->	2
	19	0.167	2	==>	1
	23	0.100	2	-->	1
	48	0.167	2	==>	1
	57	0.167	2	==>	1
	61	0.143	2	-->	1
	88	0.200	2	-->	1

node_76 --> node_72	15	0.167	1 --> 2	114	0.333	2 ==> 1
				32	0.286	1 --> 2
				47	0.500	2 ==> 1
				50	0.167	1 --> 3
				66	0.167	2 ==> 1
				116	0.636	8 ==> 6
node_72 --> node_70				8	0.267	3 --> 1
				44	1.000	1 ==> 2
				56	0.143	1 ==> 2
				102	0.200	1 --> 2
				105	0.333	1 --> 3
				110	0.500	2 --> 1
				123	0.400	2 --> 1
node_72 --> node_71				11	0.500	1 ==> 2
				40	0.500	2 ==> 1
				64	0.333	2 ==> 1
				68	0.133	1 ==> 3
				79	0.143	2 ==> 1
				84	0.222	3 --> 1
				112	1.000	1 ==> 3
				119	0.286	2 ==> 1
node_76 --> node_75				17	0.500	1 --> 2
				31	0.200	1 --> 2
				45	1.000	1 --> 2
				65	0.111	2 --> 1
				122	1.000	1 ==> 2
node_75 --> node_74				16	0.200	2 ==> 1
				28	0.600	4 ==> 3
node_74 --> node_73				7	1.000	1 ==> 2
				68	0.133	1 ==> 3
				124	0.500	2 --> 3
node_80 --> node_79				5	0.222	1 ==> 3
				8	0.267	3 --> 4
				26	0.375	2 ==> 4
				35	0.143	1 --> 2
				36	0.300	1 --> 2
				63	0.182	2 ==> 3
				70	0.333	1 ==> 2
				91	0.667	1 ==> 3
node_79 --> node_78				50	0.167	1 --> 2
				55	0.250	2 ==> 1
				71	0.222	1 --> 2
				72	0.400	2 ==> 3
				79	0.143	2 ==> 1
				84	0.222	3 --> 1
node_83 --> node_82				29	0.200	1 ==> 2

	50	0.167	1	==>	3
	57	0.167	2	==>	1
	63	0.182	2	==>	1
	67	0.500	1	==>	2
	68	0.133	1	==>	3
	75	0.182	2	==>	1
	80	0.500	1	-->	2
	93	1.000	1	==>	2
	95	0.333	2	==>	1
	115	0.333	1	==>	2
	116	0.636	8	==>	7
	120	1.000	1	==>	2
node_82 --> node_81	20	0.250	2	==>	1
	52	0.167	2	-->	1
	79	0.143	2	==>	1
	83	0.400	2	==>	3
	119	0.286	1	-->	3
node_86 --> node_85	11	0.500	1	==>	2
	26	0.375	2	==>	1
	36	0.300	1	==>	4
	46	1.000	1	==>	2
	62	0.200	1	==>	2
	63	0.182	2	==>	1
	66	0.167	2	==>	1
	71	0.222	1	==>	2
	83	0.400	2	-->	3
	87	0.375	2	==>	4
	97	0.333	2	==>	1
	100	0.200	2	==>	1
	102	0.200	1	==>	2
	113	0.500	1	-->	2
	119	0.286	1	-->	3
node_90 --> node_89	3	0.125	2	==>	1
	8	0.267	1	==>	2
	12	0.800	3	==>	4
	16	0.200	2	==>	1
	22	0.222	3	==>	1
	32	0.286	1	==>	2
	36	0.300	1	==>	4
	100	0.200	2	-->	1
	101	1.000	1	==>	2
	105	0.333	1	-->	2
	110	0.500	2	==>	1
node_94 --> node_93	26	0.375	3	-->	4
	102	0.200	1	==>	2
node_93 --> node_91	8	0.267	1	==>	5
	12	0.800	3	==>	5

					15	0.167	1	==>	2
					22	0.222	3	-->	2
					27	1.000	2	==>	1
					29	0.200	1	==>	2
					36	0.300	1	-->	3
					50	0.167	1	-->	2
					63	0.182	3	==>	2
					71	0.222	1	==>	2
					72	0.400	2	==>	3
					73	0.400	1	==>	3
					75	0.182	3	==>	2
					79	0.143	2	==>	1
					84	0.222	3	==>	1
					87	0.375	2	==>	1
					96	0.333	1	==>	2
					116	0.636	1	-->	5
node_93	-->	node_92	3	0.125	2	==>	1		
					26	0.375	4	-->	7
					32	0.286	1	==>	3
					52	0.167	2	==>	1
					54	0.333	2	==>	1
					58	1.000	2	==>	1
					59	1.000	2	==>	1
					61	0.143	2	==>	1
					105	0.333	1	-->	3
					113	0.500	1	==>	4
					119	0.286	1	-->	2
node_96	-->	node_95	18	1.000	1	==>	2		
					20	0.250	2	==>	1
					23	0.100	1	==>	2
					35	0.143	2	==>	1
					56	0.143	2	==>	1
					57	0.167	1	==>	2
					62	0.200	1	==>	2
					86	0.500	1	==>	2
					88	0.200	1	-->	2
					97	0.333	2	-->	3
					107	1.000	1	==>	2
					113	0.500	1	==>	2
					115	0.333	1	==>	2
					116	0.636	1	-->	6
					119	0.286	1	-->	3

Table 2.7.– List of apomorphies for the terminal taxa in cladogram of Fig. 111. Characters optimized using Accelerated transformation (ACCTRAN). Single lines denote ambiguous changes, lines denote unambiguous changes.

Branch	Character #	CI	Change
node_97 -->	26	0.375	3 ==> 1
<i>Pterocalla ocellata</i> Fabricius	31	0.200	2 ==> 1
	36	0.300	1 --> 2
	50	0.167	1 --> 3
	63	0.182	3 ==> 2
	73	0.400	1 ==> 2
	75	0.182	3 ==> 2
	77	0.200	1 --> 2
	85	1.000	1 ==> 2
	87	0.375	3 ==> 4
	95	0.333	2 ==> 1
	101	1.000	1 ==> 3
	105	0.333	1 --> 3
	116	0.636	1 --> 3
	118	0.500	2 ==> 1
	123	0.400	1 ==> 3
	124	0.500	2 ==> 3
node_50 --> <i>Anthomyza gracilis</i> Fallén	26	0.375	1 --> 3
node_50 --> <i>Mumetopia terminalis</i> (Loew)	21	0.200	2 ==> 1
	23	0.100	1 ==> 2
	24	0.100	2 ==> 1
	68	0.133	1 ==> 3
node_51 --> <i>Geomyza tripunctata</i> Fallén	32	0.286	2 --> 1
	43	0.333	2 ==> 3
	87	0.375	2 ==> 1
	111	0.500	1 ==> 2
node_51 --> <i>Opomyza florum</i> (Fabricius)	3	0.125	2 ==> 1
node_54 --> <i>Clusia lateralis</i> Haliday	36	0.300	1 ==> 2
	68	0.133	1 ==> 3
node_54 -->	8	0.267	4 --> 2
<i>Chaetocclusia bakeri</i> Coquillett	24	0.100	2 ==> 1
	29	0.200	2 --> 1
	39	1.000	3 ==> 4
	74	1.000	1 ==> 2
node_55 --> <i>Clusiodes ater</i>	8	0.267	4 --> 1
node_64 -->	2	0.667	1 ==> 2
<i>Echidnocephalodes barbatus</i> Lamb	8	0.267	1 ==> 4
	13	0.500	2 ==> 1
	23	0.100	1 ==> 2
	24	0.100	2 ==> 1
	55	0.250	2 ==> 1

	68	0.133	1 ==>	3
	79	0.143	1 -->	2
	102	0.200	1 ==>	2
	114	0.333	2 ==>	5
	124	0.500	2 ==>	1
node_57 --> <i>Aulacigaster bromeliae</i> ,	2	0.667	1 ==>	3
undescribed species	5	0.222	1 ==>	3
	8	0.267	1 ==>	3
	43	0.333	2 ==>	1
	105	0.333	3 ==>	4
node_57 --> <i>A.equadoriensis</i> (Hennig)	2	0.667	1 ==>	2
	24	0.100	2 ==>	1
node_58 --> <i>A.plesiomorphica</i> (Hennig)	82	0.500	1 ==>	3
node_59 --> <i>A. minuta</i> (Hennig)	24	0.100	2 ==>	1
node_59 --> <i>A.femorata</i> ,				
undescribed species	76	0.333	2 ==>	1
node_63 --> Gen.sp. (Malaysia)	9	0.500	1 ==>	3
	14	0.333	1 ==>	2
	33	1.000	1 ==>	2
	52	0.167	2 ==>	1
	61	0.143	1 ==>	2
	63	0.182	2 ==>	3
	66	0.167	2 ==>	1
	73	0.400	1 ==>	2
	82	0.500	1 ==>	3
	91	0.667	1 ==>	3
node_65 --> <i>Asteia amoena</i> Meigen	9	0.500	1 ==>	3
	14	0.333	1 ==>	2
	41	0.500	1 ==>	2
	42	0.250	2 ==>	3
	43	0.333	2 ==>	1
	63	0.182	2 ==>	1
	65	0.111	1 ==>	2
	75	0.182	2 ==>	3
	90	1.000	1 ==>	2
	97	0.333	2 ==>	1
	114	0.333	2 ==>	1
node_66 --> <i>Xenasteia palauensis</i> Hardy	1	0.667	2 ==>	3
	42	0.250	2 ==>	1
	81	1.000	2 ==>	1
node_66 --> <i>X.shalam</i>	36	0.300	2 -->	4
node_69 --> <i>Periscelis flinti</i>	8	0.267	3 -->	1
	68	0.133	1 ==>	2
	125	1.000	1 ==>	2
node_69 --> <i>Parascutops maculipennis</i>	4	1.000	1 ==>	2
	32	0.286	1 ==>	2
	35	0.143	1 -->	2

	52	0.167	2 ==>	1
	63	0.182	2 ==>	3
node_70 --> <i>Planinasus</i> sp.a	29	0.200	1 ==>	2
	32	0.286	2 -->	3
	34	0.500	1 ==>	2
	57	0.167	1 ==>	2
	69	0.083	1 ==>	2
node_70 --> <i>Diopsosoma</i> prima	5	0.222	2 -->	1
	23	0.100	1 ==>	2
	26	0.375	2 ==>	1
	71	0.222	1 ==>	2
	88	0.200	1 ==>	2
	73	0.400	1 ==>	2
node_71 --> <i>Stenomicra</i> sp.2	17	0.500	1 ==>	2
	19	0.167	1 ==>	2
	28	0.600	4 ==>	1
	61	0.143	1 ==>	2
	69	0.083	1 ==>	2
	114	0.333	1 ==>	3
node_75 --> <i>Cyamops</i> sp.n. (fossil)	5	0.222	2 -->	1
	8	0.267	3 -->	2
	24	0.100	1 ==>	2
node_71 --> <i>Stenomicra</i> sp.1	75	0.182	2 ==>	3
node_74 --> <i>C.micronesicus</i> Baptista&Mathis	5	0.222	2 -->	3
	65	0.111	1 -->	2
	79	0.143	2 ==>	1
node_73 --> <i>C.americus</i> Baptista&Mathis	56	0.143	1 ==>	2
	64	0.333	2 ==>	3
	75	0.182	2 ==>	3
	124	0.500	3 -->	4
node_73 --> <i>C.nebulosus</i> Sabrosky	114	0.333	1 ==>	3
node_78 --> <i>Neurochaeta inversa</i>	15	0.167	1 ==>	2
McAlpine	19	0.167	2 ==>	1
	23	0.100	2 -->	1
	24	0.100	1 ==>	2
	26	0.375	4 ==>	3
	36	0.300	2 -->	3
	69	0.083	2 ==>	1
	71	0.222	2 -->	3
	87	0.375	2 ==>	1
	103	1.000	1 ==>	2
node_78--> <i>Neurotaxis charis</i> McAlpine	65	0.111	1 ==>	2
	68	0.133	1 ==>	3
	84	0.222	1 -->	2
node_78--> <i>Neurocytta prisca</i> McAlpine	42	0.250	3 -->	2
	43	0.333	1 -->	2

	49	0.667	1 ==>	2
	66	0.167	2 ==>	1
	67	0.500	1 ==>	2
	98	1.000	1 ==>	2
node_82 --> <i>Nemo corticeus</i> McAlpine	28	0.600	1 ==>	2
	69	0.083	2 ==>	1
node_81--> <i>Nemula longarista</i> Freidberg	16	0.200	2 ==>	1
	22	0.222	2 ==>	3
	53	0.333	2 ==>	1
	54	0.333	2 ==>	1
	60	1.000	2 ==>	1
node_81 --> <i>Ningulus simatus</i> McAlpine	25	0.250	2 ==>	1
	26	0.375	2 ==>	6
node_85 -->	3	0.125	2 ==>	1
<i>Teratomyza neozelandica</i> Malloch	23	0.100	1 ==>	2
	55	0.250	2 ==>	1
	84	0.222	1 -->	3
	92	0.500	1 ==>	2
	113	0.500	2 -->	5
	123	0.400	1 ==>	2
node_85 --> <i>Auster sp.</i>	22	0.222	3 ==>	1
	61	0.143	1 -->	2
	65	0.111	1 -->	2
	68	0.133	1 ==>	3
	72	0.400	2 ==>	3
node_87 --> <i>Margo clausa</i> McAlpine	3	0.125	2 ==>	1
	5	0.222	1 ==>	3
	6	0.333	2 ==>	1
	8	0.267	1 ==>	3
	19	0.167	2 ==>	1
	36	0.300	1 ==>	2
	39	1.000	1 ==>	2
	69	0.083	2 ==>	1
	71	0.222	1 ==>	3
node_89 --> <i>Chyromyia flava</i>	62	0.200	1 ==>	2
	94	1.000	1 ==>	2
	99	1.000	2 ==>	1
node_89 --> <i>Gymnochiromya concolor</i>	68	0.133	2 -->	3
	97	0.333	2 ==>	3
	121	1.000	1 ==>	2
node_92 --> <i>Meoneura flaviceps</i> Collin	35	0.143	2 ==>	1
	62	0.200	1 ==>	2
node_92 --> <i>Carnus hemapterus</i> Nitzsch	19	0.167	2 ==>	1
	23	0.100	1 ==>	2
	24	0.100	2 ==>	1
	88	0.200	1 ==>	2
node_91 --> <i>Somatia aestiva</i> (Fabricius)	16	0.200	2 ==>	1

	21	0.200	2 ==>	1
	22	0.222	3 ==>	1
	23	0.100	1 ==>	2
	24	0.100	2 ==>	1
	26	0.375	7 -->	8
	35	0.143	2 ==>	1
	42	0.250	2 ==>	3
	43	0.333	2 ==>	1
	48	0.167	2 ==>	1
	53	0.333	1 ==>	2
	65	0.111	2 ==>	1
	68	0.133	2 -->	1
	69	0.083	2 ==>	1
	77	0.200	1 -->	2
	91	0.667	1 ==>	2
	104	1.000	1 ==>	2
	114	0.333	2 ==>	1
	118	0.500	2 ==>	1
	123	0.400	1 ==>	2
node_91 --> <i>Psila rosae</i> Fabricius	8	0.267	1 ==>	4
	31	0.200	2 ==>	1
	51	0.333	1 ==>	2
	56	0.143	2 ==>	1
	66	0.167	2 ==>	1
	83	0.400	2 ==>	1
	97	0.333	2 ==>	1
	100	0.200	2 ==>	1
	115	0.333	1 ==>	2
node_95 -->	9	0.500	1 ==>	3
<i>Traginops irroratus</i> Coquillett	10	1.000	1 ==>	2
	50	0.167	1 -->	3
	54	0.333	2 ==>	1
	105	0.333	1 -->	3
node_95 --> <i>Odinia</i> sp	3	0.125	2 ==>	1
	6	0.333	1 ==>	2
	8	0.267	1 ==>	4
	68	0.133	1 -->	2
	71	0.222	1 ==>	2

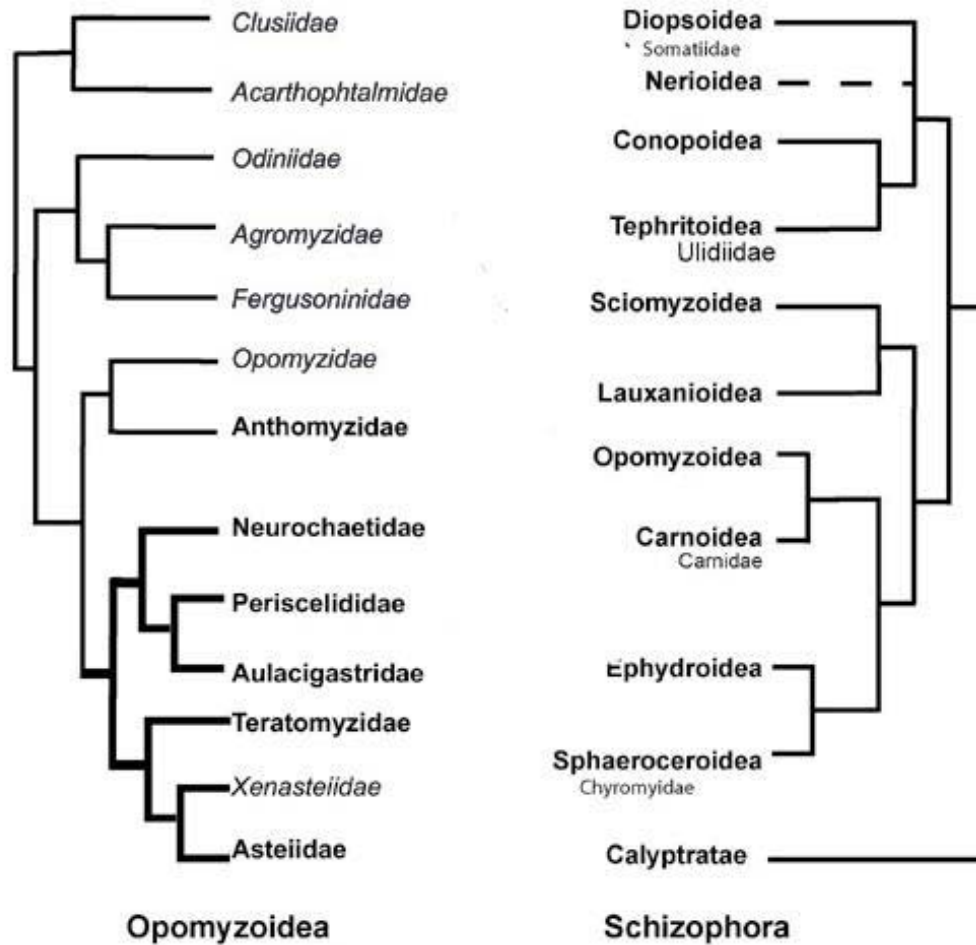


FIGURE 2.1.– Cladogram showing the phylogenetic relationships between the families of Opomyzoidea (left) and between the superfamilies of Acalyptratae (right) according to J. F. McAlpine (1989). The families in italics (left) belong in D. K. McAlpine's Opomyzoidea (1991), whereas the families in bold (black) belong in his Asteioidea. The suprafamilial placement of distant outgroups is shown in the cladogram on the right.

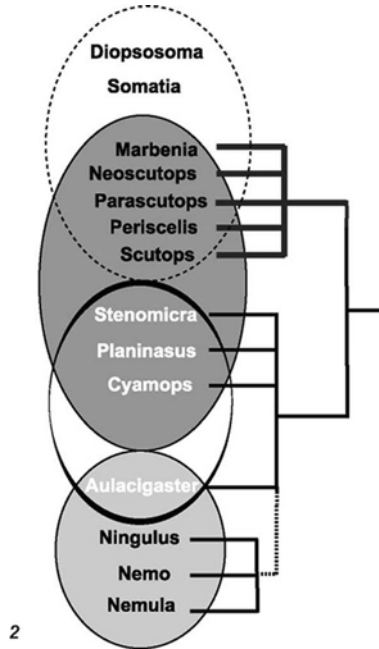
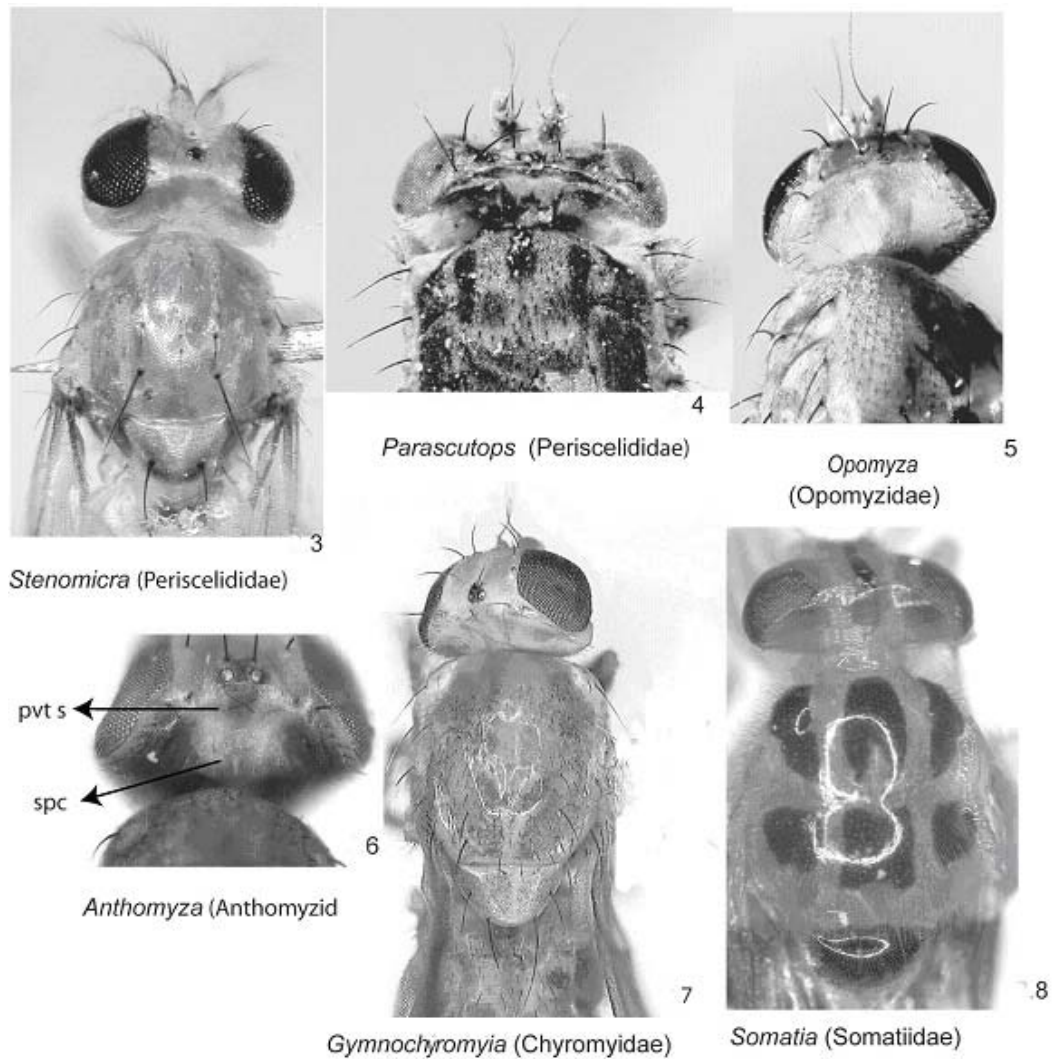
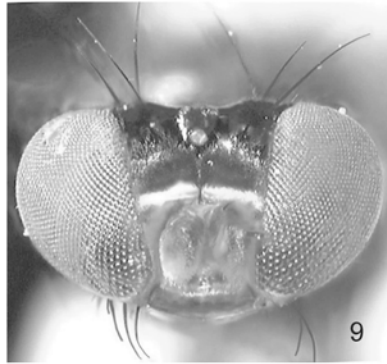


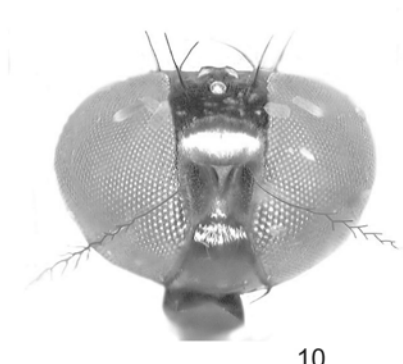
FIGURE 2.2.—Diagrammatic representation of different definitions of the families Perisclididae and Aulacigastridae. The dark grey circle represents D. K. McAlpine's definition of Perisclididae (1983), and the light grey circle represents D.K. McAlpine's Aulacigastridae (1983). Griffiths's (1972) Perisclididae is shown by the dashed lined circle. Hennig's Aulacigastridae (1971) is represented by the genera in white. The cladogram depicts the phylogenetic relationships among the genera under consideration, according to J. F. McAlpine (1989).



FIGURES 2.3-2.8.—Digital photographs of the dorsal aspect of the head and thorax of acalyptrates. 3. *Stenomicroa* sp, undescribed species (Stenomicroinae, Opomyzoidea). 4. *Parascutops* sp (Periscelidinae, Opomyzoidea). 5. *Opomyza florum* (Fabricius) (Opomyzoidea). 6. *Anthomyza gracilis* Fallén (Opomyzoidea). 7. *Gymnochiromyia concolor* (Malloch)(Sphaeroceroidea). 8. *Somatia aestiva* (Fabricius) (Diopsoidea). Not all to the same scale.



9



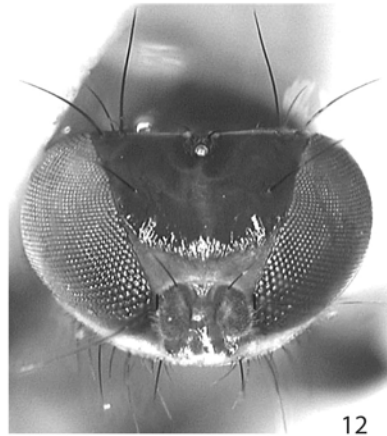
10

Aulacigaster (Aulacigastridae)



11

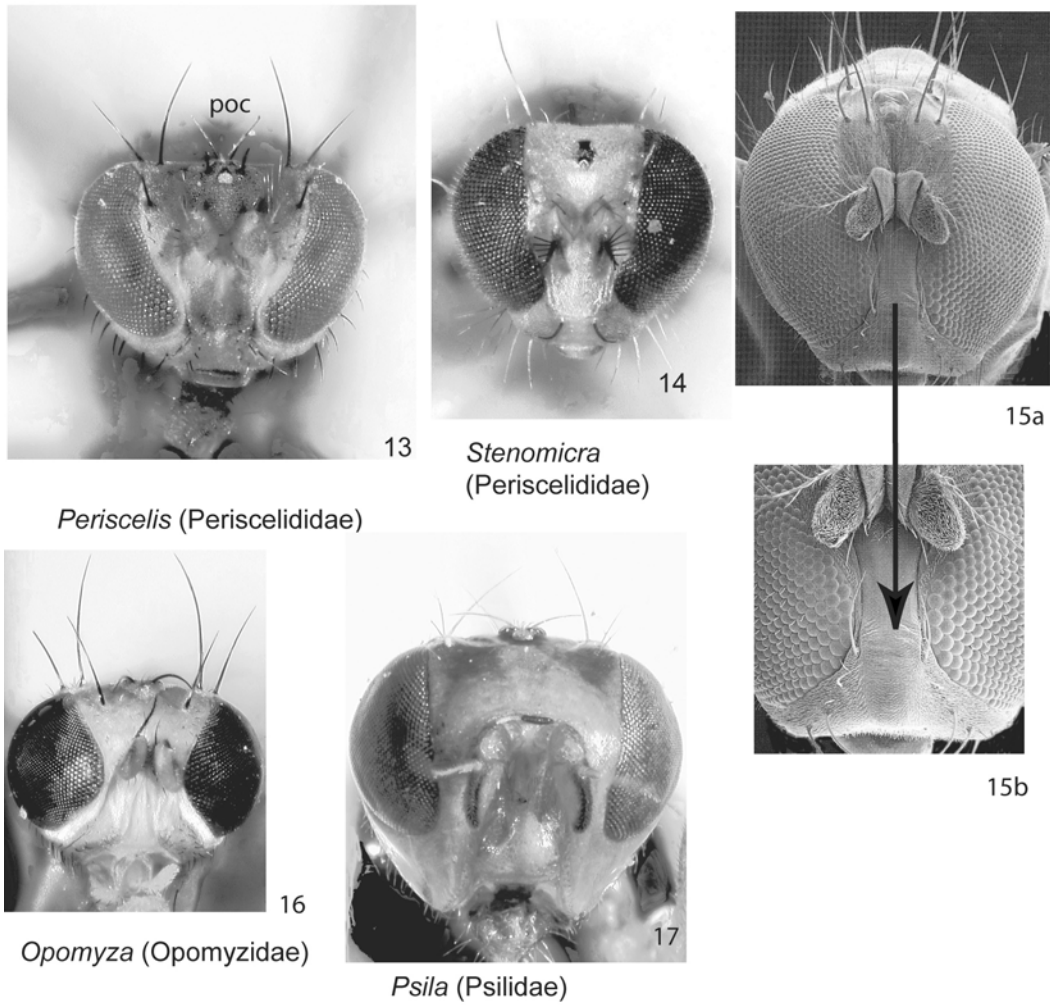
Aulacigaster (Aulacigastridae)



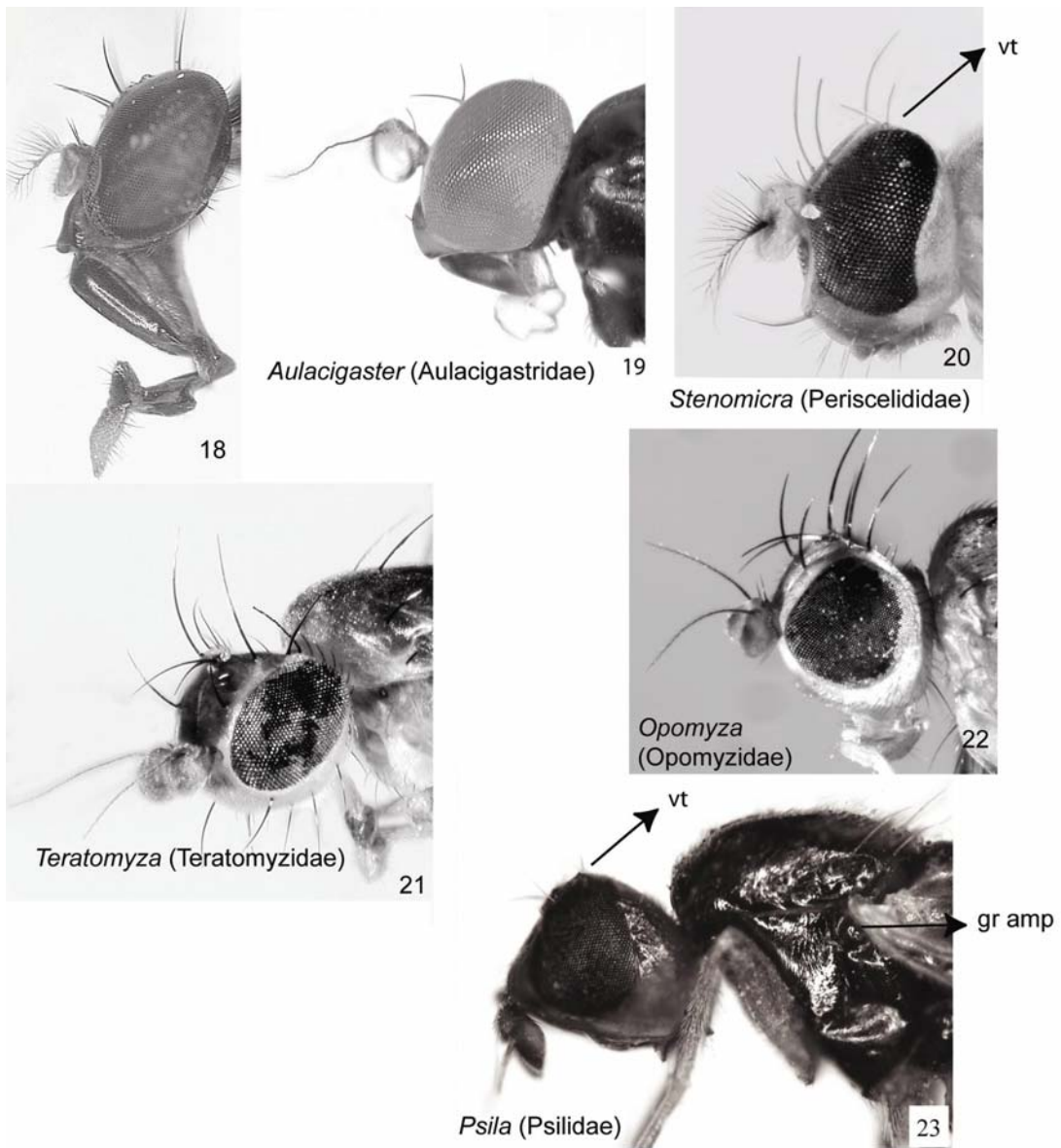
12

Undescribed genus
(Aulacigastridae)

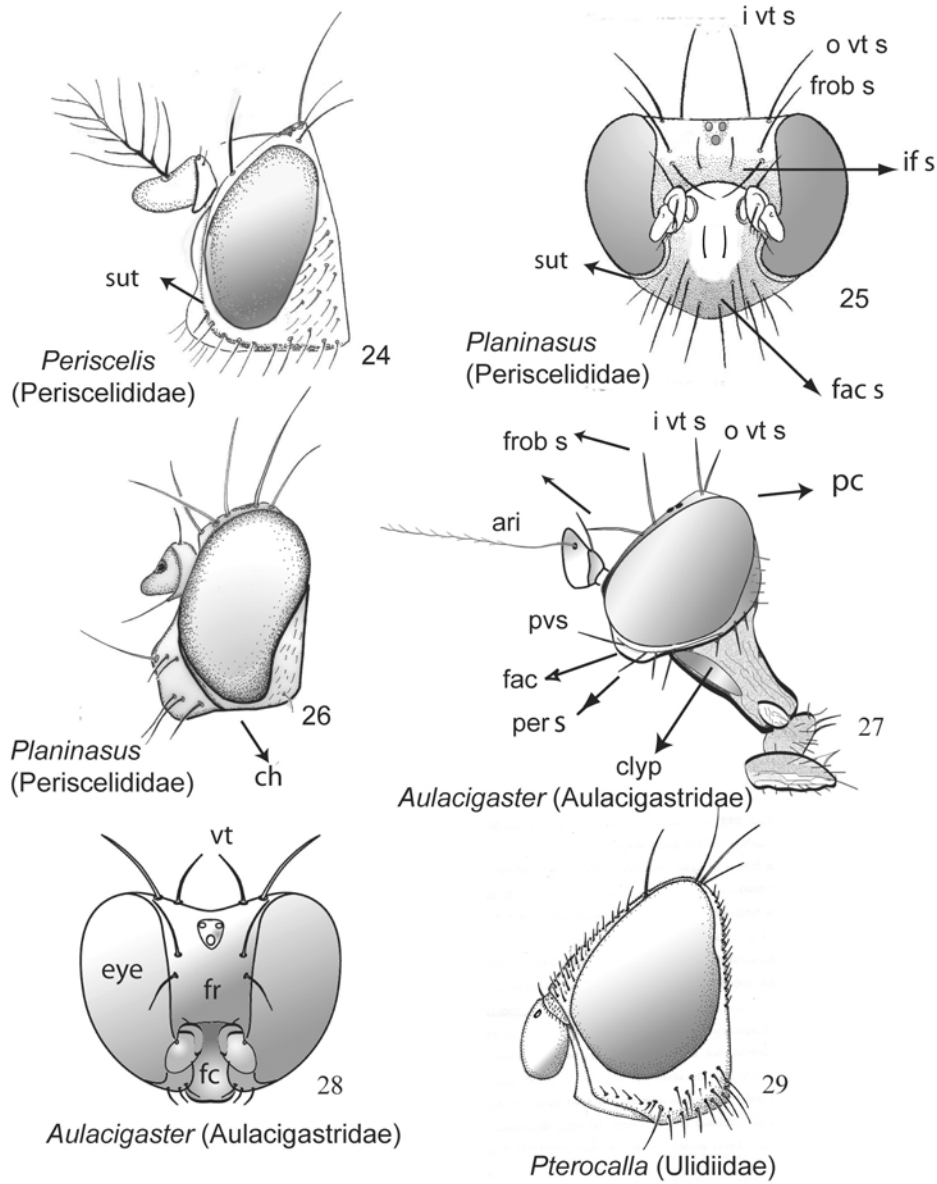
FIGURES 2.9-2.12.—Digital photographs of the anterior aspect of the head of aulacigastrids (Opomyzoidea). 9. *Aulacigaster colombiana*, undescribed species. 10. *Aulacigaster erikae*, undescribed species. 11. *Aulacigaster bromeliae*, undescribed species. 12. Undescribed genus and species (Malaysia). Not all to the same scale.



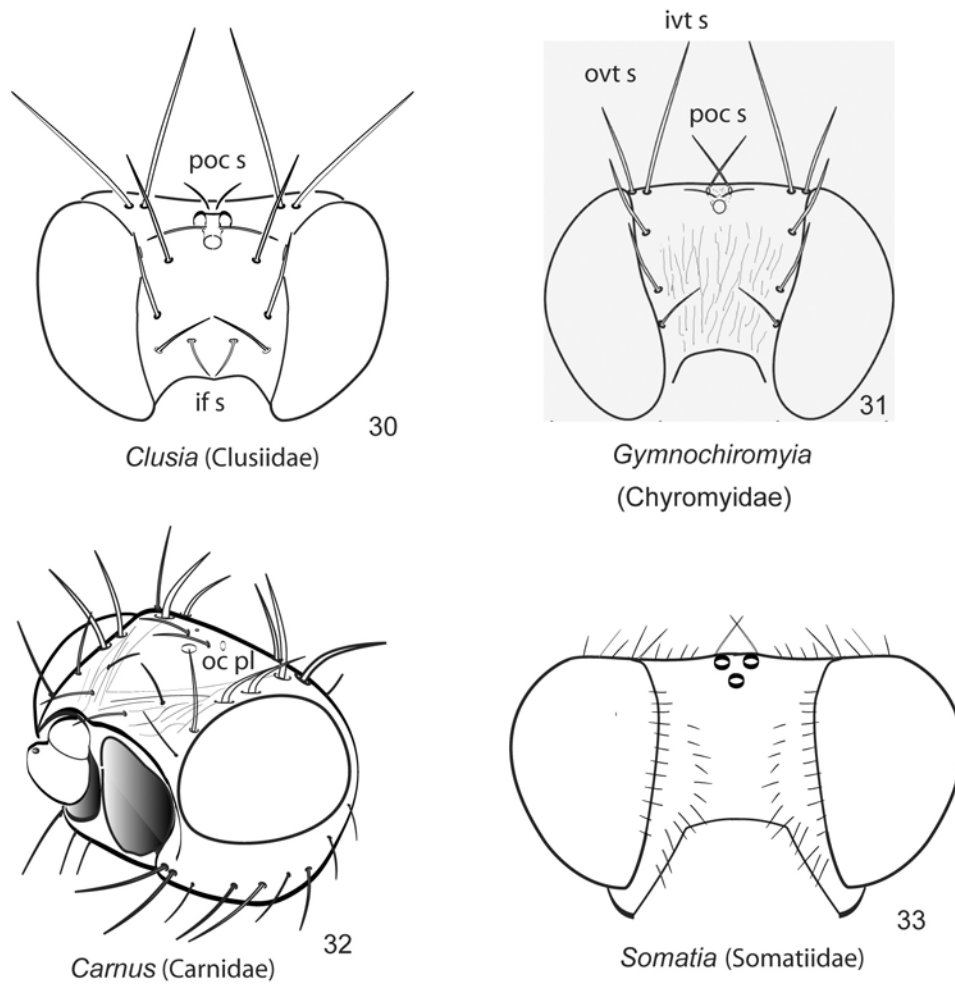
FIGURES 2.13-2.17.—Digital photographs of the anterior aspect of the heads of acalyptrates. 13 *Periscelis flinti* (Periscelidinae, Opomyzoidea). 14. *Stenomicra* sp, undescribed species (Stenomicroinae, Opomyzoidea). 2.1 a. *Cyamops neotropicus* (Stenomicroinae, Opomyzoidea); 2.15b. same, detail of face. 16. *Opomyza florum* (Opomyzoidea). 17. *Psila rosae* Fabricius (Diopsoidea). Not all to the same scale.



FIGURES 2.18-2.23.—Digital photographs of the lateral aspect of the head of acalyptrates. 18. *Aulacigaster bromeliae*, undescribed species (Opomyzoidea). 19. *Aulacigaster conspicua*, undescribed species (Opomyzoidea). 20. *Stenomicra* sp, undescribed species (Stenomicroinae, Opomyzoidea). 21. *Teratomyza neozelandica* (Opomyzoidea). 22. *Opomyza florum* (Fabricius) (Opomyzidae). 23. *Psila rosae* Fabricius (Diopsoidea). Not all to the same scale.



FIGURES 2.24-2.29.—Illustrations of the head of acalyptrates. 24. *Periscelis* sp., lateral aspect (Opomyzoidea, Periscelidinae). 25. *Planinasus ambiguous* Cresson (Opomyzoidea, Stenomicroinae), anterior aspect; 26. lateral aspect. 27. *Aulacigaster ecuadoriensis* (Opomyzoidea), lateral aspect; 28. anterior aspect. 29. *Pterocalla ocellata* Fabricius (Tephritoidea), lateral aspect. Not all to the same scale.



FIGURES 2.30-2.33.—Schematic representation of the anterior aspect of the head of acalyptrates. 30. *Clusia lateralis* Haliday (Opomyzoidea). 31. *Gymnochiromyia concolor* (Malloch) (Sphaeroceroidea). 32. *Carnus haemapterus* (Carnoidea). 33. *Somatia aestiva* (Fabricius) (Diopsoidea). Not all to the same scale.

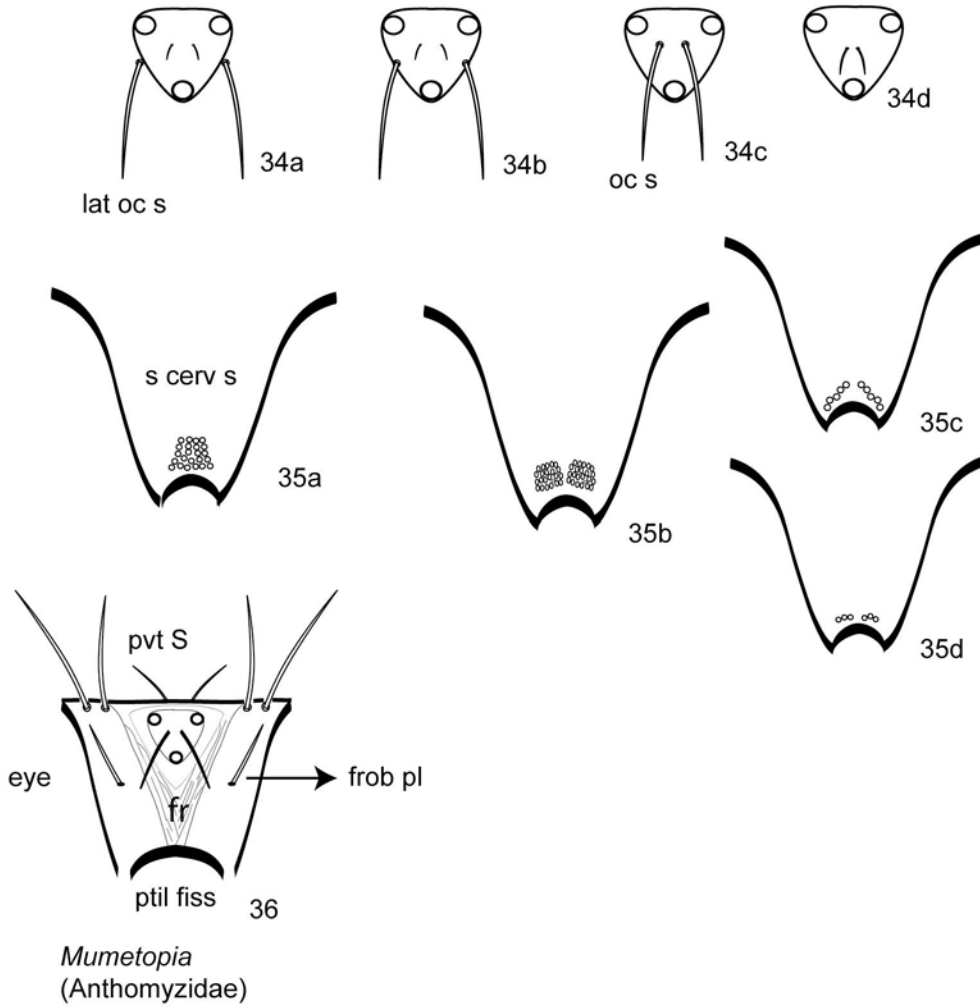
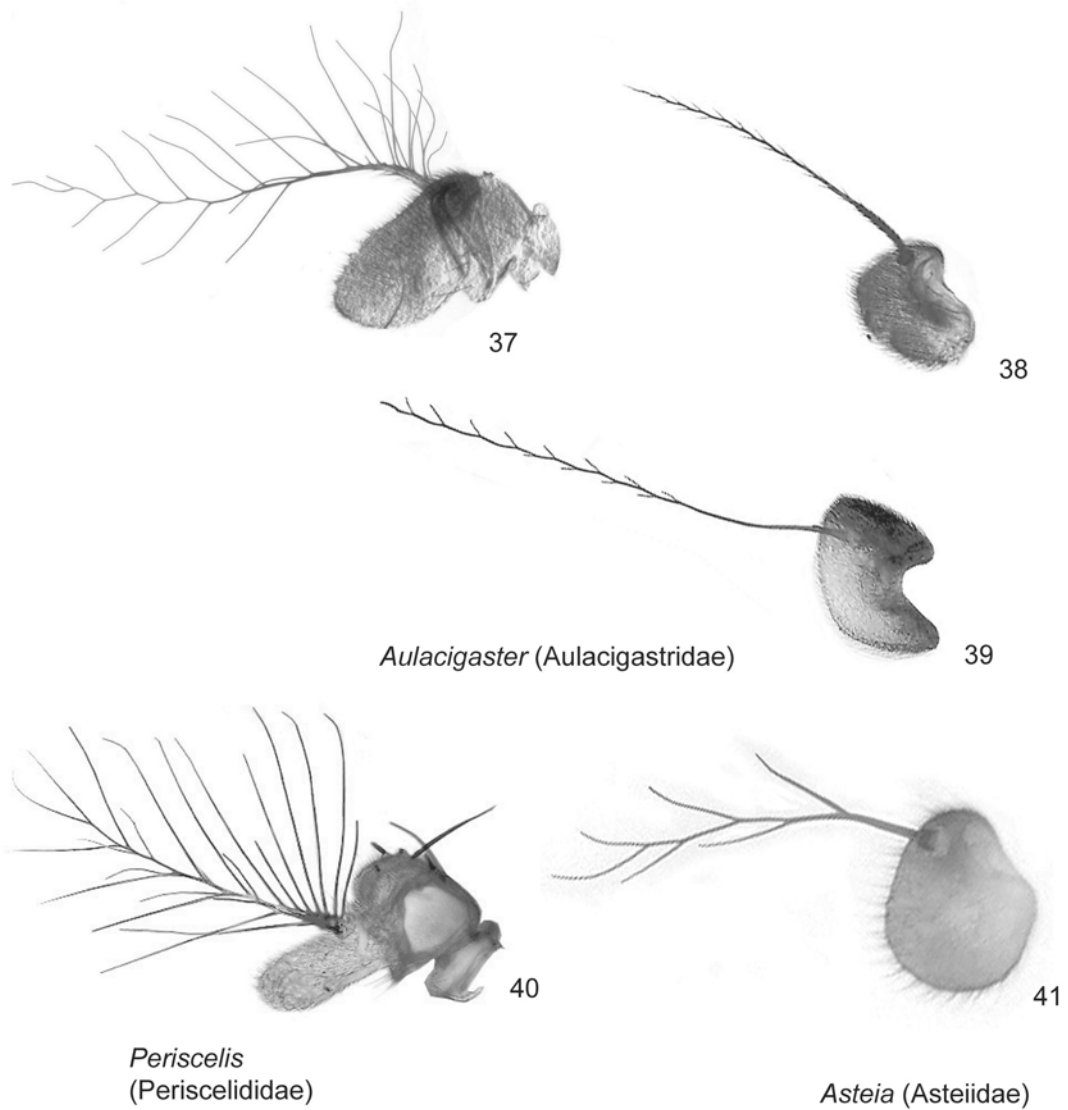
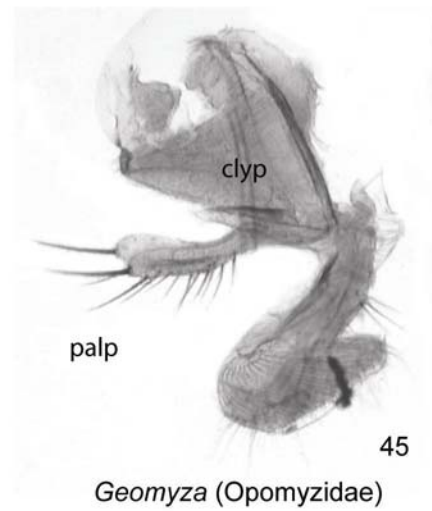
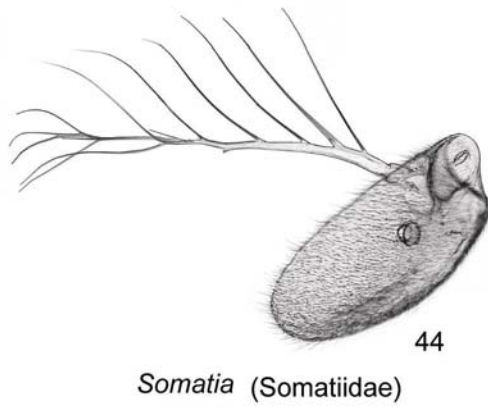
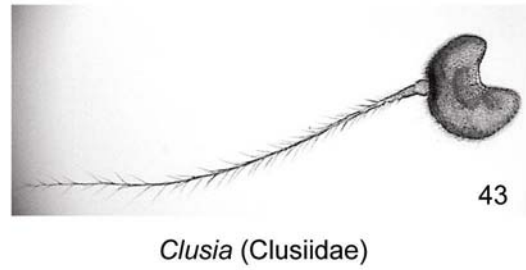
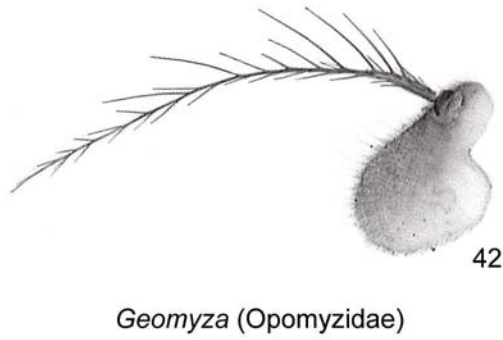


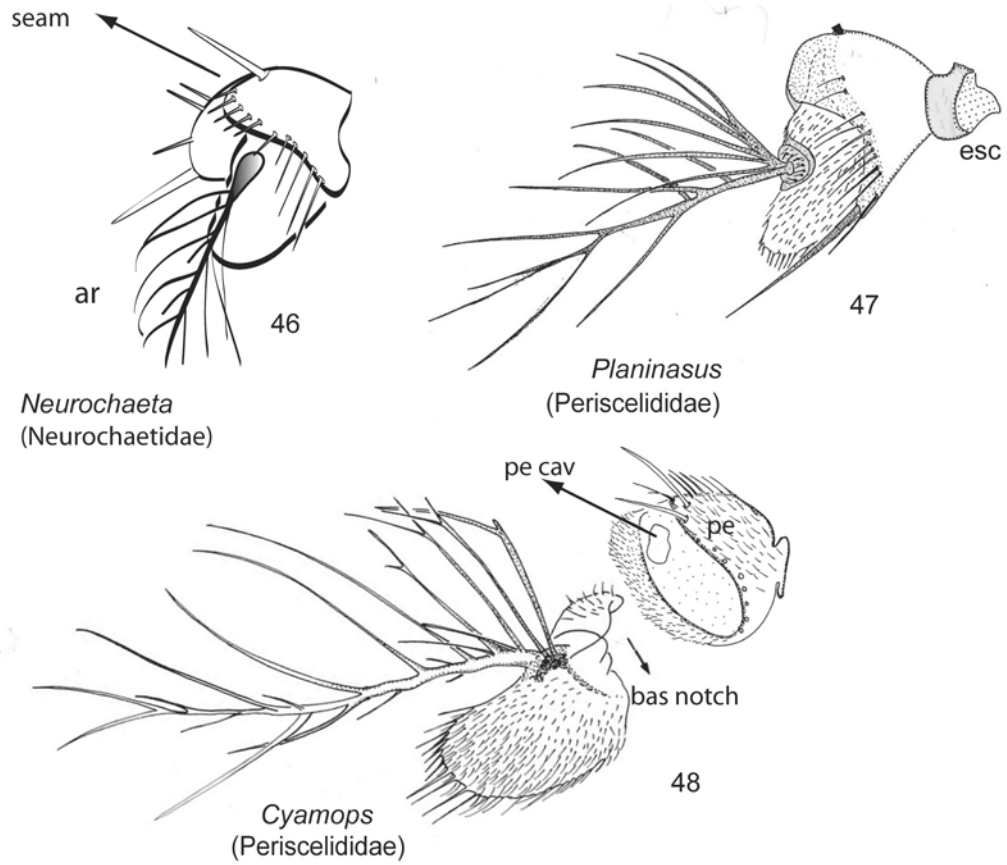
FIGURE 34 a-d.—Schematic representation of the anterior aspect of ocellar tubercle and ocellar setae, corresponding to characters 23-25. FIGURE 35 a-d. Schematic representation of the arrangement of supracervical setae on cervical region, corresponding to character 36. FIGURE 36. Frons of *Anomalochaeta guttipennis*, anterior aspect.



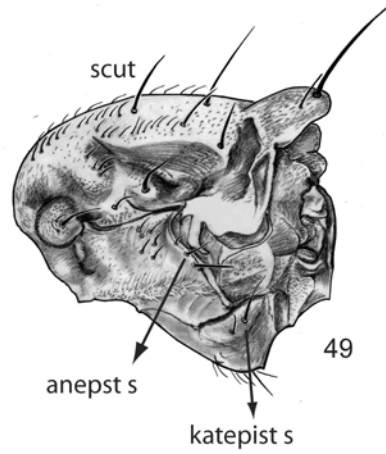
FIGURES 2.37-2.41.—Digital photographs of the lateral aspect of the antenna of opomyzoids. 37. *Aulacigaster bromeliae*, undescribed species. 38. *Aulacigaster mcalpinei* Mathis & Freidberg. 39. *Aulacigaster melanoleuca*, undescribed species. 40. *Periscelis* sp (Periscelidinae). 41. *Asteia amoena* Meigen. Not all to the same scale.



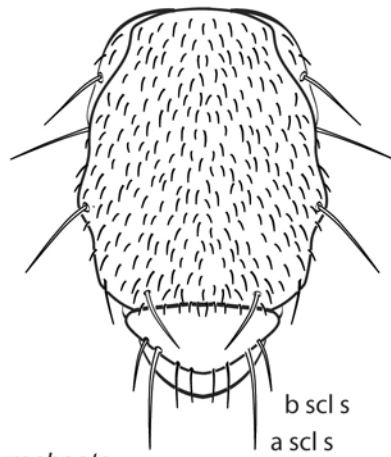
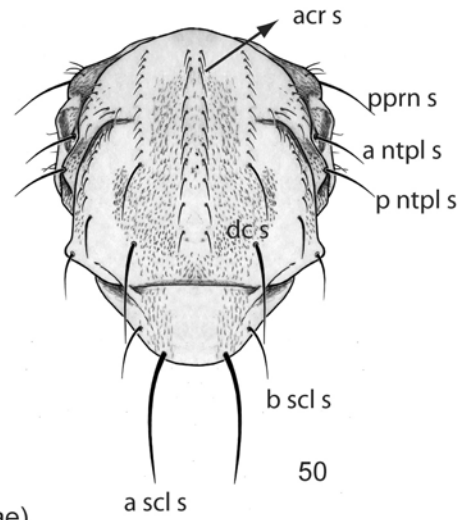
FIGURES 2.42-2.45.—Digital photographs of the lateral aspect of the antenna of acalyptrates. 42. *Geomyza tripunctata* Fallén (Opomyzoidea). 43. *Clusia lateralis* Haliday (Opomyzoidea). 44. *Somatia aestiva* (Fabricius) (Diopsoidea). FIGURE 45. Lateral aspect of the clypeus of *Geomyza* sp. (Opomyzoidea). Not all to the same scale.



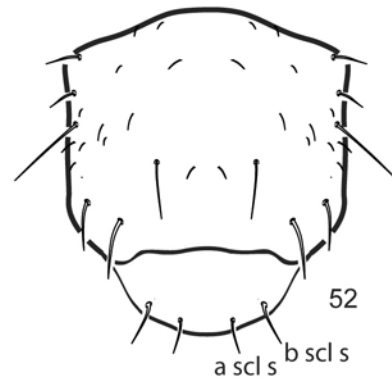
FIGURES 2.46-2.48.—Illustrations of the lateral aspect of the antenna of opomyzoids. 46. *Neurochaeta inversa*. 47. *Planinasus* sp, undescribed species (Stenomicroinae). 48. *Cyamops nebulosus* Melander (Stenomicroinae). Not all to the same scale.



Aulacigaster
(Aulacigastridae)

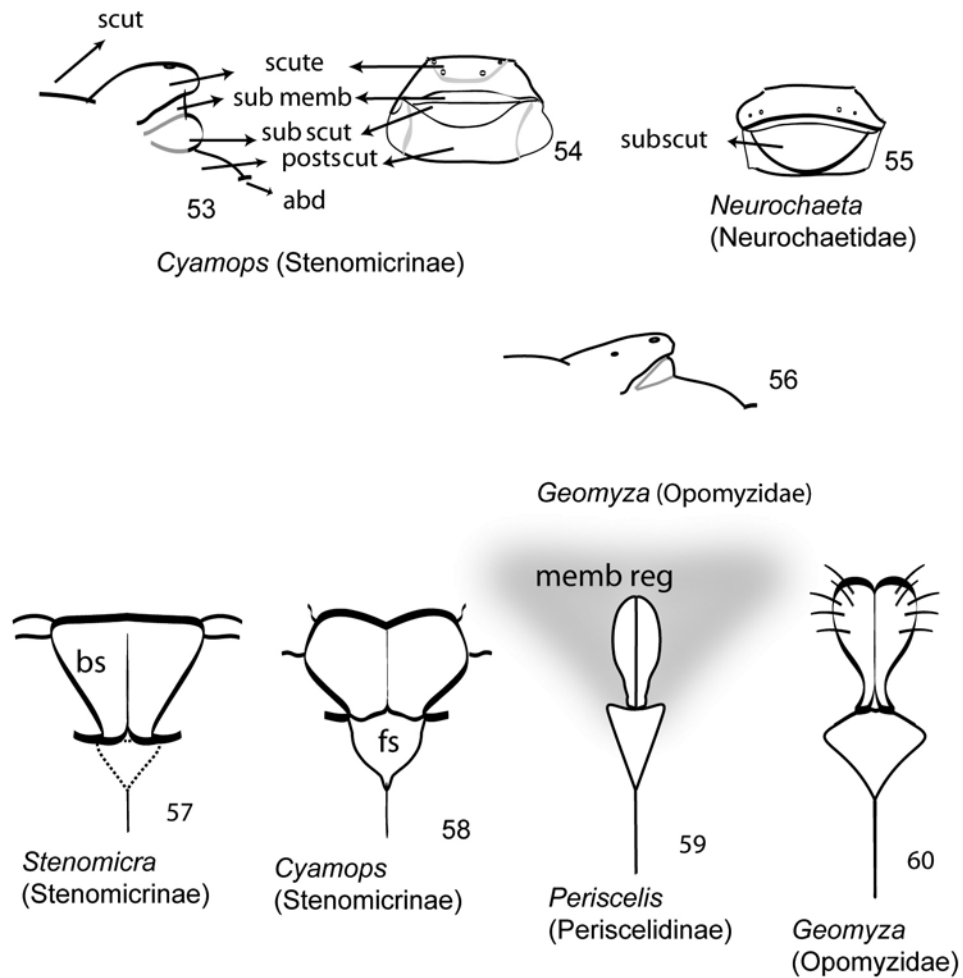


Neurochaeta
(Neurochaetidae)

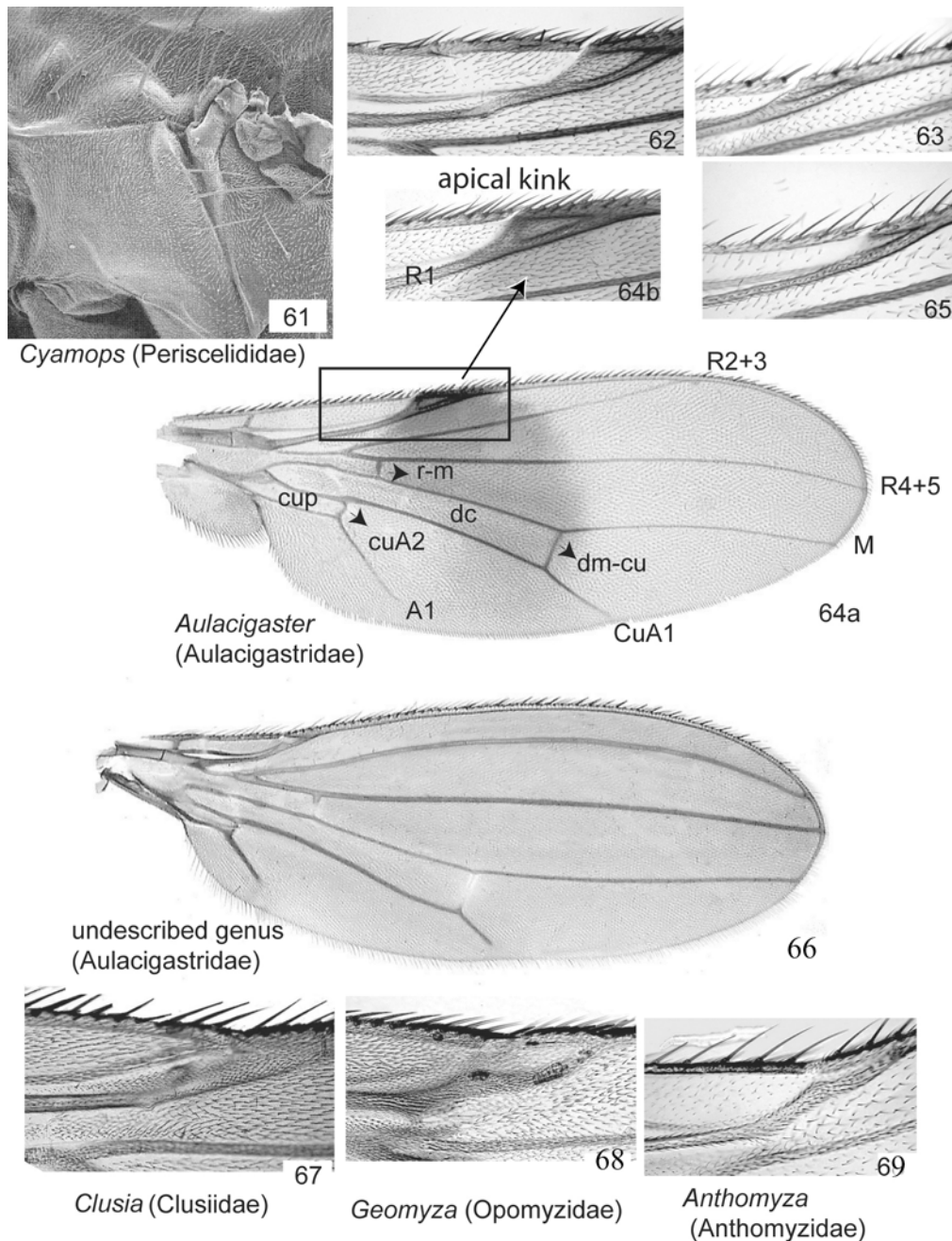


Nemula
(Neminidae)

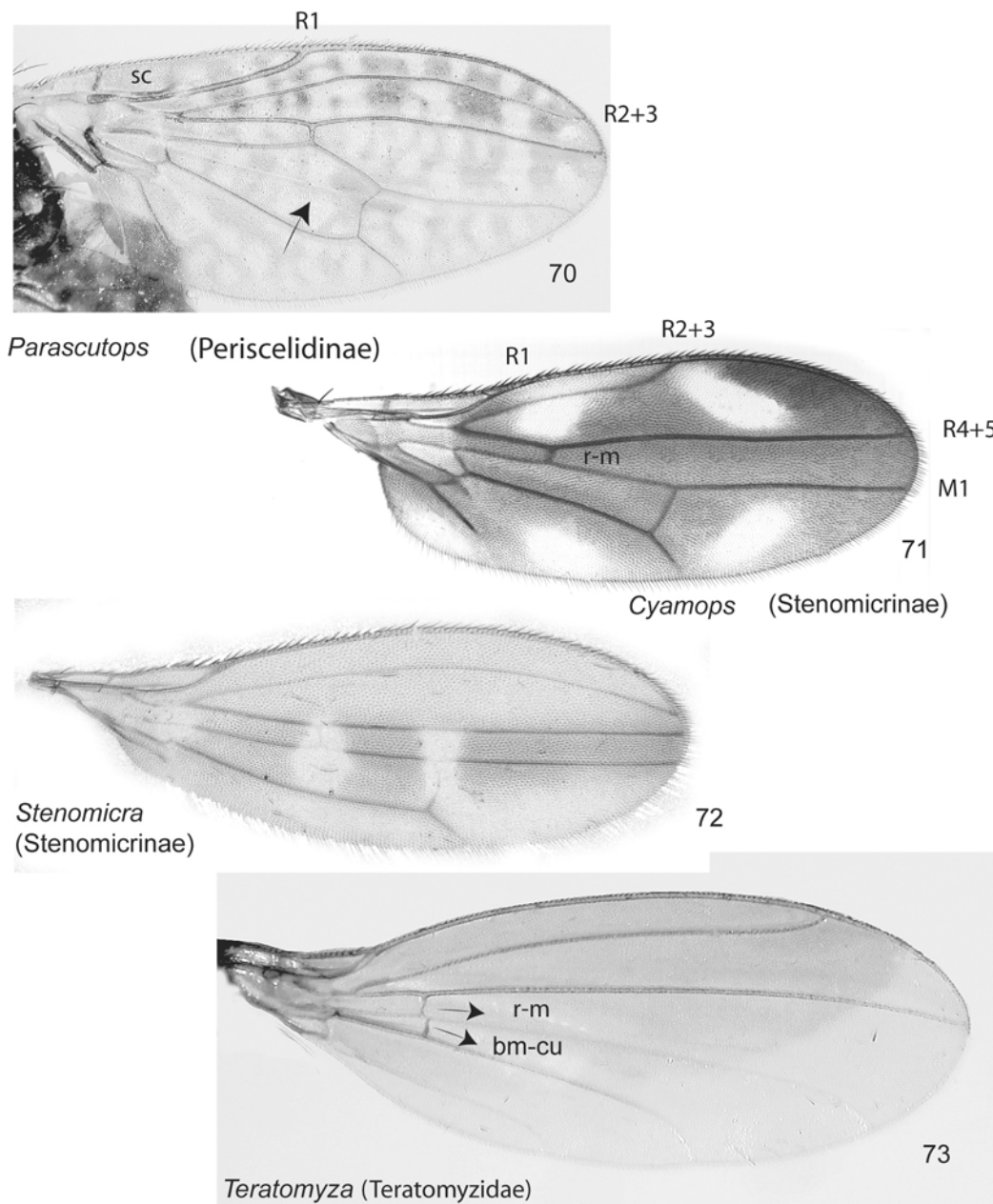
FIGURES 2.49-2.52.—Illustrations of the mesonotum of opomyzoids. 49. *Aulacigaster leucopeza*, lateral aspect; 50. Same, dorsal aspect. 51. *Neurochaeta inversa*, dorsal aspect. 52. *Nemula longarista*, dorsal aspect. Not all to the same scale.



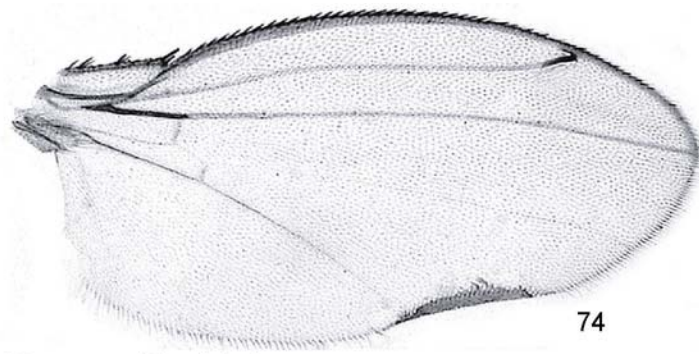
FIGURES 2.57-2.60. Ventral aspect of the proesternum of opomyzoids. 57. *Stenomicra* sp, undescribed species (Stenomicrinae). 58. *Cyamops* sp. (Stenomicrinae). 59. *Periscelis flinti* (Periscelidinae). 60. *Geomyza tripunctata*. Not all to the same scale.



FIGURES 2.62-2.69. Wings of opomyzoids. 62. *Aulacigaster* sp., detail of subcostal region. 63. *Aulacigaster melanoleuca* (Hennig), detail of subcostal region. 64. *Aulacigaster bromeliae*, undescribed species. 64a. wing; 64b. Detail of subcostal region. 65. *Aulacigaster lobata*, undescribed species, detail of subcostal region. 66. Undescribed genus of Aulacigastridae (Malaysia), wing. 67. *Clusia lateralis*, detail of subcostal region. 68. *Geomyza tripunctata*, detail of subcostal region. 69. *Anthomyza gracilis* Fallén, detail of subcostal region. Not all to the same scale.



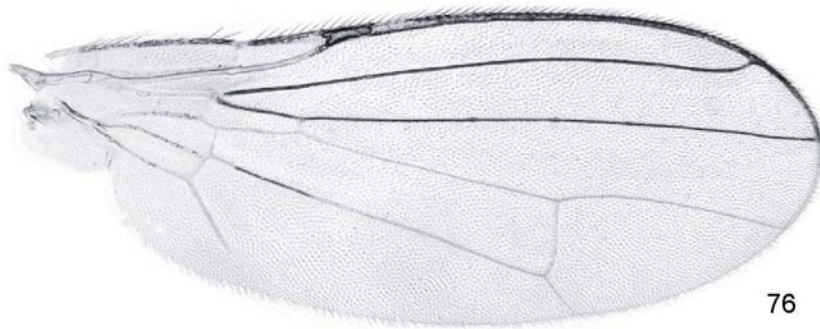
FIGURES 2.70-2.73.—Digital photographs of the wing of opomyzoids. 70. *Parascutops maculipennis*. 71. *Cyamops micronesicus* Baptista & Mathis. 72. *Stenomicra* sp, undescribed species (Stenomicrinae). 73. *Teratomyza neozelandica*. Not all to the same scale.



Meoneura (Carnidae)

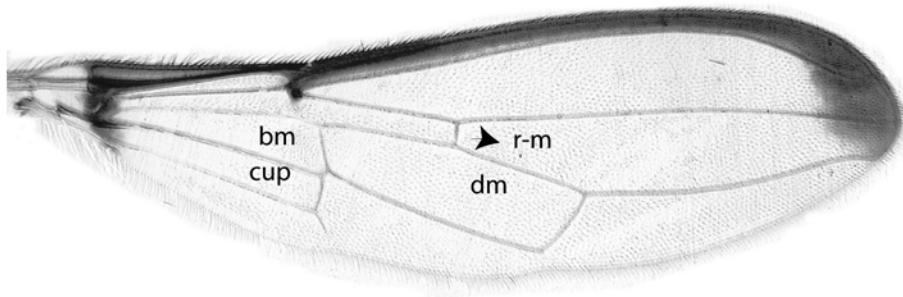


Psila (Psilidae)



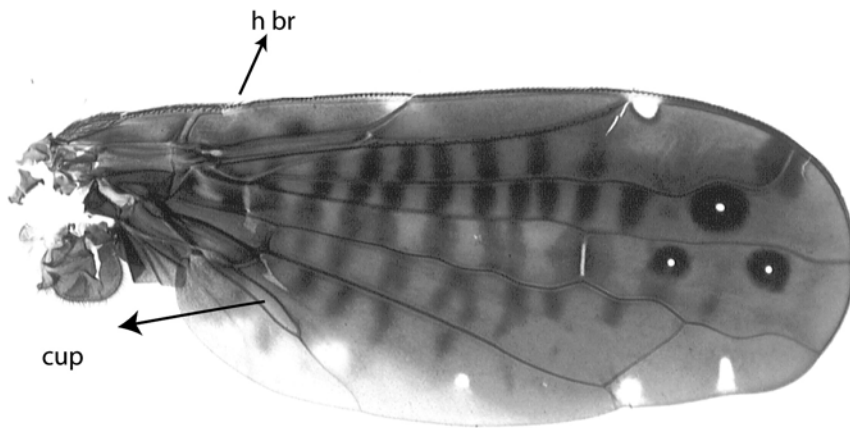
Gymnochiromyia (Chyromyidae)

FIGURES 2.74-2.76.—Digital photographs of the wing of acalyprates. 74. *Meoneura* sp (Carnoidea). 75. *Gymnochiromyia concolor* (Malloch) (Sphaeroceroidea). 76. *Psila rosae* Fabricius (Diopsoidea). Not all to the same scale.



Somatia (Somatiidae)

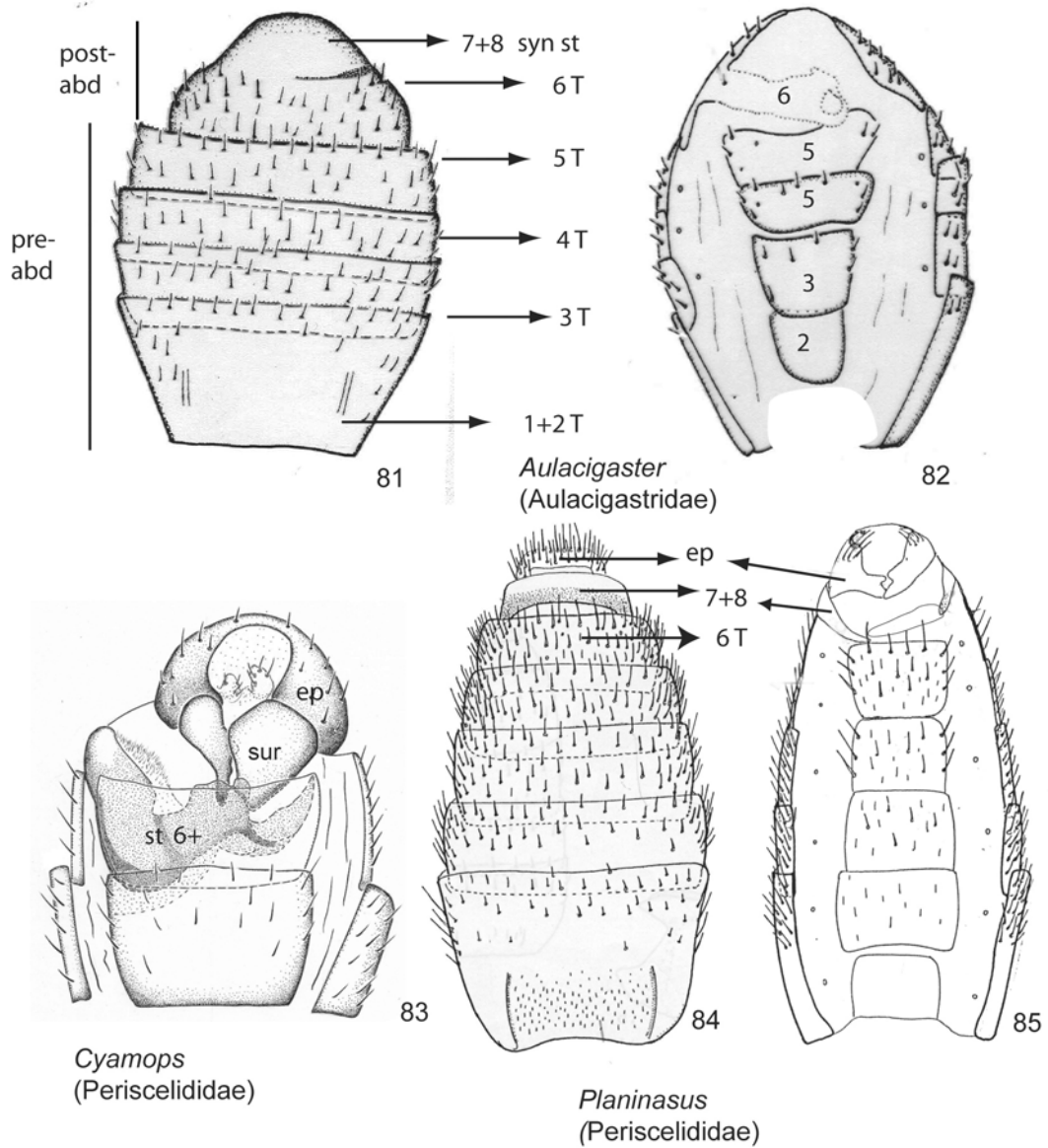
77



Pterocalla
(Ulidiidae)

78

FIGURES 2.77-2.78. Digital photographs of the wing of acalyptrates. 77. *Somatia aestiva* (Fabricius) (Diopsoidea). 78. *Pterocalla ocellata* Fabricius (Ulidiidae). Not all to the same scale.



FIGURES 2.81-2.85.—Illustrations of the male abdomen of opomyzoids. 81. *Aulacigaster bromeliae*, undescribed species, dorsal aspect; 82. Same, ventral aspect. 83. *Cyamops nebulosus*, ventral aspect. 84. *Planinasus* sp., undescribed species, dorsal aspect. 85. Same, ventral aspect. Not all to the same scale.

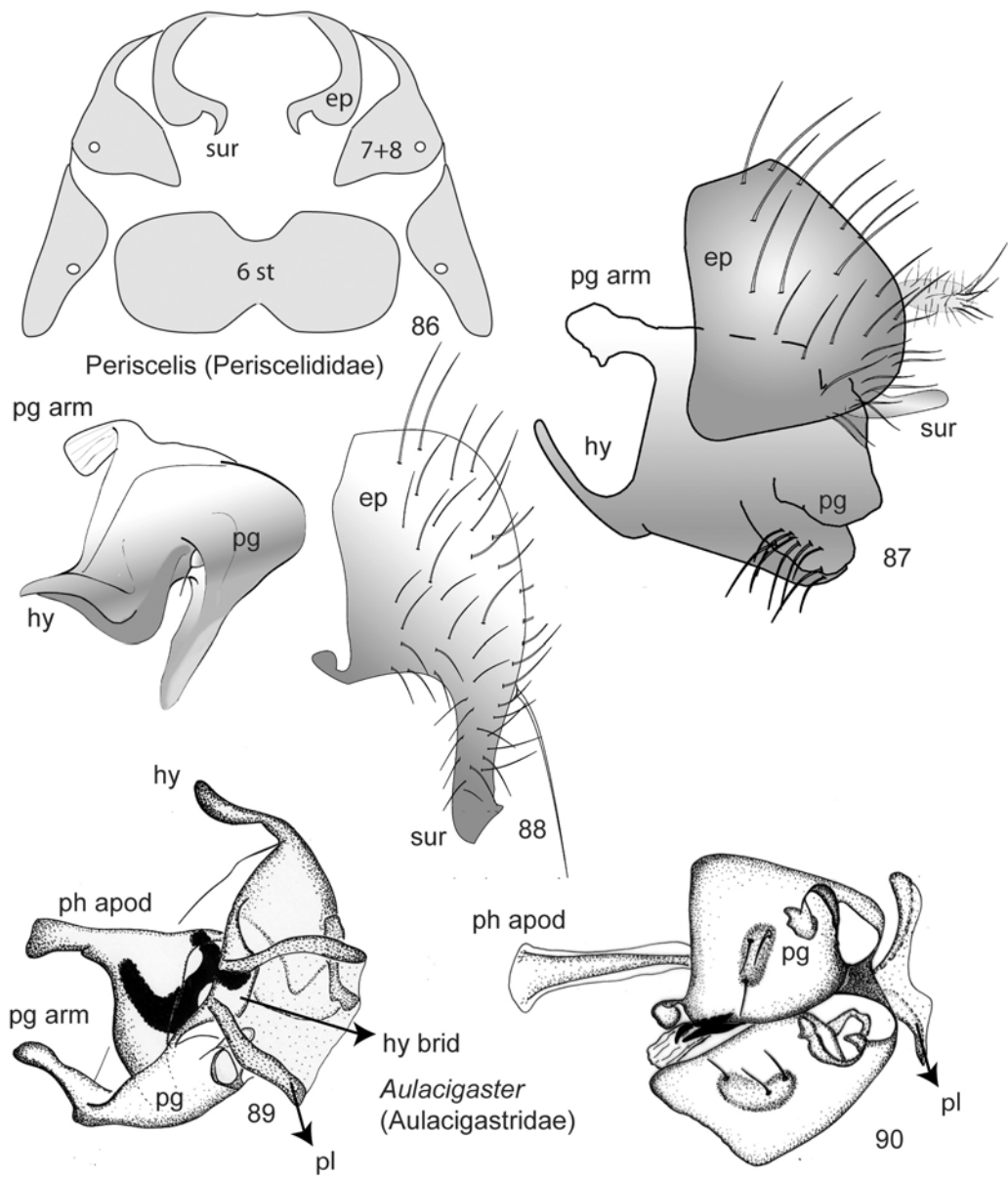
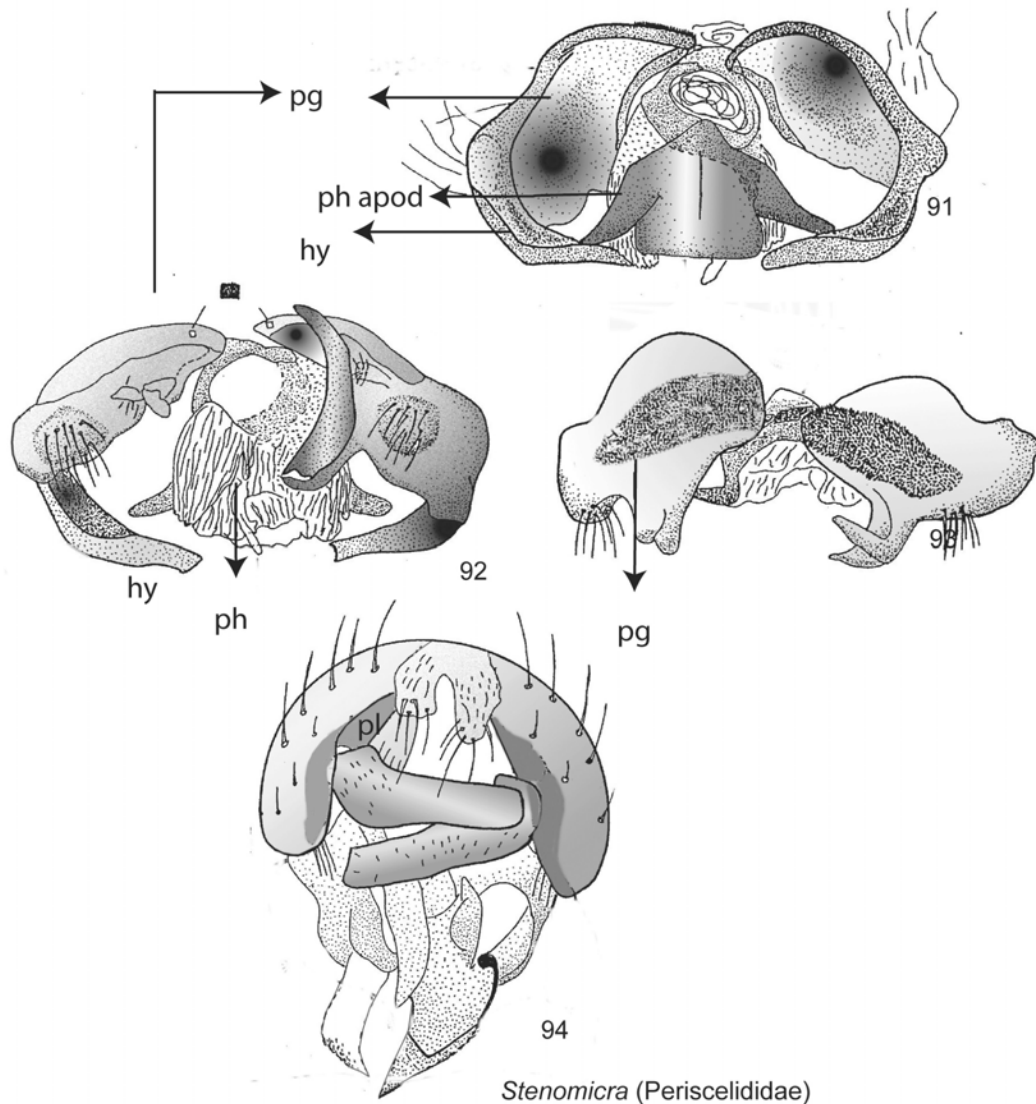
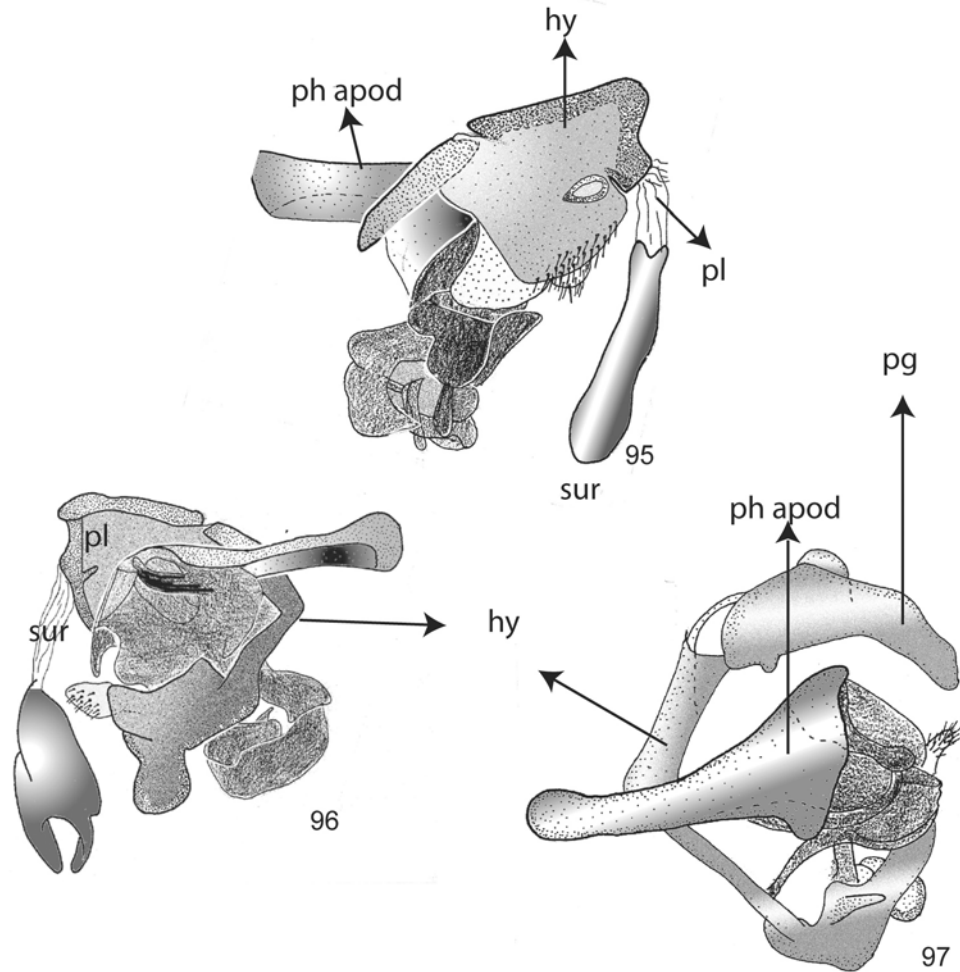


FIGURE 2.86.—Illustration of the ventral aspect of the posterior portion of the abdomen of *Periscelis annulata* (Periscelidinae). FIGURES 2.87-2.90. Male terminalia of *Aulacigaster* (Opomyzoidea). 87. *Aulacigaster* sp, epandrium and internal genitalic structures, lateral aspect. 88. *Aulacigaster* sp, epandrium and internal genitalic structures, lateral aspect. 89. *Aulacigaster bromeliae*, undescribed species, dorsal lateral aspect; 90. Same, ventral lateral aspect. Not all to the same scale.

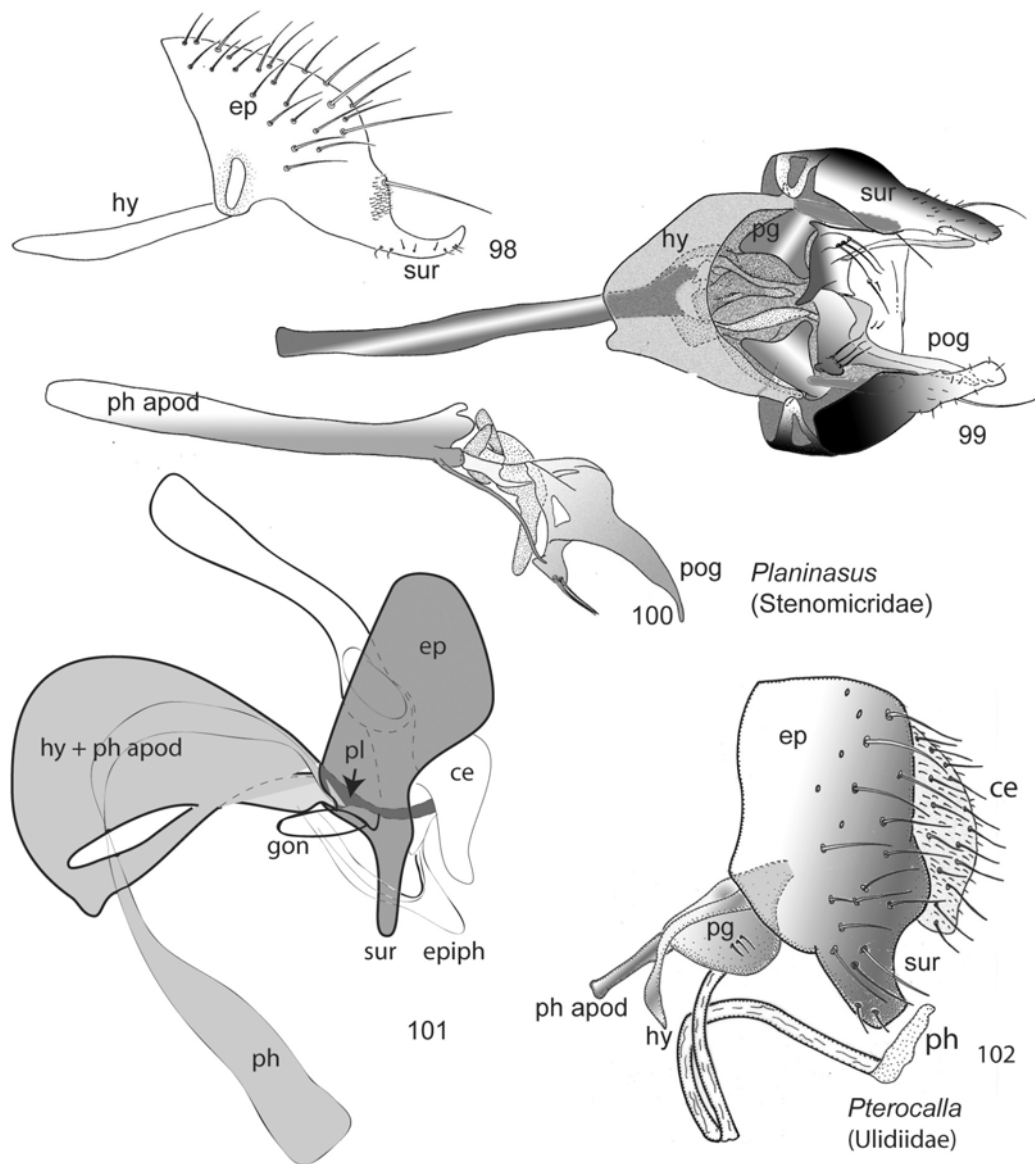


FIGURES 2.91-2.94.—Illustrations of the male terminalia of *Stenomicra* sp, undescribed species (Opomyzoidea). 91. Internal genitalic structures, dorsal aspect; 92. Same, postero-ventral aspect; 93. Same, anterior aspect; 94. Epandrium and internal genitalic structures, ventral aspect. Not all to the same scale.

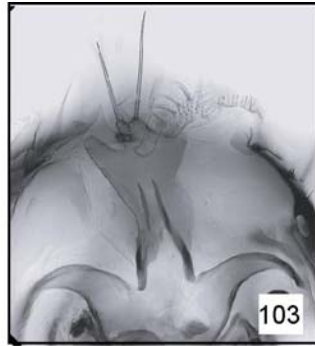


Cyamops (Periscelididae)

FIGURES 2.95-2.97.—Male terminalia of *Cyamops nebulosus* Melander (Opomyzoidea). 95. Internal genitalic structures, lateral aspect, right side; 96. Same, lateral aspect, left side; 97. Same, dorsal aspect. Not all to the same scale.



FIGURES 2.98-2.100.—Illustrations of the male terminalia of acalyptrates. 98-100. *Planinasus* sp. (Opomyzoidea). 98. Epandrium, lateral aspect; 99. Epandrium and internal genitalic structures, ventral aspect; 100. Internal genitalic structures, lateral aspect. 101. *Periscelis* sp. (Periscelidinae, Opomyzoidea), epandrium and internal genitalic structures, lateral aspect. 102. *Pterocalla ocellata* Fabricius (Ulidiidae), epandrium and internal genitalic structures, lateral aspect. Not all to the same scale.



103

Aulacigaster (Aulacigastridae)

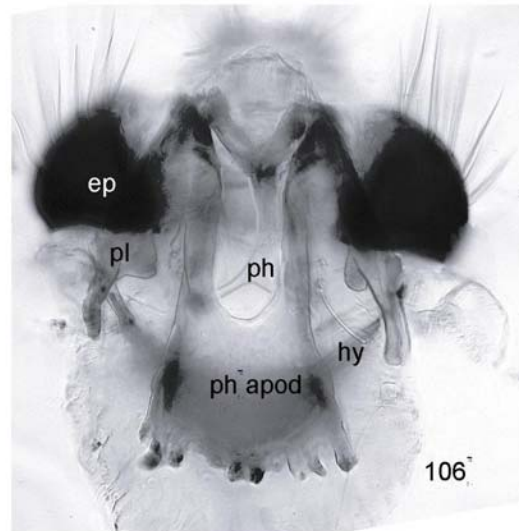


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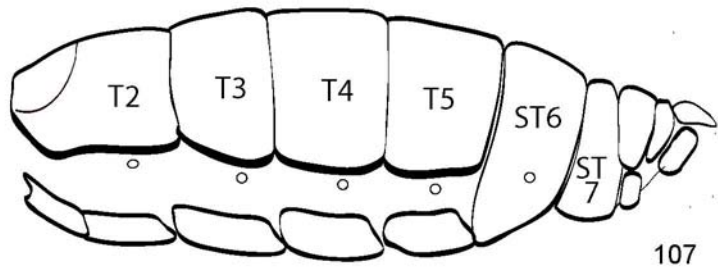
undescribed genus (Aulacigastridae)



106

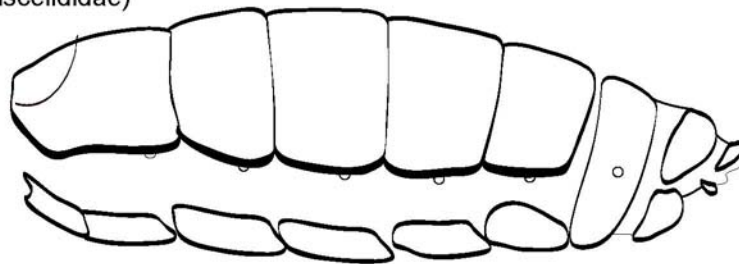
Psila (Psilidae)

FIGURES 2.103-2.106.—Digital photographs of the male terminalia of acalyptrates. 102. *Aulacigaster erika*, undescribed species (Opomyzoidea), subepandrial sclerite. 103. *Aulacigaster rufifemur*, undescribed species (Opomyzoidea), subepandrial sclerite. 104. Undescribed genus of Aulacigastridae from Malaysia (Opomyzoidea), anterior aspect; 105. Same, lateral aspect. 106. *Psila rosae* Fabricius (Diopsoidea), epandrium and internal genitalic structures, dorsal aspect. Not all to the same scale.



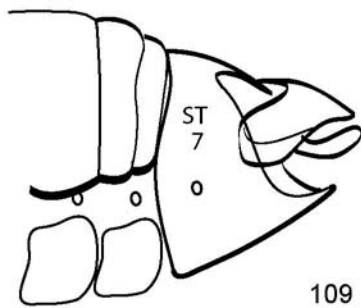
107

Cyamops (Periscelididae)



Periscelis (Periscelididae)

108



109

Stenomicra (Periscelididae)

FIGURES 2.107-2.108.—Illustrations of the lateral aspect of the female abdomen of periscelidids (Opomyzoidea). 107. *Cyamops* sp. (Stenomicrinae). 108. *Periscelis annulata* (Periscelidinae). 109. *Stenomicra* sp. (Stenomicrinae). Not all to the same scale.

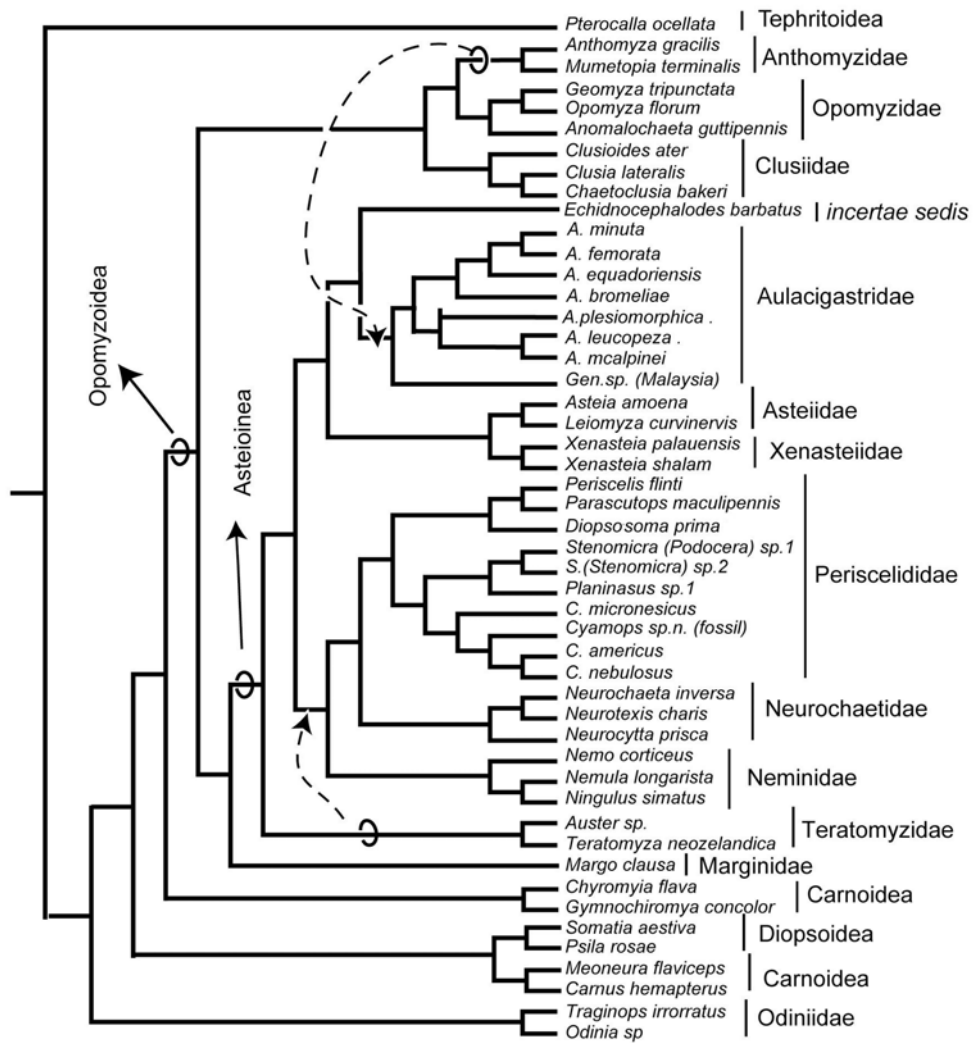


FIGURE 2.109. Strict consensus cladogram of four trees obtained with ordered characters, Goloboff weighting. Under unweighted parsimony, trees have 544 steps, consistency index of 0.32 and Retention index of 0.63. When characters are treated as unordered, the strict consensus of 4 trees (531 steps, consistency index of 0.32 and Retention index of 0.63) differs in topology as indicated by dashed lines.

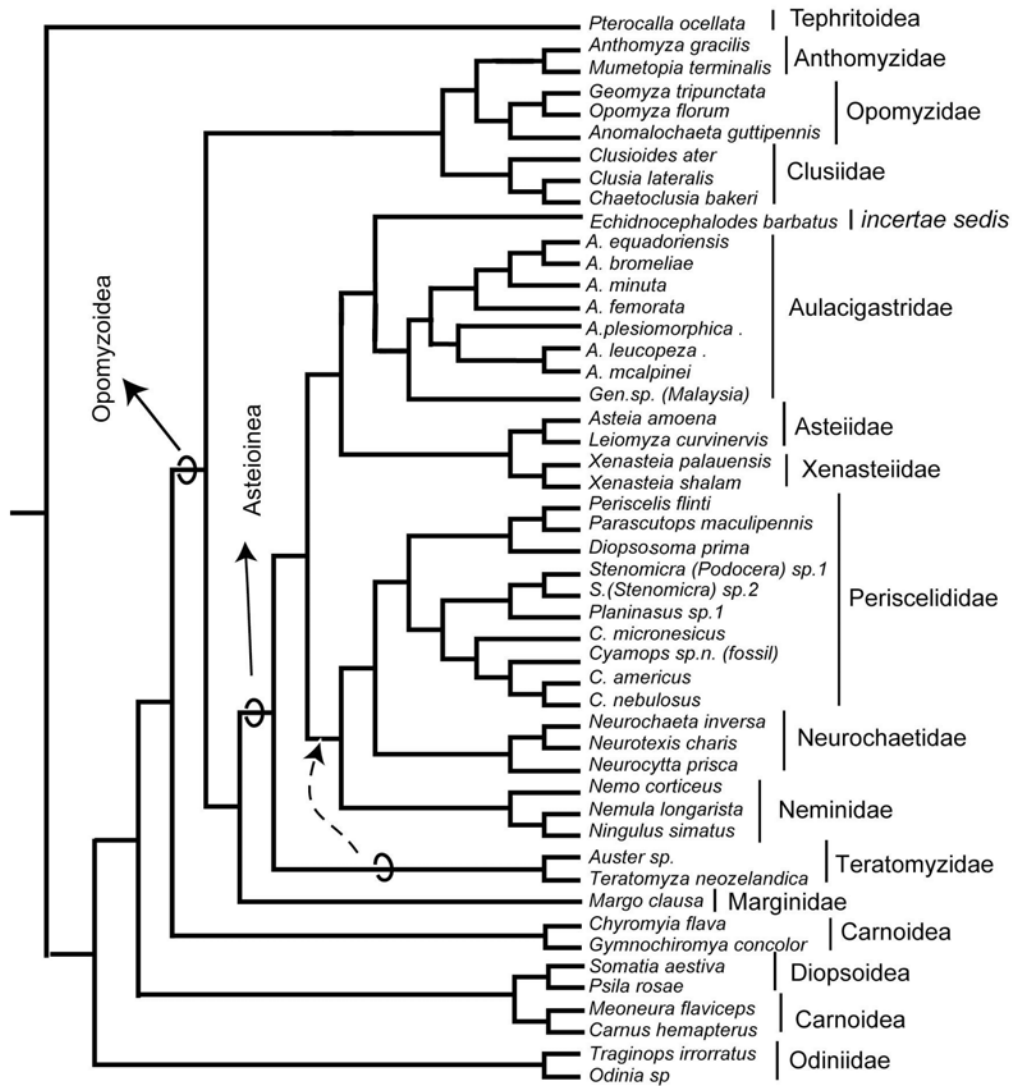


FIGURE 2.110. Strict consensus cladogram of 18 trees obtained after analysis employing ordered characters, successive weighting. Trees have 129.28 steps, consistency index of 0.5 and Retention index of 0.77. When characters are treated as unordered, the strict consensus of 37 trees (130.69 steps, consistency index of 0.57 and Retention index of 0.78) differs in topology as indicated by dashed lines, and lacks resolution within the genus *Aulacigaster*.

Chapter 3 : A REVISION OF THE GENUS *AULACIGASTER* MACQUART (DIPTERA:
AULACIGASTRIDAE)

ABSTRACT

The World species of the genus *Aulacigaster* Macquart, now numbering 42, are revised. New species are described for the Neotropical (28 spp) and Oriental (1 sp) regions, and the genus is divided into six species groups, of which five are new. Keys to the species known to occur in the Neotropical and Oriental regions, diagnosis, detailed distributional data for the species of the genus, notes on the biology and illustrations (photographs and drawings) are provided to assist species identification. A phylogenetic analysis was performed to test the monophyly of the genus *Aulacigaster* and the species-groups herein described. The ingroup includes a total of 18 exemplar species. Outgroup sampling includes exemplars from the Periscelididae, Anthomyzidae, and an undescribed genus from Malaysia. Analyses involving 4 different combinations of character weighting and character state ordering all recovered a monophyletic *Aulacigaster* and species groups.

INTRODUCTION

This revision concerns the Aulacigastridae, an obscure family of Acalyptrate Diptera. The Aulacigastridae are a relatively small group of flies that are associated with slime fluxes of deciduous trees (for example Robinson 1953; Cole and Streams 1970; Davis and Zack 1978; Mathis and Freidberg 1994; Hilger and Kassebeer 2000) or the phytotelmata of bromeliads (personal observations) and are found in the Afrotropical, Holarctic, Neotropical, and Oriental Regions. Aulacigastrid larvae are peculiar in having a long, posterior, respiratory siphon. The group has received increased attention during the last decade, not only because it has revealed surprising diversity and species richness, but also because of the challenges that its classification and characterization have posed to taxonomists (see below).

The main purpose of this revision is to describe and organize the largely unknown fauna of Aulacigastridae (Mathis and Freidberg 1994; Baptista 1998a) within the context of a phylogenetic analysis and to clarify some of the issues concerning the phylogenetic placement and characterization of the family.

The Family Aulacigastridae: historic and taxonomic background

The Aulacigastridae are currently classified in the superfamily Opomyzoidea (J. F. McAlpine 1989), as the sister-group of the family Periscelididae. Characterization of Aulacigastridae differs widely among authors (see below), and up to five genera have been assigned to it, in addition to the nominate genus, *Aulacigaster* Macquart. Duda (1924) first accorded familial status to the Aulacigastridae, and recent authors (Mathis and Freidberg 1994; Papp 1997; Baptista

1998b; and Hilger and Kassebeer 2000) have adopted a monotypic characterization for the family, as I have herein. A broader characterization of the family includes the genera *Cyamops* Melander, *Stenomicro* Coquillett, *Planinasus* Cresson, and a fossil species from Baltic amber, *ProtoAulacigaster electra* Hennig. Hennig (1958, 1965, 1969, 1971) first advocated this characterization, followed by Griffiths (1972, with the exclusion of *Stenomicro*), Teskey (1987) and J. F. McAlpine (1989). D. K. McAlpine (1978, 1983) proposed a rather different characterization that (1) transferred the genera *Stenomicro*, *Cyamops* (1978) and *Planinasus* (1983) from the Aulacigastridae to the Periscelididae, (2) excluded *ProtoAulacigaster electra* from the Aulacigastridae, and (3) described two new genera in the family, *Ningulus* (Afrotropical Region) and *Nemo* (Australian Region). Freidberg (1994) proposed the family Neminidae for *Ningulus*, *Nemo*, and his new Afrotropical genus, *Nemula*. Freidberg's work resulted again in a monotypic Aulacigastridae. Most recently, Evenhuis (1984, 1994a, 1994b) listed *ProtoAulacigaster electra* in *Aulacigaster*, and Roháček (1998) tentatively transferred the genus *Echidnocephalodes* Sabrosky from the Anthomyzidae to the Aulacigastridae.

The Genus *Aulacigaster* Macquart: historic and taxonomic background

The genus *Aulacigaster* Macquart, 1835, was described for *A. rufitarsis* Macquart 1835, a junior synonym of *A. leucopeza* (Meigen 1830). The genus remained monotypic for more than a century following its publication, and *A. leucopeza* was believed to occur in the Palearctic (type locality) and Nearctic

Regions (Christianson and Ryckman 1830; Malloch and McAtee 1924; Wirth 1955; Davis and Zack 1978, and Teskey 1978). In 1956, Hennig described the genus *Schizochroa* for a new species from Costa Rica, *S. melanoleuca*, in the Aulacigastridae. Thirteen years later, he (Hennig 1956) added three more species to *Schizochroa*, *S. plesiomorphica* (Peru), *S. minuta* and *S. ecuadoriensis* (Ecuador). D.K. McAlpine (1983) synonymized the genus *Schizochroa* with *Aulacigaster*.

Interest in the taxonomy of *Aulacigaster* has steadily increased during the last decade. Barraclough (1993) revised the Afrotropical fauna and described two new species, *A. africana* (South Africa) and *A. perata* (Cameroon). A year later, Mathis and Freidberg (1994) revised the Nearctic fauna, describing three new species: *A. neoleucopeza* and *A. mcalpinei*, which occur sympatrically and frequently at the same flux, and *A. sabroskyi*. These authors (op. cit.) also noted that previous records of *A. leucopeza* for the Nearctic Region were misidentifications of *A. neoleucopeza*. Papp (1997) revised the Palearctic fauna of *Aulacigaster*. He described two new species for that region, *A. afghanorum* (Afghanistan) and *A. falcata* (Hungary), and reported the presence of *A. neoleucopeza* Mathis and Papp in the Palearctic Region, noting that previous distributional records of *A. leucopeza* need verification.

Recently, Hilger and Kassebeer (2000) described a new species of *Aulacigaster* for the Afrotropical Region (Reunión), *A. borbonica*. The genus has now 13 available names, but a large number of undescribed species has been reported for the Neotropical Region (Mathis and Freidberg 1994; Baptista 1998). Keys are available for the Afrotropical (Barraclough, 1993), Nearctic (Mathis and

Papp 1994) and Palearctic (Papp 1997) Regions.

METHODS

General.—I have adopted the descriptive terminology of J.F. McAlpine (1981) with the modifications noted below. I follow Sabrosky (1983) in using the term “microtomentum” rather than pruinosity. Setae posterior to the pseudovibrissal seta are called peristomal setae. The nomenclature for structures of the male terminalia follows Cumming, Sinclair, and Wood (1995).

Acronyms for institutions used in the text are as follows:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.
CNC	Canadian National Collection, Ottawa, Ontario, Canada.
DEI.	Deutsche Entomologische Institut, Eberswalde, Germany.
EPNE	Escola Politécnica Nacional, Quito, Ecuador.
HMHM	Hungarian Natural History Museum, Budapest, Hungary.
MNRJ.	Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil.
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.
TAU	Tel Aviv University, Tel Aviv, Israel.
UFPR	Universidade Federal do Paraná, Curitiba, Paraná, Brazil.
UGE	University of Guelph, Guelph, Canada.

Taxonomy.—Label data of holotypes are quoted exactly as they appear on the label with a slash (/) denoting the end of a label. Clarifying comments are included within brackets.

Because specimens are small, study and illustration of the male and female

terminalia required use of a compound microscope. Photographs were taken with a Nikon Coolpix 990® digital camera and edited in Adobe Photoshop®. Illustrations and plates were manipulated with characters and information on their states within taxa was stored in DEscriptive Language for TAxonomy (DELTA)® files (Dallwitz 1980, Pankhurst 1991). The descriptions and keys were generated using the “DELTA” software package (Dallwitz, 1980; Dallwitz, M. J., T. A. Paine and E. J. Zurcher, 1993-onwards). Species descriptions are composite, including information on the holotype and other conspecific specimens. Characters used to characterize the genus and species-groups are not repeated in species descriptions. To generate such inclusive descriptions, I wrote a separate “tonath” DELTA file for the diagnosis of the genus *Aulacigaster* and species-groups, and one tonath DELTA file for each of the six species-groups. Species diagnostic descriptions were generated with the aid of Intkey (Dallwitz, 1980; Dallwitz, M. J., T. A. Paine and E. J. Zurcher, 1993-onwards). They distinguish each taxon in at least one respect from every other taxon in the genus.

The following ratios are used in the descriptions (two males and two females were measured for each species when available, cases to the contrary are indicated under the appropriate species description):

1. Wing ratio: the greatest length of wing divided by the greatest width of wing;
2. Scutal ratio: the greatest length of scutum divided by the greatest width of scutum;

3. Eye ratio: the greatest length of eye divided by the greatest height of eye.

Phylogenetic Analysis.—The phylogenetic analysis was performed with the following objectives: (1) to test the monophyly of the genus *Aulacigaster*, and (2) to test the monophyly of the species-groups herein described. To accomplish these goals, an analysis including all of the component species of the genus is unnecessary. Therefore, I opted for the exemplar approach to taxa selection (Yeates 1995). At least two exemplars representing each species group were included in the analysis. If the monophyly of a group seemed doubtful, I included additional exemplars for that group. This procedure was used with the *leucopeza* and *ecuadoriensis* groups. A total of 18 exemplar species was included in the ingroup (see Appendix 1). The outgroup was selected to account for conflicting hypothesis made by previous authors. As the sister group of the Aulacigastridae is probably to be found within the family Periscelididae *sensu stricto* (Hennig 1971; J.F. McAlpine 1989), and as some periscelidid (Stenomicroinae) genera had previously been classified as aulacigastrids, I have used, as outgroups, exemplars from the two subfamilies of Periscelididae presently recognized, Periscelidinae and Stenomicroinae (Mathis and Papp 1992). Moreover, as a previous, unpublished phylogenetic analysis (Baptista 1998a and b, 1999) had revealed the family Anthomyzidae to be closely related to the Aulacigastridae, one exemplar of this family was also included in the outgroup.

New and traditional morphological characters were combined in a quantitative phylogenetic analysis. I endeavored to include characters that seemed independent and informative at the generic- and species-group levels. Only

characters that showed obvious discrete variation were included, and for this reason, characters 9 and 16 were not used in the analysis. I did not exclude characters because of perceived levels of homoplasy, in contrast to some authors working with Diptera (see for example D. K. McAlpine 1978: 274) but in accordance with recent methodological study (Wiens and Servedio 1997; Wiens 1998; see also Poe and Wiens 2000).

Characters were coded for the analysis as either binary (15 characters) or qualitative multistate (29 characters).

The matrix was initially analyzed with a branch-and-bound search, with all characters unordered, and equally weighted. Following initial parsimony analysis, successive weighting (Farris 1969) was applied using Farris' (1989) rescaled consistency index. This approach gives highest weight to characters that have the least amount of homoplasy for the given set of trees. The foregoing analysis was then repeated after ordering some of the multistate characters (see Table 3.1), thus minimizing the amount of morphological change between states (similarity criterion). For some characters, no transformation seemed more plausible than another, and the characters were left unordered. Following parsimony analysis, the characters were weighted as described in the first analysis.

Analyses were carried out using PAUP 4.0 (Swofford 2000).

Support levels were measured using Bootstrap analysis (Felsenstein 1984) also using PAUP 4.0. A total of 100 replicates were performed using a heuristic search with tree-bisection-and-reconnection branch swapping (TBR)

RESULTS AND DISCUSSION

Taxonomy

Genus *Aulacigaster* Macquart

Aulacigaster Macquart, 1835: 579. Type species: *Aulacigaster rufitarsis* Macquart, 1835 (= *Diastata leucopeza* Meigen), by monotypy. *Aulacigaster* Wirth, 1965: 823 [Nearctic catalog] .–Papavero, 1967: 91 [Neotropical Catalog] .–Teskey, 1976: 12 [Diptera associated with trees].–Sabrosky, 1977: 230 [Oriental Catalog].–Papp, 1984: 61 [Palearctic Catalog]; Teskey, 1989: 891-894 [Manual of Nearctic Diptera].–Barraclough, 1993: 331-42 [Afrotropical species].–Mathis and Freidberg, 1994: 586–591 [Nearctic species].–Papp, 1997[8]: 225-234 [Palearctic species]; 1998: 279-284 [Manual of Palearctic Diptera].–Bachli *et al.*, 1999: 120 119-122 [Checklist, Switzerland, Italy and Greece].

Apotomella Dufour, 1846:455. Type species: *Apotomella impressifrons* Dufour, 1846: 460 [= *Diastata leucopeza* (Meigen, 1830)], by monotypy.

Ampycophora Wahlberg, 1847: 261. Type species *Ampycophora tarsata* Wahlberg, 1847, [= *Diastata leucopeza* (Meigen, 1830)], by monotypy.

Sephanilla Rondani, 1874: 276. Type species: *Sephanilla sertulata* Rondani 1874 (= *Diastata leucopeza* Meigen), by original designation (p.246).

Aulacogaster Oldenberg, 1924: 30 [unjustified emendation for *Aulacigaster*].

Schizochroa Hennig, 1956: 151-152. Type species: *Schizochroa melanoleuca*, by original designation.

DIAGNOSTIC DESCRIPTION.— Adult: Coloration: Body predominantly dark brown to black. Cervix gray microtomentose. Frons often with anterior 1/3–1/2 yellowish in ground color or bearing a transverse, large, orange band. Scutum typically uniformly microtomentose. Pleura, in some species, white on ventral half.

Morphology: Body robust (scutal ratio 1.1–1.35), or elongate (scutal ratio 1.5–1.75). Head: Head higher than long (head ratio lower than 0.9), or longer than high (head ratio higher than 1.1). Face completely sclerotized, often protruding, easily visible in profile. Gena narrow, usually less than 1/3 the width of 1st flagellomere. First flagellomere round or oval or triangular. Arista unsegmented, often rayed, zigzag, rays present on apical 2/3 of arista, dorsal and ventral rays alternating. Ocellar seta, when present, minute. Inner vertical setae typically convergent, seta at most 3/4 length of outer vertical seta. Fronto-orbital setae 2, in some species with posterior seta internal to and almost horizontally aligned with anterior seta. Setulae between fronto-orbital setae 1-2, one is proclinate. Intra-frontal seta absent. Peristomal vestiture typically consisting of weak setae following pseudovibrissal seta.

Thorax: Anepisternum bearing 1–2 setae along posterior margin. Scutellar setae 2, apical setae nearly parallel, curved posteriorly. Wing: Cell dm flat, lacking a longitudinal crease or fold. Crossvein r-m basal to middle of combined cell dm + bm. Sc vein partly fused with vein R1 apically.

Male abdomen and terminalia: Pregonital segment large, at least twice as long as tergite 5. Abdominal sternites slightly increasing in width posteriorly. Surstylus

fused with epandrium; cerci separate or partly fused. Subepandrial sclerite with caudal portion attached to cerci and proximal portion attached to hypandrial bridge. Hypandrium bearing a lateral, anterior apodeme at base of each gonopod, halves of hypandrium connected by a narrow bridge above aedeagal apodeme. Gonopods fused to hypandrium forming a shovel-like structure with a posterior lobe or projection and a few central setae. Phallapodeme cuneiform with asymmetrical posterolateral projections. Phallus short, partly sclerotized. Parameres absent.

Female abdomen and terminalia: Postabdomen distinctly shorter than preabdomen. Spermathecae often with ventral digitiform projections.

Immatures: Larva (3rd instar): Subcylindrical, amphipneustic, bearing a long, partly retractile terminal respiratory tube; integument white, almost transparent, covered with minute spicules and sensory setae, or smooth; 3 thoracic and 8 abdominal segments present; abdominal segments with ventral creeping pads bearing minute spicules; last abdominal segment with a small perianal pad; anterior spiracles small, retracted into a pair of deep, narrow pockets; posterior spiracles on apex of respiratory tube, joined other at their base, bifurcating posteriorly; cephalopharyngeal skeleton slender with well-developed mandible bearing 2 pairs of accessory teeth; hypopharyngeal and tentoropharyngeal sclerites separate. Puparium: light brown, oval in shape, with prothoracic spiracle completely everted.

DISTRIBUTION.—Worldwide, excluding Australian and Oceanic Regions.

BIOLOGY.—Information on the biology of flies of the genus *Aulacigaster* pertains to species of the *leucopeza* group. Adults and immatures are peculiar for

weeping wounds and sap fluxes of deciduous trees (Robinson 1953; Teskey 1976). A group of species (here named “the *bromeliae* group”) inhabits bromeliads in the Neotropical Region. Larvae of these species are fully aquatic and probably feed on decaying organic matter. Some adults of *Aulacigaster* were collected on freshly cut logs. A few species have been collected on Heliconiaceae leaves.

Implicit Attributes

Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable:

Adult.—Coloration: Occiput mostly subshiny to dull. Cervix grey microtomentose. Anterior portion of frons without a microtomentose band. Facial band absent. Scutum uniformly microtomentose. Pleura uniformly black. Abdomen completely dark brown to black. Pregenital segment mostly polished.

Morphology: Body robust, scutal ratio 1.1–1.35. Head: Vertex nearly straight between compound eyes. Margins of eye closer together at ventral portion of frons than at vertex. Median portion of frons not depressed. Face completely sclerotized. Gena in profile a narrow ridge circumventing ventral margin of eye. Mouth opening occupying 2/3 of ventral head axis. Palpus short, length about half that of 1st flagellomere. Clypeus stout, 1.5–2.5 times longer than wide. First flagellomere round. Arista long, distinctly zigzagged on apical 2/3 and bearing short hairs. Cephalic and thoracic setae not particularly long. Ocellar seta present. Inner vertical

setae present; convergent. Fronto-orbital setae transversely aligned. Peristomal vestiture consisting mostly of weak setae following pseudovibrissal seta. One strong peristomal seta present. Wing: C vein of male not spinose. Legs: Hindtrochanter of male without a ventral tuft of setae. Hindfemur unmodified, without ventral spines. Hindfemur of male without a conspicuous lobe and ventral spines. Hindtibia with a rounded, posteroventral projection, without apicodorsal setae.

Male abdomen and terminalia: Abdominal sternites slightly increasing in width posteriorly. Sternite 3 unmodified, with posterior margin straight. Sternite 4 unmodified, with posterior margin straight. Sternite 5 unmodified, with posterior margin straight. Cerci separate. Halves of hypandrium connected by a narrow bridge above aedeagal apodeme.

NEOTROPICAL SPECIES

The Neotropical fauna comprises 33 species, of which 30 are described in this paper. I recognize six species-groups for the Neotropical fauna. Most species are apparently endemic or of restricted distribution.

Key to the Neotropical species of *Aulacigaster* Macquart

- 1. Body robust, scutal ratio 1.1-1.35 (Fig. 3.78)2
- Body elongate, scutal ratio 1.5-1.75 (Figs. 3.34, 3.40) 34
- 2(1). Arista relatively long, bearing very short to long rays (Figs. 3.5, 3.26, 3.36b)3
-3
- Arista relatively short, appearing naked (Figs. 3.129, 3.131, 3.133)

	(Neotropical species of the <i>leucopeza</i> group)	4
3(2)	Arista distinctly zigzagged on apical 2/3 and bearing short hairs; first flagellomere round (Figs. 3.26, 3.35); clypeus stout, 1.5 to 2.5 times longer than wide (Fig. 3.35)	6
	Arista with a double row of dorsal rays on basal 1/3, and alternate rays on apical portion; 1st flagellomere elongate, decumbent (Fig. 3.5); clypeus elongate, 3.5 to 5.5 times longer than wide (Figs. 3.2, 3.6) (the <i>bromeliae</i> group)	29
4(2).	Frons bearing a horizontal, large, orange band; face in profile dorso-ventrally projected, ventral portion of face not receded (Figs. 3.132-3.133)	
 <i>A. sp. e</i> , undescribed species	
	Frons at most with a narrow, orange-brown transverse band; ventral portion of face receded (Figs. 3.129-3.131)	5
5(4)	Frons yellowish-orange on central portion, merging with black along lateral margins; facial band absent (Figs. 3.130-3.131) ... <i>A. spangleri</i> , new species	
	Frons with a transverse, narrow, orange-brown band; facial band present (Figs. 3.128-3.129)	<i>A. colombiana</i> , new species
6(3).	Frons mostly brown, at most with anterior margin pale, yellowish (as in Fig. 3.75); anepisternum mostly polished (as in Fig. 3.73)	7
	Frons with anterior 1/3 to anterior 1/2 yellowish in ground color (yellowish portion of frons invested with dense microtomentum, silver under certain angles) (Fig. 3.103); anepisternum mostly dull (the <i>plesiomorphica</i> group)	

.....	19
7(6). Abdomen with syntergite 1+2 whitish (Fig. 3.74); mesofrons with faint, but wide transverse microtomentose stripe (Fig. 3.75); hindfemur and tibia not modified, without conspicuous ventral spines ... <i>A. grimaldii</i> , new species	
Abdomen with a whitish to yellowish region over syntergite 1+2, in some cases extending to tergite 3 (as in Fig. 3.42); hindfemur and tibia modified, bearing tiny, conspicuous ventral spines; hindfemur of male often strong, bearing a basal lobe (as in Figs. 3.46, 50, 56)	9
9(8). Foretarsus mostly brown, only basitarsomere yellow; scutellum very weakly raised (Fig. 43)	<i>A. bella</i> , new species
Foretarsus mostly yellow (at most with apical and subapical tarsomere brown infuscate); scutellum moderately raised (angle with scutum approximately 45 degrees (Fig. 3.54)	10
10(9). Wing clear (at most with tip very slightly infuscate)	11
Posterior ½ of wing infuscate with brow.....	<i>A. sp.c</i> , undescribed species
11(10). Hindfemur completely yellow.....	12
Hindfemur at least partially brown	16
12(11).Hindtibia yellowish, at most very lightly brown infuscate on basal 1/3 ..	13
Hindtibia brown to black on central portion, base and apex yellowish	
.....	<i>A. lobata</i> , new species

- 13(12). Postpronotum yellow to yellowish-brownish; lobe on hindfemur of male
 approximately cylindrical; less densely microtomentose flies, usually without
 large microtomentose regions on mesofrons and mesonotum
*A. irwini*, new species
- Postpronotum concolorous with mesonotum; lobe on hindfemur of male
 approximately triangular; more densely microtomentose flies, usually with a
 large median microtomentose region on the mesofrons and microtomentum
 over mesonotum reaching anterior dorsocentral seta
 *A. formosa*, new species
- 16(11). Hindfemur dark on apical 1/3 to apical 1/2; forefemur yellowish.....17
 Hindfemur dark-brown on apical 3/5; forefemur yellow basally,
 tip darkened*A. sp. b*, undescribed species
- 17(16). Hindfemur of male without a conspicuous lobe; hindtibia yellowish
 *A. peruana*, new species
- Hindfemur of male with a conspicuous lobe; hindtibia yellowish, often with
 brown to black mark on central portion 18
- 18(17). Hindfemur of male with a basoventral lobe followed by a distinct concavity;
 postpronotum mostly polished *A. femorata*, new species
- Hindfemur of male with a basoventral lobe followed by a slight concavity;
 postpronotum microtomentose over lower and posterior margins, otherwise
 polished*A.sp.h*, undescribed species
- 19(6). Ocellar tubercle mostly polished (Fig. 3.123)*A. trifasciata*, new species

Ocellar tubercle dull microtomentose (Fig. 3.103)	20
20(19).Hindtibia without apical ventral setae.....	21
Hindtibia with strong, dark, apical ventral setae (as in Fig. 3.108)	27
21(20).Facial band absent.....	22
Facial band present (sometimes very inconspicuous, delimited as a transversely wrinkled band mostly lacking microtomentum; Figs. 99, 111)	24
22 (21) Frons white-microtomentose stripe not followed by a conspicuous velvety- black stripe (Fig. 3.103)	<i>A. erikae</i> , new species
Frons white-microtomentose stripe followed by a conspicuous velvety-black stripe (as in Fig. 3.111)	23
23(22).Antenna pale yellow to yellowish, at most infusate dorsally; face at level of pseudovibrissal seta wider than width of 1 st flagellomere; face bulbous	<i>A. bifasciata</i> , new species
Antenna brownish to brown; face at level of pseudovibrissal seta approximately the same width as the 1 st flagellomere; ventral portion of face not “bulbous,” difficult to see in lateral view	<i>A. sp. b</i> , undescribed species
24(21).Facial band delimited as a transversely wrinkled band on upper portion of face, but mostly lacking microtomentum; cerci of male and female separate	<i>A. belize</i> , new species
Facial band more distinct, grey or golden, over brown mark, on upper portion	

of face; cerci of male with cerci partly fused	25
25(24).Hindfemur yellow; surstylar lobe approximately triangular, apex strongly pointed, surface concave (Fig. 3.115)	<i>A. rufifemur</i> , new species
Hindfemur at least partly dark; surstylar lobe not as above	26
26 (25)Vertex mostly polished, microtomentum restricted to a narrow area posterior to ocellar tubercle and, in some specimens, around vertical setae; ventral portion of face not “bulbous,” difficult to see in lateral view; facial band whitish; surstylar lobe approximately rectangular, from lateral view approximately “boat-shaped” (Fig. 3.91)	<i>A. albifacies</i> , new species
Vertex mostly dull microtomentose, shiny spot, when present, reaching at most halfway to eye margin; ventral portion of face bulbous, easily seen from lateral view; facial band whitish or golden yellow (Figs. 98, 99); surstylar lobe keel-shaped, with an apical and 1-2 basal marginal setae (Fig. 3.101)	<i>A. conspicua</i> , new species
27(20) Hind trochanter of male without a ventral tuft of setae; surstylus folded ventrally to epandrium, difficult to discern (Fig. 3.104)	<i>A. kenna</i> , new species
Hind trochanter of male with a ventral tuft of setae (as in Figs. 3.110, 3.112); surstylus differentiated	28
28(27) Hind trochanter of male with a ventral, yellowish tuft of setae not borne on a projection (Fig. 3.110); surstylus approximately foot-shaped, with two subterminal setae and two basal, marginal setae (Fig. 3.106)	

.....	<i>A. proxima</i> , new species	
Hind trochanter of male with a ventral, black tuft of setae borne on a projection (Fig. 3.112); surstylus approximately triangular, with a terminal seta and two basal, marginal setae (Fig. 3.105)	<i>A. plesiomorphica</i> (Hennig)	
29(3). Median portion of frons slightly depressed from ptilinal suture to base of ocellus (Fig. 3.16)		30
Median portion of frons deeply depressed, often velvety black (Fig. 3.19)...		32
30(29). Ocellar seta absent	<i>A. serrana</i> , new species	
Ocellar seta present, though minute.....		31
31(30). Antenna infusate on dorsal margin; inner vertical seta present (Fig. 3.16)	<i>A. tibanae</i> , new species	
Antenna infusate on dorsal half; inner vertical seta absent	<i>A. lopezi</i> , new species	
32(29). Parafacial completely brown to dark brown; ocellar tubercle mostly polished; katepisternum mostly polished; inner vertical seta absent		33
Parafacial yellowish in ground color; ocellar tubercle microtomentose, subshiny; katepisternum mostly microtomentose (some specimens with a polished area dorsally); inner vertical seta present	<i>A. bromeliae</i> , new species	
33(32). Vertex entirely polished; C vein of male not spinose (Fig. 3.11)	<i>A. korneyev</i> , new species	
Vertex polished around ocellar tubercle; C vein of male bearing a few tiny,		

but conspicuous spines	<i>A. vespertina</i> , new species
34(1). Pleurae uniformly black (as in Fig. 3.83)	35
Pleurae white on lower half; legs white to pale yellow (as in Fig. 3.35) (the <i>ecuadoriensis</i> group)	39
35(34). Wing hyaline (at most with tip very slightly infusate, as in Fig. 3.85)	36.
Wing infusate with brown, mostly on apical 2/3 of cells R2+3 and R4+5 (Fig. 3.87)	<i>A. gaimarii</i> , new species
36(35). Antenna not infusate dorsally; hindtarsi with basal tarsomere brown, apical tarsomere yellowish	<i>A. nigratarsa</i> , new species
Antenna infusate along dorsal margin; hindtarsi yellowish.....	37
37(36). Hindfemur mostly dark-brown (Fig. 3.89)	<i>A. minuta</i> (Hennig)
Hindfemur mostly yellowish, tip brown infusate, or yellowish-brownish, but never dark-brown.....	38
38(37). Hindfemur of male without a conspicuous lobe	<i>A. costaricana</i> , new species
Hindfemur of male with a basoventral lobe followed by a distinct concavity (Fig. 3.81)	<i>A. appendiculata</i> , new species
39(34). First flagellomere round; face slightly convex, barely visible in profile; inner vertical seta slightly proclinate (Fig. 3.39); Sc vein incomplete, fused with vein R1 apically	<i>A. stenopteron</i> , new species
First flagellomere triangular face with dorsal 2/3 flat, ventral portion receded	

(as in Figs. 26, 35); inner vertical setae not proclinate; Sc vein partly fused with vein R1 apically but terminating on costa (Fig. 3.37a)	40
40(39). Head and thorax setae not particularly long; C vein of male bearing relatively strong, conspicuous spines	41
Head and thorax setae long; C vein of male not spinose.....	<i>A. sp. a</i> , undescribed species
41(40). Wing with apical 2/3 of cells r1 and r2+3 brown infusate (Fig. 3.37b); hindfemur of male without a conspicuous lobe.....	<i>A. melanoleuca</i> (Hennig)
Wing with apical half mostly brown; hindfemur of male with a basal lobe (Fig. 3.30)	<i>A. ecuadoriensis</i> (Hennig)

The *bromeliae* group

(Figs. 3.1-3.25)

DIAGNOSIS.—The *bromeliae* group can be distinguished from other species groups by the following combination of characters: stout, medium-sized flies, body length 2.9–4.0 mm. Coloration: Occiput typically with median occipital sclerite polished. Mesofrons mostly dark brown. Antenna often invested with whitish, pubescent hairs. Face polished, brown to black. Wing often bearing a central, brown mark.

Morphology: Head: Vertex obviously excavated between compound eyes. Head typically higher than long (head ratio lower than 0.9). Margins of eye closer together at vertex than at level of antenna. Median portion of frons slightly to broadly depressed, deep. Face in profile projected dorsoventrally, ventral portion of

face not receded. Gena in profile projected at level of anteroventral margin of eye, approximately triangular in shape, thereafter following ventral margin of eye as a narrow ridge. Clypeus elongate, 3.5–5.5 times longer than wide. First flagellomere oval, decumbent. Arista long, with a double row of dorsal rays on basal 1/3, and alternate rays on apical 2/3. Ocellar seta often present, minute. Inner vertical setae, when present, nearly cruciate. Fronto-orbital setae with posterior seta slightly internal to and almost transversely aligned with anterior seta. Peristomal area typically with one strong seta right behind pseudovibrissal seta, followed by 2 or 3 weaker setae and other setae. Wing: Sc vein partly fused with vein R1 apically, terminating on costal vein.

Male abdomen and terminalia: Surstylus fused to an internal, ventral shelf of epandrium, posteroventral. Subepandrial sclerite consisting of paired, ribbon-like sclerites separated by a membranous, central region. Halves of hypandrium connected by a plate over aedeagal apodeme. Gonopods short, wide, with a few central setulae and a posterior projection in some species.

DISTRIBUTION.—Neotropical: Brazil, Costa Rica, Ecuador.

BIOLOGY.—Species of this group are rare in collections, but conspicuous and easy to collect on leaves of bromeliads that have large “cups,” where small quantities of water accumulate. In Brazil, adults are apparently present throughout the year, although in fewer numbers during the winter. Larvae are fully aquatic and can be easily found close to the bases of the bromeliad leaflets, where they probably feed on decaying organic matter.

OBSERVATIONS.—Species of the *bromeliae* group can be easily identified by the shape of the depressed portion of the mesofrons and its coloration, the coloration of the legs, and the presence/absence of an internal vertical seta and ocellar seta.

NOTES.—The *bromeliae* group includes six species, of which all are newly described here. The group is exclusively Neotropical. Most species are from South America, but one species, *A. korneyev*, occurs in Central America (Costa Rica).

Aulacigaster bromeliae, new species

(Figs. 3.1-3.10)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: parafacial yellowish in ground color; median portion of frons broadly depressed, concave.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose or polished around ocellar tubercle. Frons with parafacial yellowish in ground color, depressed portion of frons appearing velvety. Mesofrons with a pair of silver microtomentose marks. Ocellar tubercle scarcely microtomentose, subshiny. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Palpus brownish (invested with silver microtomentose hairs). Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, mostly polished. Anepisternum polished. Katepisternum mostly microtomentose, with a polished area dorsally. Halter mostly white. Male abdomen subshiny to dull. Female abdomen bright shiny, or with dense microtomentum

medially, lateral margins of tergites nearly polished. Forecoxa yellow, forefemur yellowish, foretibia brown, foretarsus mostly brown to dark brown, yellowish on basal 1/3–1/2 of basitarsomere or completely brown to dark brown. Midcoxa brown to black, midfemur brown, midtibia yellowish or with basal portion brown to dark-brown, apical portion yellowish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown (apical and subapical). Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Wing bearing a central, brown mark.

Morphology: Head: Median portion of frons depressed, deep. Ocellar seta hair-like or minute. Inner vertical weak, less than a 1/2 of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed.

Male abdomen and terminalia: Surstylus about 1/3-1/2 length of basal margin of epandrium, posteroventral, finger-like. Anterior process of gonopod about 1/3-1/4 length of basal margin of epandrium, well-developed. Posterior projection of gonopod absent. Cercus narrow, finger-like, bearing several long and well-developed setae.

Female abdomen and terminalia: Spermathecae with ventral digitiform projections.

Measurements and ratios: Cell dm ratio 3–4. Body length 2.8–3.7 mm. Wing length 1–1.2 mm.

Immatures.—Egg- whitish, oval in shape, dorso-ventrally flattened; chorion delicately sculptured

Larva (3rd instar).—Length 6.6-.7.5 mm. Slender, subcylindrical, elongate, slightly tapering anteriorly; integument almost transparent, smooth; abdomen with 2 pairs of lateral sensory hairs on segments 1–7; ventral creeping pads bearing spines arranged in rows as follows: a pair of rows on segments 1 and 8, 2 pairs on remaining segments; 8th segment bearing a respiratory process and also a pair of lateral fleshy lobes; anterior spiracle retractable into a pair of narrow pockets, and bearing 23–26 pairs of twig-like processes, plus additional bulbs on their apical part. Respiratory tube with posterior spiracle separate at apex, bearing 3 long bristle-like interspiracular processes each. Cephalopharyngeal skeleton well-developed, large; tentopharyngeal sclerite fully sclerotized, with prominent ventral groove and a weak dorsal bridge. Mandible well-developed, with 2 pairs of accessory teeth.

Puparium.—5.6–6.4 mm long, 2.0–3.3 mm wide. Light brown, oval in shape, tapering towards apex. Posterior respiratory tube strongly retracted. Prothoracic spiracles extruded into a pair of 1.1-1.2 mm long horns each with c. 23–26 pairs of twig-like papillae.

TYPE MATERIAL.—The holotype male is labeled: “BRAZIL. Rio de Janeiro: Ilha da Marambaia, 23^o 03.6’S, 43^o 59.1’W, 4 Sep 2000, D. & Wayne N.Mathis”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and will be deposited at the UFRRJ. Paratypes are as follows: Same label as the holotype (2 ♂, 2 ♀; UFRRJ), (2 ♂, 1 ♀;

USNM). BRAZIL. Rio de Janeiro. Rio de Janeiro: Maricá, A. Baptista, L. Lopez , 27 Feb 1995 (3 ♂; MNRJ) (3 ♂; USNM).

OTHER SPECIMENS EXAMINED.—BRAZIL. Rio de Janeiro: Petrópolis, Retiro, 10 May 1984, H. S. Lopes (2 ♀; MNRJ); Teresópolis, Parque Nacional da Serra dos Órgãos, 28 Dec 1990, Jul 1996, A. & R. Baptista (2 M; USMN); same, 28 Dec 1990 (1 ♀; USNM). Rio de Janeiro, 1 Jan 1934, 1 Sep 1934, H. S. Lopes (1 ♂, 2 ♀ MNRJ); 20 Oct 1991, A. Baptista & R. Baptista “em bromélia”(3♀; MZUSP); Gávea, 3 Mar 1935, H. S. Lopes (1 ♂; MNRJ); Jardim Botânico do Rio de Janeiro, 27 Sep 1990, R. Tibana (3 ♀; MZUSP); Recreio dos Bandeirantes, 30 Sep 1974, R. Tibana (2 ♂, USNM). Santa Catarina: Ilhota, Morro do Baú, 26-27 Jan 1990, A. Chaves, R. Baptista “em bromélia” (1 ♂, 2 ♀; MNRJ). São Paulo: Salesópolis, 01-03 Mar 1992, A. Baptista & R. Baptista “em bromélia” (1 ♂, 2 ♀; MZUSP).

Immature forms.—Puparium. BRAZIL. Rio de Janeiro: Rio de Janeiro, Recreio dos Bandeirantes, Sep 1974, R. Tibana (5, MNRJ); 29 Aug 1978, R. Tibana (1, MNRJ).

Larva. BRAZIL. Rio de Janeiro: Rio de Janeiro, Recreio dos Bandeirantes, Sep 1974, R. Tibana (7, MNRJ).

DISTRIBUTION.—Neotropical: Southeast Brazil.

BIOLOGY.—I have collected immatures and adults of this species on the following species of bromeliad: *Neoregellia cruenta* (R. Graham), *Vriesea* spp, and *Canistrum lindenii* (Regel). The species occurs in bromeliads at the shore as well as inside the Atlantic forest.

ETYMOLOGY.—The specific epithet, *bromeliae*, refers to a plant genus of the family Bromeliaceae, the habitat of the species.

Aulacigaster korneyev, new species

(Figs. 3.11-3.14)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Median portion of frons broadly depressed, concave; vertex mostly polished.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Frons with mesofrons completely brown to dark brown, depressed portion of frons appearing velvety. Mesofrons with a pair of silver microtomentose marks. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, not infuscate dorsally or infuscate on dorsal half. Palpus brownish. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, mostly polished. Anepisternum polished. Katepisternum mostly polished. Halter mostly white. Male abdomen subshiny to dull. Female abdomen with dense microtomentum over tergites 1–4/5, remaining tergites mostly polished. Forecoxa yellow, forefemur yellowish, foretibia brown, foretarsus completely brown to dark brown. Midcoxa brown to black, midfemur brown, midtibia yellowish, midtarsus mostly yellowish or yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish or yellowish, apical tarsomere brown to black. Wing in females bearing a central, brown mark.

Morphology: Head: Median portion of frons depressed, deep. Inner vertical seta absent.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), triangular, apex strongly pointed.

Male abdomen and terminalia: Surstylar length subequal to the length of basal margin of epandrium; surstylus posterior, slender, with apex swollen, pointed upwards, apex approximately triangular. Anterior process of gonopod about same length of basal margin of epandrium, well-developed. Posterior projection of gonopod present. Cercus narrow, finger-like, bearing several long and well-developed setae.

Measurements and ratios: Cell dm ratio 3.1–4. Body length 2.9–3.3 mm. Wing length 0.8–1 mm.

TYPE MATERIAL.—The holotype male is labeled: “COSTA RICA. Sto. Domingo, Heredia, INBIO./29-31 Jul 01 [,] Korneyev/ INBIO”/ HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition (left basal scutellar seta broken), and is deposited in INBIO. Paratypes are as follows: Same label as the holotype (6 ♂; 5 ♀; INBIO, USNM). COSTA RICA. Heredia: Santo Domingo, INBIO, W.N. Mathis, 21 Feb 2003 (11 ♂, 3 ♀; INBIO, USNM); M. Buck and S. Marshall, 03 Oct 1999 “on bromeliad leaves” (12 ♂, 5 ♀; UGE).

DISTRIBUTION.—Neotropical: Costa Rica.

OBSERVATIONS.—*A. korneyev* is distinctive for displaying dimorphism in the wing coloration: the wing of the female is only very slightly clouded, and the wing of the male is almost hyaline. This species is similar to *A. vespertina* (see below) in the shape of the epandrium (narrow in lateral view), the presence of a distinct posterior gonopodal process, and the arrangement of the gonopodal setae. *A. korneyev* differs from *A. vespertina* by having the surstylus swollen apically and the anterior process of gonopod with blunt apex, in addition to the characters given in the key. In *A. vespertina*, the surstylus has a triangular apical process and the process of the gonopod is strongly pointed apically.

ETYMOLOGY.—The specific epithet, *korneyev*, is a genitive patronym to honor and recognize the contributions of Dr. Valery A. Korneyev to dipterology.

Aulacigaster lopezi, new species

(Fig. 3.22)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: parafacial yellowish in ground color; median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus; ocellar seta present.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Parafacial yellowish in ground color. Mesofrons microtomentose. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate on dorsal half. Palpus brownish. Scutellum dull microtomentose. Postpronotum concolorous with

mesonotum, scarcely microtomentose, subshiny. Anepisternum polished.

Katepisternum mostly polished. Male abdomen subshiny to dull. Female abdomen subshiny, or with dense microtomentum medially, lateral margins of tergites nearly polished. Forecoxa yellow, forefemur yellowish, foretibia brown, foretarsus completely brown to dark brown. Midcoxa brown to black, midfemur yellowish, midtibia yellowish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur yellow, hindtibia dark basally, yellow apically, hindtarsus yellowish, apical tarsomere brown to black. Wing bearing a central, brown mark. Morphology: Head: Median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus. Inner vertical seta absent.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed.

Male abdomen and terminalia: Surstylus about $\frac{1}{2}$ length of basal margin of epandrium, posteroventral, finger-like. Anterior process of gonopod about $\frac{1}{3}$ - $\frac{1}{2}$ length of basal margin of epandrium, weak. Posterior projection of gonopod absent. Cercus narrow, finger-like, bearing several long and well-developed setae.

Female abdomen and terminalia: Spermathecae with ventral digitiform projections.

Measurements and ratios: Cell dm ratio 7.2. Body length 7.1 mm. Wing length 2.6 mm.

TYPE MATERIAL.—The holotype male is labeled: “Salinas (Três Picos), Nova Friburgo [,] Rio de Janeiro-Brazil / XI 1991, A. Baptista & R. Baptista “em bromélia” [date and habitat handwritten].”/HOLOTYPE LABEL. The holotype is double-mounted (glued on left side to a small triangle), is in a moderate condition (head setae damaged, left outer vertical seta missing, right antenna broken, scutellar setae damaged and right wing missing) and will be deposited in the MNRJ.

Paratypes are as follows: Same label as the holotype (4 ♂, 5 ♀; MNRJ).

DISTRIBUTION.—Neotropical: Brazil, Rio de Janeiro.

BIOLOGY.—This species was collected from bromeliads in the Atlantic forest.

ETYMOLOGY.—The specific epithet, *lopezi*, is a genitive patronym to honor and recognize the contributions of Dr. Hugo de Souza Lopez to entomology in Brazil.

Aulacigaster serrana, new species

(Fig. 3.23)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus; ocellar seta absent.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons completely brown to dark brown or with parafacial yellowish in ground color. Mesofrons with a pair of silver microtomentose marks. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Palpus brownish. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, mostly polished. Anepisternum polished. Katepisternum mostly polished. Halter mostly white (infusate basally). Male abdomen bright shiny. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus completely brown to dark brown. Midcoxa brown to black, midfemur brown, midtibia with basal portion brown to dark-brown, apical portion yellowish (basal $\frac{1}{2}$), midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Wing bearing a central, brown mark.

Morphology: Head: Median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus. Ocellar seta absent. Inner vertical seta absent.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), triangular, apex strongly pointed.

Male abdomen and terminalia: Surstylus about $\frac{1}{2}$ length of basal margin of epandrium, posterior, finger-like. Anterior process of gonopod about $\frac{1}{2}$ - $\frac{1}{3}$ length of

basal margin of epandrium, weak. Posterior projection of gonopod absent. Cercus narrow, finger-like.

Measurements and ratios: Cell dm ratio based on two specimens 3–3.5. Body length 3.1–4 mm. Wing length 1–1.2 mm.

TYPE MATERIAL.—The holotype male is labeled: “Brazil. RJ [,] Teresópolis/ A. & R. Baptista [,] Jul 1996 [,] Bromeliads. The holotype is double-mounted (glued to a point on the left side), is in fair condition (eyes collapsed, left outer vertical, upper fronto-orbital and right scutellar seate setae missing), and will be deposited at the MNRJ”/ HOLOTYPE LABEL. Paratype as follows: Same label as the holotype (1 ♂; MNRJ). The abdomen has been removed and preserved in a vial attached to the specimen.

DISTRIBUTION.—Neotropical: Brazil: Rio de Janeiro.

BIOLOGY.—This species was collected from bromeliads in the Atlantic forest.

OBSERVATIONS.—This species shares, with *A. tibana*, a similar shape of the epandrium and surstylus, the orientation of the surstylus in relation to the epandrium, and the setae on the posterior margin of the epandrium. Both species are also similar in the shape and coloration of the mesofrons, but they can be easily separated by the characters given in the key.

ETYMOLOGY.—The specific epithet, *serrana*, is taken from the type locality, Parque Nacional da Serra dos Órgãos. The Portuguese word “*serra*” designates a mountain that has a craggy, irregular skyline.

Aulacigaster tibanae, new species

(Figs. 3.15-3.17, 3.24)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus; inner vertical seta present.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Frons with mesofrons completely brown to dark brown or with anterior portion of parafacials yellowish in ground color. Mesofrons microtomentose, or with a pair of silver microtomentose marks. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Palpus brownish (invested with silver microtomentose hairs). Scutellum dull microtomentose. Postpronotum concolorous with mesonotum (yellowish anteriorly), mostly polished. Anepisternum polished. Katepisternum mostly polished. Halter mostly white, or mostly yellowish. Male abdomen subshiny to dull. Female abdomen bright shiny, or with dense microtomentum medially, lateral margins of tergites nearly polished. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus completely brown to dark brown. Midcoxa brown to black, midfemur brown, midtibia with basal portion brown to dark-brown, apical portion yellowish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Wing bearing a central, brown mark.

Morphology Head: Median portion of frons slightly depressed over a transverse, triangular area from ptilinal suture to base of ocellus. Ocellar seta minute. Inner vertical setae weak, less than a ½ of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), triangular, apex strongly pointed.

Male abdomen and terminalia: Surstylus about ½ length of basal margin of epandrium, posterior, slightly sickle-shaped. Anterior process of gonopod about as long as basal margin of epandrium, well-developed. Posterior projection of gonopod absent. Cercus narrow, finger-like, bearing several long and well-developed setae.

Female abdomen and terminalia: Spermathecae with ventral digitiform projections.

Measurements and ratios: Head ratio 0.7. Cell dm ratio 2.9–3.8. Body length 2.5–3.7 mm. Wing length 1–1.3 mm.

TYPE MATERIAL.—The holotype male is labeled: “BRAZIL: PR [Paraná] [,] Curitiba [,] Morretes / A. R.P. Chaves [,] R.L.C. Baptista [,] 28-31 I 990, “Em bromélia” [labels handwritten]”/ HOLOTYPE LABEL. The holotype is double-mounted (glued to a point in a small yellow triangle), is in a fair condition (setae of head, scutellar setae, midlegs and right wing missing) and will be deposited, with most of the paratypes, in the MNRJ. Paratypes are as follows: same label data as the holotype (1 ♂, 1 ♀; MZNR); Paraná: Morretes, 09 Nov 1990, S.A.Marshall, “near antecolum” (1 ♀; UGE); same, 29 Aug 2000, D. and W.N.Mathis (1 ♀; USMN); Santa

Catarina: Ilhota, Morro do Baú, 26-27 Jan 1990, A. Chaves, R. Baptista “em bromélia”(1 ♂, 3 ♀; MNRJ).

OTHER SPECIMENS EXAMINED.—BRAZIL. Rio de Janeiro: Angra dos Reis, 8 Sep 31, L.T.(1 ♂; MNRJ).

DISTRIBUTION.—Neotropical: Brazil: Curitiba, Paraná, Rio de Janeiro.

BIOLOGY.—This species was collected in bromeliads of the Atlantic forest.

OBSERVATIONS.—See above, under *A. serrana*.

ETYMOLOGY.—The specific epithet, *tibanae*, is a genitive patronym to honor and recognize Dr. Rita Tibana, who collected many specimens of bromeliad *Aulacigaster* in the costal section of Rio de Janeiro (Brazil).

Aulacigaster vespertina, new species

(Figs. 3.18-21, 25)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Median portion of frons depressed, concave; frons with mesofrons completely brown to dark brown; vertex polished around ocellar tubercle.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex polished around ocellar tubercle. Frons with mesofrons completely brown to dark brown, depressed portion of frons appearing velvety. Mesofrons with a pair of silver microtomentose marks. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, not infuscate dorsally to infuscate on dorsal half. Palpus brownish (covered by silver microtomentum). Scutellum dull microtomentose. Postpronotum

concolorous with mesonotum, mostly polished. Anepisternum polished.

Katepisternum mostly polished. Halter mostly white. Male abdomen subshiny to dull. Female abdomen with dense microtomentum over tergites 1–4/5, remaining tergites mostly polished. Forecoxa yellow, forefemur yellowish (tip brown), foretibia brown, foretarsus completely brown to dark brown. Midcoxa brown to black, midfemur brown, midtibia yellowish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Wing bearing a central, brown mark.

Morphology: Head: Median portion of frons depressed, deep. Ocellar seta hair-like. Inner vertical seta absent.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees) (about 45 degrees), approximately triangular, apex relatively pointed.

Male abdomen and terminalia: Surstylar length subequal to the length of basal margin of epandrium; surstylus posterior, slender, with apex swollen, blunt. Anterior process of gonopod about the same length of basal margin of epandrium, well-developed. Posterior projection of gonopod present. Cercus narrow, finger-like, bearing several long and well-developed setae.

Measurements and ratios: Cell dm ratio 3.3–3.7. Body length 2.6–3.1 mm. Wing length 1.5–2.2 mm.

TYPE MATERIAL.—The holotype male is labeled: “ECUADOR. Puerto

Orellana: Rio Tiputini (0°38.2'S, 76°8.9'W), 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and will be deposited in EPNE. Paratypes are as follows: same label data as the holotype (1 ♂, 6 ♀; USNM; EPNE).

DISTRIBUTION.—Neotropical: Ecuador.

OBSERVATIONS.—See under *A. korneyev* above.

ETYMOLOGY.—The specific epithet, *vespertina*, is of Latin derivation and means “of the evening.” This species was found in late afternoons/ early evenings in the rain forest of Ecuador.

The *ecuadoriensis* group

(Figs. 3.26-3.41)

DIAGNOSIS.—The *ecuadoriensis* group can be distinguished from other species groups by the following combination of characters: relatively large, dorso-ventrally flattened flies, body length 7.3–7.8 mm. Coloration: Vertex mostly polished. Frons mostly brown, anterior margin pale, yellowish. Ocellar tubercle mostly polished. Scutum mostly devoid of microtomentum. Pleura and legs white on ventral half. Legs pale yellow.

Morphology: Body elongate, scutal ratio 1.5–1.75. Head typically longer than high (head ratio higher than 1.1). Face typically with dorsal 2/3 flat, ventral portion projected, bulbous, easily visible in profile. Gena in profile a narrow ridge circumventing ventral margin of eye. First flagellomere often triangular. Wing: Sc

vein partly fused with vein R1 apically but terminating on costal vein. Legs:
Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta.
Hindfemur of male often bearing a sub-basal lobe.

Male abdomen and terminalia: Surstylus in lateral view a wide, posterior extension of epandrium or a short, postero-ventral lobe in lateral view, cerci partly fused. Subepandrial sclerite forming a single, plate-like structure. Gonopods short, wide, with a few central setulae and an anterior projection, or with two anterior projections, one of them with 4–5 strong, stout setae.

DISTRIBUTION.—Neotropical: Costa Rica, Ecuador, Peru.

BIOLOGY.—The biology of the species belonging to this group is mostly unknown. *A. ecuadoriensis* has been collected on leaves of Heliconiaceae.

OBSERVATIONS.—Species of the *ecuadoriensis* group can be best identified by the coloration of the wings, the presence/absence of a lobe on the hindfemur of the male, the shape of the surstylus, and the shape and setation of the posterior margin of the abdominal sternites of the male.

NOTES.—The *ecuadoriensis* group includes three species, of which two were previously described. The group is exclusively Neotropical. Most species here reported (three out of four) are known from Central America (Costa Rica) only.

Aulacigaster ecuadoriensis (Hennig)

(Figs. 3.26-3.31)

Schizochroa ecuadoriensis Hennig, 1969: 610, 605 [figure of head and wing].

Type locality: Ecuador. Coca. Napo.—Papavero, 1967: 91 [Neotropical Catalog].

Aulacigaster ecuadoriensis.—D.K. McAlpine, 1983: 58 [generic combination].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: First flagellomere triangular; wing with apical half mostly brown.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Palpus white, or yellowish. Scutum mostly devoid of microtomentum. Scutellum dull microtomentose on lateral margins and apex, median portion of scutellum bright shiny. Postpronotum light brown or concolorous with mesonotum. Anepisternum subshiny. Katepisternum subshiny to dull. Halter mostly white, or mostly brown to dark brown. Abdomen with anterior margin white. Male abdomen subshiny to dull. Epandrium whitish to pale yellow on anteroventral portion. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished. Wing with apical half mostly brown.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. First flagellomere triangular. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Wing. C vein of male bearing relatively strong, conspicuous spines. Legs: Hindfemur

modified, with 2 ventral rows of spines, each spine bearing an apical seta (very inconspicuous). Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately triangular, setae on lobe yellow, 10–12, none especially elongate or strong.

Male abdomen and terminalia: Sternite 3 with posterior margin irregular. Sternite 4 with posterior margin and median portion only weakly sclerotized, posterior margin receded. Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus a short, postero-ventral lobe in lateral view. Cercus bearing 1 very long, ventral seta and 1–3 shorter setae. Gonopods with 2 posterior projections, one of them with 4–5 strong, stout setae.

Measurements and ratios: Cell dm ratio 7.5. Body length 7.8 mm. Wing length 2.1 mm.

TYPE MATERIAL.—The holotype male is labeled: “Coca, Napo R., Napo, ECUADOR, .V.1965, 250m., L. Pena/HOLOTYPUS *Schizochroa ecuadoriensis* Hg. [red][on reverse side “wing on slide” is written]”/Holotype *Schizochroa ecuadoriensis* Hennig CNC No. 9931.” The holotype is pinned directly, lacks a right wing, but otherwise is in good condition, and is deposited in the CNC (9931). Paratypes are as follows: Same label as the holotype (1 ♂, 1 ♀, CNC, 9931).

OTHER SPECIMENS EXAMINED.—ECUADOR. Provincia Pichincha: Maquipucuna Biological Research Station, River Trail, 1200 m, 27-29 Oct 1999, S.A. Marshall, “Heliconia leaves” (6 ♂, 2 ♀; UGE).

DISTRIBUTION.—Neotropical: Ecuador.

OBSERVATIONS.—This species is very similar to *A. melanoleuca* and the two species are sister-groups in the analysis. Besides the characters given in the key and diagnosis, the shape of the surstylus and of abdominal sternites four and five of the male abdomen provide good characters to distinguish both species. Male specimens of *A. ecuadoriensis* have a distinctive lobe on the hindfemur, whereas males of *A. melanoleuca* do not.

Aulacigaster melanoleuca (Hennig)

(Figs. 3.32-3.38)

Schizochroa melanoleuca Hennig, 1956: 152–154 [figure of head, wing and male postabdomen]. Type locality: Costa Rica.—Papavero, 1967: 91 [Neotropical catalog].

Aulacigaster melanoleuca.—D.K. McAlpine, 1983: 58 [generic combination].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: 1st flagellomere triangular; head and thorax setae not particularly long; wing with apical 2/3 of cells r1 and r2+3 dark brown, remaining wing light brown.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished. Antenna pale yellow to yellowish, infuscate along dorsal margin or infuscate on dorsal half. Palpus white, or yellowish. Scutum mostly devoid of microtomentum. Scutellum commonly dull microtomentose on lateral margins and apex, median portion of scutellum bright shiny. Postpronotum concolorous with mesonotum. Anepisternum subshiny. Katepisternum subshiny to dull. Halter mostly

brown to dark brown (base whitish). Abdomen with anterior margin white. Male abdomen subshiny to dull. Epandrium whitish to pale yellow on anteroventral portion. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished. Wing with apical 2/3 of cells r1 and r2+3 dark brown, remaining wing light brown.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. First flagellomere triangular. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum flat or slightly convex. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Wing: C vein of male bearing relatively strong, conspicuous spines. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male without a conspicuous lobe.

Male abdomen and terminalia: Sternite 3 with posterior margin irregular. Sternite 4 with posterior margin irregular, bearing long, thin setae. Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus a short, postero-ventral lobe in lateral view. Cercus bearing 1 very long, ventral seta and 1–3 longer setulae. Gonopods with 2 posterior projections, one of them with 4–5 strong, stout setae.

Measurements and ratios: Cell dm ratio 7.3. Body length 8 mm. Wing length 2 mm.

TYPE MATERIAL.—The holotype male is labeled “Costa Rica, Farm Hamburg am Reventazon, 8.3.28. [green]/Eing. 1926 No 54 [green]/Holotypus [red]/Coll. DEI Eberswalde.]”/HOLOTYPE LABEL. The holotype is in fair condition, the proboscis, left antenna, right wing, and abdomen beyond the first tergum are missing, and is deposited in DEI.

Paratypes are as follows: Same label as the holotype (4 ♂, 3 ♀; 2 specimens with abdomens missing; DEI).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Heredia: La Selva Biological Station, Puerto Viejo (3 km S) 1980-1997 (various dates), H. A. Hespenheide (3 ♂; UCLA; 2 ♂ 2 ♀; USNM). Guanacaste: Estación Pitilla, Santa Cecilia (9 km S), C. Moranga, Jul 1991 (3 ♂, 1 ♀; USNM). Puntarenas: Piedras Blancas (24 km W), P. Hanson, Oct 1990, “malaise trap” (2 ♀; USNM). San José, Rio Paraíso, 15-17 Feb 2003, W.N. Mathis (1 ♂; USNM).

DISTRIBUTION.—Neotropical: Costa Rica.

Aulacigaster stenoptera, new species

(3.39-3.41)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Pleurae white on lower half; 1st flagellomere round.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished. Antenna pale yellow to yellowish, not infusate dorsally or infusate along dorsal margin. Palpus white. Scutum mostly devoid of microtomentum. Scutellum

dull microtomentose. Postpronotum concolorous with mesonotum, mostly polished. Anepisternum polished. Katepisternum subshiny to dull. Halter mostly brown to dark brown. Wing mostly brown, infuscate (cells r2+3 and upper half of wing more heavily infuscate). Male abdomen subshiny to dull. Female abdomen subshiny.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent and slightly proclinate, seta $\frac{3}{4}$ length of outer vertical seta. One or 2 peristomal setae following pseudovibrissal setae present.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately triangular, setae on lobe 2-3. Hindtibia with a row of tiny ventral spines (whitish).

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded (appearing centrally divided). Surstylus in lateral view a wide, posterior extension of epandrium. Cercus bearing 1 very long, ventral seta and 1–3 longer setulae. Gonopods short, wide, with a few central setulae and a posterior projection.

Measurements and ratios: Cell dm ratio 5.8. Body length 6.1 mm. Wing length 1.7 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, Cocha Salvador, 240 m, 14 Sep 1988, A. Freidberg, W. N. Mathis]”/ HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (12 ♂ 14 ♀; USNM).

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios: Manu, Erika (near Salvación), 550 m, 5-6 Sep 1988, A. Freidberg (1 ♀; USNM); Pakitza (5 km E), Aguajal, 19 Sep 1988, A. Freidberg (7 ♂, 4 ♀; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—This species is peculiar to this group because it has the 1st flagellomere rounded and the gonopods lack a posterior projection bearing strong setae. The shape of the surstylus is also characteristic for this species.

ETYMOLOGY.—The specific epithet, *stenoptera*, is of Greek derivation and is a combination of the Greek words for narrow (*steno*) and wing (*ptera*).

Aulacigaster sp.a., undescribed species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Body elongate, scutal ratio 1.5–1.75; head and thorax setae long.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Antenna pale yellow to yellowish. Halter mostly brown to dark brown. Abdomen with anterior margin white. Wing with apical 2/3 of cells r1 and r2+3 dark brown, remaining wing light brown.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. First flagellomere triangular. Cephalic and thoracic setae long (Fig. 2.112). Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta.

OTHER SPECIMENS EXAMINED.—COSTA RICA. Monteverde, 1500 m, 29 Feb 1980, W. R. Mason (1 ♂, teneral; CNC).

DISTRIBUTION.—Neotropical: Costa Rica.

OBSERVATIONS.—This species is similar to *A. ecuadoriensis* and *A. melanoleuca* but differs from both species in having relatively elongate setae on the head and thorax. I am not describing this species here because I only have one teneral male.

The *femorata* group

(Figs. 3.42-3.72)

DIAGNOSIS.—The *femorata* group can be distinguished from other species groups by the following combination of characters: relatively small, delicate-looking flies, body length 2.5–4.3 mm. Coloration: Frons mostly brown, anterior margin pale, yellowish. Anterior portion of frons sometimes densely microtomentose on anterior $\frac{1}{6}$, silver from certain angles. Scutum typically mostly devoid of microtomentum. Anepisternum polished. Katepisternum mostly polished. Abdomen with a yellowish region over syntergite 1+2.

Morphology: Head higher than long (head ratio lower than 0.9), or longer than high (head ratio higher than 1.1). Margins of the eye nearly parallel. Face slightly convex, barely visible in profile. Gena in profile a narrow ridge circumventing ventral margin of eye. Ocellar seta present, hair-like. Inner vertical setae often convergent and slightly proclinate. Wing: Sc vein incomplete, fused with vein R1 apically. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindtibia with a row of tiny ventral spines. Hindfemur of male often bearing a sub-basal lobe.

Male abdomen and terminalia: Abdomen with a yellowish region over syntergite 1+2. Surstylus in lateral view a wide, ventroposterior extension of epandrium, cerci often partly fused. Subepandrial sclerite often forming a single, T-shaped structure. Gonopods approximately rectangular, with a long, posterior, finger-like projection. Cercus bearing one long, apical seta.

DISTRIBUTION.—Neotropical: Bolivia, Costa Rica, Ecuador, Peru. One female specimen from French Guyana.

OBSERVATIONS.—Species of the *femorata* group can be best identified by the shape of the basal lobe on the hindfemur of the male and coloration of the legs. As with the *minuta* group, the shape of the surstylus and internal male terminalia do not provide many characters that are useful in species identification.

NOTES.—The *femorata* group includes 7 species, of which are newly described here. The group is exclusively Neotropical.

Aulacigaster bella, new species

(Figs. 3.42-3.48)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; foretarsi mostly brown, basitarsomere yellow; scutellum very weakly raised.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons with a median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face pale yellow. Palpus white. Scutum dull microtomentose on anteriormost portion (anterior 1/5). Postpronotum concolorous with mesonotum, mostly polished. Halter mostly white. Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus brown to dark brown, basal tarsomere yellow. Midcoxa yellow, midfemur yellowish (tip slightly darkened in some specimens), midtibia yellowish, midtarsus mostly yellowish or yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical 1/3–1/2), hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum very weakly raised (making almost no angle with scutum), approximately triangular, apex relatively pointed. Legs: Hindfemur of male with a basoventral lobe followed by a slight concavity, lobe approximately cylindrical. Setae on lobe present.

Male abdomen and terminalia: Surstylus not particularly wide, about twice the width of posterior projection of gonopod.

Measurements and ratios: Cell dm ratio 3.3–3.6. Body length 2.8–3 mm. Wing length 1–1.4 mm.

TYPE MATERIAL.—The holotype male is labeled: “CR, Prov.Limon, Bribri (4km NE, 50 m, Dec 1989-Mar1990, P.Hanson, debu00100753”/ HOLOTYPE LABEL. The holotype is double-mounted (glued to a point in a small cardboard triangle), is in good condition (wings slightly folded) and is deposited in the UGE. Paratypes are as follows: same locality, date and collector as the holotype (4 ♂; UGE, USNM).

OTHER SPECIMENS EXAMINED.—BOLIVIA. La Paz: Mapiri (5 Km W Mapiri), 750 m, 16 Mar 2001, W. N. Mathis (2 ♂, 2 ♀; USNM). COSTA RICA. Limon Bribri, Jul-Sep 1990, P.Hanson, « Malaise trap » (1 ♂, 1 ♀; USNM). Higuito: San Mateo, Pablo Schield (1 ♂; USNM). ECUADOR. Pichincha (1 mile West of Santo Domingo de los Colorados), E.I.Schlinger, 23 Feb 1955, E.S.Rosa, (1 ♂; CAS); Zamora: Cumbaratza, 31-31 Mar 1965, 700 m, L.Pena (1 ♂; CNC).

DISTRIBUTION.—Neotropical: Costa Rica.

ETYMOLOGY.—The specific epithet, *bella*, is a Latin derivation of the word “bellus,” which means “pretty.”

NOTES.—The specimens listed as “other specimens examined” have the scutellum more strongly raised than the type series.

Aulacigaster irwini, new species

(Figs. 3.49-3.52)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; postpronotum yellow to yellowish-brownish.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face white to pale yellow. Palpus white. Scutum dull microtomentose on anteriormost portion (anterior 1/5). Scutellum dull posteriorly, anterior portion shiny, or dull microtomentose on lateral margins and apex, median portion of scutellum bright shiny. Postpronotum yellow to yellowish-brownish, mostly polished. Halter mostly white. Forecoxa yellow, forefemur yellowish or yellow basally, apex darkened, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow, hindtibia yellowish (infusate with brown at base in some

specimens), hindtarsus yellowish. Male abdomen subshiny to dull. Female abdomen subshiny.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 1 row, or 2 rows on anteriormost portion, merging into 1 row posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight. Legs: Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately cylindrical. Setae on lobe yellow, 1, apical.

Male abdomen and terminalia: Surstylus wide, almost three times the width of posterior projection of gonopod, apex foot-shaped.

Measurements and ratios: Cell dm ratio 3.5–3.9. Body length 3.1–3.3 mm. Wing length 0.9–1.1 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU: Madre de Dios: Manu, Pakitza, Rio Manu, 250 m, 120 7’S 700 58’ W, 9-23 Sep 1988, A. Freidberg”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (3 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

ETYMOLOGY.—The specific epithet, *irwini*, is a genitive patronym to honor and recognize Dr. Mike Irwin for his numerous contributions to dipterology.

Aulacigaster femorata, new species

(Figs. 3.53-3.58)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; hindfemur of male with a basoventral lobe followed by a pronounced concavity; hindfemur yellow on basal portion, apical portion dark.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow. Palpus white, or yellowish. Scutum dull microtomentose on anteriormost portion (anterior half). Scutellum dull microtomentose on lateral margins and apex, median portion of scutellum bright shiny. Postpronotum concolorous with mesonotum, mostly polished (anteriormost portion and lower margin microtomentodse). Halter mostly white (base infuscate). Pregenital segment mostly subshiny. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa yellow, midfemur yellowish or dark-brown to black apically, yellowish basally, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical 2/3 blackish), hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Female abdomen subshiny (some microtomentum on lateral margin of tergites).

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta $\frac{1}{2}$ length of outer vertical seta.

Thorax: Acrostical setae in 1 row, or in 2 rows, bifurcating posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight or approximately triangular, apex relatively pointed. Legs: Hindfemur of male with a basoventral lobe followed by a distinct concavity, lobe approximately rectangular. Setae on lobe pale yellow, 4–6.

Male abdomen and terminalia: Surstylus wide basally, almost three times the width of anterior projection of gonopod, narrowing apically, with a subbasal constriction.

Measurements and ratios: Cell dm ratio 3.4–4.1. Body length 3.3–3.5 mm. Wing length 0.9–1 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, \ Rio Manu, Pakitza, 250 m, 120 7’ S, 700 58’ W, 9-23 Sep 1988, A. Freidberg”/ HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (22 ♂; USNM); same locality and data, collected by W.N.Mathis (11 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—This species is similar to *A. lobata*. Besides the characters given in the key, *A. femorata* differs from *A. lobata* in having the basal $\frac{1}{2}$

-2/3 of the hindfemur brown to dark-brown, and in the shape of the surstylus and internal male genitalia.

ETYMOLOGY.—The specific epithet, *femorata*, is of Latin derivation.

Aulacigaster formosa, new species

(Figs. 3.61-3.62, 3.63)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; postpronotum concolorous with mesonotum; mesofrons more strongly microtomentose, with a median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta; hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately triangular.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons with a median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, not infuscate dorsally or infuscate along dorsal, apical and ventral margins (antenna infuscate in females only). Face white. Palpus white. Scutum dull microtomentose on anteriormost portion (anterior 1/5–2/3). Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, mostly polished. Halter mostly white. Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur

yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow (females with basal 1/3 infuscate with brown), hindtibia yellowish, hindtarsus yellowish.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed.

Legs: Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately triangular. Setae on lobe pale yellow, 4–6.

Male abdomen and terminalia: Surstylus not particularly wide, at most twice the width of anterior projection of gonopod; surstylus constricted subbasally.

Measurements and ratios: Cell dm ratio 2.5–3.1. Body length 2.5–2.7 mm. Wing length 0.8–0.9 mm.

TYPE MATERIAL.—The holotype male is labeled: “ECUADOR. Prt.[Puerto] Orllna: RioTiputini (0° 38.2’S, 76° 8.9’W) [,] 12-26 Aug 1999, A. Baptista, M. Kotrba”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (5 ♂, 2 ♀; USNM).

DISTRIBUTION.—Neotropical: Ecuador.

ETYMOLOGY.—The specific epithet, *formosa*, is of Latin derivation and means “beautiful.”

Aulacigaster lobata, new species

(Figs. 3.64-3.68)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; hindfemur completely yellow; hindfemur of male with a basoventral lobe followed by a distinct concavity.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly polished. Mesofrons with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow (pale). Palpus yellowish. Scutum dull microtomentose on anteriormost portion. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, microtomentose over lower and posterior margins, otherwise polished. Halter mostly white (base infusate). Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly (slightly so). Forefemur yellowish, foretarsus mostly yellowish or yellowish, apical and sometimes subapical tarsomeres brown to black. Midfemur yellowish, midtarsus mostly yellowish. Hindfemur yellow (rarely with tip brown infusate), hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta $\frac{1}{2}$ length of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed. Legs: Hindfemur of male with a basoventral lobe followed by a distinct concavity, lobe approximately rectangular. Setae on lobe pale yellow, 4–6.

Male abdomen and terminalia: Surstylus wide basally, almost four times the width of anterior projection of gonopod, strongly narrowed apically, with a subbasal constriction

Measurements and ratios: Cell dm ratio 3.5. Body length 3.3–3.5 mm. Wing length 1 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, 250m, Pakitza, 120 7’ S, 700 58’ W, 9–23 Sep 1988, W. N. Mathis”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (2 ♂; USNM); same locality and data, collected by A. Freidberg (7 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—See under *A. femorata*, above.

ETYMOLOGY.—The specific epithet, *lobata*, is of Greek derivation. The word "*lobus*" means a rounded projection or protuberance.

Aulacigaster peruana, new species

(Figs. 3.69-72)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; hindfemur of male without a conspicuous lobe.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face white to yellow. Palpus white. Scutum dull microtomentose on anteriormost portion (anterior 1/6–1/2). Scutellum dull posteriorly, anterior portion shiny (completely microtomentose of some specimens). Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Halter mostly white (base infusate). Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish, midtibia yellowish or mostly yellowish, apex brown infusate (very lightly in the male), midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical half), hindtibia yellowish, hindtarsus yellowish. Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum over anterior margin of tergites, posterior margin of tergites bright shiny (tergites 1–3 of in some specimens also with lateral microtomentum).

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed (to triangular).

Male abdomen and terminalia: Surstylus slightly directed posteriorly, wide basally, almost five times the width of anterior projection of gonopod, narrowing apically.

Measurements and ratios: Cell dm ratio 3.1–3.8. Body length 3–3.6 mm. Wing length 1–1.6 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, 250 m, Pakitza, 12 7’ S, 70 58’ W, 9-23 Sep 1988, W. N. Mathis”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype, (26 ♂, 1 ♀; USNM). Same locality and data, collected by A. Freidberg (22 ♂, 6 ♀; USNM).

OTHER SPECIMENS EXAMINED.—BOLIVIA. S. Inicua, Rio Alto Beni (1100 m), 15-18 Jan 1976, L.E. Pena (1 ♂; CNC). La Paz: Mapiri, 16 Mar 2001, A. Freidberg (2 ♂, 1 ♀; USNM). PERU. Rio Tambopata Reserve, (30 Km SW Puerto Maldorado), 19 Sep-10 Oct 1984, D.A. Grimaldi (7 ♂, 2 ♀; AMNH).

DISTRIBUTION.—Neotropical: Bolivia, Peru.

ETYMOLOGY.—Name after the country where the type series was collected, Peru.

Aulacigaster sp.b, undescribed species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; hindfemur mostly dark-brown, yellowish at basal 1/5–1/4.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face white to yellow. Palpus white. Scutum dull microtomentose on anteriormost portion. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Halter mostly white (infusate at base). Forecoxa yellow, forefemur yellow basally, apex darkened, foretibia yellowish, foretarsus mostly yellowish or yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa yellow, midfemur yellowish or dark-brown to black apically, yellowish basally, midtibia yellowish or yellowish on central portion, apex and basis brown, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur mostly dark-brown, yellowish at basal 1/5–1/4, hindtibia brown to dark-brown or brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen bright shiny (tergite 5 more uniformly microtomentose), pregenital

segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 1 row, or 2 rows on anteriormost portion, merging into 1 row posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed. Legs: Hindfemur of male with a basoventral lobe followed by a slight concavity, lobe approximately cylindrical. Setae on lobe present.

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios. Manu, Rio Manu, Pakitza, 250 m, 9–23 Sep 1988, W.N.Mathis (2 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

Aulacigaster sp.c. undescribed species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; posterior half of the wing infusate with brown.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Mesofrons mostly polished, or with a pair of silver microtomentose marks. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow. Palpus white. Scutum dull microtomentose on anteriormost portion. Scutellum dull microtomentose on lateral margins and apex, median portion of scutellum bright shiny. Postpronotum concolorous with

mesonotum, mostly polished. Halter mostly white. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish (slightly infuscate on apical 1/3 in female specimens), midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical 1/4 infuscate), hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Wing with apical 2/3 of cells r1 and r2+3 dark brown, remaining wing light brown. Male abdomen subshiny to dull. Female abdomen subshiny.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta 1/2 length of outer vertical seta.

Thorax: Acrostical setae 2 rows on anteriormost portion, merging into 1 row posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight. Legs: Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately cylindrical. Setae on lobe present. Measurements and ratios: Cell dm ratio 6.5. Body length 5.2 mm. Wing length 1.6 mm.

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 9–23 Sep 1988, A. Freidberg (1 ♀; USNM); Manu, Erika (near Salvacion), 550 m, 5–6 Sep 1988, A. Freidberg (1 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—This species was not described because of the scarcity of type-material.

Aulacigaster sp. h., undescribed species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; frons mostly brown, anterior margin pale, yellowish; foretarsi yellowish, apical tarsomere brown to black; hindfemur of male with a basoventral lobe followed by a slight concavity.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly polished. Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow. Palpus white. Scutum dull microtomentose on anteriormost portion. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, microtomentose over lower and posterior margins, otherwise polished. Halter mostly white (base infuscate). Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black (brownish). Midcoxa yellow, midfemur yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical 1/3–1/2), hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical seta ½ length of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed. Legs: Hindfemur of male with a basoventral lobe followed by a slight concavity, lobe approximately cylindrical. Setae on lobe pale yellow, 2–4.

Measurements and ratios: Cell dm ratio 3.6–3.7. Body length 3.4–3.5 mm. Wing length 1–1.1 mm.

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 120 7' S, 700 58' W, 9-23 Sep 1988, A. Freidberg.

DISTRIBUTION.—Neotropical: Peru.

The *grimaldii* group

(Figs. 73-80)

DISTRIBUTION.—Neotropical: Bolivia, Colombia, Costa Rica, Dominican Republic, Guyana, Venezuela, Panama, Peru.

OBSERVATIONS.—This species group includes only one species, which is described below (autapomorphies in bold and italics):

Aulacigaster grimaldii, new species

(Figs. 3.73-3.80)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with dorsal portion of syntergite 1+2 white. Frons mostly brown, with anterior margin pale yellowish.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished. Frons mostly brown, anterior margin pale, yellowish. Anterior portion of frons densely microtomentose anterior to fronto-orbital setae, but not silver. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow. Palpus white. Scutum strongly microtomentose medially, polished between pleural region and dorsocentral row of setae, posterior of postpronotum. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Anepisternum polished. Katepisternum mostly polished. Halter mostly white. Forecoxa yellow, forefemur yellowish, foretibia mostly brown (base yellowish), foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black (apical and subapical). Midcoxa yellow, midfemur yellowish (tip darkened), midtibia yellowish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (1/2), hindtibia yellowish, hindtarsus yellowish, apical tarsomere brown to black. Abdomen with dorsal portion of syntergite 1+2 whitish, male abdomen bright shiny. Female abdomen subshiny.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1). Face at level of pseudovibrissal seta narrower than width of 1st flagellomere, in profile projected from base of antenna to level of pseudovibrissal seta, thereafter receded to buccal opening (males) or strongly convex on ventral 2/3, easily visible in profile (females), bulbous. Ocellar seta minute. Inner vertical seta ½ length of outer vertical seta. Fronto-orbital setae with posterior seta slightly internal to and almost

transversely aligned with anterior seta. Peristomal vestiture consisting mostly of weak setae following pseudovibrissal seta (unusually thin). One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Wing: Sc vein partly fused with vein R1 apically but terminating on costa.

Male abdomen and terminalia: Sternite 3 with posterior margin and median portion only weakly sclerotized, posterior margin receded, sternite appearing medially divided. Sternite 4 strongly sclerotized, almost twice length of sternite 3. Sternite 5 asymmetrical, wider on right side. Surstylus in lateral view a wide, ventroposterior extension of epandrium. Cerci partly fused, each cercus bearing 1 very long, posteriorly porrect seta. Subepandrial sclerite Y-shaped. Gonopods short, wide, with a few central setulae and a posterior projection.

Measurements and ratios: Cell dm ratio 4.3. Body length 3.9 mm. Wing length 1.2 mm. Wing width 0.2 mm.

TYPE MATERIAL.—The holotype male is labeled: “VENEZUELA: Amazonas [,] Rio Mavaca Camp, 65° 06W-2°2’N 150 m, 16–27/III/89/ Phipps-FUDECI Expedition by Amer. Mus. Nat. Hist. D.A. Grimaldi, coll.”/ HOLOTYPE LABEL. The holotype is double mounted (glued to a cardboard triangle on the right side), is in excelent condition, and is deposited in the AMNH. Paratypes are as follows: same label as the holotype (2 ♂, 2 ♀; AMNH).

OTHER SPECIMENS EXAMINED.—BOLIVIA. La Paz: Arroyo Tuhiri (5 Km W. Mapiri), 750 m, 19 Mar 2001, S. D. Gaimari (1 ♂; USNM). COSTA RICA. Puntarenas: Peninsula de Osa, Rincon, 24 March 1991, sea level, D.A. Grimaldi, J. Stark, “sweeping in palm-mangrove forest” (2 ♂; USNM); Oct-Dec 1990, P.Hanson, “Malayse trap” (2 ♀; USNM). COLOMBIA. Rio Raposa, Aug-Oct 1964, V. H. Lee, “light trap” (2 ♀; USNM). DOMINICAN REPUBLIC. Peravia: San Jos de Ocoa (19 Mi N), 3000 ft., 30 Jul 1991, D.A. Grimaldi, J. Stark, “near stream” (1 ♂; USNM). Pony Casse. 12-14 Oct 1964, P.J. Spangler (1 ♀; USNM). GUYANA. Kumo River: Lethem, 3-6 Apr 1994, W. N. Mathis (1 ♂; USNM). PANAMA. Canal Zone: Barro Colorado Island (on fresh-cut log), 15-30 Jun 1986, D. A. Grimaldi (1 ♂; AMNH). PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 9-23 Sep 1988, A. Freidberg (1 ♂; USNM); Rio Tambopata Reserve, 30 km SW Puerto Maldonado (tropical moist forest) 19 Sep-10 Oct 1984, D.A. Grimaldi (1 ♀; AMNH).

DISTRIBUTION.—Neotropical: Dominican Republic, Guyana, Panama, Peru.

OBSERVATIONS.—Besides the characters given in the key and diagnosis, this species can be easily recognized by the sexually dimorphic shape of the face, the enlarged sternite 4 of the male abdomen, and the shape of sternite 5 are all unique to this species.

ETYMOLOGY.—The specific epithet, *grimaldii*, is a genitive patronym to honor and recognize Dr. David A. Grimaldi for his numerous contributions to dipterology.

The *minuta* group

(Figs. 3.81-3.90)

DIAGNOSIS.—The *minuta* group can be distinguished from other species groups by the following combination of characters: relatively small, slender, delicate looking, dorso-ventrally flattened flies, body length 5.4–6.1 mm. Coloration: Vertex mostly polished. Frons typically mostly brown, anterior margin pale, yellowish. Ocellar tubercle mostly polished. Scutum mostly devoid of microtomentum. Anepisternum polished. Katepisternum mostly polished.

Morphology: Head: Head typically longer than high (head ratio higher than 1.1). Face slightly convex, barely visible in profile. Gena in profile a narrow ridge circumventing ventral margin of eye. Ocellar seta absent. Inner vertical setae typically convergent. Wing: Sc vein incomplete, fused with vein R1 apically. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindtibia with a row of tiny ventral spines.

Male abdomen and terminalia: Surstylus in lateral view a wide, ventroposterior extension of epandrium; cerci separated or partly fused. Subepandrial sclerite forming a single, T-shaped structure. Gonopods approximately rectangular, with a posterior, finger-like projection and ventral, wide sclerotized plates. Cercus bearing 1 very long, ventral seta and 1–3 longer setulae.

DISTRIBUTION.—Neotropical: Bolivia, Costa Rica, Panama.

BIOLOGY.—The biology of the species belonging to this group is mostly unknown. One male of *A. appendiculata* was collected on cacao foliar nectaries. Specimens of *A. gaimarii* and *A. minuta* were collected on leaves of Heliconiaceae.

OBSERVATIONS.—Species of the *minuta* group can be best identified by the shape of the basal lobe on the hindfemur of the male and coloration of the legs: as with the *femorata* group, the shape of the surstylus and internal male terminalia do not provide many characters that are useful in species identification.

NOTES.—The *minuta* group includes four species, one previously described. The group is exclusively Neotropical.

Aulacigaster appendiculata, new species

(Figs. 3.81)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: body elongate, scutal ratio 1.5–1.75; pleurae uniformly black; hindfemur of male with a basoventral lobe followed by a distinct concavity.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Anterior portion of frons densely microtomentose on anterior 1/6, silver from certain angles. Antenna pale yellow to yellowish, infusate along dorsal margin. Palpus white. Scutum mostly devoid of microtomentum. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, mostly polished. Halter mostly yellowish. Forecoxa yellow, forefemur

yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur mostly yellowish, apex brown infusate, hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen subshiny to dull. Female abdomen with dense microtomentum over syntergite 1+2, and anterior margin of remaining segments.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent or convergent and slightly proclinate, seta $\frac{1}{2}$ length of outer vertical seta. Peristomal area with about three setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male with a basoventral lobe followed by a distinct concavity, lobe approximately rectangular, setae on lobe present. Hindtibia with a row of tiny ventral spines.

Male abdomen and terminalia: Surstyler length about three times the width of posterior projection of gonopod; surstylus slightly narrowing towards apex.

Measurements and ratios: Cell dm ratio 5.6. Body length 5 mm. Wing length 1.4 mm. Wing width 0.3 mm.

TYPE MATERIAL.—The holotype male is labeled: “COSTA RICA: Heredia [,] Pr.: La Selva Biol.[ogical] Sta.[tion] 3 Km S Pto. Viejo 10 26 N 84 01 W/ 18 Vi 1991 [,] H. A. Hespenheide”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the UCLA. Paratypes are as follows: same label as the holotype, dates as follows: 2 ♂ 1990, (1 ♂; UCLA); 8 Jul 1987 (at foliar nectaries of *Byttenaria aculeata* Jacq., plant # ?, cacao, H. A. Hespenheide (1 ♂; CAS).

DISTRIBUTION.—Neotropical: Costa Rica.

ETYMOLOGY.—The specific epithet, *appendiculata*, is of Latin derivation and means "little appendage."

OBSERVATIONS.—Females of *A. appendiculata* cannot be separated with certainty from females of *A. costaricana*.

Aulacigaster costaricana, new species

(Figs. 3.82-3.85)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: body elongate, scutal ratio 1.5–1.75; pleurae uniformly black; hindfemur of male without a conspicuous lobe.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Anterior portion of frons densely microtomentose on anterior 1/6, silver from certain angles. Antenna pale yellow to yellowish, infusate along dorsal margin. Palpus white, or yellowish. Scutum mostly devoid of

microtomentum. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, mostly polished. Halter mostly yellowish. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur mostly yellowish, apex brown infusate, hindtibia brown to dark brown, yellowish at basal fifth or brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen subshiny to dull. Female abdomen with dense microtomentum over syntergite 1+2, and anterior margin of remaining segments.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent or convergent and slightly proclinate, seta $\frac{1}{2}$ length of outer vertical seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male without a conspicuous lobe. Hindtibia with a row of tiny ventral spines.

Male abdomen and terminalia: Sternite 4 modified, posterior margin with a median weakly sclerotized area. Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylar length about three times the width of posterior projection of gonopod; surstylus slightly constricted subbasally.

Measurements and ratios: Cell dm ratio 6. Body length 5.2 mm. Wing length 1.4 mm. Wing width 0.3 mm.

TYPE MATERIAL.—The holotype male is labeled: “COSTA RICA: Heredia [,] Pr.: La Selva Biol.[ogical] Sta.[tion] 3 Km S Pto. Viejo 10 26 N 84 01 W/ 18 Vi 1991 [,] H. A. Hespenheide”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the UCLA. Paratypes are as follows: Same label as the holotype, (1 ♂; UCLA); 15 Jul 1994, (1 ♂; UCLA).

OTHER SPECIMENS EXAMINED.—COSTA RICA. La Suiza de Turrialba, P. Schild (A. L. Melander Collection), (3 ♂; 11 ♀; USNM).

DISTRIBUTION.—Neotropical. Costa Rica.

ETYMOLOGY.—The specific epithet, *costaricana*, refers to the country where the type series was collected, Costa Rica.

OBSERVATIONS.—Females of *A. costaricana* cannot be separated with certainty from females of *A. appendiculata*.

Aulacigaster gaimarii, new species

(Figs. 3.86-3.87)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: Body elongate, scutal ratio 1.5–1.75; pleurae uniformly black; wing infuscate with brown on apical 2/3.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished. Anterior portion of frons densely microtomentose on anterior 1/6, silver from certain angles. Antenna pale yellow to yellowish, not infusate dorsally or infusate along dorsal margin. Palpus white. Scutum mostly devoid of microtomentum. Scutellum dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, mostly polished. Halter mostly white. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish or dark-brown to black apically, yellowish basally, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur brown or yellow on basal portion, apical portion dark, hindtibia brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Wing mostly brown, infusate. Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum over syntergite 1+2, and anterior margin of remaining segments.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent or convergent and slightly proclinate, seta 1/2 length of outer vertical seta. One peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat or slightly convex. Basal scutellar seta less than 1/2 length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine

bearing an apical seta. Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately cylindrical, setae on lobe present. Hindtibia with a row of tiny ventral spines.

Male abdomen and terminalia: Sternite 3 with posterior margin and median portion only weakly sclerotized, posterior margin receded, sternite appearing medially divided. Sternite 4 modified, posterior margin with a median weakly sclerotized area. Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylar length about three times the width of posterior projection of gonopod; surstylus slightly narrowing towards apex, somewhat constricted subbasally.

TYPE MATERIAL.—The holotype male is labeled: “BOLIVIA: Depto. La Paz [,] 5 Km W Mapiri, Arroyo Tuhiri 750 m, 15 17.8’S 68 15.6’ W [,] 19-iii-2001, S. D. Gaimari”/HOLOTYPE LABEL The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: same label as the holotype, Mar 2001, A. Freidberg (11 ♂, 9 ♀; USNM); same locality, 16 Mar 2001, A. Freidberg (15 ♂; 7 ♀; USNM).

DISTRIBUTION.—Neotropical. Bolivia.

BIOLOGY.—The type series was collected on leaves of plants belonging to the family Heliconiaceae (S.Gaimari, personal communication).

ETYMOLOGY.—The specific epithet, *gaimarii*, is a genitive patronym to honor and recognize Dr. Stephen Gaimari, who collected this species and many other interesting acalyptrate Diptera in Bolivia.

Aulacigaster minuta (Hennig)

(Figs. 3.88-3.90)

Schizochroa minuta Hennig, 1969: 609, 605 [figure of wing]. Type locality: Ecuador. Coca. Napo.—Papavero, 1967: 91 [Neotropical catalog].

Aulacigaster minuta D.K. McAlpine, 1983: 58 [generic combination].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: body elongate, scutal ratio 1.5–1.75; hindfemur mostly dark-brown, yellowish at basal 1/5–1/4 (check).

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons mostly polished, or with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta (females without stripe). Anterior portion of frons densely microtomentose on anterior 1/6, silver from certain angles. Antenna pale yellow to yellowish, in some specimens infusate along dorsal margin. Palpus white. Scutum mostly devoid of microtomentum. Scutellum dull posteriorly, anterior portion shiny (dull along apical margin). Postpronotum concolorous with mesonotum, mostly polished. Halter mostly white, or mostly brown to dark brown. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish or dark-brown to black apically, yellowish basally, midtibia yellowish or brownish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur mostly dark-brown, yellowish at basal 1/5–1/4, hindtibia yellow basally, dark apically or brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen subshiny to dull (mostly on

lateral margin of tergites). Female abdomen with dense microtomentum over lateral margins of syntergite 1+2, remaining segments shiny.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent or convergent and slightly proclinate, seta $\frac{1}{2}$ length of outer vertical seta. Peristomal area with two to three setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately triangular, setae on lobe brown, 2, apical. Hindtibia with a row of tiny ventral spines.

Measurements and ratios: Cell dm ratio 5.4. Body length 5.2 mm. Wing length 1.2 mm. Wing width 0.2 mm.

TYPE MATERIAL.—The holotype female is labeled “Coca, Napo R., Napo, ECUADOR, 25.30.IV.65, 250 m., L. Peña/*Schizochroa minuta* Hg. HOLOTYPUS wing on slide [red]/HOLOTYPUS *Schizochroa minuta* Hennig CNC No. 9930 [red].” The holotype is in good condition (left wing is missing), and is deposited in the CNC (9930).

OTHER SPECIMENS EXAMINED.—PANAMA. Canal Zone. Corozal, 19 Jan 1929, C. H. Curran (1 ♂; AMNH); Madden Forest, 7–16 Mar 1961, S.B. Pipkin

(3 ♂; 2 ♀; USNM); Paraiso, 28 Jan-11 Feb 1911, A. Busck (2 ♂, 1 ♀; USNM); Barro Colorado Island, 18 Jul 1924, N. Banks (2 ♂, 3 ♀; AMNH). Darien: El Real (ex. *Heliconia curhispatha*), 28 Nov 1963, S. B. Pipkin (1 ♂; USNM). PERU. Loreto: Iquitos, Mar-Apr 1931, R. C. Shannon (4 ♀; USNM).

DISTRIBUTION.—Neotropical. Ecuador, Panama, Peru.

NOTES.—One specimen that otherwise fully agrees with the description of *A. minuta* has the wing very weakly infuscate with brown.

OBSERVATIONS.—This species is similar to *A. nigritarsa* in the shape of the lobe on the hind femur of the male. However, *A. minuta* can be separated from that species by having the antenna completely yellow, and by the overall coloration of the hind leg (see species' descriptions).

Aulacigaster nigritarsa, new species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: body elongate, scutal ratio 1.5–1.75; hindtibia entirely brown to dark-brown.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Mesofrons with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Anterior portion of frons densely microtomentose on anterior 1/6, silver from certain angles. Antenna pale yellow to yellowish, not infuscate dorsally. Palpus white. Scutum mostly devoid of microtomentum. Scutellum dull microtomentose, or dull posteriorly, anterior portion shiny. Postpronotum concolorous with mesonotum, mostly polished. Halter mostly yellowish. Male abdomen subshiny to dull, pregenital

segment mostly subshiny. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa yellow, midfemur yellowish, midtibia brownish or with basal portion brown to dark-brown, apical portion yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus with basal tarsomere brown, apical tarsomer yellowish.

Morphology: Head: Face at level of pseudovibrissal seta narrower than width of 1st flagellomere. Inner vertical setae convergent or convergent and slightly proclinate, seta thin, less than a ½ of outer vertical seta or ½ length of outer vertical seta. Peristomal area with about two setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat. Basal scutellar seta less than ½ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindfemur of male with a basal lobe not followed by a posterior concavity, lobe approximately cylindrical or approximately triangular. Hindtibia with a row of tiny ventral spines.

Male abdomen and terminalia Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylar length about 5 times the width of posterior projection of gonopod; surstylus slightly swollen medially, narrowing towards apex, somewhat constricted subbasally.

Measurements and ratios: Cell dm ratio 6.1. Body length 4.8 mm. Wing length 1.4 mm. Wing width 0.3 mm.

TYPE MATERIAL.—The holotype male is labeled: “Higuito [,] San MateoCR/PabloSchild Coll”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in fair condition (setae of head and mesonotum broken, right wing slightly folded, left hindfemur missing), and is deposited in the USNM. Paratypes are as follows: same label as the holotype (4 ♂, 6 ♀; USNM).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Heredia: Peninsula de Osa, Rincon, Oct-Dec 1990, “malaise trap,” P. Hanson (1 ♀; USNM).

DISTRIBUTION.—Neotropical. Costa Rica.

ETYMOLOGY.—The specific epithet, *nigritarsa*, is of Latin derivation and refers to the black (*niger*) coloration of the tarsus.

OBSERVATIONS.—See under *A. minuta*, above.

The *plesiomorphica* group

(Figs. 3.91-3.127)

DIAGNOSIS.—The *plesiomorphica* group can be distinguished from other species groups by the following combination of characters: Stout, medium-sized flies, body length 3–4.6 mm. Coloration: Frons with anterior 1/3–1/2 yellowish in ground color. Anterior portion of frons densely microtomentose, microtomentum forming a with a wide, lunate, silvery microtomentose stripe. Facial band often

present. Scutum typically uniformly microtomentose. Abdomen in a few cases with a large, white to yellowish region over syntergite 1+2.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face strongly convex on ventral 2/3, easily visible in profile. Gena in profile a narrow ridge circumventing ventral margin of eye. Fronto-orbital setae with posterior seta slightly internal to and almost transversely aligned with anterior seta. Ocellar seta present, minute. Wing: Sc vein partly fused with vein R1 apically but terminating on costa.

Male abdomen and terminalia: Surstylus a short, postero-ventral lobe in lateral view. Cerci often partly fused. Subepandrial sclerite typically forming a single, plate-like structure. Gonopods with 2 posterior projections, one of them with 4–5 strong, stout setae.

DISTRIBUTION.—Neotropical: Belize, Costa Rica, Ecuador, Guyana, Peru.

BIOLOGY.—There is little information on the biology of the species of this group. Exemplars collected by us in the rainforest were caught on tree trunks and aerial portions of large ceiba trees where no wound exuding sap flux was visible.

OBSERVATIONS.—Species of the *plesiomorphica* group can be best identified by the presence/absence of a facial band, the shape of the face, and coloration of the Legs: In some cases, species can only be identified with certainty by the shape of the surstylus and other male characters such as the shape of sternite 5, presence/absence of setae on the hind trochanter and hindtibia.

NOTES.—The *plesiomorphica* group includes 9 species, one previously described in the literature. The group is exclusively Neotropical. Two species, *A. conspicua* and *A. trifasciata*, are known from Central America.

Aulacigaster albifacies, new species

(Figs. 3.91, 3.95)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; acrostical setae in 2 rows.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose or mostly polished, with a densely microtomentose stripe posterior to ocellar triangle, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face white to yellow. Facial band present, distinct, gray or golden, over brown mark, on dorsal portion of face. Palpus white. Scutum polished on anteriormost portion, opposite postcranium. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Anepisternum mostly dull (upper posterior portion more shiny in some specimens). Katepisternum subshiny to dull. Halter mostly white. Forecoxa brown to black, forefemur brown, foretibia yellowish or brown, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown or brown to black, apex yellowish, midtibia

yellowish or brownish, midtarsus mostly yellowish or yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown or brown to black, tip yellowish, hindtibia yellowish-brownish or brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Abdomen completely dark brown to black or with a large, white to yellowish region over syntergite 1+2, male abdomen bright shiny, pregenital segment mostly subshiny. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta approximately the same width as the 1st flagellomere, not appearing “bulbous.” Inner vertical seta $\frac{1}{2}$ length of outer vertical seta to $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum strongly raised (angle with scutum more than 45 degrees), triangular, apex strongly pointed, disk of scutellum flat. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded, and bearing a tongue-like median projection. Surstylus approximately rectangular, from lateral view “box-shaped.” Cerci partly fused, each cercus bearing 1 very long, ventral seta and 1–3 longer setulae.

Measurements and ratios: Cell dm ratio 3–3.6. Body length 3–3.6 mm. Wing length 1–1.3 mm. Wing width 0.32 mm.

TYPE MATERIAL.—The holotype male is labeled: “Ecuador. Prt.[Puerto]. Orellana: RioTiputini (00 38 2’ S, 760 8 9’W) 12-26 Aug 1999, W.N.Mathis, A.Baptista, M.Kotrba.”/ HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (4 ♂, 2 ♀; USNM).

OTHER SPECIMENS EXAMINED.—GUYANA. Kanuku: Moco Moco River, 29 Apr 1995, W.N. Mathis (3 ♂, 1 ♀; USNM). PERU. Madre de Dios: Manu, Rio Manu, Iguajal, 19 Sep 1988, A. Freidberg, (2 ♂; USNM).

DISTRIBUTION.—Neotropical: Ecuador, Guyana.

BIOLOGY.—This species was collected while sweeping on trunks of ceiba (genus ???) trees in the rainforest of Ecuador. The tree trunk had no visible wound exuding sap flux.

OBSERVATIONS.—This species shares with *A. trifasciata*, the presence of a tongue-like median projection on the posterior margin of sternite 5 of the male abdomen, and a predominantly polished vertex. The surstylar lobe is also very similar in these two species.

ETYMOLOGY.—The specific epithet, *albifacies*, is of Latin derivation and refers to the white (*albus*) coloration of the facial band (*facies*).

NOTES.—The specimens from Guyana and Peru have a large, white to yellowish region over syntergite 1+2, which is not present in the type series.

Aulacigaster belize, new species

(Figs.3.92)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior ½ yellowish in ground color; face not appearing “bulbous”; hindtibia without apicodorsal setae; surstylar lobe more or less folded below the epandrium, difficult to see in lateral view.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin or with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow anteriorly, brown to black on posterior portion. Facial band present, delimited as a transversely wrinkled band on dorsal portion of face, mostly lacking microtomentum. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished. Forecoxa brown to black, forefemur brown to black, apex yellowish, foretibia yellowish (brown infusate basally), foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur

brown to black, apex yellowish, midtibia yellowish (brown infusate on basal portion), midtarsus mostly yellowish. Hindcoxa brown, femur brown to black, tip yellowish, hindtibia yellowish or dark basally, yellow apically, hindtarsus yellowish.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1) to higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere or approximately the same width as the 1st flagellomere, not appearing “bulbous.” Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), semi-circular, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus a short, postero-ventral lobe in lateral view, surstyler lobe more or less folded below the epandrium, difficult to see in lateral view, approximately foot-shaped, bearing a basal and a terminal strong setae. Cerci separated, narrow, finger-like, each cercus bearing 1 very long, ventral seta and 1–3 longer setulae.

Measurements and ratios: Cell dm ratio 3–3.6. Body length 3–3.6 mm. Wing length 1–1.1 mm. Wing width 0.32 mm.

TYPE MATERIAL.—The holotype male is labeled: “BELIZE. Stann Creek District: Cockscomb Basin Wldlfe. Sanct. (160 47' N, 880 30'W) 5-6Apr 1993, W.

Mathis. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM"/HOLOTYPE LABEL. Paratypes are as follows: Same label as the holotype (9 ♂, 6 ♀; USNM).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Puntarenas: Peninsula de Osa, Rincón, 24 Mar 1991, sea level, D.A. Grimaldi, J. Stark, "sweeping in palm-mangrove forest" (3 ♂; USNM).

DISTRIBUTION.—Neotropical: Belize, Costa Rica.

ETYMOLOGY.—The specific epithet, *belize*, refers to the country where the type-locality is located.

Aulacigaster bifasciata, new species

(Figs. 3.93, 3.96)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; face bulbous; facial band absent; frons white-microtomentose stripe followed by a conspicuous velvety-black stripe.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Face brownish. Palpus white, or yellowish. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, mostly polished. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forecoxa brown to black, forefemur brown, foretibia yellowish or yellowish-

brownish, foretarsus mostly yellowish. Midcoxa brown to black, midfemur yellowish, midtarsus mostly yellowish. Hindcoxa brown, hindfemur brown, hindtibia yellowish-brownish or brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere, bulbous. Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae 2 rows on anteriormost portion, merging into 1 row posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), semi-circular, disk of scutellum strongly convex. Basal scutellar seta $\frac{3}{4}$ length of posterior seta.

Male abdomen and terminalia: Surstylus a short, postero-ventral lobe, in lateral view somewhat inconspicuous, approximately beak-shaped. Cercus bearing 1 very long, posteriorly porrect setula.

Measurements and ratios: Cell dm ratio 3.6–3.8. Body length 3.5–4.1 mm. Wing length 1.1–1.3 mm. Wing width 0.37 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Pakitza, Rio Manu, 250 m, 120 7’S 700 58’ W, 9-23 Sep 1988, W. N. Mathis”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block

of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (3 ♂, 6 ♀; USNM).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Heredia: Prov.

Guanacaste, Estacion Santa Rosa, 300 m, 11 Feb 1996, S. Marshall (1 ♀; UGE).

Puntarenas: Peninsula de Osa, Rincón, 24 March 1991, sea level, D.A. Grimaldi, J.

Stark, “sweeping in palm-mangrove forest” 91 ♂; AMNA). GUYANA. Moco Moco Lethem, 3-6 Apr 1994, W.N. Mathis (1 ♀; AMNH).

DISTRIBUTION.—Neotropical: Costa Rica, Guyana, Peru.

ETYMOLOGY.—The specific epithet, *bifasciata*, is of Latin derivation and is a combination of the prefix “*bi-*,” which means two, and the Latin word for band (*fascia*).

Aulacigaster conspicua, new species

(Figs. 3.97-3.101)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; face bulbous; facial band present; Hindfemur brown to black on central portion, tip and base yellowish.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, without a shiny spot or with a shiny spot extended from ocellus at most half way to eye margin. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow anteriorly, brown to black on posterior portion. Facial band present, distinct, gray or

golden, over brown mark, on dorsal portion of face. Palpus white. Scutellum dull microtomentose. Postpronotum yellow to yellowish-brownish or concolorous with mesonotum, scarcely microtomentose, subshiny. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forecoxa brown to black, forefemur brown to black, apex yellowish, foretibia yellowish, foretarsus mostly yellowish or yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish, midtarsus mostly yellowish or yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown to black on central portion, apex and base yellowish, hindtibia yellowish or brown to black on central portion, base and apex yellowish, hindtarsus yellowish or yellowish, apical tarsomere brown to black. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere, bulbous. Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), semi-circular, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus keel-shaped, with an apical and 1–2 basal marginal, strong setae. Cerci partly fused, each cercus bearing 1 very long, posteriorly porrect setula.

Measurements and ratios: Cell dm ratio 3.9–4.3. Body length 3.2–3.6 mm. Wing length 1.2 mm. Wing width 0.36 mm.

TYPE MATERIAL.—The holotype male is labeled: “COSTA RICA: Puntarenas, Peninsula de Osa, Rincon [,] 24 March 1991, sea level [,] Grimaldi & Stark, sweeping in palm-mangrove forest”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition, (ventral, left fronto-orbital, scutal and scutellar setae partly broken) and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (1 ♂, 2 ♀; USNM).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Puntarenas: Rincon, Oct-Dec 1990, P. Hanson “Malaise trap” (5 ♀; USNM). PANAMA. Canal Zone: Barro Colorado Island, 10 Jan 1929, C.H.Curran (1 ♂, 1 ♀; USNM).

DISTRIBUTION.—Neotropical: Costa Rica, Panama.

ETYMOLOGY.—The specific epithet, *conspicua*, is of Latin derivation and means “prominent.”

NOTES.—The four females from Puntarenas (Costa Rica) caught by Malaise trap seem to belong to these species but are much lighter in the coloration of the legs and face.

Aulacigaster erika, new species

(Figs. 3.94, 102-3.103)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; frons white-microtomentose stripe not followed by a posterior, velvet black stripe; facial band absent.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe not followed by a posterior, velvet black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face brownish. Palpus white, or yellowish. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white (base dark). Forecoxa brown to black, foretibia yellowish, foretarsus mostly yellowish. Midcoxa brown to black, midtarsus mostly yellowish. Hindtibia yellowish-brownish or brown to black on central portion, base and apex yellowish, hindtarsus yellowish. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere, not appearing “bulbous” or bulbous. Inner vertical seta 1/2 length of outer vertical seta or 3/4 length

of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus approximately nose-shaped, apex slightly pointed. Cerci partly fused, each cercus bearing 1 very long, posteriorly porrect setula..

Measurements and ratios: Cell dm ratio 3.1–3.8. Body length 3–3.1 mm. Wing length 1–1.6 mm. Wing width 0.35 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 12^o 7’ S, 70^o 58’ W, 9-23 Sep 1988, A. Freidberg”/ HOLOTYPE LABEL The holotype is double mounted (mounted in a block of plastic), is in excellent condition (abdomen dissected, structures in an attached microvial), and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (5 ♂, 2 ♀; USNM); same label as the holotype, collected by W.N. Mathis (10 M; 3 F); Erika (near Salvación), 550 m, 5-6 Sep 1988, A. Freidberg (10 ♂, 1 ♀; USNM); same label, collected by W.N.Mathis (7 ♂, 1 ♀).

OTHER SPECIMENS EXAMINED.—ECUADOR. Puerto Orellana: Rio Tiputini, 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba (5 ♂, 2 ♀; USNM).

DISTRIBUTION.—Neotropical: Ecuador, Peru.

BIOLOGY.—This species was collected while sweeping the aerial portion of large ceiba tree roots.

ETYMOLOGY.—The specific epithet, *erika*, refers to the type-locality, Erika.

Aulacigaster kenna, new species

(Fig. 3.104)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; hindtibia with strong, dark, apicodorsal setae; hind trochanter of male without a ventral tuft of setae.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin to with a shiny spot extended from ocellus at most half way to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow anteriorly, brown to black on posterior portion. Facial band present (region of facial band “wrinkled”), delimited as a transversely wrinkled band on dorsal portion of face, mostly lacking microtomentum. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forecoxa brown to black, forefemur brown to black, apex yellowish, foretibia yellowish (brown infuscate basally), foretarsus mostly yellowish to yellowish, apical and sometimes subapical

tarsomeres brown to black. Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa brown, hindfemur brown to black, tip yellowish, hindtibia yellowish or dark basally, yellow apically, hindtarsus yellowish. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1), or higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta approximately the same width as the 1st flagellomere, not appearing “bulbous.” Inner vertical seta $\frac{1}{2}$ length of outer vertical seta to $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta. Legs: Hindtibia with strong, dark, apicodorsal setae.

Male abdomen and terminalia: Surstylus not well differentiated from folded portion of epandrium, difficult to discern in lateral view. Cerci bearing 1 very long, ventral seta and 1–3 longer setulae.

Measurements and ratios: Cell dm ratio based on the holotype only 3.8. Body length 3.8 mm. Wing length 1.3 mm. Wing width 3.4 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Erika (near Salvacion), 550 m, 5-6 Sep 1988, W. N. Mathis”/HOLOTYPE

LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition (lower right fronto-orbital seta broken), and is deposited in the USNM.

Paratypes are as follows: PERU. Madre de Dios: Manu, Rio Manu, 250m, 9-23 Sep 1988, W.N.Mathis (1 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—This species shares, with *A. proxima* and *A. plesiomorphica*, the presence of black, dorso-apical setae on the hindfemur of male and female specimens. It can be easily distinguished from the last two species by the absence of well-developed setae on the hind trochanter of the male, and by the absence of a well-developed surstyler lobe.

ETYMOLOGY.—The specific epithet, *kenna*, is a patronym to honor and thank Dr. Joseph Kenna. The name is in apposition.

Aulacigaster plesiomorphica (Hennig)

(Figs. 3.105, 110)

Schizochroa plesiomorphica Hennig, 1969: 608, 605 [figure of head and wing]. Type locality: Peru. Quincemil. Cuzco.—Papavero, 1967: 91 [Neotropical catalog].

Aulacigaster plesiomorphica D.K. McAlpine, 1983: 58 [generic combination].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: hind trochanter of male with a ventral, black tuft of setae borne on a projection.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Cervix subshiny, sparsely microtomentose. Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate on dorsal half. Face yellow anteriorly, brown to black on posterior portion. Facial band present, delimited as a transversely wrinkled band on dorsal portion of face, mostly lacking microtomentum. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forefemur brown or brown to black, apex yellowish, foretibia yellowish, foretarsus mostly yellowish. Midfemur brown or brown to black, apex yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindfemur brown or brown to black, tip yellowish, hindtibia yellowish or dark basally, yellow apically, hindtarsus yellowish. Male abdomen bright shiny, pregenital segment mostly subshiny. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face not appearing “bulbous.” Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), approximately triangular, apex relatively pointed,

disk of scutellum strongly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Legs: Hindtrochanter of male with a ventral, black tuft of setae borne on a projection. Hindtibia with strong, dark, apicodorsal setae.

Male abdomen and terminalia: Surstylus more or less folded below the epandrium, difficult to see in lateral view, approximately triangular, with 1 apical and 2 basal, marginal, strong setae. Cerci separated.

Measurements and ratios: Cell dm ratio based on two specimens 3.5. Body length 3.5 mm. Wing length 1.3–1.6 mm. Wing width 0.35 mm.

TYPE MATERIAL.—Paratypes.—One male paratype (PERU. Cuzco. Quincemil, 15–30 Oct 1962, L.Pena) seem to belong to one species, whereas the two other designated paratypes key out to *A. rufifemur*. One of these paratypes, also collected by E.L.Pena, is from Quincemil (1–15 Nov 1962 and 13–31 Aug 1962), and the other one is from Avispas, Madre de Dios (20–30 Sep 1962, L.Pena).

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios: Manu, Erika (near Salvacion), 550 m, 5–6 Sep 1988, A. Freidberg (1 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

Aulacigaster proxima, new species

(Figs. 3.106-3.109, 111-3.113)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: hind trochanter of male with a ventral, yellowish tuft of setae not borne on a projection.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin to with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Face yellow anteriorly, brown to black on posterior portion (from level of vibrissa to base of antenna). Facial band present, delimited as a transversely wrinkled band on dorsal portion of face, mostly lacking microtomentum. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny to dull microtomentose. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forecoxa brown to black, forefemur brown to black, apex yellowish, foretibia yellowish, foretarsus mostly yellowish. Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindcoxa brown, hindfemur brown to black, tip yellowish, hindtibia yellowish or dark basally, yellow apically, hindtarsus yellowish. Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1) to higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta narrower than width of 1st flagellomere, not appearing “bulbous.” Inner vertical seta

½ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum strongly raised (angle with scutum more than 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum flat. Basal scutellar seta ½ length of posterior seta (but thinner). Legs: Hindtrochanter of male with a ventral, yellowish tuft of setae not borne on a projection. Hindtibia with strong, dark, apicodorsal setae.

Male abdomen and terminalia: Sternite 4 with posterior margin and median portion only weakly sclerotized, posterior margin receded. Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus more or less folded below the epandrium, difficult to see in lateral view, approximately foot-shaped, with 2 subapical and two basal, marginal, strongly setae. Cerci separated, narrow, finger-like, each cercus bearing 1 very long, ventral seta and 1–3 longer setulae.

Measurements and ratios: Cell dm ratio 3.8–4.8. Body length 3.8–4.3 mm. Wing length 1.2–1.3 mm. Wing width 0.31 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 12 7’ S, 70 58’ W, 9-23 Sep 1988, A. Freidberg”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition (left posterior dorso-central seta missing), and is deposited in the USNM. Paratypes are as follows: Same label as the holotype, (2 ♂; USNM); same label as the holotype, collected by W.N.Mathis (11 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

ETYMOLOGY.—The specific epithet, *proxima*, is of Latin derivation and means "near."

Aulacigaster rufifemur, new species

(Figs. 3.114-3.119)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons with anterior 1/3 to anterior 1/2 yellowish in ground color; vertex with a shiny spot extended from ocellus half way to eye margin; hindfemur yellow.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Face yellow anteriorly, brown to black on posterior portion. Facial band present, distinct, gray or golden, over brown mark, on dorsal portion of face. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Foretibia yellowish, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindfemur yellow, hindtibia yellowish, hindtarsus yellowish, apical tarsomere brown to black. Male abdomen bright shiny, pregenital segment polished posteriorly, dull

anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere, not appearing “bulbous”. Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), semi-circular, disk of scutellum strongly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta (at most).

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus approximately triangular in profile, apex strongly pointed, surface concave. Cerci partly fused, each cercus bearing 1 very long, posteriorly porrect setula.

Measurements and ratios: Cell dm ratio 3.8–4.3. Body length 3.3–4.1 mm. Wing length 1.1–1.4 mm. Wing width 0.35 mm.

TYPE MATERIAL.—The holotype male is labeled: “PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 12 7' S, 70 58' W, 9-23 Sep 1988, A. Freidberg”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes.—Same label as the holotype (27 ♂, 16 ♀; USNM); same label as the holotype, collected by W.N. Mathis (8 ♂; 4 ♀).

OTHER SPECIMENS EXAMINED.—ECUADOR. Puerto Orellana: Rio Tiputini, 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba. (11 ♂, 3 ♀; USNM). PERU. Madre de Dios: Manu, Erika (near Salvacion), 550 m, 5-6 Sep 1988, A. Freidberg (1 ♀; USNM); Rio Manu, Cocha Salvador, 240 m, 14 Sep 1988, W. N. Mathis (1 ♀; USNM).

DISTRIBUTION.—Neotropical: Ecuador, Peru.

ETYMOLOGY.—The specific epithet, *rufifemur*, is of Latin derivation and is a combination of the Latin words for red (*rufus*) and thigh (*femur*).

Aulacigaster trifasciata, new species

(Figs. 3.120-3.127)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: ocellar tubercle mostly polished; abdomen with a large, white to yellowish region over syntergite 1+2.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe not followed by a posterior, velvet black stripe. Ocellar tubercle mostly polished. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face white. Facial band present, distinct, gray or golden, over brown mark, on dorsal portion of face. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white. Forecoxa yellow, forefemur yellowish, foretibia yellowish, foretarsus yellowish,

apical and sometimes subapical tarsomeres brown to black. Midcoxa yellow, midfemur yellowish (tip infuscate in some specimens), midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur yellow on basal portion, apical portion dark (apical $\frac{1}{4}$ infuscate to black), hindtibia yellowish, hindtarsus yellowish, apical tarsomere brown to black. Abdomen with a large, white to yellowish region over syntergite 1+2, male abdomen bright shiny. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face not appearing “bulbous.” Inner vertical seta $\frac{1}{2}$ length of outer vertical seta or $\frac{3}{4}$ length of outer vertical seta. One strong peristomal seta present, following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta. Legs: Hindfemur modified, with 2 ventral rows of spines, each spine bearing an apical seta. Hindtibia with a row of tiny ventral spines. Hindtibia without ventropical projections.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded, and bearing a tongue-like median projection. Surstylus from lateral view “box-shaped.” Cerci partly fused, each cercus bearing 1 very long, ventral seta and 1–3 longer setulae.

Measurements and ratios: Cell dm ratio 3.5–3.6. Body length 3.3 mm. Wing length 1.1 mm. Wing width 0.35 mm.

TYPE MATERIAL.—The holotype male is labeled: “ECUADOR. Puerto Orellana: Rio Tiputini (0° 38.2’S, 76° 8.9’W), 12–26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba.”/HOLOTYPE LABEL The holotype is double mounted (mounted in a block of plastic), is in excellent condition, and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (54 ♂, 19 ♀; USNM).

OTHER SPECIMENS EXAMINED.—COSTA RICA. Puntarenas: Peninsula de Osa, Rincon, 24 March 1991, sea level, D.A. Grimaldi, J. Stark, “sweeping in palm-mangrove forest” (1 ♂; USNM). PERU. Madre de Dios: Manu, Rio Manu, Pakitza, 250 m, 12 7’ S, 70 58’ W, 9–23 Sep 1988, A. Freidberg, W. N. Mathis (8 ♂, 4 ♀; USNM). PANAMA. Canal Zone: Barro Colorado Island, 10 Jan 1929, C.H. Curran (2 ♂; AMNH).

DISTRIBUTION.—Neotropical: Costa Rica, Ecuador, Peru.

ETYMOLOGY.—The specific epithet, *trifasciata*, is of Latin derivation and is a combination of the prefix “*tri-*,” which means three, and the Latin word for band (*fascia*).

Aulacigaster sp. d., undescribed species

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with a yellowish region over syntergite 1+2; hindfemur mostly dark-brown, yellowish at basal 1/5-1/4.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frontal white-microtomentose stripe followed by a conspicuous velvety-black stripe. Ocellar tubercle dull microtomentose. Antenna brownish to brown. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly white (base darker). Male abdomen bright shiny, pregenital segment polished posteriorly, dull anteriorly. Forecoxa brown to black, foretibia yellowish, foretarsus mostly yellowish. Midcoxa brown to black, midfemur yellowish, midtibia yellowish, midtarsus mostly yellowish. Hindfemur yellow, hindtibia yellowish, hindtarsus yellowish.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta approximately the same width as the 1st flagellomere, not appearing “bulbous.” Inner vertical seta ½ length of outer vertical seta.

Thorax: Scutellum strongly raised (angle with scutum more than 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex or strongly convex. Basal scutellar seta less than ½ length of posterior seta.

Male abdomen and terminalia: Surstylus a short, postero-ventral lobe in lateral view, surstylar lobe approximately triangular, apex strongly pointed, surface concave. Cerci separated.

MATERIAL EXAMINED.—PERU. Madre de Dios. Manu, Rio Manu, Pakitza, 250 m, 9–23 Sep 1988, A. Freidberg (1 ♂; USNM).

DISTRIBUTION.—Neotropical: Peru.

OBSERVATIONS.—I did not describe this species because it is represented by one male only.

The *leucopeza* group

(Figs. 3.128-3.154)

DIAGNOSIS.—The *leucopeza* group can be distinguished from other species groups by the following combination of characters: Stout, small to medium-sized flies, body length 1.63–4.5. Coloration: Frons typically bearing a transverse, orange to orange-brown stripe, often followed by a brown stripe or shadow. Anterior portion of frons densely microtomentose, with a narrow, anterior, silver stripe. Abdomen in a few species with a large, white to yellowish region over syntergite 1+2.

Morphology: Head: Head typically higher than long (head ratio lower than 0.9). Face in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in most species in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Arista short, with very inconspicuous, alternate hairs (arista appearing naked at low magnification) or short, with tiny, dense, alternate hairs; arista appearing straight. Ocellar seta typically minute. Fronto-orbital setae typically with posterior seta

internal to and almost horizontally aligned with anterior seta. Wing: Sc vein partly fused with vein R1 apically but terminating on costa.

Male abdomen and terminalia: Surstylus often arising from posteroventral margin of epandrium. Cerci often broad, plate-like. Subepandrial sclerite forming a single, plate-like structure. Gonopods short, wide, with a few central setae and a posterior lobe.

DISTRIBUTION.—Worldwide, excluding Australian and Oceanic Regions.

OBSERVATIONS.—Species of the *leucopeza* group can be best identified by the coloration and shape of the lower frons, the coloration of legs, the shape of the surstylus and male internal terminalia.

NOTES.—The *leucopeza* group includes 12 species, 9 previously described in the literature. Species of the *leucopeza* group are the one only to occur outside the Neotropical region. Mathis and Freidberg (1994) revised the Nearctic *Aulacigaster*, and provided a key for the species known to occur in that region. A key to the Palearctic species was published by Papp (1997). Barraclough (1993) and Hilger and Kassebeer (2000) treated the Afrotropical species of the genus.

Aulacigaster colombiana, new species

(Figs. 3.128-3.129)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons a with a transverse, narrow, orange-brownish stripe.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly polished

(microtomentose around vertical setae). Frons with a transverse, narrow, orange-brownish stripe (Fig. 3.128). Silver stripe on frons approximately straight, bright shiny (Fig. 3.128). Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, not infuscate dorsally. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protruding, ventral portion of face. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum polished. Katepisternum mostly polished. Halter mostly white. Male abdomen subshiny to dull. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown on central portion, apex and base yellowish, midtibia yellowish-brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown to black on central portion, apex and base yellowish, hindtibia yellowish, hindtarsus yellowish, apical tarsomere brown to black.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of 1st flagellomere, in profile with dorsal ½ concave, ventral portion bulbous. Gena in profile approximately ½–1/3 the width of 1st flagellomere. Cephalic and thoracic setae relatively long (Figs. 3.128-3.129). Ocellar seta very thin, but long, 1/3 length of fronto-orbital setae. Inner vertical seta ¾ length of outer vertical seta (Fig. 3.129). Peristomal area with about three setae following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), approximately triangular, apex relatively pointed, disk of scutellum slightly convex. Basal scutellar seta $\frac{3}{4}$ length of posterior seta.

Male abdomen and terminalia: Cerci bearing short setae, none especially elongate.

Measurements and ratios: Cell dm ratio based on the holotype 4.5. Body length 4.6 mm. Wing length 1.7 mm. Wing width 0.37 mm.

TYPE MATERIAL.—The holotype male is labeled: “COLOMB[ia.] Narino[.] Laguna[.] La Cocha[.] IX-26–71, GEBohart”/ HOLOTYPE LABEL. The holotype is double mounted (glued to the pin), is in regular condition [left vibrissa and scutellar setae broken, abdomen and right wing dissected and attached to a microvial], and is deposited at the USNM.

DISTRIBUTION.—Colombia.

OBSERVATIONS.—I damaged the surstylus upon dissecting the epandrium. Therefore this structure could not be described.

ETYMOLOGY.—The specific epithet, *colombiana*, refers to the country where the type series was collected.

Aulacigaster spangleri, new species

(Figs. 3.130-3.131)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: frons yellowish-orange on central portion, merging with black along lateral margins.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished, with a densely microtomentose stripe posterior to ocellar triangle. Frons yellowish-orange centrally, merging with black along lateral margins. Silver stripe on frons approximately semi-lunate. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, not infuscate dorsally. Face brownish. Facial band absent (Fig. 3.130). Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Anepisternum polished. Katepisternum mostly polished. Halter mostly white. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown (base and tip yellowish), midtibia yellowish, midtarsus mostly yellowish. Hindcoxa yellow, hindfemur brown to black on central portion, apex and base yellowish (base yellowish), hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Abdomen with a large, white to yellowish region over syntergite 1+2, male abdomen subshiny to dull. Female abdomen with dense microtomentum over anterior margin of tergites, posterior margin of tergites bright shiny.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissal seta wider than width of first flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous (Fig. 3.130). Gena in profile approximately $\frac{1}{3}$ - $\frac{1}{2}$ the width of 1st flagellomere (Fig. 3.131). Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta. Wing. Costal vein of male bearing a few tiny, but conspicuous spines.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, slightly sickle-shaped (with a long terminal seta), relatively long. Cerci broad, plate-like, bearing short setae, none especially elongate.

Measurements and ratios: Cell dm ratio 4. Body length 3.7 mm. Wing length 1.5 mm. Wing width 4 mm.

TYPE MATERIAL.—The holotype male is labeled: “COSTA RICA[,] Turrialba[,] VI-15–19–65[,] P. J. Spangler.”/HOLOTYPE LABEL. The holotype is double mounted (mounted in a block of plastic), is in good condition (vertical, scutellar and mesonotal setae broken, wings slightly folded), and is deposited in the USNM. Paratypes are as follows: Same label as the holotype (1 ♀, USNM).

DISTRIBUTION.—Costa Rica.

ETYMOLOGY.—The specific epithet, *spangleri*, is a patronym to honor and recognize the contributions of Dr. Paul Spangler to entomology.

NOTES.—I did not dissect the abdomen of this species because it was tightly attached to the body, and dissection would probably damage the holotype.

Aulacigaster sp.e, undescribed species

(Figs. 3.132-3.133)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: arista short, with very inconspicuous, alternate hairs (arista appearing naked at low magnification); face in profile dorso-ventrally projected, ventral portion of face not recessed.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly polished, with a densely microtomentose stripe posterior to ocellar triangle. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Silver stripe on frons approximately straight, bright shiny (Fig. 3.132). Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protruding, ventral portion of face (Fig. 3.132). Palpus white (Fig. 3.133). Scutum strongly microtomentose medially, polished between pleural region and dorsocentral row of setae, posterior of postpronotum. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose (Fig. 3.133). Anepisternum mostly dull. Katepisternum with anterior portion dull microtomentose, and posterior portion mostly polished. Halter mostly white (knob with dark mark). Forecoxa brown to black, forefemur brown, foretibia yellowish-brownish, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish-

brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown to black, tip yellowish, hindtibia brown to dark-brown (tip yellowish), hindtarsus yellowish, apical tarsomere brown to black. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished (tergites 6- mostly polished).

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1) (Fig. 3.133). Face at level of pseudovibrissal seta wider than width of 1st flagellomere (Fig. 3.123), in profile projected dorsoventrally, ventral portion of face not receded (Fig. 3.133). Ocellar seta very thin, but 2/3 of fronto-orbital setae. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta.

Thorax: Acrostical setae in 2 rows. Scutellum strongly raised (angle with scutum more than 45 degrees), triangular, apex strongly pointed. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

OTHER SPECIMENS EXAMINED.—PERU. Madre de Dios. Manu, Rio Manu, Pakitza, 250 m, 9–23 Sep 1988, A. Freidberg (1 ♀, 1 Sex?; USNM).

DISTRIBUTION.—Peru.

OBSERVATIONS.—Besides the characters cited in the diagnosis, this species is peculiar among the Neotropical species of the *leucopeza* group for having a wide, orange band on the anterior portion of frons.

NOTES.—this species was not fully described and named here because the type series lacks a male.

AFROTROPICAL SPECIES

The Afrotropical fauna comprises three named species belonging to the *leucopeza* group. One species, *Aulacigaster perata* Barraclough, is known only from the female.

Key to the Afrotropical species of *Aulacigaster*

1. Anterior dorsocentral seta lacking. Wing hyaline (Fig. 3.134)
..... *A. sp.* (Barraclough, 1993)
Anterior dorsocentral seta present. Wing mostly brown infuscate
..... 2
2. Palpus short, length about half that of 1st flagellomere 3
Palpus long, subequal in length to that of 1st flagellomere
..... *A. africana* Barraclough
- 3(2). Wing membrane with dark infuscation along costal margin and apex.
Abdomen completely dark brown to black; scutum uniformly
microtomentose (Cameroon) *A. perata* Barraclough
Wing membrane homogeneously dark infuscate along costal margin and
apex. Abdomen with dorsal portion of syntergite 1+2 pale in some
specimens; scutum with weakly defined microtomentose
stripes..... *A. borbonica* Hilger and Kassebeer

Aulacigaster africana Barraclough

Aulacigaster africana Barraclough 1993: 34–38 [figures of head, wing and male terminalia]. Type locality: South Africa. Natal.

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: palpus long, subequal in length to that of third antennal segment.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Frons bearing a transverse, large, orange band. Antenna brownish to brown. Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus white. Scutum dull microtomentose. Scutellum mostly devoid of microtomentum, bright shiny. Postpronotum concolorous with mesonotum, microtomentose over lower and posterior margins, otherwise polished. Katepisternum subshiny to dull. Halter mostly white. Male abdomen subshiny to dull. Forecoxa brown to black, forefemur brown, foretibia yellowish or brown, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish or brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown to black, tip yellowish, hindtibia yellowish or brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Wing membrane dark infuscate, darker along costal margin and apex.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face in profile with dorsal ½ concave, ventral portion bulbous. Gena in profile

approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Palpus long, subequal in length to that of 1st flagellomere. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. One peristomal setae following pseudovibrissal setae present.

Male abdomen and terminalia: Surstylus arising from ventral margin of epandrium, slender, slightly sickle-shaped, relatively long. Cercus bearing short setae, none especially elongate (Barraclough, 1993: Figs. 3-4).

DISTRIBUTION.—Afrotropical: South Africa.

OBSERVATIONS.—The female is not known for this species. The description herein presented is based on Barraclough (1993). According with Barraclough (1993), *A. africana* was collected from a shaded sandstone ledge.

Aulacigaster borbonica Hilger and Kassebeer

Aulacigaster borbonica Hilger and Kassebeer, 2000: 167–172 [figures of male terminalia, head and thorax]. Type locality: La Reunión. Salazie.

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: abdomen with tergite one white; frons bearing a transverse, large, orange band.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Mesofrons with a faint median microtomentose stripe from base of antenna to level of anterior fronto-orbital seta. Face brownish.

Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus white. Scutum with weakly defined microtomentose stripes. Postpronotum concolorous with mesonotum, scarcely microtomentose, subshiny. Halter mostly white. Abdomen with dorsal portion of tergite 1 white. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus brown to dark brown, basal tarsomere yellow. Midcoxa brown to black, midfemur brown, midtibia brownish, midtarsus yellowish on basal 1/3 of basitarsomere, otherwise brown. Hindcoxa brown, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish on basal 1/3 of first tarsomere, otherwise brown. Wing mostly brown, infusate.

Morphology: Head: Face in profile with dorsal 1/2 concave, ventral portion bulbous. Gena in profile approximately 1/2–1/3 the width of 1st flagellomere. Inner vertical seta 3/4 length of outer vertical seta.

Thorax: Acrostical setae in 2 rows. Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, apex swollen, blunt, relatively long. Cerci broad, plate-like, bearing short setae, none especially elongate.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, finger-like, relatively long (Fig. 2a, Hilger and Kassebeer 2000: 170). Subepandrial sclerite with cerci fused on basal 1/2, lateral arms curved posteriorly and blunt apically (Fig. 2b, Hilger and Kassebeer 2000: 170). Gonite (Fig. 2c, Hilger and Kassebeer 2000: 170) in lateral view with pointed process posterodorsally, deep, approximately rectangular.

Measurements and ratios: Body length 0.2 mm.

DISTRIBUTION.—Afrotropical: Reunión.

OBSERVATIONS.—The description herein presented is based on Hilger and Kassebeer (2000). According the authors, *A. borbonica* was collected from slime flux of the Horsetail Tree , original from Australia and introduced to Réunion by man.

Aulacigaster perata Barraclough

Aulacigaster perata Barraclough, 1993: 39–40. Type locality: Cameroon.

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: arista short, with tiny, dense, alternate hairs; facial band absent.

DIAGNOSTIC DESCRIPTION.—Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Antenna pale yellow to yellowish. Facial band present. Palpus white. Anepisternum mostly dull. Katepisternum mostly polished. Halter mostly yellowish, or mostly brown to dark brown (knob darker). Forecoxa yellow or brown to black, forefemur brown, foretibia brown, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa yellow, midfemur brown, midtibia brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa yellow, hindfemur brown, hindtibia brown to dark-brown, hindtarsus with basal tarsomere brown, apical

tarsomere yellowish. Wing mostly brown, infusate. Head: Gena in profile approximately 1/5 the width of 1st flagellomere below ventral margin of eye.

Male abdomen and terminalia: Surstylus arising from ventral margin of epandrium, approximately sickle-shaped, relatively long (Figs. 3-4 , Barraclough 1993: 35). Subepandrial sclerite with cerci fused along most of its length. Gonite (Fig. 3, Barraclough 1993: 35) in lateral view with pointed process posterodorsally, in profile more developed ventrally, approximately tongue-shaped.

DISTRIBUTION.—Afrotropical: South Africa.

OBSERVATIONS.—The description herein presented is based on Barraclough (1993). The male is not known for this species. According to Barraclough (1993), *A. perata* was collected at approximately 1500 m altitude.

NEARCTIC SPECIES

The Nearctic fauna comprises three named species. One species, *A. neoleucopeza* Mathis and Papp, also occurs in the Palearctic region (see above). A key to the Nearctic species, distributional data, descriptions and illustrations were given by Mathis and Papp (1994).

Aulacigaster neoleucopeza Mathis and Freidberg

(Figs. 3.136-3.137, 141, 154)

Aulacigaster neoleucopeza Mathis and Freidberg, 1994: 586–591 [illustration of head, thorax, and male terminalia]. Type locality: USA. Maryland. Montgomery County.–Papp, 199[8]: 229, 230–232 [comparison with *A. leucopeza*, illustrations of head and male terminalia], 233 [key for Palearctic species of *Aulacigaster*]; 1988: 280-284 [Manual of Palearctic Diptera].–Bächli *et al.*, 1999: 121 [checklist, Switzerland, Italy, and Greece].

DIAGNOSIS.–This species can be distinguished from congeners by the following combination of characters: arista short, with tiny, dense, alternate hairs; katepisternum with anterior portion dull microtomentose, and posterior portion mostly polished; scutum with weakly defined microtomentose stripes; surstylus moderately long, about 1/3 length of basal margin of epandrium in lateral view.

DIAGNOSTIC DESCRIPTION.–Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to ½-2/3 distance to eye margin. Frons bearing a transverse, large, orange band. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion (Figs. 3.136-3.137). Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus white. Scutum with weakly defined microtomentose stripes. Scutellum dull microtomentose. Postpronotum

concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull, or with a semi-lunate, ventral, strongly microtomentose stripe. Katepisternum with anterior portion dull microtomentose, and posterior portion mostly polished. Halter mostly white (knob and base with brownish marks). Forecoxa brown to black, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Three peristomal setae following pseudovibrissal setae present.

Thorax: Acrostical setae in 1 row, bifurcating posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta less than $\frac{1}{2}$ length of posterior seta or $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, finger-like, relatively long (Fig.). Subepandrial sclerite with lateral arms well sclerotized, curved posterolaterally, with slight recurved apices. Cerci with deep, narrow cleft, fused only on basal $\frac{1}{4}$ (Fig. 9, Mathis and Freidberg

1994: 588). Gonite lacking pointed projection posterodorsally, more broadly developed ventrally, approximately tongue-shaped in profile.

Female abdomen and terminalia: Spermathecae with ventral digitiform projections.

Measurements and ratios: Body length 2.35 mm. Wing width 0.51 mm.

TYPE MATERIAL.—USA. Maryland. Montgomery: Potomac, 23 Jul-23 Aug 1989, Amnon Freidberg, slime flux on oak (22 ♂, 9 ♀; TAU, USNM). Prince Georges: Camp Springs, 1 Apr 1979, G.F. Hevel (16 ♂, 7 ♀; USNM). Virginia. Stafford: Stafford (4 mi N), 14 Aug 1990, W.N. Mathis (3 ♂; USNM).

OTHER SPECIMENS EXAMINED.—CANADA. Alberta. Edmonton, 29 Apr 1924, O. Bryant (6 ♂, 4 ♀; CAS, USNM); MEXICO. Baja California Norte: San José (reared from ooze from cottonwood), 6 Nov 1953, R.E. Ryckman, C.C. Lindt (4 ♂ 1 ♀; USNM); Tecate (ex *Populus ooze*), 16 Jun 1964, R. Duke (1 ♂, 1 ♀; USNM). UNITED STATES. California. Kern: Kern Canyon, Apr 1934, A.H. Sturtevant (1 ♂, 2 ♀; USNM); Rosamond, 17 Oct 1956, A.H. Sturtevant (2 ♀; USNM); Glendora, 15 Mar 1929, A.H. Sturtevant (1 ♀; USNM). Riverside: Mecca, Cottonwood Spring, May 1939, A.H. Sturtevant (2 ♀; USNM); San Juan Canyon, 22 Jul 1953, A.H. Sturtevant (2 ♀; USNM). San Bernardino: Redlands, 27 May 1923, F.R. Cole (1 ♂, 1 ♀; USNM); San Diego: Alpine (ex. *Rhus ovata*), 12 May 1959, Moffet (1 ♀; USNM); Palomar Mountain (5300 ft), 23 Jul 1953, A.H. Sturtevant (3 ♂, 1 ♀; USNM). Santa Clara: Palo Alto, 14 Jun-17 Jul 1921, A.H. Sturtevant (4 ♂; USNM); Connecticut. Fairfield: Redding, 31 Mar 1929, A.L. Melander (1 ♀;

USNM). ILLINOIS. Flat Rock, 1915 (1 ♂, 3 ♀; USNM). Indiana. Tippecanoe: Lafayette, 26 Jul 1916, J.M. Aldrich (1 ♀; USNM). IOWA. Story: Ames, 1 Apr 1918 (1 ♀; USNM). Webster: Lehigh, 15 Apr 1955, D.M. Norris (1 ♀; USNM).

KANSAS. Maryland. Montgomery: Bethesda, 27 Jul 1965, G.C. Steyskal (4 ♂, 3 ♀; USNM); Colesville, 14 Jun 1977, W.W. Wirth (1 ♀; USNM); Glen Echo, 6 Aug 1922, J.R. Malloch (1 ♂; USNM); Plummers Island, 3 Aug 1912 (8 ♂, 5 ♀; USNM).

Prince Georges: Marlboro, May 1913, H.S. Barber (1 ♀; USNM). Massachusetts. Barnstable: Naushon Island, 30 Jul 1922, A.H. Sturtevant (1 ♀; USNM); Woods Hole, Jul-20 Sep 1922, A.H. Sturtevant (7 ♂, 8 ♀; USNM). Michigan. Wayne: Detroit, 13 Apr-18 Jul 1938, 1942, 1943, G.C. Steyskal (4 ♂, 2 ♀; USNM); Grosse Isle, 11 Jul 1948, G.C. Steyskal (1 ♀; USNM). New Hampshire. Grafton: Hanover, 31 Aug 1916, A.H. Sturtevant (1 ♂; USNM). New Jersey. Morris: Morristown, 9 Apr 1922, A.H. Sturtevant (2 ♀; USNM). New Mexico. Otero: Cloudcraft (*Pinus ponderosa*), E.J. Hay (1 ♂; USNM). Oregon. Jackson: Trail, 20 Aug 1951, A.H. Sturtevant (2 ♂; USNM). Union: U. Lick Creek (28 mi SE Union, 4280 ft, sap flow), 23 Apr 1977, R.S. Zack (1 ♂; USNM). Wallowa: Elgin (22 mi N, *Alnus seep*), 20 May 1977, E.S. Davis (1 ♀; USNM). PENNSYLVANIA. Philadelphia: Roxborough, 30 Apr 1910 (2 ♂; USNM). SOUTH DAKOTA. Brule: Chamberlain, 25 Jun 1948, A.H. Sturtevant (1 ♂, 3 ♀; USNM). UTAH. Washington: Zion National Park, 7 Jun 1934, A.H. Sturtevant (3 ♂, 1 ♀, 1ex; USNM). VERMONT. Orange: Fairlee, 5 Aug 1956, A.H. Sturtevant (1 ♂; USNM). Virginia. Fairfax: Dead Run, R.C. Shannon (8 ♂, 9 ♀; USNM). Washington. Walla Walla: Walla Walla, Mill Creek, 2-6 Jul 1922,

V.N. Argo, A.L. Melander (16 ♂, 8 ♀; USNM). Washington, D.C. 19 Jun-17 Aug 1913, 1944 (2 ♂, 1 ♀; USNM). Wisconsin. Dane: 29 Apr 1951, R.H. Jones (1 ♂; USNM).

DISTRIBUTION.—Nearctic: Canada (AB, BC, MN, NB, ON, PQ, SQ), Mexico (BCN), USA (AZ, CA, CT, IA, ID, IL, IN, KS, MA, MD, MI, MN, NH, NJ, NM, NV, NY, OR, PA, SD, UT, VA, VT, WA). Palearctic: Hungary, Switzerland.

BIOLOGY.—Collected by beer/wine traps (Bachli, 1999).

Aulacigaster mcalpinei Mathis and Freidberg

Aulacigaster mcalpinei Mathis and Freidberg, 1994: 593–597 [illustration of head, thorax, male terminalia and spermathecae]. Type locality: USA. Maryland. Montgomery County.

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: vertex with a shiny spot extended from ocellus at most half way to eye margin; surstylus broad, beak like, wider than width of apical portion of aedeagal apodeme.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infuscate along dorsal margin (to upper 2/3). Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protrudent,

ventral portion of face. Palpus white. Scutum with weakly defined microtomentose stripes. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum. Anepisternum with a semi-lunate, ventral, strongly microtomentose stripe. Katepisternum mostly polished. Halter mostly white (knob mostly dark-brown anteriorly). Forecoxa brown to black, foretibia yellowish, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal ½ concave, ventral portion bulbous. Gena in profile approximately ½–1/3 the width of 1st flagellomere. Inner vertical seta ¾ length of outer vertical seta. Three of four peristomal setae following pseudovibrissal setae present.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta ½ length of posterior seta.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, broad basally, shaped as a beak, relatively long (Fig.). Subepandrial sclerite with cerci mostly fused, lateral arms curved posteriorly and pointed apically (Fig. 22, Mathis and Freidberg 1994: 595). Gonite (Fig. 21, Mathis and Freidberg

1994: 595) in lateral view with pointed process posterodorsally, approximately rectangular.

Female abdomen and terminalia: Spermathecae with ventral digitiform projections.

Measurements and ratios: Body length 2.6 mm. Wing width 0.4 mm.

TYPE MATERIAL.—Paratypes: USA. Maryland. Montgomery: Potomac, 23 Jul-23 Aug 1989, Amnon Freidberg, slime flux on oak (17 ♂, 15 ♀; TAU, USNM). Connecticut. Fairfield: Redding, 31 Mar 1929, A.L. Melander (4 ♂, 4 ♀; USNM). New Hampshire. Hillsboro: Hollis (Beaver Brook Association), 20 Apr 1980, N.E. Woodley (14 ♂, 8 ♀; NEW, USNM). Virginia. Fairfax: Dead Run (at sap tree, at sap sugar maple), 8 Mar-28 Jul 1914, 1915, 1916, 1925, R.C., E.M. Shannon (17 ♂, 21 ♀; USNM).

OTHER SPECIMENS EXAMINED.— UNITED STATES. Arkansas.

Garland: Hot Springs National Park, 29 Aug-13 Sep 1943, B.C. Marshall (2 ♀; USNM). Florida. Alachua: Gainesville, 22 May 1957, H.V. Weems (3 ♂; USNM). Illinois. Cook: Chicago (1 ♀; USNM). Macoupin: Carlinville, Robertson (1 ♂; USNM). Indiana. Dubois: Ireland (in trap), 17 Jul 1965, O. Mund (1 ♂; USNM). Maryland. Montgomery: Colesville (Malaise trap), 26 Jun 1977, W.W. Wirth (1 ♀; USNM); Glen Echo, 23 Jul-6 Aug 1922, J.R. Malloch (1 ♂, 2 ♀; USNM); Plummers Island, 25 Mar-18 Aug, 1912, 1914, 1916, W.L. McAtee, R.C. Shannon (5 ♂, 3 ♀; USNM). Prince Georges: College Park, 29 Jun 1933, C.T. Greene (1 ♂; USNM). Massachusetts. Middlesex: Cambridge, 7-16 Jul 1981, N.E. Woodley (3 ♀; NEW).

Suffolk: Boston (Arnold Arboretum), 18 Apr 1980, N.E. Woodley (3 ♂, 1 ♀; NEW).
Michigan. Livingston: Es. George Reserve, 16 Apr 1950, K. Bohnsack (1 ♀;
USNM). Washtenaw: Ann Arbor, 30 Apr 1936, G.C. Steyskal (1 ♀; USNM).
Wayne: Detroit, 29 Aug 1943, G.C. Steyskal (1 ♀; USNM); Grosse Isle, 2 Apr 1957,
G.C. Steyskal (1 ♀; USNM). NEW YORK. Tomkins: Ithaca, 15 Apr 1913, H.
Morrison (2 ♀; USNM). Virginia. Alexandria, Maywood (at oak sap), 4 May 1916,
W.L. McAtee (1 ♂; USNM). Falls Church, Holmes Run (light trap), 14 Jun-23 Aug
1961, W.W. Wirth (1 ♂, 1 ♀; USNM). Scotts Run, Stubblefield Falls (on *Pinus
virginiana*), J.R. Malloch (1 ♂, 1 ♀; USNM). Shenandoah: Big Meadows, 15 Jun
1941, A.L. Melander (1 ♀; USNM). Washington, D.C. 3 Mar-4 Aug 1927, H.S.
Barber (1 ♂, 1 ♀; USNM).

Aulacigaster sabroskyi Mathis and Freidberg

Aulacigaster sabroskyi Mathis and Freidberg, 1994: 591–593 [illustration of
male terminalia and spermathecae]. USA. Arizona. Portal.

DIAGNOSIS.—This species can be distinguished from congeners by the
following combination of characters: katapisternum mostly microtomentose, with a
shiny area posteriorly, below the posterior katapisternal seta; surstylus short, less
than 1/6 the basal portion of epandrium in lateral view.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly
densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to
eye margin. Frons bearing a transverse, large, orange band, frontal orange band

merging into dark-brown ventrally. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus white. Scutum with weakly defined microtomentose stripes. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum mostly microtomentose, with a shiny area posteriorly, below the posterior katepisternal seta. Halter mostly white. Forecoxa brown to black, foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull, pregenital segment polished posteriorly, dull anteriorly. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Three to four peristomal setae following pseudovibrissal setae present.

Thorax: Acrostical setae in 1 row, bifurcating posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoidal, apex nearly

straight, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, finger-like, relatively short. Subepandrial sclerite (Fig. 13, Mathis and Freidberg 1994: 591) with lateral arms narrow, well sclerotized, more or less parallel sided, curved evenly posteriorly. Cerci fused on basal $\frac{1}{2}$. Gonite (Fig. 12, Mathis and Freidberg 1994: 591) with a small pointed projection posterodorsally, approximately rectangular in profile.

Measurements and ratios: Body length 2–2.2 mm. Wing width 0.43 mm.

TYPE MATERIAL.—USA. Arizona, Portal 4800 Ft. VI-5- 1967, C.W. Sabrosky, “At bleeding sap, cottonwood” (8 ♂, 2 ♀; USNM, TAU). Arizona. Cochise: Portal (slime flux on tree), 17 May 1973, C.W. Sabrosky (5 ♂, 2 ♀; USNM); Portal, Turkey Creek (6400 ft), 18 May 1973, C.W. Sabrosky (1 ♂; USNM); Carrizo, 26 Sep 1954, A.H. Sturtevant (1 ♂; USNM). New Mexico. Catron: Whitewater Canyon (ulcer on Sycamore tree), 1 Jun 1972, W.W. Wirth (3 ♂, 3 ♀; USNM).

DISTRIBUTION.—Nearctic: Mexico (CHI), USA (AZ, NM).

PALEARCTIC SPECIES

The Palearctic fauna comprises three named species belonging to the *leucopeza* group. One species, *A. neoleucopeza* Mathis and Papp, also occurs in the Nearctic region (see above under “Holarctic species.” A key to the Palearctic *Aulacigaster*

was given by Papp (1997).

Aulacigaster afghanorum Papp

(Figs. 3.148-3.149, 152)

Aulacigaster afghanorum Papp, 1997[8]: 226, 227–229 [figures of male terminalia]. Type locality: Afghanistan. Kabul, Aliabad; 1988: 279–284 [Manual of Palearctic Diptera].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: surstylus slender, approximately finger-like, making a wide angle with anterior margin of epandrium.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: vertex scarcely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, not infuscate dorsally. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus yellowish. Scutellum dull microtomentose. Postpronotum yellow to yellowish-brownish, dull microtomentose. Anepisternum mostly dull. Katepisternum subshiny to dull. Halter mostly yellowish. Epandrium mostly dark brown to black. Forecoxa brown to black, forefemur brown or brown to black, apex yellowish, foretibia brown, foretarsus brown to dark brown, basal tarsomere yellow. Midcoxa brown to black, midfemur brown, midtibia brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown, hindtibia

brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull, pregenital segment mostly polished.

Morphology: Head: head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Chaetotaxy. Ocellar seta minute. Inner vertical seta $\frac{3}{4}$ the length of outer vertical seta. Fronto-orbital setae with posterior seta internal to and almost horizontally aligned with anterior seta. Peristomal vestiture consisting of relatively well-developed setae. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, finger-like, relatively long. Subepandrial sclerite (Fig. 9, Papp 1997: 229) with lateral arms narrow, well sclerotized, tapering towards pointed apex, directed sideways. Cerci completely separated. Gonite (Fig. 3, Papp 1997: 227) with a small pointed projection posterodorsally, shallow ventrally, approximately rectangular to trapezoid in profile.

Measurements and ratios: Cell dm ratio 1.63–2.75. Body length 1.88–2.8 mm. Wing length 0.78–1.1 mm.

TYPE MATERIAL.—The holotype male is labeled: Afghanistan [,] Kabul, Aliabad/ University Park, 1800 m [,] 21.4.1974/ No. 49 [,] L. Papp/ *Aulacigaster leucopeza* Meig. [handwritten] det. L. Papp 1986/ Partypus *Aulacigaster afghanorum* L. Papp [white label with red borders, species name handwritten]. The specimen is double mounted (minuten in cardbox), is in excellent condition, and is deposited in the HMHM.

DISTRIBUTION.—Palearctic: Afghanistan.

Aulacigaster falcata Papp

(Figs. 3.150)

Aulacigaster falcata Papp, 1997[8]: 226–229 [figures of male terminalia].

Type locality: Hungary, Kunfeh'et'o.falcate; 1988: 279–284 [Manual of Palearctic Diptera].—Bächli *et al.*, 1999: 120 [checklist, Switzerland, Italy, and Greece].

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: surstylus slender, approximately sickle-shaped.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protrudent, ventral portion of

face. Palpus white. Scutellum dull microtomentose. Postpronotum yellow to yellowish-brownish, dull microtomentose. Anepisternum mostly dull. Katepisternum with anterior portion dull microtomentose, and posterior portion mostly polished. Halter mostly white, or mostly yellowish. Forecoxa brown to black, forefemur brown, foretibia brown, foretarsus brown to dark brown, basal tarsomere yellow (1–3). Midcoxa brown to black, midfemur brown, midtibia brownish, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindcoxa brown, hindfemur brown, hindtibia brown to dark-brown, hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull, pregenital segment mostly subshiny. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Chaetotaxy: Ocellar seta minute. Inner vertical seta $\frac{3}{4}$ the length of outer vertical seta. Fronto-orbital setae with posterior seta internal to and almost horizontally aligned with anterior seta. Setulae between fronto-orbital setae 1, proclinate. Peristomal vestiture consisting of relatively well-developed setae. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ the length of posterior seta.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, slightly sickle-shaped, relatively long. Subepandrial sclerite (Fig. 10, Papp 1997: 229) with lateral arms broad, well sclerotized, tapering towards apex, slightly curved posteriorly. Cerci completely separated. Gonite (Fig. 4, Papp 1997: 227) with a small pointed projection posterodorsally, more developed ventrally, approximately tongue-shaped in profile.

Measurements and ratios: Cell dm ratio 1.92–2.71. Body length 2.17–2.88 mm. Wing length 0.8–1 mm.

TYPE MATERIAL.—Paratype: Hungary. Kiskunsági National Park, Kunfehértó, 15 Jul 1982, L. Papp (1 ♂; USNM).

OTHER SPECIMENS EXAMINED.—Budapest. Pestszeöntlorinc, Halmi-erdő, 11 Jul 1998, L. Papp, “tölgifák sebeiről” (1 ♂, 1 ♀; USNM)

DISTRIBUTION.—Palearctic: Greece, Hungary, and Switzerland.

Aulacigaster leucopeza (Meigen,)

(Fig. 151)

Aulacigaster leucopeza (Meigen)

Diastata leucopeza Meigen, 1830: 100. Type locality: unknown (Baumhauer coll.”).

Aulacigaster leucopeza.—Robinson 1953: 77–83 [description of biology and immature stages].—Chandler, 1987: ?? [?].—Teskey, 1987: 891, 894 [illustrations, manual Nearctic Diptera].—Mathis and Freidberg, 1994: 583 [locality data].—Bächli,

1997: 33 [faunistic and host record.–Bachli *et al.*, 1999: 120–121 [checklist, Switzerland, Italy and Greece].–Papp, 1997[8]: 228, 231–233 [illustrations and key for Palearctic species]; 1988: 279–284 [Manual of Palearctic Diptera].

Aulacigaster rufitarsis Macquart, 1835: 580. Type locality: Liège (Belgium).

Diastata diadema Meigen, 1838: 379. Type locality: “Lüetticher Gegend” [= near Liège] (Belgium).

Apotomella impressifrons Dufour, 1846: 460. Type locality: France.

Ampycophora tarsata Wahlberg, 1847: 261. Type locality: Sweden.

Sephanilla sertulata Rondani 1874: 268.

DIAGNOSTIC DESCRIPTION.–Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin or with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frons bearing a transverse, large, orange band. Silver stripe on frons approximately straight. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin or infusate on dorsal half. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protrudent, ventral portion of face. Palpus white. Scutum with weakly defined microtomentose stripes. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum mostly microtomentose, with a shiny area posteriorly, below the posterior katepisternal seta. Halter mostly white. Forecoxa brown to black, forefemur brown to black, apex yellowish, foretibia brown, foretarsus yellowish, apical and

sometimes subapical tarsomeres brown to black (3 apical). Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish on central portion, apex and basis brown, midtarsus yellowish, apical and subapical tarsomere brownish to dark brown (3 apical). Hindcoxa brown, hindfemur brown to black, tip yellowish, hindtibia brown to dark brown, basal and central portion yellowish, hindtarsus yellowish, apical tarsomere brown to black. Male abdomen subshiny to dull. Female abdomen with dense microtomentum medially, lateral margins of tergites nearly polished.

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Three to four peristomal setae following pseudovibrissal setae present.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Surstylus arising from posteroventral margin of epandrium, slender, finger-like, relatively long. Subepandrial sclerite (Fig. 11, Papp 1997: 229) with lateral arms narrow, well sclerotized, curved evenly posteriorly. Cerci completely separated. Gonite (Figs. 15-16, Papp 1997: 231) with a small pointed projection posterodorsally, more developed ventrally, approximately tongue-shaped in profile.

BIOLOGY.—Collected by beer/wine traps (Bachli, 1999).

DISTRIBUTION.—Palearctic. France, England, Germany, Hungary, Israel, Italy, Poland, Spain, Sweden, Switzerland.

ORIENTAL SPECIES

The presence of the undescribed *Aulacigaster* in the Oriental region had been previously documented by Delfinado and Hardy (1977). One species is herein described, and two others are mentioned, all belonging to the *leucopeza* group.

Key to the Oriental species of *Aulacigaster* Macquart

1. Vertex mostly microtomentose; facial band absent (Figs. 3.145-3.146); scutum with weakly defined microtomentose stripes (Nepal)
..... *A. sp. g*, undescribed species
- Vertex with a shiny area between hind ocellus and margin of eye facial band present (Figs. 3.142, 3.143); scutum without obvious stripes2
- 2(1). Shiny spot of vertex small, extended from ocellus at most half way to eye margin (Fig. 3.142); scutum uniformly microtomentose (Sri-Lanka) *A. sp. f* undescribed species
- Shiny spot of vertex large, extended from ocellus 2/3 to eye margin (Fig. 3.143); scutum polished opposite to postcranium (India)
.....*A. india*, new species

Aulacigaster india, new species

(Figs. 3.141-3.142)

DIAGNOSIS.—This species can be distinguished from congeners by the following combination of characters: arista short, with tiny, dense, alternate hairs; scutum polished on anteriormost portion, opposite to postcranium.

DIAGNOSTIC DESCRIPTION.—Coloration and vestiture: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus to 2/3 distance to eye margin. Frons bearing a transverse, large, orange band, frontal orange band merging into dark-brown ventrally (dark-brown region interrupted in some specimens). Silver stripe on frons approximately straight, weak. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infuscate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protruding, ventral portion of face. Palpus white. Scutum polished on anteriormost portion, opposite postcranium. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum with anterior portion dull microtomentose, and posterior portion mostly polished. Halter mostly white, or mostly yellowish ((knob with brown area)). Forecoxa brown to black, foretibia yellowish (tip and sometimes basis dark), foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black (apical and subapical). Midcoxa brown to black, midfemur brown to black, apex yellowish, midtibia yellowish on central portion,

apex and basis brown (tip, and sometimes basis brown), midtarsus yellowish-brownish. Hindfemur brown to black, tip yellowish, hindtibia mostly yellow, base and apex infuscate with brown, hindtarsus yellowish, apical tarsomere brown to black (apical and subapical).

Morphology: Head: Head higher than long (head ratio lower than 0.9). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal $\frac{1}{2}$ concave, ventral portion bulbous. Gena in profile approximately $\frac{1}{2}$ – $\frac{1}{3}$ the width of 1st flagellomere. Inner vertical seta $\frac{3}{4}$ length of outer vertical seta. Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum strongly convex. Basal scutellar seta $\frac{1}{2}$ length of posterior seta.

Male abdomen and terminalia: Sternite 5 with a central, more membranous area, posterior margin appearing receded. Surstylus arising from posteroventral margin of epandrium, slender, finger-like, relatively long. Cercus partly fused, bearing short setae, none especially elongate.

Measurements and ratios: Cell dm ratio 2.7–3.3. Body length 3–3.6 mm. Wing length 1–1.3 mm. Wing width 0.36 mm.

TYPE MATERIAL.—The holotype male is labeled: “INDIA: Meghalaya Mawphlang (20 km W. Shillong) 21Apr[il] 1980 [,] A[.]Freidberg”/HOLOTYPE LABEL. The holotype is double mounted (minuten in a block of plastic), is in excellent condition (abdomen dissected, structures in an attached microvial), and is

deposited in the USNM. Paratypes are as follows: Same label as the holotype (3 ♀; USNM).

DISTRIBUTION.—India.

ETYMOLOGY.—The specific epithet, *india*, refers to the country where the type series was collected. The name is in apposition.

Aulacigaster sp.f, undescribed species

(Figs. 3.141-3.146)

DIAGNOSIS.—This species can be distinguished from congeners by the following characters: cheek in profile approximately 1/5 the width of 1st flagellomere below ventral margin of eye.

DIAGNOSTIC DESCRIPTION.—Coloration: Vertex mostly densely microtomentose, with a shiny spot extended from ocellus at most half way to eye margin. Frons bearing a transverse, large, orange band. Silver stripe on frons approximately straight, bright shiny. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate along dorsal margin. Face yellow, with a transverse brown mark on dorsal portion. Facial band present, sharply defined, transverse, on protruding, ventral portion of face. Palpus white. Scutellum dull microtomentose. Postpronotum concolorous with mesonotum, dull microtomentose. Anepisternum mostly dull. Katepisternum mostly microtomentose, with a shiny area posteriorly, below the posterior katepisternal seta. Halter mostly brown to dark brown. Forecoxa brown to black. Midcoxa brown to black, midtarsus yellowish,

apical and subapical tarsomere brownish to dark brown. Hindtarsus yellowish, apical tarsomere brown to black. Male abdomen bright shiny.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1), or longer than high (head ratio higher than 1.1). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal ½ concave, ventral portion bulbous. Gena in profile approximately 1/5 the width of 1st flagellomere below ventral margin of eye. Inner vertical seta ½ length of outer vertical seta. Peristomal area with about one seta following pseudovibrissal seta.

Thorax: Acrostical setae in 2 rows. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta less than ½ length of posterior seta.

OTHER SPECIMENS EXAMINED.—SRI LANKA. Kan.?? District, Kandi Udawattakele Sanctuary, 22 Mar 1981, K.V.Krombein, T.Wijesinhe and L.Weeratunge (1 ♂, USNM).

DISTRIBUTION.—Oriental: Sri Lanka.

NOTES.—This species was not described because one male only represents it.

Aulacigaster sp. g, undescribed species

(Figs. 3.145-3.146)

DIAGNOSIS.– This species can be distinguished from congeners by the following characters: Arista short, with very inconspicuous, alternate hairs (arista appearing naked at low magnification); facial band absent; frons bearing a transverse, large, orange band.

DIAGNOSTIC DESCRIPTION.–Coloration: Vertex mostly densely microtomentose, without a shiny spot (a small dot lateral to posterior ocellus is however present). Frons bearing a transverse, large, orange band, frontal orange band not merging into dark-brown ventrally. Anterior portion of frons densely microtomentose, with a faint, narrow, anterior silvery stripe (Fig.??), not followed by a black stripe or shadow. Ocellar tubercle dull microtomentose. Antenna pale yellow to yellowish, infusate on dorsal half or infusate along dorsal margin. Face yellow anteriorly, brown to black on posterior portion. Palpus white. Scutum with weakly defined microtomentose stripes. Scutellum dull microtomentose. Postpronotum yellow to yellowish-brownish, dull microtomentose. Anepisternum mostly dull (with a silver, transverse, ill-defined stripe). Katepisternum mostly polished, or with anterior portion dull microtomentose, and posterior portion mostly polished. Halter mostly white (base slightly infusate). Forecoxa brown to black, forefemur brown to black, apex yellowish (tip yellowish), foretarsus yellowish, apical and sometimes subapical tarsomeres brown to black. Midcoxa brown to black, midfemur brown to

black, apex yellowish (tip yellowish), midtarsus yellowish, apical and subapical tarsomere brownish to dark brown. Hindfemur brown to black, tip yellowish (tip yellowish), hindtarsus yellowish, apical tarsomere brown to black. Female abdomen subshiny.

Morphology: Head: Head round, about as high as long (head ratio 0.9 to 1.1). Face at level of pseudovibrissa wider than width of 1st flagellomere, in profile with dorsal ½ concave, ventral portion bulbous. Gena in profile approximately ½–1/3 the width of 1st flagellomere. Inner vertical seta ¾ length of outer vertical seta.

Peristomal area with about 4 setae following pseudovibrissal seta.

Thorax: Acrostical setae in 1 row, bifurcating posteriorly. Scutellum slightly raised (angle with scutum approximately 45 degrees), trapezoid, apex nearly straight, disk of scutellum slightly convex. Basal scutellar seta ½ length of posterior seta.

OTHER SPECIMENS EXAMINED.—NEPAL. Can.?? Nepal expedition, 26 May 1967, “malaise trap.” (2 F; USNM).

DISTRIBUTION.—Oriental: Nepal.

NOTES.—This species was not described because it is represented by females only.

Morphology and character coding

In this section I describe the morphological variation observed and the characters extracted from it. The character codings are summarized in Table 3.1.

Discussions of phylogenetic distribution of character states refer to the ‘best estimate’ phylogeny (see below) shown in Fig. 3.155.

Coloration and vestiture

1. The anterior portion of the frons, or lower frons, is concolorous with the remaining frons in the ground-plan of *Aulacigaster* (1) (as in Figs. 3.16, 3.19, 3.27). A yellow lower frons (2) (as in Figs. 3.103, 3.111) occurs in species of the *plesiomorphica* group, except *A. tripuncata*. This state is convergent with that present in the undescribed genus from Malaysia. Species of the *leucopeza* group have the lower portion of the frons orange (3) (as for ex. in Figs. 3.132, 3.135), a synapomorphy for the group. In some species, the orange coloration of the lower frons is somewhat infuscate with brown (as in Figs. 3.128, 3.130).

3. In the outgroup, and in species belonging to the *plesiomorphica*, *bromeliae* and *leucopeza* groups, the scutum is uniformly microtomentose (1). A reduction in the microtomentum coverage of the scutum (2-4) happens in the apical species of *Aulacigaster*. State 2 is a synapomorphy uniting *grimaldii*, *femorata*, *minuta* and *ecuadoriensis* groups.

4. The pleural region white on lower half (2-4) (as in Fig. 3.35) is a synapomorphy for the species of the *ecuadoriensis* group, excluding *A. stenoptera*. In most opomyzoids, the pleural region is homogeneous in color.

5. In species of the *femorata* group, the syntergite 1+2 has a large, yellow central region (2) (as in Fig. 3.42). This state is not present in any other aulacigastrid group.

6. Species of the *ecuadoriensis* and *minuta* groups have the body elongate and somewhat dorsoventrally flattened (2) (as in Figs. 3.35, 3.83). According with this analysis, the dorsoventral compression of the body is a synapomorphy for these two groups. It also occurs in the Neurochaetidae and other Opomyzoidea.

7. The vertex is straight between the compound eyes (1) in the ground-plan of the Aulacigastridae, but it can be excavated. This excavation may be semilunate (3), an autapomorphy for the species of the *bromeliae* group (Figs. 3.16, 3.19), or approximately V-shaped (2) (Fig. 3.27), a state found in species of the *ecuadoriensis* group and in *Echidnocephalodes barbatus (incertae sedis)*.

8. The frontal margins of the eye usually diverge towards the top of the head, making the frons wider posteriorly, or they are sub-parallel (1) (as for ex. Figs. 3.128, 3.130, 3.132). In the *bromeliae* group, the frontal margins of the eyes conspicuously converge posteriorly (2) (as in Figs. 3.16, 3.19), an autapomorphic condition. In the Opomyzoidea, this state is also present in the Marginidae (D.K. McAlpine 1992:170, Fig. 2) and Neurochaetidae, as well as in some species of *Cyamops*.

Morphology of the head, and head appendages

9. A completely sclerotized face is a synapomorphy for the Asteioinea (J.F. McAlpine 1989) (1). In this analysis, it is present in *Cyamops* and *Periscelis*, as well as in the undescribed genus from Malaysia and *Aulacigaster*. Only the Anthomyzidae have a weakly sclerotized face (2).

10. The cheek of aulacigastrids ranges from narrow to wide (1-4). The cheek is wide (1/3-1/2 the width of the 1st flagellomere) (1) in species of the *leucopeza* group (as for ex. in Figs 3.129, 3.140). A narrower cheek (1/5 the width of 1st flagellomere) occurs in the undescribed genus from Malaysia (2). The cheek in the species of the *bromeliae* group is triangular in profile, being narrowest below the ventral margin of the eye, a synapomorphy for the group (3) (as in Figs. 3.6, 3.15, 3.18). In species of the *plesiomorphica*, *femorata*, *minuta* and *ecuadoriensis* groups, the cheek is very narrow throughout its range, a synapomorphy for these groups that evolved independently in *A. grimaldii* (4) (as for ex. in Figs. 3.35, 3.49, 3.73, 3.83). Because it is difficult to separate this character into discrete states, it was excluded from the analysis.

11. Only species of the *bromeliae* group have the clypeus elongate, a synapomorphy for the group (2) (as in Figs. 3.2, 3.6).

12. In the ground plan of *Aulacigaster*, the pedicel is round (1) (as in Fig. 3.43). An oval, decumbent pedicel is a synapomorphy for the species of the *bromeliae* group (2) (as in Fig. 3.5). It also occurs in the outgroup genera *Cyamops* and *Periscelis* (Periscelididae). A triangular pedicel is a synapomorphy for the species of the *ecuadoriensis* group (as in Figs. 3.26, 3.35), with the exception of *A. stenoptera* (Fig. 3.39), which has a round pedicel.

13. An unsegmented arista (1) is a synapomorphy for the *Aulacigaster* in this analysis and the undescribed genus from Malaysia. Outgroup taxa have the arista 2

or 3-segmented (see chapter 2 of this dissertation; see D.K. McAlpine 2002 for an account of arista segmentation in schizophorous Diptera).

14. In the ground plan of *Aulacigaster*, the pedicel articulates with the first flagellomere by means of a membrane that inserts into a basal cavity of the 1st flagellomere (1) (as in Fig. 2.44). In the Periscelididae and Neurochaetidae, the first flagellomere is constricted basally into a basal notch that is inserted deeply into a central cavity of the pedicel (2) (as in Fig. 2.48), a synapomorphy for these two families (see chapter 2). In this analysis, it resulted autapomorphic for the Periscelididae.

15. A pubescent arista has rays arising from the dorsal, lateral and ventral sides of the arista axis, and is characteristic of the Anthomyzidae, among the outgroup taxa (1). A bare arista has no hairs or rays on the arista axis. This state is characteristic of the undescribed genus from Malaysia, and some Neotropical *Aulacigaster* belonging to the *leucopeza* group (2). Most aulacigastrids, however, have the arista distinctly zigzagged (3) (as in Fig. 3.38), with short rays alternating on the dorsal and ventral axis, a synapomorphy for *Aulacigaster*. The arista of species of the *bromeliae* group, and species of *Periscelis* and *Cyamops*, have a double row of dorsal rays on basal 1/3, and alternate rays on apical portion (4) (as in Fig. 3.5). The optimization of this character was ambiguous at the base of the aulacigastrid phylogeny.

16. The ocellar seta is present in the ground plan of the *Aulacigaster* (1). Species of *ecuadoriensis* and *minuta* groups lack an ocellar seta (2). This state

evolved independently in both groups, according with this analysis. The ocellar seta is also lacking in *Cyamops* (Periscelididae) and many other opomyzoid taxa.

17. I have coded the ocellar seta as reduced when it is hair-like in appearance (1). All other degrees of development of this seta were coded as well developed (2). A strong ocellar seta is present in the ground-plan of the Opomyzoidea and Asteioinea. The optimization of this character resulted ambiguous at the base of the aulacigastrid phylogeny.

18. The absence of the inner vertical seta (Fig. 3.16) is an autapomorphy for *A. korneyev* (Fig. 3.19) and *C. nebulosus*, in this analysis. All other taxa have an inner vertical seta.

19. The absence of the postocellar seta (1) is part of the ground plan of the Aulacigastridae, according with this analysis. The postocellar seta is absent in several opomyzoid taxa. It is present (2) in most acalyprates.

20. The presence of only two fronto-orbital setae is part of the ground plan of the Aulacigastridae, according with this analysis. Most asteioids have two fronto-orbital setae (2), a synapomorphy uniting this group with the Marginidae.

21. The reduction in the number of rows of acrostical setae (1) is a synapomorphy for all groups of *Aulacigaster*, excluding the *leucopeza* group, where most species have 2 rows of acrostical setae.

Thorax morphology

22. The presence of a greater ampulla (2) unites all groups against the Anthomyzidae, in this analysis.

23. The presence of a fold on cell dm (2) is a synapomorphy for the Periscelididae, in this analysis.

Wing

24. The *Aulacigaster* and the undescribed genus from Malaysia have the crossvein r-m basal to middle of combined cell dm + bm (2), a synapomorphy for the Aulacigastridae in the modified sensu proposed in chapter 2 of this dissertation.

25. The presence of a kink on vein R1 (2) is characteristic of the Aulacigastridae, and Anthomyzidae. The optimization of this character resulted ambiguous at the base of the aulacigastrid phylogeny.

26. In the ground plan the *Aulacigaster* the costal vein of the male has no spines. In the undescribed genus from Malaysia, and in some species of the *ecuadoriensis* (3.37b) and *bromeliae* (Figs. 3.11, 3.21) groups, the costal vein of the male bears relatively strong, conspicuous spines (2 and 3). The spines present on the costal vein of the species of the *ecuadoriensis* group are stronger and more conspicuous, and for that reason, I have coded it as a different state (3).

27. In the ground plan of the Aulacigastridae, the subcostal vein is fused with vein R1 apically, but still reaching the costal vein (1) (as in Fig. 3.4a, 3.37a). This state is present in Anthomyzidae as well. The subcosta is incomplete but free from R1 in the Periscelididae and most asteioid taxa (2). In species of *Aulacigaster* belonging to the *femorata* (see Fig. 3.68a) and *minuta* groups, the subcosta is fused with vein R1, but it does not reach the costal vein (3). This reduction in the sclerotization of the sc vein is a synapomorphy for the apical groups of *Aulacigaster*,

i.e., the clade sister to the *grimaldii* group, but it reverses again in the apical species of the *ecuadoriensis* group.

Legs

28. In most taxa, the hindfemur of male and female is unmodified (1) (as in Fig. 3.12). In a few species of the *plesiomorphica* group, and in the *femorata*, *ecuadoriensis* and the *minuta* groups, the hindfemur and hindtibia have ventral rows of tiny spines, each spine bearing an apical seta (2) (as in Fig. 3.56). A similar state is also present in *A. tripunctata*, which belongs in the *plesiomorphica* group. The optimization of this character resulted ambiguous at node that above the *bromeliae* group.

Male abdomen and terminalia

29. In the *Aulacigaster*, tergite 6 is fused with the pregenital segment (1) (as in Figs. 3.42, 3.43). The optimization of this character resulted ambiguous at the base of the aulacigastrid phylogeny.

30. The surstylus is fused with the epandrium (2) (as in Figs. 3.31, 3.48) in the Aulacigastridae. Most outgroup taxa (but not *Periscelis*) have the surstylus freely articulated with the epandrium (1). In species of the *bromeliae* group, the surstylus is fused with an inner corner of epandrium (3), a synapomorphy for the group.

31. In the ground plan of the Aulacigastridae, the surstylus is narrow, often finger-like, arising from ventral or posterior ventral margin of epandrium (1) (as in Figs. 3.22-3.25). It is shaped like a lobe in species of the *plesiomorphica* (3.91-3.94), and *ecuadoriensis* groups (2) (Figs. 3.31, 3.32); it can be ventral, ventral posterior or

posterior in position. In apical aulacigastrids, the surstylus is a wide projection of the posterior ventral margin of the epandrium (3) (as in Fig. 3.48). This character failed to unambiguously support any group within the genus *Aulacigaster*.

32. A plate-like subepandrial sclerite (as in Fig. 3.36) belongs in the ground plan of the Aulacigastridae (1). This state is also characteristic of most outgroup taxa; the subepandrial sclerite is T-shaped (as in Fig. 3.45) in species of the *femorata* and *minuta* groups (2), being Y-shaped (as in Fig. 3.79) in *A. grimaldii* (3), a state unique to this species. This character failed to unambiguously support any group within the genus *Aulacigaster*.

33. The presence of lateral, anterior apodeme arising at base of each gonopod (2) (Fig. 3.14) is a synapomorphy for the Aulacigastridae.

34. In the ground plan of the *Aulacigaster*, the gonopod has one or 2 anterior projections that do not bear strong setae (as in Fig. 3.14). In the *plesiomorphica* and *ecuadoriensis* groups (excluding *A. stenoptera*), the gonopod has convergently developed a posterior projection bearing 4-5 strong setae (see Figs. 3.31, 3.91, 3.94). According with this analysis, both groups acquired this state independently.

35. The aedeagal apodeme has no posterior lateral projections that shield the base of the aedeagus in most taxa (1). It is cuneiform, with asymmetrical posterolateral projections in *Aulacigaster* (2). In the Periscelidinae, it is extremely modified, fused with the hypandrium (3). This character failed to unambiguously support any group within the genus *Aulacigaster*.

36. In the *minuta* group the ventral portions of the gonopods are strongly sclerotized, forming a pair of ventral, dark plates (2), a synapomorphy for the group. These plates are absent in the other taxa (1).

37. The posterior portion of the hypandrium is very weakly sclerotized in *Aulacigaster*, a synapomorphy for the genus (2) (Fig. 3.14). It is usually well sclerotized.

Phylogenetic analysis

The optimal trees (Figs. 3.155-3.156) resulting under the four combinations of character ordering and weighting methods are characterized in Table 3.2.

Resolution was higher when phylogenetic orderings among character states were taken into account. Under unweighted parsimony, treating characters as unordered resulted in 37 most parsimonious (MP) trees, the *strict consensus* of which recovered only the species groups and the genera represented by more than one species. Inclusion of character orderings reduced the number of MP trees to 18, and resolved the relationships among the species-groups. When successive weighting was applied, the same number of trees was recovered, regardless of whether character state orderings were applied or not. The trees found with ordered characters are not in conflict with those supported by unordered characters, suggesting that the orderings reflect additional phylogenetic signal.

The major features of the phylogeny, supported by all analyses, are as follows. First, all of the genera and families represented by more than one exemplar are recovered. Second, all of the species groups recognized by me within the genus *Aulacigaster* are recovered with bootstrap support of 70 or higher. Third, when successive weighting is applied, the *leucopeza* group is consistently basal, followed by the *bromeliae* and the *plesiomorphica* groups. The relationships between the apical *Aulacigaster*, consisting of the *femorata*, the *ecuadoriensis* and the *grimaldii* groups differed in some trees found when character orderings were not applied.

In my analyses, both character ordering and weighting against seeming homoplasy (i.e., disagreement with other characters) appeared to enhance phylogenetic signal, providing increased tree resolution that was generally compatible with groupings supported without such ordering or weighting. I therefore place most credence in, and center my discussion on, the trees found using both character ordering and successive weighting (Figs. 3.155-3.156).

Phylogenetic relationships among 16 species of *Aulacigaster*, and 4 other species, used as outgroups, are presented in Fig. 3.157. Clades supported by bootstrap values higher than 50% are indicated by circled numbers in Fig. 3.156.

The *leucopeza* group is supported by two unambiguous, non-homoplasious synapomorphies, the orange coloration of the lower frons (character 1, state 3; Figs. 3.132, 3.135) and the shape of the frontal microtomentose stripe (character 2, state 4; Figs. 3.132, 3.135). This group occurs in all zoogeographic regions except the Australian and Oceanic regions.

The Neotropical species of *Aulacigaster* form a clade that is supported by one unambiguous (albeit homoplasious) synapomorphy, a reduction in the number of rows of acrostical setae (character 21, state 1). The *bromeliae* group, which is basal to the remaining Neotropical aulacigastrids, is supported by 6 unambiguous synapomorphies: the semi-lunate, excavated vertex (character 7, state 3; Figs. 3.16, 3.19); the eye margins converging posteriorly on the vertex (character 8, state 2; Figs. 3.16, 3.19); the enlarged clypeus (character 11, state 2; Figs. 3.2, 3.6); the oval, decumbent 1st flagellomere (character 12, state 2; Fig. 3.5); and the fusion of the surstylus with an inner corner of the epandrium (character 30, state 3). Species of the *bromeliae* group differ from all other aulacigastrids in having an aquatic larva that lives in the phytotelmata of bromeliads (see Figs. 3.1-3.2 for habitus; Fig. 3.10 for immature).

There is no unambiguous synapomorphy supporting the clade containing the Neotropical *Aulacigaster*, excluding the *bromeliae* group. When characters are optimized using accelerated transformation (ACCTRAN), the possession of spines on the hind femur and tibia (character 28, state 2; Fig. 3.56, 3.69) and the lobe-like surstylus (character 31, state 2; Figs. 3.91-3.94) are synapomorphies for this clade. However, if delayed transformation (DELTRAN) is used to optimize the same characters, the modified femur is a synapomorphy for *A. tripunctata*, and for the sister clade of the *plesiomorphica* group. Similarly, the lobe-like surstylus can be optimized a synapomorphy for the *plesiomorphica* group, and for the *ecuadoriensis* group.

The *plesiomorphica* group is supported by two unambiguous synapomorphies, the shape of the microtomentose band on the lower frons (character 2, state 3; Fig. 3.111), and the presence of strong setae on the posterior gonopodal projection (character 34, state 2; Figs. 3.31, 3.91, 3.94). The last character state is homoplasious with the condition found in the *ecuadoriensis* group.

The apical groups of *Aulacigaster* are the *grimaldii* group (monotypic), the *femorata* group, the *ecuadoriensis* group and the *minuta* group. *A. grimaldii* is basal. The remaining *Aulacigaster* form a clade characterized by a reduction in the microtomentum coverage of the scutum (character 3, state 3), and a reduction in the sclerotization of vein sc (character 27, state 1; Fig. 3.68a).

The *femorata* group is characterized by a yellow dorsal region on syntergite 1+2 (character 5, state 2; Fig. 3.42)). The *ecuadoriensis* and *minuta* groups are sister-groups. Species in these groups show a further reduction in the microtomentum of the scutum (character 3, state 4), an elongate, dorso-ventrally flattened body (character 6, state 2; Figs. 3.35, 3.83); and the complete reduction of the ocellar setae (character 16, state 1). The *ecuadoriensis* group is unique in having the lower half of the pleural region, and legs, white (character 4, state 2; Fig. 3.35), and also in having the vertex excavated as a "V" (character 7, state 3; Fig. 3.27). Species of the *minuta* group are peculiar for having a dark-brown sclerotization of the ventral portion of the gonopods, which looks like a pair of ventral plates when viewed ventrally (character 36, state 2).

The results of this work support D.K. McAlpine's (1983) synonymy of Hennig's genus *Schizochroa* with *Aulacigaster*, because *Schizochroa* resulted polyphyletic in my analysis.

Table 3.1.– List of characters

1. Coloration of lower frons: 1. concolorous with the rest of the frons; 2. yellow on lower 1/3-2/3; 3. orange on lower 1/3-2/3;
2. Microtomentum coverage of anterior portion of frons: 1. not forming a microtomentose stripe; 2. forming a narrow, anterior, silver stripe; 3. forming a wide, lunate, silvery microtomentose stripe
3. Microtomentum coverage of scutum: 1. uniform; 2. absent between pleural region and dorsocentral row of setae, posteriorly to postpronotum; 3. at most reaching midline of mesonotum; 4. nearly absent. Ordered.
4. Coloration of pleural region: 1. uniformly black; 2. white on lower half.
5. Coloration of abdominal tergites 1+2: 1. without a yellowish region dorsally; 2. with a yellowish region dorsally
6. Shape of body: 1. robust, scutal ratio 1.1–1.35; 2. elongate, scutal ratio 1.5–1.75
7. Shape of vertex, between compound eyes: 1. nearly straight; 2. U-excavated; 3. V-excavated.
8. Margins of eye: 1. not encroaching on the posterior portion of the frons 3. encroaching on the posterior portion of the frons.
9. Sclerotization of face: 1. homogeneous; 2. weak on midline
10. Cheek, in profile (shape): 1. as wide as 1st flagellomere; 2. approximately 1/2–1/3 the width of 1st flagellomere; 3. approximately 1/5 the width of 1st flagellomere below ventral margin of eye; 4. projected at level of anteroventral margin of eye, approximately triangular in shape, thereafter following ventral margin of eye as a narrow ridge; 5. a narrow ridge circumventing ventral margin of eye.
11. Clypeus (proportions): 1. stout, 1.5 to 2.5 times longer than wide; 2. elongate, 3.5-5.5 times longer than wide
12. First flagellomere (shape): 1. round; 2. oval, decumbent; 3. triangular.
13. Presence of basal segmentation of the arista: 1. absent; 2. present.
14. Articulation of pedicel with 1st flagellomere: 1. pedicel with a median membrane fitting into a cavity on the 1st flagellomere; 2. pedicel with a median hole into which basal projection of the 1st flagellomere fits

15. Arista (shape): 1. with tiny, dense, alternate hairs (pubescent); 2. with very inconspicuous, alternate hairs (arista appearing naked at low magnification); 3. distinctly zigzagged on apical 2/3 and bearing short hairs; 4. with a double row of dorsal rays on basal 1/3, and alternate rays on apical portion.
16. Ocellar seta (whether present): 1. absent; 2. present.
17. Development of ocellar seta: 1. weak, hair-like; 2. strong, seta-like.
18. Presence of inner vertical seta: 1. absent; 2. present.
19. Presence of postocellar seta: 1. absent; 2. present
20. Number of fronto-orbital setae: 1.1; 2.2; 3.3. Ordered.
21. Acrostical setae: 1. in 1 row; 2. in 1 row, bifurcating posteriorly; 3. in 2 rows; 4. 2 rows on anteriormost portion, merging into 1 row posteriorly
22. Greater ampulla: 1. absent; 2. present.
23. Presence of a fold on cell dm: 1. absent; 2. present, running along entire length of cell dm.
24. Position of crossvein r-m: 1. at middle of combined cell dm + dm; 2. basal to middle of combined cell dm + bm.
25. Presence of apical kink on vein R1: 1. absent; 2. present.
26. C vein of male: 1. not spinose; 2. bearing a few tiny, but conspicuous spines; 3. bearing relatively strong, conspicuous spines. Ordered.
27. Sc vein: 1. incomplete, fused with vein R1 apically, and reaching costal vein; 2. incomplete and not fused with vein R1 apically; 3. incomplete, fused with vein R1 apically, not reaching costal vein.
28. Hindfemur: 1. not modified, and without ventral spines (well-delimited); 2. modified, with two ventral rows of spines, each spine bearing an apical seta
29. Preabdomen: 1. consisting of 5 segments; 2. consisting of 6 segments.
30. Surstylus: 1. articulated with epandrium; 2. fused with epandrium
3. fused to an inner corner of epandrium. Ordered.
31. Shape of surstylus: 1. thin, ventral to posterior; 2. lobe-like, ventral to posterior; 3. a wide, ventral posterior extension of the epandrium.

32. Subepandrial sclerite: 1. plate-like; 2. T-shaped; 3. Y-shaped; 4. paired, rod-like.

33. Male genitalia: 1. not bearing a lateral, anterior apodeme arising at base of each gonopod; 2. bearing a lateral, anterior apodeme arising at base of each gonopods

34. Gonopods: 1. Without strongly setose posterior projection; 2. with posterior projection bearing 4-5 strong setae.

35. Phallapodeme: 1. rod-like, without posterior lateral projections that shield base of aedeagus; 2. cuneiform, with asymmetrical posterolateral projections; 3. fused with hypandrium.

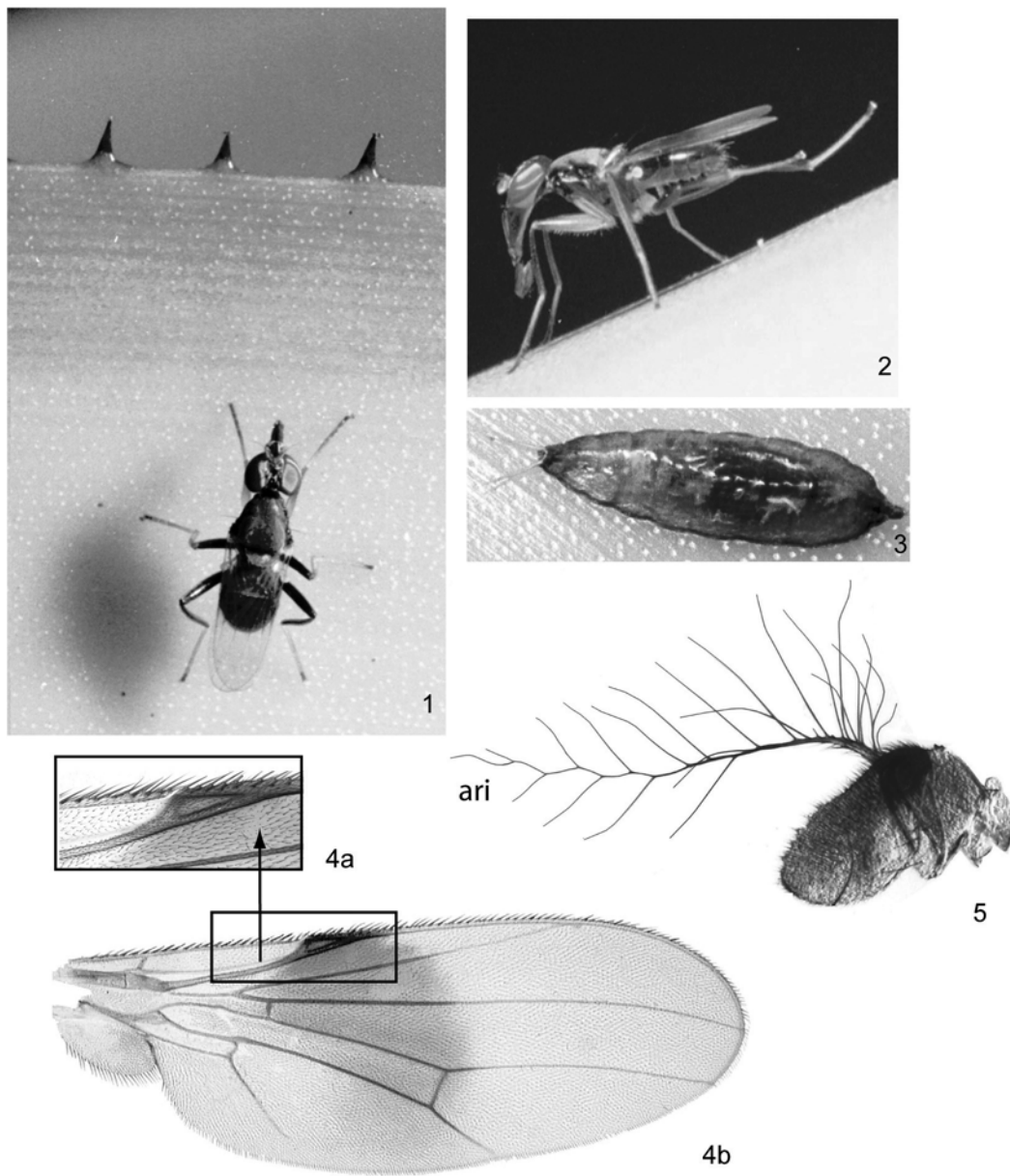
36. Gonopods: 1. without a dark-brown ventral structure; 2. with a dark-brown ventral structure

37. Posterior portion of hypandrium: 1. strongly sclerotized; 2. weakly sclerotized

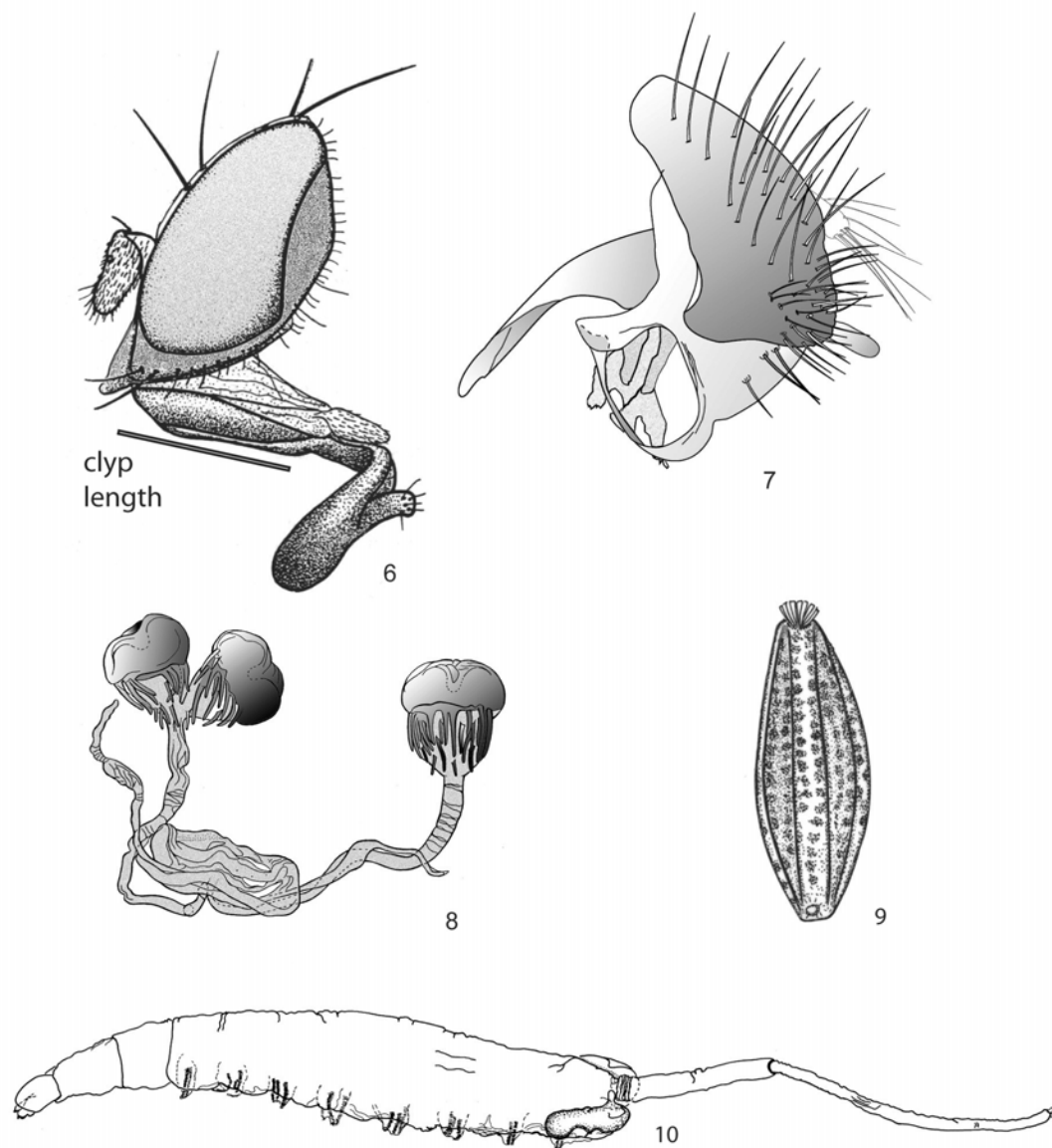
Table 3.2.– Summary of the results of four analyses performed with combinations of character ordering and weighting schemes.

The numbers on top refer to the analysis, 1-4.

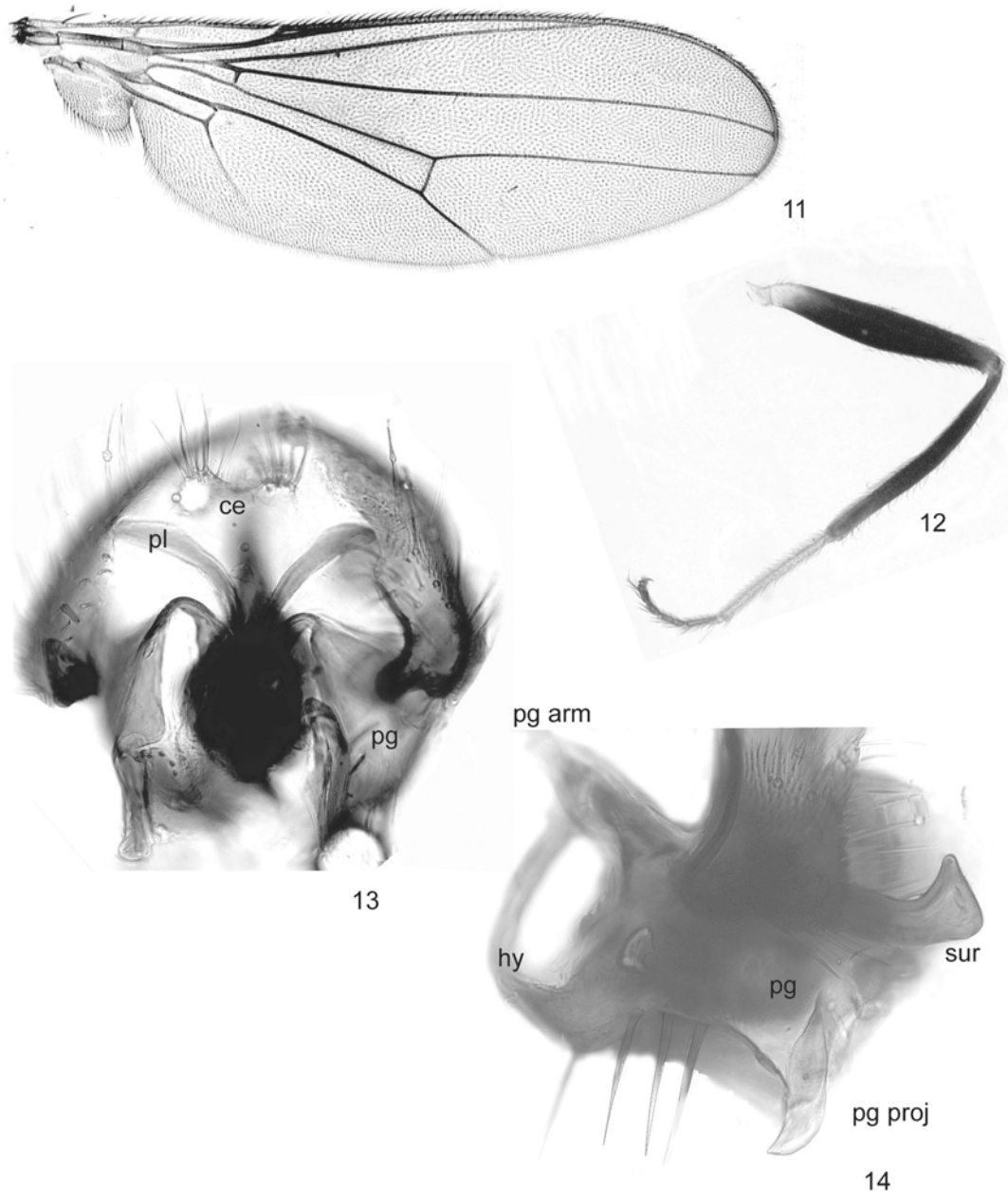
Reference	1	2	3	4
Characters ordered	N	N	Y	Y
Successive weighting	N	Y	N	Y
Cladograms found	38	6	18	6
Steps	77	53	78	53
CI	0.73	0.80	0.82	0.80
RI	0.80	0.87	0.65	0.887



FIGURES 3.1-3.5.—Digital photographs of *Aulacigaster bromeliae*, new species (The *bromeliae* group, Neotropical region). 1. *Habitus*, dorsal aspect, on bromeliad leaf; 2. Same, lateral aspect; 3. Puparium, dorsal aspect, on bromeliad leaf; 4a. costal section of wing; 4b. Wing; 5. Left antenna, internal aspect. Not all to the same scale.



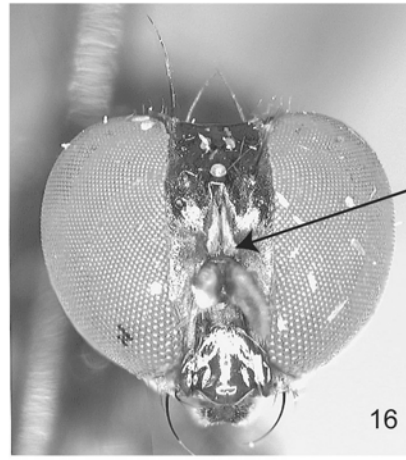
FIGURES 3.6-3.10.—Illustrations of *Aulacigaster bromeliae*, new species (The *bromeliae* group, Neotropical region). 6. Head, lateral aspect; 7. Epandrium and internal genitalic structures (male), lateral aspect; 8. Spermathecae; 9. Egg; 10. Larva, first instar, lateral aspect. Not all to the same scale.



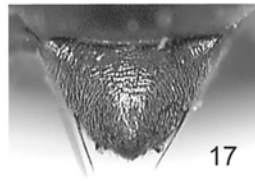
FIGURES 3.11-3.14.—Digital photographs of *Aulacigaster korneyev*, new species (The *bromeliae* group, Neotropical region). 11. Wing; 12. Hindleg, dorsal aspect; 13. Epandrium and internal genitalic structures (male), posterior aspect; 14. Same, lateral aspect. Not all to the same scale.



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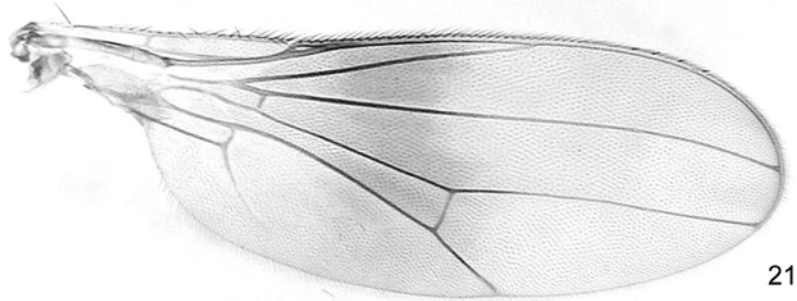
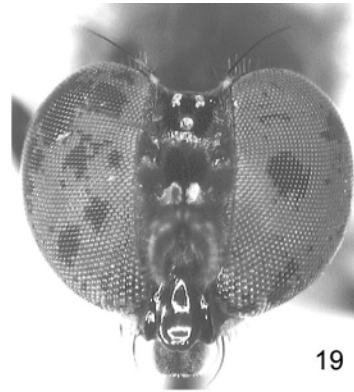


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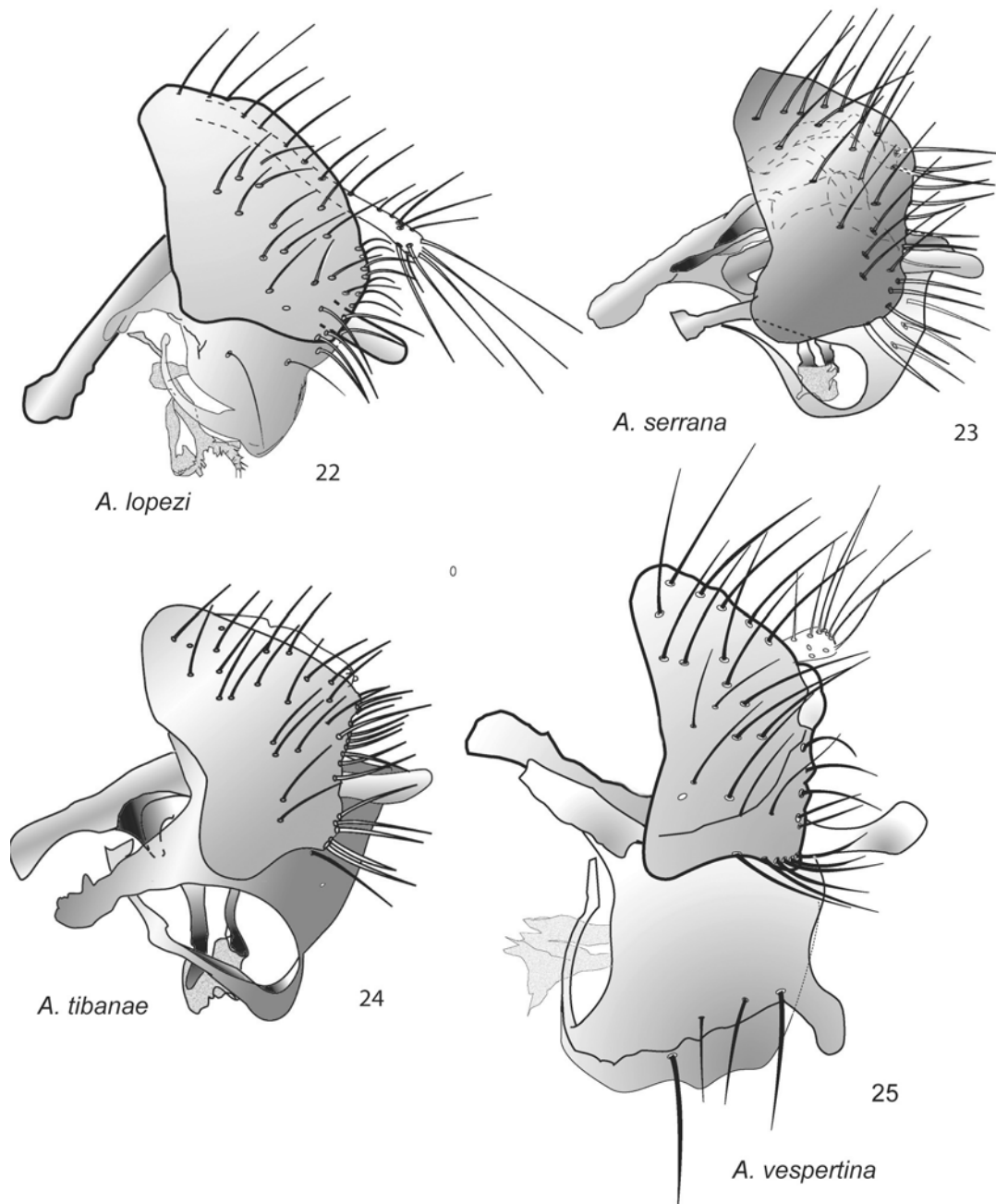


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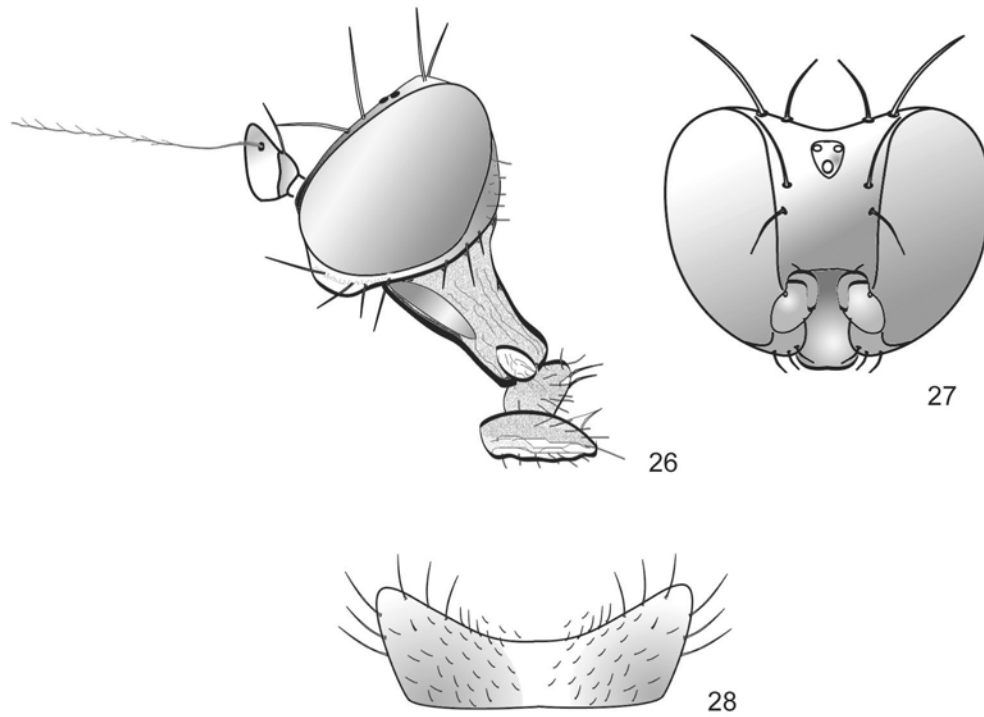
FIGURES 3.15-3.17.—Digital photographs of *Aulacigaster tibanae*, new species (The *bromeliae* group, Neotropical region). 15. Head, lateral aspect; 16. Same, frontal aspect; 17. Scutellum, anterior dorsal aspect. Not all to the same scale.



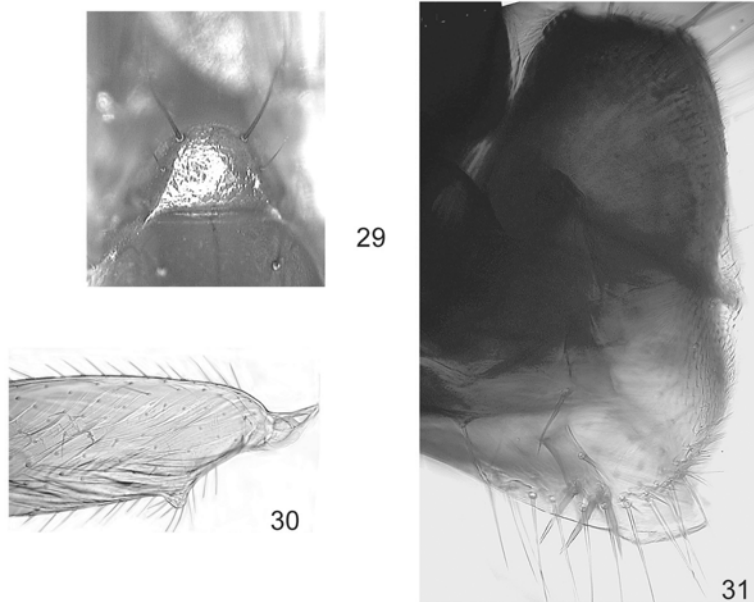
FIGURES 3.18-3.21.—Digital photographs of *Aulacigaster vespertina*, new species (The *bromeliae* group, Neotropical region). 18. Head, lateral aspect; 19. Same, frontal aspect; 20. Thorax, dorsal aspect; 21. Wing. Not all to the same scale.



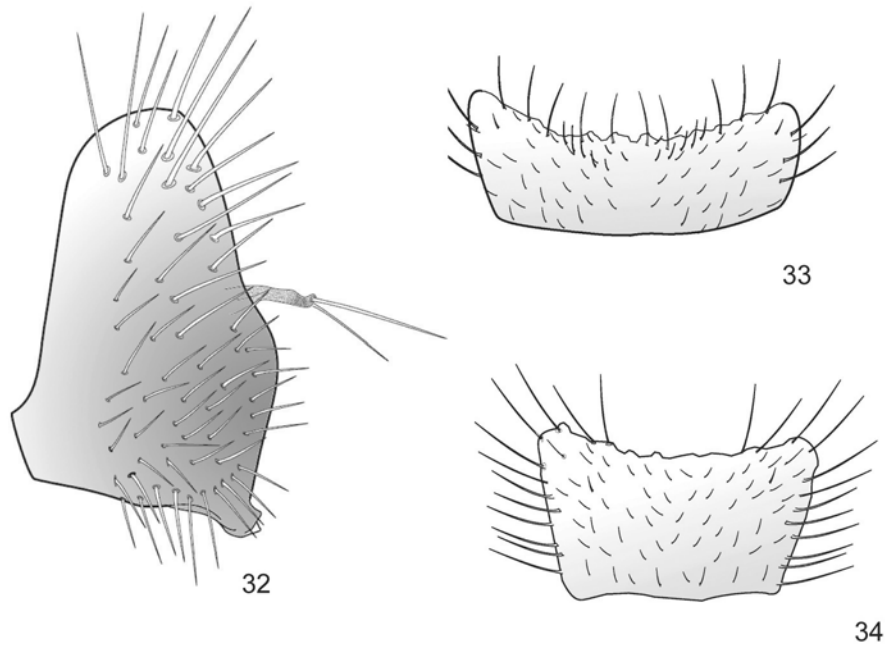
FIGURES 3.22-3.25.—Illustrations of the epandrium and internal genitalic structures (male) of aulacigastrids (The *bromeliae* group, Neotropical region). 22. *Aulacigaster lopezi*, new species; 23. *Aulacigaster serrana*, new species; 24. *Aulacigaster tibanae*, new species; 25. *Aulacigaster vespertina*, new species. Not all to the same scale.



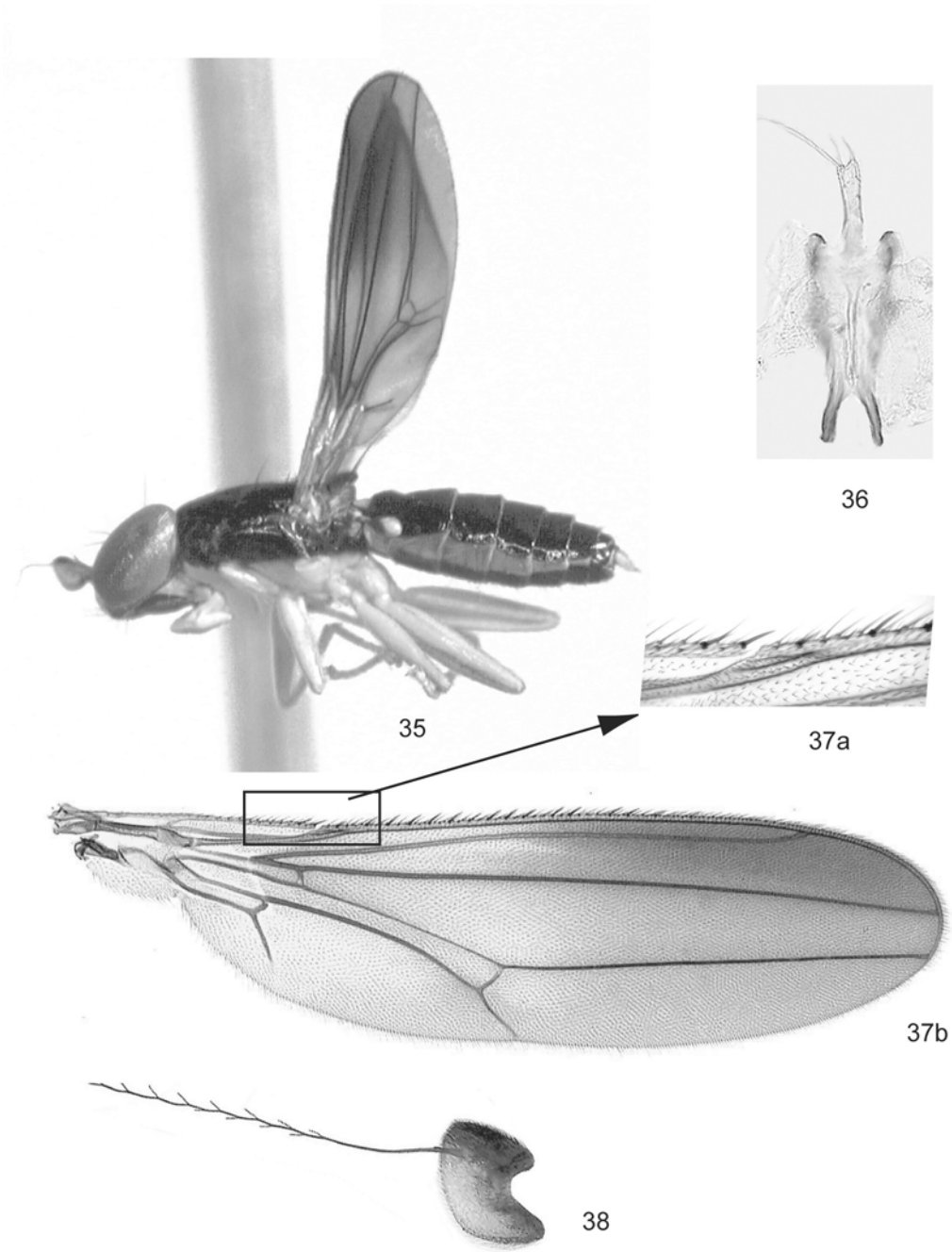
FIGURES 3.26-3.28.—Illustrations of *Aulacigaster ecuadoriensis* (Hennig) (The *ecuadoriensis* group, Neotropical region). 26. Head, lateral aspect; 27. Same, frontal aspect; 28. Abdominal sternite 5 (male), ventral aspect. Not all to the same scale.



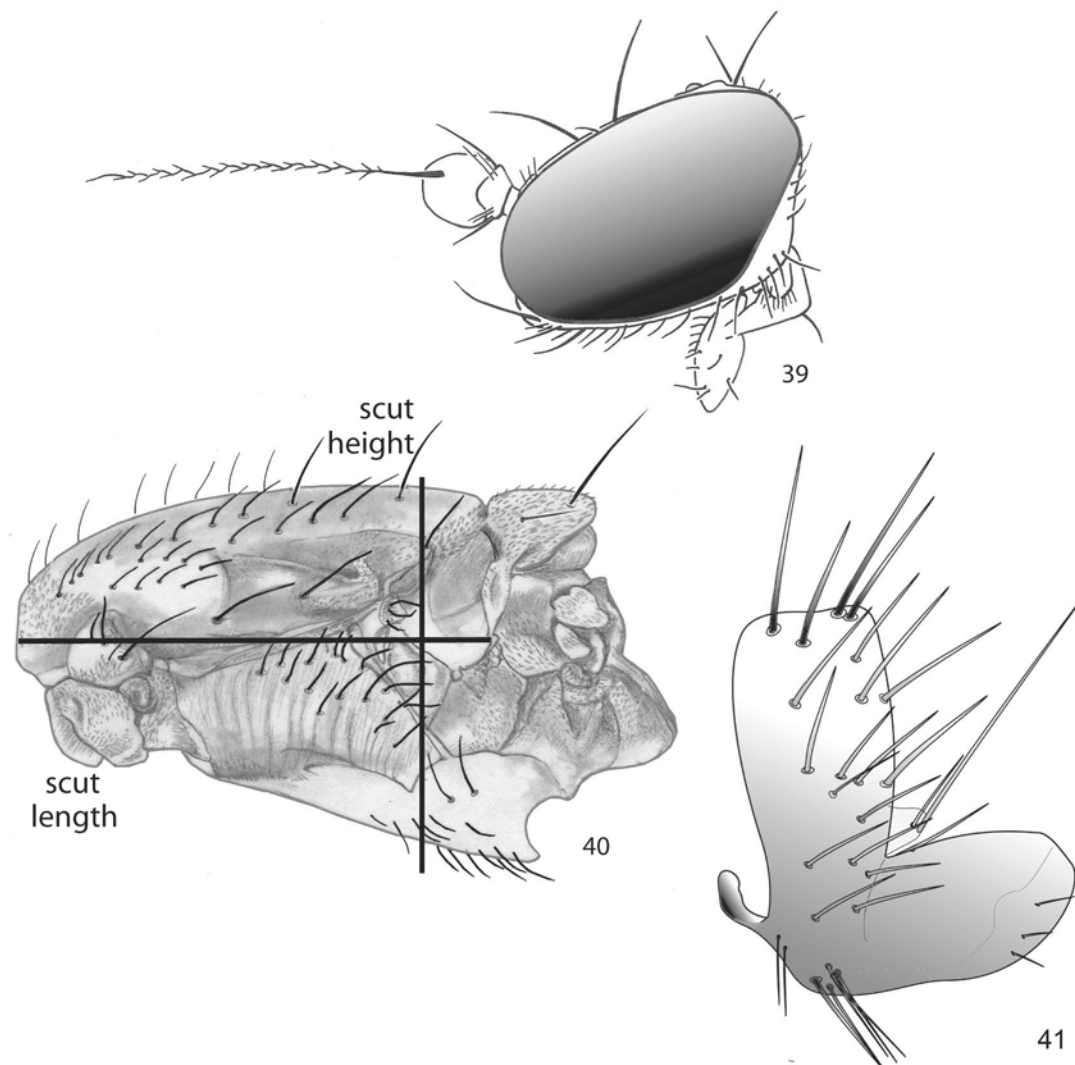
FIGURES 3.29-3.31.—Digital photographs of *Aulacigaster ecuadoriensis* (Hennig) (The *ecuadoriensis* group, Neotropical region). 29. Scutellum, dorsal aspect; 30. Hindfemur of male, ventral aspect; 31. Epandrium and internal genitalic structures (male), lateral aspect. Not all to the same scale.



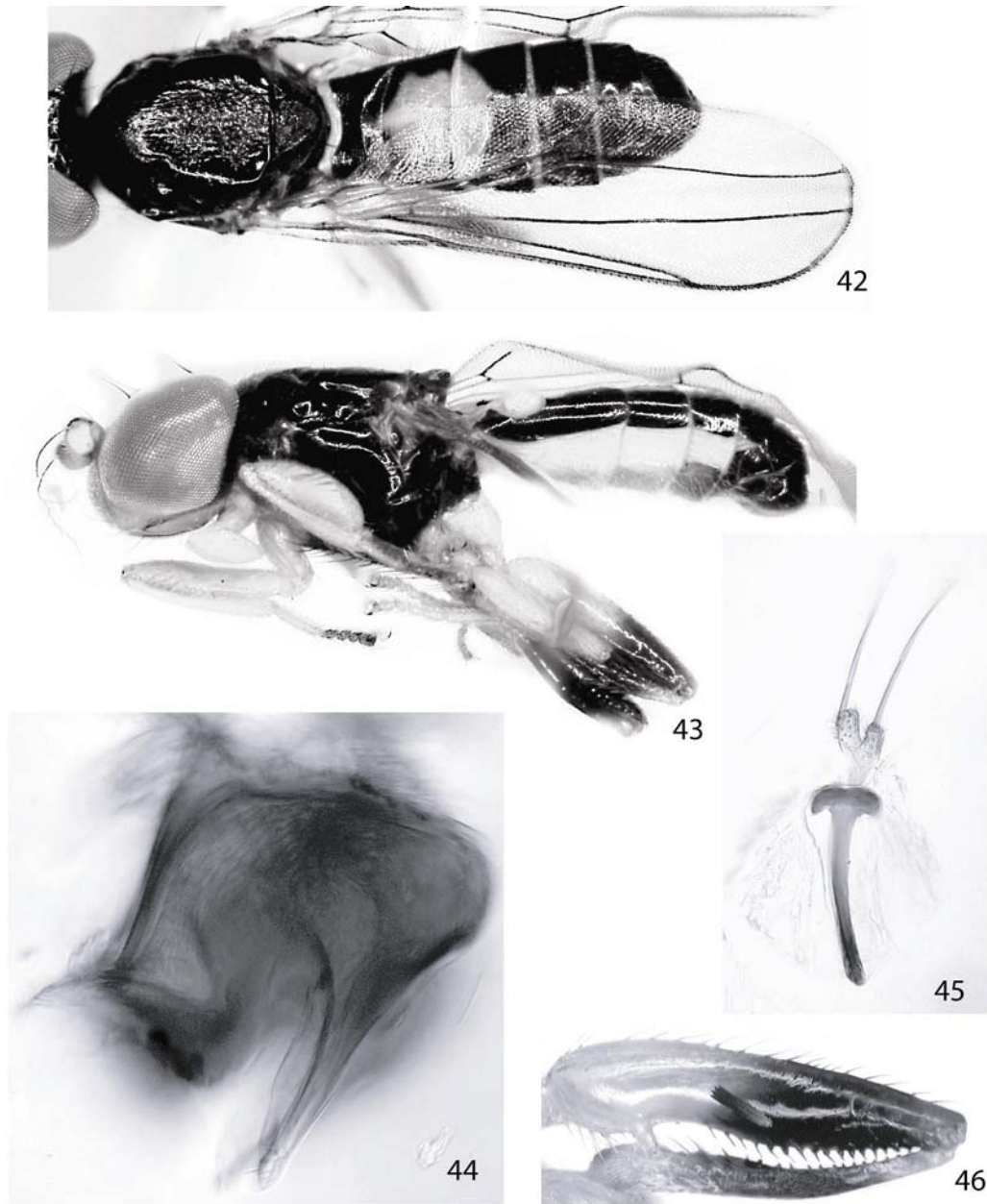
FIGURES 3.32-3.34.— Illustrations of *Aulacigaster melanoleuca* (Hennig) (The *ecuadoriensis* group, Neotropical region). 32. Epandrium, lateral aspect; 33. Abdominal sternite 4 (male), ventral aspect; 34. Abdominal sternite 5 (male), ventral aspect. Not all to the same scale.



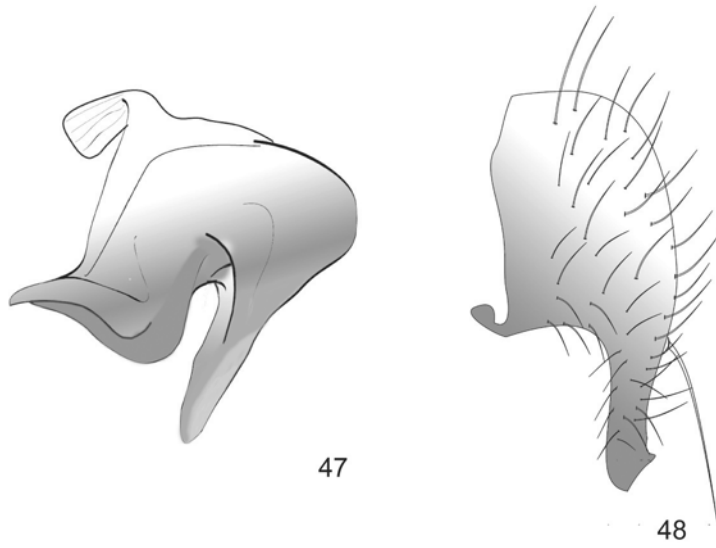
FIGURES 3.35-3.38.— Digital photographs of *Aulacigaster melanoleuca* (Hennig) (The *ecuadoriensis* group, Neotropical region). 35. Entire specimen, lateral aspect; 36. Subepandrial sclerite, ventral aspect; 37a. costal section of the wing; 37b. Wing; 38. Antenna, internal aspect. Not all to the same scale.



FIGURES 3.39-3.41.— Illustrations of *Aulacigaster stenoptera*, new species (The *ecuadoriensis* group, Neotropical region). 39. Head, lateral aspect; 40. Thorax, lateral aspect; 41. Epandrium, lateral aspect. Not all to the same scale.



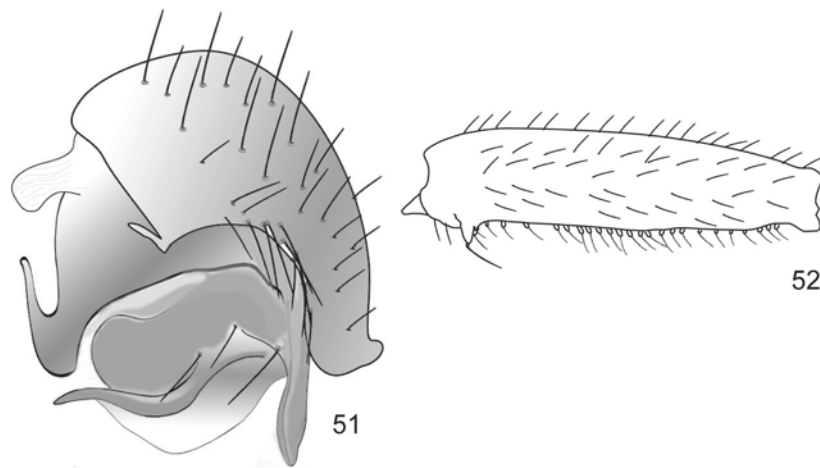
FIGURES 3.42-3.46.— Digital photographs of *Aulacigaster bella*, new species (The *femorata* group, Neotropical region). 42. Thorax and abdomen, dorsal aspect; 43. Entire specimen, lateral aspect; 44. Internal genitalic structures (male), lateral aspect; 45. Subepandrial sclerite, ventral aspect; 46. Hindfemur (male), ventral aspect. Not all to the same scale.



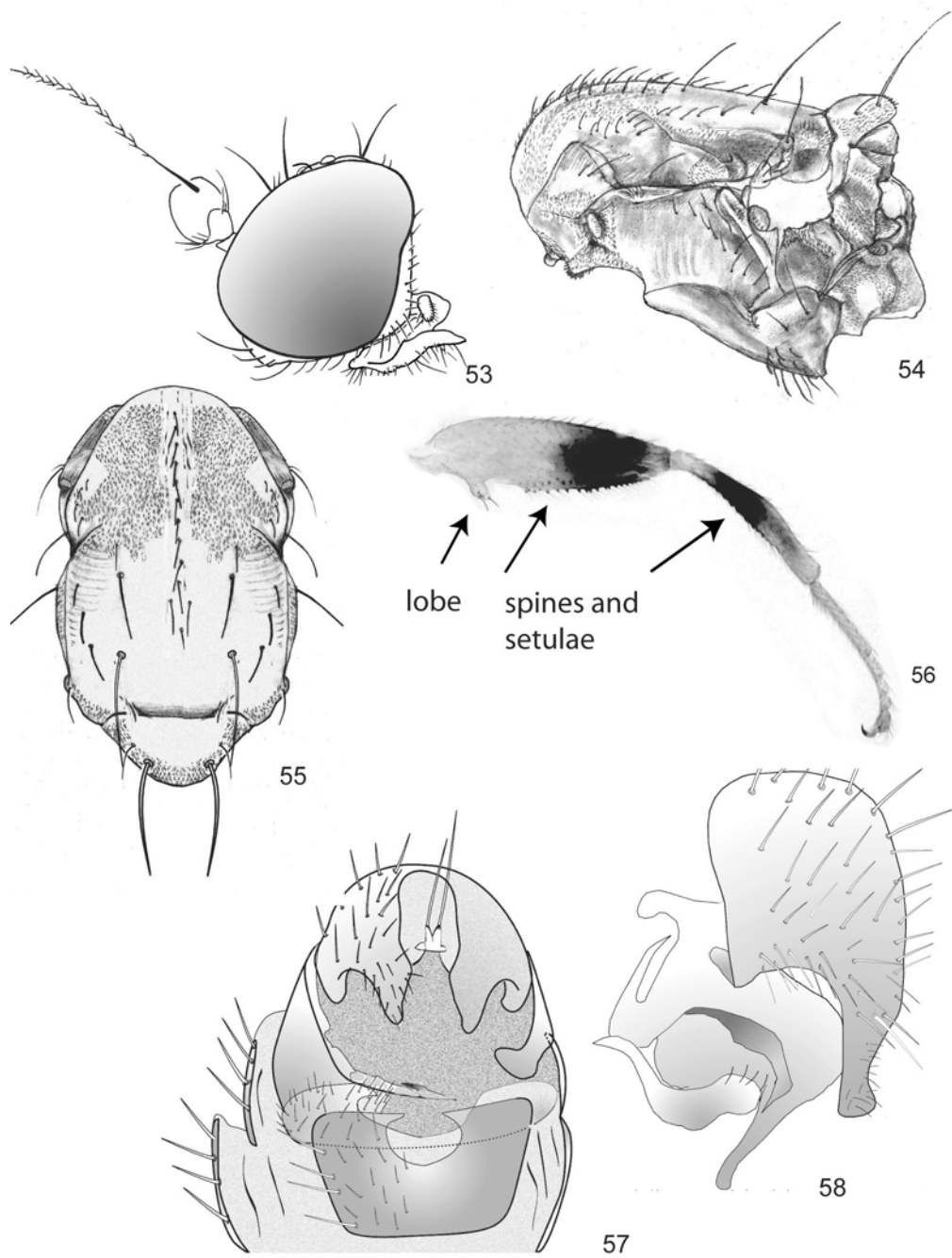
FIGURES 3.47-3.48.—Illustrations of *Aulacigaster bella*, new species (The *femorata* group, Neotropical region). 47. Internal genitalic structures (male). 48. Epandrium, lateral aspect.



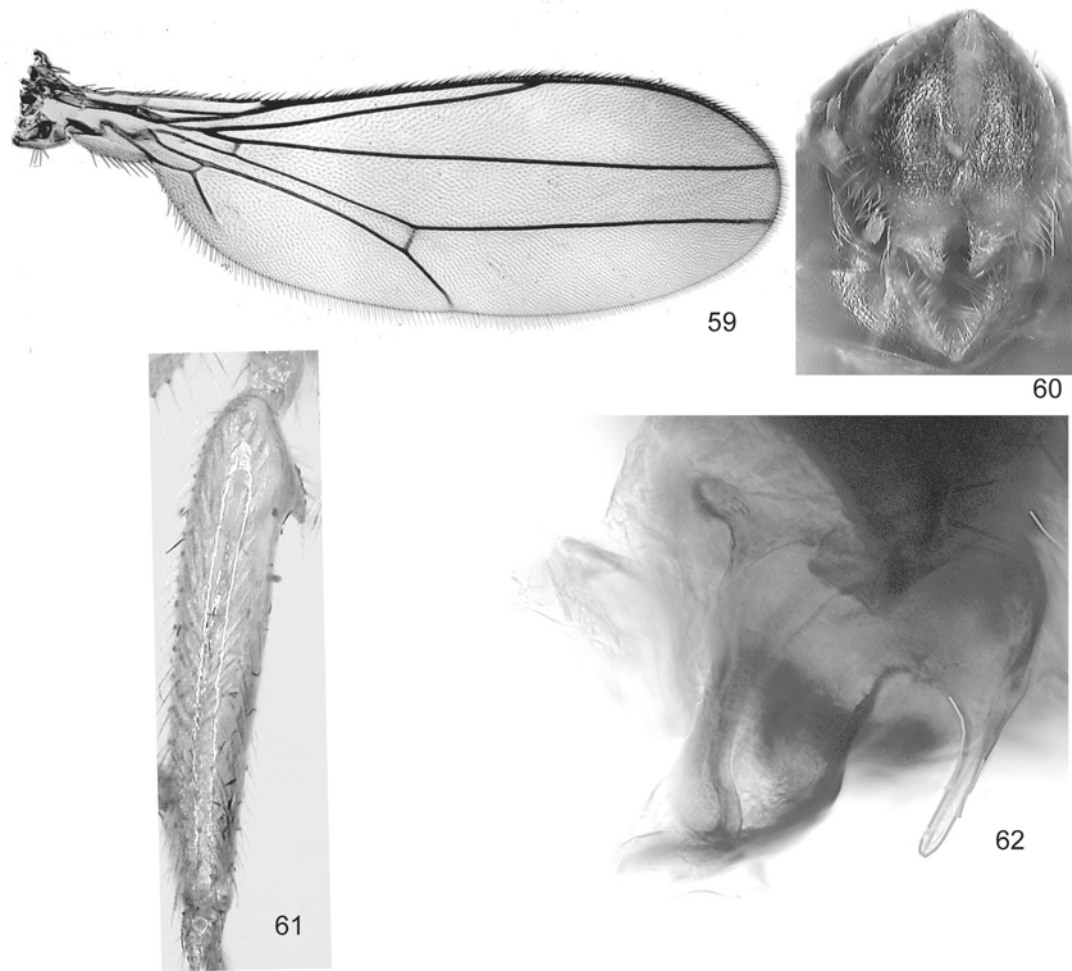
FIGURES 3.49-3.50.—Digital photographs of *Aulacigaster irwini*, new species (The *femorata* group, Neotropical region). 49. Entire specimen, lateral aspect (wings omitted); 50. Hindfemur (male), dorsal posterior aspect. Not all to the same scale.



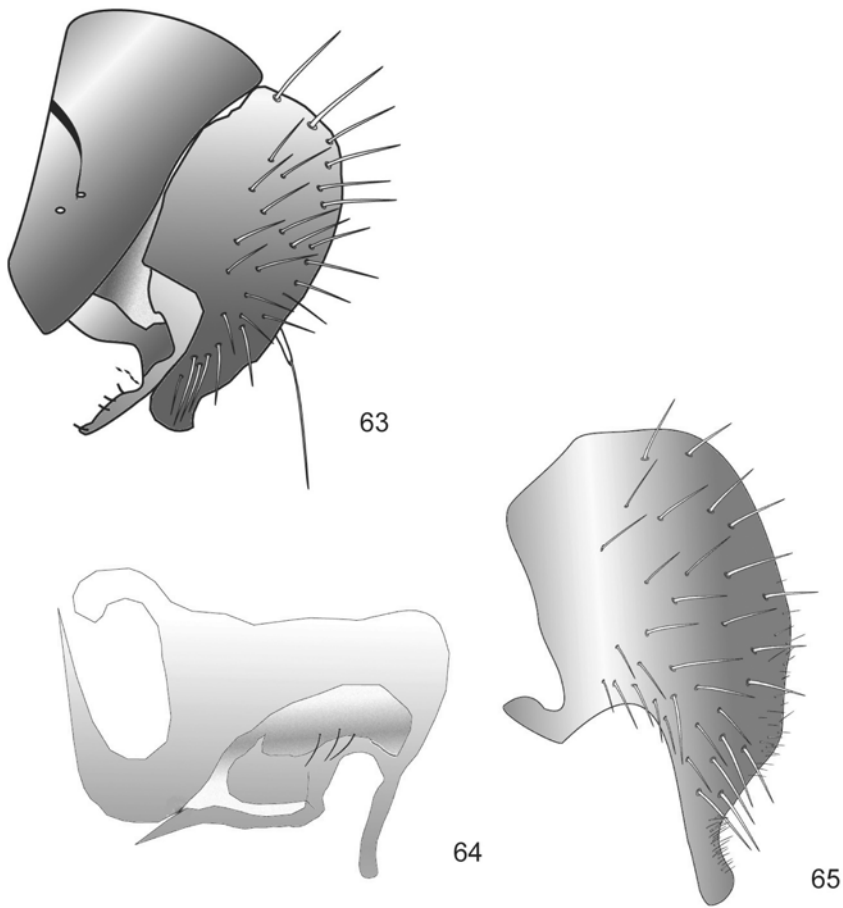
FIGURES 3.51-3.52.—Illustrations of *Aulacigaster irwini*, new species (The *femorata* group, Neotropical region). 51. Epandrium and internal genitalic structures (male), lateral aspect; 52. Hind femur (male), lateral ventral aspect. Not to the same scale.



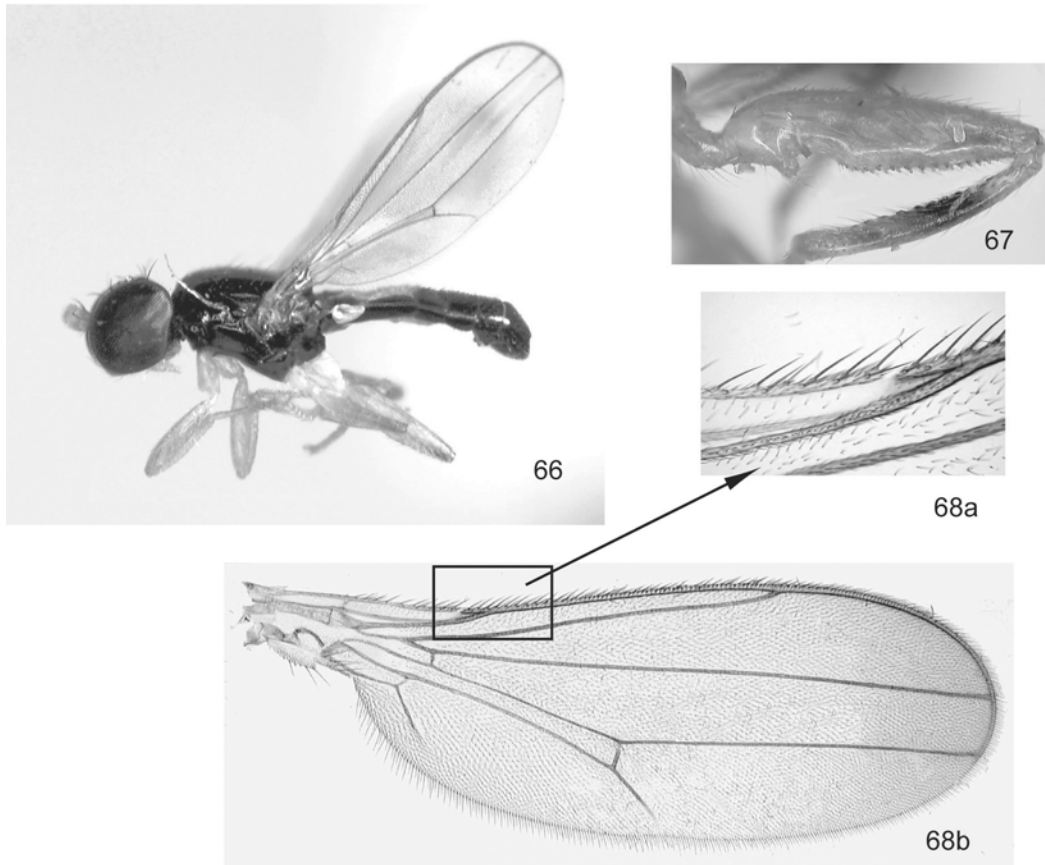
FIGURES 3.53-3.58.—Illustrations of *Aulacigaster femorata*, new species (The *femorata* group, Neotropical region). 53. Head, lateral aspect; 54. Thorax, lateral aspect; 55. Same, dorsal aspect; 56. Hindfemur (male), ventral aspect; 57. Male postabdomen, ventral aspect; 58. Epandrium and internal structures (male), lateral aspect. Not to the same scale.



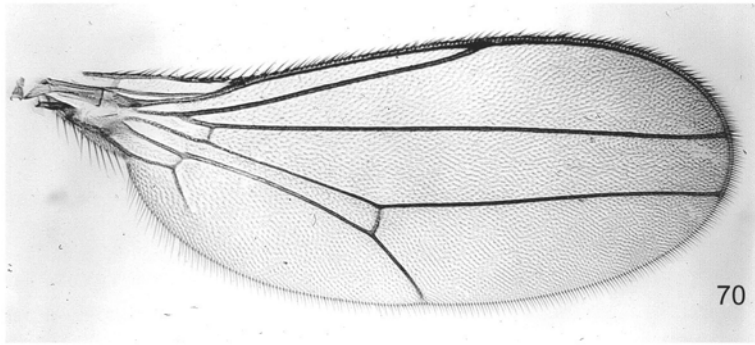
FIGURES 3.59-3.62.—Digital photographs of aulacigastrids (The *femorata* group, Neotropical region). 59- 60. *Aulacigaster femorata*, new species. 59. Wing; 60. Epandrium and abdominal sternite 6 (male), ventral aspect. 60- 61. *Aulacigaster formosa*, new species. 59. Hindfemur (male), postero-dorsal aspect; 60. Internal genitalic structures (male), lateral aspect. Not all to the same scale.



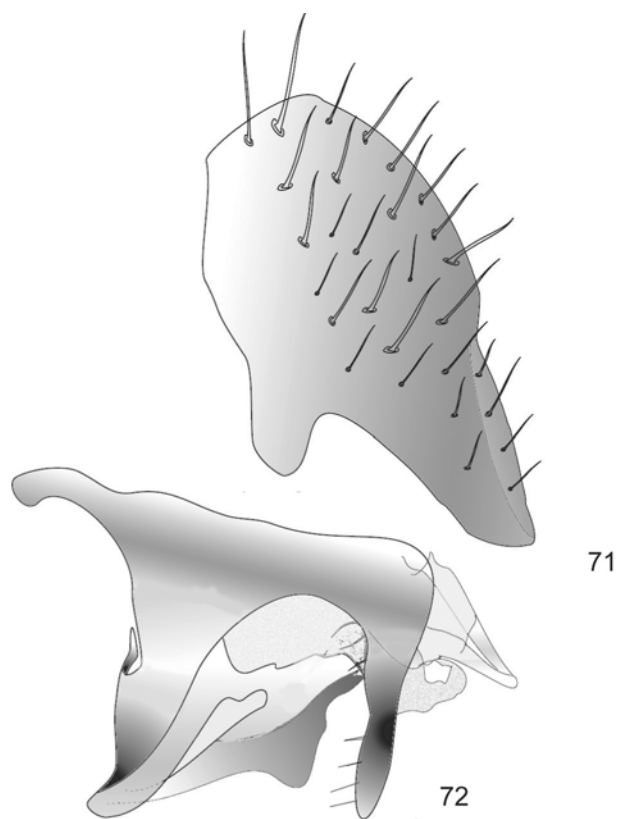
FIGURES 3.63-3.65.—Illustrations of the male terminalia of aulacigastrids (The *femorata* group, Neotropical region). 63. *Aulacigaster formosa*, new species, postabdomen and epandrium, lateral aspect. 64- 65. *Aulacigaster lobata* new species. 64. Internal genitalic structures (male), lateral aspect; 65. Epandrium, lateral aspect. Not all to the same scale.



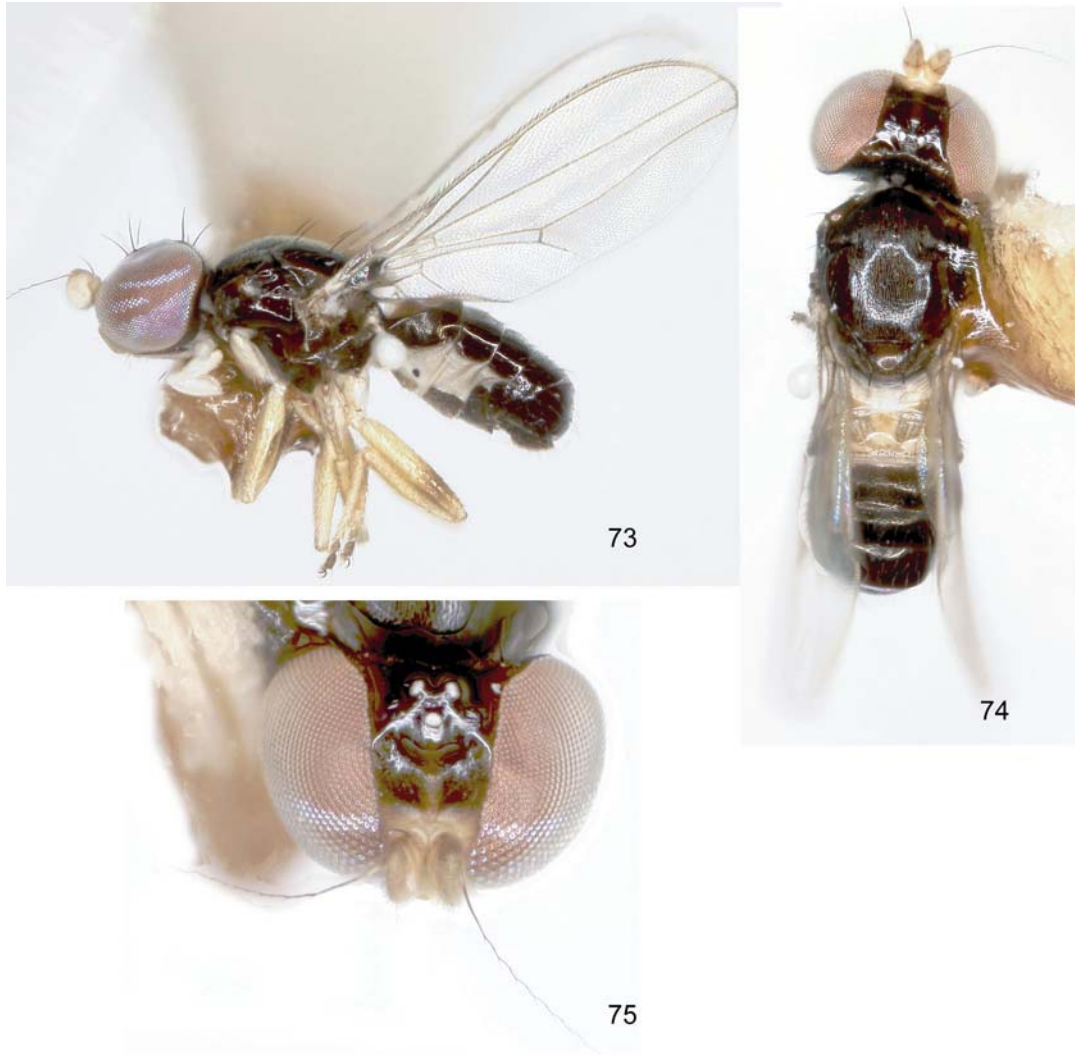
FIGURES 3.66-3.68.— Digital photographs of *Aulacigaster lobata*, new species (The *femorata* group, Neotropical region). 66. Entire specimen, lateral aspect; 67. Hindfemur (male), postero-ventral aspect; 68a. costal section of wing; 68b. Wing. Not all to the same scale.



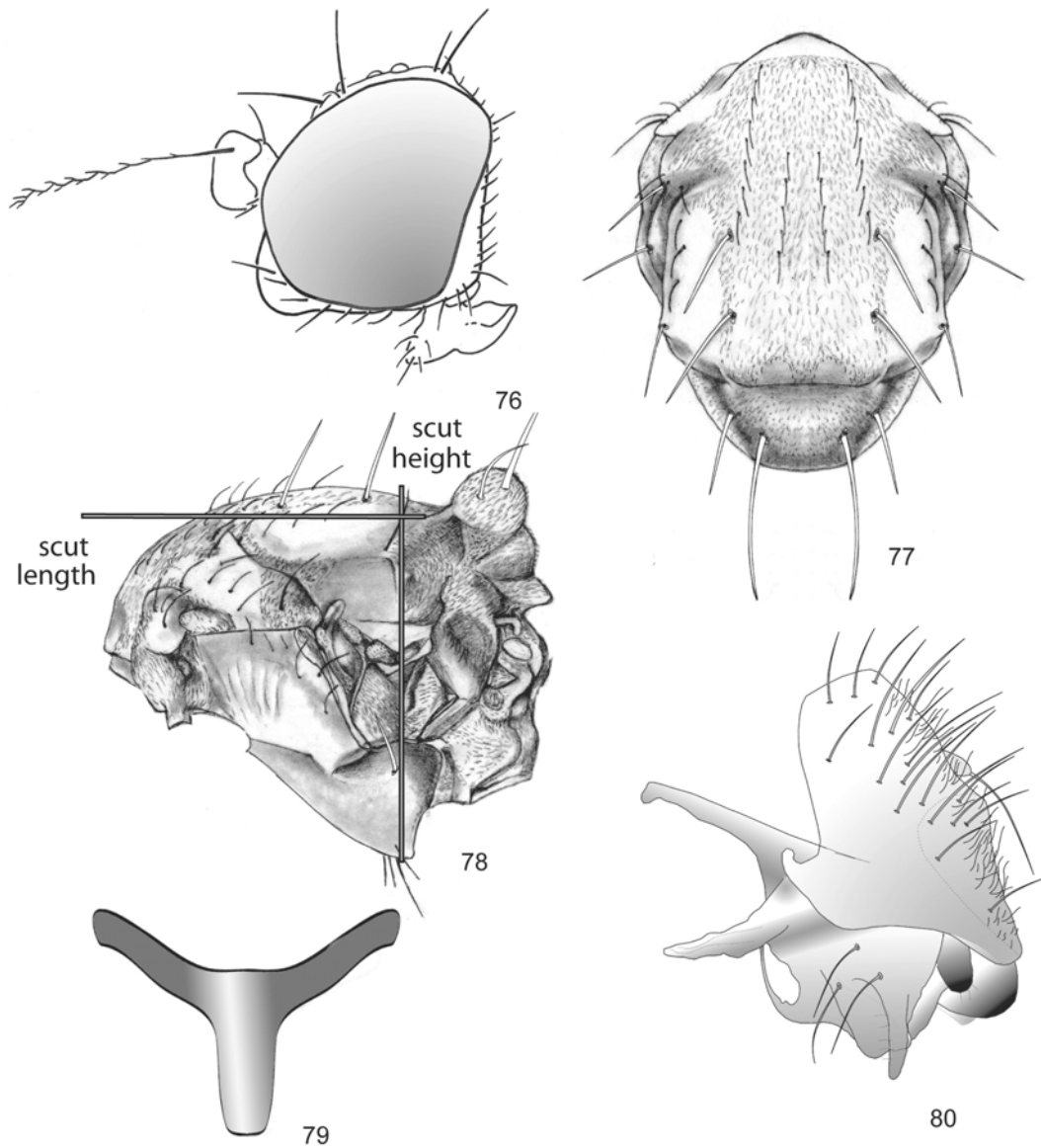
FIGURES 3.69-3.70.— Digital photographs of *Aulacigaster peruana* new species (The *femorata* group, Neotropical region). 69. Hindfemur (male), dorsal aspect; 70. Wing. Not to the same scale.



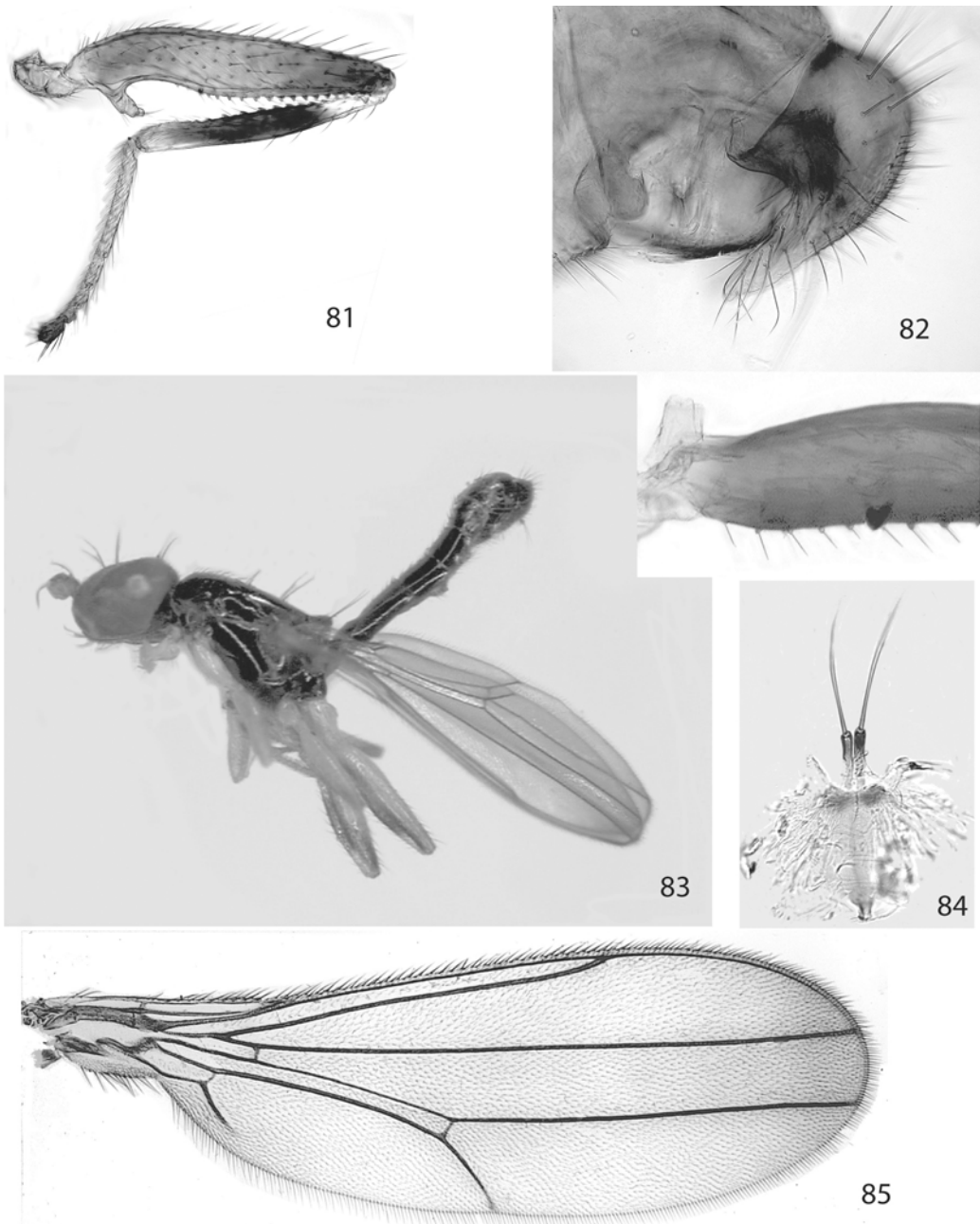
FIGURES 3.71-3.72.—Illustrations of *Aulacigaster peruana* new species (The *femorata* group, Neotropical region). 71. Epandrium, lateral aspect; 72. Internal genitalic structures (male), lateral aspect.



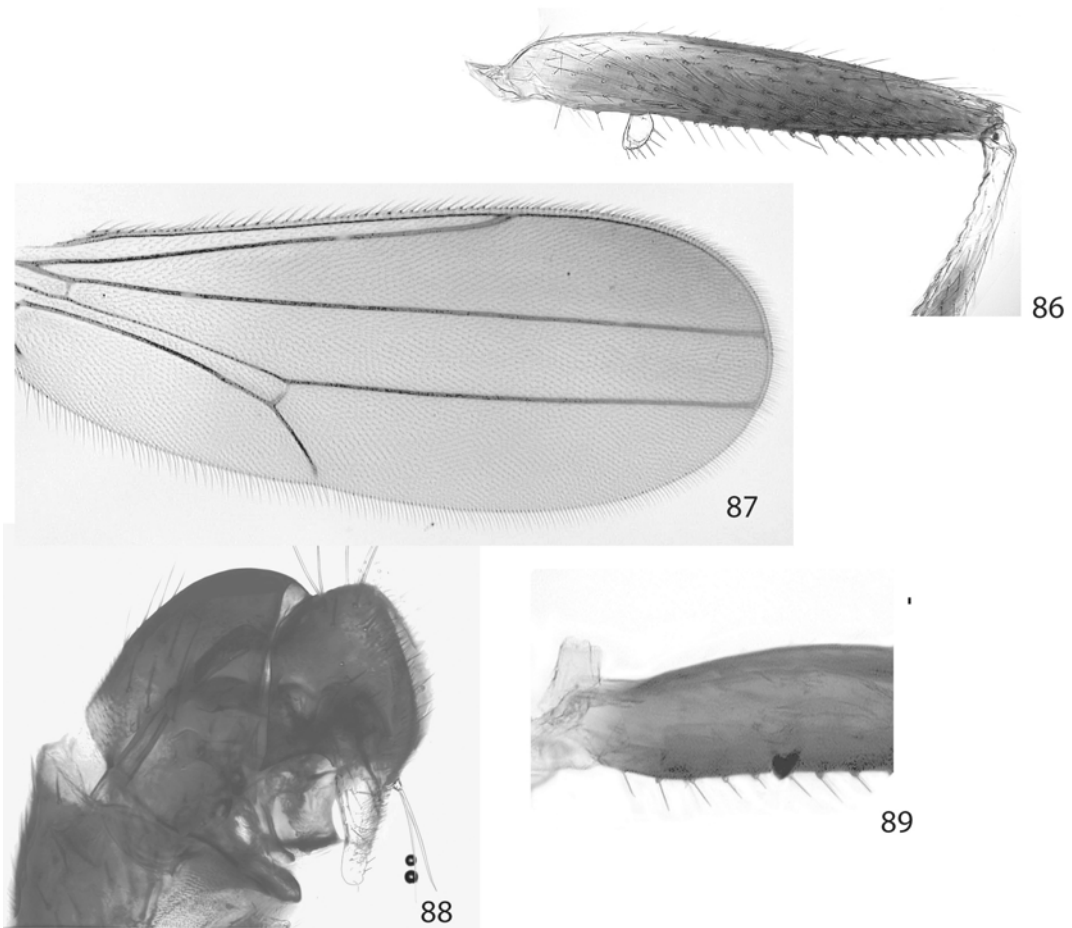
FIGURES 3.73-3.75.— Digital photographs of *Aulacigaster* Grimaldi, new species (The *grimaldii* group, Neotropical region). 73. Entire specimen, lateral aspect; 74. Same, dorsal aspect; 75. Head, frontal aspect. Not all to the same scale.4.



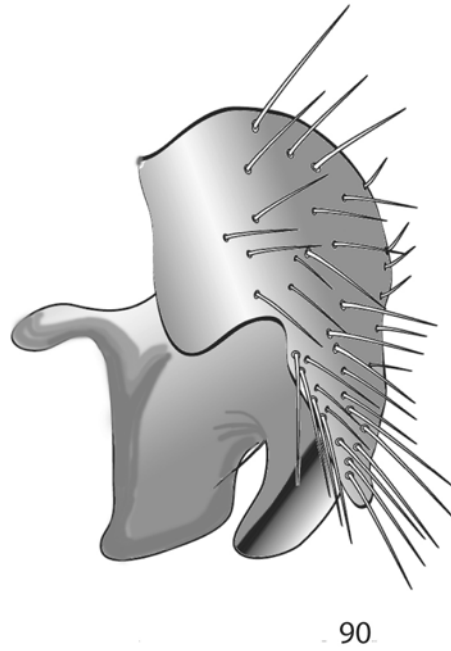
FIGURES 3.76-3.80.— Illustrations of *Aulacigaster* Grimaldi, new species (The *grimaldii* group, Neotropical region). 76. Head, lateral aspect; 77. Thorax, dorsal aspect; 78. Same, lateral aspect; 79. Subepandrial sclerite, dorsal aspect (cerci omitted); 80. Epandrium and internal genitalic structures (male), lateral aspect. Not all to the same scale.



FIGURES 3.81-3.85.—Digital photographs of aulacigastrids (The *minuta* group, Neotropical region). 81. *Aulacigaster appendiculata*, new species, hindfemur (male), ventral aspect. 82- 85. *Aulacigaster costaricana*, new species. 82. Epandrium, lateral aspect; 83. Entire specimen, lateral aspect; 84. Subepandrial sclerite, ventral aspect; 85. Wing. Not all to the same scale.

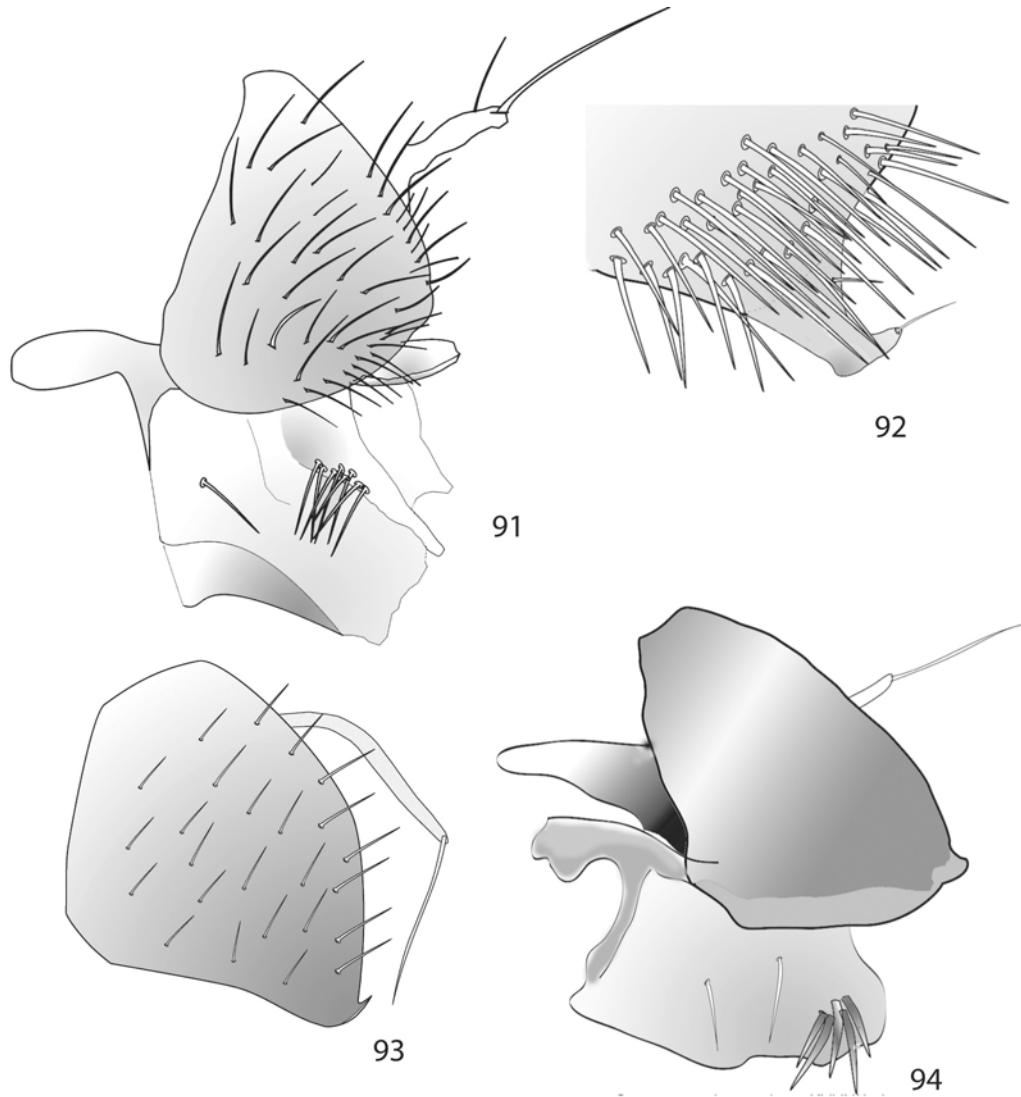


FIGURES 3.86-3.89.—Digital photographs of aulacigastrids (The *minuta* group, Neotropical region). 86- 87. *Aulacigaster gaimarii*, new species. 86. Hindfemur (male), dorsal aspect; 87. Wing. 88- 89. *Aulacigaster minuta* (Hennig). 88. Male postabdomen and epandrium, lateral aspect; 89. Hindfemur (male), dorsal aspect. Not all to the same scale.

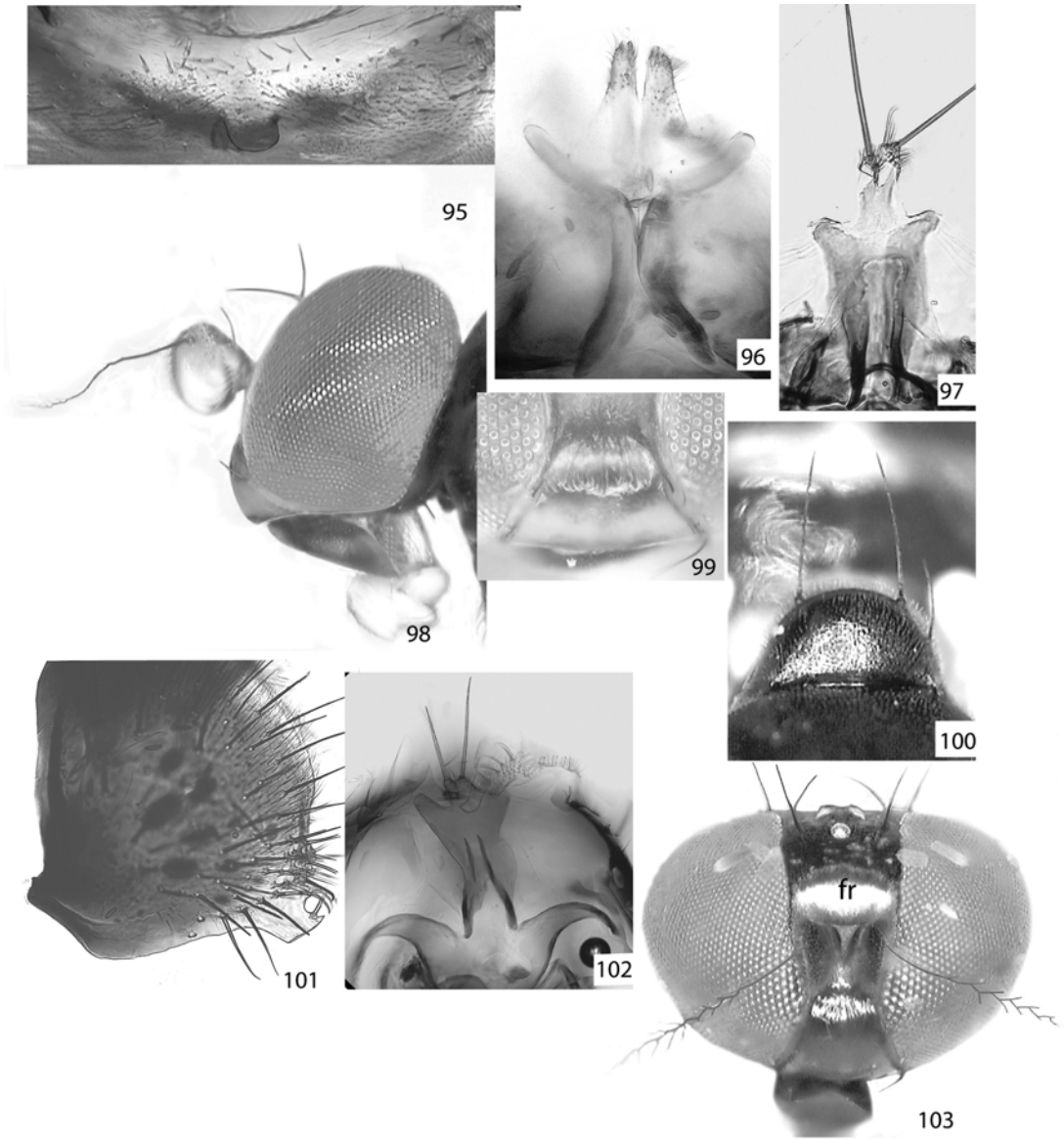


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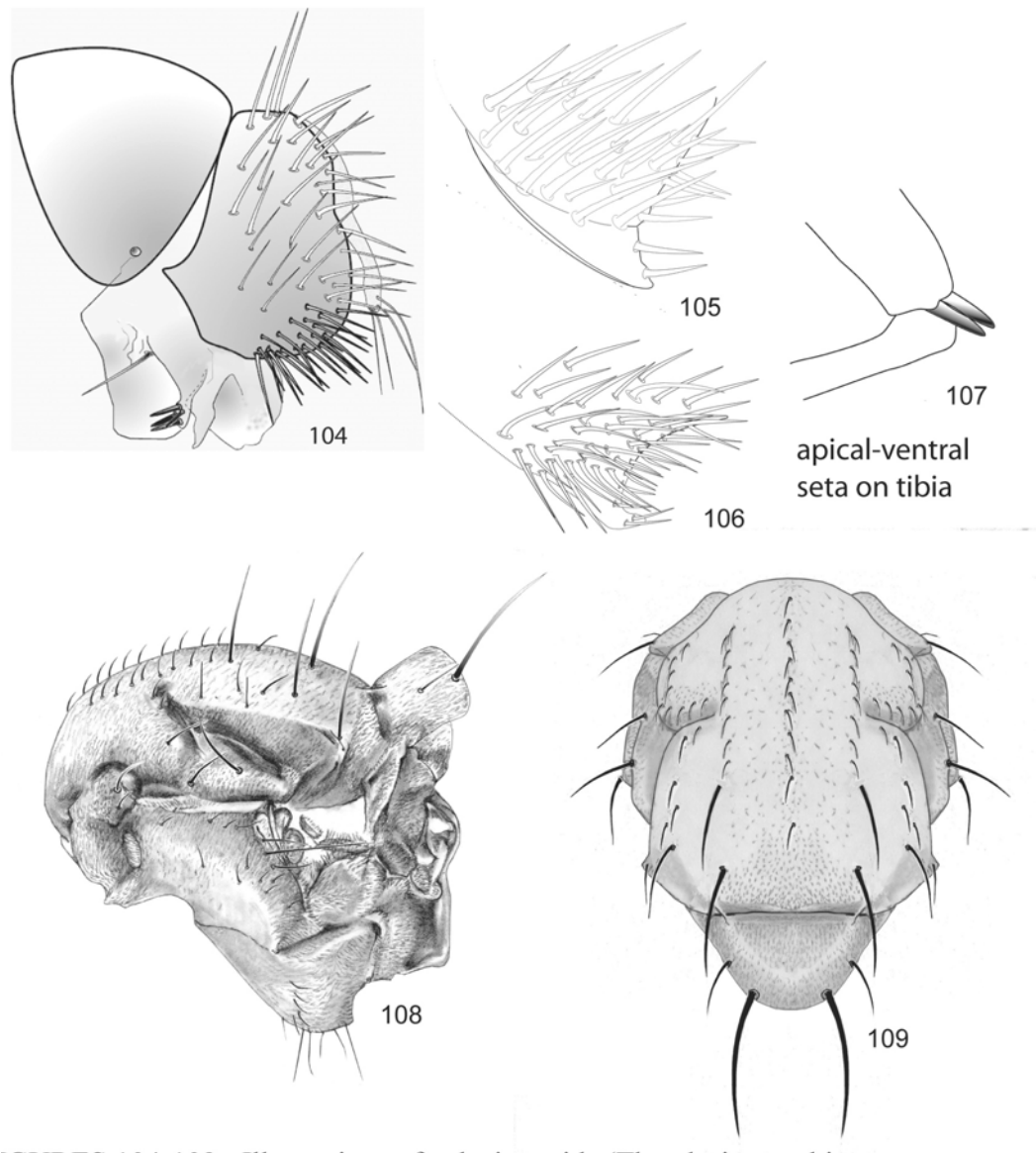
FIGURE 3.90.—Illustration of the epandrium and internal genitalic structures (male), of *Aulacigaster minuta* (Hennig) (The *minuta* group, Neotropical region), lateral aspect.



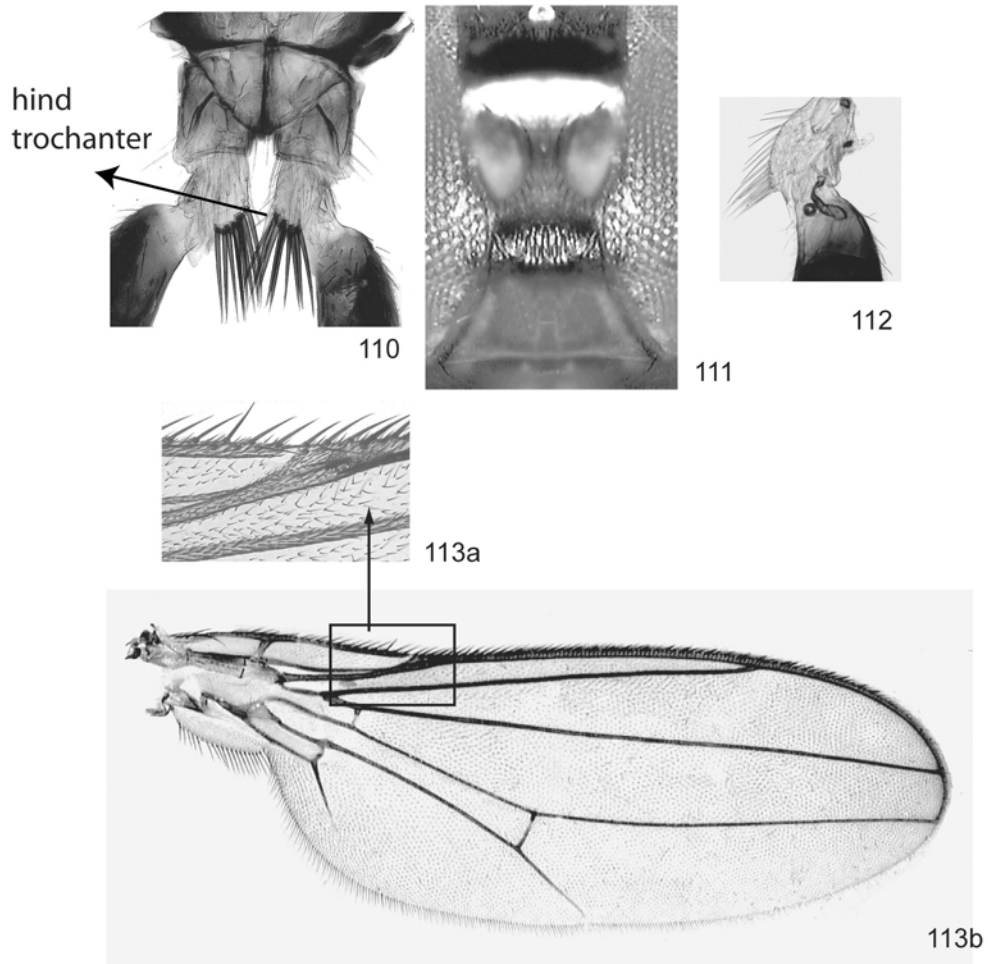
FIGURES 3.91-3.94.—Illustrations of the terminalia and internal genitalic structures (male) of aulacigastrids (The *plesiomorphica* group, Neotropical region), lateral aspect. 91. *Aulacigaster albifacies*, new species, epandrium and internal genitalic structures. 92. *Aulacigaster belize*, new species, surstylus (lateral ventral aspect). 93. *Aulacigaster bifasciata*, new species, epandrium. 94. *Aulacigaster erikae*, new species, epandrium (setae omitted). Not all to the same scale.



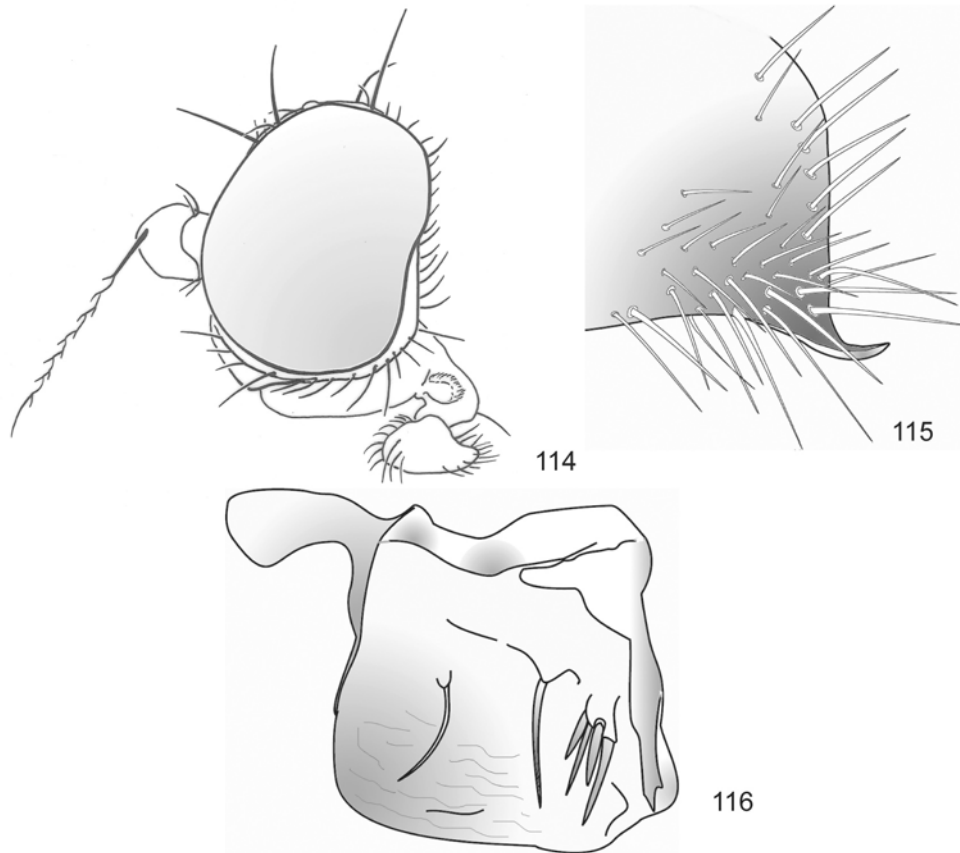
FIGURES 3.95-3.103.—Digital photographs of aulacigastrids (The *pleiomorphica* group, Neotropical region). 95. *Aulacigaster albifacies*, new species, abdominal sternite 5 (male), ventral aspect. 96. *Aulacigaster bifasciata*, new species, subepandrial sclerite, ventral aspect. 97- 101. *Aulacigaster conspicua*, new species. 97. Subepandrial sclerite, dorsal aspect; 98. Head, lateral aspect; 99. Face, frontal aspect; 100. Scutellum, dorsal aspect; 101. Epandrium, lateral aspect. 102- 103. *Aulacigaster erikae*, new species. 102. Subepandrial sclerite, ventral aspect; 103. Head, frontal aspect. Not all to the same scale.



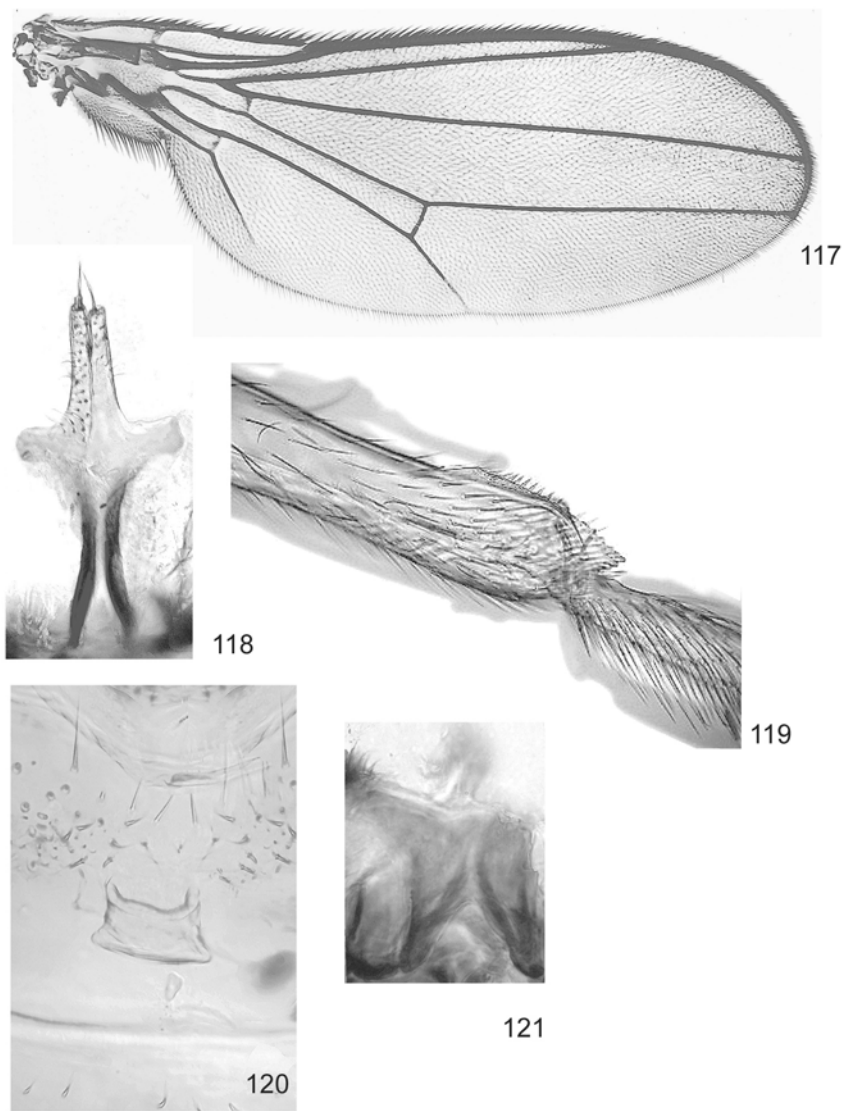
FIGURES 3.104-3.109.—Illustrations of aulacigastrids (The *plesiomorphica* group, Neotropical region). 104. *Aulacigaster kenna*, new species, postabdomen, epandrium and internal genitalic structures (male), lateral aspect. 105. *Aulacigaster plesiomorphica* (Hennig), sustylus, ventro-lateral aspect. 106- 109. *Aulacigaster proxima*, new species. 106. Sustylus, ventro-lateral aspect; 107. Hindtibia, dorsal aspect; 108. Thorax, lateral aspect. 109. Same, dorsal aspect. Not all to the same scale.



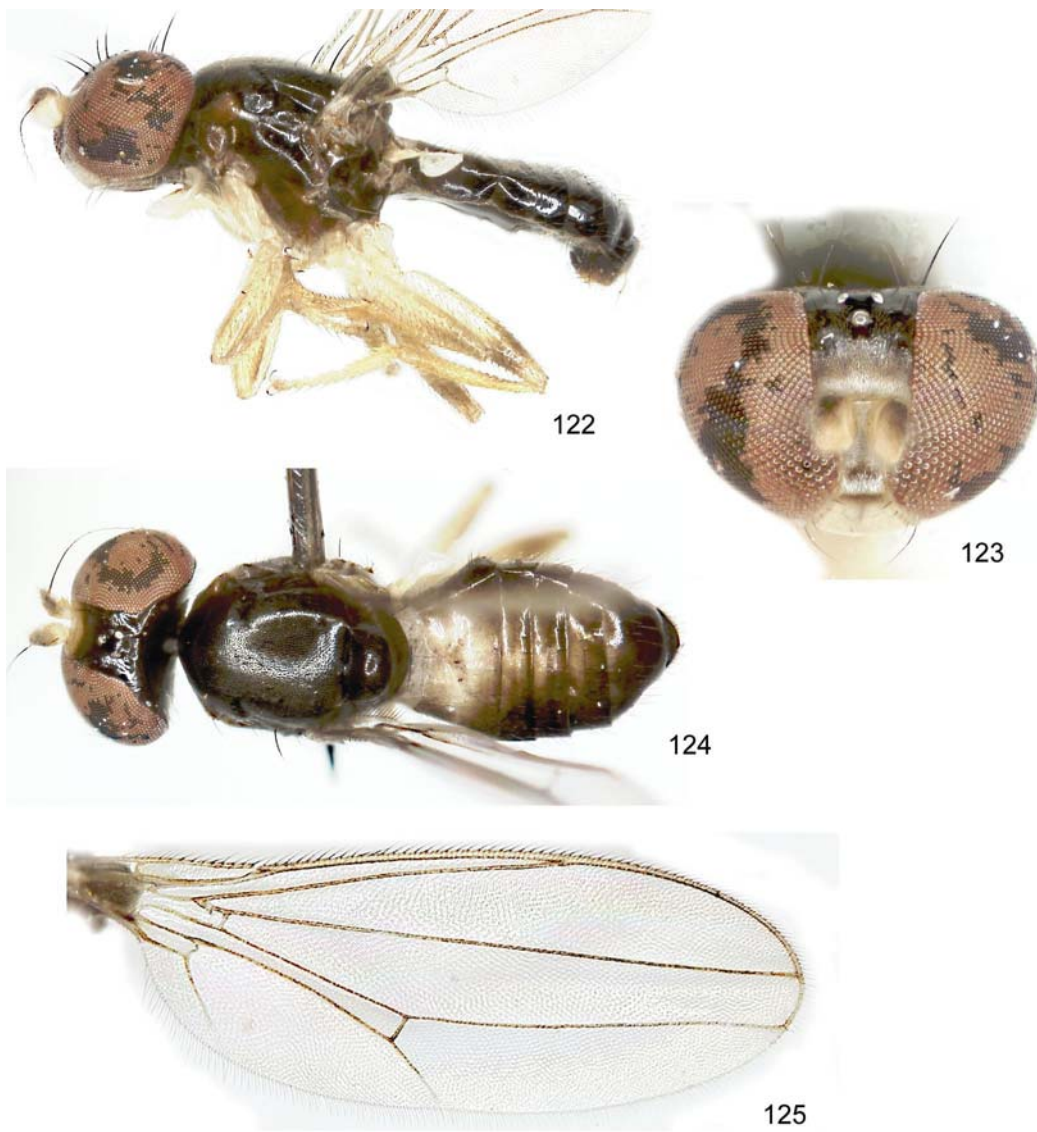
FIGURES 3.110-3.113.— Digital photographs of aulacigastrids (The *plesiomorphica* group, Neotropical region). 110. *Aulacigaster plesiomorphica* (Hennig), hind trochanter of male, posterior aspect. 3.111-3.113. *Aulacigaster proxima*, new species. 111. Mesofrons, frontal aspect; 112. Hind trochanter (male), posterior aspect. 113. Mesofrons and face, ventral frontal aspect; 113a. costal section of wing; 113b. Wing. Not all to the same scale.



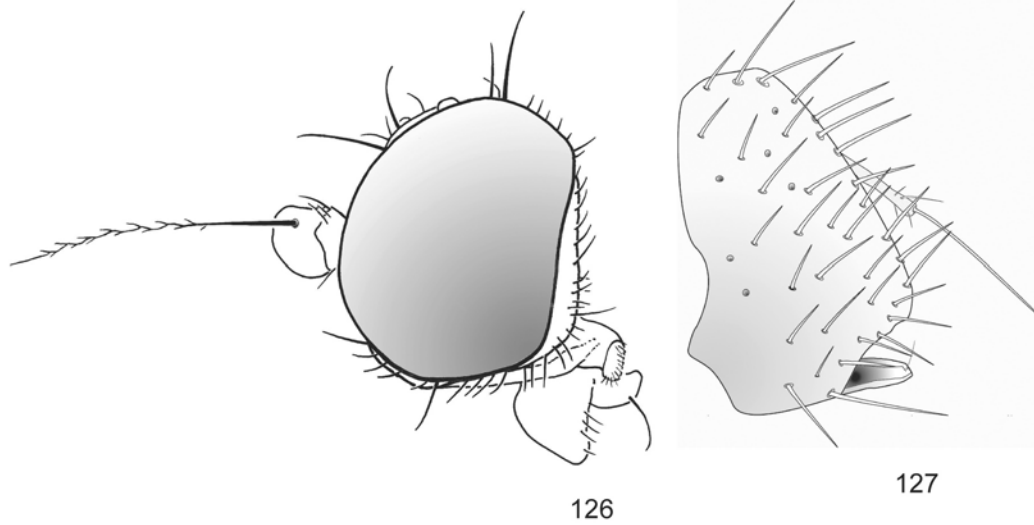
FIGURES 3.114-3.116.— Illustrations of *Aulacigaster rufifemur*, new species (The *plesiomorphica* group, Neotropical region). 114. Head, lateral aspect; 115. Surstylus, lateral aspect. 116. Internal genitalic structures (male), lateral aspect. Not all to the same scale.



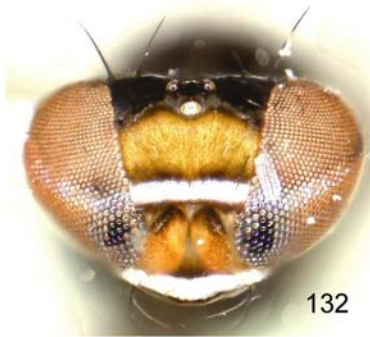
FIGURES 3.117-3.121.— Digital photographs of aulacigastrids (The *plesiomorphica* group, Neotropical region). 117- 119. *Aulacigaster rufifemur*, new species. 117. Wing; 118. Subepandrial sclerite, dorsal aspect; 119. Hindtibia of male, ventral aspect. 120- 121. *Aulacigaster trifasciata*, new species. 120. Abdominal sternite 5 (male), ventral aspect; 121. Subepandrial sclerite, dorsal aspect. Not all to the same scale.



FIGURES 3.122-3.125.— Digital photographs of *Aulacigaster trifasciata*, new species (The *pleiomorphica* group, Neotropical region). 122. Entire specimen, lateral aspect; 123. Head, frontal aspect; 124. Entire specimen, dorsal aspect; 125. Wing. Not all to the same scale.



FIGURES 3.126-3.127.— Illustrations of *Aulacigaster trifasciata*, new species (The *plesiomorphica* group, Neotropical region). 126. Head, lateral aspect; 127. Epandrium, lateral aspect. Not all to the same scale.



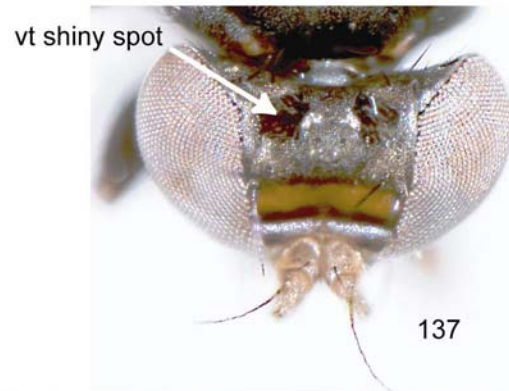
FIGURES 3.128-3.133.—Digital photographs of aulacigastrids (The *leucopeza* group, Neotropical region). 128- 129. *Aulacigaster colombiana*, new species. 128. Head, frontal aspect; 129. Same, lateral aspect. 130- 131. *Aulacigaster spangleri*, new species. 130. Head, frontal aspect; 131. Same, lateral aspect. 132- 133. *Aulacigaster* sp.e., undescribed species. 132. Head, frontal aspect; 133. Same, lateral aspect. Not all to the same scale.



FIGURES 3.134-3.135.—Digital photographs of *Aulacigaster* sp. (undescribed species, Afrotropical region). 134. Entire specimen, lateral aspect; 135. Head, frontal aspect. Not all to the same scale.



136



137



138

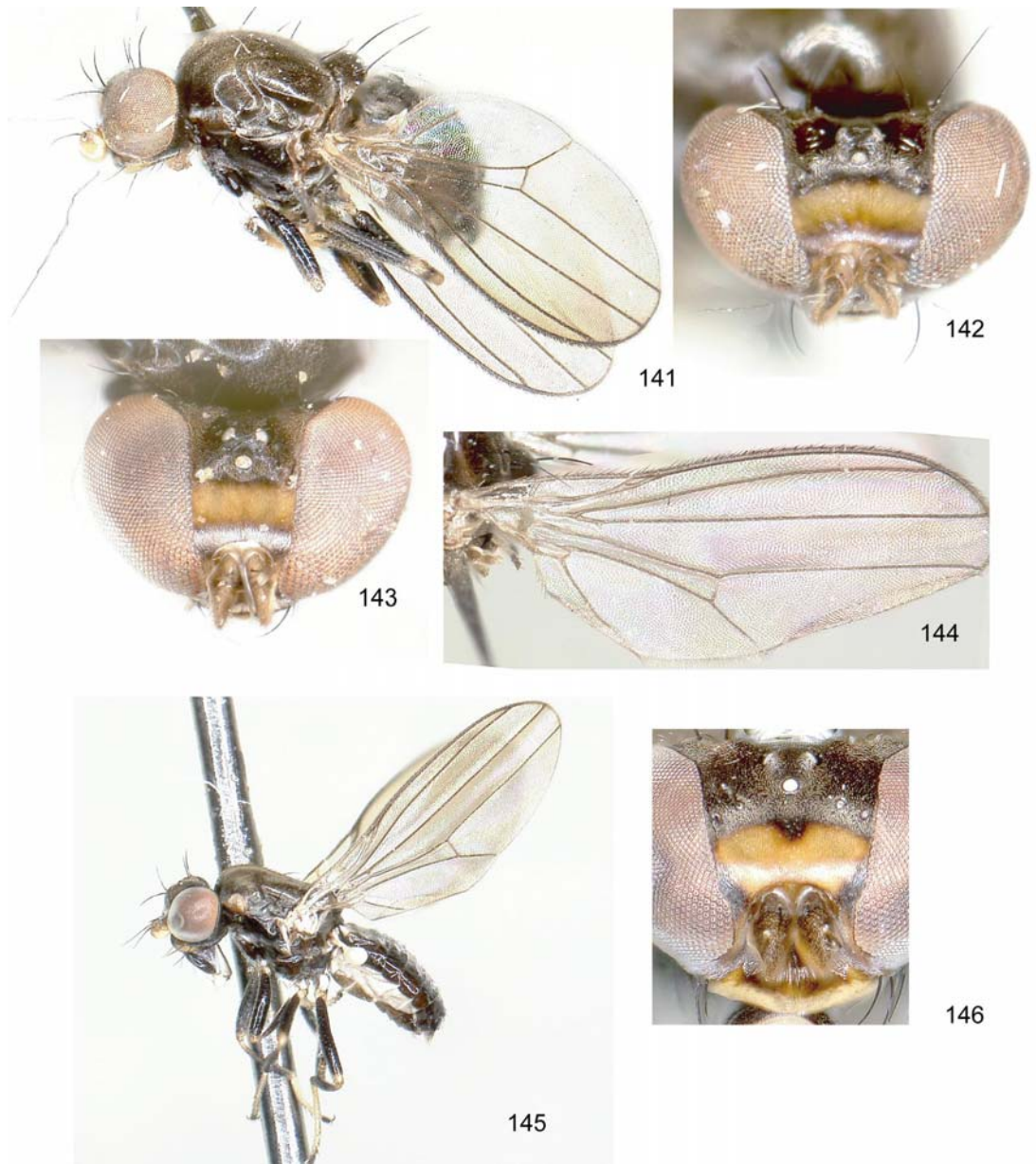


139

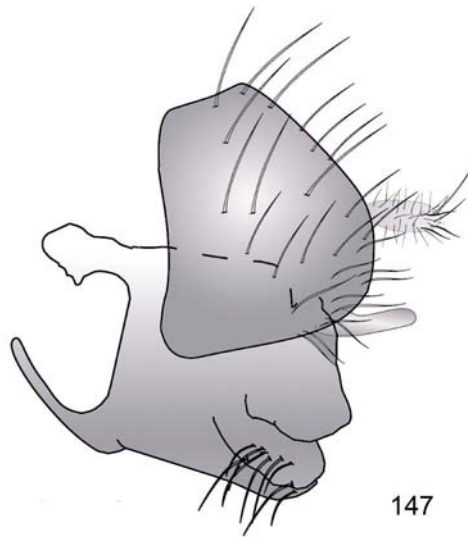


140

FIGURES 3.136-3.140.—Digital photographs of aulacigastrids (The *leucopeza* group, Nearctic region). 136- 137. *Aulacigaster neoleucopeza*. 136. Detail of frons; 137. Head, dorsal frontal aspect. 138. *Aulacigaster mcalpinei* Mathis& Freidberg, head, frontal aspect. 139. *Aulacigaster sabroskyi* Mathis and Freidberg. Head, frontal aspect.

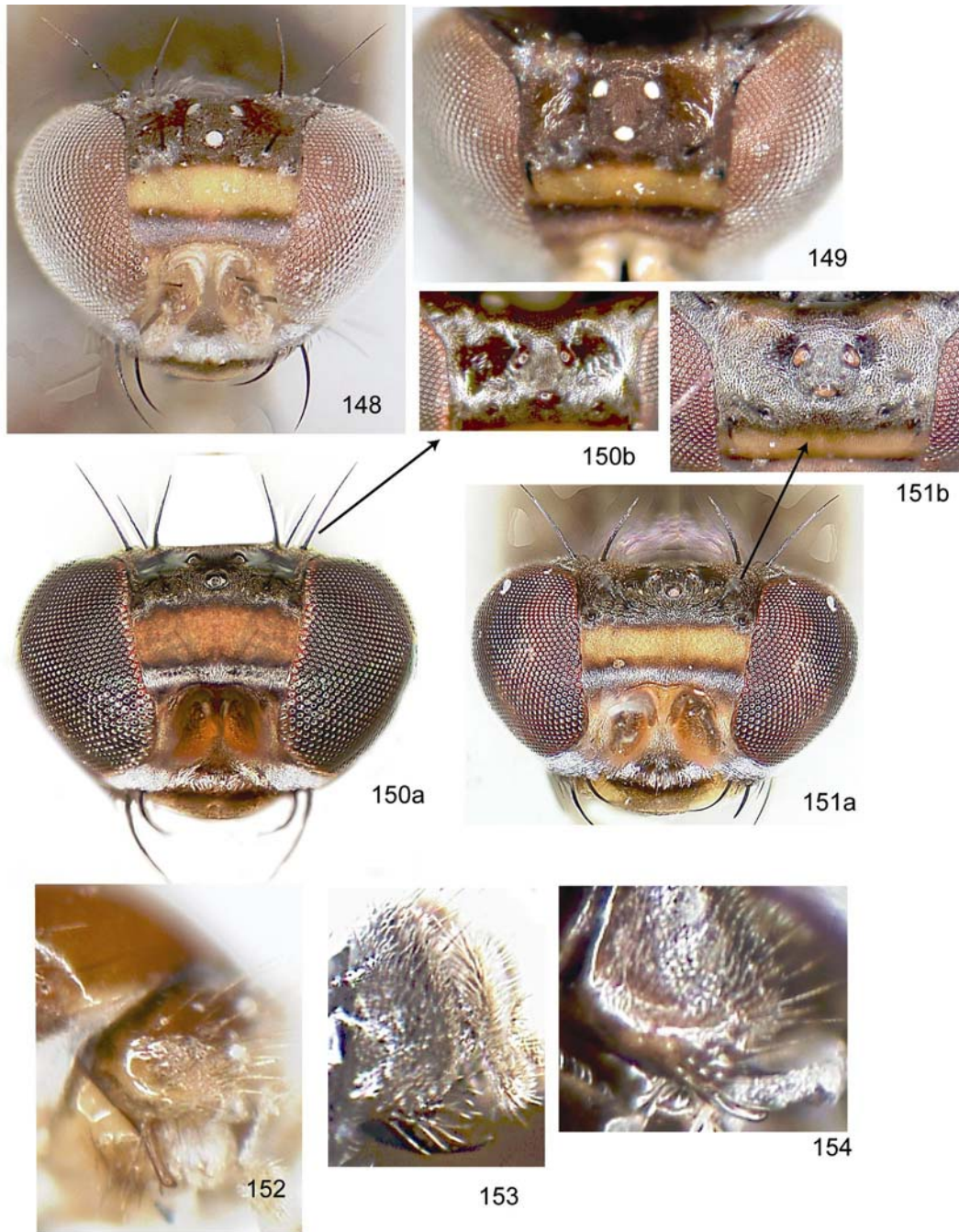


FIGURES 3.141-3.146.—Digital photographs of aulacigastrids (The *leucopeza* group, Oriental region). 141- 142. *Aulacigaster india*, new species. 141. Entire specimen, lateral aspect; 142. Head, frontal aspect. 143- 144. *Aulacigaster* sp.f, undescribed species. 143. Head, frontal aspect; 144. Wing. 145- 146. *Aulacigaster* sp.g, undescribed species. 145. Entire specimen, lateral aspect; 146. Detail of frons. Not all to the same scale.



147

FIGURE 3.147.— Illustration of the epandrium and internal genitalic structures (male) of *Aulacigaster indiana*, new species (The *leucopeza* group, Oriental region).



FIGURES 3.148-3.154.—Digital photographs of aulacigastrids (The *leucopeza* group, Palearctic region). 148- 149. *Aulacigaster afghanorum*. 148; Head, frontal aspect; 149. Same, dorsal frontal aspect. 150 a-b. *Aulacigaster falcata*. 150a. Head, frontal aspect; 150b. Detail of vertex. 151 a-b. *Aulacigaster leucopeza*. 151 a. Head, frontal aspect; 151 b. Detail of vertex. FIGURES 3.152-3.154. Epandrium, lateral aspect. 152. *Aulacigaster afghanorum*. 153. *Aulacigaster falcata*. 154. *Aulacigaster neoleucopeza*. Not all to the same scale.

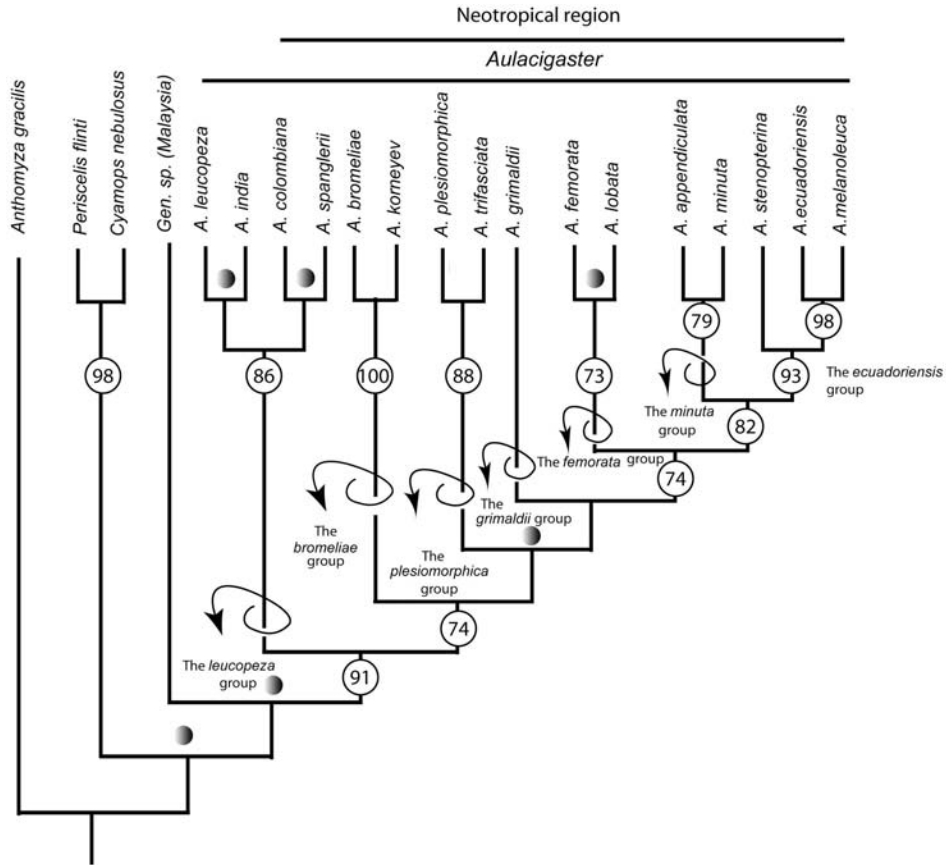


FIGURE 3.155.— One of six cladograms generated using ordered characters, and successive weighting. Trees have 53 steps, consistency index of 0.80, and Retention index of 0.88. Grey dots indicate where the branches collapse in the strict consensus cladogram. Bootstrap support is shown below the branch nodes.

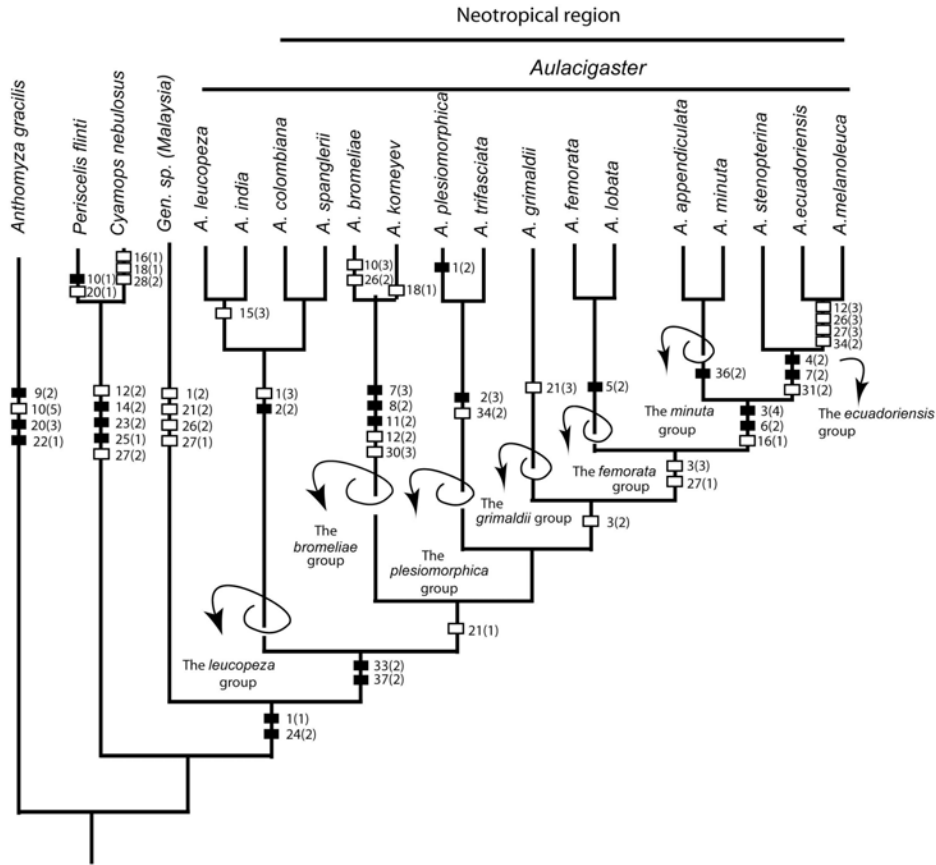


FIGURE 3.156.—One of the six cladograms generated using ordered characters, successive weighting. Trees have 53 steps, consistency index of 0.80 and Retention index of 0.88. Black rectangles indicate unambiguous, unique changes. White rectangles indicate unambiguous, homoplasious changes. Ambiguous changes are omitted. Numbers for the characters correspond to those used in text. Character states within brackets.

Chapter 4 : The internal female reproductive tract of opomyzoidea (Diptera, Schizophora)

ABSTRACT

The internal female reproductive tract of six species of Opomyzidae is described, representing three of the four known genera of the family. It is then compared with the female tract of other opomyzoid families. The general pattern, shared by all families, comprises a tubular membranous vagina, two or three ovoid to elongate sclerotized spermathecae, a ventral receptacle and long accessory glands. Most interspecific variation is in the shape and ornamentation of the spermathecae, and sclerotization of the duct and apex of spermathecal ducts and accessory gland ducts, and number of chambers in the multi-chambered ventral receptacle. The following structures do not seem to vary inside individual families of Opomyzoidea, and may prove informative for phylogenetic analyses, in addition to the number of spermathecae: the presence/ absence of multiple chambers in the ventral receptacle; the degree of sclerotization and shape of the ventral receptacle; and the presence of a ring-shaped sclerotization on the wall of the vagina, posterior to the ventral receptacle.

INTRODUCTION

The phylogenetic relationships among the families of acalyprate Schizophora are an ongoing controversy (McAlpine 1989, Yeates & Wiegmann 1999). The internal female reproductive tract has been suggested as a potential source of

phylogenetically informative characters for resolving these relationships (Sturtevant 1925, 1926, Hennig 1958, Griffiths 1972, McAlpine 1989). During the last decade, this character system has received increased attention (e. g. Kotrba 1993, 1995, Roháček 1993, 1998a, 1998 b, 1999, Meier *et al.* 1997, Caloren & Marshall 1998, Brake 2000). Besides helping to resolve the phylogeny, detailed knowledge of the morphology of these organs may help us to understand their role in reproductive biology, particularly the possibilities of postcopulatory sexual selection, such as sperm competition and cryptic female choice, which are very active topics in evolutionary biology (e. g. Eberhard 1985, 1996, Otronen & Siva-Jothy 1991, Ward 1993, Hellriegel & Ward 1998). For many acalyprate families, however, the female reproductive tract remains undescribed.

In this chapter I investigate and compare the morphology of the internal female reproductive tract of a few opomyzoid families, as well as other taxa that have been previously believed to lie close to or within the Opomyzoidea. (J.F.McAlpine 1989).

METHODS

This study is mostly based on dissection of fresh material, although some species could only be investigated from dried specimens after maceration in KOH. Dissection of fresh material gave much better results, especially regarding the less sclerotized parts. However, macerated material was sufficient for comparison of the most important characters, such as the condition of the spermathecae and the ventral receptacle. As specimens are largely destroyed by dissection, museum specimens of otherwise poor condition and/or lacking locality data were chosen for the study.

After dissection, the female reproductive tract was embedded in polyvinyl lactophenol with an admixture of chlorazol black E. The preparations were then studied in bright field as well as DIC contrast using an Olympus BX50 equipped with a drawing tube and Olympus SC35 camera.

Descriptions are based on the study of one or a few specimens per species. The descriptions focus on the morphology of the anterior part of the vagina and associated organs. These organs are internally lined with cuticle and provide a number of distinct morphological characters for systematics. The terminology of morphological structures follows a recent glossary (Kotrba 2000). The term “sclerotized” is used for structures consisting of darkened cuticle.

RESULTS

Superfamily Opomyzoidea

Internal female reproductive tract of Opomyzidae, general description

The internal female reproductive tract of Opomyzidae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, paired spermathecae and accessory glands, and a multi-chambered ventral receptacle (Kotrba and Baptista, 2000: Fig. 1).

The vagina is an elongate muscular tube lined internally by thin cuticle. It has an enlarged portion posterior to the ventral receptacle, which is very pronounced in some species. When empty, the inner vaginal wall forms numerous folds. It

contains no sclerotized elements apart from some areas with sclerotized spines in *Anomalochaeta*.

The two ovoid to elongate sclerotized spermathecae are surrounded by a layer of glandular epithelium (Kotrba and Baptista, 2000: Fig. 1). In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter. The spermathecal ducts are lined by thick, annulated cuticle and surrounded by longitudinal muscles. In some species they are thinner and/or sclerotized at their base and/or apex.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are slightly to considerably longer than the spermathecae (ducts plus capsules). Their membranous ducts are surrounded by predominantly circular muscles. The elongate glandular portion is surrounded by glandular epithelium in which round end apparatus can be discerned. It has an apical tubular extension (Kotrba and Baptista, 2000: Fig. 1).

The ducts of the spermathecae and accessory glands open dorsally into the genital papilla (Kotrba and Baptista, 2000: Fig. 1). This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The ventral receptacle arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It is

surrounded by musculature. Into the anterodorsal portion of the ventral receptacle open two to many ovoid cuticular chambers (Kotrba and Baptista, 2000: Fig. 1).

Anomalochaeta guttipennis

(Kotrba and Baptista, 2000: Fig. 1).

DESCRIPTION.—Spermathecae ovoid, slightly invaginated and slightly telescoped basally. Spermathecal walls smooth, with a few wart-like protrusions from which the end apparatus of gland cells originate. Spermathecal ducts comparatively short and wide, narrower at base and apex, slightly annulate. Accessory glands in total about twice as long as the spermathecae. Ventral receptacle with two large chambers, each with a diameter of about 12 μm , and two much smaller chambers on each side. Anteroventral wall of the ventral receptacle and apical portions of the large chambers slightly sclerotized. Vagina widest immediately posterior to insertion of ventral receptacle and spermathecae. Lateral walls of vagina studded with sclerotized cuticular denticles.

MATERIAL EXAMINED.—One dried specimen, coll. USNM (Manatuska, Alaska, leg. J. C. Chamberlin, 27 May 1944).

REMARKS.—The ovaries of this *Anomalochaeta* specimen contained about 10 mature eggs.

Geomyza balachowskyi

(Kotrba and Baptista, 2000: Fig. 2a-c).

DESCRIPTION.—Spermathecae ovoid, slightly longer than wide, slightly invaginated basally and apically. Spermathecal walls ornamented with transverse wrinkles and a few wart-like protrusions from which the end apparatus of gland cells originate. Spermathecal ducts comparatively short and distinctly annulate. Accessory glands could not be traced. Ventral receptacle with about 10 chambers, each with a diameter of about 8 μm . Vagina widest immediately posterior to insertion of ventral receptacle and spermathecae. Ventral receptacle and vagina without sclerotized structures.

MATERIAL EXAMINED.—One dried specimen, coll. MNHUB, no locality data.

REMARKS.—In another undetermined specimen of the *combinata* group that is very similar to *G. balachowskyi*, the ventral receptacle has 7 chambers, each with a diameter of about 8 μm . The accessory glands in total about twice as long as the spermathecae. In this specimen the vagina has a distinct pouchlike enlargement ventrally, just posterior to the ventral receptacle.

Geomyza tripunctata

(Kotrba and Baptista, 2000: Fig. 7 a-b).

DESCRIPTION.—Spermathecae conoid, distinctly longer than wide (about 1.5x), and slightly invaginated basally. Spermathecal walls with irregular, mostly longitudinal wrinkles and a few wart-like protrusions from which the end apparatus of gland cells originate. Spermathecal ducts comparatively long and narrow, distinctly annulate. Basal portions of spermathecal ducts narrower, ornamented with

irregular lobular ridges, and distinctly sclerotized. Apical portions of spermathecal ducts sclerotized as well. Accessory glands in total a little longer than spermathecae. Ventral receptacle with 6 to 8 chambers, each with a diameter of about 9 μm . One of the specimens seemed to have a few additional, much more delicately lined chambers posterior to these. Vagina with pouch-like enlargement posterior to ventral receptacle. Ventral receptacle and vagina without sclerotized structures.

MATERIAL EXAMINED.—Two fresh specimens from Munich, Germany, and one specimen in alcohol from Ottawa, Canada.

REMARKS.—The Canadian specimen differs in the following respects: Spermathecae ovoid, slightly longer than wide, and slightly invaginated basally. Their walls mostly smooth with a few wart-like protrusions from which the end apparatus of gland cells originate. Genital papilla sclerotized around opening of spermathecal ducts. Ventral receptacle with 6 chambers, each with a diameter of about 8 μm . Its anterodorsal wall slightly pigmented. Vagina with some pigmented specks in its posterior portion.

Opomyza germinationis

(Kotrba and Baptista, 2000: Fig. 3a-b)

DESCRIPTION.—Spermathecae round to ovoid, one distinctly larger than the other, slightly telescoped basally. In one of the specimens collected in Munich larger spermatheca apically divided in two. Spermathecal walls mostly smooth with scattered wart-like protrusions or spinules from which the end apparatus of gland cells originate. Spermathecal ducts relatively short and wide, slightly annulate,

strongly sclerotized along apical fourth. Basal portion of spermathecal ducts narrower and slightly sclerotized as well. Accessory glands in total distinctly longer than spermathecae. Ventral receptacle with 8-10 chambers, each with a diameter of about 7 μm . Vagina with large pouch posterior to ventral receptacle. Ventral receptacle and vagina without sclerotized structures.

MATERIAL EXAMINED.—Four fresh specimens from Brandenburg, Germany, and two fresh specimens from Munich, Germany.

Opomyza florum

(Kotrba and Baptista, 2000: Figs. 4a, 5, 6)

DESCRIPTION.—Spermathecae elongate, about 4 to 6 times longer than wide, not telescoped basally. Spermathecal walls ornamented with narrowly spaced, transverse wrinkles and a few wart-like protrusions from which the end apparatus of gland cells originate. Spermathecal ducts comparatively long and narrow, slightly annulate. Their apical ends slightly thicker and as sclerotized as spermathecal capsules. Accessory glands in total a little longer than spermathecae. Ventral receptacle with 25 to 30 chambers, each with a diameter of about 5-6 μm . Vagina enlarged posterior to ventral receptacle with many transverse folds. Ventral receptacle and vagina without sclerotized structures.

MATERIAL EXAMINED.—Five fresh specimens from Brandenburg, Germany, and one fresh specimen from Munich, Germany.

Opomyza punctella

DESCRIPTION.—Spermathecae elongate, about 3 times longer than wide, not telescoped basally. Their walls ornamented with narrowly spaced transverse wrinkles and a few wart-like protrusions from which the end apparatus of gland cells originate. Spermathecal ducts similar to those of *O. florum*, but not sclerotized apically or basally. Accessory glands in total distinctly longer than spermathecae. Ventral receptacle with about 17 chambers, each with a diameter of about 5.5 μm . Vagina enlarged posterior to ventral receptacle with many transverse folds. Ventral receptacle and vagina without sclerotized structures.

MATERIAL EXAMINED.—One dried specimen, coll. MNHUB, no locality data.

Internal female reproductive tract of Clusiidae, general description

The internal female reproductive tract of Clusiidae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, paired spermathecae, paired accessory glands, and a thick-walled ventral receptacle.

The vagina approximately is slightly longer than wide, not sclerotized and has an additional ventral evagination directly posterior to ventral receptacle.

The spermathecae are cylindrical or mushroom-shaped, with smooth walls. In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are slightly to considerably longer than the spermathecae (ducts *plus*

capsules), thinner at base, enlarging apically, with a thin apical projection. The elongate glandular portion is surrounded by glandular epithelium in which round end apparatus can be discerned. It has an apical tubular extension.

The spermathecal duct bifurcates close to apex. The ducts of the spermathecae and accessory glands open dorsally into the genital papilla. This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The ventral receptacle is thick-walled and arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It consists of only one chamber, and is surrounded by musculature.

OBSERVATIONS.—For further details, see Caloren & Marshall 1998.

Clusia lateralis

DESCRIPTION.—Spermathecal wall smooth. Spermathecal ducts wide, short and thick-walled, smooth; base and apex not sclerotized. Ventral receptacle thick-walled and sclerotized (sclerotization at tip only) .Walls of vagina not sclerotized, with an additional ventral evagination directly posterior to ventral receptacle.

Clusioides ater

DESCRIPTION.—Spermathecae cylindrical, sclerotized at constricted, apical portion, swollen portion thick-walled. Spermathecal wall smooth, base strongly telescoped, apex smooth. Spermathecal ducts wide, short and thick-walled, smooth;

base and apex not sclerotized. Base of accessory gland duct not sclerotized. Ventral receptacle thick-walled and sclerotized at tip. Vagina approximately as wide as long, with an additional ventral evagination of vagina directly posterior to ventral receptacle.

Internal female reproductive tract of Anthomyzidae, general description

The internal female reproductive tract of Anthomyzidae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, two spermathecae, paired accessory glands, and a membranous ventral receptacle that has only one chamber.

The vagina is wider than long, with walls posterior to ventral receptacle sclerotized, forming a large ring.

The spermathecae are round to oval with smooth walls. In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are shorter than the spermathecae (total) and lack an apical tubular extension (Roháček, 1993, 1998 a, 1998 b, 1999).

The spermathecal duct bifurcates close to apex. The ducts of the spermathecae and accessory glands open dorsally into the genital papilla. This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The multi-chambered ventral receptacle is membranous and arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It is surrounded by musculature.

Anthomyza gracilis

DESCRIPTION.—Spermathecae round to oval. Spermathecal wall smooth, with broadly scattered denticles, base not telescoped. Apparatus in spermathecal glands not conspicuous. Spermathecal ducts thin, long and thin walled, smooth. Apex of spermathecal duct sclerotized, bent by more than 90 degrees. Accessory glands approximately as long as wide, slightly narrower apically; base of accessory gland duct not sclerotized. Ventral receptacle membranous. Vagina considerably longer than wide, walls of vagina sclerotized posterior to ventral receptacle (forming a ring); ring large.

MATERIAL EXAMINED.— USA. New Mexico: Questa, RedR. 26 May 1969, W.W.Wirth, river margin (1 ♀; USNM).

REMARKS.—This observation was based on dried material.

Mumetopia terminalis

DESCRIPTION.—Spermathecae tear-drop shaped. Spermathecal wall smooth, with denticles present along basal half, base not telescoped. Apparatus in spermathecal glands not conspicuous. Spermathecal ducts wide, short and thick-walled, smooth. Apex of spermathecal duct not sclerotized. Ventral receptacle thick-

walled and sclerotized (sclerotization only partial, at tip). Vagina approximately as wide as long.

MATERIAL EXAMINED.— USA. West Virginia: Granberry Glades, 16 Jun 1970, G. Steyskal, Det. Sabrosky (1 ♀ USNM).

REMARKS.—This observation was based on dried material.

Suprafamily Asteioinea

Internal female reproductive tract of Aulacigastridae, general description

(Kotrba and Baptista, 2000: Fig. 4b)

The internal female reproductive tract of Aulacigastridae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, three spermathecae, paired accessory glands, and a multi-chambered ventral receptacle.

The vagina approximately as wide as long, with walls posterior to ventral receptacle sclerotized, forming a large ring.

The spermathecae are cylindrical or mushroom-shaped, with smooth walls. In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are slightly to considerably longer than the spermathecae (ducts plus capsules), thinner at base, enlarging apically, with a thin apical projection. The

elongate glandular portion is surrounded by glandular epithelium in which round end apparatus can be discerned. It has an apical tubular extension.

The duct that contains two spermathecae bifurcates close to apex. The ducts of the spermathecae and accessory glands open dorsally into the genital papilla. This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The multi-chambered ventral receptacle is membranous and arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It is surrounded by musculature. Into the anterodorsal portion of the ventral receptacle open two to many ovoid cuticular chambers.

Aulacigaster vespertina, undescribed species

DESCRIPTION.—Spermathecae approximately round, wall smooth, base of with marginal digitiform projections. Spermathecal ducts wide, short and thick-walled, smooth, bifurcating very close to base of spermatheca. Apex and base of spermathecal duct not sclerotized. Accessory glands thinner at base, enlarging apically, with a thin apical projection. Base of accessory gland duct not sclerotized. Ventral receptacle membranous, approximately fan-shaped, with approximately 20 chambers. Walls of vagina sclerotized posterior to ventral receptacle, forming a large plate, and a ring posterior to it. Additional ventral evagination of vagina absent.

MATERIAL EXAMINED.—ECUADOR. Puerto Orellana: Rio Tiputini

(0°38.2'S, 76°8.9'W), 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba (1 ♀; USNM). Slide prepared from fresh material.

Aulacigaster mcalpinei

DESCRIPTION.—Spermathecae cylindrical, walls wrinkled and bearing basal denticles. Base of spermatheca slightly telescoped, apex invaginated, central portion bearing a central evagination. Spermathecal ducts wide, short and thick-walled, smooth, bifurcating very close to base of spermatheca, apex and base of spermathecal duct sclerotized. Accessory glands thinner at base, enlarging apically, with a thin apical projection; base of accessory gland duct weakly sclerotized. Ventral receptacle membranous, with internal chambers. Vagina approximately as wide as long, walls of vagina sclerotized posterior to ventral receptacle (forming a ring), ring short. Additional ventral evagination of vagina absent.

MATERIAL EXAMINED.—USA. Maryland. Montgomery: Potomac, 23 Jul-23 Aug 1989, Amnon Freidberg, slime flux on oak (1 ♀; USNM).

Internal female reproductive tract of Periscelididae, general description

The internal female reproductive tract of Periscelididae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, two to four spermathecae, paired accessory glands, and a simple or a multi-chambered ventral receptacle.

The vagina is approximately wider than long, and the walls are not sclerotized.

The spermathecae are round to oval, with smooth walls. In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are slightly to considerably longer than the spermathecae (ducts plus capsules), thinner at base, enlarging apically.

The spermathecal duct bifurcates close to apex. The ducts of the spermathecae and accessory glands open dorsally into the genital papilla. This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The ventral receptacle is membranous and arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It is surrounded by musculature.

Periscelidinae

Periscelis flinti

DESCRIPTION.—Spermathecae 3, significantly reduced, round to oval. Spermathecal wall smooth, base slightly telescoped, apex smooth. Spermathecal ducts wide, short and thick-walled, very wrinkled, bifurcating very close to base of spermatheca. Apex and base of spermathecal duct sclerotized, bent by less than 90 degrees. Ventral receptacle membranous. Vagina approximately as wide as long, or slightly longer than wide, walls of vagina not sclerotized.

MATERIAL EXAMINED.—USA. VA. Stafford Co.. Stafford, 14 Aug 1990, W.N.Mathis, also Det. (1 ♀; USNM).

Stenomicrinae

Stenomicra (Podocera), sp., undescribed species

DESCRIPTION.—Two, round to oval spermathecae. Spermathecal wall ornamented, base not telescoped and bearing basal denticles, apex smooth. Apparatus in spermathecal glands not conspicuous. Spermathecal ducts slightly wrinkled, base and apex not sclerotized. Ventral receptacle membranous and with several visible chambers. Vagina approximately as wide as long, sclerotized dorsal-anterior to, or at, genital papilla.

MATERIAL EXAMINED.—ECUADOR. Puerto Orellana: Rio Tiputini (0°38.2'S, 76°8.9'W), 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba (1 ♀; USNM). Slide prepared from fresh material.

Stenomicra (Stenomicra) sp., undescribed species

DESCRIPTION.—Two round spermathecae. Spermathecal wall smooth, base not telescoped, apex smooth. Spermathecal ducts thin, long and thin walled, smooth, apex and base not sclerotized. Ventral receptacle thick-walled and with several visible chambers. Vagina approximately as wide as long.

MATERIAL EXAMINED.—ECUADOR. Puerto Orellana: Rio Tiputini (0°38.2'S, 76°8.9'W), 12-26 Aug 1999, W. N. Mathis, A. Baptista, M. Kotrba (1 ♀; USNM). Slide prepared from fresh material.

Cyamops nebulosus

DESCRIPTION.—Three round to oval spermathecae. Spermathecal wall smooth, base not telescoped, apex smooth. Spermathecal ducts wide, short and thick-walled, smooth, bifurcating very close to base of spermatheca, apex and base not sclerotized. Ventral receptacle thick-walled and not sclerotized.

MATERIAL EXAMINED.—USA. No additional information. (1 ♀; USNM).

REMARKS.—This observation was based on dried material.

Internal female reproductive tract of Asteiidae

Leiomyza laevigata

DESCRIPTION.—Two oval to round spermathecae present. Spermathecal wall smooth, base not telescoped, apex smooth. Spermathecal ducts wide, short and thick-walled, slightly wrinkled. Apex of spermathecal duct sclerotized, bent by less than 90 degrees, base slightly sclerotized. Base of accessory gland duct slightly sclerotized. Ventral receptacle membranous, with several internal chambers. Vagina approximately as wide as long, walls of vagina sclerotized posterior to ventral receptacle (forming a ring), ring short.

Internal female reproductive tract of Neminidae

Nemo corticeus

DESCRIPTION.—Two oval to round spermathecae present significantly small, round to oval. Spermathecal wall smooth, with evenly distributed denticles, base not telescoped, apex smooth. Apparatus in spermathecal glands not conspicuous. Spermathecal ducts thin, long and thin walled, slightly wrinkled, apex and base not sclerotized. Base of accessory gland duct not sclerotized. Ventral receptacle thick-walled and not sclerotized, with internal chambers. Walls of vagina sclerotized posterior to ventral receptacle (forming a ring), ring short.

MATERIAL EXAMINED.—USA. No additional information. (1 ♀; USNM).

REMARKS.—This observation was based on dried material.NSW: Hartley Vale Rd; Blue Mtns. 10 Nov 1990, D.K.McAlpine. McAlpine Det. (1 ♀; USNM).

Superfamily Diopsoidea

Somatia aestiva

DESCRIPTION.—Two spermathecae present, elongate. Spermathecal wall smooth, with broadly scattered denticles, base not telescoped, apex smooth. Spermathecal ducts smooth; base and apex not sclerotized. Base of accessory gland duct not sclerotized. Ventral receptacle membranous, with only one chamber. Additional ventral evagination of vagina present on the anterior 1/3 of the vagina.

MATERIAL EXAMINED.—Costa Rica. Pedregosa. D. L. Rounds. ALMelander Collection 1961. A.L.Norbom Det, 1988. (1 ♀; USNM).

REMARKS.—This observation was based on dried material.

Incertae sedis

Internal female reproductive tract of Odiniidae, general description

The internal female reproductive tract of Odiniidae comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, paired spermathecae and accessory glands, and a thick-walled ventral receptacle that consists of only one chamber.

The vagina is an elongate muscular tube lined internally by thin cuticle. It has an enlarged portion posterior to the ventral receptacle, which is very pronounced in some species. When empty, the inner vaginal wall forms numerous folds. It contains no sclerotized elements apart from some areas with sclerotized spines in *Anomalochaeta*.

The two ovoid to elongate sclerotized spermathecae are surrounded by a layer of glandular epithelium. In fresh material the cuticular end apparatus of the gland cells can be discerned. Their tiny ducts open into the spermathecal wall, often into small wart-like protrusions of the latter. The spermathecal ducts are lined by thick, annulated cuticle and surrounded by longitudinal muscles. In some species they are thinner and/or sclerotized at their base and/or apex.

The accessory glands in total (ducts plus glandular portions plus apical extensions) are slightly to considerably longer than the spermathecae (ducts plus capsules). Their membranous ducts are surrounded by predominantly circular muscles. The elongate glandular portion is surrounded by glandular epithelium in which round end apparatus can be discerned. It has an apical tubular extension.

The ducts of the spermathecae and accessory glands open dorsally into the genital papilla. This is an internal protuberance of the anterodorsal vaginal wall, which projects anteroventrally towards the entrance of the ventral receptacle.

The ventral receptacle is thick-walled and arises from the anteroventral portion of the vagina, opposite the opening of the ducts of the spermathecae and accessory glands. From there it projects anteriorly along the basal portion of the common oviduct. It is surrounded by musculature.

Odinia sp.

DIAGNOSTIC DESCRIPTION.—Spermathecae sclerotized centrally, but with base and apex membranous. Spermathecal wall smooth. Spermathecal ducts wide, short and thick-walled, slightly wrinkled, base and apex not sclerotized. Base of accessory gland duct not sclerotized.

MATERIAL EXAMINED.—USA. Maryland. Montg:Bethesda. Jul 1972. G.E.Steyskal. (1 ♀; USNM).

Traginops sp.

DIAGNOSTIC DESCRIPTION.—Spermathecae transversely oval. Spermathecal wall smooth, base strongly telescoped, apex smooth. Spermathecal ducts wide, short and thick-walled, very wrinkled, base and apex not sclerotized. Base of accessory gland duct sclerotized.

MATERIAL EXAMINED.—USA. Virginia. Stafford Co, Stafford, 14 Aug

1990, W.N.Mathis. S.D.Gaimari Det. (1 ♀; USNM).

DISCUSSION

The internal female reproductive tract shows little variation across species of the same family. Differences occur predominantly in the shape and ornamentation of the spermathecae, the number and size of chambers of the ventral receptacle (when it is multi-chambered), and whether the spermathecal and gland ducts are sclerotized at the base and apex. Between families, the major differences are in the shape and the degree of sclerotization of the ventral receptacle, and whether it has one or more chambers; the length of the vagina relative to its width; the presence of sclerotization and additional chambers in the wall of the vagina.

My investigation of the internal female reproductive tract has not revealed any putative synapomorphies for the Opomyzoidea. The following putative synapomorphies can be advanced for some of the included families:

1) The spermathecae of Anthomyzidae are often adorned with long spines, as are those of Asteiidae.

2) A sclerotized ring is present in the ventral vaginal wall of most Anthomyzidae (Roháček 1998 b), *Aulacigaster* Macquart and *Nemo* McAlpine.

3) The multi-chambered condition of the ventral receptacle, absent in other superfamilies, is present in *Aulacigaster*, *Leiomyza* Macquart, *Stenomicro* Coquillett and the unplaced Neotropical genus *Mallochianamyia* Santos-Neto (Wheeler 2000).

Where the ventral receptacle of the acalyprate Schizophora has been studied in detail, it has been found to store spermatozoa prior to fertilization and to serve as the fertilization site (e. g. Miller 1965, Solinas & Nuzzaci 1984, Kotrba 1993). In some of the Opomyzidae studied by me, filamentous spermatozoa were clearly visible within the ventral receptacle.

The morphological variation found in the ventral receptacle of the Opomyzidae across species is remarkable in that a negative correlation exists between the number and the diameter of the chambers (Kotrba and Baptista 2000). As a result, the overall volume of the chambers combined stays more or less the same. Possibly the number of chambers does not so much affect the number of stored spermatozoa as it affects their individual allocation prior to fertilization. The morphology of multi-chambered ventral receptacles in particular has been studied in detail in *Dacus oleae* Gmel. (Tephritidae, Solinas & Nuzzaci 1984) and *Cyrtodiopsis whitei* Curran (Diopsidae, Kotrba 1993). In the latter, their possible adaptive value with respect to sperm competition was discussed by Kotrba (1993). Moreover, variation in the morphology of the ventral receptacle was found to be correlated with the length of the spermatozoa across species in Diopsidae (Kotrba 1995, Presgraves *et al.* 1999), and a similar correlation was discovered in Drosophilidae (Hihara & Kurokawa 1987, Pitnick *et al.* 1999). These results suggest that the study of the multi-chambered ventral receptacle in acalyprate Schizophora, its evolution and its significance with respect to sperm competition and cryptic female choice, constitutes a promising topic for future research.

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