

To Bill,  
With best wishes, and appreciation  
for BRF funding (pgs. 291-312:  
Cladochaeta inversa) — Dave

MONOGRAPH ON THE  
SPITTLEBUG FLIES,  
GENUS *CLADOCHAETA*  
(DIPTERA: DROSOPHILIDAE:  
CLADOCHAETINI)

DAVID GRIMALDI  
TAM NGUYEN

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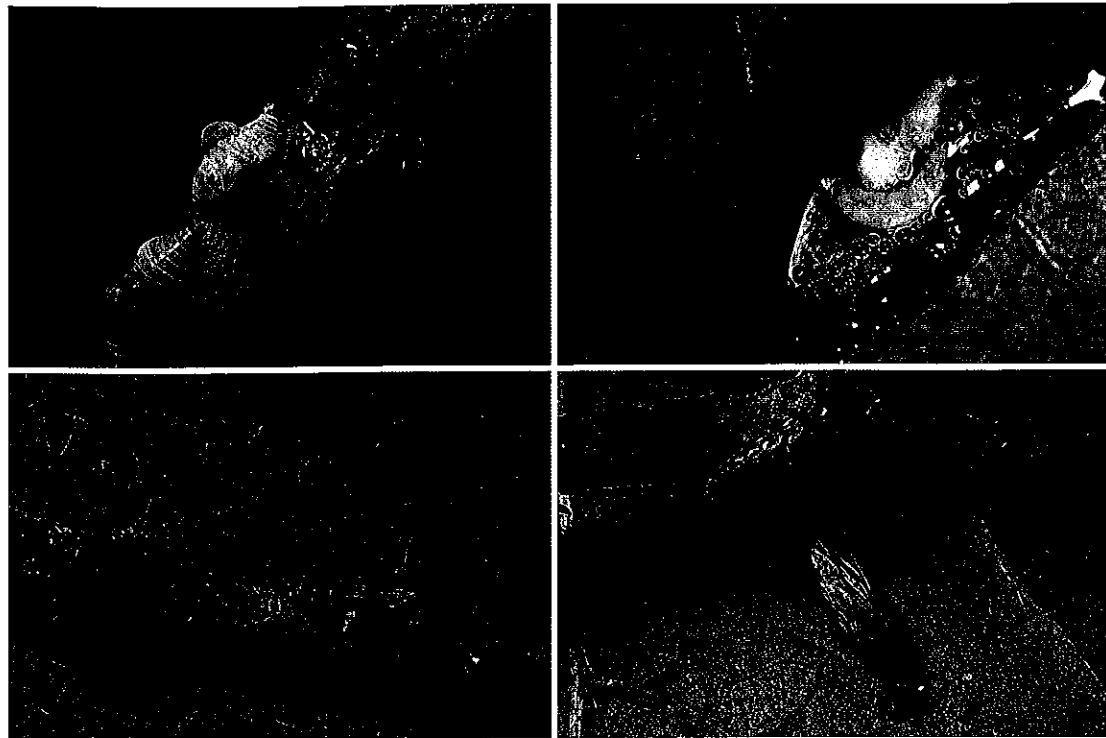
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Life history of the eastern North American species, *Cladochaeta inversa*, with the alder spittlebug, *Clastoptera obtusa*. **Top** (left): Three spittlebug nymphs, middle one with fly larva. (right): Nymph with mature fly larva. **Bottom**: Newly eclosed adult fly. (Photos by Steve Marshall, University of Guelph)

## ABSTRACT

Species of the New World genus *Cladochaeta* are revised, and the natural history of several of them is presented. From 14 described species in the genus, there now are 119 total, based on 105 new species, primarily Neotropical. The distributions of the three described species of North American *Cladochaeta* (*floridana*, *inversa*, and *sturtevantii*) are detailed for the first time. Four new North American species are described: *C. wilhansoni*, from Utah; *C. dracula* and *C. heedi*, both from Arizona; and *C. florinversa*, from southern Florida.

The newly described Neotropical species are the following: *abarista*, *abbrevifusca*, *abeja*, *abrupta*, *adusta*, *akantha*, *albifrons*, *ambidextra*, *amblyharpa*, *antalba*, *aquila*, *arthrostyla*, *austrinversa*, *bispina*, *brunnea*, *calvovis*, *carinata*, *centetor*, *chaeta*, *chelifera*, *crassa*, *dejecta*, *devriesi*, *dextra*, *dikra*, *diminuta*, *dolichofrons*, *dominicana*, *dominitica*, *ectopia*, *erecta*, *fasciata*, *fuscora*, *genuinus*, *glans*, *glapica*, *hadruncu*, *hamula*, *hermani*, *hodita*, *howdeni*, *incessa*, *inornata*, *jamaicensis*, *janzeni*, *labidia*, *laevacerca*, *longistyla*, *masneri*, *mathisi*, *mexinversa*, *mystaca*, *neblina*, *neoinversa*, *neosimplex*, *obscura*, *obunca*, *onyx*, *ostia*, *paravolsella*, *paulhansoni*, *polia*, *proctobarba*, *propenicula*, *pruinopleura*, *pseudikra*, *pseudunca*, *psychotria*, *ranhyae*, *reversa*, *robusta*, *santana*, *sclerostyla*, *sepia*, *sicula*, *similex*, *simplex*, *spinacosta*, *spinula*, *spira*, *starki*, *sternospina*, *telescopica*, *tepui*, *tica*, *trauma*, *tricerabops*, *tripunctata*, *tubula*, *unca*, *vapida*, *venebula*, *verdifrons*, *vermes*, *vittata*, *vivipara*, *volsella*, *vomica*, *wirthi*, *yanomama*, and *zurquia*. Grimaldi and Nguyen are the authors of all newly described species. *Cladochaeta taeniatipennis* (Duda) and *C. peruviana* (Duda) are transferred to *Cladochaeta* from the genus *Diathoneura*, the former species being the type species of *Diathoneura*.

Illustrations and discussions of the adult diagnostic features of each species are provided, as are distributions. Female terminalia are plesiomorphic to most Drosophilinae by lacking pegs on the oviscapt, and variation in the terminal sternites and tergites of females was found to be as species-specific as male genitalia. Females have non-sclerotized sperm receptacles (apparently the ventral receptacles), but no diagnostic variation was found in these structures. Male genitalia provided most characters for classification of species in the genus, which is basically a system of species groups as presented here.

Larvae of *C. inversa* and *C. floridana* are described and illustrated. They are highly modified for acalyptrate Diptera by possessing 6 pairs of prolegs, each with a rosette of creeping welt spinules; the cephalopharyngeal skeleton is unsclerotized, except for the minute, very sharp mandibular hooks; and the posterior pair of spiracles is very long and telescoping, adapting the larva to being submerged in spittle. Five Neotropical species are recorded as being viviparous.

Host records are summarized, and various new ones presented. Hosts are almost always spittlebug nymphs (Auchenorrhyncha: Cercopidae). A larva of *Cladochaeta* attaches itself to the dorsum of its host's abdomen, where it makes minute holes presumably for feeding on hemolymph. An ephydrid is reported as living in the spittle masses of the cercopid, *Tomaspis inca*, in Costa Rica; it is saprophagous, not parasitic; this is a habit previously unknown for that family. Several records of adventitious spittlebug associations in the Drosophilidae are also reported. In lieu of experimental data, all evidence indicates that the larvae of *Cladochaeta* are parasitic.

The great increase in species diversity makes this group the most speciose genus of Drosophilidae endemic to the Western Hemisphere.

## INTRODUCTION

The Drosophilidae are among the most ecologically diverse Diptera in terms of their breeding habits. There are species that breed in decaying fruits and cacti, highly toxic mushrooms, living flowers, and even in the nephric exudates of land crabs. Some species mine leaves and stems, and others are predators of frog eggs, sessile homopterans, blackfly larvae, or spider eggs. The saprophytic habit is clearly ancestral for the family, and also the most common habit, which

makes those species whose larvae are intimately associated with spittlebugs of such unusual interest.

The association of drosophilid larvae from the New World with spittlebug nymphs has been known for some 60 years. Despite all this time, there is still some controversy over whether the larvae of *Cladochaeta* are parasites or inquiline, the latter being an association having no effect on the host. Our interest in these flies began, in fact, as a result

of their bizarre life histories. Experiments are the best way to assess whether fly larvae are parasitic or just inquilines, but these have proven to be too difficult to perform thus far. Although we have little to contribute toward experimentally proving parasitism of the larvae, the morphological and behavioral evidence strongly favors that interpretation. Questions arose during our work: Are the spittlebug parasites a monophyletic group, or has the habit evolved several times? How closely associated are *Cladochaeta* and certain spittlebug species (e.g., do their ranges overlap closely)? What is an ancestral habit that led to this parasitism? Knowing that scores of undescribed species existed and that distributions were not at all documented made any phylogenetic and biogeographic work premature. Thus, a thorough revision of the genus was in order.

Like the true habits of the larvae, the taxonomic history of the genus *Cladochaeta* has also been somewhat controversial in drosophilid systematics. In 1900 the genus was erected by the Smithsonian dipterist D. W. Coquillett (1856–1911) for the Neotropical species *C. nebulosa*. The generic name reflected the fact that this species has a single branch on the arista. When J. R. Malloch described *Clastopteromyia* in 1924, for the eastern North American species *inversa*, he named the genus for the bizarre habit of the larva. The name *Clastopteromyia* has been used virtually synonymously with *Cladochaeta* until fairly recently (e.g., Pipkin, 1966), and it was not until the paper by Wheeler and Takada (1971) that *Clastopteromyia* was recognized as a junior synonym of *Cladochaeta*. Alfred Sturtevant, despite his insightful and seminal work (e.g., Sturtevant, 1921), gave little attention to *Cladochaeta*. Frota-Pessoa (1947) worked on the genus, but almost solely on Brazilian species; he placed most of the species in the Neotropical genus *Diathoneura*. Wheeler and Takada (1971) recognized the close relationship between *Cladochaeta* and *Diathoneura*, and agreed with Frota-Pessoa that limits of the 2 genera were not apparent. Later, in the world catalog of drosophilids, Wheeler (1981) was uncertain as to the generic position of many species of *Cladochaeta* and *Diathoneura*. Grimaldi (1990) outlined the

morphological and phylogenetic evidence of a sister-group relationship between *Cladochaeta* and *Diathoneura*. Lastly, Vilela and Bächli (1990) provided a diagnosis for a monophyletic genus *Cladochaeta*, in which they included 13 described species. The basis of their work was a restudy of the type specimens. Here, we report more than 100 additional new species for the genus.

## MATERIALS AND METHODS

Individual specimens were first sorted into gross morphospecies on the basis of external characteristics. Genitalia were then dissected where individuals showed sufficiently distinct or consistent differences. Individuals from different localities were routinely dissected, even if they were externally indistinguishable. All dissected specimens were given unique, consecutive numbers (up to no. 325); these numbers are provided under each species account. Dissection techniques were described elsewhere (Grimaldi, 1987); genitalia were mounted on microscope slides using the glycerine jelly technique. Generally, an oblique terminal and a full lateral view of the male genitalia were observed and illustrated. We broke with traditional illustration methods by rendering male genitalia with pen-and-ink and pencil drawings. This was necessary to best portray depth and spatial relationships for these complicated structures, as well as the degree of sclerotization of various lobes.

Morphological terminology follows Grimaldi (1990) with one exception. In that monograph, the paraphyses of *Cladochaeta* were erroneously referred to as surstyli. In the present study, we tried to decipher variation in female terminalia, not just male terminalia, with the result that species were found to be as diagnosable on the basis of female genitalia as for male genitalia. However, only in cases where the species possessed distinctive external features (presumably shared by both sexes) was the description of a new species made using only female specimens. Also, females are known for only about half of the species. Species-level taxonomy is more stable if based on a set of characters comparable among them all—in this case, the highly elaborate male genitalia.



Male and female flies collected at the same spot were generally associated as conspecifics on the basis of color (especially of the pleura), wing pattern, arisal branching pattern, and proportions of the head.

Certain proportions of the head were found to be diagnostic after gross visual comparisons, and these were then measured for the reliability of the differences. These proportions (being the greatest distance for each measurement) were cheek depth (CD), eye depth (ED), face width (FW), and head width (HW). Thorax length (ThL), from the anterior margin of the notum to the posterior tip of the scutellum, was measured as a general index of body size. CD, ED, and ThL were measured in lateral view; the other 2 distances were measured in frontal view. Measurements were made with a Zeiss SV8 stereomicroscope and a digital stage micrometer. Since measurement error of the micrometer was  $\pm 0.0001$  mm, most of the error resulted from slight distortions of the specimens, positioning of specimens during measurement, and crosshair alignment. Thus, 2 measurements of each specimen were taken, with the second measurement taken after the specimen was removed from the mount and repositioned in it. Each individual value is an average of the 2 measurements. Mean and range of the measurements are given, and where five or more individuals of the same sex of a species were measured, the standard error is also given. Ratios of CD/ED and FW/HW were calculated. Approximately 6400 measurements were taken for this study; they are cited in the species accounts where diagnostic and are summarized in the Appendix. All measurements are in millimeters.

Cladistic analyses of the relationships of species and species groups would be extremely premature at this point. As we discuss at the end of this monograph, there are an estimated 800 species of *Cladochaeta*, but only 122 species (15%) are named and described. Given the dramatic effects that missing taxa and characters have on cladistic analyses, it is most prudent to consider phylogenetic relationships when the fauna is better surveyed. We have, however, included comments under certain species accounts of possible relationships among species based on

obviously homologous features. Likewise, we have not included a key to the species, for several reasons. First, virtually all species require dissection of genitalia for accurate identification, and the best way to confirm a species identity is to simply compare the dissections with the illustrations. Second, such a key would be very tedious to use with so many genitalic characters. Third, the key will become quickly out of date as new species are described.

**COLLECTING TECHNIQUES:** The methods that appear most effective in obtaining specimens are (1) sweeping understory vegetation with a fine net and (2) Malaise (Flight Intercept) traps. Given the opportunity, searching for larvae in spittle masses and enclosing the spittle mass with a bag of fine mesh is an excellent approach. The bags must be routinely checked for emergent flies. Some fine series of specimens were also obtained in samples of canopyfogging and UV-light traps. Specimens are best preserved in 70% ethanol, then critical-point dried (to prevent collapse) and glued to points on pins. Generally, *Cladochaeta* can be found in any vegetated areas where cercopids are likely to be found; however, at least in the tropics, there seems to be a rough correlation between the number of *Cladochaeta* species and the floristic diversity and age of the forest.

#### ACKNOWLEDGMENTS

Numerous people have been extremely helpful as a source of information and specimens; for their efforts we are extremely grateful. We thank Vinton Thompson (Roosevelt University, Chicago: specimens and host information); Daniel Hilburn (Dept. of Agriculture and Fisheries, Bermuda: specimens and host information from Bermuda); Karl Valley and Al Wheeler (Pennsylvania Dept. of Agriculture: larval and adult specimens and host information from Pennsylvania and Florida); Al Wheeler also provided published and unpublished information on *Scaptomyza* in *Lepyronia* spittle masses); Tom Eisner (Section of Neurobiology and Behavior, Cornell University: larval specimens and host information from Arizona); Wilford Hanson (Entomology Dept., Utah

State University: a large series of adults from the western U.S. and Central America); Wayne Mathis and Hollis Williams (Entomology Dept., Smithsonian Institution: loaned a large series of adults from the USNM collection); and Brian Pitkin and Laszlo Papp (The Natural History Museum, London, and the Hungarian Natural History Museum, Budapest; respectively: loans of holotypes). Chen Young (Carnegie Museum), Jeff Cumming (Biosystematics Research Centre, Ottawa), and Paul H. Arnaud, Jr. (California Academy of Sciences, San Francisco) loaned many interesting specimens from those collections. Ben Foote (Kent State University, Ohio) kindly provided extensive data on the phenology of *Cladochaeta inversa* in Ohio, and Steve Marshall (University Guelph, Ontario) provided additional notes on the life history of *C. inversa* in Ontario.

Henk Wolda (Smithsonian Tropical Research Institute, Panama) allowed DG to spend many tedious hours screening through his Chiriqui light-trap samples, and the Malaise trap samples from Paul Hanson (University Costa Rica, San José) were an equally valuable source of specimens. Kyle Harms (Princeton University) provided a valuable, small series of specimens reared in Monteverde, Costa Rica. Peling Fong-Melville (AMNH) assisted with the scanning electron microscopy, and Sally Goodman rendered the final genitalic illustrations of about 20 species. The beautiful map of South America, produced at the Smithsonian Institution,

was kindly provided by Wayne Mathis. Field research on *Cladochaeta inversa* in New York was funded by a grant to D. G. from the Black Rock Forest Consortium.

We are especially grateful to Gerhard Bächli, Wayne Mathis, and Steve Marshall for having waded through the original manuscript and providing us with detailed comments and editorial changes. Their advice greatly improved the monograph.

For the many others not mentioned here, we have acknowledged their contributions under the accounts of various species named after them.

#### COLLECTIONS, DEPOSITORIES, AND ACRONYMS

AMNH	American Museum of Natural History, New York
CAS	California Academy of Sciences, San Francisco
CMNH	Carnegie Museum of Natural History, Pittsburgh
CNC	Canadian National Collection, Ottawa
HNHM	Hungarian Natural History Museum, Budapest
INBio	Instituto Nacional da Biodiversidad, San José
NHM	Natural History Museum, London
NMNH	National Museum of Natural History, Washington, D.C.
USU	Utah State University, Logan, Utah.

Specimens from the Museu da Zoologia, Universidade da São Paulo, Brazil, were not available for study. Very few specimens from Brazil were, in fact, studied for this project, so there is a huge gap in our knowledge of *Cladochaeta* from this area of the neotropics.

#### TAXONOMY AND DISTRIBUTIONS

##### GENUS *CLADOCHAETA*

*Cladochaeta* Coquillett, 1900: 263. Type species: *C. nebulosa* Coq. 1900.

*Clastopteromyia* Malloch, 1924: 31. Type species: *Drosophila inversa* Walker, 1861.

*Cladochaeta*: Wheeler and Takada, 1971: 232 (synonymy of *Clastopteromyia* with *Cladochaeta*).

**DIAGNOSIS:** Face without carina or with shallow carina. Arista with a single ventral branch, at apex (except for in *C. taeniatipennis*) (fig. 1a). Eyes bare or with sparse, thin (not ribbed at SEM magnifications) interfa-

cetal setulae (fig. 1c, d). Frons with dense microtrichia and generally with scattered, fine, inclinate interfrontal setulae (fig. 2a). Proboscis with small, apical fleshy lobe (fig. 2b), as in *Diathoneura*.

**Wings:** Hyaline or with diffuse infuscation, especially in costal region and over cross vein dm-cu and at apex of vein  $R_{2+3}$ . Veins  $A_1 + CuA_2$  and  $A_2$  lost or extremely vestigial. Costal vein extended to apex of vein M, but costal spinules end midway between apices of  $R_{2+3}$  and M. Cross veins bm-br and bm-cu lost; cell br open basally. Notal

coloration light to dark tan, light or dark brown in some species; the abdomen always darker (brown to black), often with diffuse, light median spots or bands. Pleura often with a darker, diffuse brown longitudinal band.

Male genitalia: Cerci without long setae, with only setulae, ventral margins often extended and narrowed ventrad; surstyli clavate, with setulae, but without peg prensisetae (fig. 2c), usually folded ventrad; aedeagus reduced, sometimes to just a U-shaped sclerite, with apical diaphanous membrane; paraphyses elaborately developed into large, hooked, sclerotized structures, with a large, broad dorsal sclerite uniting them; hypandrium usually with ventral keel.

Female genitalia: Oviscapt not developed; terminal sternite (9) either resembling penultimate one or slightly or entirely separated medially, but without narrow anterior bridge and broad lateral surfaces, nor with pegs (fig. 2d). Spermathecal capsule vestigial or absent; ventral receptacle well developed but not sclerotized.

The most important work thus far on this genus is the study of type specimens by Vilela and Bächli (1990). In this study they presented a diagnosis of the genus far superior to any other; some of these characters are

given in the diagnosis above. A careful diagnosis enabled them to draw clear boundaries between *Cladochaeta* and *Diathoneura*. In many respects *Diathoneura* is more modified than *Cladochaeta*, such as in the following characteristics: oviscapt with pegs (the apicalmost one being large in some species); surstyli crescentic, usually with peg prensisetae (seven species lack these pegs); wing with anal lobe but usually the anal veins completely lost.

We disagree with Vilela and Bächli (1990) on the placement of only 2 species: *C. taeniatipennis* Duda and *D. peruviana*, which they placed in *Diathoneura*. Our justification for this transfer is given under the accounts for those species. The former species is the type species of *Diathoneura*, which would imply either that *Diathoneura* be synonymized with *Cladochaeta* or that another type species be designated for the 35 species remaining in *Diathoneura*. The latter option would be far more preferable not only for nomenclatural stability, but because both generic names reflect monophyletic taxa. Grimaldi (1990) described features indicating why *Diathoneura* and *Cladochaeta* were monophyletic sister-groups comprising the tribe Cladochaetini. The tribe is entirely New World in distribution, principally Neotropical.

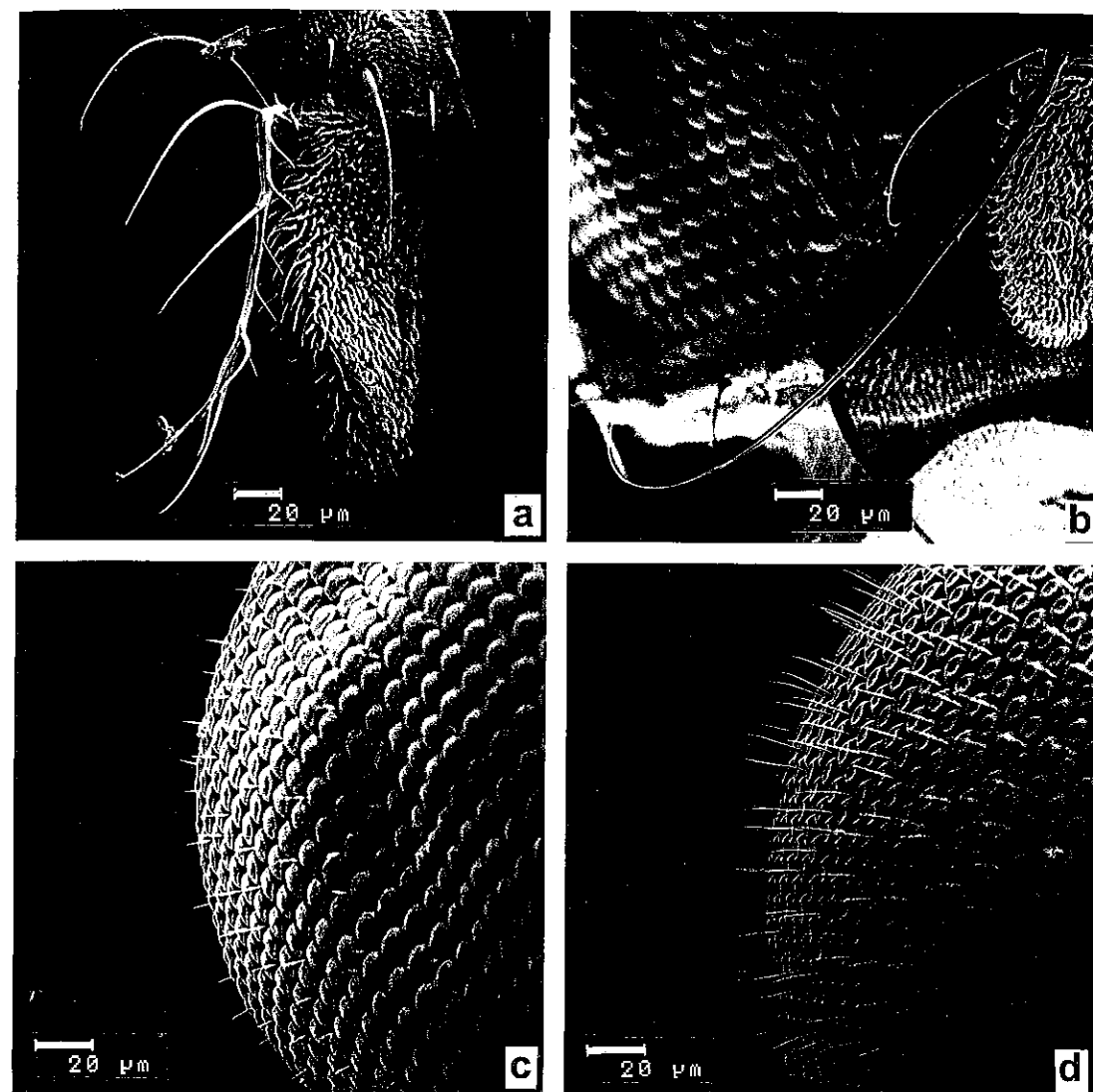


Fig. 1. Scanning electron micrographs of *Cladochaeta* characters. a, b: arista. a. *C. inversa*. b. *C. nebulosa*. c, d: eyes, with interfacetal setulae. c. *C. nebulosa*. d. *C. inversa*.

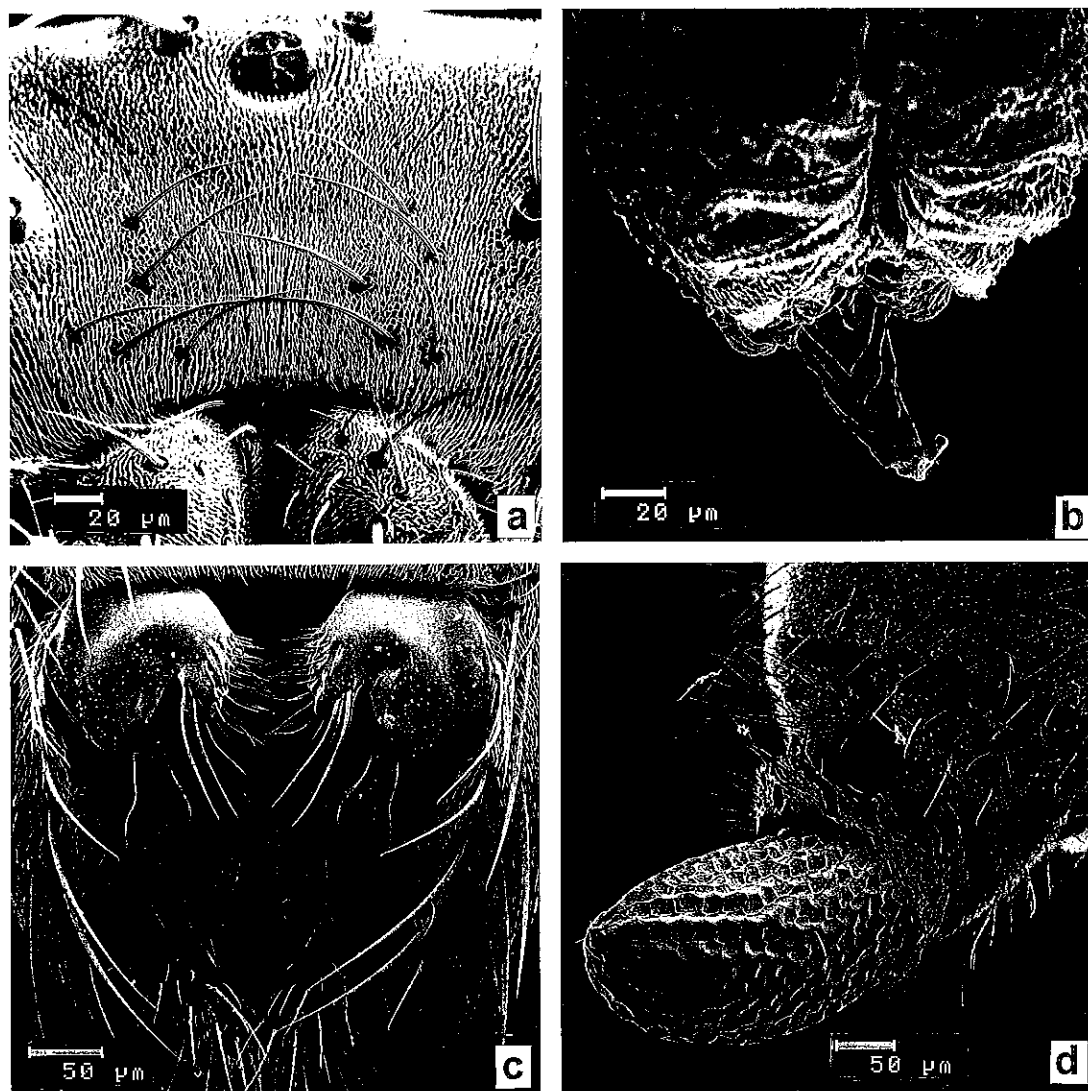


Fig. 2. Scanning electron micrographs of *Cladochaeta* characters. **a.** frons of *C. inversa*. **b.** tip of labellum, *C. nebulosa*. **c.** external male genitalia, *C. inversa*. **d.** oviscapt with egg, *C. nebulosa*.

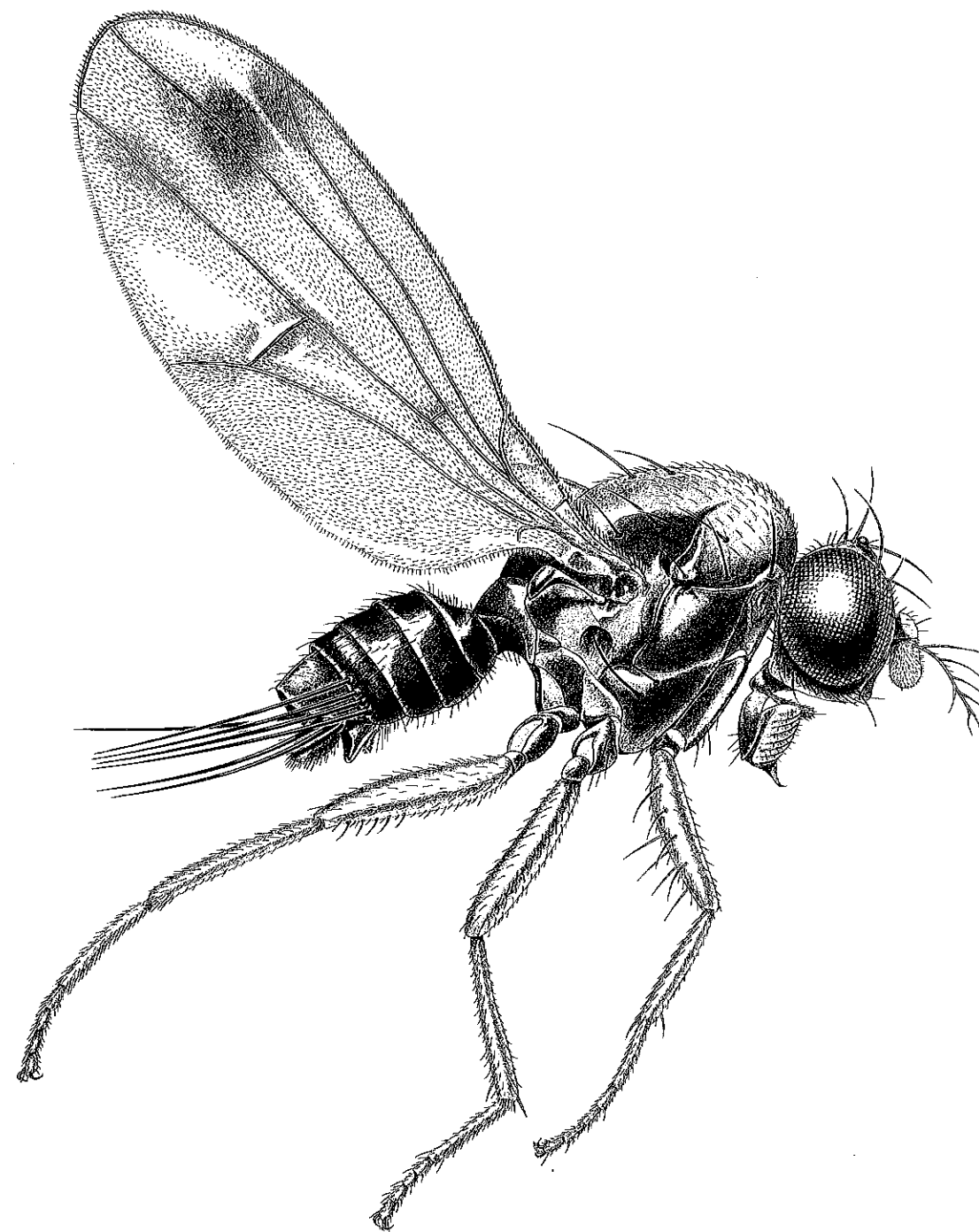


Fig. 3. Lateral habitus of *C. bomplandi*.

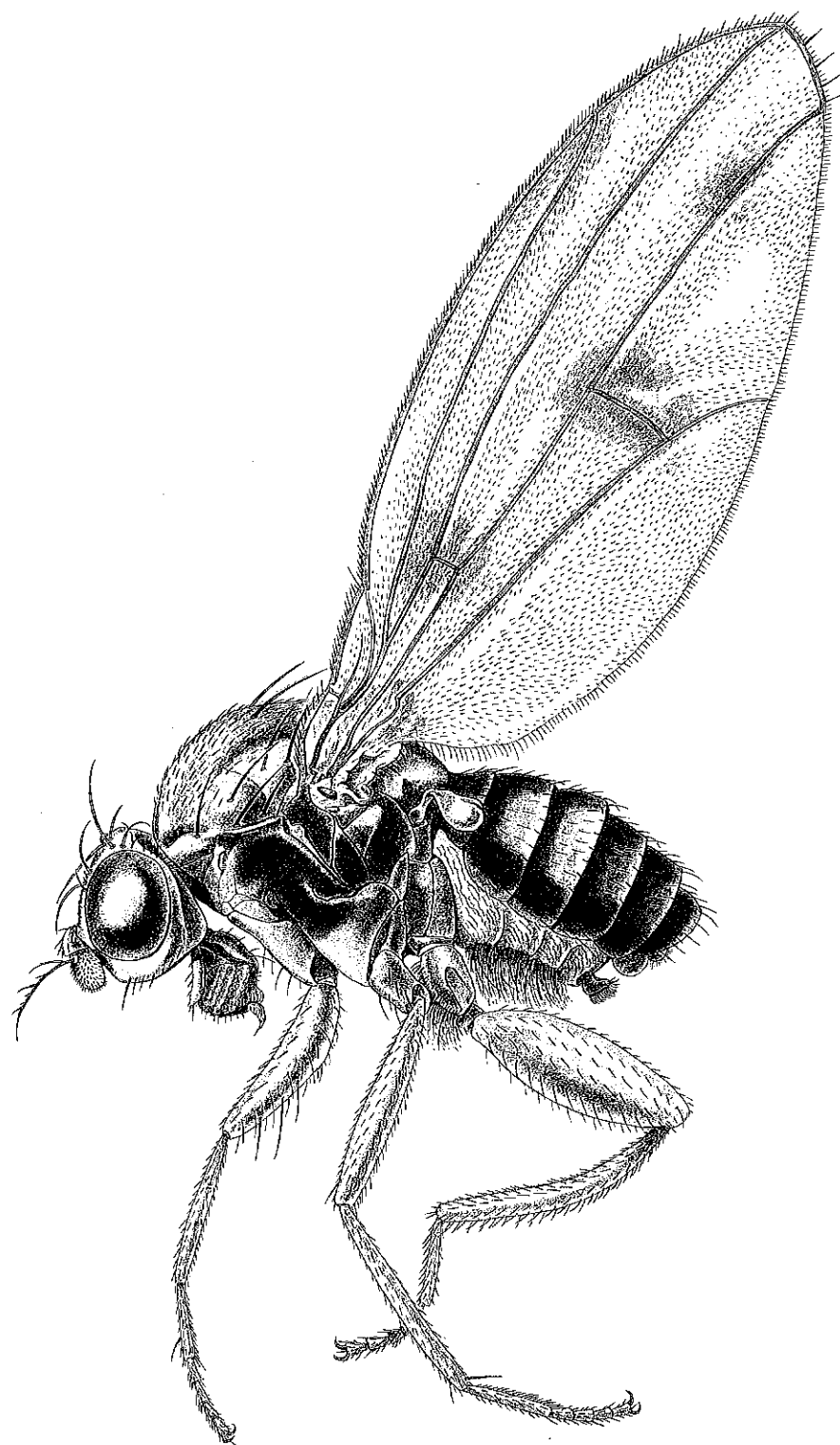


Fig. 4. Lateral habitus of *C. crassa*, n. sp.

### NEBULOSA SPECIES GROUP

DIAGNOSIS: Antenna with arista bare, only one dorsal branch (except in 3 species: *ectopia*, *floridana*, and *wirthi*). Most species with at least clouds on crossveins, often also with large clouds on distal third and costal margin of wing. Male genitalia distinctive: aedeagus a laterally flattened, usually entirely membranous lobe, flanked by sclerotized paraphyses that are usually long, thin, and asymmetrical. Female terminalia with apical tergite always devoid of setae; apical sternite always bilobed and often completely divided, each lobe with about 8–10 fine setulae.

#### *Cladochaeta adumbrata* (Duda)

Figure 13

*Diathoneura adumbrata* Duda, 1925: 178; Wheeler, 1963: 54.

DIAGNOSIS: Head and notum generally tan to yellow, with pleuron brownish; wing with light infuscation overall, darker clouds on x-veins; male genitalia with paraphyses sclerotized, left one well developed, right one vestigial and without hooked, ventral portion.

DESCRIPTION: HEAD: Eyes with very sparse, very short, fine setulae (seemingly bare); greatest length of eye (in lateral view) in line with greatest depth of head. Head of moderate length (HL/HD = 0.85). Pedicel and flagellomere I uniformly brown. Arista with just basal branch, without small branches on main branch. Front brown (yellow in some females) and of moderate length (measurements). Frontal-orbital setae: Proclinate not midway along length of frons, slightly closer to ptilinal suture; anterior reclinate small, ca. 3× the length of frontal-orbital setulae, slightly posterolateral to proclinate and midway between 2 large ipsilateral orbitals; posterior reclinate equal in size to proclinate; post. reclinate slightly closer to ipsilateral proclinate or midway between it and inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face brown (yellow in some females), all with oral margin and cheeks light to dark brown; face of moderate width (FW/HW = 0.33 [N = 6]). Cheeks extremely shallow (CD/ED = 0.09).

THORAX: Notum and scutellum evenly

brown (yellow in females). Anterior dorso-centrals 0.7× the length of posterior dorso-centrals; posterior dorsocentrals much closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 4–6 irregular rows. Anterior scutellars slightly parallel, close to base of scutellum; posterior scutellars cruciate for about one-fourth their length. Pleuron brown, with some small lighter areas, especially ventral tip of katepisternum. One large postpronotal lobe setae; anterior katepisternal seta one-half the size of posterior katepisternal seta. Legs almost all yellow; forecoxa light brown; forefemur with 3 long lateral and 2 long ventral setae. Halter light brown (yellow in females). Wing with light, diffuse infuscation. Infuscation very light on costal edge and apical third of wing, over vein  $R_{4+5}$ ; darkest as small clouds surrounding x-veins r-m and dm-cu, cloud on dm-cu barely extended to vein  $CuA_1$ . Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly bent.

ABDOMEN: Female terminalia with penultimate tergite incomplete dorsally; apical tergite with thin, kinked bridge between epi/hypoproct and apical sternite. Apical sternite bilobed, with ventral floor connecting them. Diamond-shaped window between sternite and tergal bridge. Male genitalia: Cercus with long, thin ventral lobe, directed ventrad; anteromesal margin of cercus turned very slightly inward. Epandrium taller than wide, height ca. 1.5× width. Ventrolateral halves of epandrium (epandrial lobes) not long and narrow, expanded in middle then tapered apicad; with row of 6 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphyses heavily sclerotized, with left one fully developed (covering entire length of aedeagus) and strongly hooked; right one vestigial. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium narrow, with deep ventral keel; gonopods forming a "Y" with hypandrium, arms of gonopods deep and laterally flattened with keel along basal part of ventral margin. Surstyli irregular in shape; short, broad, with outer surface bearing ca. 50 fine setulae. Apical sternites not examined.

TYPES: Holotype, Male: COSTA RICA: La Suiza de Turrialba, 31/III/21, in the HHNM.

The type was dissected and illustrated by Vi-lela and Bächli (1990: fig. 4A-M). The species was previously known only from the holotype, to which we can now add the females and additional male records.

OTHER MATERIAL EXAMINED: COSTA RICA: *Limon*: Ambri (Talamanca), 26/VII/75, W. J. Hanson, 3♂, 2♀; 1♂ (DAG no. 45), 1♀ (DAG no. 46) with genitalia dissected; dissected male in the AMNH, others in the UTSC. PANAMA: *Chiriqui*: David, 2200 ft, 24/VII/64, A. Broce, light trap (1♂, no. 212; 1♀, not dissected) (NMNH).

*Cladochaeta ambidextra*, new species

Figures 5, 14

DIAGNOSIS: Body yellowish; male genitalia most distinctive: paraphyses sclerotized, relatively long and equally well developed; surstyli large, clavate, with row of stiff setae on one edge.

DESCRIPTION: HEAD: Eyes completely bare; greatest length of eye oblique in lateral view. Head relatively long (HL/HD = 0.90). Pedicel dark brown, flagellomere I with anterior surface dark brown; remainder of antenna yellow. Arista with just basal branch, without small branches on trunk. Front yellow, long and sloping. Frontal-orbital setae: Procline orbitals midway along length of frons; anterior reclinate very small, ca. 2× the length of frontal-orbital setulae, just posterolateral to procline; posterior reclinate equal in size to procline, midway between ipsilateral procline and inner vertical seta. Inner vertical seta in line with ipsilateral procline and post. reclinate. Face yellow, including oral margin; wide (FW/HW = 0.33). Cheeks yellow and of moderate depth (CD/ED = 0.20 [holotype]).

THORAX: Notum and scutellum yellow. Anterior dorsocentrals 0.7× the length of posterior dorsocentrals; posterior dorsocentrals slightly closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellars slightly divergent, close to base of scutellum; posterior scutellars cruciate for one-fourth their length. Pleuron yellow. One large postpronotal lobe setae; anterior katepisternal seta one-half the size of posterior katepisternal seta. Legs entirely yellow; forefemur with lateroventral

row of 3 long setae and dorsolateral row of 5 setae (most proximal and distal ones longest). Halter all yellow. Wing patterning unknown (wing is shredded on the only known specimen, only the costal edge remains).

ABDOMEN: Female terminalia unknown. Male genitalia: Cercus with thin ventral lobe, turned laterad; anteromesal margin of cercus turned inward. Epandrium taller than wide, height ca. 2× width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, slightly tapered, with row of 4–5 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphysis heavily sclerotized and about equally developed, length extended to end of epandrium; left one with more curvature. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium (narrow?); gonopods forming a "Y" with hypandrium, arms of gonopods narrow and with slight keel along ventral margin. Surstyli clavate with broad, flat apical surface bearing ca. 30 stiff setulae on perimeter of apical surface, with ones on dorsal surface longer and denser. Apical sternites not examined.

TYPE: Holotype, Male: MEXICO: *Chiapas*: 7 mi SE San Cristobal, 28/V/69, 7000 ft, H. J. Teskey. Genitalia dissected (DAG no. 34), in the CNC. Specimen is quite greasy, making the true hues of the yellow body coloration difficult to discern.

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Latin *dextra* (right-handed) and *ambi* (both), referring to equal development of both paraphyses in the male genitalia.

*Cladochaeta bupeo*, new species

Figures 5, 7, 10, 15

DIAGNOSIS: Body generally light and yellowish, with dark brown areas on ventral parts of thorax (in males); aedeagus very large and laterally flattened (externally very visible); left paraphysis tightly curled, right paraphysis very long and thin.

DESCRIPTION: HEAD: Eyes with very sparse, short, fine setulae; greatest length of eye oblique in lateral view. Head of moderate length (HL/HD = 0.82 [holotype]). Pedicel

and flagellomere I yellow. Arista with just basal branch, without small branches on main branch. Front yellow and of moderate length. Frontal-orbital setae: Proclinate midway along length of frons; anterior reclinate small, ca. 3× the length of frontal-orbital setulae, slightly posterolateral to procline; posterior reclinate equal in size to procline, midway between ipsilateral procline and inner vertical seta. Inner vertical seta in line with ipsilateral procline and post. reclinate. Face yellow, including oral margin; relatively narrow (FW/HW = 0.30 [N = 14]). Cheeks yellow and of moderate depth (CD/ED = 0.10). Probsocis and palps entirely light yellow in females, yellow to dark brown in males.

THORAX: Notum and scutellum yellow. Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentrals much closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 6 irregular rows; acrostichal immediately anterior to ant. dorsocentral seta enlarged, ca. 2× the length of other acrostichals. Anterior scutellars slightly parallel, close to base of scutellum; posterior scutellars barely cruciate. Pleuron entirely yellow in females. Pleuron mostly yellow in males, but with diffuse, light brown stripe running through middle of propisternum and anepisternum; anterior half of katepisternum (to which forecoxa adpresses) dark brown to black in parts of some specimens; apical half of forecoxa dark brown; prosternum brown. One large postpronotal lobe setae; anterior katepisternal seta one-half the size of posterior katepisternal seta. Legs entirely yellow (except dark forecoxa in males); forefemur with 2 long ventrolateral and 2 long dorsolateral setae (smaller other ones). Halter all yellow. Wing with vein  $R_{2+3}$  slightly sinuous (not straight); apex of wing more rounded than pointed; veins  $R_{4+5}$  and M parallel; x-vein dm-cu straight, nearly perpendicular to vein M. Slight infuscation at apex of wing surrounding apex of vein  $R_{2+3}$  and extended to  $R_{4+5}$ ; small, very light clouds on x-veins r-m and dm-cu; rest of wing hyaline.

ABDOMEN: Female terminalia with apical tergite short, ventral margin distant from apical sternite. Apical sternite divided into pair of small, rounded lobes not connected to

each other. Penultimate tergite an inverted "U" shape. Male genitalia: Cercus with broad, flat ventral lobe, turned slightly laterad. Epandrium taller than wide, height ca. 1.7× the width. Ventrolateral halves of epandrium (epandrial lobes) tapered apicad, with row of 6 stiff long setae. Aedeagus mostly membranous, very large (nearly the size of epandrium) and laterally flat; base flat, flared, with wrinkles. Dorsal rim of aedeagus bent slightly to the left, sclerotized, with groove for right paraphysis. Paraphyses very thin, sclerotized, forming long curving hooks. Left paraphysis most sclerotized at base, very lightly sclerotized apically; wrapped around dorsal and posterior margins of aedeagus, apex almost reaching base of ventral part of aedeagus. Right paraphysis longer, extended well beyond epandrium; more sclerotized than left paraphysis, particularly throughout entire length of paraphysis; distal third of paraphysis turned sharply anteriorly; proximal third of paraphysis presumably fitting into groove on dorsal rim of aedeagus, distal third of paraphysis free of aedeagus. Aedeagal apodeme narrow and troughlike, with small dorsal keel; standing upright and articulating with bases of paraphyses and gonopods. Hypandrium of moderate width, with ventral keel; gonopods considerably narrowed apicad. Surstyli slightly hatchet-shaped, with large apical lobe pointing posteriorly, smaller dorsal lobe, and thin neck; large apical lobe bearing ca. 35 minute setulae on lateral surface and on rim of apical surface. Apical sternites not examined.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Boquete, VIII/58, W. B. Heed et al. (not dissected). Paratypes: Same data, 3♂ (no. 199 and UT slide no. 305), 3♀ (no. 200) (AMNH).

OTHER MATERIAL EXAMINED: PANAMA: *Chiriqui*: David, 24/VII/64, A. Broce, light trap (2♂, 4♀) (NMNH); Cerro Campana, VII/67, W. W. Wirth (3♂) (NMNH).

ETYMOLOGY: Latin prefix *bu*, meaning large, and *peos* (Greek for penis) in reference to the conspicuous aedeagus this species has, which is the largest in the *nebulosa* group.

*Cladochaeta dominicana*, new species

Figures 5, 7, 10, 16

DIAGNOSIS: Wing with dark clouds over apical third of vein  $R_{2+3}$  and x-veins r-m and



dm-cu; pleuron, forecoxa, and sternites dark brown in males (contrasting with yellowish notum); male genitalia with left paraphysis vestigial, right one long, arched, with apex flattened. Surstyli clavate, with row of 4–5 stiff setae on ventral edge.

DESCRIPTION: HEAD: Eyes completely bare; greatest length of eye (in lateral view) in line with greatest depth of head. Head short in lateral view (HL/HD = 0.74). Pedicel ochre, flagellomere I brown. Arista with just basal branch, without small branches on main branch. Front ochre to light brown and of moderate length. Frontal-orbital setae: Proclinate midway along length of frons; anterior reclinate small, ca. 3× the length of frontal-orbital setulae, slightly postero-lateral to proclinate; post. reclinate slightly closer to ipsilateral proclinate than to inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face light brown, lighter than flagellomere I; face narrow (FW/HW = 0.29 [N = 11]). Cheeks yellow; of moderate depth (CD/ED = 0.11).

THORAX: Notum and scutellum evenly yellow to ochre. Anterior dorsocentrals 0.7× the length of posterior dorsocentrals; posterior dorsocentrals much closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 4–6 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral is enlarged, ca. 1.5× length of other acrostichals. Anterior scutellars slightly convergent, close to base of scutellum; posterior scutellars convergent. Pleuron, prosternum and forecoxa dark brown in males, with some small lighter areas, especially ventral tip of katapisternum; pleuron lighter brown in females, with katapisternum entirely yellow and forecoxa almost white. Legs almost all yellow (except dark forecoxa in males); forefemur with 1 long dorsolateral and 1 long ventrolateral setae. Halter yellow. Wing with distinct pattern of infuscation: dark cloud over apical third of vein  $R_{2+3}$ , with much lighter infuscation apical and over  $R_{4+5}$  and apex of vein M; x-veins r-m and dm-cu with dark clouds; dm-cu with cloud extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  turned slightly costad. Veins  $R_{4+5}$  and M slightly divergent. X-vein dm-cu straight.

ABDOMEN: Tergites completely and evenly dark brown in males and females. Female

terminalia with apical tergite having large opening for epi-/hypoproct; tergite without setae, well sclerotized. Ventrolateral lobes of tergite triangular. Apical sternite bilobed, completely divided; each lobe with medial end rounded, bearing ca. 8 long, fine setulae. Male genitalia: Cercus with thin ventral lobe, directed ventrad; anteromesal margin of cercus turned slightly inward. Epandrium taller than wide, height ca. 1.5× the width. Ventrolateral halves of epandrium (epandrial lobes) long but not narrow, expanded slightly in middle then slightly tapered apically with row of 5 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Right paraphysis heavily sclerotized, very long and thin (extended to end of epandrium), bow-shaped. Left paraphysis vestigial: short, with minute apical hook, slightly sclerotized. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium broad, with deep ventral keel. Surstyli clavate; base long and narrow, with club-shaped apex bearing ca. 20 minute setulae on dorsomedial surface and 4 long, stiff, fine setae on ventral surface. Apical sternites not examined.

TYPES: Holotype, Male: HISPANIOLA (DOMINICAN REPUBLIC): *Pedernales Prov.*: 20 km NE Pedernales, 29/II/92, 1500 m, D. Grimaldi & J. Stark (not dissected; in AMNH). Paratypes: 2♂ (1 dissected, no. DAG 268), 6♀, with same labels as holotype (in AMNH); DOMINICAN REPUBLIC: *Pedernales Prov.*: Sr.[Sierra] de Batoruco, "Las Abejas," 1300 m, 17/II/89, L. Masner, cloud forest, 1♂ (dissected, DAG no. 66) (CNC), 1♀ (dissected, DAG no. 65) (CNC); 1♂, "Upper Las Abejas," 38 km NNW Cabo Rojo, 18-09N, 71-38W, 1350 m, 22/VII/90, L. Masner, "sweeping in mesic deciduous forest" (DAG no. 264) (CMNH).

OTHER MATERIAL EXAMINED: DOMINICAN REPUBLIC: *La Vega Prov.*: Paso de la Vaca, Mons. Nouel-Constanza Rd., 1500 m, 27/XII/55, J. Maldonado-Capriles (1♀; dissected, DAG no. 64) (AMNH).

ETYMOLOGY: In reference to the locality of this species, the Dominican Republic.

DISCUSSION: For possible relationships, see discussion under *jamaicensis* and *masneri*.

### *Cladochaeta ectopia*, new species

Figures 5, 7, 10, 17

DIAGNOSIS: Easily recognized, within this group, by arista with 3 short dorsal branches and terminal fork; notum yellowish, pleuron light brown; wing evenly dusky but without clouds; male genitalia distinct: setae on ventral lobe of epandrium in patch, left paraphysis vestigial, right paraphysis very long and looped near dorsal end of aedeagus.

DESCRIPTION: HEAD: Eyes with dense, short, fine setulae; greatest length of eye (in lateral view) in line with greatest depth of head. Head rather long in lateral view (HL/HD = 0.80 [holotype]). Pedicel and flagellomere I light brown. Arista not highly reduced, with 3 short dorsal branches, row of 4–5 minute medial branches, plus apical fork; branch d-1 slightly closer to d-2 than to d-3; apical fork with dorsal branch one-half the length of ventral branch. Front light brown with bluish pruinescence (especially at oblique angles) and of moderate length. Frontal-orbital setae: Proclinate midway between inner vertical and ptilinal suture; anterior reclinate minute, barely distinguishable from frontal-orbital setulae; post. reclinate slightly closer to ipsilateral inner vertical than to proclinate seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face yellowish, relatively narrow (FW/HW = 0.31 [N = 3]). Cheeks yellow and rather shallow (CD/ED = 0.08).

THORAX: Notum and scutellum evenly yellow to ochre. Anterior dorsocentrals 0.6× the length of posterior dorsocentrals; posterior dorsocentrals closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 6 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral not enlarged. Anterior scutellars parallel; posterior scutellars barely cruciate. Pleuron light brown, except for katapisternum (yellow). Legs almost all yellow, including male forecoxae; forefemur with 1 long dorsolateral and 2 long ventrolateral setae. Entire wing lightly and evenly fuscous, without areas of darker infuscation. Membrane with dense microtrichiae, but not so long or dense as in *mathisi*. Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. Apex of

wing not rounded, slightly pointed. X-vein dm-cu straight.

ABDOMEN: Tergites an even, medium brown. Female terminalia: Apical tergite with thin bridge between foramen and sternal concavity, ventrolateral corners broad; concavity above apical sternite is hemispherical. Apical sternite not divided at tip, but basal part divided into 2 lateral arms. Male genitalia: Cercus without thin ventral lobe, ventrolateral corners pointed. Epandrium slightly taller than wide, height ca. 1.2× the width. Ventrolateral halves of epandrium (epandrial lobes) broad, apically truncate; epandrial setae not in row along ventral lobe, but in cluster of 20 fine, long, curved setae (largest one is dorsalmost). Aedeagus slightly sclerotized, pistol-shaped, with shorter lobe projected posteriad, longer lobe directed ventrad. Left paraphysis vestigial; right paraphysis very long and thin. Right paraphysis lightly sclerotized, projected posteriad, then folded sharply and curved downward along left side of aedeagus nearly to apex of aedeagus. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium rounded, with shallow ventral keel. Surstylus a simple lobe; elongate, with numerous fine setulae on apical part of mesal surface. Apical sternites not examined.

TYPE: Holotype, Male: DOMINICA (West Indies): Pont Cassé, 1.7 mi E, 12/III/65, W. W. Wirth (not dissected). Paratypes: DOMINICA: 1♂, Freshwater Lake, 6/III/65 (no. 180); 1♀, Pont Cassé, 10/III/65 (no. 181) (all in NMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Greek *ektopios*, meaning out of place, odd, strange; in reference to apparent relationship in the *nebulosa* group based on genitalia, but not on other characters (e.g., the lack of distinctive, bifurcate arista).

### *Cladochaeta floridana* (Malloch)

Figures 5, 7, 10, 13

*Clastopterymyia floridana* Malloch, 1924: 10.  
*Cladochaeta floridana*; Wheeler and Takada, 1971: 234.

DIAGNOSIS: Arista generally with only one

long basal, dorsal branch, sometimes with several other much shorter ones. Male genitalia: Paraphyses bilaterally symmetrical; surstyli apically blunt, not hooked; hypandrium without large lateral arms.

REDESCRIPTION: HEAD: Eyes virtually bare of fine setulae; greatest length of eye (in lateral view) in line with greatest depth of head. Head of intermediate length in lateral view (HL/HD = 0.80). Pedicel and flagellomere I light brown. Arista not entirely reduced, with row of 6–7 minute branches on medial edge, plus longer branch (ca. 3× the length of small ones) between minute branches 4–5; apical fork very small, with very short dorsal branch. [N.B.: Holotype male and several females in series examined from Gold Head Branch State Park, Florida, mentioned below have 3 relatively long, evenly spaced dorsal branches, without any small medial branches.] Front ochre and of moderate length. Frontal-orbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca. 2× length of frontal-orbital setulae, in line with setulae; post. reclinate closer to proclinate than to inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan and of moderate width (FW/HW = 0.33 [N = 9]). Cheeks yellow and rather shallow (CD/ED = 0.10).

THORAX: Notum and scutellum evenly yellow to ochre. Anterior dorsocentrals 0.7× the length of posterior dorsocentrals; posterior dorsocentrals closer to scutellar margin than to anterior dorsocentrals. Acrostichals in 4 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral enlarged ca. 1.6× length of other acrostichals. Anterior scutellars parallel; posterior scutellars barely cruciate. Pleuron light brown, with some yellow areas. Legs yellow; forefemur with 1 long dorsolateral and 2 long ventrolateral setae. Wing with light, diffuse infuscation. Very light, even wing infuscation over apical two-thirds of vein  $R_{2+3}$  and not meeting vein  $R_{4+5}$  until apical third, then extended down to apex of vein M; small, slightly darker clouds over x-veins r-m and dm-cu; cloud over dm-cu barely extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  turned abruptly costad. Veins  $R_{4+5}$  and M slightly divergent. X-vein dm-cu straight.

ABDOMEN: Female terminalia: Penultimate tergite with deep, thin, inverted U-shaped sclerite. Apical tergite tall and narrow, with round foramen close to dorsal margin. Ventral margin of apical tergite with pointed, sclerotized tooth. Apical sternite divided into pair of narrow, club-shaped structures flanking tooth, with setulae on bulbous tip of "club." Male genitalia: Cercus with broad, flat ventral lobe, directed ventrad, apex slightly curled inward. Epandrium taller than wide, height ca. 1.5× width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, tapered apically, with row of 7 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphyses heavily sclerotized and very strongly hooked. Left paraphysis more developed than right one, about twice the size; left paraphysis extended to end of epandrium. Aedeagal apodeme typical of species group: troughlike, but broad, articulating with bases of paraphyses and hypandrium. Hypandrium oval with concave disk, ventral keel shallow; arms of gonopods short and stout. Surstyli long and slightly clavate; apex triangular in posterior view and slightly broader than neck, with broad, flat apical surface; posteromedial surface with ca. 25 minute setulae, 16 slightly larger, stiff ones on outside margin. Apical sternites not examined.

TYPE: Holotype, Male: FLORIDA: Fort Lauderdale, II/18/19, A. Wetmore. USNM type no. 26699. Dissected and figured by Vilela and Bächli (1990). Male genitalia and other features redescribed here.

OTHER MATERIAL EXAMINED: FLORIDA: *Clay Co.*: Gold Head Branch State Park, F. W. Mead, 22/XII/57 (1♂, 2♀); *Dade Co.*: Hialeah, 19/II/67, C. Stegmaier (2♀); Royal Palm Hammock, Everglades National Park, 19/XII/49, G. S. Walley (1♀); *Hendry Co.*: La Belle, 16/VII/39, Oman (1♀); *Highlands Co.*: Archbold Biological Station, S. W. Frost, 24/I/61 (1♀); Fort Worth (county unknown), Slosson (1♀).

DISCUSSION: Vilela and Bächli (1990) first noted that the species discussed and illustrated by Wheeler and Takada (1971) was undescribed, and not *C. floridana*, as had been mentioned. That species is described here (under the *inversa* group) as *C. florinversa*. *C. floridana* is problematic. The male

genitalia of specimen no. 39 match exactly the type specimen; however, the arista differs considerably, as discussed above. Moreover, there is a third type of arista that appears in Floridian specimens: the true *nebulosa* type (entirely bifurcate, no other branches), which appears in females from Hialeah, Ft. Worth, La Belle, and Royal Palm Hammock (Everglades National Park). Unfortunately, no associated males from these series were available for study.

### *Cladochaeta genuinus*, new species

Figures 5, 7, 10, 18

DIAGNOSIS: Notum yellowish, pleuron very light brown; wing with light infuscation on costal edge, cloud over x-vein dm-cu only. Male genitalia: Left paraphysis small, sharply hooked; right paraphysis long and thin, looped dorsally and pointed downward at apex; surstyli clavate, with broad medial surfaces having numerous fine setulae.

DESCRIPTION: HEAD: Eyes with very sparse, fine setulae; greatest length of eye (in lateral view) in line with greatest depth of head. Head of intermediate length in lateral view (HL/HD = 0.77 [holotype]). Pedicel and flagellomere I light brown. Arista with just basal branch, no minute medial branches. Front ochre and of moderate length. Frontal-orbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca. 2× length of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, rather narrow (FW/HW = 0.31 [N = 20]). Cheeks yellow, somewhat shallow (CD/ED = 0.08).

THORAX: Notum and scutellum evenly tan. Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentral about midway between scutellar margin and ipsilateral anterior dorsocentral, or slightly closer to scutellar margin. Acrostichals in 6 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral not enlarged. Anterior scutellars parallel; posterior scutellars barely cruciate. Pleuron slightly darker than notum. Legs yellow; forefemur with 1 long dorsolateral and 2 long ventrolateral setae. Wing with very light, diffuse infuscation

over entire blade. X-veins r-m and dm-cu with small, slightly darker clouds; cloud over dm-cu barely extended to vein  $CuA_1$ . Apex of vein  $R_{2+3}$  turned abruptly costad. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu straight.

ABDOMEN: Tergites even, light brown. Female terminalia: Apical tergite small, virtually a ring around foramen, with slight ventrolateral lobes. Apical sternite completely divided into pair of lobes, each with flat, lateral arm and bulbous end bearing setulae. Median sclerite ventrally between lobes, with pointed lobe extended dorsad between sternal lobes. Male genitalia: Cercus with deep ventral lobe, turned slightly laterad; anteromesal surface of cercus broad and turned inward, with 4–5 long setulae. Epandrium taller than wide, height ca. 1.7× width. Ventrolateral halves of epandrium (epandrial lobes) tapered apicad; with row of 6 stiff setae. Aedeagus saddle-shaped and apparently membranous but not diaphanous as in many other *nebulosa* group species; no sclerotization; small right flange at ventral part of apex. Paraphyses heavily sclerotized, especially right one (left paraphysis vestigial), which fits into ridge of aedeagus. Right paraphysis thin and long, extended to end of epandrium, with sharp bend near middle and apex projected straight downward. Left paraphysis short, with thin, sharp, strongly curved apical hook. Aedeagal apodeme troughlike, short, with median bulge. Hypandrium oval in full view; gonopods forming a "Y" with hypandrium; arms of gonopods with deep ventral keel and flat dorsal surfaces near apices. Surstyli clavate, with broad, flat apical surface and small knob on proximal end of dorsal surface; bears ca. 50 minute setulae on broad mesal surface, some on dorsal margin, and slightly longer ones on ventral surface. Apical sternites not examined.

TYPES: Holotype: Male: GUATEMALA: Tikal, 13/II/79, G. E. Bohart (in the AMNH). Paratypes: 11 males and females, coll. 13–16/II/79 from same locality as holotype (series split between AMNH and UTSC). Two males (DAG nos. 23, 24), 1 female (DAG no. 25) dissected.

OTHER MATERIAL EXAMINED: CUBA: Havana, I–II/15 (1♂, no. 213; 1♀, no. 214) (NMNH). HONDURAS: F.M.: El Zamorano, XI–XII/70, G. M. Freytag, (\*1♂, no.

162; 1♀) (CAS). EL SALVADOR: San Salvador, 5/XII/53, W. B. Heed (\*2♂; nos. 41, 42). HONDURAS: Roatan Island, 27/II/79, G. E. Bohart (\*2♀), 1/I/80, G. E. Bohart (\*1♀); San Pedro Sula, 23/II/79 (\*3♂); La Ceiba 25/II/79 (1♂, 1♀). MEXICO: Jalisco: Puerto Vallarta, G. E. Bohart, 25/I/84 (2♂), 5–10/XII/85 (1♂), P. H. & M. Arnaud, 1/I/71 (1♂), 31/XII/70 (1♂). Quintana Roo: Cozumel S. Miguel, 29/I/81, G. E. Bohart (\*1♀, no. 30; \*1♂, no. 29, 9 others). Sinaloa: 12 mi S Mazatlan, XII/17/63, L. B. & C. W. O'Brien (\*1♀, no. 33). Tampico: Tampico, XII/5, P. C. Bishop (\*1♂, no. 37). Vera Cruz: Fortin de las Flores, 2/V/85, 925 m, A. Freidberg (\*1♀, no. 32; \*2♂, no. 31), and VI/64, light trap, F. S. Blanton (1♂, no. 207) (NMNH); 15 mi W Tiapacoyan, 28/II/72, F. Parker & D. Miller (1♂, no. 202); Motzorongo, I/1892, H. Osborn (1♂); San Rafael, III/14, Townsend (1♂).

ETYMOLOGY: In reference to genuine or true, regarding the widespread nature of this species and its identity distinct from *nebulosa*. *C. nebulosa* was formerly thought to have been widespread throughout the Caribbean and Central America, but now seems restricted to Puerto Rico.

DISCUSSION: This species ranges from El Salvador to the middle of Mexico.

#### *Cladochaeta hodita*, new species

Figures 5, 7, 11, 19

DIAGNOSIS: Body generally yellowish and otherwise with few distinguishing external characters, best identified on basis of male genitalia: paraphyses sclerotized, left one slightly more developed than right, with acute hook; surstylus simple, lobate, with numerous fine setae over most of surface. Best distinguished from *C. adumbrata* by greater development of right paraphysis and by surstyli. Some specimens have infuscation on the wing along the apical half of radial veins.

DESCRIPTION: HEAD: Eyes completely bare; greatest length of eye (in lateral view) in line with greatest depth of head. Head of intermediate length in lateral view (HL/HD = 0.88 [holotype]). Pedicel and flagellomere I light brown. Arista with just basal branch, no minute medial branches. Front tan and of moderate length (measurements). Frontal-or-

bital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca. 3× length of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, rather narrow (FW/HW = 0.29 [N = 35]). Cheeks yellow and very shallow (CD/ED = 0.08).

THORAX: Notum, scutellum, and pleuron evenly yellow; forecoxa almost white. Anterior dorsocentrals 0.7× the length of posterior dorsocentrals; posterior dorsocentral closer to scutellar margin than to ipsilateral anterior dorsocentral. Acrostichals in 4 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral slightly enlarged. Anterior scutellars parallel; posterior scutellars slightly cruciate. Pleuron same color as notum, not darker; ventromedial area of katepisternum and prosternum dark brown in males (light yellow in females). Legs yellow; forefemur with 1 long dorsolateral and 2 long ventrolateral setae. Wing with very light infuscation on apex and costal edge. Infuscation surrounding apices of veins  $R_{2+3}$ ,  $R_{4+5}$ , and M, with narrow, slightly hyaline windows between these veins. X-veins r-m and dm-cu with small clouds of darker infuscation. Apex of vein  $R_{2+3}$  turned abruptly costad. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu straight.

ABDOMEN: Tergites light brown to dark brown. Female terminalia: Identical in specimens from Panama, Trinidad, and Costa Rica. All sclerites very lightly sclerotized. Apical tergite most sclerotized, ca. 1.5× taller than wide, with small slit in middle, demarcating where apical sternite was fused. Apical sternite with pair of small lobes, but divided very little. Male genitalia: Cercus with long, thin ventral lobe, projected ventrad; anteromesal margin of cercus turned inward. Epandrium taller than wide, height ca. 1.6× the width. Ventrolateral halves of epandrium (epandrial lobes) widest in middle, then tapered apically, with row of 5 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphyses heavily sclerotized and nearly equally developed, left slightly larger. Base of paraphysis stout, apical half strongly hooked and narrow, extended to only about one-half length of aedeagus.

Aedeagal apodeme troughlike, narrow, articulating with bridge between bases of paraphyses and with bases of gonopods; apodeme flared outward in middle. Hypandrium narrow, with shallow ventral keel; arms of gonopods deep and laterally flattened, with flattened dorsal surface. Surstyli simple, lobelike, with slightly pointed apex; bearing ca. 30 minute setulae on outer surface. Apical sternites not examined.

TYPES: Holotype: Male: TRINIDAD: Arima: Blanchisseuse Rd., 2000 ft, 28–31/XII/81, M. S. Adams (genitalia not dissected, in the AMNH). Paratypes: 8 males and females, with same label data as holotype; 1♂ (DAG no. 51), 1♀ (DAG no. 52) dissected. All in the AMNH.

OTHER MATERIAL EXAMINED: COSTA RICA: Guanacaste: Cerro El Hacha, 300 m, V–IX/87, D. H. Janzen, ex: Malaise trap in understory, park loc. 17–52 (13♀, 1 dissected, no. 50); La Suiza de Turrialba, Pablo Schild (no date) (1♂, no. 218; 3♀, no. 219). EL SALVADOR: Laguna de Zapotitan, XII/53, W. B. Heed (10♂, no number indicated; 17♀) (AMNH). NICARAGUA: El Recreo, VI/54, W. B. Heed (3♂, UT no. 56.68) (AMNH). PANAMA: Darien: Patino Pt., 17/VIII/52, F. S. Blanton (5; 1♀ dissected [no. 42]); Canal Zone: Ft. Clayton, 22/IX/52, F. S. Blanton (1♂ dissected, no. 43); Playa Santa Clara, 2/VII/67, W. W. Wirth (1♂, no. 204; 1♀, no. 205) (NMNH). TRINIDAD: Sangre Grande, XII/55, W. B. Heed (1♂, no. 236) (AMNH).

ETYMOLOGY: From Greek *hodites* (traveler), in reference to the widest distribution of all species in the genus.

DISCUSSION: The species probably extends from Trinidad to the Canal Zone in Panama, and perhaps to the northwestern corner of Costa Rica. Unfortunately the Costa Rican specimens are matched only on the basis of the female genitalia, which are exactly like the Trinidadian and Panamanian specimens. It would be important to eventually obtain males of this species from Guanacaste. Variation in the male genitalia is documented in figure 19.

#### *Cladochaeta incesa*, new species

Figure 20

DIAGNOSIS: Indistinguishable from most other species in group; identified best on ba-

sis of male genitalia. Anterior reclinate orbital lateral to proclinate; wing with clouds over both crossveins; male genitalia with right paraphysis long and slightly twisted, left one short, both heavily sclerotized; surstylus clavate, with mesal surface concave and with dorsal, sclerotized tooth, and apical fringe of 8 long setae.

TYPES: Holotype, Male: PANAMA: Chiriqui, VIII/55, W. B. Heed (dissected, no. 55) (in AMNH). Male terminalia of a similar species were figured by Wheeler and Takada (1971), which they identified as *C. infumata* (Duda) (unfortunately, the specimens on which this is based cannot be found). As discussed later, we conclude that *C. infumata* is not in the *nebulosa* group.

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: Derived from *incessant*, referring to the number of *Cladochaeta* species.

#### *Cladochaeta jamaicensis*, new species

Figures 5, 7, 11, 21

DIAGNOSIS: Notum yellowish, pleuron light brown (much darker in some males); wing with very dark clouds on apex of  $R_{2+3}$  and x-vein dm-cu. Male genitalia also similar to *C. dominicana*, distinguished by the following: right paraphysis longer, more sinuous; apical club of surstylus slightly larger, with row of only 3 stiff setae.

DESCRIPTION: HEAD: Eyes completely bare; greatest length of eye (in lateral view) in line with greatest depth of head. Head of intermediate length in lateral view (HL/HD = 0.79 [female paratype]). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, minute remnants of 4–5 medial branches. Front tan and of moderate length (measurements), rather narrow. Frontal-orbital setae: Proclinate midway between ptilinal suture and ipsilateral inner vertical seta; anterior reclinate larger than in most species, about one-third the length of other orbital setae; post. reclinate closer to proclinate than to inner vertical seta. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan and rather narrow (FW/HW = 0.28 [N = 18]). Cheeks yellow and of moderate depth (CD/ED = 0.10).



THORAX: Notum, scutellum, and pleuron evenly tan; forecoxa very light; pleuron slightly darker than notum (even in females), except for katepisternum. Anterior dorsocentrals 0.9× length of posterior dorsocentrals; posterior dorsocentral much closer to scutellar margin than to ipsilateral anterior dorsocentral. Acrostichals in 6 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral enlarged, ca. 2× size of other acrostichals. Anterior scutellars parallel; posterior scutellars slightly cruciate. Legs yellow; forefemur with 1 very long dorsolateral and 2 slightly shorter ventrolateral setae. Halter tan. Wing most similar to *C. dominicana*, with pattern of distinct infuscation: dark cloud over apical third of vein  $R_{2+3}$  (with truncate apical margin), with much lighter infuscation apicad and over apices of  $R_{4+5}$  and vein M; x-veins r-m and dm-cu with dark clouds; dm-cu with cloud extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  turned slightly costad. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu slightly bent.

ABDOMEN: Tergites even, light brown; apical tergite yellow in females. Female terminalia very simple. Apical tergite with narrow bridge between epi-/hypoproct and apical sternite. Apical sternite bilobed; apically separated, connected anteriorly by narrow bridge; pair of apical lobes each with ca. 10 fine, stiff setae. Male genitalia: Cercus with long, thin ventral lobe projected mostly under epandrium; ventral margin of cercus with sclerotized, short, pointed lobe. Epandrium taller than wide, height ca. 1.8× width. Ventrolateral halves of epandrium (epandrial lobes) slightly tapered apically, with row of 5 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphysis heavily sclerotized, right one very well developed and left one vestigial. Right paraphysis very long and thin, curved and slightly twisted, extended slightly beyond end of epandrium. Left paraphysis a simple lobe, with apex not extended beyond outer level of aedeagus. Aedeagal apodeme troughlike, narrow, and long, standing upright with articulations between bases of paraphyses and hypandrium; base of aedeagal apodeme bifid; apex of apodeme curled into a tube. Hypandrium very small, U-shaped; arms of gonopods very long, thin, and rodlike, articulating

into deep notch at base of surstylus. Surstyli clavate, with flared, broad, and flat apical surface; bearing ca. 30 minute setulae on mesal surface; row of 3 long, stiff subapical setae on ventral margin. Apical sternites not examined.

TYPES: Holotype, Male: JAMAICA: Hardwar Gap, 29/VII/66, Howden & Becker (not dissected) (in the CNC). Paratypes: 29 males and females, with same label data as holotype (collecting dates vary: 10/VII, 13/VII, 25/VII, 29/VII), also in the CNC; 2 males and 2 females deposited in the AMNH. One ♀ (DAG no. 68), 1♂ (DAG no. 71) dissected.

OTHER MATERIAL EXAMINED: JAMAICA: Falmouth, IV/60, F. D. Bennett, ex: spittle, *Clastoptera flavidorsa* on *Casuarina* (1♂ dissected) (in AMNH); Hardwar Gap, 10/III/70, Wirth & Farr (1♂, no. 210; 1♀, no. 211) (NMNH).

ETYMOLOGY: In reference to the Jamaican locality of this species.

DISCUSSION: This species appears most closely related to *dominicana* based on the wing with very dark spots at the apex of vein  $R_{2+3}$ , over dm-cu, and with lighter clouds over most of the apex. Both species appear closely related to *masneri* based on the shape of the surstylus.

#### *Cladochaeta masneri*, new species

Figures 6, 8, 11, 21

DIAGNOSIS: Best distinguished externally from other Hispaniolan species based on less developed wing infuscation and overall light body color. Male genitalia: Left paraphysis vestigial, right paraphysis well developed, but not longer than aedeagus; surstylus with unique array of 2–3 rows of short, stiff setae on dorsomedial edge of surstylus.

DESCRIPTION: HEAD: Eyes with sparse, short setulae; greatest length of eye (in lateral view) slightly oblique to line of greatest depth of head. Head of intermediate length in lateral view (HL/HD = 0.82 [holotype]). Pedicel yellow, flagellomere I light ochre. Arista with large basal branch, no vestiges of even minute medial branches. Front tan and of moderate length and width (measurements). Frontalorbital setae: Proclinate midway between ptilinal suture and ipsilateral

inner vertical seta; anterior reclinate very small, barely distinguishable from frontal-orbital setulae, to 2× the size of setulae; post. reclinate midway between inner vertical seta and proclinate. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, rather narrow (FW/HW = 0.29 [N = 2]). Cheeks yellow and of moderate depth (CD/ED = 0.09).

THORAX: Notum, scutellum, and pleuron evenly yellow. Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentral closer to scutellar margin than to ipsilateral anterior dorsocentral. Acrostichals in 6 irregular rows; acrostichal setula immediately anterior to ant. dorsocentral only slightly larger than other acrostichals. Anterior scutellars parallel; posterior scutellars slightly cruciate. Legs yellow; forefemur with row of 3 long dorsolateral setae (on proximal half) and ventrolateral row of 4 long setae (distal half). Halter tan. Apical third of wing with very light pattern of infuscation extended from costal vein to vein M; thin, very slightly hyaline strip between apex of  $R_{2+3}$  and  $R_{4+5}$ ; very slight, small clouds over x-veins dm-cu and r-m. Apex of vein  $R_{2+3}$  turned abruptly costad. Veins  $R_{4+5}$  and M almost perfectly parallel. Crossvein dm-cu slightly bent and slightly oblique to vein  $CuA_1$ .

ABDOMEN: Female terminalia very simple, barely sclerotized; apical tergite with deep bridge between epi-/hypoproct and apical sternite. Apical sternite not divided, but with pair of small lobes, each with ca. 8 fine setulae. Male genitalia: Cercus with long, flat ventral lobe directed ventrad. Epandrium taller than wide, height ca. 1.7× width. Ventrolateral halves of epandrium (epandrial lobes) of equal width along length, slightly tapered at apex, with row of 5 stiff long setae. Aedeagus bulbous and membranous, with slight sclerotization on dorsoapical portion where shallow groove accommodates right paraphysis. Paraphyses heavily sclerotized, left one vestigial, right one very well developed. Right paraphysis long and thin, with length extended almost to end of epandrium and tip bent anteriad. Left paraphysis a simple lobe, not extended even to apical margin of aedeagus. Aedeagal apodeme typically troughlike but very broad, especially

near articulation with paraphyses. Hypandrium of moderate width, with very deep ventral keel; gonopods deep at base, considerably narrowed apicad. Surstyli ca. 2.5× longer than at widest point, with broad, roughly triangular apical surface. Mesal surface with ca. 35 minute setulae; proximal part of dorsal ridge with ca. 25 stout, stiff setulae. Apical sternites not examined.

TYPES: Holotype, Male: HISPANIOLA (HAITI): Kenscoff, 4000 ft, II/56, W. B. Heed. Genitalia dissected (DAG no. 56) (in the AMNH). Paratypes: Same label data as holotype, 1♂, \*1♀ [DAG no. 55], in the AMNH.

OTHER MATERIAL EXAMINED: HISPANIOLA (DOMINICAN REPUBLIC): La Cumbre (Puerto Plata), 21–24/III/78, L. Masner (\*2♀, DAG no. 67) (in CNC).

ETYMOLOGY: Patronym in honor of Lubomir Masner (Biosystematic Research Centre, Ottawa), a premier scientist of insect diversity.

DISCUSSION: This species appears most closely related to 2 other Caribbean species (*dominicana* and *jamaicensis*) based on clavate surstyli with a row of stiff, stout setae at medial edge of the base of the club.

#### *Cladochaeta mathisi*, new species

Figures 6, 8, 22

DIAGNOSIS: Brown body, with slight bluish pruinescence on pedicel and flagellomere I and pleuron; relatively long anterior reclinate orbital seta (nearly one-half length of proclinate); apical scutellar setae cruciate for about half their length; male genitalia with paraphyses stout, very heavily sclerotized; surstyli large, rounded, very setulose, with toothlike lobe.

DESCRIPTION: HEAD: Eyes with very sparse, very short setulae; greatest length of eye (in lateral view) in line with greatest depth of head. Head rather short in lateral view (HL/HD = 0.75 [holotype]). Pedicel and flagellomere I brown, with bluish pruinescence. Arista with large basal branch, no vestiges of even minute medial branches. Front brown and of moderate length and width. Frontal-orbital setae: Proclinate midway between ptilinal suture and ipsilateral inner vertical seta; anterior reclinate relatively large, nearly

one-half the size of proclinate seta; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, fairly wide, and rather high (FW/HW = 0.36). Cheeks yellow and fairly deep (CD/ED = 0.13).

**THORAX:** Notum, scutellum, and pleuron brown; pleuron (especially anepisternum) with slight bluish pruinescence. Anterior dorsocentrals 0.8× the length of posterior dorsocentrals; posterior dorsocentral closer to scutellar margin than to ipsilateral anterior dorsocentral. Acrostichals in 6 even rows; acrostichal setula immediately anterior to ant. dorsocentral ca. 2× the size of other acrostichals. Anterior scutellars parallel; posterior scutellars strongly cruciate (for half their length). Legs even, light brown; forefemur with row of 3 dorsolateral setae, distal one longest (on proximal half), and ventrolateral row of 7 setae (distal 2 setae twice the length of others). Halter light brown. Entire wing evenly and lightly fuscous, with dense covering of microtrichiae giving membrane an hirsute appearance. Slightly darker infuscation over costal edge, extended to apex. X-vein r-m slightly clouded, vein dm-cu with larger, darker cloud barely extended to CuA<sub>1</sub>. Wing infuscation: Veins R<sub>4+5</sub> and M parallel. Crossvein dm-cu straight.

**ABDOMEN:** Female terminalia unknown. Male genitalia: Cercus with ventral lobe tapered to apical point, turned slightly laterad; apex lying under epandrium. Epandrium taller than wide, height ca. 1.5× width. Ventrolateral halves of epandrium (epandrial lobes) tapered, with row of 6 stiff long setae; apex of lobe with concave mesal surface. Aedeagus sclerotized, somewhat tubular, slightly longer than right paraphysis, barely protruding beyond bends in paraphyses. Paraphyses very heavily sclerotized and stout. Left paraphysis acutely hooked, with ventral arm about half the width of basal part; tip of paraphysis bent slightly inward around aedeagus. Right paraphysis of about equal width throughout, apex blunt, lying close to outer rim of aedeagus. Aedeagal apodeme rather short, fairly broad, dorsally scoop-shaped. Hypandrium very broad, with shallow ventral keel; gonopods barely sclerotized. Surstylus sclerotized, mostly round, with broad,

very flat, tooth-shaped medial lobe (devoid of setae); outer surface of surstylus with 60–70 fine, fairly long setae. Apical sternites not examined.

**TYPE:** Holotype, Male: COLOMBIA: *Antioquia*: El Retiro (5 km N), Quebrada Boqueron, 26/II/84, W. N. Mathis (dissected, DAG no. 203) (NMNH).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Named for a friend and esteemed colleague, Wayne Mathis, curator of Diptera at the NMNH, and who collected the only known specimen of this species.

**DISCUSSION:** For possible relationships, see *sclerostyla*.

### *Cladochaeta neblina*, new species

Figures 6, 23

**DIAGNOSIS:** Easily distinguished externally based on even, light brown body color, with anterior half of frons white and contrasting with rest of body; head rather long in lateral view, with face short and sloping backward; cheek very deep; wing hyaline; male genitalia with both paraphyses equally well developed, apex of left paraphysis spatulate; surstylus with medial lobe hooked anteriorly.

**DESCRIPTION:** **HEAD:** Eyes virtually bare; greatest length of eye (in lateral view) oblique to line of greatest depth of head. Head quite long in lateral view (HL/HD = 0.85 [holotype]). Pedicel ochre, flagellomere I brown. Arista with large basal branch, no vestiges of even minute medial branches. Front long and wide; anterior half white, posterodorsal half brown, with diffuse area between. Frontalorbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, only twice the size of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, relatively wide, short, and receding backward (FW/HW = 0.33). Cheeks tan and deep (CD/ED = 0.13 [HT]).

**THORAX:** Notum, scutellum, and pleuron even, light brown. Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentral very close to scutellar margin. Acrostichals in 6 uneven rows; ac-

rostichal setula immediately anterior to ant. dorsocentral barely larger than other acrostichals. Anterior and posterior scutellars parallel. Legs light, even brown; forefemur with 1 dorsolateral seta and 2 ventrolateral setae, all in middle of femur. Halter light brown. Entire wing hyaline, without infuscation. Apex of vein R<sub>2+3</sub> gradually meeting costal vein (not abruptly turned costad). Veins R<sub>4+5</sub> and M virtually parallel. X-vein dm-cu straight.

**ABDOMEN:** Tergites dark, even brown. Female terminalia unknown. Male genitalia: Cercus with short ventrolateral lobe; anteromesal margin of cercus turned slightly inward. Epandrium taller than wide, height ca. 2× the width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, slightly tapered, with row of 4–5 stiff long setae. Aedeagus bulbous and membranous, laterally flattened, no sclerotization; ventral margin extended almost to tip of right paraphysis and slightly beyond ventral margin of epandrium. Both paraphyses heavily sclerotized and about equally developed, with lengths extended beyond ventral margin of epandrium; left paraphysis curved inward (unlike right one, pointed downward), with expanded, leaf-shaped apex. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium with slightly concave anterior margin, very shallow ventral margin, about equal in length to gonopods; gonopods without keel along ventral margin. Surstyli clavate, with broad, flat apical surface; lobe lying along dorsal edge bearing ca. 30 stiff setulae; apex with row of 4 long, stiff setae. Apical sternites not examined.

**TYPE:** Holotype, Male: VENEZUELA: *Amazonas Territory*: Cerro de la Neblina, Camp II, 2100 m, 0°50'N, 65°59'W, 30/I/85, Malaise trap at edge of open bog and *Bonnetia* scrub, W. E. Steiner (dissected, DAG no. 201) (NMNH).

**OTHER MATERIAL EXAMINED:** Known only from the type specimen.

**ETYMOLOGY:** Taken directly from the type and only known locality, Cerro de la Neblina, in southern Venezuela. An intensive survey of the flora and fauna of this, the highest

tepui, was made by several North American and Venezuelan institutions in 1985.

### *Cladochaeta nebulosa* Coquillett

Figures 6, 8, 11, 24

*Cladochaeta nebulosa* Coquillett, 1900: 263; Wheeler, 1957: 103; Wheeler and Takada, 1971 (male genitalia); Vilela & Bächli, 1990: 12 (re-description, description of type female genitalia).

**DIAGNOSIS:** Endemic to Puerto Rico and distinguished externally from sympatric congeners by presence of infuscation on wings, by female genitalia, and especially by male genitalia with both paraphyses equally well developed and apex of surstylus bilobed.

**REDESCRIPTION:** **HEAD:** Eyes virtually bare; greatest length of eye (in lateral view) in line with greatest depth of head. Head of moderate length in lateral view (HL/HD = 0.80). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, no vestiges of even minute medial branches. Front of moderate length and width; evenly tan. Frontal-orbital setae: Proclinate midway between ptilinal suture and ipsilateral inner vertical seta; anterior reclinate relatively large, ca. 2.5× size of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, relatively narrow, of moderate height (FW/HW = 0.33 [N = 5]). Cheeks tan and of moderate depth (CD/ED = 0.09).

**THORAX:** Notum, scutellum, and pleuron evenly tan. Anterior dorsocentrals 0.8× length of posterior dorsocentrals; posterior dorsocentral midway between scutellar margin and anterior dorsocentral. Acrostichals in 6 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral barely larger than other acrostichals. Anterior scutellars parallel; posterior scutellars cruciate for one-third their length. Legs light, even tan; forefemur with 1 dorsolateral seta and 2 ventrolateral setae, on proximal half of femur. Halter light brown. Wing with very light, diffuse infuscation over most of vein R<sub>2+3</sub>, apical third of vein R<sub>4+5</sub> (not reaching to vein M); x-veins r-m and dm-cu with slightly darker, small clouds of infuscation. Apex of vein R<sub>2+3</sub> turned abruptly costad. Veins R<sub>4+5</sub> and

M slightly divergent for apical third. X-vein dm-cu straight.

ABDOMEN: Tergites even, dark brown in males and females. Female terminalia: Apical tergite tall and narrow, no sclerotized bridge between epi-/hypoproct and apical sternite, with narrow slit in this membrane near sternite. Apical sternite bilobed but not divided; each lobe with flat arms slightly projected laterad; lobe with ca. 8 fine setulae. Male genitalia: Cercus and epandrium not available for study. Distal part of aedeagus bulbous and membranous, proximal part slightly sclerotized and tubular. Paraphyses heavily sclerotized and about equally developed, both extended to middle of gonopods. Paraphyses thin, evenly curved. Aedeagal apodeme troughlike, but apex flared where it articulates with base of aedeagus. End of gonopods forked where articulating with bases of gonopods. Hypandrium oval, with shallow ventral keel; arms of gonopods long and thin, tapered apically. Surstyli short, apical end split into 2 thin lobes; both lobes with long, thin, stiff setulae, dorsal one with 2, ventral one with row of 5 (increasing in length apicad). Apical sternites not examined.

TYPE: Holotype, Female: PUERTO RICO: Arroyo, Feb. 1899, August Busck, USNM type no. 4341 (in the NMNH). The genitalia were dissected and the wing removed and slide mounted by Vilela and Bächli (1990); both were illustrated.

OTHER MATERIAL EXAMINED: PUERTO RICO: Bayamon, I/1899, Aug. Busck (\*1 ♀, no. 62); Adjuntas, Guilarte Peak, 13/II/54, J. Maldonado, S. Medina (\*2 ♀, no. 61); Mayaguez, I/1899, Aug. Busck (1 ♀), 1/XI/32, A. S. Harley (1 ♀); Aguadilla, I/1899, Aug. Busck; Vieques I., II/1899, Aug. Busck (1 ♀); no specific locality in Puerto Rico, 14/XI/59, F. D. Bennett, ex: *Clastoptera* spittle (\*1 ♂, no. 63).

DISCUSSION: Identification of the assorted females cited above is based on the match in the genitalia between these and the holotype female. I found no evidence for the presence of a sclerotized strip on the inner wall of the last female tergite in *C. nebulosa*, as is reported by Vilela and Bächli (1990), although the specimens that I examined agree in all other details.

*Cladochaeta pruinopleura*, new species

Figures 6, 25

DIAGNOSIS: Body light brown, with bluish pruinescence on anterior part of pleuron (possibly for males only) and frons; wing long and rather narrow, with obvious infuscation pattern (described below); male genitalia with aedeagus large, somewhat sclerotized; left paraphysis vestigial, right one stout, heavily sclerotized and with pointed apex.

DESCRIPTION: HEAD: Eyes with very sparse, short setulae; greatest length of eye (in lateral view) slightly oblique to line of greatest depth of head. Head quite long in lateral view (HL/HD = 0.85 [holotype]). Pedicel and flagellomere I light brown. Arista with large basal branch, no vestiges of even minute medial branches. Front slightly long, of moderate width; evenly light brown, with light bluish pruinescence in anterior (facial) view. Frontal-orbital setae: Proclinate slightly midway between ptilinal suture and ipsilateral inner vertical seta; anterior reclinate small, ca. 2.5× size of frontal-orbital setulae; post. reclinate slightly closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan and of moderate depth and width (FW/HW = 0.31 [N = 3]). Cheeks tan and of moderate depth (CD/ED = 0.10).

THORAX: Notum and scutellum ochre; pleuron light brown, with light bluish pruinescence, especially on anterior half of anepisternum and on proepisternum (most obvious at an oblique anterior angle). Anterior dorsocentrals 0.7× the length of posterior dorsocentrals; posterior dorsocentral closer to scutellar margin. Acrostichals in 6 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral twice the size of other acrostichals. Anterior scutellars parallel; posterior scutellars cruciate at very tips. Legs yellowish; forefemur with 1 dorsolateral seta and 2 ventrolateral setae, on apical half of femur. Halter light brown. Wing with infuscation over most of costal edge, over vein  $R_{4+5}$ ; extended to vein M but faded apicad. X-vein r-m with very slight infuscation; dm-cu with larger, darker cloud entirely covering the vein. Veins  $R_{4+5}$  and M slightly divergent. X-vein dm-cu slightly bent.

ABDOMEN: Tergites dark, even brown. Female terminalia unknown. Male genitalia: Cercus with thin ventral lobe turned laterad, ventral margin of cercus flat. Epandrium taller than wide, height ca. 1.5× width. Ventrolateral halves of epandrium (epandrial lobes) acutely tapered at apex, with row of 7–8 stiff long setae. Aedeagus large, laterally flattened, slightly sclerotized especially dorsally. Dorsal surface of aedeagus flattened, not curved, with pit, and rim with wide groove (probably to fit right paraphysis). Left paraphysis diminutive, barely sclerotized; apex does not reach to posterior margin of aedeagus. Right paraphysis heavily sclerotized and well developed, length extended nearly to ventral margin of epandrium. Left paraphysis with sharp kink in basal half, apical half nearly straight and tapered to a blunt point. Aedeagal apodeme lightly sclerotized. Hypandrium with deep ventral keel (depth greater toward epandrium); gonopods long, deep, and laterally flat. Surstyli boat-shaped and laterally flat, with tall, flat apical surface; apical surface bearing ca. 100 minute setulae, ventral "elbow" of surstylus with 4 long, fine setae. Apical sternites not examined.

TYPE: Holotype, Male: COLOMBIA: Medellín: Coffee finca, 5000 ft, XI/55, W. B. Heed (not dissected)(AMNH). Paratypes: Same data, 2 males (1 dissected, no. 193)(AMNH).

OTHER MATERIAL EXAMINED: Known only from type series.

ETYMOLOGY: *Pruina* (Latin for frost), *pleura*, referring to the bluish pruinescence seen on the pleura when viewed at certain angles, which is one of the distinguishing characters.

DISCUSSION: For possible relationships, see *sclerstyla* below.

*Cladochaeta sclerstyla*, new species

Figures 6, 8, 11, 26

DIAGNOSIS: Body brown, pleuron darker (with bluish pruinescence); wing with clouds on x-veins, diffuse apical infuscation; male easily identified externally by heavily sclerotized surstyli, internally by vestigial left paraphysis, dorsal portion of aedeagus heavily sclerotized, and well-developed right paraphysis.

DESCRIPTION: HEAD: Eyes virtually bare;

greatest length of eye (in lateral view) in line with greatest depth of head. Head quite high in lateral view (HL/HD = 0.78 [holotype]). Pedicel light brown, flagellomere I slightly darker. Arista with large basal branch, several vestiges of minute medial branches present. Front slightly long and of moderate width; light brown anteriorly, darker brown on ocellar triangle and surrounding triangle (this dark area with light bluish pruinescence in anterior [facial] view). Frontal-orbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca. 1.5× size of frontal-orbital setulae; post. reclinate slightly closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan and of moderate width and height (FW/HW = 0.31 [N = 2]). Cheeks tan and of moderate depth (CD/ED = 0.12).

THORAX: Notum and scutellum ochre to light brown; pleuron darker brown, with some light bluish pruinescence (most obvious at an oblique anterior angle), katapisternum lighter. Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentral very close to scutellar margin. Acrostichals in 6 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral apparently the same size of other acrostichals. Anterior scutellars parallel; posterior scutellars cruciate for about one-third their length. Legs yellowish, forecoxa nearly white; forefemur with 1 long dorsolateral seta and 2 slightly shorter ventrolateral setae, on apical half of femur. Halter light brown. Entire wing lightly fuscous, with darker, diffuse infuscation on apical half of costal edge, over vein  $R_{4+5}$  and extended to M. Infuscation darkest as small clouds over x-veins r-m and dm-cu. Cloud entirely covering dm-cu, extended slightly past M and  $CuA_1$ . Veins  $R_{4+5}$  and M parallel. X-vein dm-cu very slightly bent.

ABDOMEN: Tergites dark, even brown. Female terminalia: Apical tergite without foramen (not encircling epi-/hypoproct), mostly sclerotized, with long ventral arms. Apical sternite with base divided into pair of narrow lobes; tip of sternite setulose, not divided. (A female from Monteverde, Costa Rica [no. 47, fig. 12], is very similar to *sclerstyla*, except

that in no. 47 the apical tergite is slightly taller and narrower and the apical sternite is shorter.) Male genitalia: Cercus with ventral margin nearly flat, lateral corner with slight point; mesal margins of cerci touching ventrally. Epandrium taller than wide, height ca.  $1.3\times$  the width. Ventrolateral halves of epandrium (epandrial lobes) abruptly tapered at apical third of lobe, with row of 6 stiff long setae; small preapical knob on mesal margin. Aedeagus deep, sclerotized (most dorsally); dorsal surface flat; outer surface convex, with fine groove for right paraphysis. Left paraphysis small, lobelike, extended to outer margin of aedeagus; lightly sclerotized. Right paraphysis heavily sclerotized and much longer, length extended to slightly past ventral margin of aedeagus. Left paraphysis fits close to aedeagus, with apical two-thirds bent slightly to the left and nearly straight; apex sharp. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium. Hypandrium of moderate width, with ventral keel deep. Gonopods laterally flattened and tapered apically. Surstyli with large, bulbous apical club; portions of apical club heavily sclerotized; apical surface of club with ca. 70 minute setulae and 3 long, sharp ones on ventral "elbow." Apical sternite a simple, setose, bilobed plate.

TYPE: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, VIII/1-IX/4/84, 2100 m, H. Wolda (dissected, no. 197). Paratype: Same data, 1♀ (no. 198) (AMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 types.

ETYMOLOGY: From *sclerotized*, as well as root of surstylus, referring to the heavily sclerotized surstyli (in the male), which is one distinguishing feature.

DISCUSSION: This species appears most closely related to *mathisi* and *pruinopleura* on the basis of heavily sclerotized male genitalia, including the aedeagus, hypandrium, epandrium, parts of the surstyli, and particularly the right paraphysis, which also is very short.

#### *Cladochaeta spira*, new species

Figures 6, 8, 11, 27

DIAGNOSIS: Thorax generally light brown, most with fine, light bluish pruinescence;

wing with infuscation on costal edge and over x-vein dm-cu; male genitalia most diagnostic. Paraphyses heavily sclerotized, with left one vestigial, right one arched, long, thin, and sinuous. Aedeagus a thin pendulous lobe; surstylus shape distinct. Apical sternites heavily setose.

DESCRIPTION: HEAD: Eyes virtually bare; greatest length of eye (in lateral view) oblique to line of greatest depth of head. Head long in lateral view (HL/HD = 0.90 [holotype]). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, vestiges of ca. 6 minute medial branches present. Front relatively long, rather narrow; light, cream-colored anteriorly; shiny, golden posterodorsally. Frontal-orbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca.  $2\times$  size of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face tan, narrow, of moderate height (FW/HW = 0.36 [N = 5]). Cheeks tan and moderately deep (CD/ED = 0.12).

THORAX: Notum and scutellum light brown; pleuron slightly darker; most of thorax with light bluish pruinescence (most obvious at an oblique anterior angle). Anterior dorsocentrals  $0.8\times$  length of posterior dorsocentrals; posterior dorsocentral slightly closer to scutellar margin. Acrostichals in 4 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral obviously larger than other acrostichals, ca.  $2.5\times$  the size. Anterior scutellars parallel; posterior scutellars cruciate for about one-third their length. Legs yellowish, forecoxa nearly white; forefemur with 1 long dorsolateral seta and 3 slightly shorter ventrolateral setae, on apical half of femur. Halter light brown. Wing with infuscation: dark cloud over apical half of vein  $R_{2+3}$ , extended to halfway between this vein and  $R_{4+5}$ ; small cloud over x-vein dm-cu, barely extended to vein  $CuA_1$ ; no cloud over x-vein r-m. Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu perfectly straight, perpendicular to vein M.

ABDOMEN: Tergites light to dark, even brown. Female terminalia barely sclerotized. Apical tergite small, somewhat hemispheri-

cal, with truncate ventral margin; foramen present. Apical sternite with apex divided into setulose lobes, connected basally by thin sclerite having triangular portion in middle. Male genitalia: Cercus with long flat ventral lobe directed ventrad. Epandrium taller than wide, height ca.  $1.6\times$  width. Ventrolateral halves of epandrium (epandrial lobes) of equal width along length, slightly tapered at apex, with row of 8 stiff long setae. Aedeagus bulbous and membranous; apparently without groove to accommodate right paraphysis. Paraphyses heavily sclerotized; left one vestigial, right one very well developed. Right paraphysis long and thin, length extended beyond ventral margin of epandrium; base broad, abruptly thinned at dorsal bend and of uniform thickness distad; curved gently inward and then slightly outward, with tip pointing straight downward. Left paraphysis a simple lobe, not extended even to apical margin of aedeagus. Aedeagal apodeme typically troughlike but with lateral bulges in center. Hypandrium with ventral keel of moderate depth; gonopods relatively short. Surstylus foot-shaped, with broad base; narrower, tapered apical lobe at right angle to base; apical half with row of 4 fine, stiff setae, and microtrichia at very apex. Apical sternites with dense, stiff setae; setae on penultimate sternite without median separation; setae on apical sternite divided in middle and this sternite with slight median constriction.

TYPES: Holotype, Male: DOMINICAN REPUBLIC: *Pedernales*: 9.7 km NE Los Arroyos, 18-16N, 71-44W, 2070 m, 15-16/VII/90, J. E. Rawlins et al. (CMNH). Paratypes: Same label data, 1♂ (no. 263, CMNH), 3♀ (CMNH, 1 in AMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: *Speira* (Greek for coiled, twisted), in reference to the shape of the left paraphysis.

#### *Cladochaeta tepui*, new species

Figures 6, 28

DIAGNOSIS: Externally not very distinctive from the other *nebulosa* group species with infusate wings and a light brown body. Genitalia most diagnostic: simple, with small, sclerotized paraphyses of nearly the same size

(acutely hooked); aedeagus baglike; epandrium stout; surstyli simple, setose.

DESCRIPTION: HEAD: Eyes virtually bare; greatest length of eye (in lateral view) in line with greatest depth of head. Head high in lateral view (HL/HD = 0.76 [holotype]). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, no vestiges of minute medial branches present. Front relatively long, rather narrow; frontal vittae light brown, frontal-orbital plates yellowish. Frontal-orbital setae: Proclinate slightly closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca.  $2.5\times$  size of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face light brown, fairly narrow (FW/HW = 0.29). Cheeks tan and moderately shallow (CD/ED = 0.08).

THORAX: Notum and scutellum tan to light brown; pleuron slightly darker, with most of pleuron with light bluish pruinescence (most obvious at an oblique anterior angle) and kat-episternum contrastingly yellow. Anterior dorsocentrals  $0.6\times$  length of posterior dorsocentrals; posterior dorsocentral closer to scutellar margin. Acrostichals in 4 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral apparently undifferentiated from other acrostichals. Anterior scutellars parallel; posterior scutellars cruciate for about one-third their length. Legs yellowish, forecoxa whitish; forefemur with 1 long dorsolateral seta and 1 slightly shorter ventrolateral seta, on apical half of femur. Halter light brown. Wing with costal half infusate; infuscation slightly darker apicad and extended to apex of vein M. X-veins r-m and dm-cu with slightly darker infuscation; cloud on vein dm-cu darkest surrounding joint of dm-cu and M. Apex of vein  $R_{2+3}$  turned abruptly costad, not gradually joined to costal vein. Wing tip very slightly pointed. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu straight.

ABDOMEN: Tergites dark, even brown. Female terminalia unknown. Male genitalia: Cercus without thin ventral lobe, but slightly distended ventrad. Epandrium only slightly taller than wide. Ventrolateral halves of epandrium (epandrial lobes) broad, slightly tapered apically, with row of 5-7 stiff, short setae. Aedeagus bulbous and very membranous, no



sclerotization. Paraphyses heavily sclerotized, very strongly hooked, nearly equally developed (left one slightly larger), but both rather small. Length of paraphyses extended to about one-third the length of aedeagus. Aedeagal apodeme unsclerotized, without keel. Hypandrium small, scoop-shaped, and shallow; gonopods narrow. Surstyli simple, lobate; outer surface bearing ca. 35 minute stiff setulae. Apical sternites not examined.

TYPE: Holotype, Male: VENEZUELA: *Boliviar*: Guaiquinima tepui camp I, 63°30'W, 55°5'N, 1150 m, Feb. 24–28, 1990, D. Grimaldi (in AMNH) (genitalia dissected, DAG no. 144).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: Directly from *tepui*, the term for the distinctive flat-topped sandstone mountains of the Guiana Shield.

*Cladochaeta vermes*, new species

Figures 6, 8, 29

DIAGNOSIS: Externally distinguished by the 2 faint brown vittae on the pleuron and the nearly hyaline wing. Male genitalia with left paraphysis very small, right one long and thin, kinked in middle; posterodorsal rim of aedeagus sclerotized; surstylus clavate, with broad apical surface.

DESCRIPTION: HEAD: Eyes virtually bare; greatest length of eye (in lateral view) slightly oblique to line of greatest depth of head. Head slightly high in lateral view (HL/HD = 0.78 [holotype]). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, no vestiges of minute medial branches present. Front of moderate length and width (measurements); entire front evenly tan. Frontal-orbital setae: Proclinate midway between ptilinal suture and ipsilateral inner vertical seta; anterior reclinate very small, barely distinguishable from frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face evenly tan, fairly narrow (FW/HW = 0.29). Cheeks tan and of average height (CD/ED = 0.11).

THORAX: Notum and scutellum tan. Dorsal part of pleuron slightly darker than notum; middle of pleuron with very light brown, diffuse vitta; katepisternum yellow, with some

bluish pruinescence (most obvious at an oblique anterior angle). Anterior dorsocentrals 0.7× length of posterior dorsocentrals; posterior dorsocentral slightly closer to scutellar margin. Acrostichals in 4 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral apparently undifferentiated from other acrostichals. Anterior scutellars parallel; posterior scutellars damaged in single specimen. Legs yellowish, forecoxa whitish; forefemur with 1 long dorsolateral seta and 2 slightly shorter ventrolateral setae, on apical half of femur. Halter light brown. Wing nearly completely hyaline, with very slight infuscation over apical tip of vein  $R_{2+3}$  and x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  gradually meeting costal vein; veins  $R_{4+5}$  and M perfectly parallel. X-vein dm-cu nearly straight, perpendicular to vein M. Wing tip rounded.

ABDOMEN: Tergites even, light brown. Female terminalia unknown. Male genitalia: Cercus with ventral extension but no distinct lobe. Epandrium slightly taller than wide, height ca. 1.3× width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, not tapered, with row of 5 stiff long setae. Aedeagus bulbous and membranous, no sclerotization. Paraphyses heavily sclerotized and very thin. Left paraphysis (vestigial? very long?: difficult to tell from drawing, or is this the posterodorsal rim of aedeagus?) extended to well past end of epandrium, with curve toward middle; right one about half the length, with very little curvature on part facing downward. Aedeagal apodeme typical of species group: troughlike, narrow, very long, articulating with bases of paraphyses and aedeagus and with gonopods. Hypandrium very small, U-shaped, without ventral keel; gonopods long and thin. Surstyli simple, lobate, with broad, flat apical surface; bearing ca. 20 minute setulae on mesal surface; lateral surface with about 5 longer, thin setulae. Apical sternites not examined.

TYPE: Holotype, Male: VENEZUELA: *Aragua*: Rancho Grande, 26/II/89, D. A. Grimaldi (in AMNH) (genitalia dissected, DAG no. 134).

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From Latin *vermis* (worm), for the long thin undulating paraphysis in the male genitalia.

*Cladochaeta wirthi*, new species

Figures 6, 8, 12, 30

DIAGNOSIS: Costal half of wing with light, even infuscation; body color yellowish; male genitalia with left paraphysis well developed and strongly hooked, right one smaller; surstyli clavate, with broad apical surface having numerous fine setulae.

DESCRIPTION: HEAD: Eyes with very sparse, short setulae; greatest length of eye (in lateral view) in line with greatest depth of head. Head of moderate depth in lateral view (HL/HD = 0.83 [holotype]). Pedicel ochre, flagellomere I light brown. Arista with large basal branch, no vestiges of minute medial branches present. Front of moderate length and width; frontal vittae shiny, golden; frontal-orbital plates lighter, yellow. Frontal-orbital setae: Proclinate closer to ptilinal suture than to ipsilateral inner vertical seta; anterior reclinate small, ca. 1.5× size of frontal-orbital setulae; post. reclinate closer to proclinate than to inner vertical. Inner vertical seta in line with ipsilateral proclinate and post. reclinate. Face evenly tan, of moderate width and height (FW/HW = 0.31). Cheeks tan; slightly shallow (CD/ED = 0.09).

THORAX: Notum and scutellum very light tan, pleuron slightly darker. Anterior dorsocentrals 0.8× length of posterior dorsocentrals; posterior dorsocentral slightly closer to scutellar margin. Acrostichals in 4 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral slightly larger than other acrostichals. Anterior scutellars slightly divergent; posterior scutellars cruciate for ca. 0.4× their length. Legs yellowish, forecoxa whitish; forefemur with 1 long dorsolateral seta and 2 slightly shorter ventrolateral setae, on apical half of femur. Halter light brown. Wing with diffuse, light infuscation over costal half of wing, extended to between veins  $R_{4+5}$  and M, and to wing tip. X-vein r-m without infuscation; dm-cu with slight cloud, barely extended to vein  $CuA_1$ . Wing tip not rounded; slightly pointed, with apex at tip of vein  $R_{4+5}$ . Apex of vein  $R_{2+3}$  turned costad, not gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. X-vein dm-cu straight.

ABDOMEN: Female terminalia barely sclerotized. Apical tergite with portion ventral to foramen deep. Apical sternite completely di-

vided into pair of widely separated, setulose lobes. Male genitalia: Cercus without thin ventral lobe, ventral margin flat. Epandrium much taller than wide, height slightly more than twice the width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, tapered apically, with row of 7 stiff long setae. Aedeagus bulbous, membranous, and irregular in shape, with lightly sclerotized dorsal knob (without a distinct outer rim and groove). Left paraphysis well developed, heavily sclerotized, and strongly hooked, with length extended nearly to aedeagal apodeme; thickness of paraphysis base nearly 3 times that of apical hooked part. Right paraphysis strongly sclerotized but very short; extended slightly beyond outer margin of aedeagus. Aedeagal apodeme typical of species group: troughlike, narrow, articulating with bases of paraphyses and hypandrium, with very small keel on anterior surface. Hypandrium of moderate width, with shallow ventral keel; gonopods narrow and laterally flattened. Surstyli clavate; apical surface broad, flat, with ca. 60 fine setulae. Apical sternites not examined.

TYPE: Holotype, Male: DOMINICA (West Indies): Clarke Hall, 1–10/II, W. W. Wirth (dissected, DAG no. 217). Paratypes: 2♂ (nos. 215, 217), 2♀ (no. 216) (NMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: In honor of the late Willis W. Wirth, an accomplished dipterist who worked at the Systematic Entomology Laboratory (USDA) and collected many valuable series of *Cladochaeta* specimens, particularly from Dominica.

*Cladochaeta nebulosa* group sp. A

DIAGNOSIS: This species is very similar to but distinct from *C. nebulosa*. Species A has no infuscation on the wing, and the female terminalia differ. *C. nebulosa* has an apodeme curled under on the ventral margin of the last tergite (the lateral margins of the last tergite are also slightly constricted in *C. nebulosa*, but almost parallel in this species, as seen in posterior view). Also in posterior view, the epi-/hypoproct are deeper in *C. nebulosa*, but are broader than high in this species. Measurements: HL/HD = 0.77, CD/ED = 0.11. Males not known.

SPECIMENS EXAMINED: 3♀ (1 dissected, no. 60); PUERTO RICO: El Yunque, Mar. 20–22, 1954, J. Maldonado, S. Medina (not dissected) (in the AMNH).

DISCUSSION: Unfortunately, there is no data on the altitude where the type series was collected. El Yunque is a mountainous area, with some parts having cloud forest at altitudes of 1500 m. It is possible that *nebulosa* and sp. A, even though macrosympatric on Puerto Rico, are altitudinally separated.

*Cladochaeta nebulosa* group sp. B

Figure 9 (wing)

DIAGNOSIS: Wing with slight infuscation, very similar to *nebulosa*; female terminalia greatly differ between the 2 species. Females from 2 islands in the Greater Antilles were matched on the basis of the terminalia, diagnostic for the species as follows: terminal tergite broad and rounded dorsally, with arch on ventral margin that almost touches ventral margin of hole for cercus; oviscapt plates separated from terminal tergite, lateral parts broad and flat, lightly sclerotized; ventral sclerite triangular, with narrow, pointed, apical portion turned upright and lying between terminal lobes of oviscapt. Male genitalia unknown. Measurements: HL/HD = 0.82, 0.78 (Cuban specimen); CD/ED = 0.90 (both specimens).

MATERIAL EXAMINED: JAMAICA: 4000 ft, Hardware Gap, 25/VII/66, Howden & Becker (\*1♀, no. 69; CNC); Try., Good Hope, 22/VIII/66, H. F. Howden (1♀; CNC); near Bath, II/56, W. B. Heed (1♀; AMNH). CUBA: Cristo, Oriente, 3/X/13 (\*1♀, no. 59); Puerto Boniato, Santiago de Cuba, M. Breuer, I–II/56 (1♀; AMNH).

DISCUSSION: The Jamaican specimen examined (no. 69) differs from the Cuban specimen (no. 59) by having the arch of the ventral margin of the last tergite virtually touching the ventral margin of the hole in which the cercus lies. Also, the oviscapt plates are slightly closer in the Jamaican specimen, and the lateral arms of these are more heavily sclerotized. Otherwise, the terminalia are very similar.

Other *nebulosa* group species

In addition to the undescribed species known only from females and presented

above, the female terminalia of 4 additional undescribed species are presented in figure 12. There are numerous other *nebulosa* group females unassociated with males that we did not dissect, but these 6 species should suffice in showing the extent of still undescribed species.

*nebulosa* group sp. C

Distinct from other species in the group by long ventrolateral arms of the apical tergite. Apical tergite with very narrow bridge between foramen and ventral margin. Apical sternite completely divided into pair of close setulose lobes. Pair of small asymmetrical sclerites just beneath lobes.

SPECIMEN: BRAZIL: Nova Teutonia, F. Plaumann coll. Dissected (no. 36).

*nebulosa* group sp. D

Apical tergite sclerotized; bridge between foramen and ventral margin incomplete. Apical sternite divided into pair of lobes; narrow sclerotized sclerite lying just above lobes.

SPECIMEN: VENEZUELA: Aragua, Rancho Grande. Dissected (no. 40). Wing is also figured (fig. 9).

*nebulosa* group sp. E

Similar to *C. infumata*. Terminalia barely sclerotized, with narrow bridge between foramen and ventral margin (this bridge incomplete in holotype of *infumata*). Apical sternite mostly divided into pair of lobes, each with short, truncate lateral lobe. Sternite lobes connected to apical tergite and to each other by ventral floor.

SPECIMEN: COSTA RICA: Turrialba. Dissected (no. 147).

*nebulosa* group sp. F

Terminalia barely sclerotized. Apical tergite with foramen, bridge between foramen and ventral margin deep. Apical sternite mostly separated, connected narrowly to tergum. Small triangular sclerite ventral to sternite lobes.

SPECIMEN: COSTA RICA: Turrialba. Dissected (no. 147).

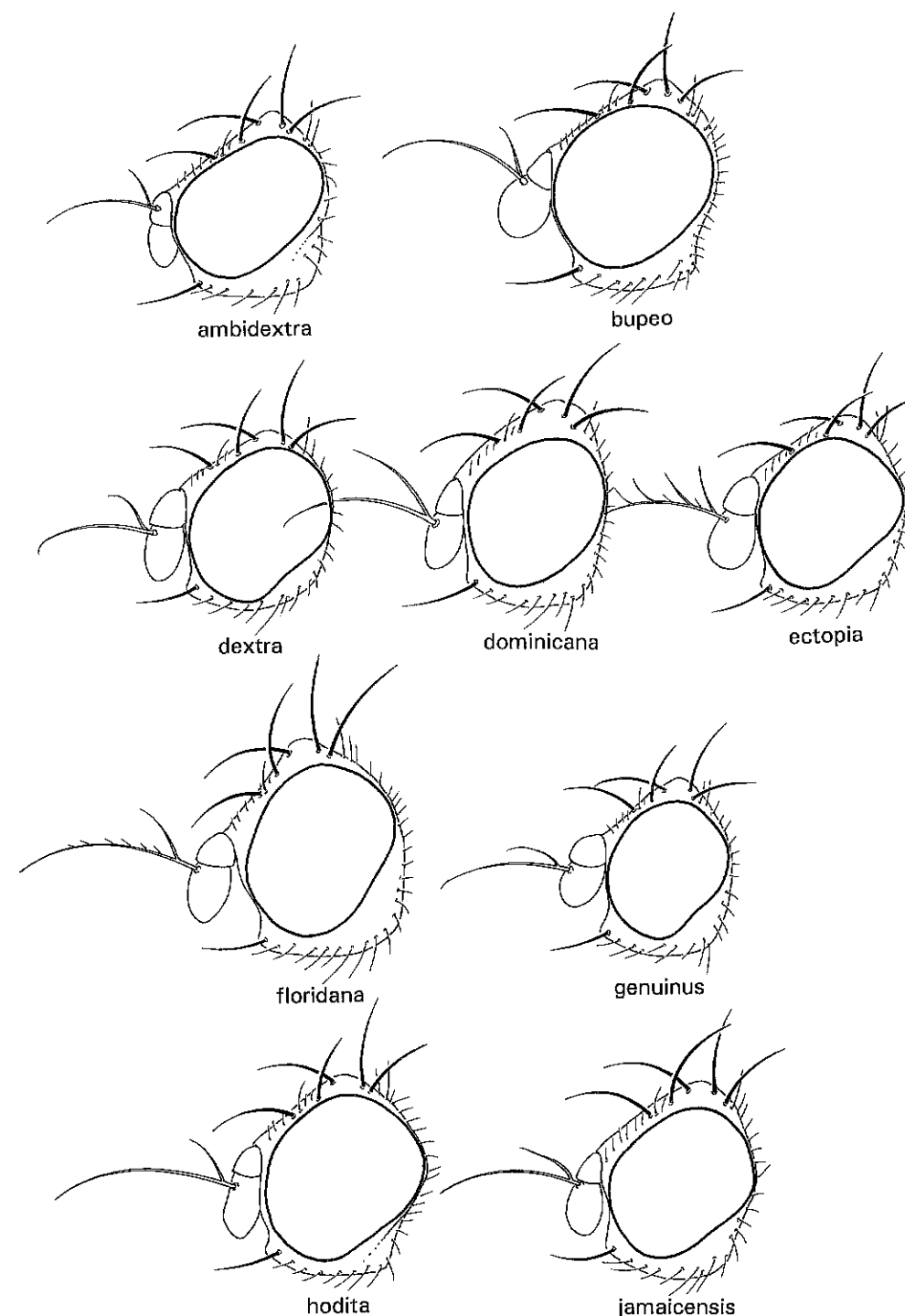
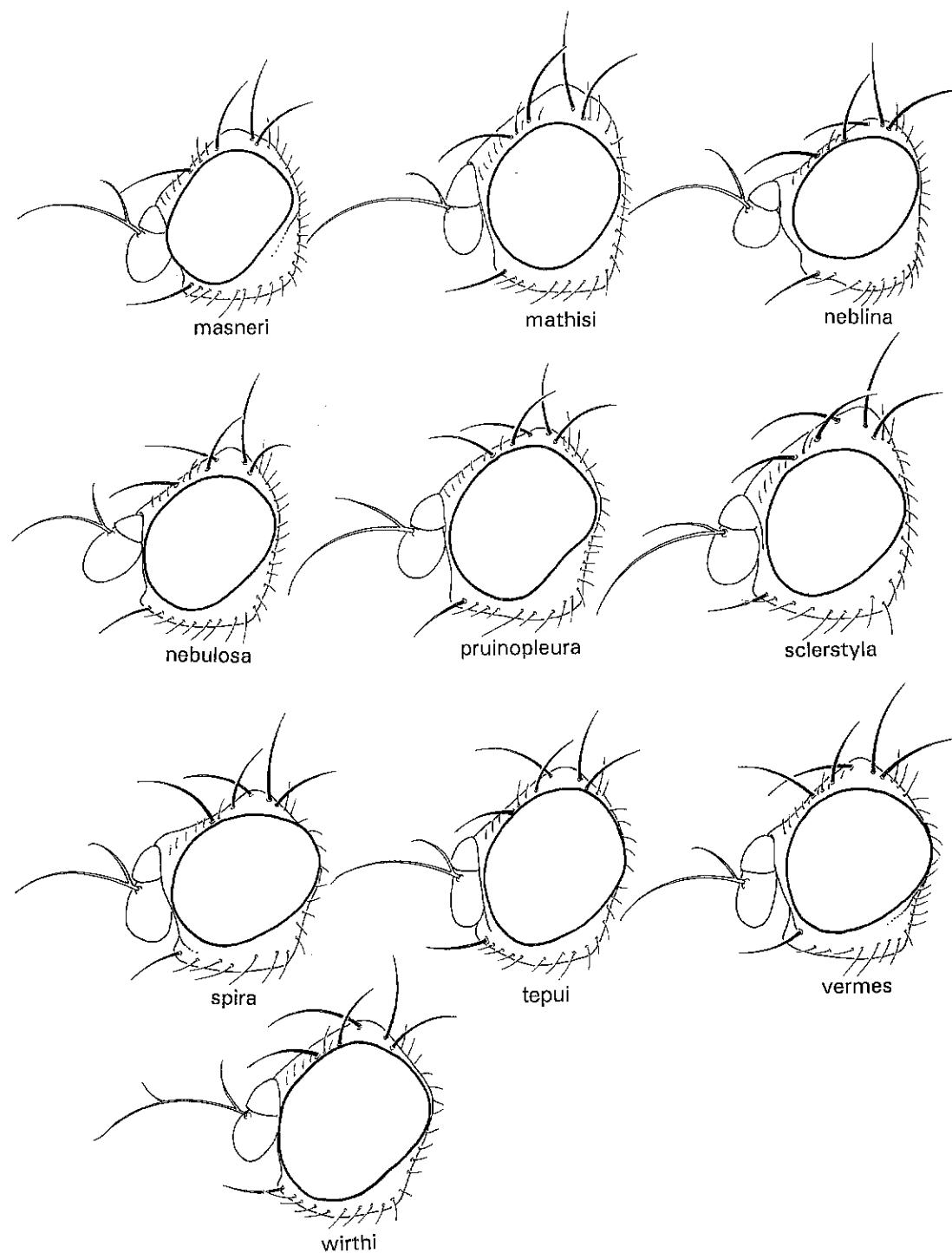
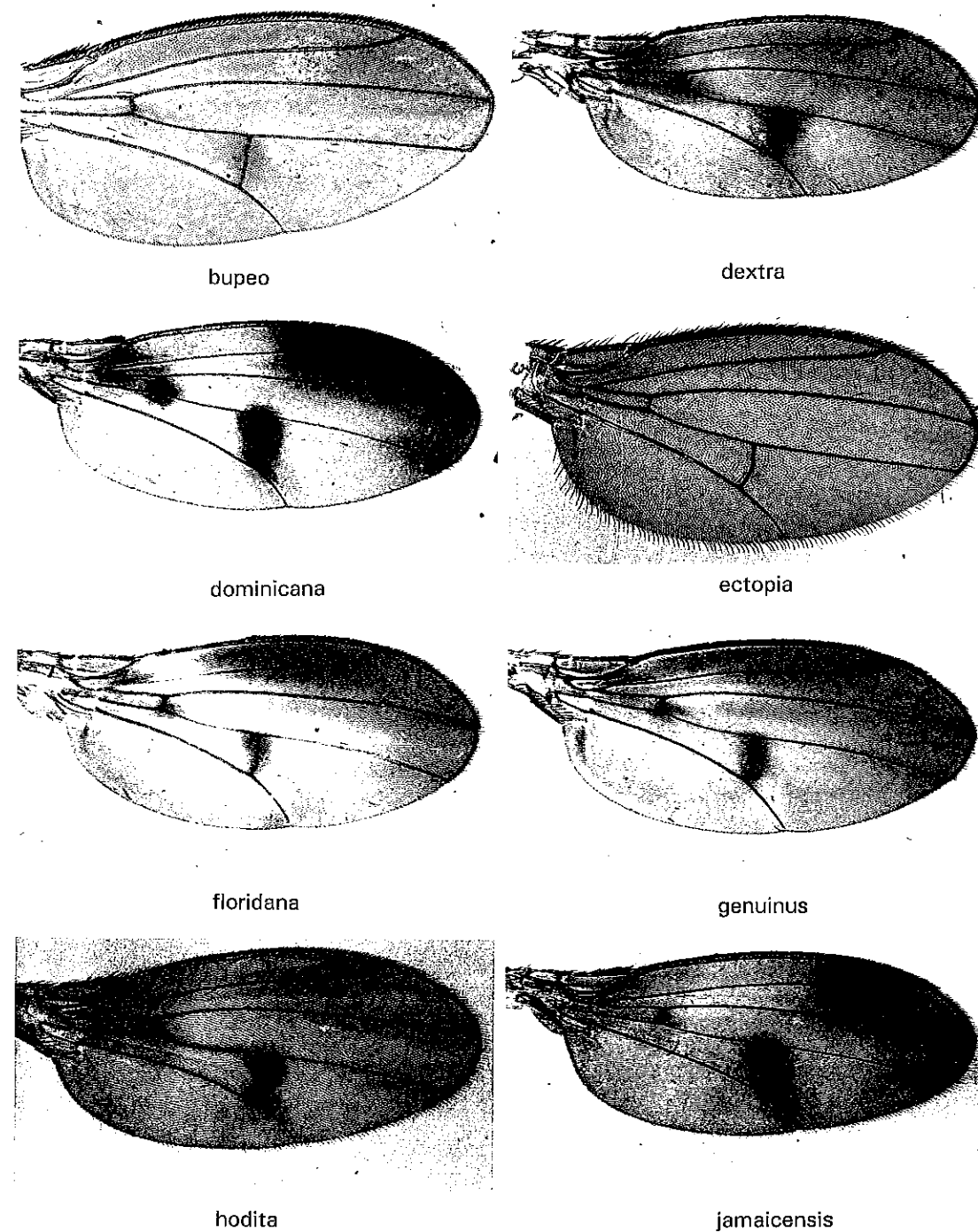
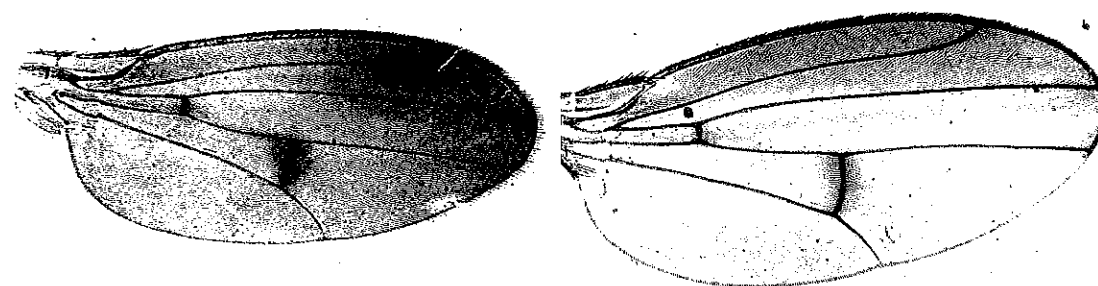


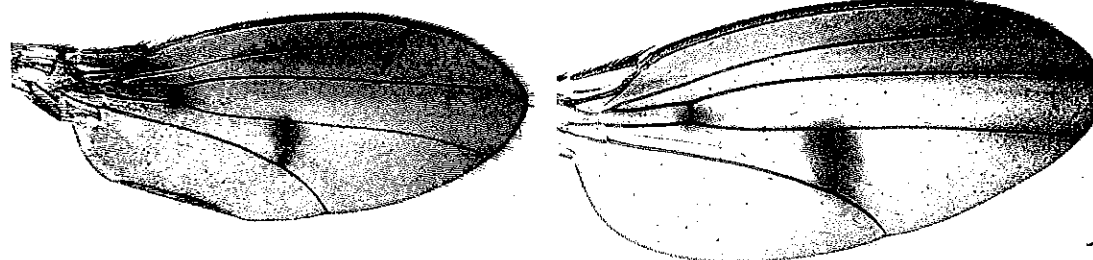
Fig. 5. Heads of *nebulosa* group species.

Fig. 6. Heads of *nebulosa* group species (continued).Fig. 7. Wings of *nebulosa* group species.



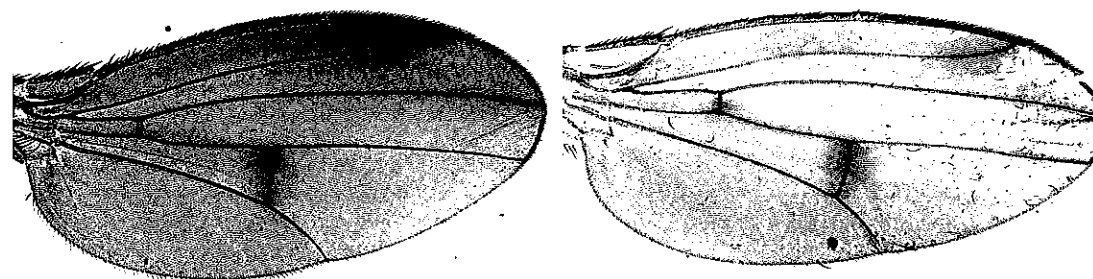
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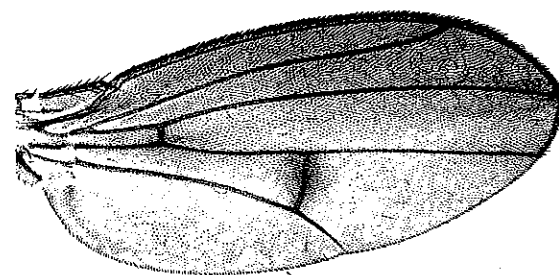
nebulosa

sclerstyla

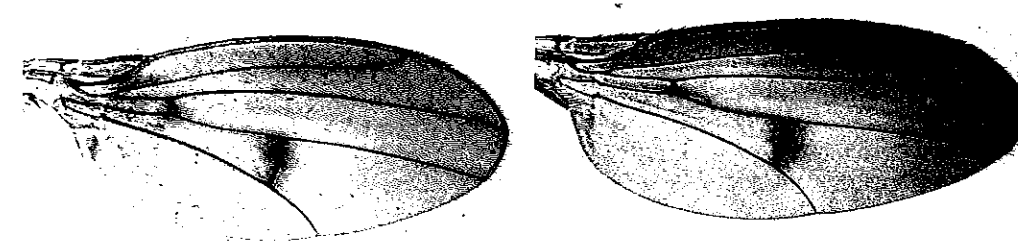


spira

vermes

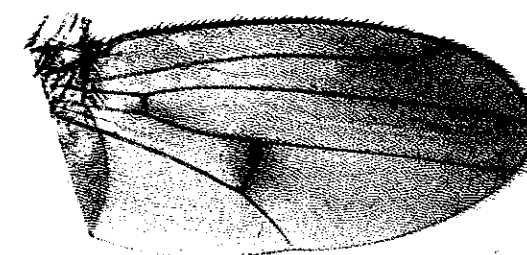


wirthi

Fig. 8. Wings of *nebulosa* group species (continued).

Jamaica (♀69, sp. "B")

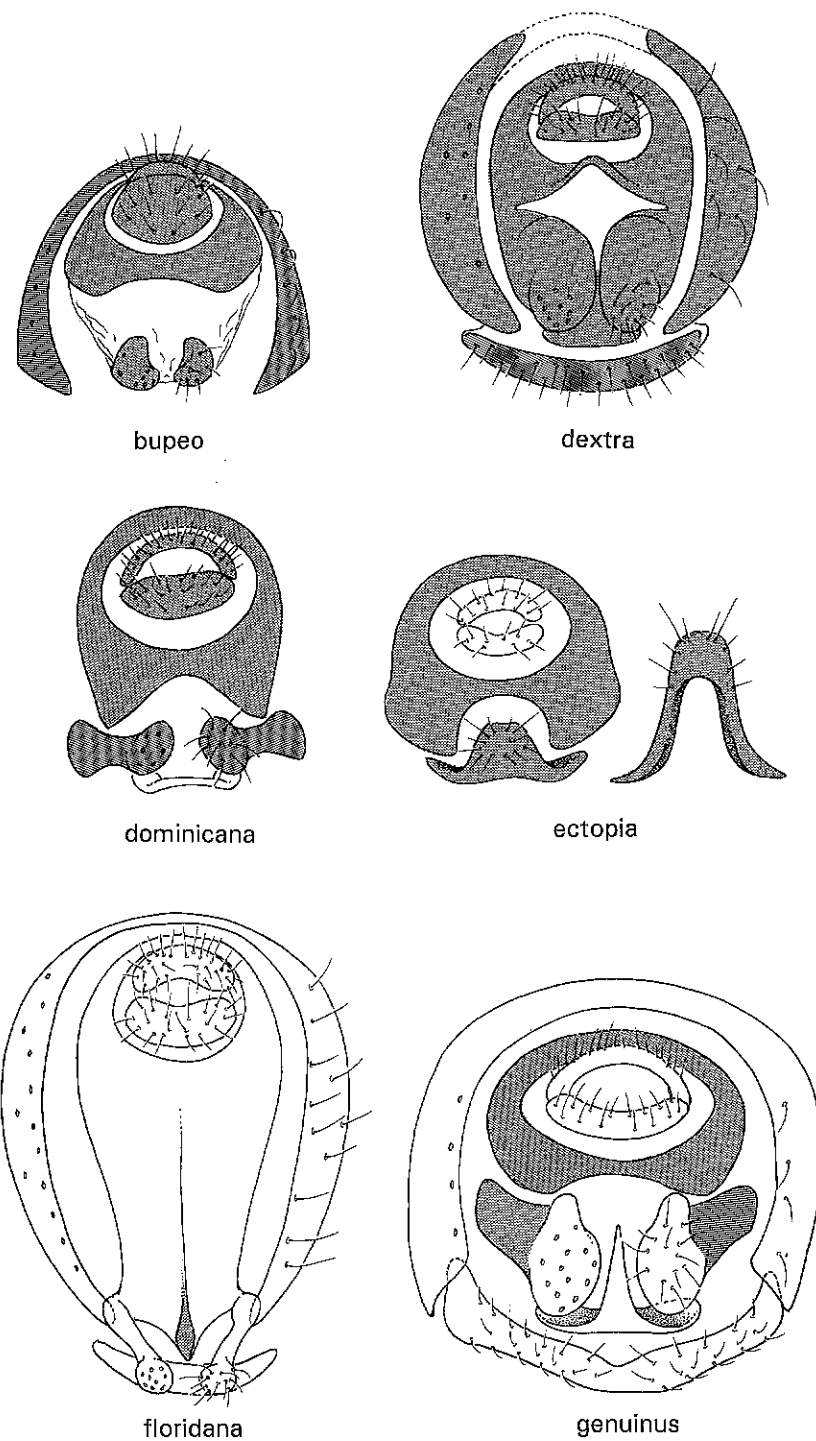
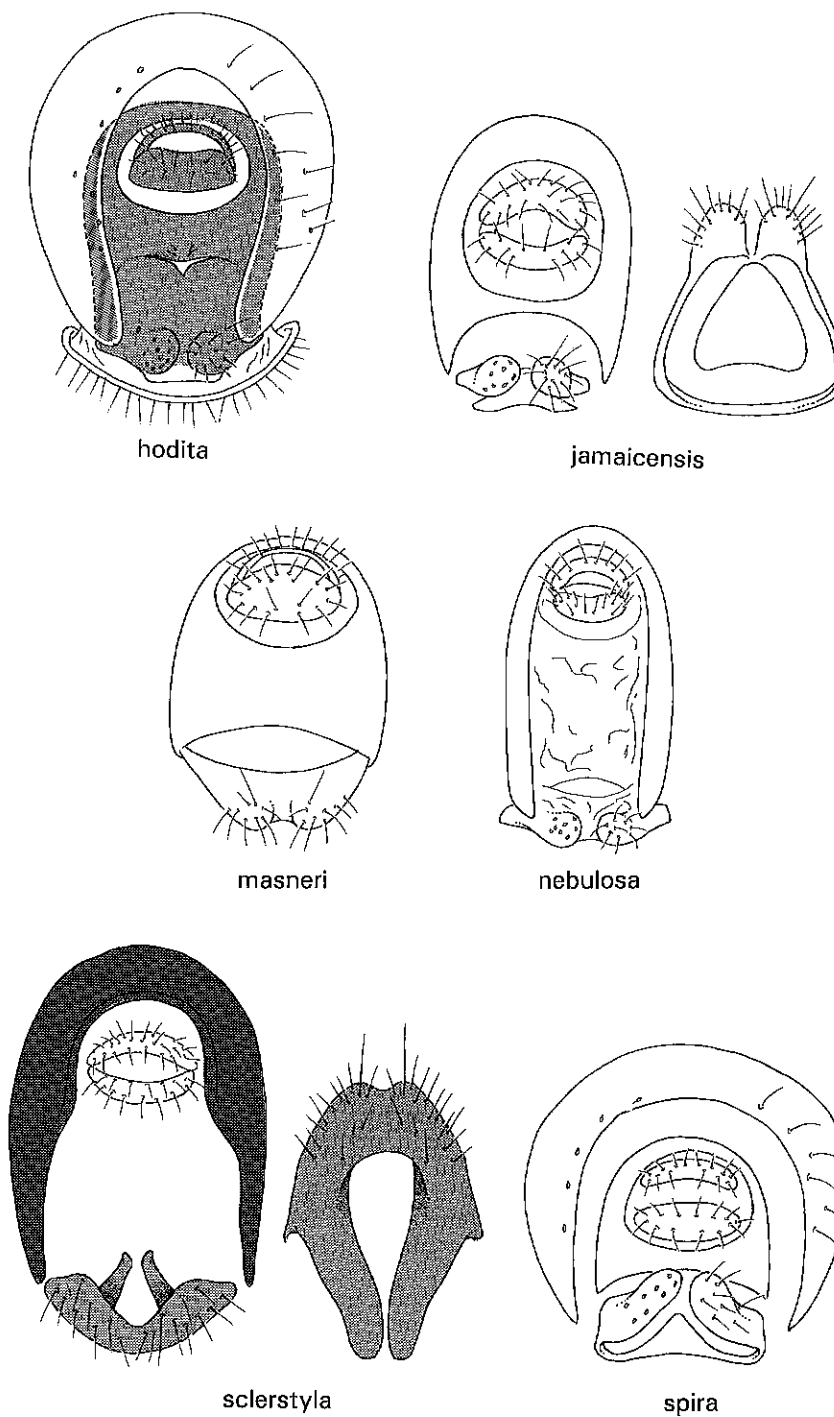
Rancho Grande, Venezuela (♀40, sp. "D")



St. Vincent, British West Indies

Fig. 9. Wings of several undescribed *nebulosa* group species (females) (see text for numbers).



Fig. 10. Female terminalia of *nebulosa* group species (posterior view).Fig. 11. Female terminalia of *nebulosa* group species (continued).

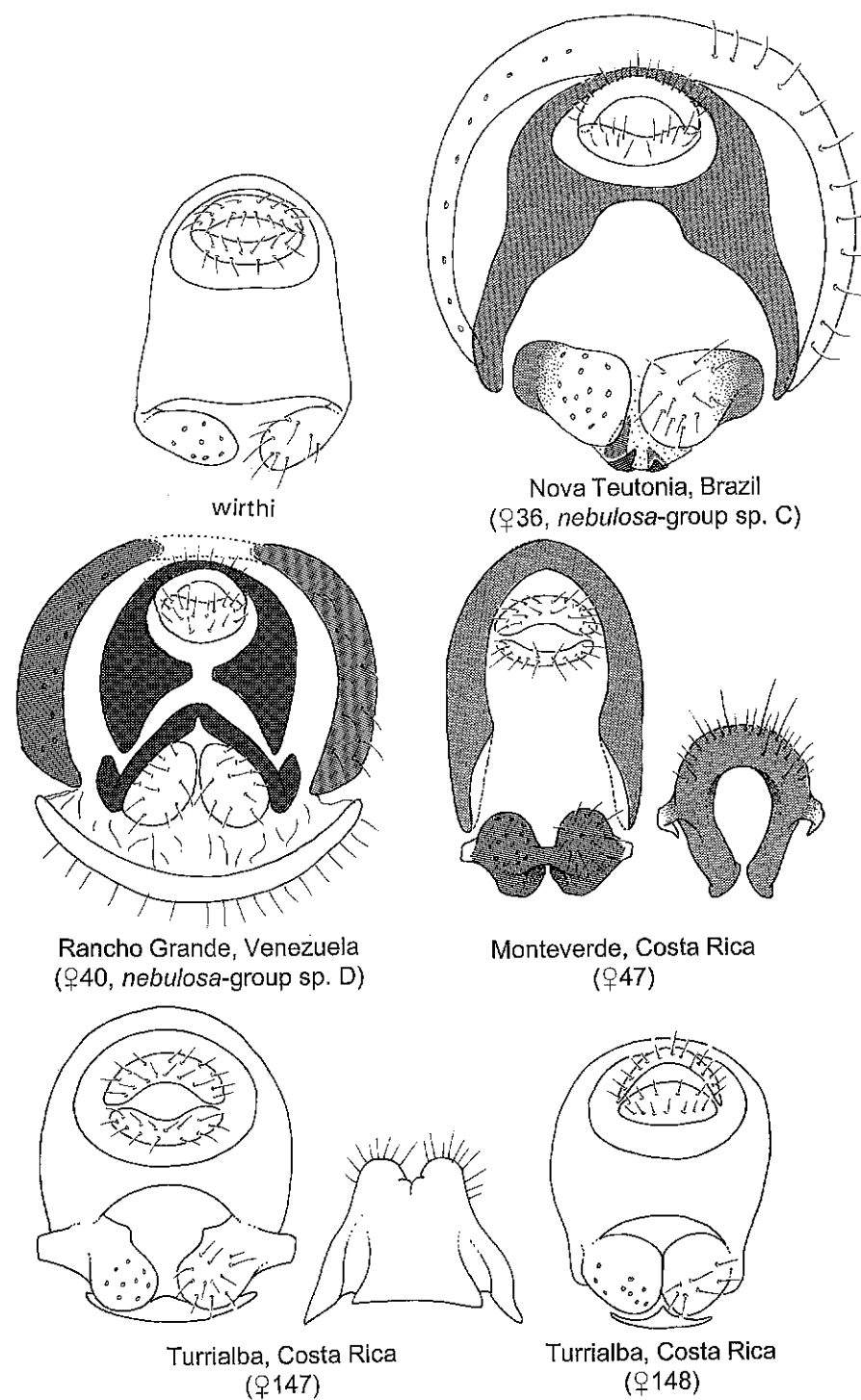


Fig. 12. Female terminalia of *nebulosa* group species, mostly undescribed species (see text for numbers).

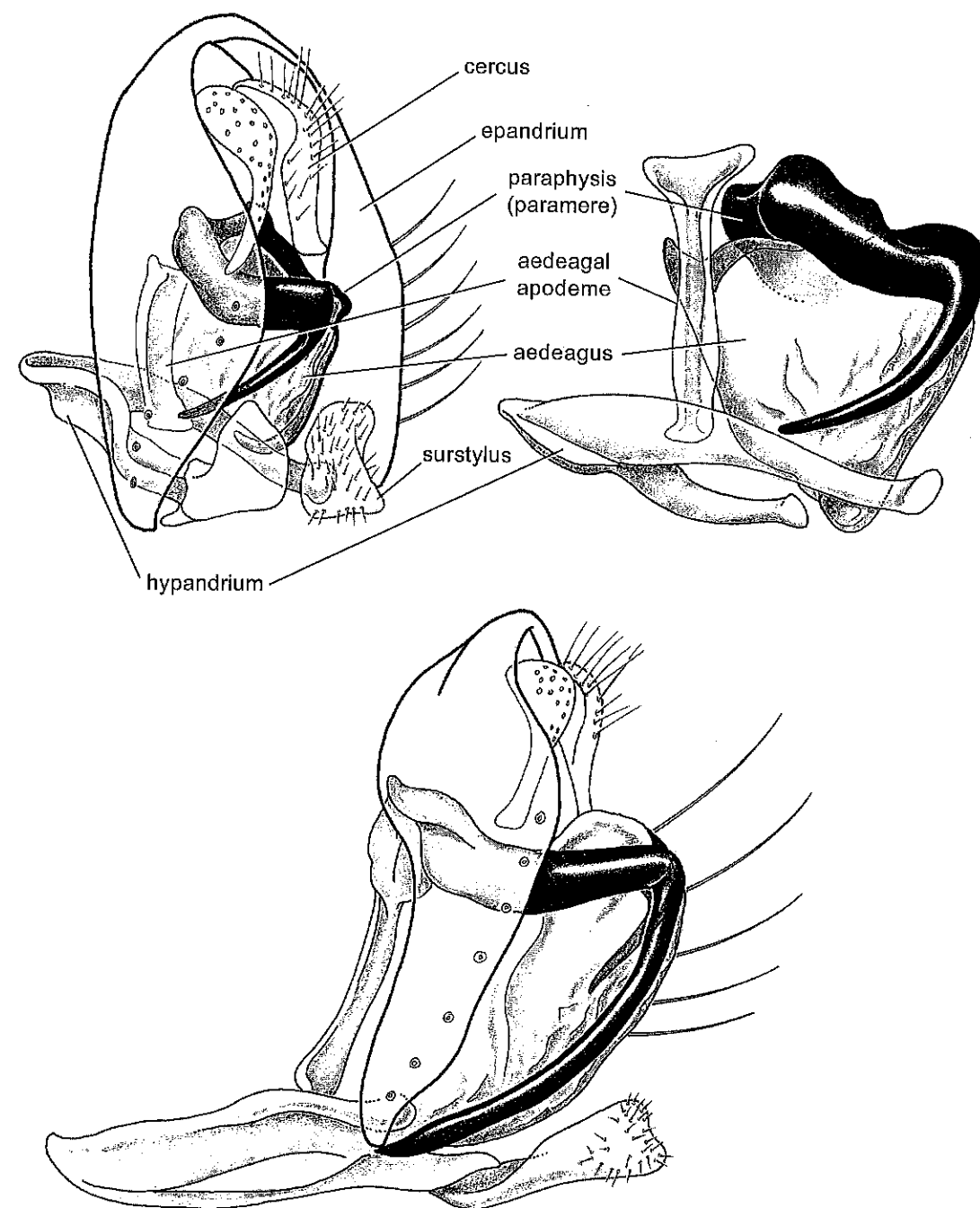


Fig. 13. Male terminalia of *C. adumbrata* (above) and *C. floridana* (below).



Fig. 14. Male terminalia of *C. ambidextra*.



Fig. 15. Male terminalia of *C. bupeo*.



Fig. 16. Male terminalia of *C. dominicana*.

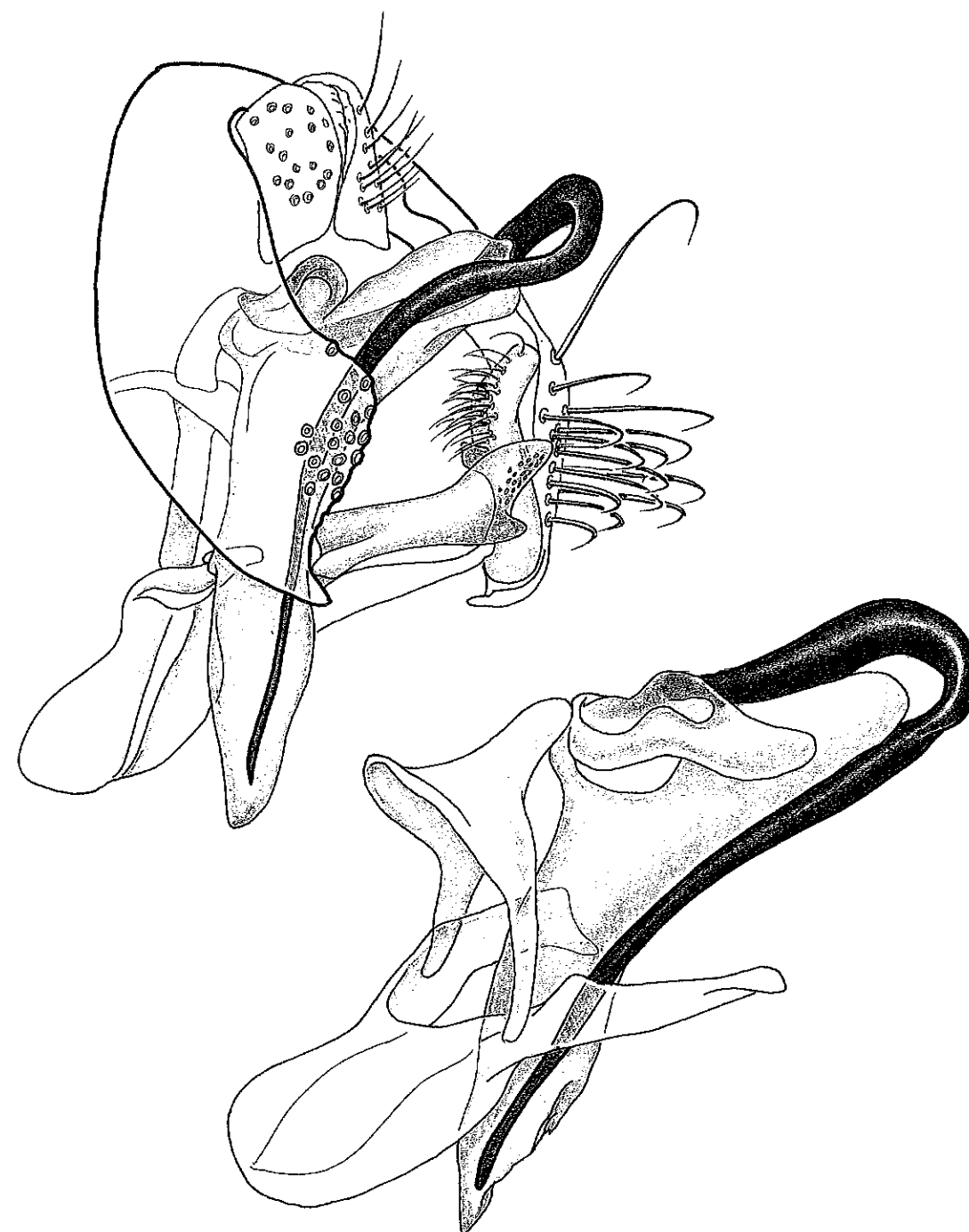


Fig. 17. Male terminalia of *C. ectopia*.



Fig. 18. Male terminalia of *C. genuinus*.

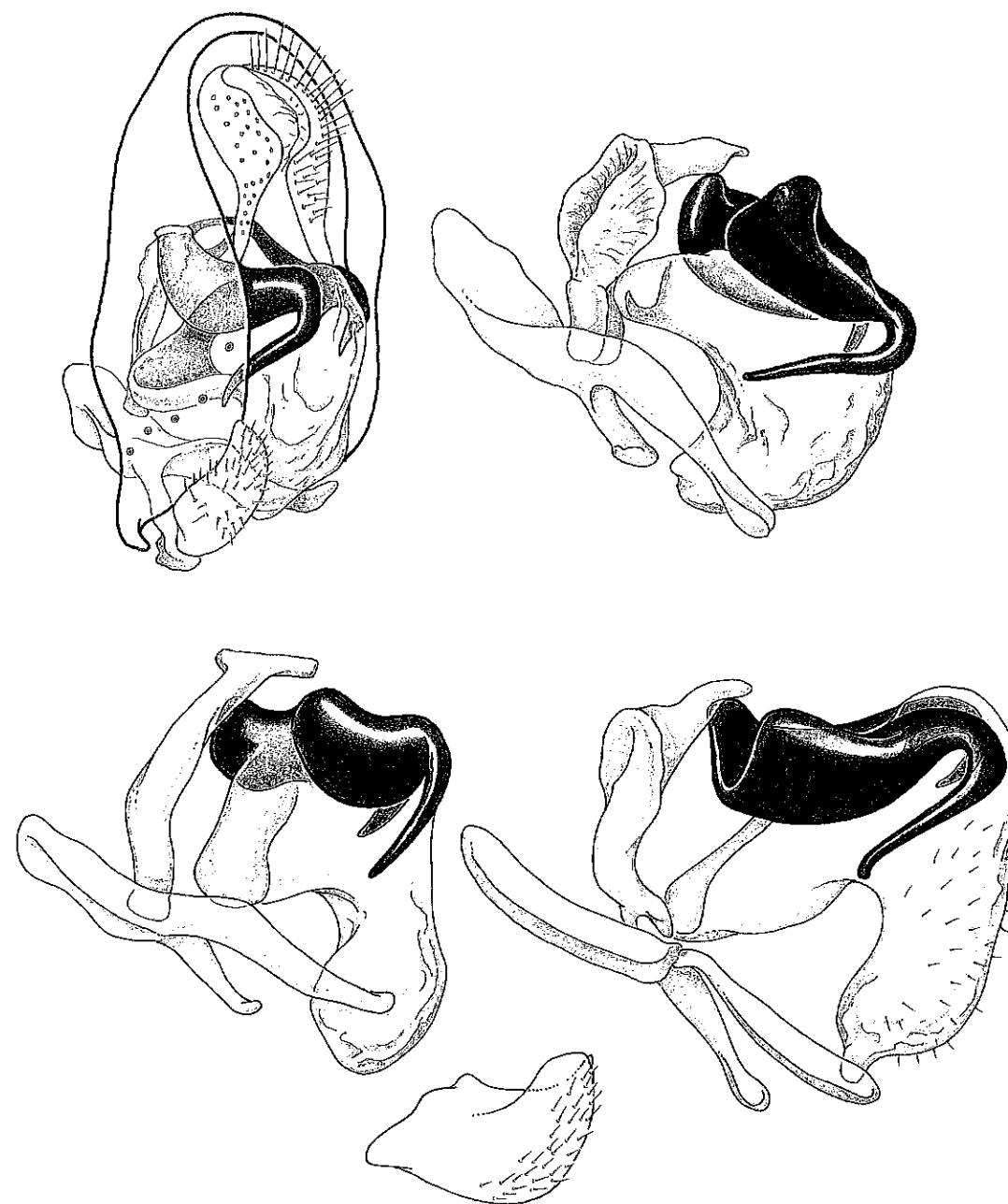


Fig. 19. Male terminalia of *C. hodita*, showing some intraspecific variation.

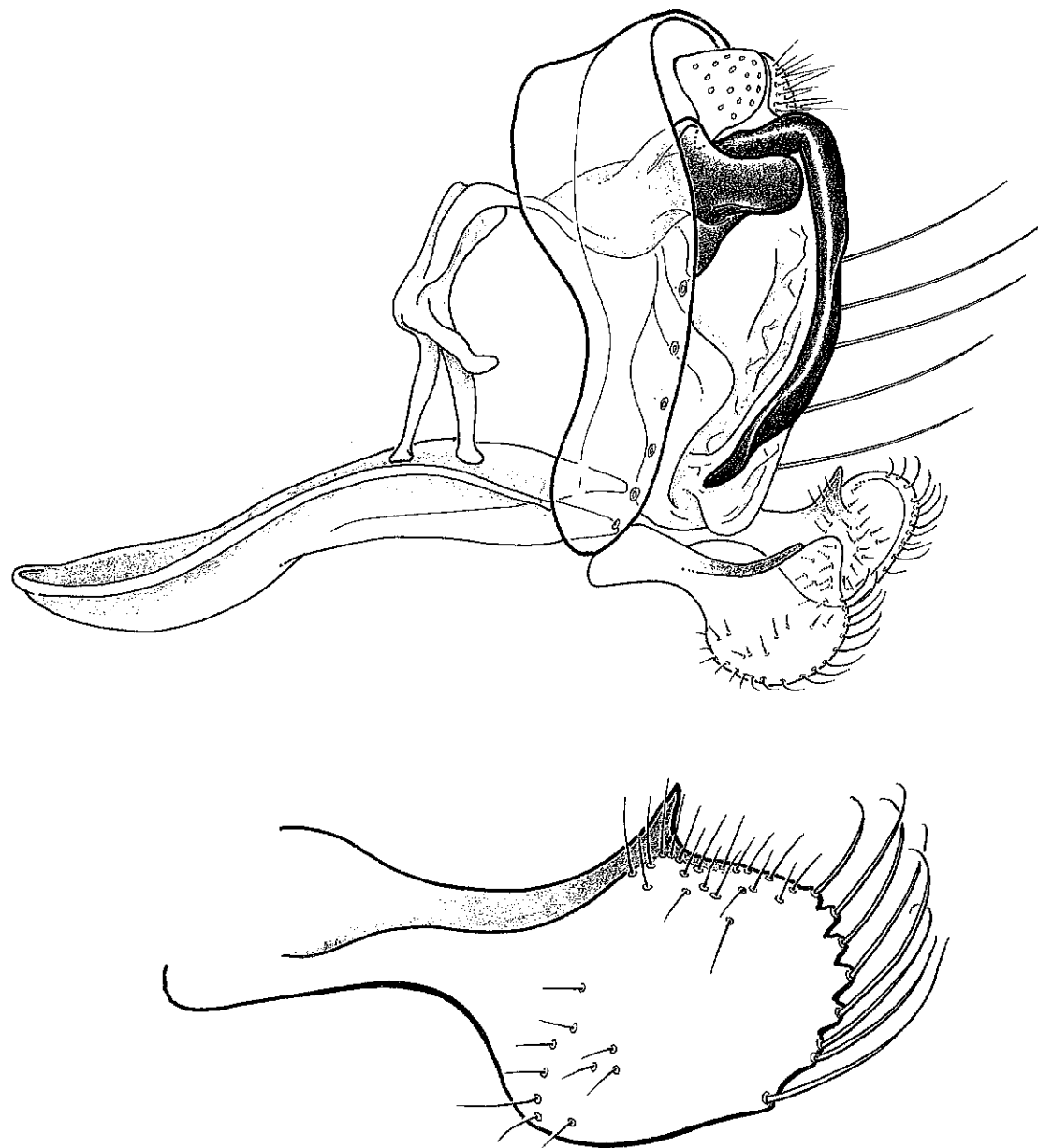


Fig. 20. Male terminalia of *C. incessa*.

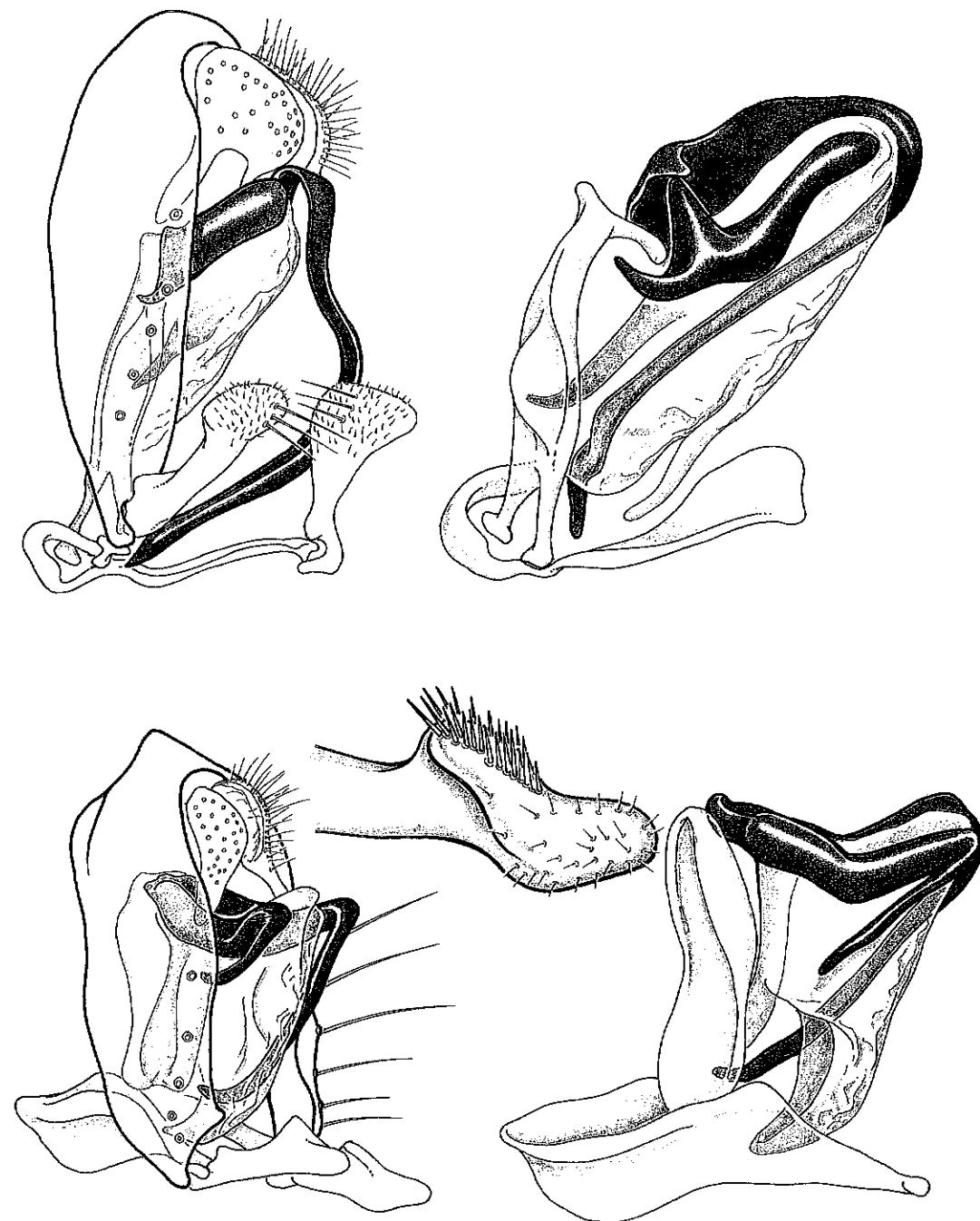


Fig. 21. Male terminalia of *C. jamaicensis* (above) and *C. masneri* (below).

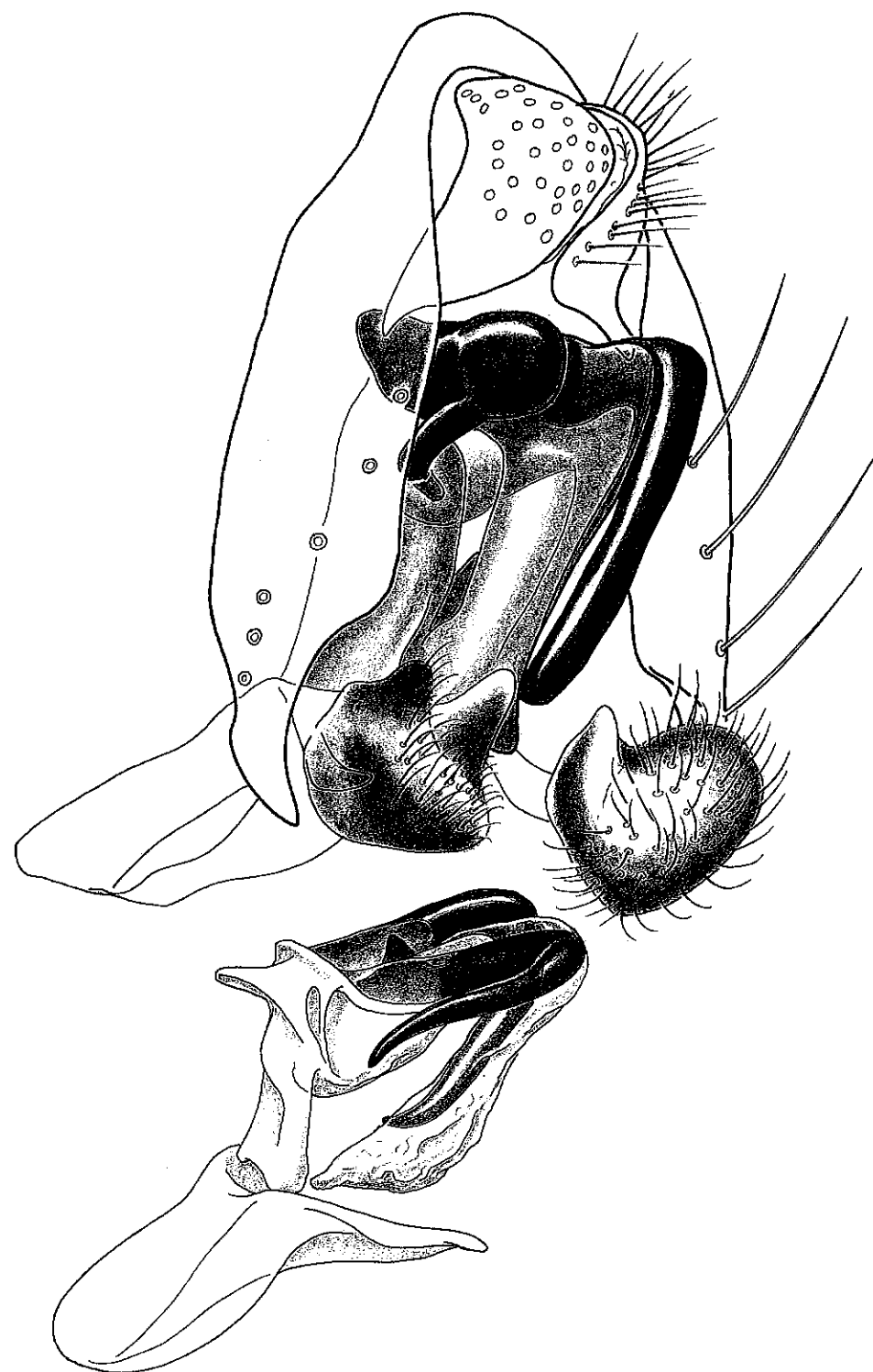


Fig. 22. Male terminalia of *C. mathisi*.



Fig. 23. Male terminalia of *C. neblina*.

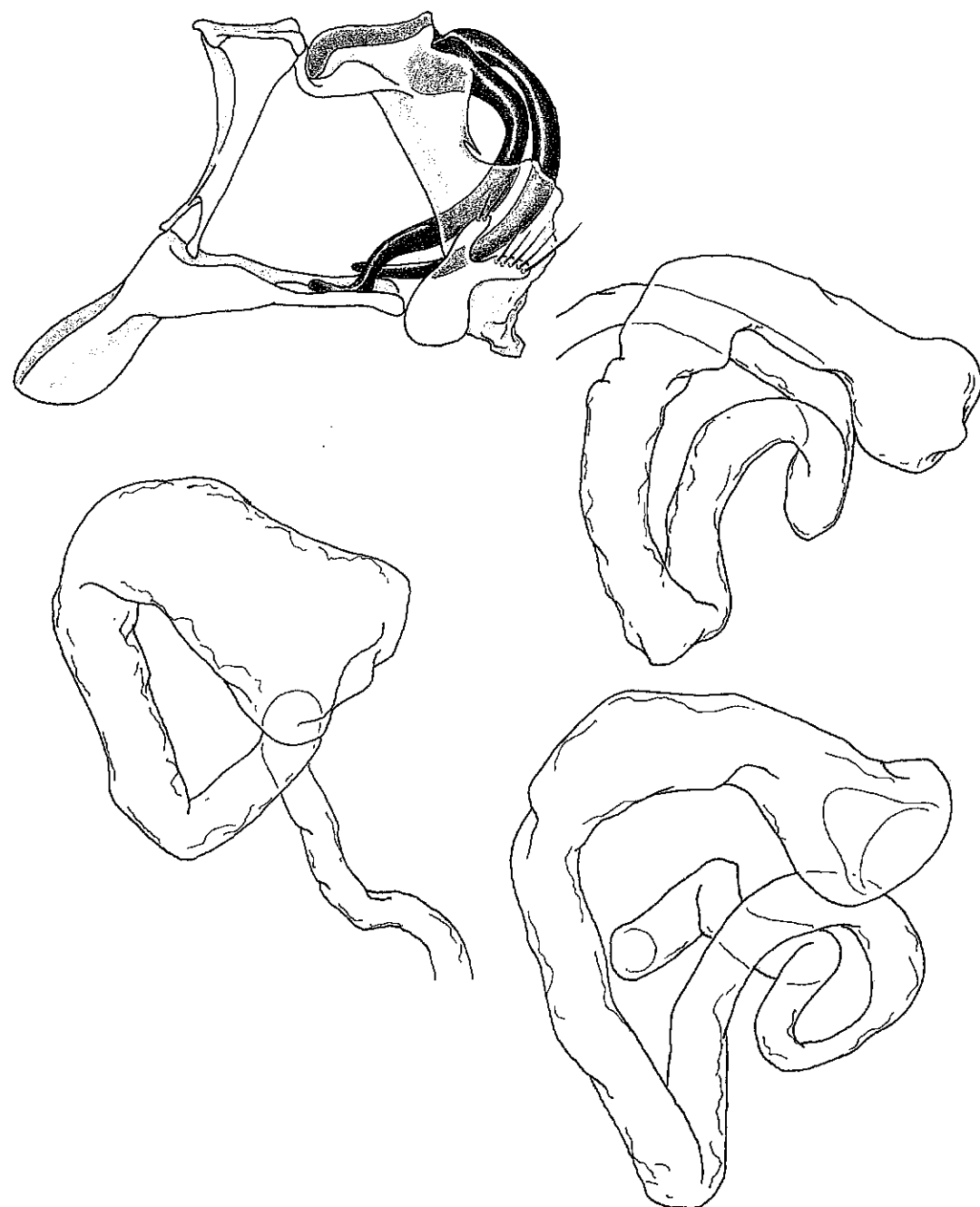


Fig. 24. Male terminalia of *C. nebulosa* (without epandrium), and ventral receptacles (female) of 3 specimens.

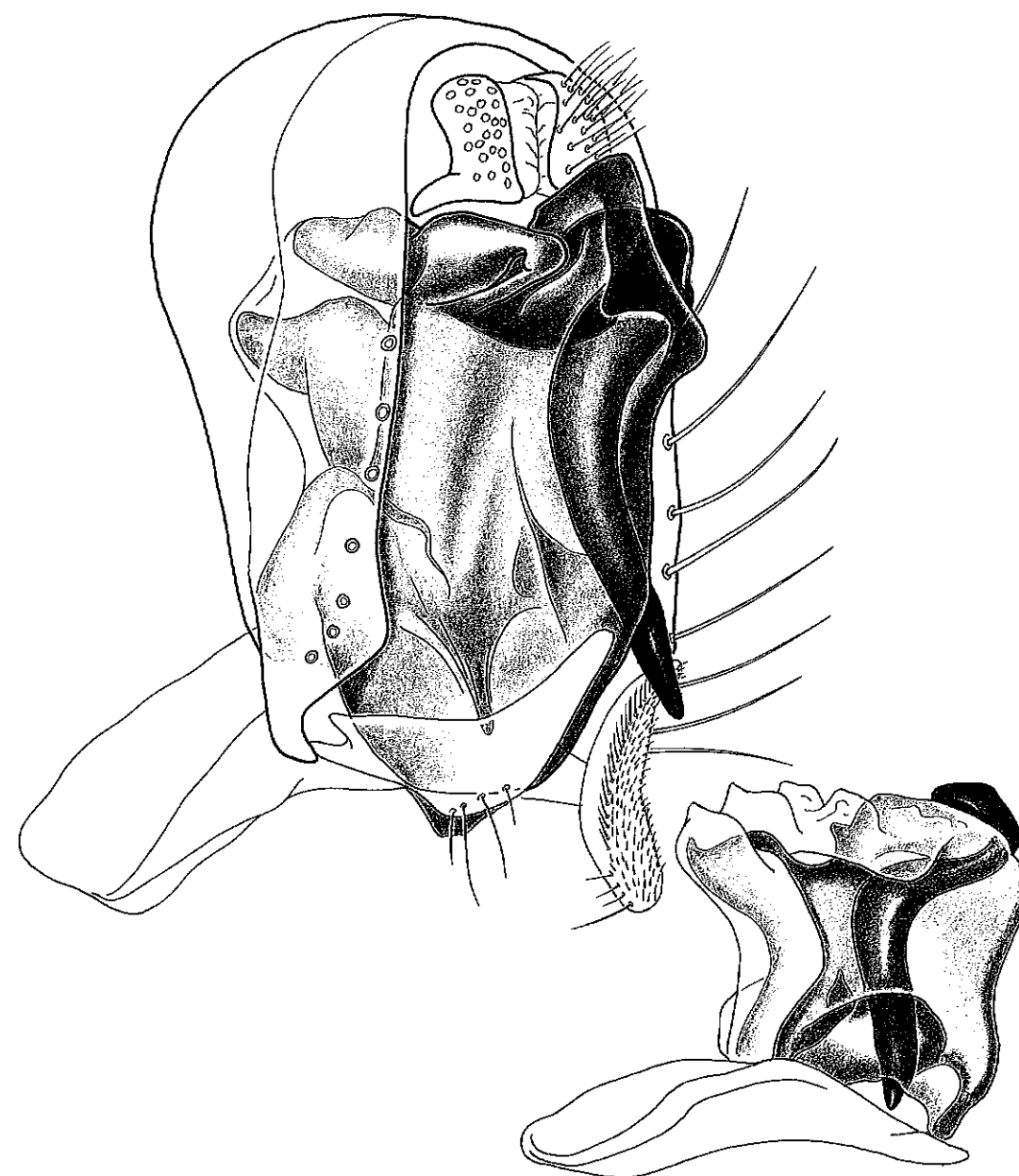


Fig. 25. Male terminalia of *C. pruinopleura*.



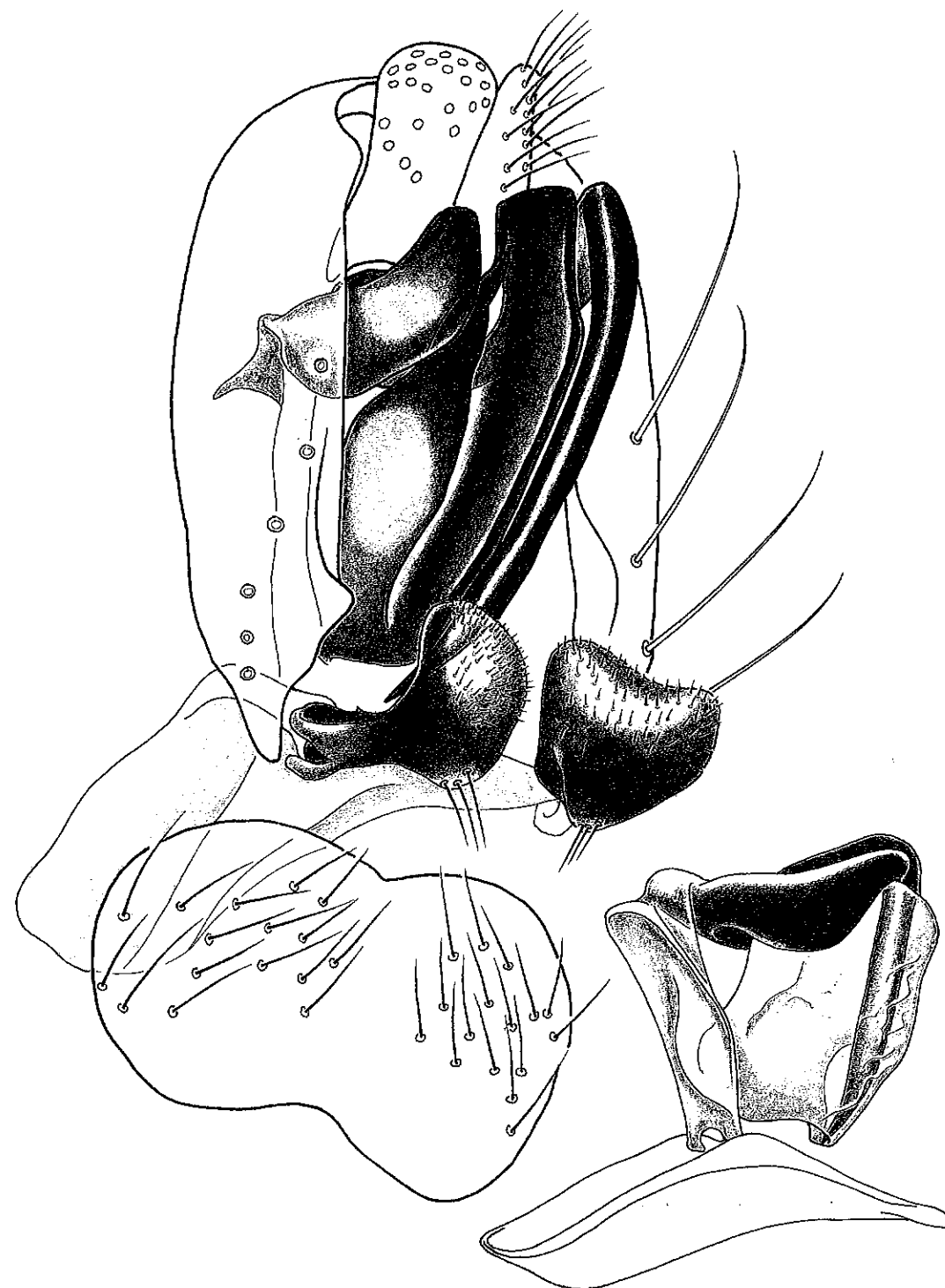


Fig. 26. Male terminalia of *C. sclerstyla*.



Fig. 27. Male terminalia of *C. spira*.



Fig. 28. Male terminalia of *C. tepui*.

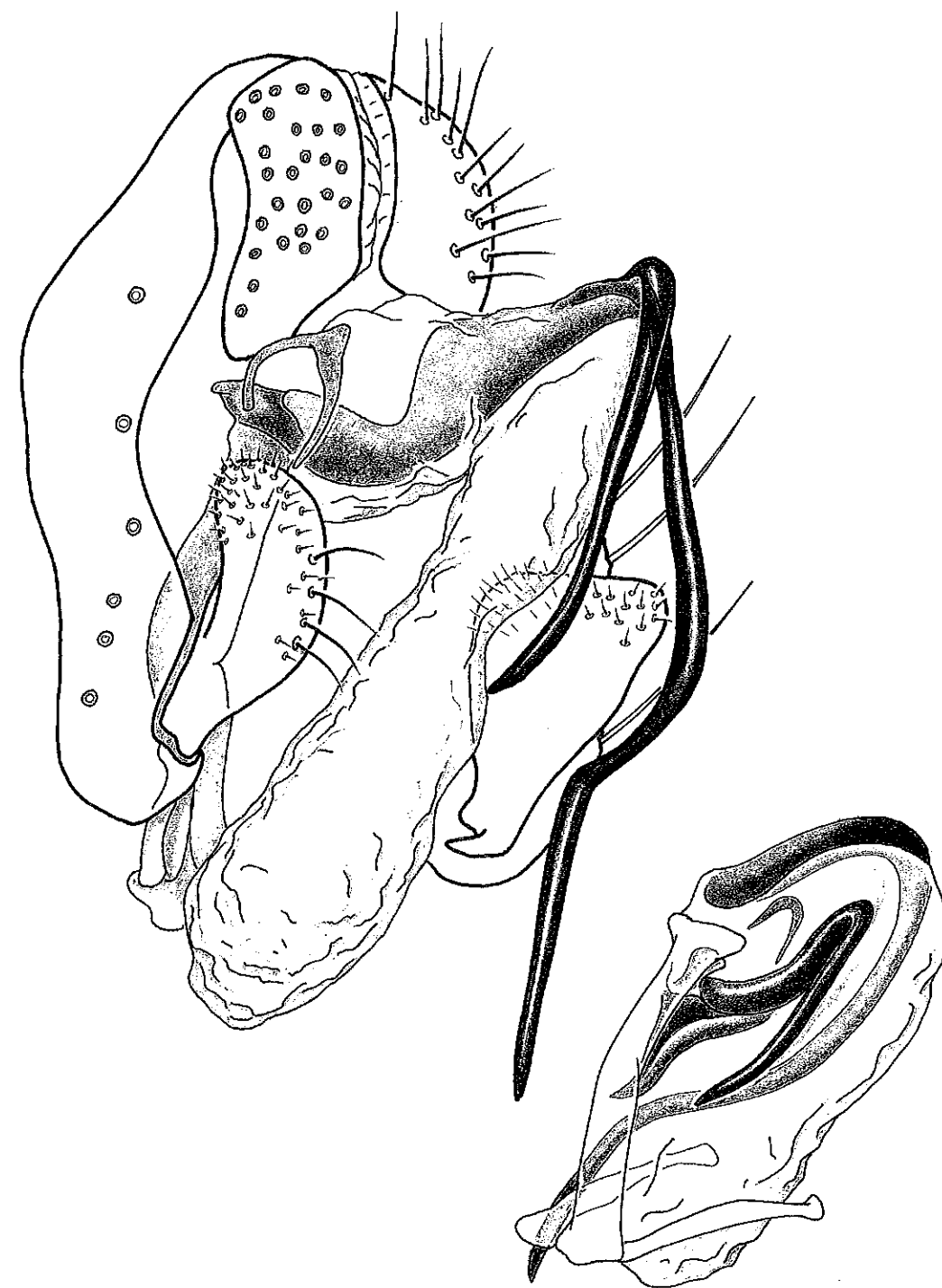
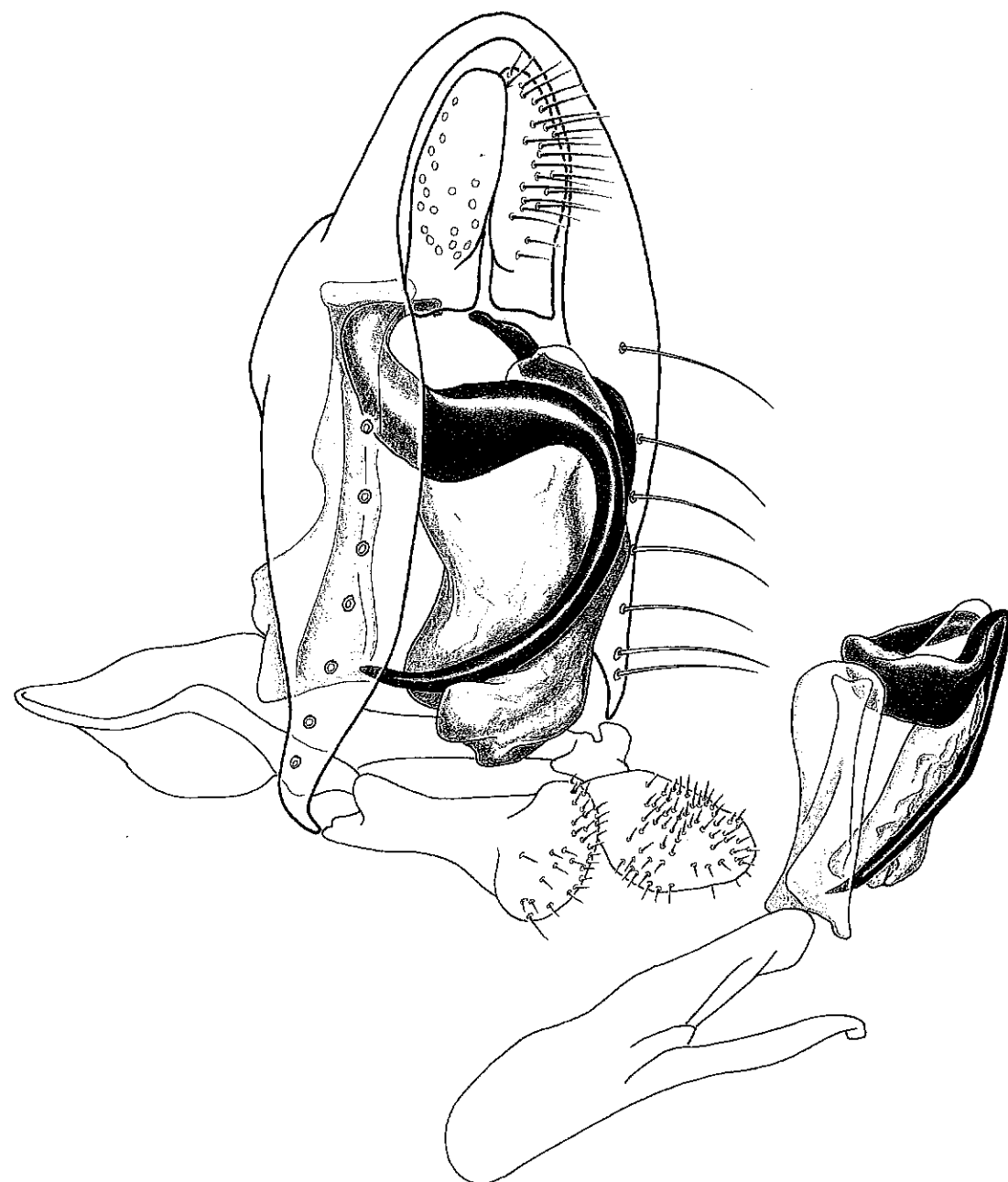
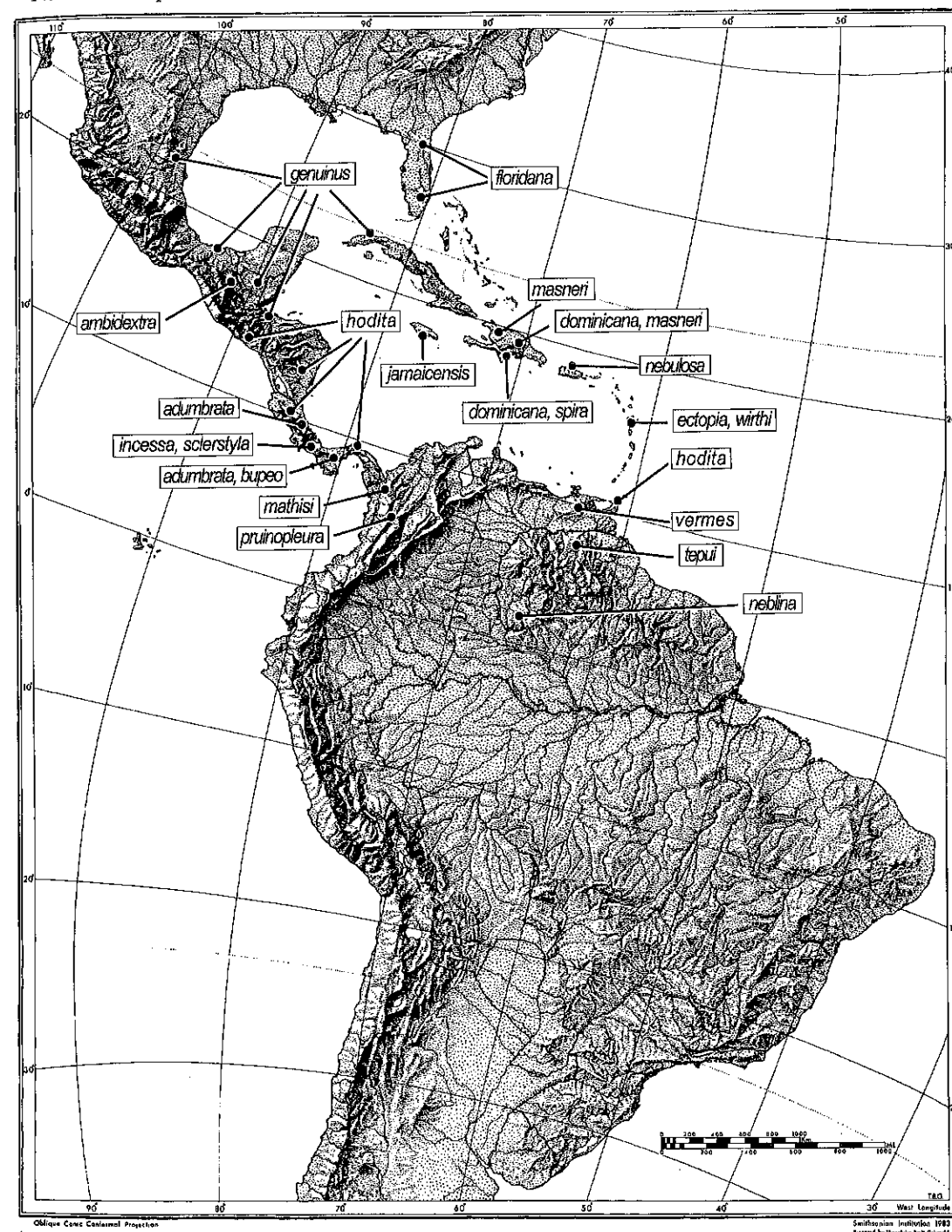


Fig. 29. Male terminalia of *C. vermes*.

Fig. 30. Male terminalia of *C. wirthi*.

## Nebulosa Group

Fig. 31. Distributions of *nebulosa* group species.

## INVERSA SPECIES GROUP

DIAGNOSIS: Interorbital and orbital setulae usually quite long and stout. Most species with wing having a light, diffuse infuscation over the costal edge, but considerably darker in some species and usually extended to apex of vein  $R_{4+5}$ . Vein  $R_{2+3}$  very slightly curved, straight, or almost straight. X-vein dm-cu slightly bent in most species. Clouds over x-veins r-m and dm-cu smaller and lighter than in *nebulosa* group species. *C. spinacosta* much different than other species (see description).

*Cladochaeta austrinversa*, new species

Figures 32, 34, 39

DIAGNOSIS: One of only few South American species in the group and apparently widely disjunct from the others. With enlarged prescutellar acrostichal setulae. Wing broad, with dark, diffuse costal infuscation. Cercus of male with long, broad ventral lobe. Male genitalia with paraphyses widely separated and broad; dorsal lobes short (one-half length of ventral lobes); dorsal lobes hooked; surstylus pointed.

DESCRIPTION: HEAD: Eyes with sparse, fine setulae; greatest length in line with greatest height of head. Head quite tall (HL/HD = 0.76 [holotype]). Pedicel, flagellomere I, and frons ochre. Arista with 4 dorsal branches, evenly spaced; apical fork short (dorsal branch one-half the length of ventral branch of fork); ventral branch midway between branches d-3 and d-4. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital one-third the size of proclinate; exactly lateral to proclinate. Frons of moderate length and width, with 5–6 long interorbital setulae per side, on anterior half. Face tan and of moderate depth and width (FW/HW = 0.33 [N = 2]). Cheeks tan, of moderate depth (CD/ED = 0.13).

THORAX: Notum and scutellum ochre to light tan; pleura slightly lighter. Anterior dorsocentral setae one-half the length of posterior dorsocentrals; post. dorsocentral slightly closer to ant. dorsocentral than to scutellar margin. Three pairs of enlarged prescutellar acrostichals; posteromedial pair largest, ca.

2.5× size of smallest acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta slightly enlarged, 1.5× size of smallest acrostichals. Anterior and posterior scutellar setae damaged in both specimens. Two large postpronotal lobe setae present. Legs light yellow; apical half of forefemur with 2 long dorsolateral and 2 ventrolateral setae. Halter light brown. Entire wing evenly and lightly fuscous, membrane with dense microtrichiae. Darker, diffuse infuscation at costal edge, barely reaching vein  $R_{4+5}$  except at its apex. Costal spinules typically short, but stout and dense. X-vein r-m without cloud of infuscation; dm-cu with barely perceptible cloud. Vein  $R_{2+3}$  virtually straight. X-vein dm-cu slightly bent.

ABDOMEN: Tergites dark, even brown. Female terminalia unknown. Male genitalia: Cercus with ventrolateral lobe, lightly sclerotized; ventromedial margin of cercus with group of 7–8 minute setulae. Epandrium slightly higher than wide, height ca. 1.2× the width. Ventrolateral halves of epandrium (epandrial lobes) broad (length ca. 3× the width), each lobe with row of 5 long, stiff setae (2 dorsalmost ones are largest). Paraphyses heavily sclerotized; halves are widely separated. Dorsal lobes short, not quite half the length of ventral lobes; ventral lobes slightly convergent at apices. A sharp, spine-like lateral lobe is attached to base of ventral lobe; lateral lobes pointed ventrally and medially. Aedeagus membranous, lying between dorsal and ventral lobes of paraphyses and extended slightly beyond apices of ventral lobes; apex slightly sclerotized. Aedeagal apodeme upright, narrow, troughlike. Hypandrium of moderate width, with deep ventral keel. Surstyli with apex pointed and triangular in lateral view, with row of ca. 20 fine setae on apical edge; triangular apex sclerotized. Apical sternites not examined.

TYPES: Holotype, Male: PERU: Lima, 26/VIII/14, H. S. Parish (dissected, no. 168). Paratype: same data, 1♂ (no. 167) (NMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: From Latin *austri* (southern) and *inversa*, in reference to the most southerly record of the species group.

*Cladochaeta dracula*, new species

Figures 32–34, 37, 40

DIAGNOSIS: Most similar to *C. heedi*. Best distinguished on basis of following: postpronotal lobe with 1 large setae (not 2 setae, as in *heedi*), prescutellar acrostichals not enlarged (large pair in *heedi*), arista with ventral branch opposite d-4 or closer to it in *heedi* (closer to d-3 in *dracula*); notum yellowish, pleuron light brown; male genitalia with toothlike median lobe of paraphysis shorter in *dracula*, aedeagus slightly larger in *dracula*. Female terminalia distinctly different in *dracula*: apical tergite unsclerotized, striplike (short); cerci much smaller relative to penultimate tergite; apical sternite (oviscapt) in ventral view a thin, U-shaped sclerite with small median plate having 10–12 minute setulae and anteromedian apodeme attached to internal V-shaped sclerite with bulbous ends.

DESCRIPTION: HEAD: Eyes with short, dense setulae; greatest length of eye in line with greatest height of head. Head of moderate height. Pedicel and flagellomere I light brown. Arista with 3–4 dorsal branches (3 in holotype, with branch d-4 missing), branch d-2 closer to d-1 than to d-3; apical fork with dorsal branch one-half the length of ventral branch; ventral branch closer to d-3 than to d-4; row of 8–9 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to slightly posterior of proclinate. Frons yellow to light brown (darker around ocellar triangle in some specimens); of moderate length and width, with 3–4 long interorbital setulae per side near ptilinal suture. Face tan to yellow and of moderate depth and width (FW/HW = 0.33 [N = 6]). Cheeks tan and relatively high for species in the group (CD/ED = 0.18).

THORAX: Notum and scutellum ochre to light brown, with slight bluish pruinescence; pleuron darker in spots. Anterior dorsocentral setae 0.5–0.6× length of posterior dorsocentrals; post. dorsocentral slightly closer to scutellar margin than to ant. dorsocentral or midway between them. Acrostichal setulae in 6 even rows; prescutellar ones and those anterior to ant. dorsocentral not en-

larged. Anterior scutellar setae slightly convergent, posterior scutellar strongly convergent or cruciate slightly to strongly (e.g., for one-half their length). One large postpronotal lobe seta present. Legs yellow; apical half of forefemur with 1 long dorsolateral seta and 2 ventrolateral setae. Halter light brown. Wing with light, evenly diffuse infuscation over costal edge, not reaching vein  $R_{4+5}$  until its apex; faded toward apex of vein  $R_{4+5}$ . Very light clouds surrounding x-veins r-m and dm-cu; cloud over dm-cu barely extended to vein  $CuA_1$ . Vein  $R_{2+3}$  almost straight. X-vein dm-cu straight.

ABDOMEN: Tergites even light brown in males and females, including epandrium. Female terminalia: Apical tergite a very narrow strip, mostly hidden by penultimate tergite. Apical sternite also a very thin strip, inverted and U-shaped, with small oval, median sclerite bearing ca. 10 minute setulae. Small median sclerite connected to pair of internal scoop-shaped apodemes. Male genitalia: Cercus with long ventrolateral lobe, length nearly equal to that of cercus. Ventrolateral halves of epandrium (epandrial lobes) relatively narrow (length ca. 4× width), each lobe with even row of 6 long, stiff setae. Paraphyses heavily sclerotized; halves are widely separated. Paraphyses with apical halves strongly hooked ventrally and then inward. A small spurlike medial lobe lies near middle of each paraphysis. Aedeagus with sclerotized preapical lateral flanges and ventroapical "tongue," dorsal part membranous; apex turned upward; aedeagus lying between paraphyses. Aedeagal apodeme projected inward, not upright; with forked base where both arms articulate with apices of paraphyses; "stem" of aedeagal apodeme 1.5× the length of arms. Hypandrium narrow, with small lateral flanges; gonopods long and curved upward. Surstyli simple, lobelike, unsclerotized, with ca. 20 fine setae on lateral surface and apical edge. Apical sternites not examined.

TYPES: Holotype, Female: ARIZONA: Gila Co.: Jones Water C. G., 30/VII/85, Wilford J. Hanson (in AMNH) (genitalia not dissected). Paratypes: 3♀, 1♂, from same series as holotype (2♀ dissected, nos. 2, 3; 1♂, no. 1) (in AMNH and UTSC).

OTHER MATERIAL EXAMINED: ARIZONA:

*Cochise Co.*; Southwestern Research Station, 5 mi W Portal, 5400 ft, 7/X/68, V. D. Roth, "reared from wild grape," (1♂, 1♀).

ETYMOLOGY: Although the larval habits are unknown, it can safely be presumed that the species feeds on hemolymph, analogous to the mythical human.

DISCUSSION: Two specimens from the Southwestern Research Station were labeled as "bred from wild grape," but most likely they were breeding on a spittlebug living on the grape.

*Cladochaeta florinversa*, new species

Figures 32–34, 37, 40

DIAGNOSIS: Arista with 4–5 relatively short dorsal branches; thorax and head generally yellow (dorsal portion of pleuron very light brown); costal half of wing infuscate, without clouds over x-veins; 2 postpronotal lobe setae; enlarged prescutellar acrostichal setulae; male genitalia with paraphyses somewhat flattened and curved backward and under; small medial lobes at bases of paraphyses, with apices that touch. Restricted to southern Florida and Bermuda; possibly occurs in the Bahamas.

DESCRIPTION: HEAD: Eyes with short, dense setulae; greatest length of eye in line with greatest height of head. Head relatively tall. Pedicel and flagellomere I yellow. Arista generally with 4 dorsal branches (a short branch, d-5, in 1 Bermuda specimen); dorsal branches evenly spaced; apical fork with dorsal and ventral branches of similar lengths; ventral branch opposite or distal to branch d-4; row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture 1.5× distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to proclinate. Frons yellow and of moderate length and width, with 3–4 long interorbital setulae per side near ptilinal suture. Ocellar triangle yellow. Face yellow and of moderate depth and rather narrow (FW/HW = 0.30 [N = 7]). Cheeks yellow, rather shallow (CD/ED = 0.12).

THORAX: Notum and scutellum yellow; notopleural area and dorsal half of pleuron slightly darker. Anterior dorsocentral setae 0.5× length of posterior dorsocentrals; post.

dorsocentral closer to scutellar margin than to ant. dorsocentral. Acrostichal setulae in 6 even rows. Three pairs of enlarged prescutellar acrostichals present: posterolateral pair largest, other 2 pairs 1.5× size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta enlarged (1.5× size of other acrostichals). Anterior scutellar setae parallel, posterior scutellar strongly cruciate, for one-third to one-fourth their length. Two large postpronotal lobe setae present. Legs yellow; forefemur with 2 long dorsolateral setae and row of 3 ventrolateral (slightly shorter) setae. Halter knob light brown. Wing with dark infuscation over costal edge; extended to vein R<sub>4+5</sub>, but faded. No clouds of infuscation surrounding x-veins r-m and dm-cu. Vein R<sub>2+3</sub> very slightly curved, not straight. X-vein dm-cu slightly bent.

ABDOMEN: Tergites even, medium brown, with diffuse, lighter areas in middle. Female terminalia: Apical tergite narrowed dorsally; broader laterally, extended almost to apical sternite. Apical sternite a narrow, inverted U-shaped sclerite with squared apex. Apex with 2 small rounded surfaces, each bearing one stouter setula and 5–6 finer setulae. Lateral arms extended well beneath penultimate sternite. Beneath sternite is internal sclerite: striplike, with ends folded anteriorad. Male genitalia: Cercus with short ventrolateral lobe. Epandrium only slightly higher than wide. Ventrolateral halves of epandrium (epandrial lobes) relatively wide (length ca. 2.8× width), each lobe with even row of 6 stiff setae of moderate length. Paraphyses heavily sclerotized, with halves widely separated. Paraphyses with apical halves strongly hooked ventrally and then inward. A small spurlike medial lobe lies at base of each paraphysis; apices of medial spurs touching. Aedeagus unsclerotized, narrow; a membranous trough that is apically tapered. Aedeagal apodeme upright, narrow, slightly S-shaped. Hypandrium broad, with shallow ventral keel; gonopods short and flat. Surstyli are simple lobes, tapered apically to rounded apex; unsclerotized, with ca. 30 fine setae on lateral surface near apex and on apical edge. Apical sternites not examined.

TYPES: Holotype, Male: FLORIDA: *Martin Co.*: Sewalls Point, A. G. Wheeler, coll. Pupa collected 1/V/82; adult emerged 3/V/

82. Reared from spittle mass on *Clastoptera undulata* on *Casuarina equisetifolia*. Genitalia not dissected. Paratypes: FLORIDA: *Monroe Co.*: Big Pine Key, A. G. Wheeler, Jr., coll. Spittle mass collected 21/III/80, fly emerged 6–7/IV/80. ex: spittlemass *C. undulata* on *Casuarina equisetifolia*, 2♂, 2♀ (1 of each dissected, DAG nos. 17, 18). Types in the AMNH.

OTHER MATERIAL EXAMINED: BAHAMAS: Grand Bahama Island, Xanadu Beach, 23/VI/87, W. E. Steiner & M. J. and R. Molineaux (3♂, 1♀; nos. 189, 190) (NMNH). BERMUDA (BRITISH COMMONWEALTH): St. George's Parish, Ferry Reach, 6/X/88, D. J. Hilburn (numerous males, females, larvae) FLORIDA: *Clay Co.*: Gold Head Branch State Park, 22/XII/57 (1♂). *Dade Co.*: Homestead, Bayfront Pk., (5♂, 3♀), "ex spittlemass of *Clastoptera undulata* on *Casuarina equisetifolia*, larva coll. 8/IV/81, fly emerged 21–22/IV/81." Hollywood, 10/XI/54, "on *Stenotaphrum secundatum*," (1♂). Hialeah, 21/III/67, C. Stegmeier (1♂).

ETYMOLOGY: From Florida, the locality, and *inversa*, a close relative.

DISCUSSION: This is the species that was figured by Wheeler and Takada (1971), but which was erroneously thought to be *C. floridana*, as Vilela and Bächli (1990) had indicated. All of the rearing records indicate it to be from *Clastoptera* on *Casuarina*, except for one on *Stenotaphrum*. Since *Casuarina* is an ornamental tree that has been extensively transported and cultivated, it is possible that southern Florida and Bermuda do not represent the natural range of *florinversa*.

*Cladochaeta heedi*, new species

Figures 32–34, 36

DIAGNOSIS: Very similar to *C. dracula*, as described in diagnosis for that species (above), but with 2 large setae (not 1) on postpronotal lobe and pair of large prescutellar acrostichal setae present. Female terminalia in *heedi* distinctively different from *dracula*: apical tergite sclerotized, dorsomedial surface longest and with minute medial notch on anterior margin; cerci larger relative to penultimate tergite; apical sternite (oviscapt) in ventral view a U-shaped sclerite with stout lateral arms; median part of "U" with-

out small plate, but very narrow, with row of 12 fine, fairly long setulae, no trace of an anteromedian apodeme attached or an internal V-shaped sclerite.

DESCRIPTION: Very similar to *C. dracula*. Differences are as follows: HEAD: Arista with 4–5 dorsal branches (4 in holotype, missing apparently branch d-4); apical fork with dorsal branch very small; ventral branch opposite or closer to d-4 than to d-3.

THORAX: Pair of enlarged prescutellar setulae present, 2× size of other acrostichals. Two large postpronotal lobe setae present, of nearly equal sizes, or ventral one slightly smaller.

ABDOMEN: Female terminalia: Apical tergite heavily sclerotized, saddle-shaped, with broad dorsal surface, narrow lateral portions. Apical sternite an inverted U-shaped sclerite with broad lateral arms; apical surface with row of ca. 12 fine setulae. Lateral arms of sternite extended slightly beneath penultimate tergite. Male genitalia: Similar to *C. dracula* except that *heedi* has the following characteristics: paraphyses slightly shorter, with basal portion thinner; inner spurlike lobe longer and thinner; surstylus slightly broader in lateral view, apex more tapered, and with fewer (ca. 15 vs. 20) setulae. Distinctive features that *heedi* shares with *dracula* are paraphyses strongly hooked ventrad and inward, with spurlike medial lobe; aedeagus with sclerotized preapical lateral flange and ventroapical tongue, rest of aedeagus membranous.

TYPE: Holotype, Male: ARIZONA: *Pima Co.*: near Tucson, Bear Canyon, Catalina Mountains, ca. 6000 ft, W. B. Heed, 4/X/59. Genitalia not dissected. Paratypes: 5 males and females (1 of each dissected, DAG nos. 7, 8), with same label data. All types in the AMNH.

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Patronym in honor of William B. Heed (University of Arizona), collector of this series and whom we feel is the finest *Drosophila* naturalist.

*Cladochaeta inversa* Walker

Figures 32–34, 36, 41

*Drosophila inversa* Walker, 1861: 331. Sturtevant, 1921: 71.



*Cladochaeta inversa*: Wheeler and Takada, 1971: 234. (Biology references are reviewed under the section on life history.)

**DIAGNOSIS:** The only species of the genus from northeastern North America. Costal infuscation on wing fairly extensive; body mostly yellow; arista with 4–5 dorsal branches; pair of large prescutellar acrostichal setulae. Male genitalia: Paraphyses strongly hooked anteroventrad, longer and thinner than any other species in group; cercus with long ventral lobe; surstyli broad, with rounded base and pointed tip. Of species with both sexes known, genitalia unique for group, as described below.

**REDESCRIPTION:** **HEAD:** Eyes with short, fine, and dense setulae; greatest length of eye in line with greatest height of head. Head relatively high and short in lateral view. Pedicel ochre, flagellomere I light brown. Arista with 4–5 dorsal branches; ventral branch usually opposite d-4, sometimes even midway between d-3 and d-4; row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to pitilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to (and sometimes also slightly posterior to) proclinate. Frons with frontal vittae and frontal-orbital plates yellowish; ocellar triangle slightly darker. Frons of medium height and width. Interorbital setulae relatively long and fine; 4–5 per side. Face yellow and of moderate depth and width (FW/HW = 0.32 [N = 24]). Cheeks yellow and of slightly shallow (CD/ED = 0.14).

**THORAX:** Notum and scutellum ochre; notopleural area very light, diffuse brown. Anterior dorsocentral seta 0.6× length of posterior dorsocentrals; post. dorsocentral slightly closer to scutellar margin than to ant. dorsocentral or midway between them. Acrostichal setulae in 6 even rows. Pair of enlarged prescutellar acrostichals present, twice the size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta enlarged (1.5× the average size). Anterior scutellar setae parallel, posterior scutellars slightly cruciate. Two large setae on postpronotal lobe, dorsal one slightly longer and thicker. Legs yellow; forefemur with 1–

2 long dorsolateral setae (in middle of femur) and row of 3–4 ventrolateral (slightly shorter) setae, on distal half of femur. Halter knob light brown. Wing with diffuse infuscation over costal edge; darkest near costa and over vein  $R_{2+3}$ , faded toward radial veins, extended to apices of veins  $R_{4+5}$  and M. Very slight clouds on x-veins r-m and dm-cu, barely perceptible. Vein  $R_{2+3}$  very slightly curved, not straight. X-vein dm-cu straight.

**ABDOMEN:** Tergites dark to medium, evenly brown, with lighter median areas on some tergites. Female terminalia with apical tergite sclerotized, narrower dorsally; laterally, arms broader and extended ventrad to almost touching and forming complete ring. Apical sternite with broad, subrectangular sclerite bearing row of ca. 6 fine, stiff setulae on posterior edge. Sternite with short pair of broad arms, slightly twisted. Male genitalia: Cercus with long ventrolateral lobe, unsclerotized. Epandrium higher than wide, height ca. 1.5× width. Ventrolateral halves of epandrium (epandrial lobes) narrow (length ca. 4× the width), each lobe with even row of 5 long, stiff setae. Paraphyses heavily sclerotized; halves widely separated, relatively narrow; apical half hooked ventrad and inward. Medial lobe on each paraphysis attached to high hump at base of paraphysis; medial lobe long and thin, projected posteriad, not mediad, lying along base of paraphysis. Lateral lobes not present on paraphyses, but small window present where lobe would be. Aedeagus narrow, membranous, lying between medial lobes of paraphyses and extended beyond apices of medial lobes. Aedeagal apodeme with posterior portion upright, narrow; anterior portion triangular in lateral view; entire structure like a compressed funnel. Hypandrium broad, with deep ventral keel. Gonopods short, flat. Surstyli with apex pointed, with broad round base in lateral view; ca. 20 fine setae on apical part of medial surface. Apical sternite unmodified.

**TYPE:** The type was not examined but (if it still exists) is probably in the Natural History Museum, London. Since the American specimen that Walker described came from the eastern U.S., and only one widespread species occurs in this area, there should be no taxonomic confusion.

**MATERIAL EXAMINED:** CANADA: *Manito-*

*ba*: Bald Head Hills, 12 km N Glenboro, 4/VIII/83, K. N. Barber (1♂). **ONTARIO:** Burlington, Bronte Ck. P. P., 21/VIII/83, K. Barber (1♂); Constance Bay, 1/X/53 (1♀); Lake Jarvis, 20/VIII/52 (2♂); Guelph, 21–22/VIII/80, K. Barber (7♀, 3♂), 21/VIII/71 K. Deacon (1♂), 10/VIII/76, E. Innes (1♂); Marmora, 20/VIII/52 (10♂, 16♀), “swept from hemlock [*Tsuga canadensis*],” “swept, white pine [*Pinus strobus*],” “taken on cedar”; Otawa, 24/VIII/59 (1♂); Maynooth, 5/IX/53 (1♀); Point Pelee, 9/IX/54 (2♂), 13/IX/78, W. Ralley (2♀), 9/VII/80, K. N. Barber (2♂); Port Credit, 14/VIII/38 (1♂); Wainfleet Bog, 8 km S Wellard, 29/IX–5/X/87 D2C, R. Sterling (1♀); Windsor, 11/VII/76, S. Marshall (1♂). **QUEBEC:** Old Chelsea, 31/VIII/58 (1♀); Wakefield, 26/VI/46 (1♂).

**UNITED STATES:** **GEORGIA:** Stone Mountain, 26/X/47 (2♂, 1♀). **INDIANA:** Lafayette, 1/VIII (1♀, 1♂). **ILLINOIS:** Cook Co.: Algonquin, Little Red Schoolhouse (2♀, 1♂), “reared from *Clastoptera proteus* nymph”; Algonquin, 2/X/09 (1♂). **LOUISIANA:** County?: New Iberia, “pecan twigs,” 8/X/29 (1♀). **MARYLAND:** Glen Echo, 2/VIII/22 (2♂, 4♀). **MASSACHUSETTS:** Beverly, 28/VIII/1869 (1♂); Holliston, 15/VII (1♂), 15/IX (1♂); Newton, 18/IX (1♂). **MICHIGAN:** Bridgeman, 5/VII/86 (1♂, 1♀), “reared from *Clastoptera obtusa* nymph”; Houghton Co.: 20/VIII/59 (2♂); Kalamazoo Co.: Gull Lake Biological Station, 21/VIII/64 (1♂); Lapeer Co.: Deerfield Twp., 11/VIII/46, “white pine” (2♀); Montcalm Co.: 12/IV/59 (1♀); Wayne Co.: VII/61 (1♀). **MINNESOTA:** Eaglesnest, 30/VII/59 (1♂); Olmstead Co.: “inquiline from *Clastoptera froth*” (1♂, 1♀, 2 empty puparia), Olmstead Co.: VII/05, “from *Clastoptera froth*,” C. N. Ainslie (2♂). **MISSISSIPPI:** Agricultural College, 8/VIII/20 (1♂). **NEW HAMPSHIRE:** “White Mountains” (1♂). **NEW JERSEY:** Fort Lee, 2/X/21 (1♂); Wildwood, VII/12 (1♂). **NEW YORK:** Delaware Co.: Cadosia & vic. (7♂, 4♀), “ex: spittle of *Clastoptera obtusa* on alder, pupa coll. 5/VII/80, fly emerged 10/VII/80, 11/VII, 12/VII/80; Long Island: Huntington, Kalbfleish Research Station, 15/VII/62 (1♂, 1♀); Montauk, 6/VI/51 (1♂); Niagara Co.: Olcott, 1/IX/24, M. C. VanDuzee (1♂); Riverhead, 20/VII/28 (1♀); New York City, IX/19 (3♀);

Tompkins Co.: Ithaca (1♂, no date); county?: Rainbow Lake, 25/VIII/40, L. Blevins (1♂). **OHIO:** Portage Co.: Kent, VIII–IX/various years (numerous ♂, ♀, larvae). **PENNSYLVANIA:** Blair Co.: McKee, 10/VI/73, D. J. Shetlar (1 ♀); Dauphin Co.: Harrisburg, Wildwood Park (3♂, 2♀) “ex: spittle of *Clastoptera obtusa* on alder, pupa coll. 18/VI/81, adult emer. 19–21/VI/81; W. Hanover Twp., Rt. 443, Fishing Creek Valley School (8♂, 4♀) (same host data as for Wildwood Pk.). **VIRGINIA:** Chain Bridge, 18/IX/21, J. R. Malloch (3♀, 1♂); Falls Church, Holmes Run, 10–17/IX/60 and 12/IX/61 (3♂, 3♀) “light trap”; **WISCONSIN:** Door Co.: 20/VIII/59, R. F. Brocks (1♂).

**DISCUSSION:** Wheeler and Takada (1971) mentioned this species as being widespread over the northeastern United States (also parts of southeastern Canada), and suggested that the northern part of *inversa*'s distribution may extend as far west as Wisconsin and Minnesota. Based on the close comparison made here of the male genitalia of western and eastern specimens, this does appear to be the case. We present some detailed information on the phenology and host biology of this species at the end of the monograph.

#### *Cladochaeta mexinversa*, new species

Figures 32–34, 36, 42

**DIAGNOSIS:** Body mostly yellow; anterior reclinate orbital setae slightly anterolateral to proclimates; male genitalia with paraphyses having pair of widely separated ventral lobes and pair of short, broad, paddle-shaped median lobes.

**DESCRIPTION:** **HEAD:** Eyes with short, fine, and sparse setulae; greatest length of eye in line with greatest height of head. Head relatively high and short in lateral view (HL/HD = 0.76 [HT]). Pedicel and flagellomere I mostly yellow, with some light brown. Arista with 4 evenly spaced dorsal branches; apical fork small to minute; ventral branch slightly closer to d-3 than to d-4; row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to pitilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to (more often also slightly anterior to) proclinate. Frons

with frontal vittae and frontal-orbital plates yellow; ocellar triangle yellow, with dark brown circle surrounding each ocellus. Frons of medium height and width. Interorbital setulae relatively long and fine; 6 per side. Face yellow and of moderate depth and width (FW/HW = 0.32 [N = 2]). Cheeks yellow and of moderate depth (CD/ED = 0.13).

THORAX: Notum and scutellum even light yellow; notopleural area very diffusely fuscous. Anterior dorsocentral seta  $0.6\times$  length of posterior dorsocentrals; post. dorsocentral midway between scutellar margin and anterior dorsocentral. Acrostichal setulae in 6 even rows. Pair of enlarged prescutellar acrostichals present, but only  $1.5\times$  size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta barely larger than other acrostichals. Anterior scutellar setae parallel, posterior scutellars cruciate for  $0.3\times$  their length. Three large setae on postpronotal lobe, dorsalmost and ventralmost ones ca.  $0.7\times$  length of middle seta. Legs yellow; forefemur with 1–3 long dorsolateral setae (in middle of femur) and row of 3–4 ventrolateral (slightly shorter) setae, on distal half of femur. Halter knob light brown. Wing with dark diffuse infuscation on apical half of costal edge; extended to, and faded toward, apex of vein  $R_{4+5}$ ; darkest part of costal infuscation at apex of vein  $R_{2+3}$ . Very slight clouds surrounding x-veins r-m and dm-cu; cloud over dm-cu barely extended to vein  $CuA_1$ . Vein  $R_{2+3}$  very slightly curved, not straight. X-vein dm-cu slightly sinuous.

ABDOMEN: Tergites light brown. Female terminalia mostly sclerotized, including tergites and epi-/hypoproct. Apical tergite dorsally with median lobe bearing notch; lateral arms extended to slightly beneath apical sternite. Apical sternite broad, with convex lateral margins; apical margin truncate, slightly irregular, with row of ca. 12 stiff setulae. Male genitalia: cercus with long, gradually tapered ventrolateral lobe, unsclerotized. Epandrium only slightly higher than wide. Ventrolateral halves of epandrium (epandrial lobes) broad (length ca.  $3\times$  width), each lobe with even row of 5 long, stiff setae. Paraphyses heavily sclerotized; halves are very widely separated. Dorsal lobes of intermediate length, about half the length of ventral lobes; sclerotized; ventral lobes extended to

ventral margins of surstyli, straight, pointed downward (not curved inward), very widely separated (by distance about equal to width of cerci). Broad, blunt lateral lobe attached to base of ventral lobe; sclerotized. Pair of short, paddle-shaped lobes attached to medial surface of paraphysis bases, lying beneath aedeagus and posteroventrally to bridge between paraphysis; sclerotized. Aedeagus entirely membranous, apical half slightly trough-shaped; extended almost to apices of ventral lobes. Hypandrium broad, with shallow ventral keel; gonopods long and thin. Surstyli with ventroapical part pointed in lateral view, with slight lateral keel; row of ca. 20 fine setae on apical edge; apical third of surstylus sclerotized; base typically broad for species group. Apical sternites not examined.

TYPES: Holotype, Male: MEXICO: *Chiapas*: San Cristobal de Las Casas, 7087 ft, 3–7/VI/1969, B. V. Peterson (dissected, no. 100; in CNC). Paratype: MEXICO: *Chiapas*: 7 mi SE San Cristobal, 28/V/69, 7000 ft, H. J. Teskey (not dissected, but abdomen lost).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Adapted from Mexico, the locality of the species, and *inversa*, the group to which it belongs.

#### *Cladochaeta neoinversa*, new species

Figures 32, 35, 38, 43

DIAGNOSIS: Body yellow; 1 large postpronotal seta; pair of prescutellar setae, only  $1.5\times$  size of acrostichals; wing with diffuse light apical and costal infuscation; male genitalia similar to *inversa*, but with differences as described below.

DESCRIPTION: HEAD: Eyes with short, fine, and dense setulae; greatest length of eye in line with greatest height of head. Head relatively high and short in lateral view (HL/HD = 0.65 [HT]). Pedicel and flagellomere I mostly yellow, with some light brown. Arista with 3–4 evenly spaced dorsal branches; apical fork relatively large; ventral branch midway between d-3 and d-4; row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture  $1.5\times$  distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to proclinate. Frons

with frontal vittae golden and shining, frontal-orbital plates light yellow; ocellar triangle yellow, with dark brown circle surrounding each ocellus. Frons slightly short and of medium width. Interorbital setulae relatively long and fine; 5–6 per side. Face yellow and of moderate depth and width (FW/HW = 0.31 [N = 6]). Cheeks yellow and of moderate depth (CD/ED = 0.13).

THORAX: Notum, scutellum, and pleuron evenly light yellow. Anterior dorsocentral seta one-half the length of posterior dorsocentrals; post. dorsocentral midway between scutellar margin and anterior dorsocentral. Acrostichal setulae in 6 even rows. Pair of enlarged prescutellar acrostichals present, but only  $1.5\times$  size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta barely larger than other acrostichals. Anterior scutellar setae parallel, posterior scutellars cruciate for one-fourth their length. One large seta on postpronotal lobe. Legs yellow; forefemur with 1 long dorsolateral seta (in middle of femur) and row of 3 ventrolateral (slightly shorter) setae, on distal half of femur. Halter knob light brown. Wing with very light, diffuse infuscation over apical half of costal edge, very faded toward vein M. Barely perceptible clouds of infuscation on x-veins r-m and dm-cu. Vein  $R_{2+3}$  very slightly curved, not straight. X-vein dm-cu slightly bent in the middle.

ABDOMEN: Tergites light brown, with diffuse yellow areas on tergites I–IV; last tergite yellow in females. Female terminalia: Similar to *inversa* except that ends of sclerotized apical tergite are curled dorsad; apical sternite is deeper, and lateral arms are farther apart. Male genitalia: Similar to *inversa* except that *neoinversa* has the following characteristics: paraphyses with medial lobes shorter, blunt, and with broader base; lateral surface of paraphysis base without small window, but with short lobe; ventrolateral surface of main paraphysis hook with small spur near middle; aedeagus also membranous but with slightly more sclerotization at edges. Surstylus with apex not upturned or as pointed. Features shared with *inversa* are long, tapered ventrolateral lobe of cercus; strongly hooked paraphyses, with well-developed medial lobes; even row of 5 stiff setae on each

epandrial lobe; surstylus with broad, rounded base and apex with long, fine setae.

TYPES: Holotype, Male: MEXICO: *San Luis Potosi*: El Bonito, 7 mi S of Ciudad Valles, 300 ft, 20/XII/1970. P. H. & M. Arnaud. Genitalia dissected (no. 73). Paratypes: 3 females, with same label data as holotype (1 dissected, no. 74). All in the CAS, with 1 paratype in the AMNH.

OTHER MATERIAL EXAMINED: MEXICO: *San Luis Potosi*: Tamazunchale, 400 ft, 22/XII/1970, P. H. & M. Arnaud (1, not dissected); Distrito Federal, 15 mi S El Guarda, 14/XI/46, (1♂, dissected, no. 72).

ETYMOLOGY: From “new” *inversa*, in reference to the group in which it belongs.

#### *Cladochaeta paradoxa* (Lamb)

Figures 38, 44

*Drosophila paradoxa* Lamb, 1918: 159; Sturtevant, 1921: 72 (redescription).

*Clastopteromyia paradoxa*: Sturtevant, 1942: 27; Frota-Pessoa, 1947: 217.

*Cladochaeta paradoxa*: Wheeler, 1981: 34; Vilela & Bächli, 1990: 12.

DIAGNOSIS: Best distinguished from other members of the *inversa* group based on details of the paraphyses and surstyli, as described below. Known only from Trinidad.

REDESCRIPTION: Wing with dark, diffuse infuscation over costal edge, wing tip, and crossveins. Infuscation on costal edge faded proximad. Small clouds of infuscation over x-veins r-m and dm-cu, cloud on dm-cu barely extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel, slightly curved. Crossvein dm-cu straight. Wing tip slightly pointed.

Male genitalia: Difficult to discern relative positions of structures, because of distortion in only slide-mounted (holotype) specimen. Paraphyses with thin, apical hooks; smaller, subbasal hook. Aedeagus mostly membranous, with pair of small sclerotized rods flanking apex. Surstyli with broad base; tapered to thin apical sclerotized lobe bearing numerous fine short setulae.

TYPES: Lectotype, male (designated by Vilela and Bächli [1990]), from TRINIDAD: St. Joseph, 5/XII/17, C. B. Williams. The pinned specimen itself is badly damaged,

having lost the head, and the remainder of the specimen is glued onto a plastic square. The genitalia are very distorted on a microscope slide mount (see fig. 44). Vilela and Bächli (1990) also designated 2 paralectotype females. All types in the BMNH.

**MATERIAL EXAMINED:** The lectotype male and slide preparation. We have not seen any material of this species other than the original type specimens; presumably it has not been collected for the last 70 years.

**DISCUSSION:** Vilela and Bächli (1990) stated that the "male terminalia of this species [*paradoxa*] seem to be very similar to those by Wheeler and Takada (1971: 235 [sic]) for a specimen collected in Ontario, Canada, and identified by them as *Cladochaeta inversa*, whose type is apparently lost." The species to which Wheeler and Takada referred was indeed *C. inversa*, based simply on their illustrations. In addition, our examination of the specimens from Marmora, Ontario (the specimens studied by Wheeler and Takada, in the CNC), indicates that there is no question about their identity as *C. inversa*. *C. paradoxa* is indeed in the *inversa* group, and is only the second species of this predominantly Nearctic group known from South America. The other species is *C. austrinversa* from Peru.

*Cladochaeta reversa*, new species

Figures 32, 33, 41

**DIAGNOSIS:** Body yellow; wing with very light, diffuse costal infuscation; arisal branches long, with 4 dorsals and 1 ventral; male genitalia with paraphyses very distinct within the species group, as described below.

**DESCRIPTION:** HEAD: Eyes with short, fine, and sparse setulae; greatest length of eye in line with greatest height of head. Head relatively high and short in lateral view (HL/HD = 0.78 [holotype]). Pedicel and flagellomere I mostly yellow, with some light brown. Arista with 4 long dorsal branches; apical fork relatively large; ventral branch either midway between d-3 and d-4 or directly opposite d-4 (variation seen in only known specimen); row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate.

Anterior reclinate orbital one-half the size of proclinate; exactly lateral to proclinate. Frons with frontal vittae dull tan, frontal-orbital plates slightly lighter; ocellar triangle light brown. Frons slightly short and of medium width. Interorbital setulae of medium lengths, with 4 per side. Face yellow and of moderate depth and width (FW/HW = 0.32 [N = 1]). Cheeks yellow and shallow (CD/ED = 0.10).

**THORAX:** Notum, scutellum, and pleuron yellowish tan. Anterior dorsocentral setae very different in single known specimen: left one half the length of posterior dorsocentrals; right one much smaller, fine and 0.3× size of posterior dorsocentral. Posterior dorsocentral seta midway between scutellar margin and anterior dorsocentral. Acrostichal setulae in 6 uneven rows. Pair of enlarged prescutellar acrostichals present, 1.5× the size of other acrostichals. Pair of acrostichals immediately anterior to ant. dorsocentral setae as different as are ant. dorsocentrals: left one slightly stouter than other acrostichals but barely longer; right one with no noticeable difference. Anterior scutellar setae parallel, posterior scutellars lost in holotype. Two large setae on postpronotal lobe, ventral one 0.6× length of other. Legs yellow; forefemur with 1 very long (2 shorter) dorsolateral seta and row of 3 ventrolateral setae (1 very long and 2 shorter, proximal ones). Halter knob tan. Wing almost entirely hyaline except for very light, diffuse infuscation at costal margin, extended to apex of vein  $R_{2+3}$ . No clouds surrounding x-veins r-m and dm-cu. Vein  $R_{2+3}$  virtually straight. X-vein dm-cu slightly bent.

**ABDOMEN:** Female terminalia unknown. Male genitalia: Cercus with short, thin ventrolateral lobe, unsclerotized. Epandrium only slightly higher than wide. Ventrolateral halves of epandrium (epandrial lobes) broad (length ca. 2.5× width), each lobe with uneven row of 7–8 stiff setae of intermediate length (dorsalmost one nearly twice the length of others). Paraphyses heavily sclerotized, joined with aedeagus into complicated structure. Dorsal lobes of paraphyses curved gently inward, equal in length to ventral lobes; ventral lobes anterior to dorsal ones, apices sharp. Aedeagus sclerotized, broad, equal in length to dorsal lobes of pa-

raphyses; with sclerotized "harness" internally, no membranous structures seen. Aedeagal apodeme large, with forked posterior part (ends of arms articulating with bases of paraphyses); trunk short, deep, laterally flat. Hypandrium small; gonopods wide and short. Surstyli relatively long, base broad; apex with dorsal spur and small ventral lobe minutely hooked, with ca. 20 fine setae on dorsal spur; apical lobes sclerotized.

**TYPE:** Holotype, Male: EL SALVADOR: San Salvador, I/54, W. B. Heed (dissected, DAG no. 241) (AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the holotype specimen.

**ETYMOLOGY:** In reference to no particular structure, just another name indicating placement in the *inversa* species group.

*Cladochaeta spinacosta*, new species

Figures 32–33, 35, 45

**DIAGNOSIS:** Easily distinguished externally by row of 7 stout, long, spinelike setae on costal margin of wing (apical ones larger, and possibly in males only); wing infuscation dark and extensive; male genitalia also distinct: paraphyses are simple, stout, heavily sclerotized, pointed lobes; surstylus stout, with rounded base, heavily sclerotized.

**DESCRIPTION:** HEAD: Eyes with short, fine, and sparse setulae; greatest length of eye in line with greatest height of head. Head of moderate depth and length in lateral view (HL/HD = 0.84 [HT]). Pedicel mostly yellow, flagellomere I light brown. Arista with 4 dorsal branches; apical fork relatively large; ventral branch midway between d-3 and d-4; row of 7–8 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to proclinate. Frons with frontal vittae golden, slightly shiny; frontal orbital plates and ocellar triangle of similar hue but not shiny. Frons of moderate length and width. Interorbital setulae relatively long, row of 3 per side pointing at opposite setula. Face yellow, of moderate depth and fairly narrow (FW/HW = 0.28 [N = 1]). Cheeks yellow and very shallow (CD/ED = 0.07).

**THORAX:** Notum, scutellum, and pleuron yellowish tan. Anterior dorsocentral very short, 0.3× length of posterior dorsocentral. Posterior dorsocentral seta slightly closer to anterior dorsocentral than to scutellar margin. Acrostichal setulae in 6 uneven rows. Pair of enlarged prescutellar acrostichals present, twice the size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta barely differentiated from other acrostichals. Anterior scutellar setae parallel, posterior scutellars cruciate for 0.3× their length. Postpronotal lobe with 1 large and 1 smaller seta. Legs yellow; forefemur with 2 long dorsolateral setae and row of 3 ventrolateral setae. Halter knob light brown. Wing unique within the genus: apical half with dark infuscation extended from costal edge to apical third of vein M. Clouds surrounding x-veins r-m and dm-cu dark and large; cloud over dm-cu extended to slightly past veins M and CuA<sub>1</sub>. Costal vein with row of 7 large spinelike setae; evenly increased in size apicad. Largest seta ca. 4.5× thickness of costa, lying slightly apical to apex of vein  $R_{2+3}$ .  $R_{2+3}$  virtually straight. X-vein dm-cu slightly bent in the middle.

**ABDOMEN:** Female terminalia unknown. Male genitalia: Cercus with long ventrolateral lobe, apex lying beneath epandrium; lobe sclerotized. Ventrolateral halves of epandrium (epandrial lobes) relatively broad (length ca. 3× width), each lobe with even row of 6 long, stiff setae. Paraphyses very heavily sclerotized; apically crossed; right one slightly longer than left and bent to left, touching margin of epandrium. Paraphyses quite broad, not hooked inward; without lateral or medial lobes. Aedeagus lying in a sclerotized trough, dorsal part membranous; apex turned slightly upward; projected posteriorly. Aedeagal apodeme projected inward, with posterior end upright; triangular in lateral view. Hypandrium broad, with deep ventral keel; gonopods short and deep, with small knob at apex. Surstyli with broad, round base and hooked apical lobe that is pointed dorsad; heavily sclerotized, with ca. 15 thick, stiff setae on medial margin of apical hook. Apical sternites not examined.

**TYPE:** Holotype, Male: PANAMA: Canal Zone: Colón, VII/79, canopy fogging, E. M. Broadhead (dissected, no. 153) (AMNH).



OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Latin *spina* (thorn) and *costa* (costal vein) for the large stout setae on the costal vein.

DISCUSSION: Placement of this species in the *inversa* species group is based on the structure of the aedeagus and the surstyli. The paraphyses are quite distinct from any other species in the group.

*Cladochaeta spinula*, new species

Figures 33, 46

DIAGNOSIS: Easily distinguished externally (perhaps in males only) based on wing with costal vein having row of 12 stout setae, which are twice the length of other spinule-like setae. Costal half of wing very lightly infuscate. Male genitalia distinctive: paraphyses with 3 pairs of long lobes, the dorsomedial pair (partially surrounding aedeagus) exceptionally long.

DESCRIPTION: HEAD: Eyes with short, fine, and sparse setulae; greatest length of eye in line with greatest height of head. Head quite deep and short in lateral view (HL/HD = 0.69 [HT]). Pedicel mostly yellow, flagellomere I light brown. Arista badly damaged in holotype (only known specimen), apparently with 3 dorsal branches; apical fork relatively large; ventral branch midway between d-2 and d-3; row of 7-8 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital broken off in holotype, size undeterminable; exactly lateral to proclinate. Frons yellowish and of moderate length and width. Interorbital setulae relatively short, 3-4 per side. Face yellow and of moderate depth and width (FW/HW = 0.33 [N = 1]). Cheeks yellow and fairly shallow (CD/ED = 0.10).

THORAX: Notum, scutellum, and pleuron yellowish. Anterior dorsocentrals broken off in holotype. Posterior dorsocentral seta midway between anterior dorsocentral and scutellar margin. Acrostichal setulae in 6 uneven rows. Three pairs of enlarged prescutellar acrostichals present, 1.5× size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta barely differentiated

from other acrostichals. Anterior scutellar setae slightly divergent, posterior scutellars barely cruciate. Postpronotal lobe with 1 very long seta. Legs yellow; forefemur with 1 long dorsolateral seta and row of 3 ventrolateral setae. Halter knob yellow. Wing similar to *spinacosta*, but with enlarged spinelike setae more numerous and not so large. Costal vein with row of ca. 12 setae that are stouter and about twice the length of other, spinule-like setae; row extended to slightly past apex of vein  $R_{2+3}$ , not increasing in size apicad. Wing with diffuse infuscation over most of costal edge, extended to between veins  $R_{4+5}$  and M. X-vein r-m without cloud; dm-cu with slight cloud. Vein  $R_{2+3}$  straight, not slightly curved even at apex. X-vein dm-cu slightly bent.

ABDOMEN: Female terminalia unknown. Male genitalia: Cercus with long, tapered ventrolateral lobe, unsclerotized. Epandrium about as high as wide. Ventrolateral halves of epandrium (epandrial lobes) very broad (length about twice the width), each lobe with uneven row of 8-9 stiff setae of intermediate length (dorsalmost one longer than the others). Paraphyses heavily sclerotized. Dorsal lobes of paraphyses hooked inward, approximately equal in length to ventral lobes; ventral lobes lateral to dorsal ones, pointed straight down. Aedeagus membranous, equal in length to dorsal lobes of paraphyses; flanked by pair of long, sclerotized median paraphysial lobes, equal in length to aedeagus. Aedeagal apodeme narrow, forked; hypandrium with deep ventral keel, short gonopod arms. Surstyli with broad, rounded base; narrow, apical half turned upward; apex with dorsal lobe and ventral spur; dorsal lobe with ca. 35 fine setae; lobe and spur sclerotized.

TYPE: Holotype, Male: COSTA RICA: *Higuito*: San Mateo, Pablo Schild (no date) (dissected, no. 238) (NMNH). This specimen is in bad condition. It was originally mounted to a "minuten" crafted from a needlelike thorn, and then glued to the side of the minuten. The right wing is half gone; the left wing is badly torn. Some major setae are damaged and lost, and the entire body is covered with a moldy flocculence, including some hyphae below the head.

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: In reference to the stout costal spines on the wing, which are much shorter than in *spinacosta*.

*Cladochaeta sturtevanti* Wheeler and Takada

Figures 33, 35, 38, 47

*Cladochaeta sturtevanti* Wheeler and Takada, 1971: 234, 236 (latter is figure of male genitalia).

DIAGNOSIS: Body yellow; wing with infuscation variable: costal half dark to barely infuscate; male genitalia distinctive for the paraphysis with 3 pairs of lobes; male and female genitalia most similar to *C. wilhansoni* and distinguished from it as described above in *wilhansoni* diagnosis.

DESCRIPTION: HEAD: Eyes with short, fine, and sparse setulae; greatest length of eye in line with greatest height of head. Head of moderate height and length in lateral view. Pedicel mostly yellow, flagellomere I light brown. Arista with 4 (rarely 5) dorsal branches; apical fork relatively small, sometimes minute; ventral branch closer to d-4 than to d-3 (opposite d-4 in specimens with 5 dorsal branches); row of 6-7 minute medial branches. Frontal-orbital setae: Distance from proclinate to ptilinal suture twice the distance between this seta and post. reclinate. Anterior reclinate orbital quite small, 0.3× or less than the size of proclinate; exactly lateral to proclinate to lying midway between ipsilateral orbitals. Frons with frontal vittae golden and slightly shiny, frontal-orbital plates slightly lighter; ocellar triangle yellow with some light brown. Frons of moderate length and width. Interorbital setulae fairly long, 6-7 per side. Face yellow, rather deep and of moderate width (FW/HW = 0.34 [N = 19]). Cheeks yellow and rather deep (CD/ED = 0.16).

THORAX: Notum, scutellum, and pleuron yellow. Anterior dorsocentral setae one-half the length of posterior dorsocentral. Posterior dorsocentral seta slightly closer to scutellar margin than to anterior dorsocentral. Acrostichal setulae in 6 even rows. Prescutellar acrostichals 1.5× larger than other acrostichals. Acrostichal immediately anterior to ant. dor-

socentral seta barely distinguishable from other acrostichals. Anterior scutellar setae parallel, posterior scutellars slightly cruciate. Two large setae on postpronotal lobe, ventral one 0.8× length of other. Legs yellow; forefemur with 1 long dorsolateral seta and row of 3 ventrolateral setae. Halter knob yellow. Wing with very light, diffuse infuscation over costal edge, faded considerably toward apex of vein  $R_{4+5}$ . (There is considerable variation in darkness of infuscation, perhaps depending on temperature [e.g., season, altitude, latitude] at which flies developed.) Clouds surrounding x-veins r-m and dm-cu very small and light, barely perceptible. Vein  $R_{2+3}$  very slightly curved at apex, otherwise almost straight. X-vein dm-cu slightly bent in middle.

ABDOMEN: Anterior tergites yellowish, grading to light brown posteriorly. Female terminalia: Apical tergite sclerotized, dorso-medially incomplete (some specimens with intercalary sclerite in this space). Posterodorsal margin of penultimate tergite with deep, square notch (also sometimes with intercalary sclerite). Apical sternite a striplike, inverted U-shaped sclerite with row ca. 6 fine, stiff setulae on each half of apical lobes. Male genitalia: Cerci large, with thin ventrolateral lobe. Ventrolateral halves of epandrium (epandrial lobes) broad, length ca. 2.5× width; each lobe with row of long, stiff setae. Paraphyses heavily sclerotized, with 3 pairs of sharp lobes. Medial pair of lobes flanking membranous aedeagus forming a trough; length nearly extended to apices of main lobe of paraphysis. Main lobe lying alongside medial lobe, turned slightly mediad and apical half turned inward (anteriad). Lateral lobe attached to base of main lobe, pointed anteriad. Halves of paraphyses connected by thin dorsal bridge. Hypandrium small, with very shallow ventral keel; gonopods broad and flat. Surstyli fairly long (length ca. 3× width), slightly curved, with apex having ventral, sclerotized tooth. Apical third of surstylus with ca. 40 minute setulae on mesal surface; row of ca. 12 longer setulae on edge of lobe dorsal to tooth.

TYPES: Holotype, Male: CALIFORNIA: *Los Angeles Co.*: Arcadia 15/X/49, M. R. Wheeler (in the NMNH). Paratypes are the specimens mentioned below from Arcadia,

Pasadena, and Tujunga, California (all in the AMNH).

OTHER MATERIAL EXAMINED: CALIFORNIA: *Alameda Co.*: University California Berkeley campus, 27/X/68, P. H. Arnaud, Jr. (1♀); *Los Angeles Co.*: Arcadia, 15/X/49 (4♂, 6♀); Angeles Crest Highway, Arroyo Seco, 1000 m, 29/VII/77 (1♂\*, 1♀\*); Pasadena 6/I/45 (1♂, 2♀) "bred cercopid on *Artemisia*," 30/V/45 (2♀) "bred cercopid on *Baccharis*," X/45 (1♂) "bred cercopid on *Lepidospartum*" (1♂), and "bred cercopid on *Senecio douglasii*," 23/VIII/49 (1♂, 4♀); Tujunga, 1/VIII/49 (6♂, 4♀), with 3 *Clastoptera lineaticollis* host vouchers; *Marin Co.*: Mill Valley, 7/X/45 (1♂); Alpine Lake, Lily Pond, 1500 ft, 27/II/69, D. D. Munroe (1♂\*, 2♀); Mount Tamalpais, Rock Springs, 15/IX/79, 600 m, P. H. Arnaud, Jr. (1♀\*); *Napa Co.*: Napa, 22/VII/70 (1♂) "ex: spittle mass of *Clastoptera* on cypress"; *San Mateo Co.*: San Mateo Co. Mem. Park, 12/VIII/59, P. H. Arnaud, Jr. (1♂\*, 3♀); county unknown: Santa Anita Canyon, 3/VIII/49 (1♂), 5/XII/49 (1♂), 18/IV/50 (1♂). UTAH: *Washington Co.*: Zion National Park, Lava Pt., 7800 ft, 8–21/IX/82 (1♂); Paradise Canyon, 13–19/V/83 (1♂). WASHINGTON: Eaton, 23/VIII/49 (1♂).

DISCUSSION: Wheeler and Takada (1971: 234) mentioned that "another (undescribed) species apparently occurs in northern California. We have seen 2 specimens from Mill Valley, Marin County with the body noticeably larger and darker, and with the wings much more heavily clouded." Only one of these 2 specimens has been found and reexamined; it is slightly larger than other specimens of *sturtevantii*, and the wing infuscation is only barely more noticeable. The male genitalia agree perfectly with those of *sturtevantii* specimens from other parts of the range. The specimens of *C. inversa* from southern California to which Wheeler (1952) referred were undoubtedly *C. sturtevantii*. *Cladochaeta sturtevantii* is now known to extend even farther north into Washington and east to southern Utah. Overall body coloration can be rather variable, for the specimens from Zion National Park, Utah (1♂ dissected), are considerably darker than even the Mill Valley, California, specimen. The paraphyses as figured by Wheeler and Takada

(1971: fig. 17a) are not nearly so thick (see, instead, fig. 47).

*Cladochaeta wilhansoni*, new species

Figures 35, 37, 47

DIAGNOSIS: Externally distinguished by frons mostly dark brown to black brown; costal infuscation on wing with discrete (not diffuse) boundary; postpronotal lobe with 1 large seta, smaller one about half the size. Also distinguished by male and female genitalia. Males with paraphyses with rudimentary "medial lobe" (troughlike structure flanking the aedeagus in *sturtevantii*, the closest relative); apex of surstylus with ventral, sclerotized point that is longer and thinner than in *sturtevantii*. Females with last sternite (oviscapt) in ventral view with apex abruptly tapered, not gradually as in *sturtevantii*; in *wilhansoni* the penultimate tergite has a shallower median notch on the posterior margin and no intercalary sclerites present within this notch, with the terminal tergite (narrow and medially divided) unsclerotized.

DESCRIPTION: HEAD: Eyes with very sparse, short setulae; greatest length of eye in line with greatest height of head. Head of moderate height and length. Pedicel ochre, flagellomere I light brown. Arista with 3–4 evenly spaced dorsal branches; if just 3 dorsals, then terminal fork large; position of ventral branch variable between fork and d-3 (or closer to d-4 than to d-3 if 4 dorsal branches); row of 5–6 minute medial branches. Frontal-orbital setae: Distance from proclinate to pitilinal suture 1.5× distance between this seta and post. reclinate. Anterior reclinate orbital one-half the size of proclinate; exactly lateral to (and sometimes also slightly posterior to) proclinate. Frons with frontal vittae medium brown to black-brown, with yellowish frontal-orbital plates; frons slightly short and rather wide. Ocellar triangle black. Face light brown and of moderate depth and relatively wide (FW/HW = 0.32 [N = 11]). Cheeks yellow and of moderate depth (CD/ED = 0.16).

THORAX: Notum and scutellum ochre; notopleural area and dorsal half of pleuron light brown. Anterior dorsocentral setae one-half the length of posterior dorsocentrals; post. dorsocentral closer to scutellar margin than

to ant. dorsocentral. Acrostichal setulae in 6 even rows. Pair of enlarged prescutellar acrostichals present, twice the size of other acrostichals. Acrostichal immediately anterior to ant. dorsocentral seta enlarged (1.5× size of other acrostichals). Anterior scutellar setae parallel, posterior scutellar slightly convergent to slightly or strongly cruciate (one-third their length). One large seta on postpronotal lobe, dorsal to one 0.6× its size. Legs yellow; forefemur with 1 long dorso-lateral seta and row of 3 widely spaced ventrolateral (slightly shorter) setae. Halter knob light brown. Wing with light infuscation at costal edge, surrounding most of vein  $R_{2+3}$ , with discrete (not faded) edges. No clouds of infuscation surrounding x-veins r-m and dm-cu. Vein  $R_{2+3}$  very slightly curved at apex, otherwise almost straight. X-vein dm-cu slightly bent.

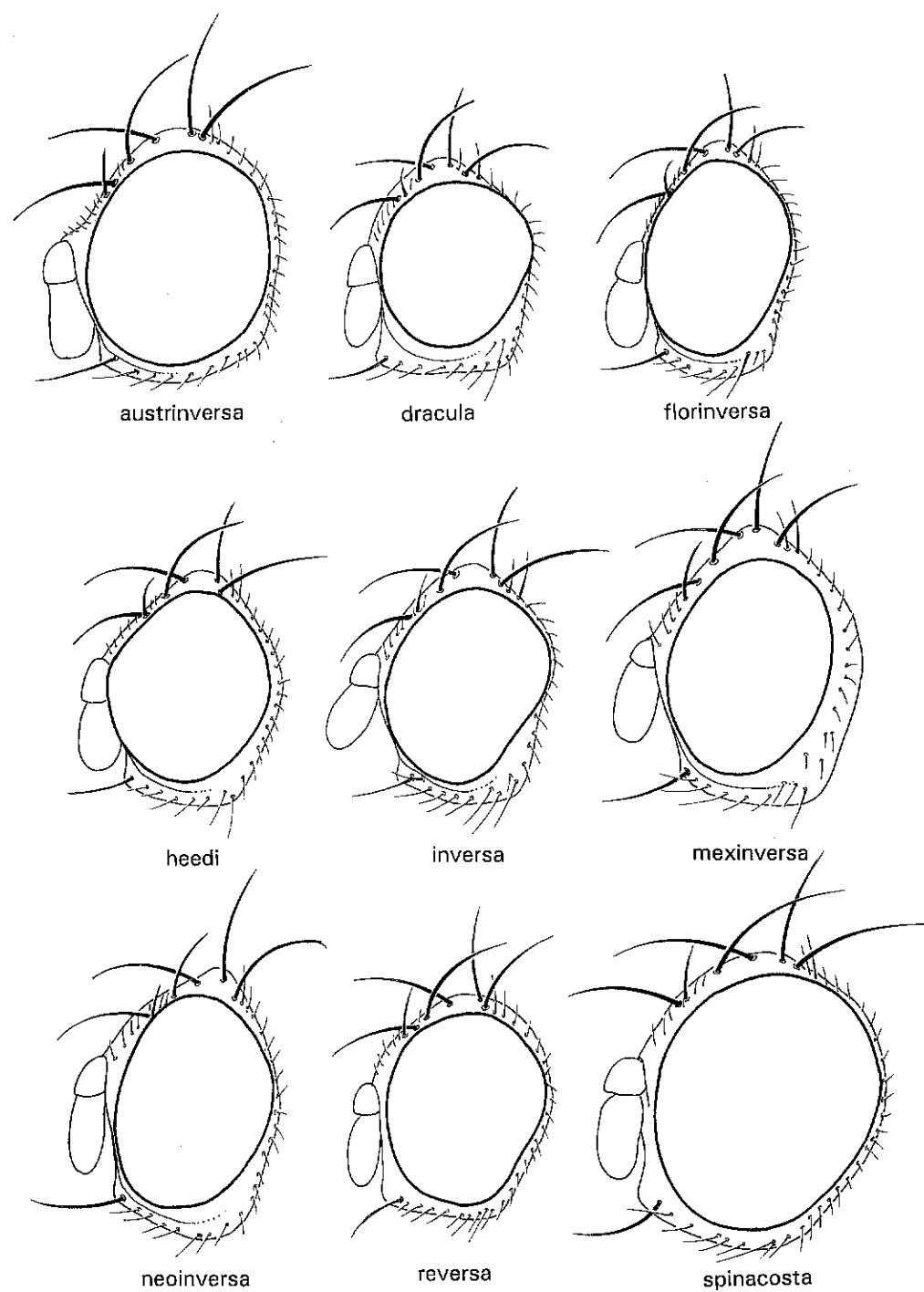
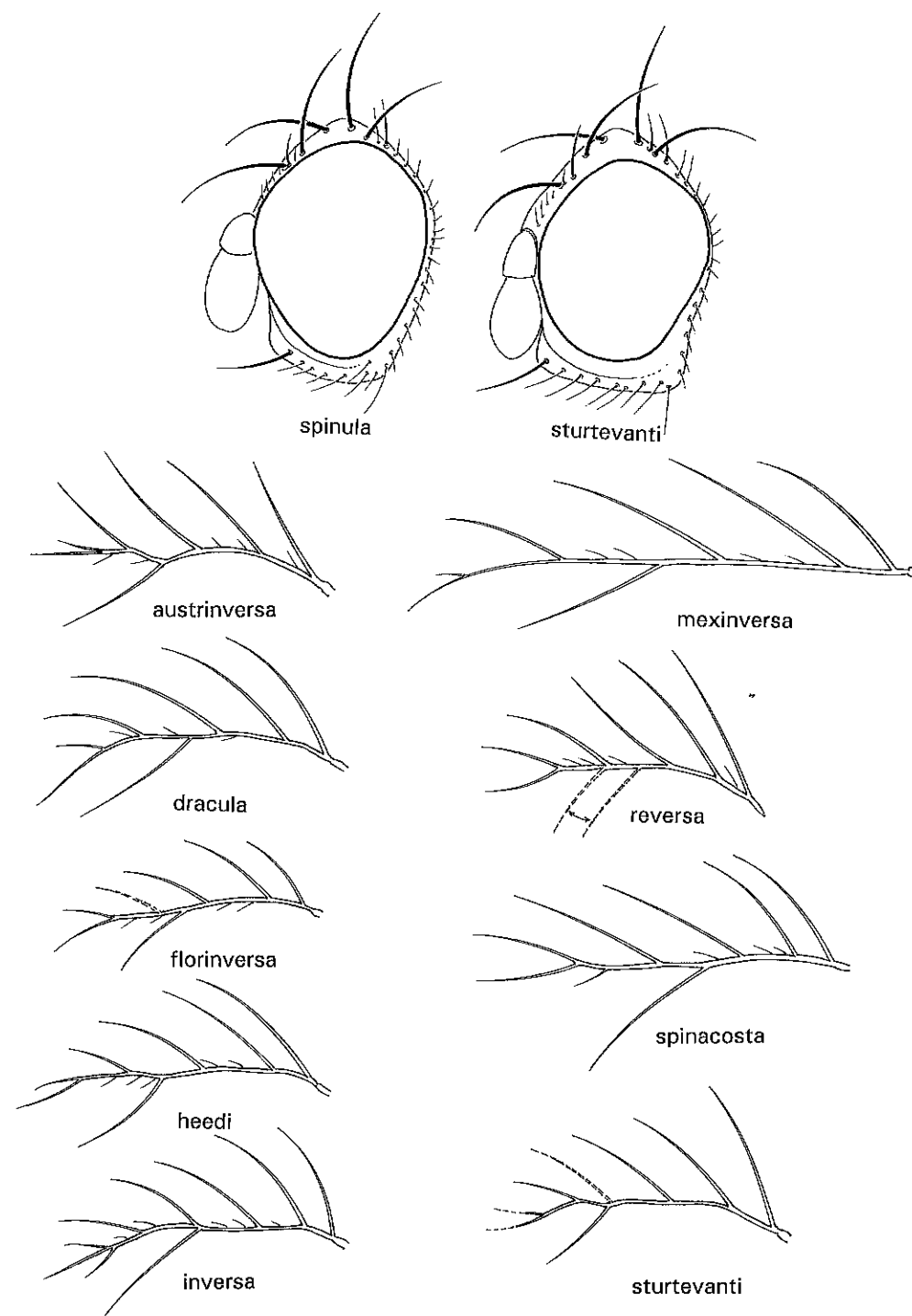
ABDOMEN: Tergites even, chocolate brown, with slightly lighter areas in the middle of some tergites. Female terminalia: Apical tergite barely extended ventrally; dorsomedially incomplete. Epiproct with medial point on anterior margin of dorsal surface. Apical sternite Y-shaped, with truncate apical margin bearing row of ca. 7 fine setulae on each half. Lateral arms of sternite long, extended

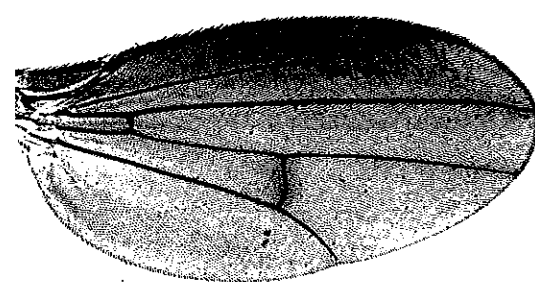
to ca. 0.4× length of penultimate sternite. Male genitalia: Similar to *C. sturtevantii* except that *wilhansoni* has the following characteristics: paraphysis with apices of medial lobes not projected inward (anteriad), but straight downward (ventrad); medial lobes slightly shorter and with a small window on medial edge near middle; lateral lobes of paraphyses thinner, of about same length as in *C. sturtevantii*. Aedeagus entirely membranous, without sclerotized trough covering ventral and lateral surfaces (as in *sturtevantii*). Surstylus slightly thinner in lateral view, with ventroapical point longer and thinner and small lateral flange at base of point. Apex of surstylus with fewer setulae (ca. 10 vs. at least 20 in *sturtevantii*).

TYPES: Holotype, Male: UTAH: *Washington Co.*: Zion National Park, Lava Pt., 7800 ft, 8–21/IX/82, C. Riley Nelson (in AMNH). Not dissected. In addition, there are 2 males (both dissected, nos. 4, 5) and 3 females (1 dissected, no. 6); all paratypes from the same series (in AMNH and Utah St. collection).

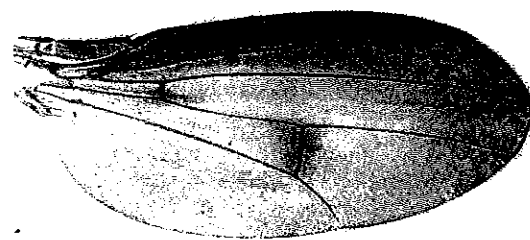
OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Patronym in honor of Wilford Hanson (Utah State University), collector of many interesting specimens of Drosophilidae and other Diptera.

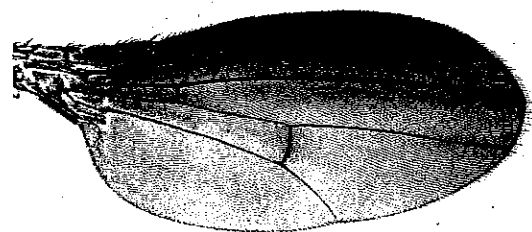
Fig. 32. Heads of *inversa* group species.Fig. 33. Heads and aristae of *inversa* group species.



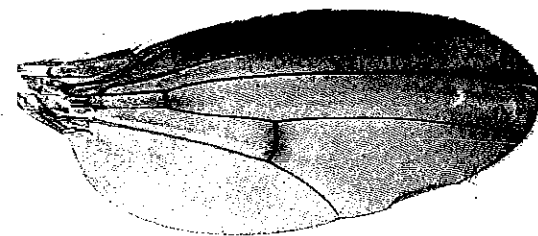
austrinversa



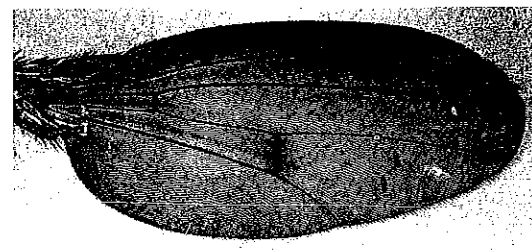
dracula



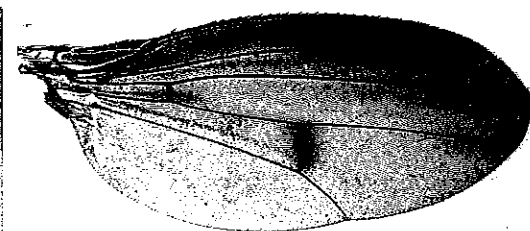
florinversa



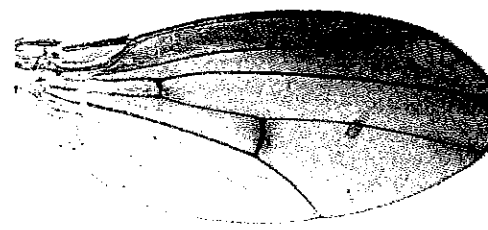
heedii



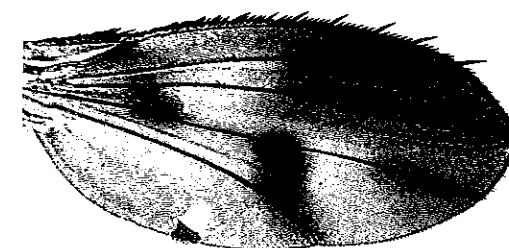
inversa



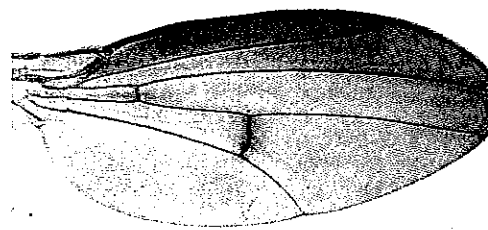
mexinversa

Fig. 34. Wings of *inversa* group species.

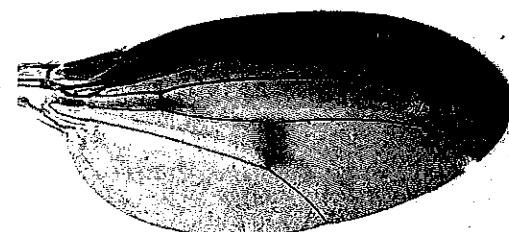
neoinversa



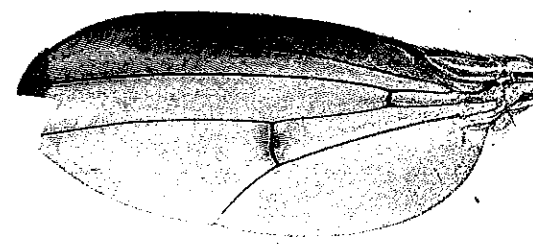
spinacosta



sturtevantii

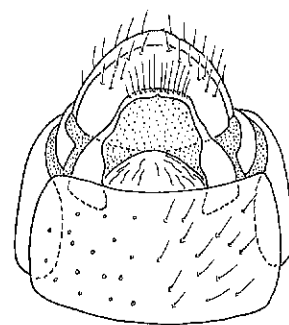


sturtevantii

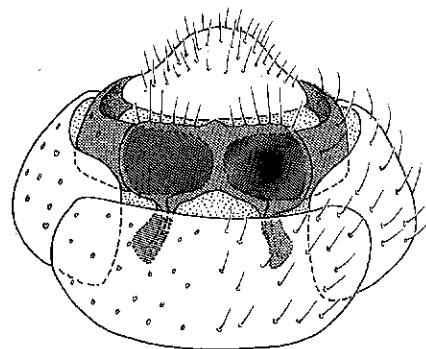
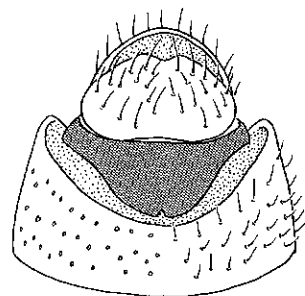


wilhansonii

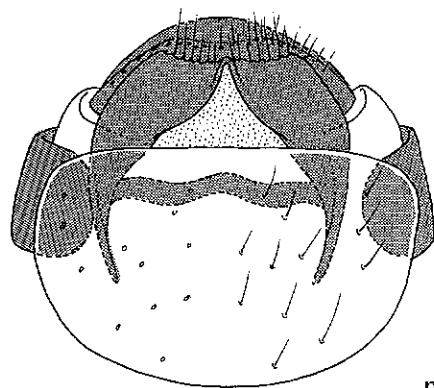
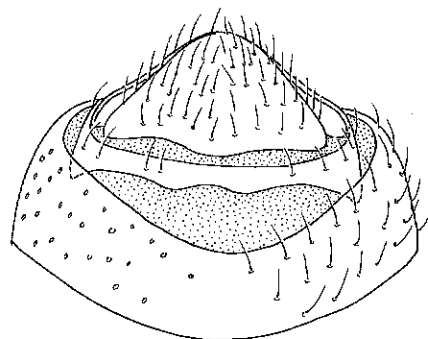
Fig. 35. Wings of *inversa* group species (continued); some variation is shown with 2 specimens of *C. sturtevantii*.



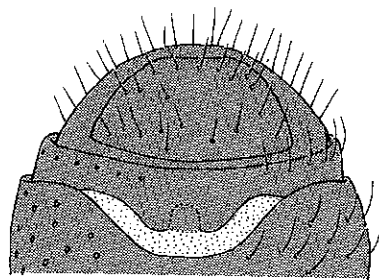
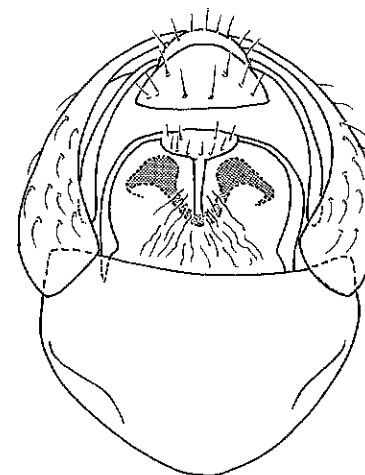
heedi



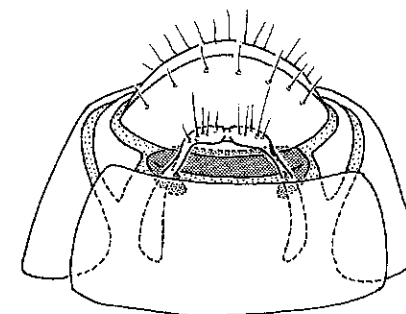
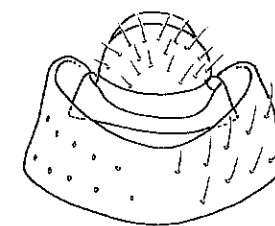
inversa



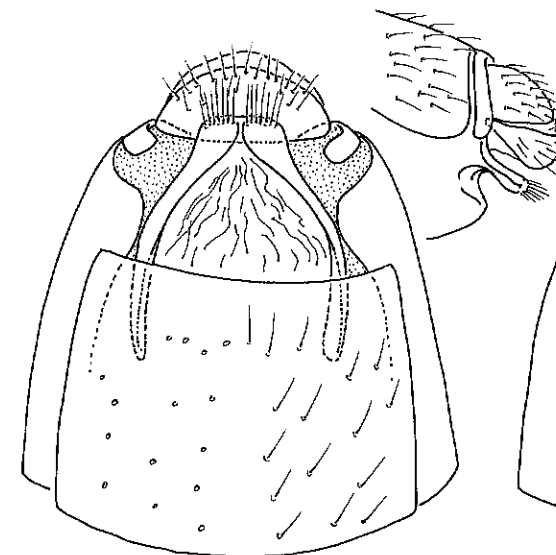
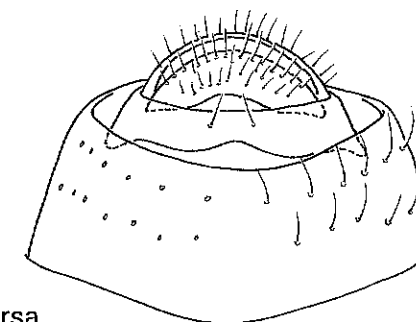
mexinversa

Fig. 36. Female terminalia of *inversa* group species, ventral (left) and dorsal (right) views.

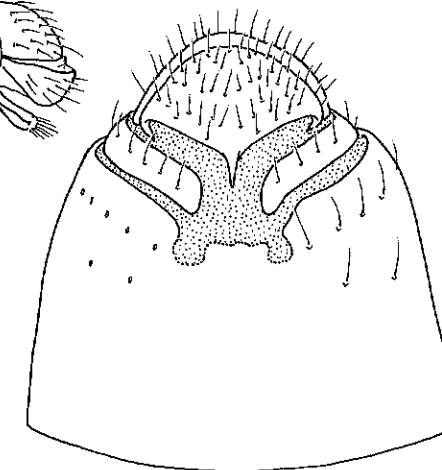
dracula

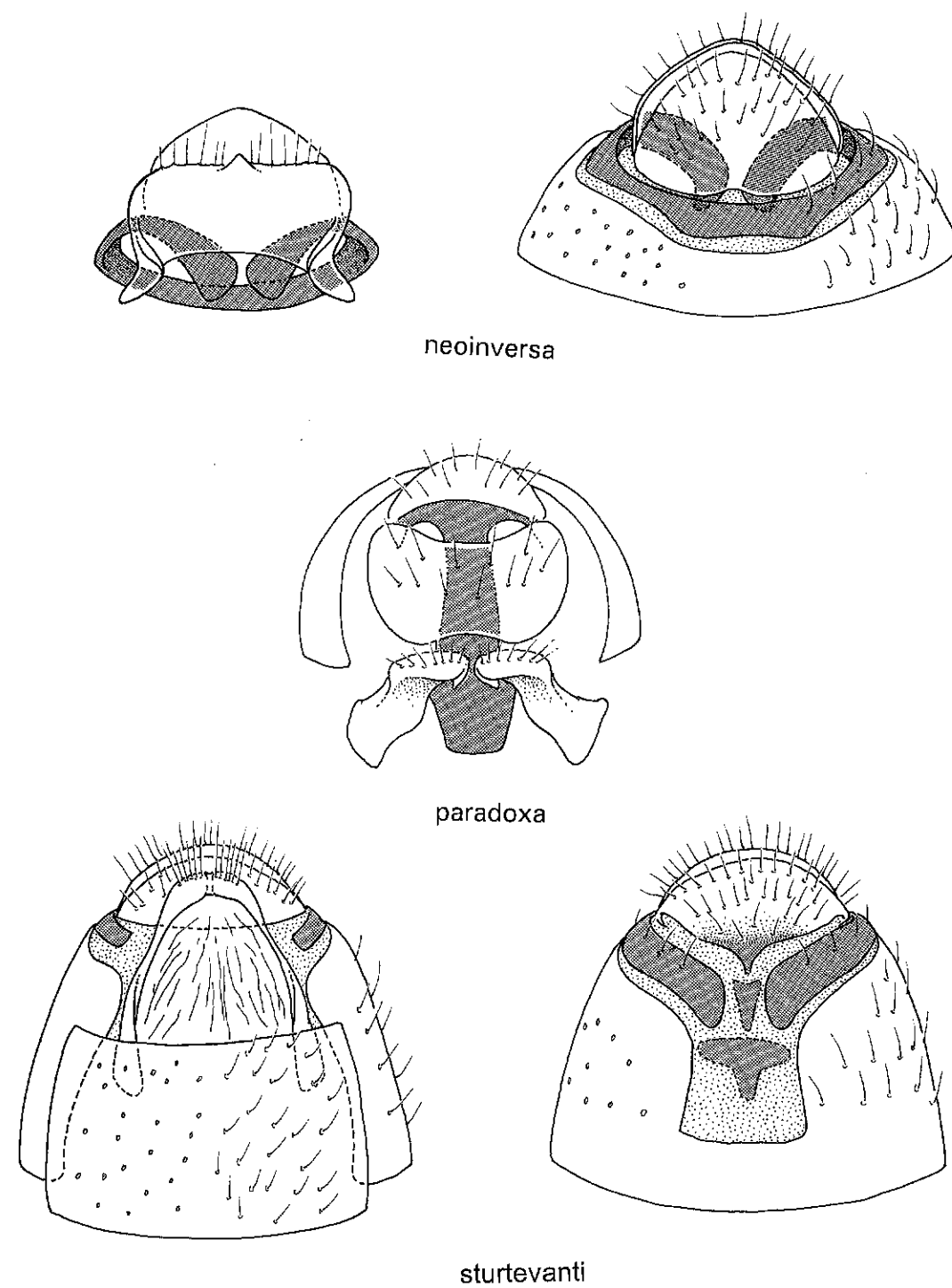


florinversa



wilhansonii

Fig. 37. Female terminalia of *inversa* group species (continued).

Fig. 38. Female terminalia of *inversa* group species (continued).Fig. 39. Male terminalia of *C. austrinversa*.



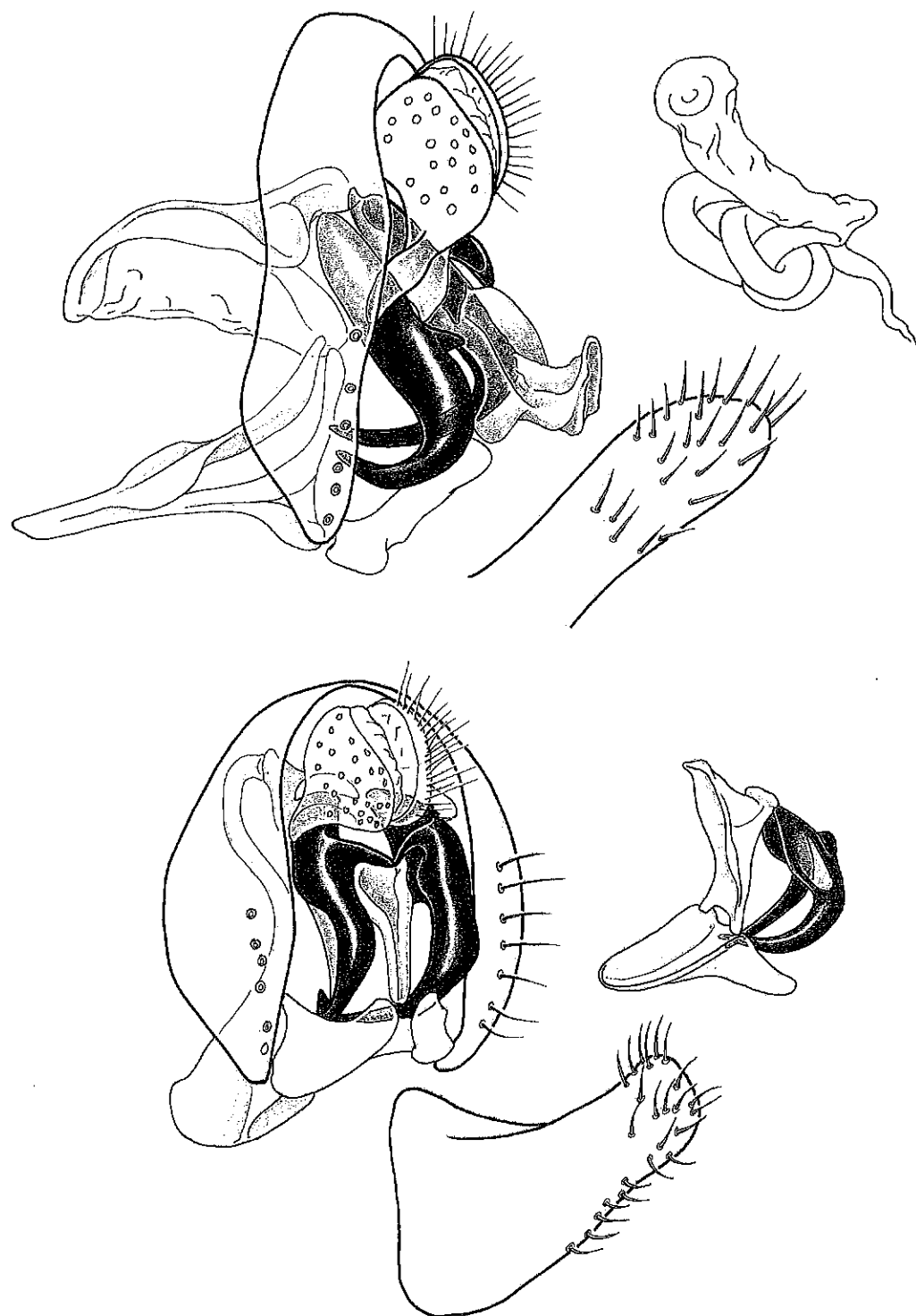


Fig. 40. Male terminalia of *C. dracula* (above), with female ventral receptacle; and *C. florinversa* (below).

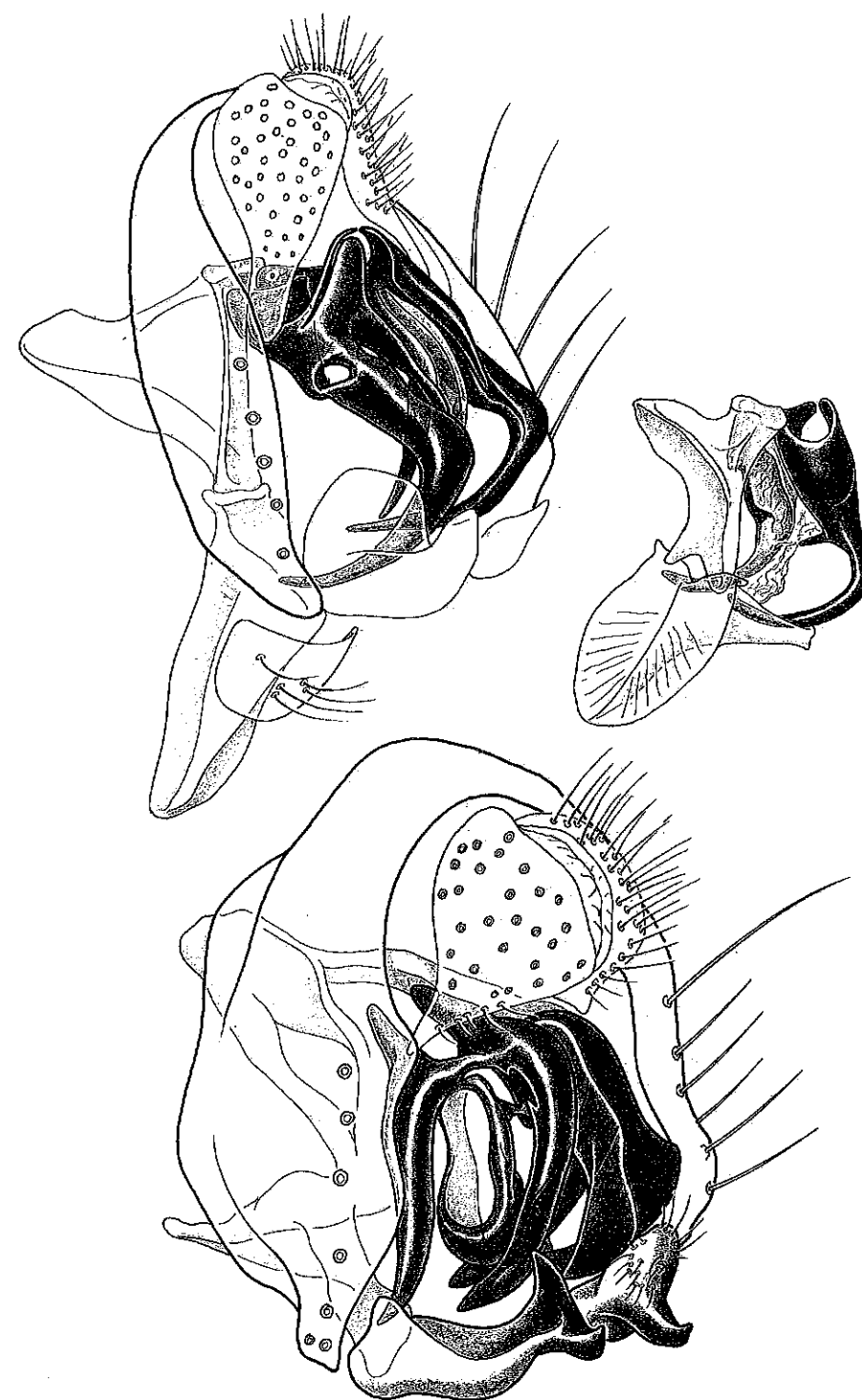


Fig. 41. Male terminalia of *C. inversa* (above) and *C. reversa* (below).

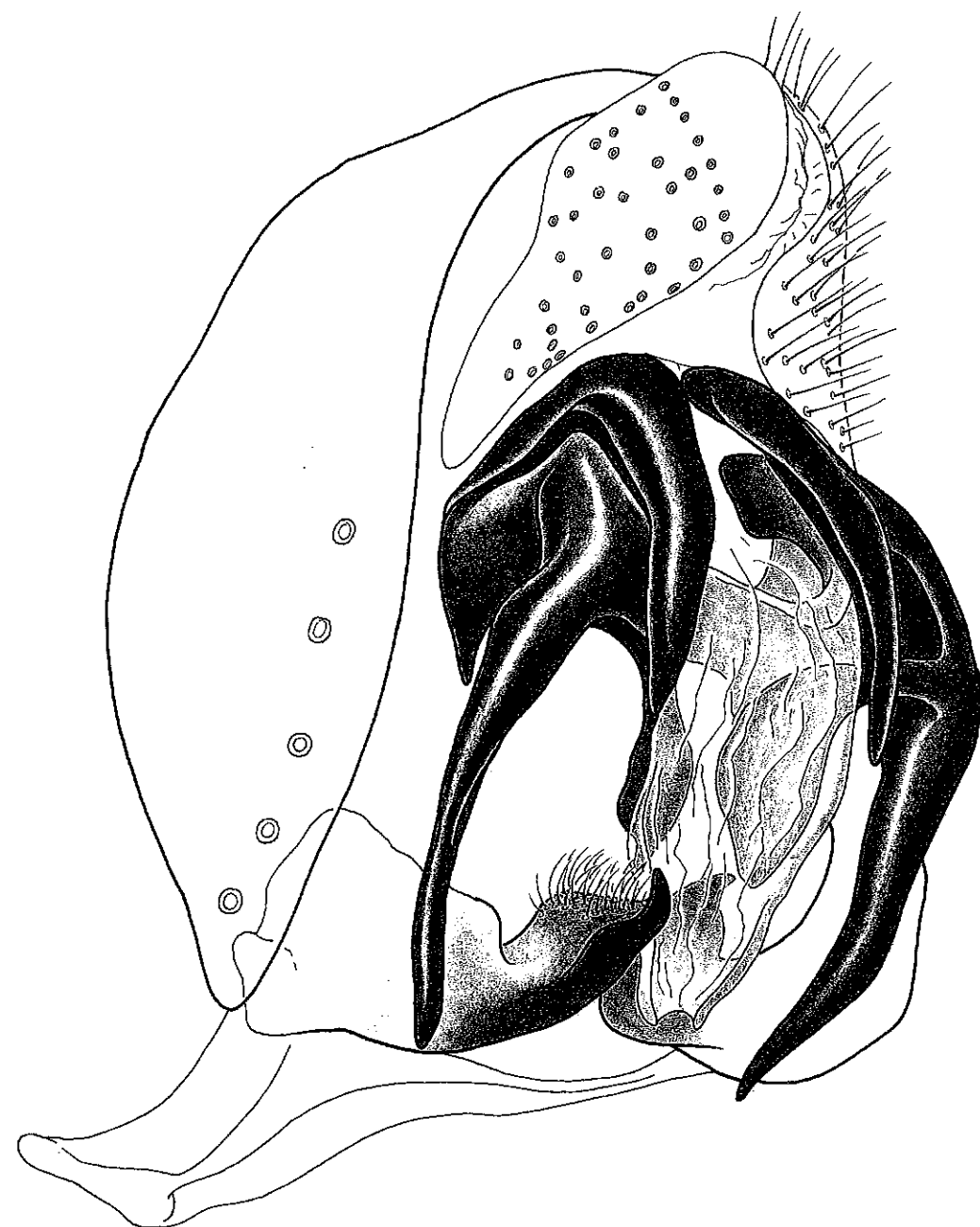


Fig. 42. Male terminalia of *C. mexinversa*.

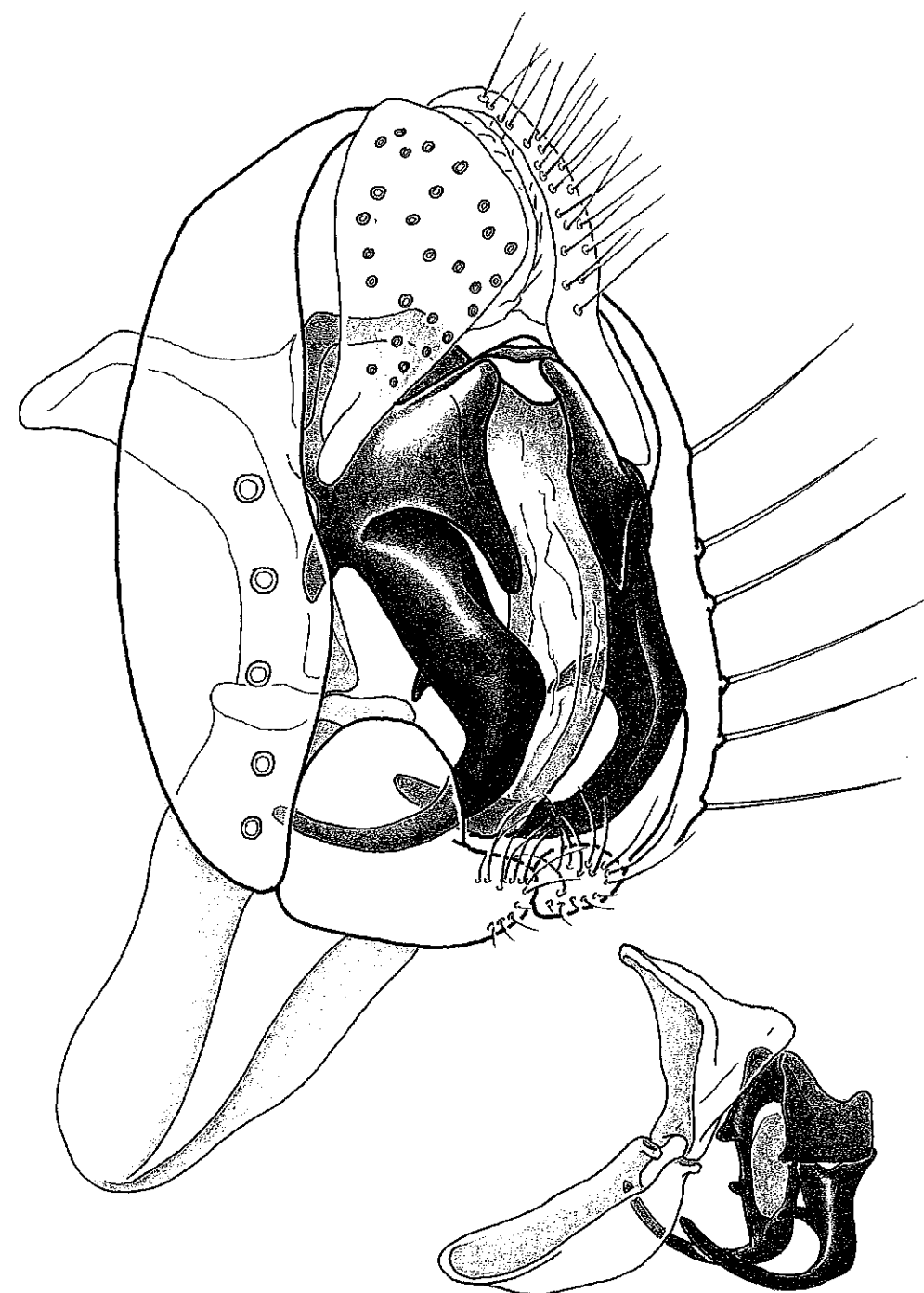


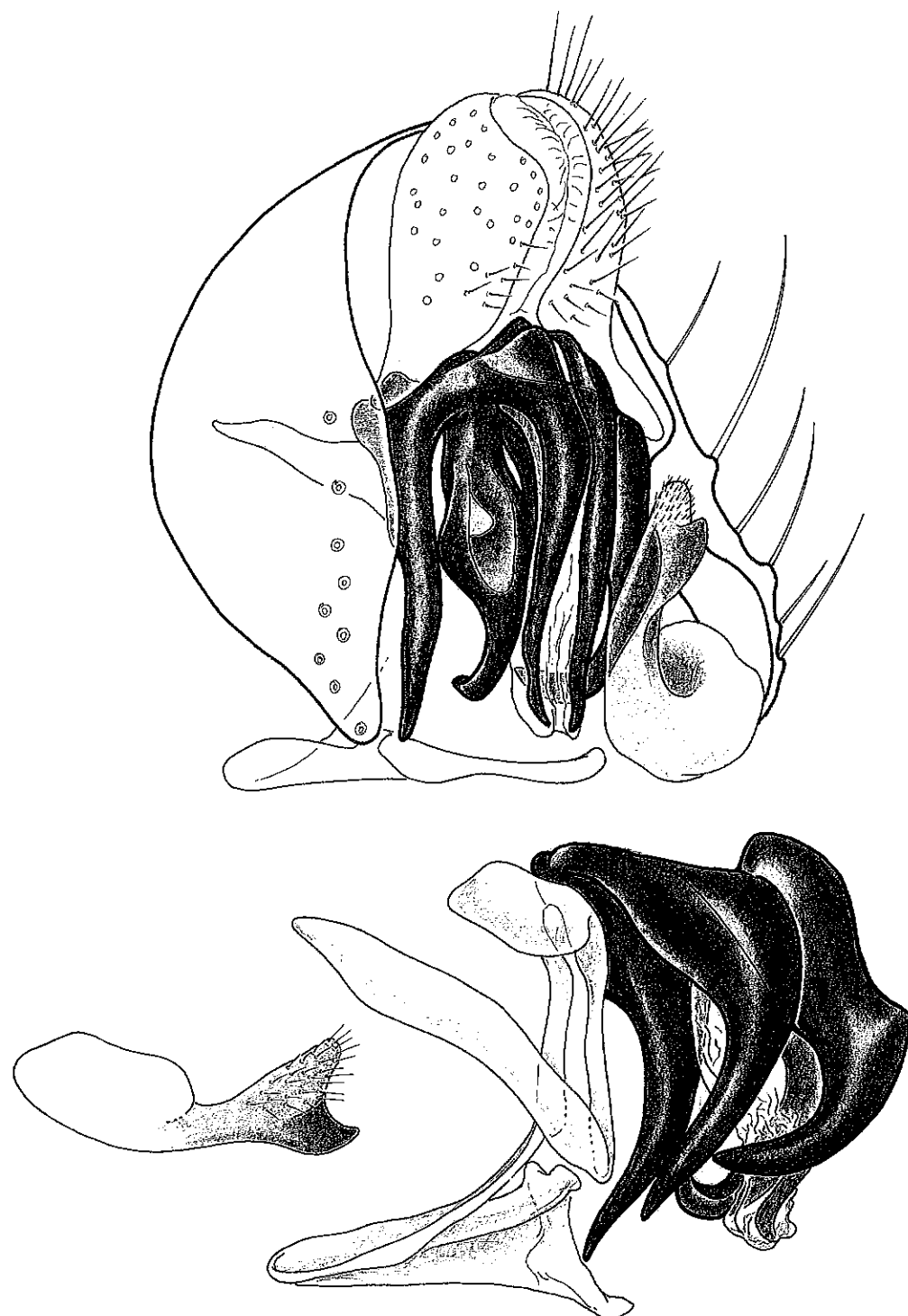
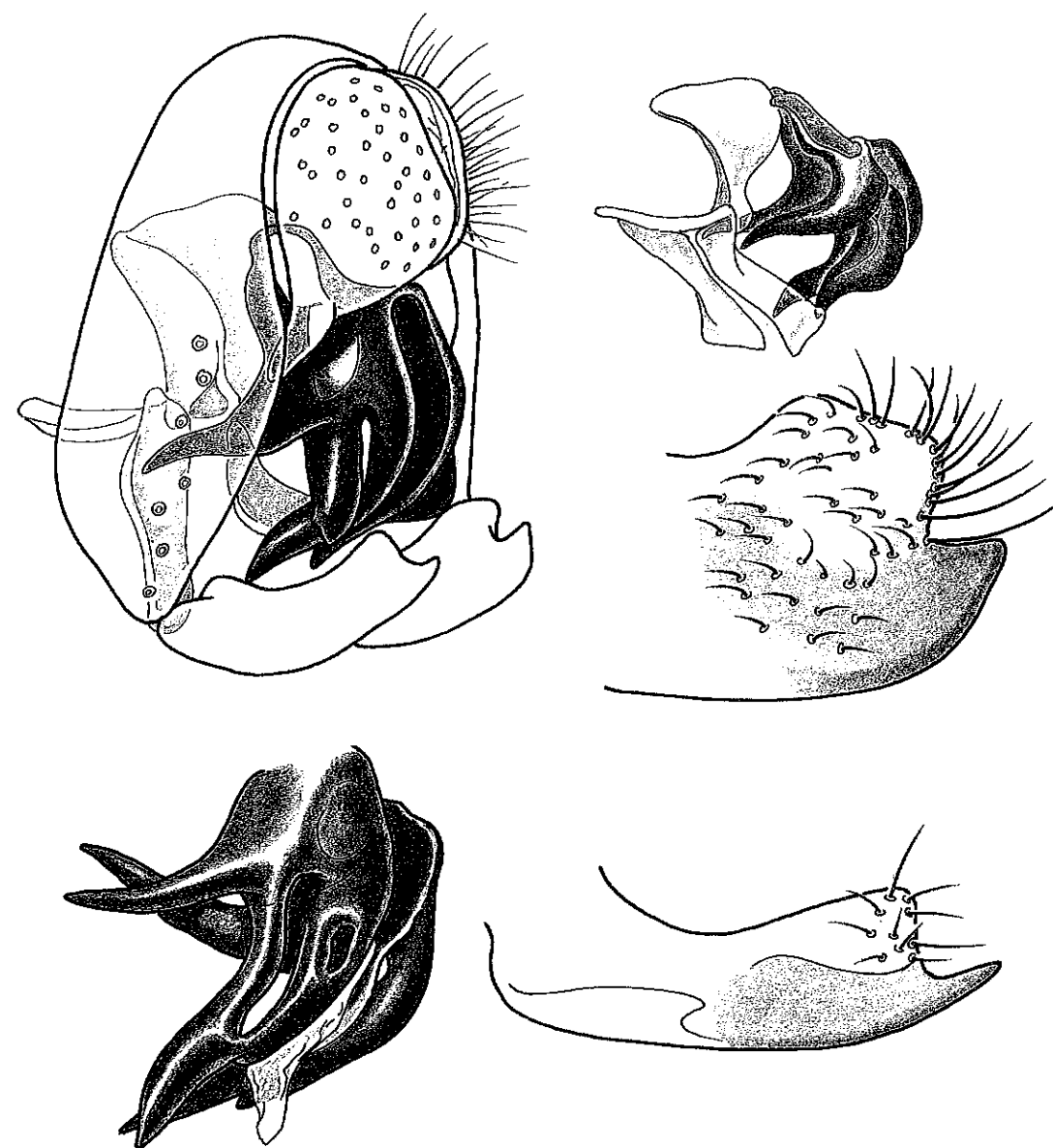
Fig. 43. Male terminalia of *C. neoinversa*.



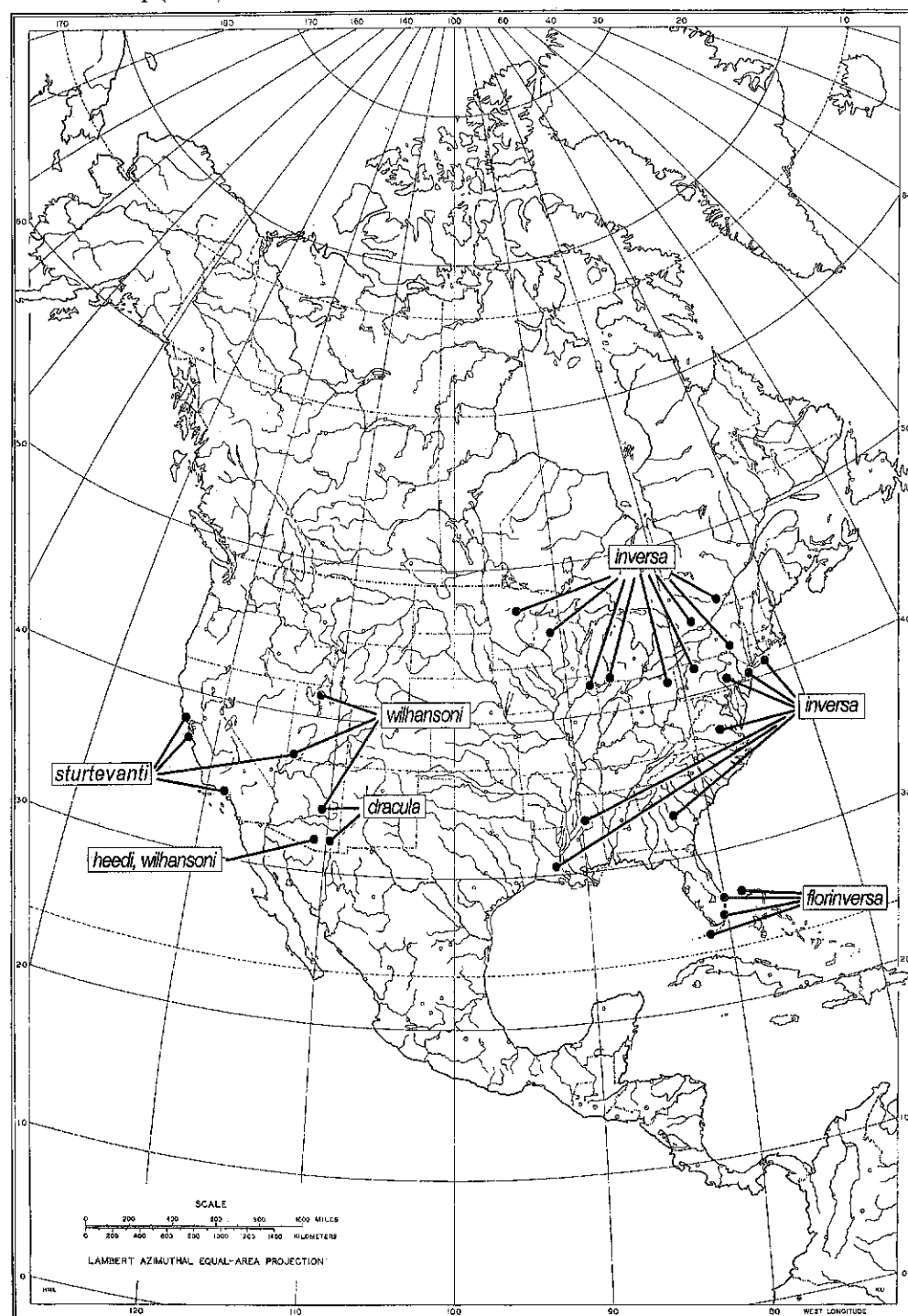
Fig. 44. Male terminalia of *C. paradoxa* (type). Specimen is distorted from having been mounted on a glass slide.



Fig. 45. Male terminalia of *C. spinacosta*.

Fig. 46. Male terminalia of *C. spinula*.Fig. 47. Male terminalia of *C. sturtevantii* (above) and *C. wilhansonii* (below, portions only).

## Inversa Group (Part 1)

Fig. 48. Distribution of Nearctic *inversa* group species.

## Inversa Group (Part 2)

Fig. 49. Distribution of Neotropical *inversa* group species.

## SORORIA SPECIES GROUP

**DIAGNOSIS:** Extremely variable: crossvein dm-cu usually clouded; hind femur usually with comb of stiff setae on apical half of ventral surface; male genitalia with paraphyses well developed and heavily sclerotized, of equal sizes, either pronged and straight, twisted, or even spiraled; distiphallus membranous, often with fine scales or spicules.

*Cladochaeta abeja*, new species

Figures 50, 52, 57

**DIAGNOSIS:** Wing evenly and lightly dusky, without noticeable clouds; arista with 1 ventral and 4 dorsal branches; pleura brown, contrasting with light notum. Male genitalia: Paraphyses heavily sclerotized and stout, distiphallus membranous and finely scaled, surstyli with fringe of fine, long setae on apical edge. Known only from the southwestern mountains of the Dominican Republic.

**DESCRIPTION:** HEAD: Moderate height and length; front flat. Eyes virtually bare, without interfacetal setulae; lower hind margin without indentation. Antenna with pedicel and first flagellomere brown; arista with 1 ventral and 4 dorsal branches, with ventral one between d-3 and d-4. Front dull, light brown, with slight bluish pruinescence when viewed anteriorly; 8 tiny interfrontal setulae present. Frontal-orbital setae: Proclinate orbitals ca.  $0.8\times$  size of posterior reclinate orbitals; anterior reclinate orbitals small, ca.  $0.3\times$  size of proclinate orbitals. Posterior reclinate orbitals slightly closer to ipsilateral proclinate than to inner vertical. Face light brown, with slight carina; relatively broad (FW/HW = 0.34). Cheeks light yellow, shallow (CD/ED = 0.10). Proboscis light yellow, palps light brown.

**THORAX:** Notum, scutellum, and postnotum ochre. Most of pleura light brown. Anterior dorsocentrals lost in only known specimen; posterior dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Scutellar setae lost in type specimen. Postpronotal lobe with 1 large seta, smaller ventral one. Legs entirely yellow; setae on forefemur rubbed off in type. Entire wing lightly and evenly dusky, with slightly darker infuscation on costal edge; very slight infuscation over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  gradually meeting

costal vein, not turned costad. Veins  $R_{4+5}$  and M virtually parallel. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light brown

**ABDOMEN:** Tergites light brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe; ventral margin flat. Epandrium height ca.  $1.5\times$  width of epandrium. Ventrolateral halves of epandrium gradually tapered to points; each with row of 7 long, stiff setae. Aedeagus membranous, bulbous, with minute papillae lying between apices of paraphysis arms. Paraphyses heavily sclerotized, forcepslike; meet very close medially on dorsal half, then curve outward and around distiphallus on apical half; apices blunt? Paraphyses with sclerotized anterior extension, apex joined to posterior groove of aedeagal apodeme. Paraphyses joined by very narrow dorsal bridge. Sclerotized "horn" lying between distiphallus and aedeagal apodeme, projected anteriorly. Aedeagal apodeme upright, troughlike; dorsal part tentlike, with thin lateral walls and sclerotized ridge. Surstyli very lightly sclerotized, with narrow arms and apices broad, laterally flattened. Apical margins with 3 groups of long thin setae (5–6 setae each); apical surface with ca. 20 minute setulae. Pair of lobes immediately ventral to surstyli, apparently articulated with bases of surstyli, with each lobe with pair of long, thin, subapical setae. Ventral to these lobes is another pair of lobes with ca. 6 apical setulae, apparently extensions of gonopods or at least articulated with apices of gonopods. Hypandrium very broad, with ventral keel considerably deeper posteriorly.

**TYPE:** Holotype, Male: HISPANIOLA: DOMINICAN REPUBLIC: *Pedernales*: "Upper Las Abejas," 38 km NNW Cabo Rojo;  $18^{\circ}09'N$ ,  $71^{\circ}38'W$ ; 1350 m, 22/VII/90, L. Masner, "sweeping mesic deciduous forest." Dissected (no. 262, in CMNH).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Taken directly from the local name of the type locality, meaning "bees." This is an isolated, moist tropical forest nestled among extensive pine forests in the Sierra de Baoruco.

*Cladochaeta abrupta*, new species

Figures 50, 52, 53, 55, 58

**DIAGNOSIS:** Very recognizable externally based on distinct wing pattern, with abrupt distal edge to costal infuscation; male hind femur and tibia with comb of large, stiff setae; surstyli (male genitalia) very distinctive, each with heavily sclerotized, anvil-shaped lobe. As for *abeja*, known only from the southwestern mountains of the Dominican Republic.

**DESCRIPTION:** HEAD: Moderate height and length; front flat. Eyes with very sparse, short, fine pile; lower hind margin without indentation. Antenna with pedicel and first flagellomere light brown; base of flagellomere I light on inside surface; arista with 1 ventral and 3–4 dorsal branches, with ventral one between apical dorsal branch and apical fork. Front dull, light brown; without pruinescence; 6–7 fairly long interfrontal setulae present. Frontal-orbital setae: Proclinate orbitals nearly equal in size to posterior reclinate orbitals; anterior reclinate orbitals very small, ca.  $0.2\times$  size of proclinate orbitals. Posterior reclinate orbitals slightly closer to ipsilateral proclinate than to inner vertical. Face light brown to tan; completely without carina, of moderate width (FW/HW = 0.29 [N = 2]). Cheeks light yellow, shallow (CD/ED = 0.15). Proboscis and palps light yellow.

**THORAX:** Notum, scutellum, and postnotum ochre and dull. Most of pleura light brown, katapisternum yellow. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellar setae convergent; apical scutellar setae cruciate for about half their length. Postpronotal lobe with 1 large seta, ventral one about half the length and thickness. Legs entirely yellow; forefemur with 1 long dorsolateral seta, row of 3 ventrolateral setae. Hind femur with longitudinal row of 9–10 long, stiff setae on ventral surface; hind tibia with smaller comb of 5 shorter setae, on apical half. Wing with light, diffuse infuscation over costal half, with very slight clouds of infuscation over x-veins r-m and dm-cu; cloud on dm-cu barely extended to  $CuA_1$ . Dark clouds at costal vein just distal to radial break and at apex of vein  $R_{2+3}$ .

Cloud at apex of vein  $R_{2+3}$  with truncate apical margin; between this margin and wing apex is a light window. Apex of vein  $R_{2+3}$  turned toward costal vein (not gradually meeting it). Veins  $R_{4+5}$  and M slightly divergent. Crossvein slightly bent. Wing tip rounded. Halter yellow, with tip light brown.

**ABDOMEN:** All tergites dark brown. Female terminalia: Evenly and lightly sclerotized, with small, short, and broad sclerite immediately below hypoproct. Apical sternite deeply divided into 2 lateral lobes, with narrow ribbon connecting lobes anteriorly; this ribbon folded in middle. Apices of sternal lobes with 4 fine setulae; apical tergite without setae. Male genitalia: Cercus without ventral lobe; ventral margin flat and with lightly sclerotized strip. Epandrium height ca.  $1.3\times$  width of epandrium. Ventrolateral halves of epandrium not tapered to points; each with row of 6 long, stiff setae. Tip of epandrial lobe with sclerotized strip. Aedeagus lying between portions of paraphysis arms that are curved downward. Aedeagus slightly flat laterally, with dorsal lobe; bare (without papillae); lightly sclerotized, more so on apical margin and troughlike strip connected to base of paraphyses and aedeagal apodeme; ventral arm(s) connected to bulbous apex and broad aedeagal apodeme. Paraphyses heavily sclerotized, forcepslike; bases slightly converged medially, width ca.  $2.5\times$  that of apices. Apical half of paraphysis turned sharply ventrad, at almost  $90^{\circ}$  angle with basal part; apical half slightly curved. Paraphyses joined by very narrow dorsal bridge. Aedeagal apodeme upright, troughlike, and very broad. Surstyli without narrow arms; lightly sclerotized, with 3 small lobes and long, laterally flattened dorsal lobe that is anvil-shaped in lateral view. Large dorsal lobe of surstylus without setulae, well sclerotized; row of 4 fine setulae on ventral lobe, ca. 25 minute setulae on apical surface. Hypandrium large, with anterior margin rounded; ventral keel considerably deeper posteriorly and splitting off to each gonopod. Apical sternites not studied.

**TYPES:** Holotype, Male: HISPANIOLA: DOMINICAN REPUBLIC: *Pedernales* Prov.: 20 km NE Pedernales, "Las Abejas," 26/II/92, D. Grimaldi & J. Stark, in isolated deciduous forest. Dissected (no. 267), in



AMNH). Paratypes: 2♀, with same labels as holotype (in AMNH); also 2♂, *Pedernales*: "Upper Las Abejas," 38 km NNW Cabo Rojo; 18°09'N, 71°38'W; 1350 m, 22/VII/90, L. Masner, "sweeping mesic deciduous forest," 1♂ dissected (no. 261). Both specimens in the CMNH.

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: In reference to the abrupt apical margin of the dark cloud in the wing.

*Cladochaeta adusta*, new species

Figures 50, 52, 55, 59

DIAGNOSIS: Pleura and most of head dark brown; wings evenly and lightly fuscous; male genitalia with surstylus having pair of sclerotized, toothlike lobes at base; surstyli long, thin, folded at base (see description below).

DESCRIPTION: HEAD: Moderate height and length. Eyes completely bare; lower hind margin very slightly indented. Antenna with pedicel and first flagellomere brown; arista with 1 ventral and 4 dorsal branches, ventral one between d-3 and d-4. Front velvety brown; without pruinescence; 6-7 interfrontal setulae present. Frontal-orbital setae: Proclinate orbitals nearly equal in size to posterior reclinate; anterior reclinate orbitals small, ca. 0.3× size of proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Face dark brown, with slight carina on dorsal half, relatively broad (FW/HW = 0.34). Cheeks light brown and shallow (CD/ED = 0.13). Labium and palps light brown; labellum light yellow.

THORAX: Notum ochre; scutellum and postnotum light brown. Most of pleura dark brown, including katapisternum. Anterior dorsocentrals ca. 0.7× size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 8 irregular rows. Anterior scutellar setae parallel; apical scutellar setae convergent but not cruciate. Postpronotal lobe with 1 large seta, ventral one ca. 0.3× the length and thickness. Legs mostly yellow, outer surfaces of femora with light, diffuse brown; forefemur with 1 long dorsolateral seta, row of 3 ventrolateral setae. Wing entirely fuscous, with darker, diffuse infuscation over

costal half, but without small clouds over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed. Halter yellowish.

ABDOMEN: Tergites evenly dark brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe but lateral margin elongate and pointed; without lightly sclerotized strip on ventral margin. Epan-drium height about equal to width. Ventro-lateral halves of epan-drium not tapered to points, apex blunt with small posterior lobe; each half with row of 6-7 long, stiff setae. Aedeagus lying between middle portions of paraphysis arms, just above where paraphysis arms cross. Aedeagus membranous, bulbous, bare, without papillae. Paraphyses heavily sclerotized, slightly flattened; sharply hooked, with acute bend at basal third. Paraphyses with bases slightly divergent, then convergent after basal fold, and crossed at apical third. Narrow dorsal bridge between paraphyses not observed. Aedeagal apodeme broad, slightly trough-shaped, with anterior surface concave. Surstyli without narrow arms; lightly sclerotized; with broad, round basal part and dorsal lobe. Basal part with ca. 16 setae near medial half. Dorsal lobe of surstylus roughly triangular, with pair of sclerotized, toothlike spines on basal part of medial margin and 1 fine seta at base of lower spine. Apical part of dorsal surstylar lobe with 20-25 fine, slightly curved setae on medial margin. Hypandrium small, with anterior margin rounded; ventral keel deep. Gonopods short.

TYPE: Holotype, Male, COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 900 m, sweeping in forest, III/91, D. Grimaldi. Genitalia dissected (no. 130).

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From the Latin for brown.

*Cladochaeta centetor*, new species

Figures 50, 52, 53, 55, 60

DIAGNOSIS: Body mostly yellow; arista with 3 dorsal branches, no ventral ones; wing virtually hyaline, very slight costal infuscation; male hind femur with ventral comb of

ca. 5 long setae; paraphyses (male genitalia) heavily sclerotized, short, stout, with sharp tips; surstylus simple, with ventroapical comb of 20-25 fine, curved setae (longest ones apically).

DESCRIPTION: HEAD: Relatively long in lateral view. Eyes with dense, short, fine pilosity; no indentation on lower hind margin. Antenna with pedicel and first flagellomere yellow. Arista with 3-4 dorsal branches, no ventral one. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: Proclinate orbitals ca. 0.8× length of posterior reclinate; anterior reclinate minute, barely distinguishable from frontal-orbital setulae, immediately lateral to proclinate; posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae short, parallel. Face flat, yellow, relatively narrow for group (FW/HW = 0.30 [N = 11]); cheeks yellow, very shallow (CD/ED = 0.10). Proboscis and palps yellow.

THORAX: Notum, scutellum, postnotum, and pleura yellow. Anterior dorsocentrals ca. 0.9× size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 regular rows. Anterior scutellar setae parallel; apical scutellar setae possibly divergent (preservation in specimen ambiguous). Postpronotal lobe with 1 large seta; ventral one ca. 0.9× length, slightly thinner. Legs light yellow. Forefemur with 1 long dorsolateral seta, 2 ventrolateral setae; hind femur of male with ventrolateral row of 5 long setae (lengths of setae equal to or slightly longer than width of femur); hind tarsi of male with 5-6 pairs enlarged setae on dorsal surface. Wing virtually hyaline, except for very light, diffuse infuscation on costal edge, extended slightly past  $R_{2+3}$  and to its apex. Crossvein r-m slightly clouded; no cloud on dm-cu. Apex of vein  $R_{2+3}$  slightly turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip rounded. Halter yellow.

ABDOMEN: Tergites I-V light brown, VI and VII yellow. Female terminalia lightly and evenly sclerotized; apical tergite without setulae, with narrow bridge below opening for epi-/hypoproct; posterolateral corners of the epan-drium developed into pair of flat, oval lobes, margin with ca. 6 fine setulae; sclerotized sclerite between (tergal?) lobes

turned ventrad, then dorsad, ending in broad lateral lobes. Male genitalia: Cercus with only small ventral lobe; ventrolateral surface expanded, flat, lightly sclerotized. Ventral margin of each cercus, near middle, with 2 small, stiff setae very close together. Epan-drium slightly higher than wide; height ca. 1.2× width. Ventrolateral halves of epan-drium tapered to fine apex; each half with 2 rows of 10 long, stiff setae (row nearest margin with larger setae). Aedeagus with heavily sclerotized, short basal rod, which splits off into paired, sclerotized arms; distiphallus membranous but not bulbous. Paraphyses heavily sclerotized; tapered to sharp point, fanglike; pointed downward (these arms about equal in length to surstyli). Paraphyses apparently without dorsal bridge between them. Aedeagal apodeme weakly sclerotized, broad, and short. Surstyli simple lobes, without narrow arms; barely sclerotized. Apex of surstylus with row of 4 long, thin curved setae (lengths about half the length of surstylus); ventral margin with ca. 15 finer, shorter setae; mesal surface with ca. 24 fine, short setulae scattered on apical half. Hypandrium small, without centralized ventral keel; with pair of keels fused to long, tapered gonopods present near lateral margins. Apical sternite simple, not modified much from anterior sternites.

TYPES: Holotype, Male: DOMINICA (West Indies): Clarke Hall, 1-10/III/65, W. W. Wirth, light trap (not dissected). Paratypes: DOMINICA: Clarke Hall, 21-31/III, 11/V, 21-28/II, 11-20/II, 1-10/II/65 (5♂, no. 187; 9♀, no. 188) (1♂, 2♀ in AMNH; all others, including holotype, in NMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Greek *kenteo* (spur, sting, prick), in reference to the sharp pair of paraphyses of the male genitalia.

*Cladochaeta chaeta*, new species

Figures 50, 52, 53, 55, 61

DIAGNOSIS: Arista with 3 dorsal branches and no ventral branch; hind femur of male with short row 4-5 large setae on ventrolateral surface, but lengths not exceeding width of femur. Male genitalia similar to *C. chaeta*, except that in *chaeta* the paraphyses are thin-

ner, the ventral halves of cerci broader, and the surstyli have different shapes and very long apical setae (about the same length as length of surstylus).

DESCRIPTION: HEAD: Moderate depth and width. Eyes with sparse, short, fine pilosity; lower hind margin of eye with very slight indentation. Antenna with pedicel and first flagellomere yellow. Arista with 3 dorsal branches, no ventral one; apical fork long, branches slightly shorter than dorsal branches. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: Proclinate orbitals ca.  $0.9\times$  length of posterior reclines; anterior reclines minute, barely distinguishable from frontal-orbital setulae, slightly posterolateral to proclines; posterior recline much closer to ipsilateral procline than to inner vertical. Postocellar setae short, parallel to slightly convergent. Face flat, yellow, and of moderate width (FW/HW = 0.32 [N = 10]); cheeks yellow and very shallow (CD/ED = 0.08). Proboscis and palps yellow.

THORAX: Notum, scutellum, postnotum, and pleura yellow. Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 regular rows. Anterior scutellar setae parallel; apical scutellar setae cruciate for about one-fourth their length. Postpronotal lobe with 1 large seta; ventral one about one-half the length and slightly thinner. Legs light yellow. Forefemur with 1 long dorsolateral seta, row of 3 ventrolateral setae; hind femur of male with small ventrolateral row of 4–5 long setae (lengths of setae slightly less than width of femur); hind tarsi of male with 5–6 pairs enlarged setae on dorsal surface. Entire wing very lightly and evenly fuscous, with slightly darker, small clouds on crossveins, especially dm-cu. Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly bent in middle. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: All tergites evenly light brown. Female terminalia: Mostly lightly and evenly sclerotized (except epi-/hypoproct); apical tergite without setulae; narrow bridge present below opening for epi-/hypoproct; posterior lobes broadly attached to tergite; each lobe with ca. 15 fine setae; ventrolateral corner of

apical tergite pointed. Male genitalia: Cercus without thin ventral lobe but posteroventral surface very broad, slightly concave, and lightly sclerotized with light window near ventral margin. Epandrium height slightly greater than width. Ventrolateral halves of epandrium slightly tapered but apex blunt; each half with 2 rows of 14 long, stiff setae. Aedeagus lying between apical parts of paraphysis arms. Aedeagus extremely membranous; bulbous, bare (without papillae). Paraphyses heavily sclerotized, pointed downward (these arms about equal in length to surstyli), apices pointed. Paraphyses with stout dorsal bridge between them, about equal in thickness to paraphysis arm. Aedeagal apodeme sclerotized, with flared, fanlike anterior portion, broadly connected to V-shaped portion with apices of arms articulated with bent bases of paraphyses. Ventral part of aedeagal apodeme with pair of small lobes articulating between bases of gonopods. Surstyli without narrow arms, roughly triangular in broadest (lateral) view, with long apical lobe; barely sclerotized. Apical lobe of surstylus with 1 very long, thin curved seta at apex (length slightly greater than length of surstylus). Ventromedial margin of surstylus with row of ca. 25 fine setae, decreased in length toward base of surstylus (subapical setae about half the length of long, apical seta). Hypandrium small, without centralized ventral keel broad; keels of long, tapered gonopods present. Apical sternites not observed.

TYPES: Holotype, Male: PANAMA: Canal Zone: Colón, VII/79, canopy fogging, E. M. Broadhead (not dissected). Paratypes: Same data (5♂, 2♀, nos. 155, 156) (AMNH).

OTHER MATERIAL EXAMINED: HONDURAS: Roatan Island (west), 1/I/80, G. E. Bohart (in UTSU) (Genitalia dissected, DAG no. 94). PANAMA: Chiriqui: David, 2200 ft, 2/VII/64, A. Broce, light trap (5♂, no. 178; 1♀, no. 179) (NMNH).

ETYMOLOGY: From Greek *chaite* (long hair), in reference to the long fine setae at the apices of the surstyli in the male.

*Cladochaeta hermani*, new species

Figures 50, 52, 53, 61

DIAGNOSIS: Genitalia differ subtly with *C. laevacerca*: epandrium shorter in *hermani*

relative to paraphyses, apex of surstylus rounded (vs. pointed) in *hermani*; left paraphysis with ostia at base in *hermani* (not present in *laevacerca*); hypandrium slightly longer in relation to width in *hermani*.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with very sparse, short, fine pilosity; lower hind margin of eye without even slight indentation. Antenna with pedicel and first flagellomere yellow. Arista with 3 dorsal branches, no ventral one; branches of apical fork of moderate length. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: Proclinate orbitals ca.  $0.9\times$  length of posterior reclines; anterior reclines minute, barely distinguishable from frontal-orbital setulae, almost immediately lateral to proclines; posterior recline much closer to ipsilateral procline than to inner vertical. Postocellar setae of moderate length; parallel to slightly convergent. Face flat, yellow, and of moderate width (FW/HW = 0.29 [N = 5]); cheeks yellow and very shallow (CD/ED = 0.08). Proboscis and palps yellow.

THORAX: Entire thorax light yellow. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals approx. midway between scutellum and ant. dorsocentrals. Acrostichals in 4 irregular rows. Anterior scutellar setae parallel; apical scutellar setae slightly cruciate. Postpronotal lobe with 1 large seta; ventral one ca.  $0.7\times$  length and roughly the same thickness. Legs light yellow. Forefemur with 1 long dorsolateral seta, row of 3 ventrolateral setae; hind femur with small ventrolateral row of 4 setae longer than most setulae on leg (lengths of setae about three-fourths the width of femur); hind tarsi of male with 5–6 pairs enlarged setae on dorsal surface. Wing with infuscation very light on costal edge; with very slight infuscation over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly toward costal vein. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites light brown. Female terminalia sclerotized; apical tergite with pair of small setulae laterally; narrow bridge between epi-/hypoproct; pair of small postero-medial lobes on tergite, each with ca. 10 fine setulae; small, flat, slightly sclerotized scler-

ite ventral to each tergal lobe, upturned, ending in small, folded, heavily sclerotized sclerite. Male genitalia: Similar to *C. laevacerca* except that this species has the following differences: surstylus not pointed and curved; setae on ventral margin of surstylus not as long, apical setae longer; apex of left paraphysis slightly hooked, right paraphysis considerably longer than the left (only barely longer in *laevacerca*); hypandrium slightly longer.

TYPES: Holotype, Male: NICARAGUA: Bluefields, W. B. Heed coll. (in AMNH). Genitalia dissected (no. 252). Paratypes: 3♀, 1♂, with same labels as holotype (all in AMNH).

OTHER MATERIAL EXAMINED: Known only from type series.

ETYMOLOGY: Patronym for Lee Herman, curator of Coleoptera at the AMNH, colleague and friend.

*Cladochaeta howdeni*, new species

Figures 50, 52, 53, 55, 62

DIAGNOSIS: Thorax mostly yellow, pleura with diffuse vitta in middle; anterior reclinate orbital seta minute, indistinguishable from frontal-orbital setulae; wing hyaline; paraphyses heavily sclerotized, slender, curved slightly outward on apical half; surstylus slender, with narrow apical lobe and long apical seta. Restricted to Jamaica.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with very sparse, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel yellow and first flagellomere light brown. Arista with 1 ventral and 4 dorsal branches; ventral branch between d-3 and d-4; branches of apical fork of moderate length. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: Proclinate orbitals equal in length to posterior reclines; anterior reclines minute, in line with and equal in size to frontal-orbital setulae, immediately lateral to proclines; posterior recline much closer to ipsilateral procline than to inner vertical. Postocellar setae of moderate length; upright and parallel. Face flat, yellow, and of moderate width (FW/HW = 0.32 [N = 11]); cheeks yellow and shallow (CD/ED = 0.10). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum yellow; pleura mostly yellow but with diffuse, light brown vitta between notopleural edge and katepisternum, running length of pleura, sometimes with light infuscation on dorsal edge of katepisternum. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals approximately midway between scutellum and ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae slightly cruciate. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow. Forefemur with 1 long dorsolateral seta, 2 ventrolateral setae; hind femur of male without enlarged setae. Wing without any infuscation, even the slight clouds over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  slightly turned costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M slightly divergent, not parallel. Crossvein slightly curved, not straight. Wing tip rounded, not slightly pointed. Halter yellow.

ABDOMEN: All tergites evenly dark brown. Female terminalia very distinctive; sclerotized: apical tergite without setae, broad, shallow; apical sternite almost entirely divided into pair of large lobes; each lobe with ca. 12 setulae. Male genitalia: Cercus without thin ventral lobe, but ventral margin with sclerotized strip turned inward. Epandrium height equal to width. Ventrolateral halves of epandrium deeply concave on posterior margin; each half with row of 6–8 long, stiff setae. Aedeagus lying between apical parts of paraphysis arms. Aedeagus mostly membranous, with some sclerotization; apex split, each half with small sclerite on mesal surface. Paraphyses heavily sclerotized, pointed downward (these arms ca.  $1.5\times$  length of surstyli), apices pointed. Bases of paraphyses parallel, apical halves slightly divergent. Paraphyses with stout dorsal bridge between them. Aedeagal apodeme lightly sclerotized, with flared, fanlike anterior portion. Surstyli with narrow arms and apical knob; knob with apical lobe; surstylus barely sclerotized. Apical lobe of surstylus with 1 long, thin curved seta at apex (length slightly greater than length of apical lobe). Dorsal surface of surstylus with row of 6–8 fine setae; ventral surface with 10–12 smaller, fine setulae. Hypandrium fan-shaped, with ventral keel flared

out to apices of gonopods. Apical sternites not observed.

TYPES: Holotype, Male: JAMAICA: Hermitage Reservoir, X–XI/57, M. Wasserman (not dissected). Paratypes: Same data (2♂, dissected, no. 251).

OTHER MATERIAL EXAMINED: JAMAICA: 4000 ft, Hardwar Gap, 25/VII/66, Howden & Becker (CNC) (1♂, 1♀); Try, Good Hope, 22/VIII/66, H. F. Howden (6♂ + ♀, DAG nos. 111, 112, respectively) (CNC); near Bath, II/56, W. B. Heed (3♂, 4♀) (AMNH); Windsor, VII/58, W. B. Heed & M. Wasserman (1♀) (AMNH).

ETYMOLOGY: Patronym in honor of Henry Howden (Carleton University, Ottawa), coleopterist and collector of many of the specimens. His collections from Jamaica in the CNC are an extremely valuable resource for Caribbean insect systematics.

*Cladochaeta labidia*, new species

Figures 50, 52, 53, 62

DIAGNOSIS: Similar and closely related to *C. howdeni* based on 4 dorsal (rarely 3) and 1 ventral arisal branches; minute ant. reclinate orbital seta; diffuse, light brown pleural vitta; shapes of paraphyses similar and with small sclerites flanking membranous distiphallus. Differs from *howdeni* principally in male genitalia: apical halves of paraphyses not turned slightly outward, but actually curved subtly inward; surstylus without thin apical lobe; tip of epandrium not as narrow as in *howdeni*.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with dense, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel and first flagellomere yellow to light brown. Arista with 1 ventral and 3–4 dorsal branches; ventral branch between d-3 and d-4 (sometimes opposite d-3); branches of apical fork rather large, lengths about equal to d-3. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: Proclinate orbitals equal in length to posterior reclines; anterior reclines minute, about twice the size to frontal-orbital setulae, immediately lateral to proclines; posterior reclinate midway between ipsilateral proclinate and inner vertical. Postocellar setae of moderate length; upright and slightly

convergent. Face flat, yellow, and of moderate width ( $FW/HW = 0.33$  [ $N = 7$ ]); cheeks yellow and of moderate depth ( $CD/ED = 0.10$ ). Proboscis and palps yellow.

THORAX: Notum ochre to light brown; scutellum diffuse, light brown; postnotum light brown; pleura mostly yellow but with diffuse, light brown vitta from notopleural edge to anterior portion of katepisternum, running length of pleura. Anterior dorsocentrals small, about half the size of posterior dorsocentrals; post. dorsocentrals approx. midway between scutellum and ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae cruciate for ca.  $0.3\times$  their length. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow. Forefemur with 1 long dorsolateral seta and 2 ventrolateral setae; hind femur of male without enlarged setae. Wing entirely hyaline, without infuscation even as tiny clouds on crossveins. Apex of vein  $R_{2+3}$  turned slightly costad, but not abruptly. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly bent in middle. Wing tip rounded, with row of ca. 7–8 fine, longer setulae on edge. Halter light yellow.

ABDOMEN: Tergites evenly light brown. Female terminalia simple, very lightly sclerotized; apical tergite with single, small seta on each lateral lobe; tergite a simple, inverted U-shaped sclerite; apical sternite bilobed but not completely divided; medial lobes small, rounded, with ca. 8 fine, long setulae. Male genitalia: Cercus without thin ventral lobe; ventral margin with sclerotized strip turned inward. Epandrium height ca.  $1.3\times$  width. Ventrolateral halves of epandrium concave on posterior margin, apex slightly hooked posteriad; each half with row of 6 stiff setae. Aedeagus lying between apical parts of paraphysis arms. Aedeagus mostly membranous, with some sclerotization; apex split, each half with small sclerite on very apex; small membranous lobe in middle of aedeagus, on posterior surface. Paraphyses heavily sclerotized, pointed downward and nearly straight (length ca.  $0.6\times$  height of epandrium). Medial margins of paraphyses much closer at bases; apical halves thinner and slightly concave (lying close to lateral surfaces of aedeagus). Bases of paraphyses with

narrow dorsal bridge between them and each with a lateral flange pointed anteriad. Aedeagal apodeme sclerotized. Surstyli clavate, with narrow arms and apical knob deeply bilobed; surstylus barely sclerotized. Hypandrium with ventral keel. Apical sternites not studied.

TYPES: Holotype, Male: COLOMBIA: Buenaventura, IX/56, M. Wasserman (dissected, no. 250). Paratypes: Same data (3♀, none dissected) (all in AMNH).

OTHER MATERIAL EXAMINED: PANAMA: Canal Zone: Gamboa, VII/67, W. W. Wirth, Malaise trap (1♂, no. 191; 1♀, no. 192) (NMNH); Darien Prov.: Patino Point, 13/IX/52, F. S. Blanton (DAG no. 90) (NMNH).

ETYMOLOGY: From Greek *labidion* (tweezers, tongs), in reference to the paraphyses in the male genitalia.

*Cladochaeta laevacerca*, new species

Figures 50, 52, 53, 55, 63

DIAGNOSIS: Distinguished externally by 3–4 dorsal arisal branches and lack of ventral branch; hind femur with row of 4 stiff setae on ventroapical margin; pleura with 2 diffuse, light brown vittae (sometimes barely visible). Very similar to *C. hermani*, but best distinguished by subtleties of male genitalia, as discussed in the diagnosis for that species.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with dense, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel yellow, first flagellomere light brown. Arista with 3–4 dorsal branches, no ventral branch; branches of apical fork rather large, lengths about equal to d-3. Front yellow; frontal vittae shiny, golden. Frontal-orbital setae: proclinate orbitals ca.  $0.9\times$  length of posterior reclines; anterior reclines minute, ca.  $2\times$  size of frontal-orbital setulae, lateral and slightly posterior to proclines; posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate length; parallel, projected backward. Face flat, yellow, quite narrow ( $FW/HW = 0.28$  [ $N = 4$ ]); cheeks yellow and shallow ( $CD/ED = 0.08$ ). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum ochre; pleura with very diffuse (sometimes barely visible), light brown vitta along no-

topleural edge and across anepisternum/katatergite. Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae cruciate for ca.  $0.3\times$  their length. Postpronotal lobe with 1 large seta, ventral one ca.  $0.4\times$  the size. Legs entirely light yellow. Forefemur with 1 long dorsolateral seta and 2 ventrolateral setae; hind femur of male with row of 4 long, stiff setae, lengths about equal to width of femur. Wing with extremely light, diffuse infuscation over costal half of wing, and with a small hyaline window lying between the apices of veins  $R_{2+3}$  and  $R_{4+5}$ . Very slight, small clouds over x-veins r-m and dm-cu, cloud on dm-cu barely extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  gradually meeting costal vein, then turned very slightly costad. Veins  $R_{4+5}$  and M parallel, but with a slight kink in  $R_{4+5}$ . Crossvein dm-cu straight; slightly oblique, not perpendicular, to vein M. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: All tergites evenly light brown. Female terminalia barely sclerotized; apical tergite without setae; pair of small posteroventral setose lobes, apparently portion of apical sternite and fused to tergite; membranous area between lobes. Male genitalia: Cercus without thin ventral lobe; ventral half broad, sclerotized, and concave, particularly medial margins. Posteromesal corner of cercus with pair of closely spaced, thin setae. Epandrium height equal to width. Ventrolateral halves of epandrium with apices barely tapered; each half with 2 uneven rows of 8 stiff setae. Aedeagus lying between apical parts of paraphysis arms. Aedeagus bulbous and entirely membranous. Paraphyses heavily sclerotized, curved directly downward from base and nearly straight (length ca.  $0.6\times$  height of epandrium), apices pointed. Bases of paraphyses with narrow dorsal bridge between them. Aedeagal apodeme sclerotized, anterior portion fan-shaped; posterior part V-shaped, with stout arms articulating with bases of paraphyses. Surstyli laterally flattened, with pointed apex; barely sclerotized; ventral margin with irregular rows of ca. 30 setae (apical 2–3 ones largest). Hypandrium quadrate, without centralized

ventral keel but with pair of lateral keels formed from bases of gonopods. Gonopods long, deep, laterally flattened, tapered apicad where they articulate with bases of surstyli. Apical sternites not studied.

TYPES: Holotype, Male: TRINIDAD: *Arima*: Blanchisseuse Rd., 2000 ft, 3–9/II/82, Morton S. Adams. Genitalia not dissected. Paratypes: 2♂ (1 dissected, no. 81a), 1♀ (dissected, no. 87), with same label data as holotype. All in the AMNH.

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From the Latin *laeva* (left), and referring to the greater size of the left cercus (male).

DISCUSSION: This species is closely related to *hermani* and *chaeta* based on the asymmetrical cerci; surstyli with long, fine apical setae; and the short, straight, sharp paraphyses (*centetor* is closely related to these 3 species based on the last 2 characters).

#### *Cladochaeta minuta* (Duda)

Figures 50, 52

*Diathoneura minuta* Duda, 1925: 182; Wheeler, 1963: 55 (designated lectotype, redescription, figured male genitalia).

*Cladochaeta minuta*: Vilela and Bächli, 1990: 11. (new combination; redescription; designated paralectotypes; illustrated genitalia).

DIAGNOSIS: Male genitalia distinct for the pair of sclerotized, hooked paraphyses that are equal in size; concave surstyli with outer (posterior lobe) truncate, inner lobe with median tip bearing 5–6 scalelike, long setae.

DESCRIPTION: Described in detail by Vilela and Bächli (1990) based on type material.

Wing: Very light infuscation on costal edge and apical third of wing; very slight infuscation over x-veins r-m and dm-cu, cloud on dm-cu barely extended to  $CuA_1$ . Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M slightly divergent. Crossvein straight. Wing tip slightly pointed.

ABDOMEN: Female terminalia with opening for epi-/hypoproct large, very narrow ventral bridge; apical sternite bilobed, lobes projected beyond apex of proctiger in lateral view, with ca. 8 fine setulae on each lobe.

Male genitalia (figured by Vilela and Bächli, 1990: figs. 7, 8): Cercus without thin ventral lobe; ventral margin flat. Epandrium height slightly greater than width. Ventrolateral halves of epandrium with apices slightly tapered; each half with a row of 6 long, stiff setae. Aedeagus lying between parts of paraphysis arms that are turned downward. Dorsal part of aedeagus very membranous, with minute spicules on ventroapical tip; lateral parts of aedeagus slightly sclerotized, fingerlike, projected posteriad. Paraphyses heavily sclerotized, strongly hooked downward, equally developed and apically pointed. Paraphyses with broad dorsal bridge between them. Aedeagal apodeme lightly sclerotized, funnel-shaped, anteroventral portion fan-shaped and flanged; posterior part slightly bifid, with tiny arms articulated with bases of surstyli. Surstyli cupped, with broad, flat anterior (inner) and posterior lobes; outer surface of posterior lobe with 15–16 fine setulae on medial margin, anterior lobe with 5–6 long scalelike setae on medial margin. Hypandrium with rounded anterior margin, short centralized ventral keel. Gonopods long, deep, laterally flattened, tapered apicad where they articulate with bases of surstyli. Apical sternites not studied.

TYPES: Lectotype, Male: COSTA RICA: Suiza de Turrialba, 14/V/21. The following type labels are attached to this specimen: "*D. minuta* type det. Dr. O. Duda, syntypus"; "Lectotype *minuta* Duda selected by M. R. Wheeler, June 1962"; and "*Cladochaeta minuta* (Duda) Bächli & Vilela det. 1990." Specimen is in the HNHM. Paralectotypes: 1♂ and 2♀, with essentially same data. Both females, as well as lectotype male, were dissected by Vilela and Bächli (1990). Specimens in the HNHM, except male paralectotype (in ZMB).

OTHER MATERIAL EXAMINED: Known only from the type series.

DISCUSSION: Vilela and Bächli examined the type series and found that one female specimen designated as a paralectotype by Wheeler (1963: 55) was a different species. They illustrated the genitalia of this specimen (their fig. 8h, i), which indeed is distinctly different from the other female paralectotypes of *C. minuta*.

#### *Cladochaeta mystaca*, new species

Figures 50, 56, 64, 65

DIAGNOSIS: Distinguished externally by the bizarre growth of vibrissae, which are convergent and have tips that form one full spiral with each other in a double helix (possibly found in males only). Also, antennae with pedicel having numerous, fine, long setulae; male genitalia with long, thin, sclerotized paraphyses, each of which is twisted into a full spiral. Female unknown. Known only from southern Mexico.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with dense, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel yellow, having numerous, fine, long setulae; first flagellomere light brown. Arista with 3 dorsal branches, one short ventral branch between d-3 and apical fork; branches of apical fork rather short, lengths about half that of d-3. Front ochre, dull; interfrontal setulae relatively large, equal in size and slightly larger than anterior reclinate orbital seta. Frontal-orbital setae: Proclinate orbitals ca.  $0.8\times$  length of posterior reclinate; anterior reclinate small, ca.  $3\times$  size of proclinate, lateral to proclinate; posterior reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate length; convergent. Face flat, yellow, and broad (FW/HW = 0.36); cheeks yellow and of moderate depth (CD/ED = 0.18); vibrissae long, thin, convergent, tips form one full spiral with each other (a double helix). Proboscis and palps yellow.

THORAX: Entire thorax (including pleura) yellow. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 8 irregular rows. Anterior scutellar setae convergent; apical scutellar setae cruciate for ca.  $0.3\times$  their length. Postpronotal lobe with 1 large seta, ventral one ca.  $0.3\times$  the size. Legs entirely light yellow. Forefemur with row of 3 stiff dorsolateral setae, row of 3 ventrolateral setae; hind femur of male with row of 5 stiff, erect setae, lengths ca.  $0.3\times$  width of femur. Wing with diffuse infuscation over costal edge of wing, darkest surrounding apices of veins  $R_{2+3}$  and  $R_{4+5}$ , extended down to apex of vein M along wing margin. Slight cloud



of infuscation over x-vein dm-cu, barely extended to CuA<sub>1</sub>; no cloud over vein r-m. Vein R<sub>2+3</sub> virtually straight, gradually meeting costal vein, apex not turned slightly costad. Veins R<sub>4+5</sub> and M parallel. Crossvein dm-cu slightly bent. Wing tip rounded, not slightly pointed.

ABDOMEN: Tergites evenly light brown. Female terminalia unknown. Male genitalia: Cercus without thin ventral lobe; without sclerotized strip on ventral margin. Epandrium height slightly greater than width. Ventrolateral halves of epandrium barely tapered, each half with row of 5 stiff setae. Aedeagus lying between apical halves of paraphyses. Aedeagus large, entirely and very membranous. Paraphyses heavily sclerotized, pointed downward, forming nearly a complete spiral (length slightly greater than height of the epandrium). Medial margins of paraphyses touching at basal third, then flared laterad in middle; sharply folded inward and around aedeagus, then touching preapically, then diverged at apices. Apices with small knobs. Bases of paraphyses with narrow dorsal bridge between them and with shallow "hood" anterior to bridge (aedeagal apodeme). Surstyli are simple lobes without narrow arms; barely sclerotized; with ca. 40 fine setulae on broad posterior surface. Hypandrium wide, quadrate, anterior margin slightly crenulate, ventral keel barely present. Aedeagal apodeme very broad. Apical sternites not studied.

TYPE: Holotype, Male: MEXICO: *Sinaloa*: 20 mi E Concordia, 3000 ft, 8/VIII/64 (in CNC) (genitalia dissected, DAG no. 102).

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From Greek *mystax* (mustache), referring to the bizarre, twisted vibrissae, which probably occur only in the male.

DISCUSSION: D. K. McAlpine (1976) reported spiral vibrissae in some male clusiid flies. In these instances the pair of vibrissae project straight forward and are twisted into a gentle spiral of approximately 1 revolution. For some of these species the males also have broadened heads. McAlpine hypothesized that the spiral vibrissae are employed by fighting males, perhaps to lock against those of an opponent. The spiral vibrissae in

*C. mystaca* differ considerably since they do not stick out forward from the face (they are almost turned upward) nor are they appreciably stouter than vibrissae seen in other *Cladochaeta*. They curl inward and intertwine at the apices. If this is a male character, it is intriguing as to how it might function in combat or otherwise.

*Cladochaeta obscura*, new species

Figures 50, 52, 66

DIAGNOSIS: Distinctly tiny species (ThL = 0.47 mm, type specimen only), with notum and dorsal part of pleura light brown; anterior reclinate orbital seta minute; male genitalia most similar to *C. howdeni*, except that *obscura* has paraphyses slightly stouter; distiphallus membranous, but without pair of small sclerites flanking it; surstylus completely different, composed of 2 apical lobes (tips bearing 4–5 setae) and broad basal lobe. Known only from the Canal Zone, Panama.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with dense, short, fine pilosity; lower hind margin of eye without slight indentation. Antenna with pedicel and first flagellomere light brown. Arista with 4 dorsal branches, one ventral branch between d-3 and d-4; branches of apical fork 0.6–0.7× that of d-4. Front bronze, shiny; interfrontal setulae minute, sparse. Frontal-orbital setae: Procline orbitals equal in length to posterior reclines; anterior reclines minute, same size as frontal-orbital setulae, lateral to proclines; posterior reclinate midway between ipsilateral procline and inner vertical. Postocellar setae very small, only slightly larger than interfrontal setulae. Face flat, light brown, and of moderate width (FW/HW = 0.32); cheeks yellow and slightly shallow (CD/ED = 0.13). Proboscis and palps light brown.

THORAX: Notum, scutellum, and postnotum light brown; dorsal half of pleura and katepisternum a similar light brown; ventral half of katepisternum yellow. Anterior dorsocentrals ca. 0.7× size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae convergent but not cruciate. Postpronotal lobe with 1 large

seta, ventral one not present (perhaps lost from specimen). Legs yellowish and light brown. Forefemur with 1 dorsolateral seta and 2 ventrolateral setae; hind femur of male with 1 stouter, erect seta, length about one-half the width of femur. Wing entirely hyaline, without infuscation even as small clouds over crossveins. Apex of vein R<sub>2+3</sub> gradually meeting costal vein, not turned abruptly costad. Veins R<sub>4+5</sub> and M slightly divergent. Crossvein dm-cu slightly bent in middle. Wing tip very rounded. Halter light brown.

ABDOMEN: Tergites evenly dark brown. Female terminalia unknown. Male genitalia: Cercus without thin ventral lobe; ventral margin flat but not sclerotized. Epandrium slightly higher than wide, height ca. 1.3× width. Ventrolateral halves of epandrium with apical half of posterior margin deeply concave; each half with row of 4 short, stiff setae. Aedeagus protruding between paraphyses. Distiphallus membranous, with slightly sclerotized floor; without papillae. Paraphyses heavily sclerotized; symmetrical; bases (dorsally) with lateral flanges, lobes pointed downward and curved slightly outward. Aedeagal apodeme broad, convex, sclerotized. Surstyli trilobed; medial lobe longest and thinnest, bearing 4 fine, curved setae and 1 thicker seta; ventral lobe with 4 fine setae; lateral lobe concave, without setae; paraphyses barely sclerotized. Hypandrium with anterior margin rounded, with shallow centralized ventral keel. Gonopods deep, laterally flattened; tapered apicad where they articulate with bases of surstyli. Apical sternites not studied.

TYPE: Holotype, Male: PANAMA: *Canal Zone*: Barro Colorado Island, VII/67, W. W. Wirth (dissected, no. 175) (NMNH).

OTHER MATERIAL EXAMINED: Known only from type specimen.

ETYMOLOGY: From Latin *obscurus*, in reference to this tiny fly with few distinctive features.

*Cladochaeta propenicula*, new species

Figures 50, 52, 54, 65, 67

DIAGNOSIS: A tiny species (ThL = 0.60 mm [♂], 0.70 [♀]); anterior dorsocentral seta small, ca. 0.3× size of posterior dorsocentral; male foreleg with tarsomere I having brush

of thick, short, fine pile; male genitalia with paraphyses heavily sclerotized, twisted into a three-quarter spiral; aedeagus large, membranous; surstylus thin, slightly bilobed apically, with 2 long setae.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with sparse, short, fine pilosity; lower hind margin of eye with very slight indentation. Antenna with pedicel yellow and first flagellomere tan to light brown. Arista with 3 dorsal branches (rarely with 4); one ventral branch between d-3 and d-4 or between d-3 and apical fork; branches of apical fork short. Front entirely yellowish; interfrontal setulae very sparse and minute. Frontal-orbital setae: Procline orbitals equal in size to posterior reclines; anterior reclines minute, slightly larger than frontal-orbital setulae, directly lateral to proclines; posterior reclinate midway between ipsilateral procline and inner vertical. Postocellar setae of moderate size, about half the size of proclines. Face flat, yellow, and low and wide (FW/HW = 0.32 [N = 6]); cheeks yellow, shallow (CD/ED = 0.09). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum yellow; very light infuscation on pleura. Anterior dorsocentrals very small, ca. 0.3× size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6–8 irregular rows. Anterior scutellar setae parallel; apical scutellar setae convergent but not cruciate. Postpronotal lobe with 1 large seta; ventral one much finer, about half the length. Legs entirely light yellowish. Forefemur with 1 dorsolateral seta and 2 larger ventrolateral setae; hind femur without larger, erect setae. Wing almost entirely hyaline except for light, diffuse infuscation on costal edge. Infuscation extended slightly past R<sub>2+3</sub> up to its apex. No clouds on crossveins. Apex of vein R<sub>2+3</sub> gradually meeting costal vein, not turned abruptly costad. Veins R<sub>4+5</sub> and M parallel. Crossvein dm-cu slightly curved. Wing tip rounded. Halter light yellow.

ABDOMEN: Tergites light brown. Female terminalia sclerotized; apical tergite narrow, without setae, a simple inverted U-shaped sclerite (not connected beneath epi-/hypoproct). Apical sternite a narrow, U-shaped sclerite with ca. 8 fine setulae on small,

rounded apical surfaces. Male genitalia (description based on male from Mexico; discrepancies with Peruvian specimen are noted where applicable): Cercus without thin ventral lobe, ventrolateral corner pointed; without sclerotized strip on ventral margin. Epanthrium higher than wide; height ca.  $1.5\times$  width. Ventrolateral halves of epanthrium tapered, each half with row of 4–5 stiff setae. Aedeagus mostly membranous, with slight sclerotization; large, scoop-shaped; projecting between paraphyses where they diverge in apical half; dorsal walls of distiphallus folded inward (but not meeting medially), apex with circular opening (Peruvian specimen with simple, bulbous, and very membranous distiphallus). Paraphyses heavily sclerotized, each forming a three-quarter downward spiral. Bases of paraphyses with narrow dorsal bridge between them, then touching at basal third (forming roof over distiphallus) (not touching in Peruvian specimen), then diverged laterad in middle and then turned anteriorly (lying behind [anterior to] distiphallus); crossed preapically (not crossed in Peruvian specimen). Apices with small knobs or slightly bilobed (apical knob barely evident in Peruvian specimen). Aedeagal apodeme lightly sclerotized (more so in Peruvian specimen), broad, and platelike. Surstyli not sclerotized; clavate, with apical knobs barely bilobed (slightly more bilobed in Peruvian specimen); each lobe with long, thin, curved seta at apex, and ca. 7 finer ones one-half the length between them. Hypandrium rounded, with shallow ventral keel. Apical sternites not studied.

**TYPES:** Holotype, Male: EL SALVADOR: San Salvador, 20/1/54, W. B. Heed (not dissected). Paratypes: Same data (1♂, dissected no. 255; 2♀) (all in AMNH). Also, MEXICO: Yucatán: Mérida, IX–X/55, W. B. Heed (1♂, no. 224) (AMNH).

**OTHER MATERIAL EXAMINED:** PERU: Uribamba, IX/55, Th. Dobzhansky & C. Pavan (1♂, no. 255) (AMNH).

**ETYMOLOGY:** *pro-* (fore) and Latin *peniculus* (brush), for the fine dense mat of setulae on the male forelegs.

**DISCUSSION:** There is variation in the male genitalia of specimens from the 3 localities. Genitalia of males from El Salvador (type locality) and Mexico agree very closely, but

the specimen from Peru differs somewhat from the Central American ones as detailed in the description above. The specimens from Peru possibly represent a different species. No differences were found in the foretarsal brush.

*Cladochaeta psychotria*, new species

Figures 50, 52, 68

**DIAGNOSIS:** Arista with 1 ventral and 4 dorsal branches; wing hyaline, with arched costal edge; male genitalia heavily sclerotized, especially paraphyses; paraphyses long, with 2 prongs. Surstylus large, elaborate, with small basal and median lobes, each with stout seta; thin dorsoapical lobe, preapical row of 9–10 fine, stiff setulae.

**DESCRIPTION:** **HEAD:** Relatively high (HD/HL = 1.42). Eyes completely bare; lower hind margin of eye with very slight emargination. Antenna with pedicel light brown, first flagellomere darker brown. Arista with 4 dorsal branches of nearly equal size; one ventral branch between d-3 and d-4; branches of apical fork short (half the size of proximal branches). Front entirely light brown, with very slight, greenish pruinescence; interfrontal setulae small, in 2 rows of 3. Frontal-orbital setae: Proclinate orbital equal to size of posterior reclinate; anterior reclinate  $0.3\times$  thickness and length of proclinate, posterior to and slightly lateral to proclinate; posterior reclinate slightly closer to proclinate than to ipsilateral inner vertical seta. Postocellar setae of moderate size, about half the size of proclinate. Face carinate; light brown, particularly near oral margin, and with slight greenish pruinescence; face relatively low (FW/HW = 0.33); cheeks shallow (CD/ED = 0.07). Proboscis and palps light brown.

**THORAX:** Notum, scutellum, and postnotum dark tan; pleura with dark brown infuscation down to about middle of katapisternum. Anterior dorsocentrals about half the size of posterior dorsocentrals; post. dorsocentrals equidistant between scutellum and ant. dorsocentrals. Acrostichals in 6–8 irregular rows; prescutellar acrostichals not enlarged. Anterior and posterior scutellar setae parallel. Postpronotal lobe with 1 large seta. One large and 1 short notopleural seta. Legs

mostly light in color. Forefemur with 1 dorsolateral seta and row of 3 ventrolateral setae; ventral surface of hind femur without thicker, stiff setae. Wing very lightly fuscous, virtually completely hyaline; without any dark clouds even on crossveins. Vein  $R_{2+3}$  straight, apex gradually meeting costal vein, not turned even slightly costad. Veins  $R_{4+5}$  and M parallel. Crossvein m-cu straight, perpendicular to vein M. Costal edge distinctly arched, wing tip slightly pointed, making overall shape of wing almost lanceolate. Tip of wing with row of 6 fine, stiff larger setulae between apices of veins  $R_{4+5}$  and M. Halter light.

**ABDOMEN:** Tergites dark brown. Female terminalia unknown. Male genitalia: Cercus with ventral margin simple. Epanthrium much taller than wide; height ca.  $1.5\times$  width. Ventrolateral halves of epanthrium distinctly tapered; each half with row of 6 stiff setae. Aedeagus sclerotized, best seen in lateral view; basally with 2 dorsal, heavily sclerotized horns projecting into a scoop-shaped aedeagal apodeme; anteriorly surface of aedeagus flat, straight, nearly equal to length of paraphyses. Paraphyses long,  $0.7\times$  height of epanthrium; heavily sclerotized, apices sharp, and pointed downward; each half with 2 prongs, with inner (mesal) prong slightly shorter and thicker than lateral one. Paraphyses joined dorsally by thin anterior band. Surstyli complex, with small basal lobe having stout, stiff seta; long, thin dorsoapical lobe curved laterad; preapical row of 9–10 fine, stiff setae; surstylus barely sclerotized. Hypandrium small, narrow, entirely clavate; without ventral keel at stem.

**TYPES:** Holotype, Male: COSTA RICA: Monteverde, VIII/96, Kyle P. Harms, ex: *Psychotria* sp. [Rubiaceae] as larvae. Dissected (no. 324). Paratype: Male, with same data as holotype; dissected (no. 325). Both specimens in AMNH.

**OTHER MATERIAL EXAMINED:** Known only from the 2 type specimens.

**ETYMOLOGY:** Taken directly from the host plant, *Psychotria*.

**DISCUSSION:** According to the notes provided by Kyle Harms, the larvae appear to have been breeding within the flowers of *Psychotria* and are not associated with any spittlebug. This may be the only definitive

record of a *Cladochaeta* not associated with spittlebugs, and certainly deserves further investigation.

*Cladochaeta robusta*, new species

Figures 51, 52, 54, 56, 69

**DIAGNOSIS:** A large species (ThL = 0.92–1.01 mm) with dark brown face and pleura; arista with 4 short dorsal branches (1 ventral one); male genitalia heavily sclerotized, including paraphyses; paraphyses with very long apical prong; surstylus with thin medial lobe having broad, apically serrate scale.

**DESCRIPTION:** **HEAD:** Relatively long compared to depth. Eyes with sparse, short, very fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel light and dark brown, flagellomere I light brown. Arista with 4 short dorsal branches; 1 ventral branch, between d-4 and apical fork; branches of apical fork very short, sometimes dorsal branch of apical fork lost. Front entirely light brown; interfrontal setulae large, about same length as anterior reclinate orbital, pointed backward. Frontal-orbital setae: Proclinate orbital ca.  $0.7\times$  size of posterior reclinate; anterior reclinate about half the thickness and length of proclinate, posterior to and slightly lateral to proclinate; posterior reclinate slightly closer to ipsilateral inner vertical seta than to proclinate. Postocellar setae of moderate size, slightly smaller than proclinate. Face mostly flat, with very small carina; brown; relatively broad (FW/HW = 0.32 [N = 9]); cheeks yellow above facial suture (brown below it), broad (CD/ED = 0.09). Proboscis yellow.

**THORAX:** Notum and scutellum yellow; postnotum dark brown; pleura almost entirely dark brown (contrasting with light forecoxa). Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 8 irregular rows; one immediately in front of ant. dorsocentral slightly larger than other acrostichals; prescutellar acrostichals not enlarged. Anterior scutellar setae parallel; apical scutellar setae cruciate for  $0.2\times$  their length. Postpronotal lobe with 1 large seta; ventral one much finer, about half the length. Legs entirely yellow. Forefemur with 1 dorsolateral seta and



row of 5 ventrolateral setae; ventral surface of hind femur with row of 8–9 slightly thicker, stiff setae, lengths about half the width of femur. Wing very lightly and diffusely fuscous, without any dark clouds even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned even slightly costad. Veins  $R_{4+5}$  and M parallel. Crossvein m-cu straight, perpendicular to vein M. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites dark brown. Female terminalia sclerotized; penultimate tergite dorsally incomplete. Apical tergite small, without setulae, an inverted U-shaped sclerite (not connected beneath epi-/hypoproct). Apical sternite turned upward; thin, inverted U-shaped sclerite, with ca. 8 stiff setulae along margin. Just beneath apical sternite is another heavily sclerotized sclerite, slightly trough-shaped, with another small sclerite beneath it and adpressed to penultimate sternite. Male genitalia: Epandrium taller than wide; height ca.  $1.4\times$  width. Ventrolateral halves of epandrium slightly tapered; each half with row of 10 long, stiff setae. Aedeagus very heavily sclerotized; basal part with 2 flat arms, which converge into common neck. Distiphallus bulbous, with 2 blunt, curved processes at apex; other apical portion of aedeagus membranous. Paraphyses long (slightly longer than height of epandrium); heavily sclerotized; both arms closely opposed and straight, like forceps; pointed downward; apices pointed. Paraphyses joined dorsally into broad, hoodlike structure. Aedeagal apodeme of standard proportions. Surstyli without narrow arms, roughly L-shaped in broadest (lateral) view, with long, thin dorsoapical lobe; barely sclerotized. Apical lobe of surstylus with bizarre pectinate scale at apex. Ventromedial margin of surstylus with row of 7–8 fine setae (2 much longer than others) and 4–5 smaller setae on ventral margin. Hypandrium large; nearly oval, with deep, centralized ventral keel; gonopods stout. Apical sternite divided into 2 simple, setose, paramedian plates.

Types: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII–4/IX/84, 2100 ft, H. Wolda. Not dissected. Paratypes: Series of 5♂ and 3♀, with same data as holotype (in AMNH).

OTHER MATERIAL EXAMINED: Known only from type series.

ETYMOLOGY: In reference to large body size.

*Cladochaeta sepia*, new species

Figures 51, 52, 70

DIAGNOSIS: A small species (ThL = 0.64 mm), with body mostly light brown, including all of thorax; male genitalia with paraphyses heavily sclerotized, hooked inward; distiphallus a thin, membranous lobe ventrally flanked by pair of sclerotized lobes; surstylus bilobed.

DESCRIPTION: HEAD: Moderate depth. Eyes with dense, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel light brown, flagellomere I slightly darker. Arista with 4 dorsal branches; 1 ventral branch between d-3 and d-4; branches of apical fork very short. Front golden and shiny, ocellar triangle dark brown; interfrontal setulae of moderate length, ca. 8 present. Frontal-orbital setae: Proclinate orbital same size as posterior reclinate; anterior reclinate very small, slightly larger than frontal-orbital setulae; directly lateral to proclimates; posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate size, ca.  $0.6\times$  size of proclimates. Face flat, brown, and of moderate width (FW/HW = 0.31 [N = 1]); cheeks yellow and relatively shallow (CD/ED = 0.11). Proboscis yellow; palps light brown.

THORAX: Notum, scutellum, postnotum, and pleura brown. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals closer to ant. dorsocentrals than to scutellum. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae just barely cruciate. Postpronotal lobe with 1 large seta; much finer ventral one apparently lost. Legs entirely light brown. Forefemur with 1 dorsolateral seta and row of 3 ventrolateral setae; ventral surface of hind femur without enlarged, stiff setae. Entire wing hyaline, with neither light diffuse infuscation nor clouds on x-veins r-m and dm-cu. Vein  $R_{2+3}$  very slightly curved, not straight. X-vein dm-cu straight. Halter light brown.

ABDOMEN: Tergites dark brown. Male genitalia: Cercus without thin ventral lobe; ventral margin flat, slightly sclerotized. Epandrium slightly higher than wide, height ca.  $1.2\times$  width. Ventrolateral halves of epandrium with apical half of posterior margin concave; each half with row of 6 stiff setae of moderate lengths. Aedeagus protruding between and below paraphyses; pointed downward. Distiphallus membranous, with minute membranous scales/papillae at apex. Pair of thin sclerotized lobes lying behind and along aedeagus; slightly shorter than membranous part. Paraphyses heavily sclerotized; symmetrical; bases connected dorsally by thin bridge, lobes pointed downward and then hooked strongly inward (anteriad). Aedeagal apodeme higher than long, scoop-shaped. Surstyli trilobed; medial lobe short and broad, with row of 5 fine setae (dorso-medial one longest); dorsolateral lobe longer, with ca. 14 short, fine setae in irregular row; ventral lobe short and broad. Hypandrium with anterior margin rounded, ventral keel shallow. Gonopods deep, laterally flattened; tapered apicad where they articulate with bases of surstyli. Apical sternites not studied.

TYPE: Holotype, Male: COSTA RICA: La Suiza de Turrialba, August (no year), Pablo Schild (dissected, no. 165) (NMNH). The specimen is in poor condition. It is covered with loose mycelia, and the left wing is shredded and the right wing torn. The specimen is mounted on a very fine, sharp plant spine, typical for many of Schild's specimens.

OTHER MATERIAL EXAMINED: Known only from the type specimen.

ETYMOLOGY: From Latin *sepia*, in reference to the brown body.

*Cladochaeta sororia* (Williston)

Figures 51, 52, 54, 56, 70

*Drosophila sororia* Williston, 1896: 408. TL: St. Vincent, B.V.I.; Wheeler, 1981: 66 (catalogue). *Cladochaeta sororia* (Williston), Vilela and Bächli, 1990: 14 (new combination, lectotype designation, redescription).

DIAGNOSIS: An externally indistinctive yellow species with small clouds of infuscation on the crossveins and part of the costa. Vilela and Bächli (1990) did not mention the very

setose terminal sternite, which is one of the best diagnostic external features for males of this species. Male genitalia: Aedeagus membranous and bulbous, with paraphyses heavily sclerotized and broad; left paraphysis broader.

DESCRIPTION: HEAD: Moderate depth and width. Eyes with dense, short, fine pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel yellow and first flagellomere light brown. Arista with 3 dorsal branches (rarely with 4), no ventral branch; branches of apical fork equal in length to dorsal ones. Front light, tan; interfrontal setulae of moderate size, with ca. 10 present. Frontal-orbital setae: Proclinate orbitals ca.  $0.8\times$  length of posterior reclimates; anterior reclimates minute, slightly larger than frontal-orbital setulae, lateral and slightly posterior to proclimates (sometimes almost directly posterior to proclinate); posterior reclinate midway between ipsilateral proclinate and inner vertical, or slightly closer to proclinate. Postocellar setae of moderate size, about half the size of proclimates. Face flat and yellow (FW/HW = 0.32 [N = 21]); cheeks yellow and shallow (CD/ED = 0.10). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum yellow; very light infuscation on pleura. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel to slightly convergent; apical scutellar setae convergent but not cruciate. Postpronotal lobe with 1 large seta; ventral one much finer, ca.  $0.6\times$  the length. Legs entirely light yellowish. Forefemur with 1 dorsolateral seta and 2 larger ventrolateral setae; hind femur without larger, erect setae. Wing with light, diffuse infuscation over apex of vein  $R_{2+3}$  and extended down to veins  $R_{4+5}$  and M, leaving apical hyaline spot. Clouds of infuscation over x-veins r-m and dm-cu darkest parts of wing; cloud on dm-cu extended slightly past  $R_{4+5}$  and to level of  $CuA_1$ . Apex of vein  $R_{2+3}$  not gradually meeting costal vein but turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight, but very oblique, not perpendicular, to vein M. Wing tip rounded, not slightly pointed. Halter light yellow.

ABDOMEN: Tergites tan to light brown. Female terminalia: Apical tergite without setulae, barely sclerotized; posteroventral portion of tergite with small median lobe, bearing fine setulae; small invaginated apodeme beneath lobe connected to broad, triangular apodeme that is abruptly turned vertically. Internal apodemes sclerotized. Male genitalia: Cercus without thin ventral lobe; ventral margin flat, sclerotized, with pair of short, sharp setulae near middle; lateral margin of cercus with flat, slightly sclerotized rim. Epandrium height ca. 0.6x width. Ventrolateral halves of epandrium with apices barely tapered; each half with 2 uneven rows of 12–14 short, stiff setae. Aedeagus protruding between paraphyses. Distiphallus bulbous, with membranous ventral portion and slightly sclerotized roof, without papillae; basal portion lightly sclerotized. Paraphyses heavily sclerotized, apical halves curved directly downward from base. Paraphyses asymmetrical; left paraphysis paddle-shaped, right one apically pointed. Posterior portions of paraphyses about equal in length to surstyli. Aedeagal apodeme of standard dimensions, scoop-shaped. Surstyli bilobed, with apical lobe bearing ca. 22–23 long, thin, curved setae; barely sclerotized. Hypandrium with anterior margin nearly flat, without centralized ventral keel but with pair of lateral keels formed from bases of gonopods. Gonopods widely separated; long, deep, laterally flattened; tapered apically where they articulate with bases of surstyli. Apical sternite divided slightly into 2 lobes, each with ca. 50 short, stiff setae arranged in irregular rows.

TYPES: Lectotype, Male: BRITISH WEST INDIES: ST. VINCENT: Windward Side, 1907–66, H. H. Smith. Lectotype and 1♂ and 2♀ paralectotypes designated by Vilela and Bächli (1990), some of them dissected (all in NHM).

OTHER MATERIAL EXAMINED: COLOMBIA: Buenaventura, IX/56, M. Wasserman (3♂, no. 258; 1♀) (AMNH). COSTA RICA: San José Prov.: Perez Zeledon, VIII/62, F. S. Blanton, light trap, (1♂, no. 174) (NMNH); Higuato, San Mateo, Pablo Schild (2♀) (NMNH); Turrialba, W. B. Heed et al., VII–VIII/56 (1♂, UT no. 292; 8♀). ECUADOR: Chimborazo, VII/55, L. Castillo (1♀) (NMNH). NICARAGUA: El Recreo, VI/54,

W. B. Heed (2♂, no. 259; 4♀). PANAMA: Canal Zone: Pipeline Road, VII/67, F. S. Blanton (1♂, no. 193) (NMNH); Balboa, W. B. Heed, X–XI/55 (1♂, no. 260) (AMNH); Summit, XI/46, N. H. L. Krauss (2♀) (NMNH); Darien: Jaque, 14/VII/53, F. S. Blanton (1♂, 1♀) (NMNH). PERU: Madre de Dios: Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 19/IX–10/X/84, 12°12'S, 69°16'W, D. Grimaldi (1♂, no. 161) (AMNH). TRINIDAD: Arima: Blanchisseuse Rd., 2000 ft, 3–9/II/82, Morton S. Adams, 5♂ (1 dissected, no. 83), 7♀ (no. 84) (AMNH). VENEZUELA: Cumanacoa, X–XI/56, M. Wasserman (2♀) (AMNH).

*Cladochaeta starki*, new species

Figures 51, 52, 54, 56, 71

DIAGNOSIS: Notum and scutellum yellow, pleura brown; wings dusky but without clouds; male genitalia with long, sclerotized, twisted paraphyses; distiphallus membranous, bulbous, finely scaled.

DESCRIPTION: HEAD: Relatively long. Eyes virtually bare; lower hind margin of eye without slight indentation. Antenna with pedicel ochre and flagellomere I light brown. Arista with 4 dorsal branches; 1 ventral branch between d-3 and d-4; branches of apical fork usually very short to minute. Top of head shiny, golden; ocellar triangle brown; interfrontal setulae sparse and fine, with ca. 6 present. Frontal-orbital setae: Procline orbital about same size as posterior reclinate; anterior reclinate minute, about twice the size of frontal-orbital setulae; posterolateral to proclinate; posterior reclinate slightly closer to ipsilateral procline than to inner vertical. Postocellar setae of moderate size, ca. 0.6x size of proclinate. Face flat, brown, and broad (FW/HW = 0.36 [N = 4]); cheeks yellow and shallow (CD/ED = 0.07). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum yellow; pleura mostly brown, ventral third of katepisternum yellow. Anterior dorsocentrals ca. 0.7x size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae just barely cruciate. Postpronotal lobe with 1 large seta; much finer ven-

tral one, ca. 0.7x its length. Legs entirely yellow. Forefemur with 1 dorsolateral seta and row of 3 ventrolateral setae; ventral surface of hind femur without enlarged, stiff setae. Wing entirely and evenly fuscous; without clouds of darker, diffuse infuscation, even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not abruptly turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved.

ABDOMEN: Tergites dark brown. Female genitalia: Apical tergite sclerotized, without setae; ventrolateral corners of tergite twisted and concave. Apical sternite modified into pair of rounded lobes connected medially, each with ca. 15 fine setulae and 1 larger setula dorsally; flat, short apodeme attached anterolaterally to each lobe. Male genitalia: Cercus without ventral lobe; ventral margin slightly rounded, not flat, without sclerotized strip. Epandrium much higher than wide; height about twice the width. Ventrolateral halves of epandrium narrow, tapered to small hook with blunt apex; each half with row of 5 long, stiff setae. Distiphallus membranous, bulbous, with minute papillae covering most of posterior surface; projected between distal parts of paraphyses. Aedeagus with stout, slightly sclerotized, tubular shaft; distiphallus with narrow lateral arms connected anteriorly; ventral part of distiphallus a flat, membranous, papillate lobe. Paraphyses heavily sclerotized, forceps-like; flat and slightly twisted; meet very close medially on dorsal half, then curved outward and around distiphallus on apical half; tips pointed. Paraphyses with sclerotized, folded anterior extension, articulating with aedeagal apodeme; joined by very narrow dorsal bridge, with a central extension pointed and directed anteriorly. Aedeagal apodeme with broad, flanged anterior portion and V-shaped posterior portion with arms articulated to bases of paraphyses. Surstyli very lightly sclerotized, somewhat clavate. Apex of surstylus bilobed, with ca. 15 minute setulae on lateral surface and ca. 12 long fine setae on dorsal part of apical margin. Immediately ventral to surstyli is pair of lobes with sparse setae, which appear to be remnants of sternite. Hypandrium oval, without ventral keel. Terminal sternites not studied.

TYPES: Holotype, Male: COSTA RICA:

Puntarenas: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi. Genitalia dissected (no. 126). Paratypes: 3♀, with same label data as holotype (1 dissected, no. 127).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Patronym for Julian Stark, former Senior Scientific Assistant at the AMNH, who provided much support in curation, research, and fieldwork.

*Cladochaeta sternospina*, new species

Figures 51, 52, 54, 72

DIAGNOSIS: Immediately recognizable externally based on flat, long head, arista with only 2 dorsal branches; 1 large basal one, 1 minute apical one; male genitalia with stout, short, sclerotized paraphyses; most distinctive for simple, toothlike spine on posterior margin of apical sternite and bifid spine on penultimate sternite.

DESCRIPTION: HEAD: Relatively long and shallow; frons long, flat, and sloping. Eyes virtually bare; lower hind margin of eye without slight indentation. Antenna with pedicel light yellow, flagellomere I whitish. Arista highly reduced, with 2 dorsal branches, 1 large basal one, 1 minute apical one. Frons dull, light brown, anterior margin light yellow; interfrontal setulae sparse and fine, ca. 4–5 present. Frontal-orbital setae: Procline orbital same size as posterior reclinate; anterior reclinate minute, indistinguishable from frontal-orbital setulae; posterior reclinate slightly closer to ipsilateral procline than to inner vertical. Postocellar setae small, twice the size of interfrontal setulae. Face flat, very low, tips of flagellomere I extended to oral margin; face light yellow (FW/HW = 0.36 [N = 4]); cheeks light yellow and deep (CD/ED = 0.16). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum tan; pleura slightly lighter. Anterior dorsocentrals ca. 0.7x size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae just barely cruciate. Postpronotal lobe with 1 large

seta; much finer ventral one, ca.  $0.6\times$  its length. Legs entirely whitish yellow. Forefemur with 1 dorsolateral seta and row of 3 ventrolateral setae; ventral surface of hind femur with row of 5 enlarged, stiff setae, lengths about equal to width of femur; hind tibia with row of 3 long, stiff setae on dorsal surface of apical third. Wing entirely hyaline; without clouds of darker, diffuse infuscation, even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not abruptly turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip rounded, not slightly pointed. Halter tan.

**ABDOMEN:** Tergites light brown. Female terminalia unsclerotized, very simple; apical tergite without setae, apparently connected to apical sternite. Apical sternite unmodified, not divided at all, cup-like, with ca. 20 long, fine setulae. Male genitalia: Cercus with small ventrolateral lobe; ventral margin without sclerotized strip. Epandrium higher than wide; height ca.  $1.3\times$  width. Ventrolateral halves of epandrium tapered to apical point; each half with row of 8 long, stiff setae of very similar lengths. Distiphallus membranous, mostly covered by paraphyses, with minute papillae. Paraphyses heavily sclerotized, especially apical halves; hooked, such that apices point inward (anteriad); tips pointed. Paraphyses joined by very narrow dorsal bridge. Aedeagal apodeme tall and narrow. Surstyli very lightly sclerotized, somewhat clavate. Apex of surstylus with dull, sclerotized point; mesal surface with ca. 40 setulae and 3 longer, fine setae on dorsal part of apical margin. Hypandrium very broad, without ventral keel. Last 2 terminal sternites with medial spines; apical sternite with 2 spines (1 lying over the other), penultimate sternite with bilobed spine. Sternal spines sclerotized and with dense microtrichia.

**TYPES:** Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-4/IX/84, 2100 m, H. Wolda (not dissected). Paratypes: 1♂, 2♀, with same data as holotype (dissected ♂, no. 195; ♀, no. 196).

**OTHER MATERIAL EXAMINED:** Known only from type series.

**ETYMOLOGY:** Named in reference to spines on apical and penultimate sternites in male.

**DISCUSSION:** This species is similar to one that we have not named, because the body of the specimen was lost on the only specimen. The genitalia of the unnamed species (fig. 72) has similar paraphyses, with most substantial differences being on the surstyli.

*Cladochaeta uniradiata* (Duda)

Figures 51, 52, 54, 56, 73

*Diathoneura uniradiata* Duda, 1925: 181; Wheeler, 1963: 57 (redescription, figures of male and female genitalia [types], lectotype designation); Wheeler, 1981: 35 (world catalog).

*Clastopteromyia uniradiata* (Duda), Frota-Pessoa, 1947: 218.

*Cladochaeta uniradiata* (Duda), Vilela & Bächli, 1990: 15 (redescription, figured male and female genitalia).

**DIAGNOSIS:** A distinctive, large species (thorax length 1.05 mm); arista with 1 ventral and 5 dorsal branches; ventral branch between d-4 and d-5. Face of moderate width (FW/HW = 0.33 [N = 8]); cheek very shallow (CD/ED = 0.08). Pleura, scutellum, postnotum, and legs are light, diffuse brown; notum lighter, ochre; wings evenly dusky brown, with lighter area surrounding vein  $CuA_1$ . Male genitalia with surstylus large, having small apical lobe bearing 4-5 long, fine setae; most of surstylus covered with numerous fine setulae. Paraphyses heavily sclerotized, slightly spiraled (see description below).

**REDESCRIPTION:** For body, see redescription by Vilela and Bächli (1990). Female terminalia: Apical tergite with row of 5 setae on each side; apical sternite completely divided into 2 long lateral lobes, with flat posterior surface. In lateral view each lobe L-shaped, apex of lobe with dense, stiff microtrichia. Male genitalia: Cercus without thin ventral lobe, ventral margin flat but not sclerotized. Epandrium much higher than wide; height  $2.3\times$  width. Ventrolateral halves of epandrium tapered to very thin, long lobes; each half with row of 6 long, stiff setae. Aedeagus lying between apical halves of paraphysis arms. Aedeagus lightly sclerotized, with tubular ventral portion (distiphallus); anterior to aedeagus a sclerotized, horn-shaped lobe pointed posteriad. Paraphyses

heavily sclerotized and slightly spiraled; basal part (dorsal) broad, with narrow dorsal bridge; arms of paraphyses curved downward, meeting medially, then divergent and apically curved medially and anteriad. Aedeagal apodeme of standard shape; narrow, upright, trough-shaped, lightly sclerotized. Surstyli without narrow arms; lightly sclerotized, with kidney-shaped basal part and small, thin apical lobe. Basal part with ca. 90 short, spiculelike setae on mesal surface; apical lobe with 5 long fine setae on apex. Hypandrium fan-shaped, flat, sclerotized, with median ventral keel? Gonopods very deep. Apical sternite bilobed; medial surfaces of both lobes turned inward, each with ca. 25 short, spiculelike setae.

**TYPES:** Lectotype (designated by Wheeler [1963]; dissected by Vilela and Bächli [1990]). Male: COSTA RICA: Suiza de Turrialba, 7/V/21. Paralectotypes: 3♂, 2♀, with same locality data but different dates of collection: 21/V (1♀), 20/VI (1♂) (in Zoological Museum, Berlin), 29/VI (1♂). Lectotype and all but one paralectotype in NHM.

**OTHER MATERIAL EXAMINED:** COSTA RICA: Turrialba, 22/IX, Pablo Schild (1♂, dissected, no. 169; 2♀, 1 dissected [no. 170]) (all in NMNH).

*Cladochaeta venebula*, new species

Figures 51, 52, 56, 74

**DIAGNOSIS:** Wing is distinctive, especially infuscation along the longitudinal veins; arista with 3 short dorsal branches (no ventral branch); pleura slightly darker than notum; hind femur with row of 8-10 long setae on ventral surface; male genitalia with paraphyses heavily sclerotized, pointed, long, each twisted into complete spiral.

**DESCRIPTION:** HEAD: Relatively long; frons long, flat, and sloping. Eyes with very short, sparse setulae; lower hind margin of eye virtually without slight indentation. Antenna with pedicel and flagellomere I light brown. Arista with 3 short dorsal branches; apical fork of moderate size; no ventral branches. Frons light brown, with slightly bluish pruinosity when viewed at anterior angle; interfrontal setulae fairly stout, ca. 10 present. Frontal-orbital setae: Proclinate orbital ca.

$0.8\times$  size of posterior reclinate; anterior reclinate minute, indistinguishable from frontal-orbital setulae; posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate size, ca.  $0.8\times$  length of proclimates. Face flat, yellow, and high (FW/HW = 0.31 [N = 2]); cheeks very light yellow and of moderate depth (CD/ED = 0.13). Proboscis and palps yellow.

**THORAX:** Notum, scutellum, and postnotum very light brown; pleura slightly darker. Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 irregular rows. Anterior scutellar setae parallel; apical scutellar setae just barely cruciate. Postpronotal lobe with 1 large seta; ventral one slightly finer and shorter. Legs entirely whitish yellow. Forefemur with 1 dorsolateral seta and 2 ventrolateral setae; ventral surface of hind femur with row 8-10 enlarged, stiff setae, lengths about equal to width of femur; numerous fine, shorter ones at base of femur. Wing with distinct markings; diffuse, brownish infuscation along all longitudinal and crossveins, except costal vein, leaving hyaline areas of varying thickness between the veins. Vein  $R_{2+3}$  virtually straight, with extreme tip slightly upturned. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly rounded. Halter light brown.

**ABDOMEN:** Tergites light brown. Female terminalia unknown. Male genitalia: Cercus without thin ventral lobe; without sclerotized strip on ventral margin. Epandrium considerably higher than wide; height ca.  $1.6\times$  width. Ventrolateral halves of epandrium long, each with a dorsal and ventral concavity on posterior margin; 1 long stiff seta on median lobe between concavities. Row of 3 smaller, stiff setae ventral to large one on point, largest (dorsalmost one) of these ca.  $0.6\times$  length of medial seta. Distiphallus very membranous, projected between apical halves of paraphyses, flaplike. Paraphyses heavily sclerotized, each forming a complete, downward spiral gradually tapered at apex. Basal part of paraphyses horizontal and parallel, then turned sharply ventrad and touching at middle, then flared laterad, then sharp-

ly folded inward and around the membranous distiphallus; touching preapically, then diverged at apices. Tips of paraphyses sharp, turned inward, reaching to ventral margin of epandrium. Bases of paraphyses with very narrow dorsal bridge between them. Aedeagal apodeme upright, like a funnel compressed laterally. Surstyli small, unsclerotized; without narrow arm, with apex bilobed and small ventral lobe; dorsoapical lobe with row of 6 fine, curved setae at apex (none on ventroapical lobe); ventral lobe and base of surstylus with several fine papillae. Hypandrium small, with rounded anterior margin; with shallow, sclerotized ventral keel. Apical sternites not studied.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-4/IX/84, 2100 m, H. Wolda (not dissected). Paratype: Same data (1♂, dissected, no. 229) (both in AMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: From Latin *vena* (vein), for wing vein, and *nebula* (cloud, mist), in reference to the distinctive infuscation along the longitudinal veins.

DISCUSSION: There appears to be a natural grouping of species, including *venebula*, defined by paraphyses that are twisted into a spiral: *abeja*, *abrupta*, *mystaca*, *propenicula*, *starki*, and *uniradiata*. *Cladochaeta venebula* and *C. mystaca* appear particularly closely related based on paraphyses with a complete spiral.

*Cladochaeta vomica*, new species

Figures 51, 52, 75

DIAGNOSIS: Wing entirely hyaline; arista with 1 ventral, and 3 dorsal branches; anterior reclinate orbital seta minute, slightly anteroventral to proclinate. Paraphyses large, heavily sclerotized, joined dorsally; strongly hook-shaped, with apices pointed anteriorly; surstylus broad in lateral view, with fringe of setulae on distal edge.

DESCRIPTION: HEAD: Moderate depth and length. Eyes completely bare; lower hind margin of eye with very slight emargination. Antenna with pedicel light brown, flagellomere I slightly darker. Arista with 3 long dor-

sal branches; 1 ventral branch of length equal to d-3; apical fork asymmetrical, dorsal branch very short. Frons ochre, ocellar triangle and bases of frontal-orbital setae brown; interfrontal setulae sparse and fine, with 4-5 present. Frontal-orbital setae: Proclinate orbital slightly shorter than posterior reclinate. Anterior reclinate minute, slightly larger than interfrontal setulae; lateral and slightly anterior to anterior reclinate. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, twice the size of interfrontal setulae. Face flat, light brown, and of moderate width (FW/HW = 0.34 [N = 2]); cheeks light yellow and of moderate depth (CD/ED = 0.14 [♂], 0.07 [♀]). Proboscis and palps light brown.

THORAX: Notum ochre; scutellum and postnotum slightly darker; pleura entirely light brown. Anterior dorsocentrals ca. 0.6× size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 irregular rows. Anterior scutellar setae parallel; apical scutellar setae just barely cruciate. Postpronotal lobe with 1 large seta and much finer, ventral one, ca. 0.8× its length. Legs entirely light tan-yellow. Forefemur with 1 dorsolateral seta; ventral surface of hind femur without row of larger, stiff setae; hind tibia with stiff, thin, preapical seta on dorsal surface. Wing lightly and evenly fuscous/brown, hyaline, without clouds even on crossveins. Vein R<sub>2+3</sub> very slightly sinuous, slightly curved apically. Veins R<sub>4+5</sub> and M parallel. Crossvein dm-cu bent very slightly in middle, essentially perpendicular to vein M. Wing tip slightly pointed. Halter very light.

ABDOMEN: Tergites brown. Female terminalia with preapical tergite divided dorsally; apical tergite complete, articulating ventrally with pair of triangular, sparsely setose lobes, lobes heavily sclerotized and shiny on mesal surfaces. Very small, crescentic sclerite (sternite?) with heavily sclerotized, shiny "button" in middle just ventral to apical tergite. Male genitalia: Cercus with flat ventral margin, ventrolateral lobes slightly more sclerotized than rest of cercus. Epandrium higher than wide; height ca. 1.7× width; dorsal part a very thin strip. Ventrolateral halves of

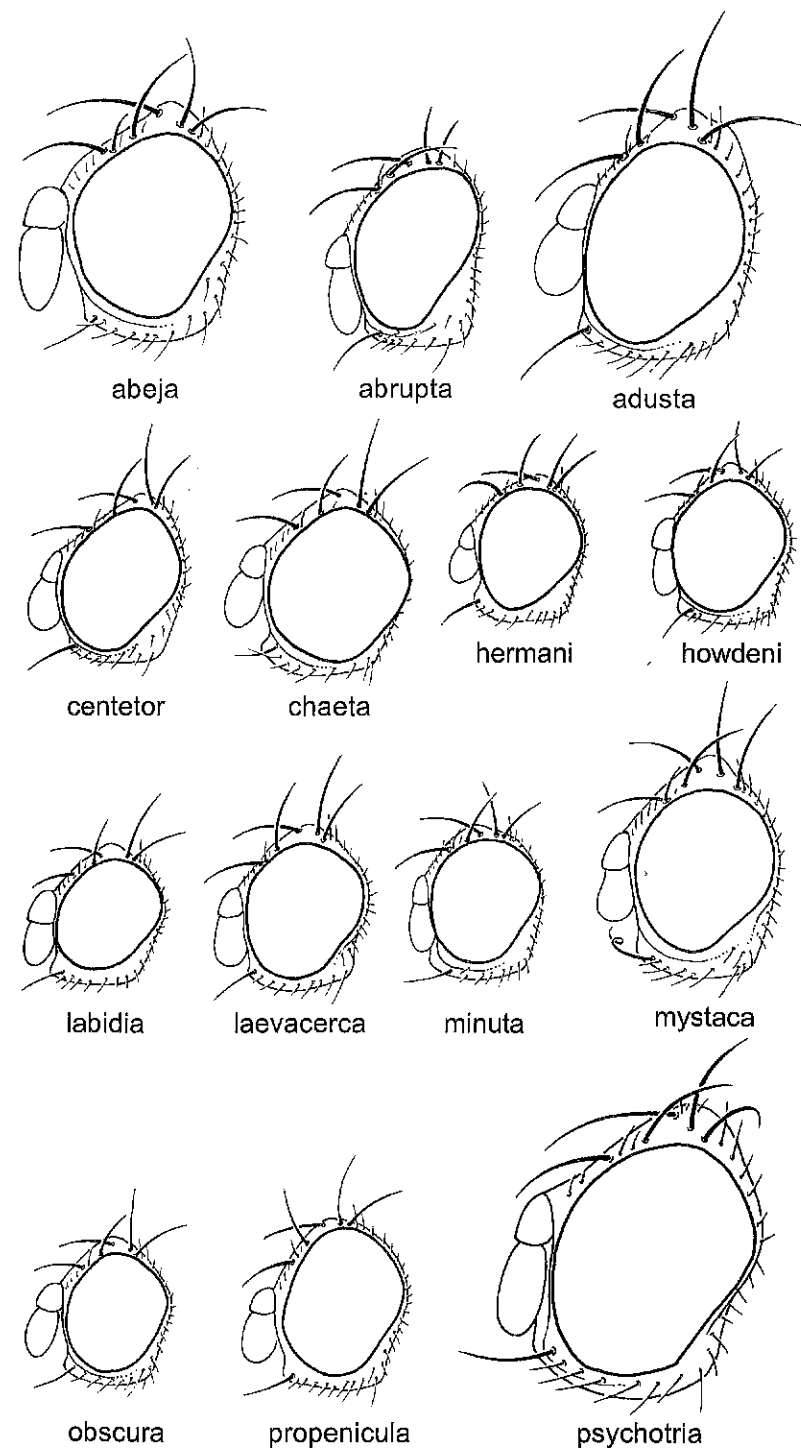
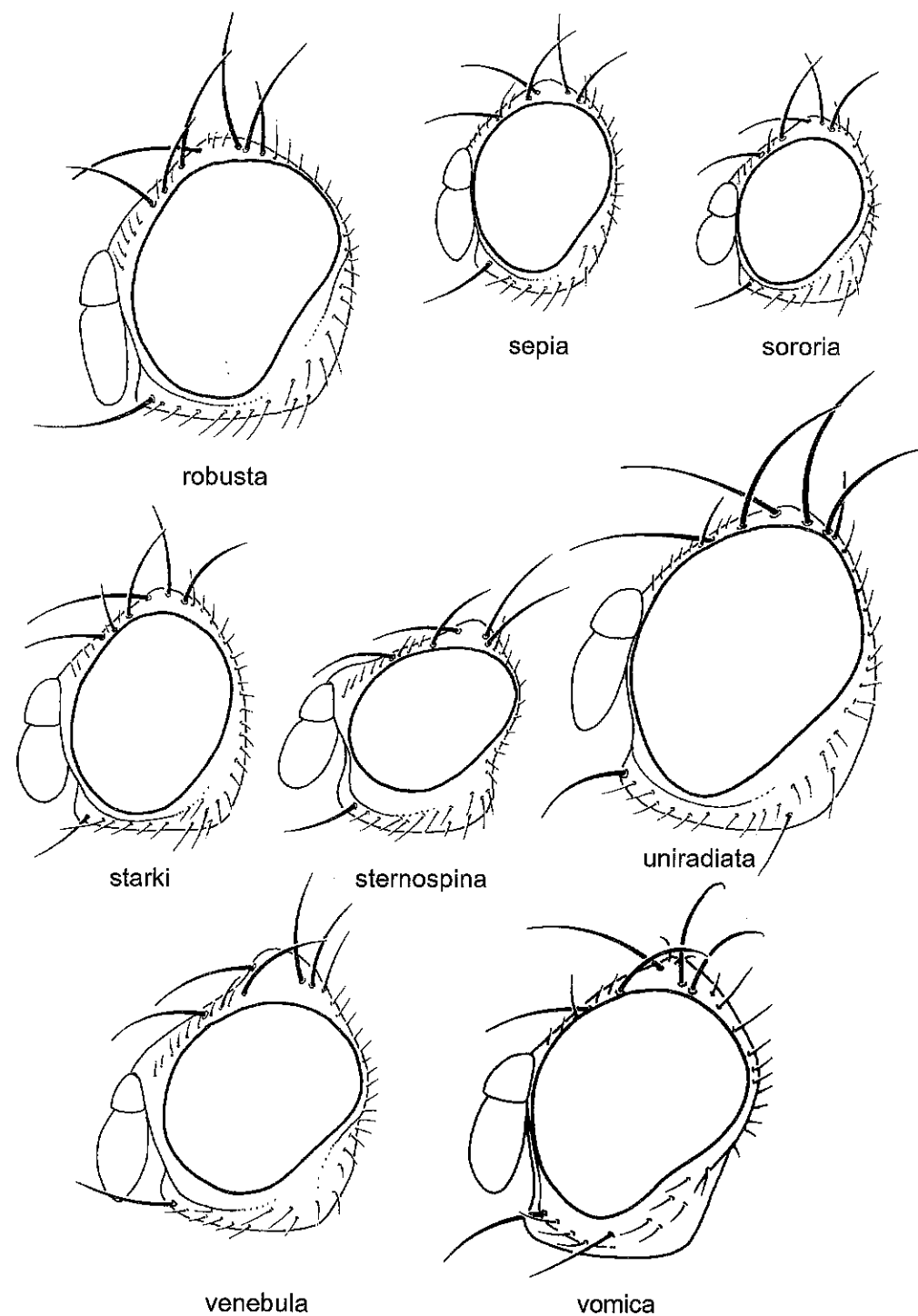
epandrium broadened in lateral view; each half with row of 6 stiff setae, diminished evenly in size ventrad. Aedeagus reduced to sclerotized "hood" anterodorsal to paraphyses. Paraphyses heavily sclerotized, hook-shaped (particularly so in lateral view), such that apices point inward (anteriorly); tips pointed. Paraphyses joined by dorsal bridge, with T-shaped lobe dorsally. Median, sclerotized lobe lies just anterior (beneath) paraphyses. Aedeagal apodeme large, articulating with anterior surface of aedeagus and ventrally with bases of hypandrial arms. Surstyli lightly sclerotized, somewhat triangular

in lateral (broadest) view, with row of fine setulae on apical margin. Hypandrium with 2 broad arms, no central keel on stem.

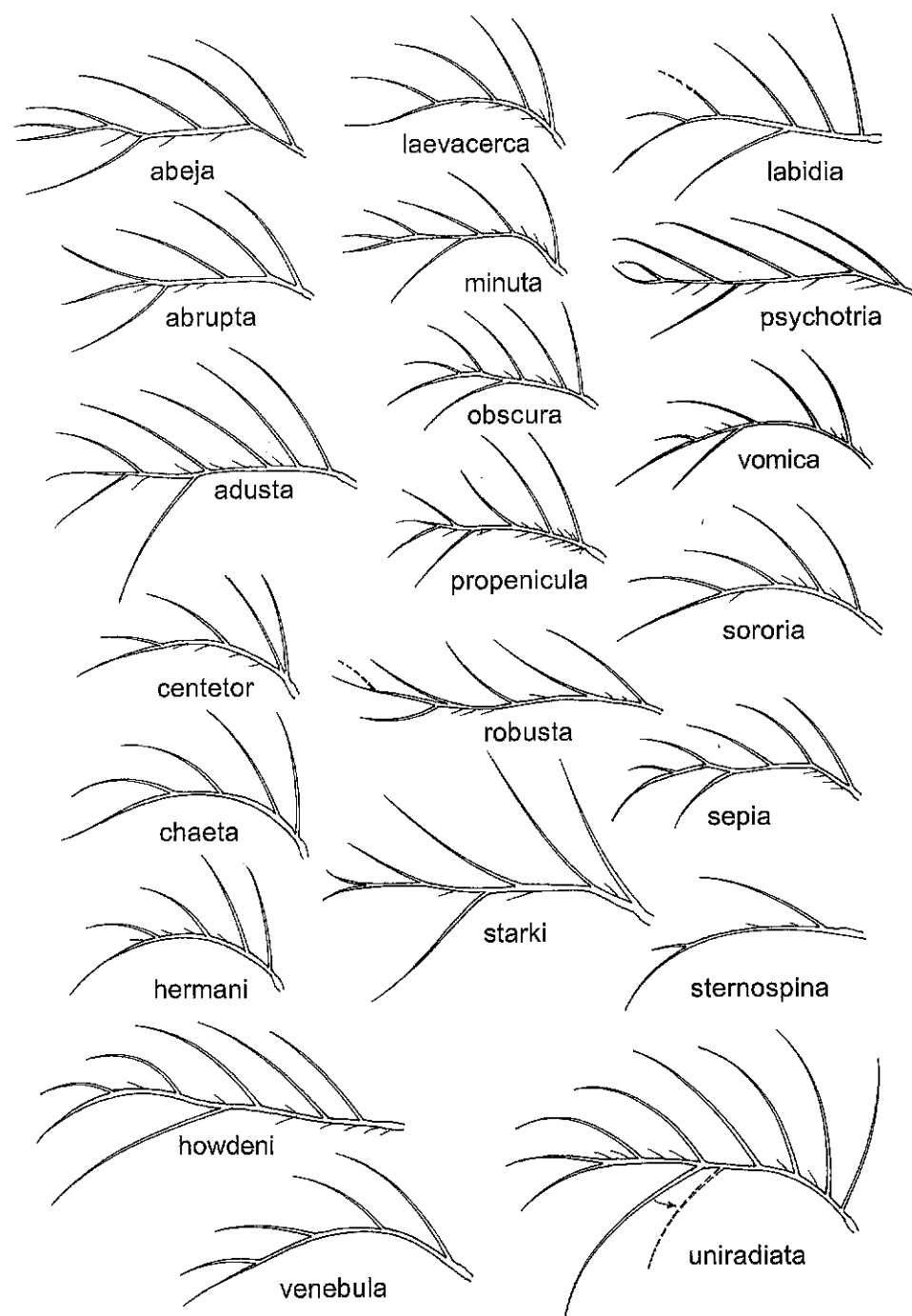
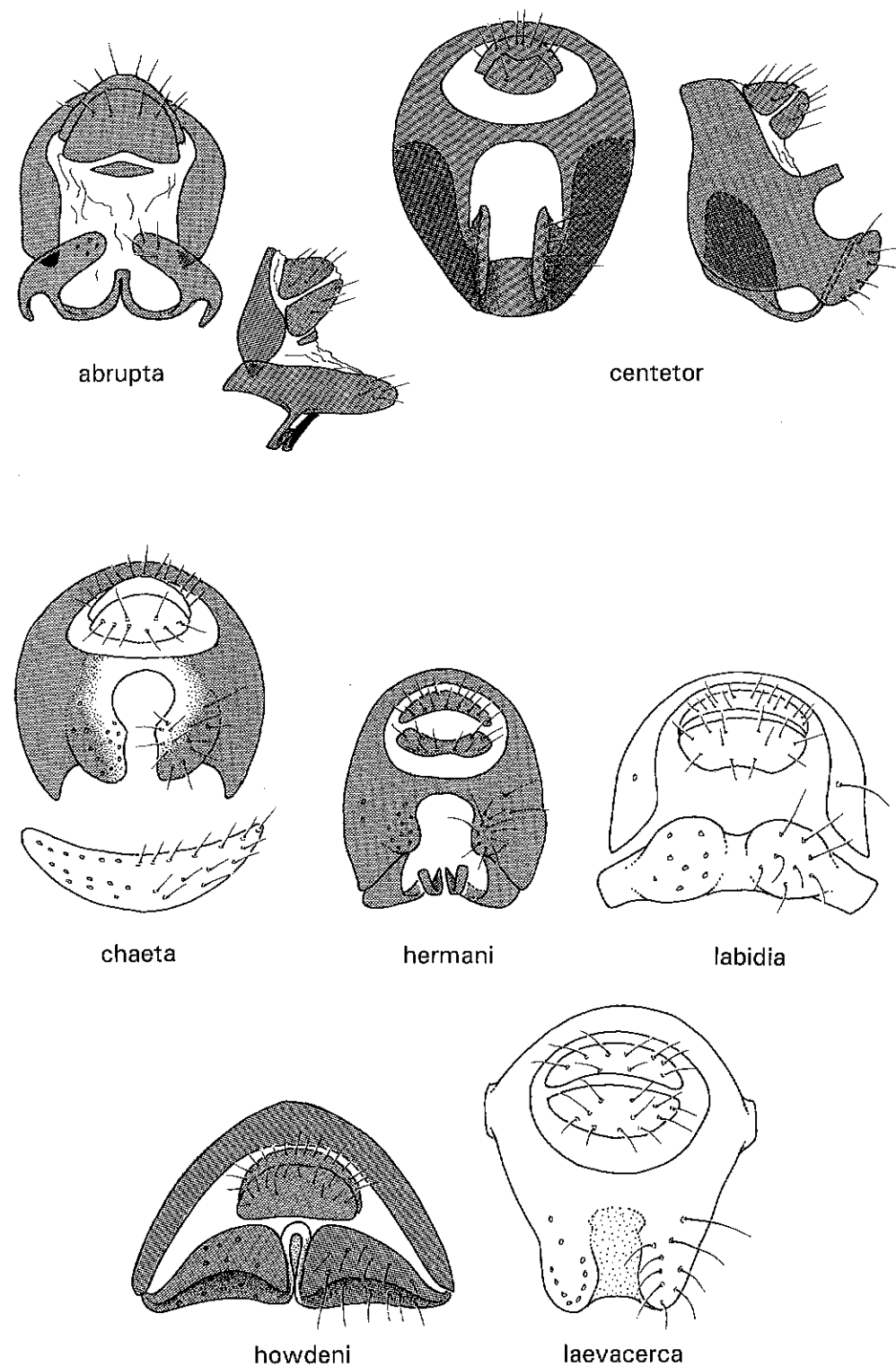
TYPES: Holotype, Male: COSTA RICA: *San José*: Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 312). Paratype: Female, same data as holotype, not dissected. Both specimens in AMNH.

OTHER MATERIAL EXAMINED: Known only from types.

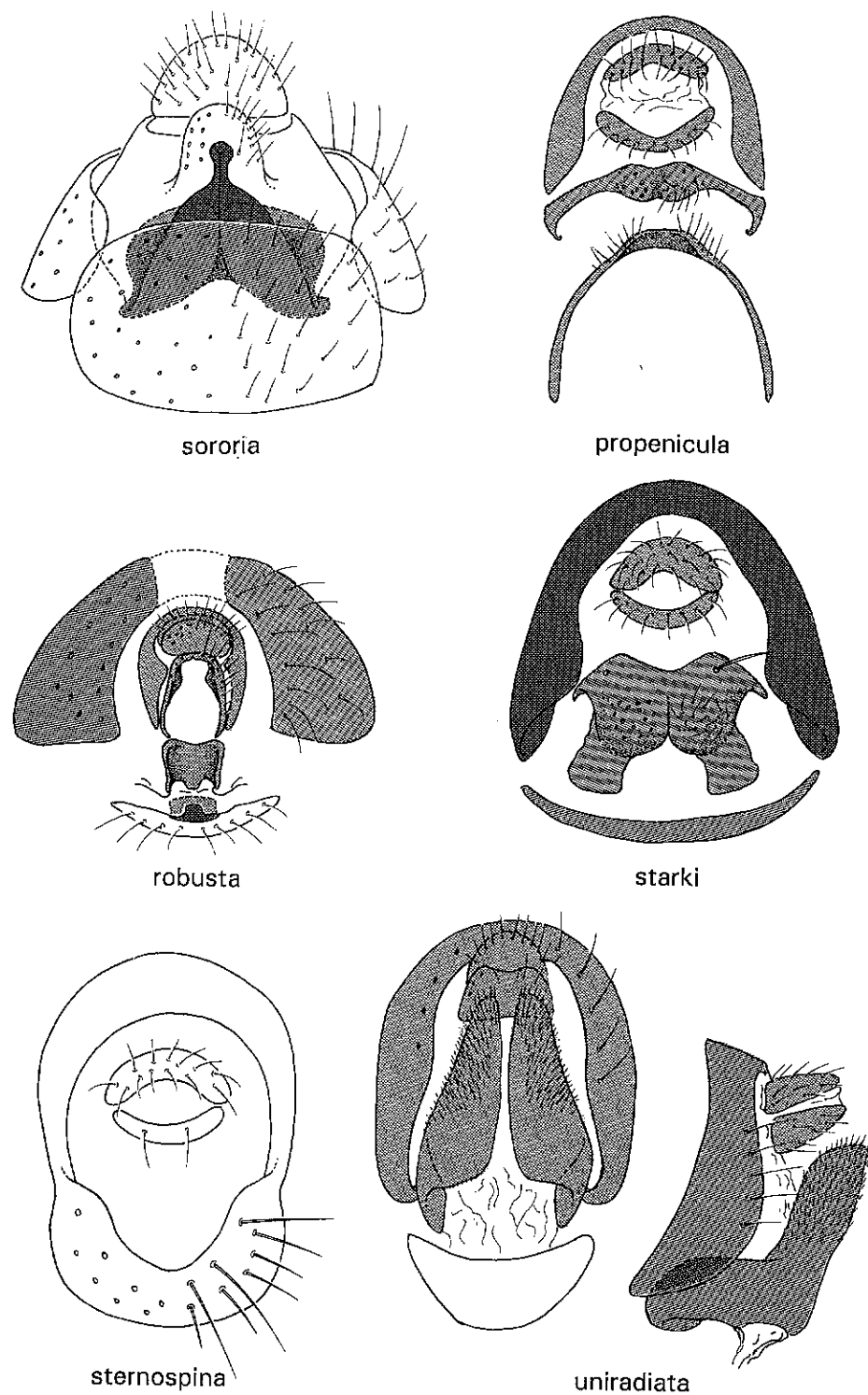
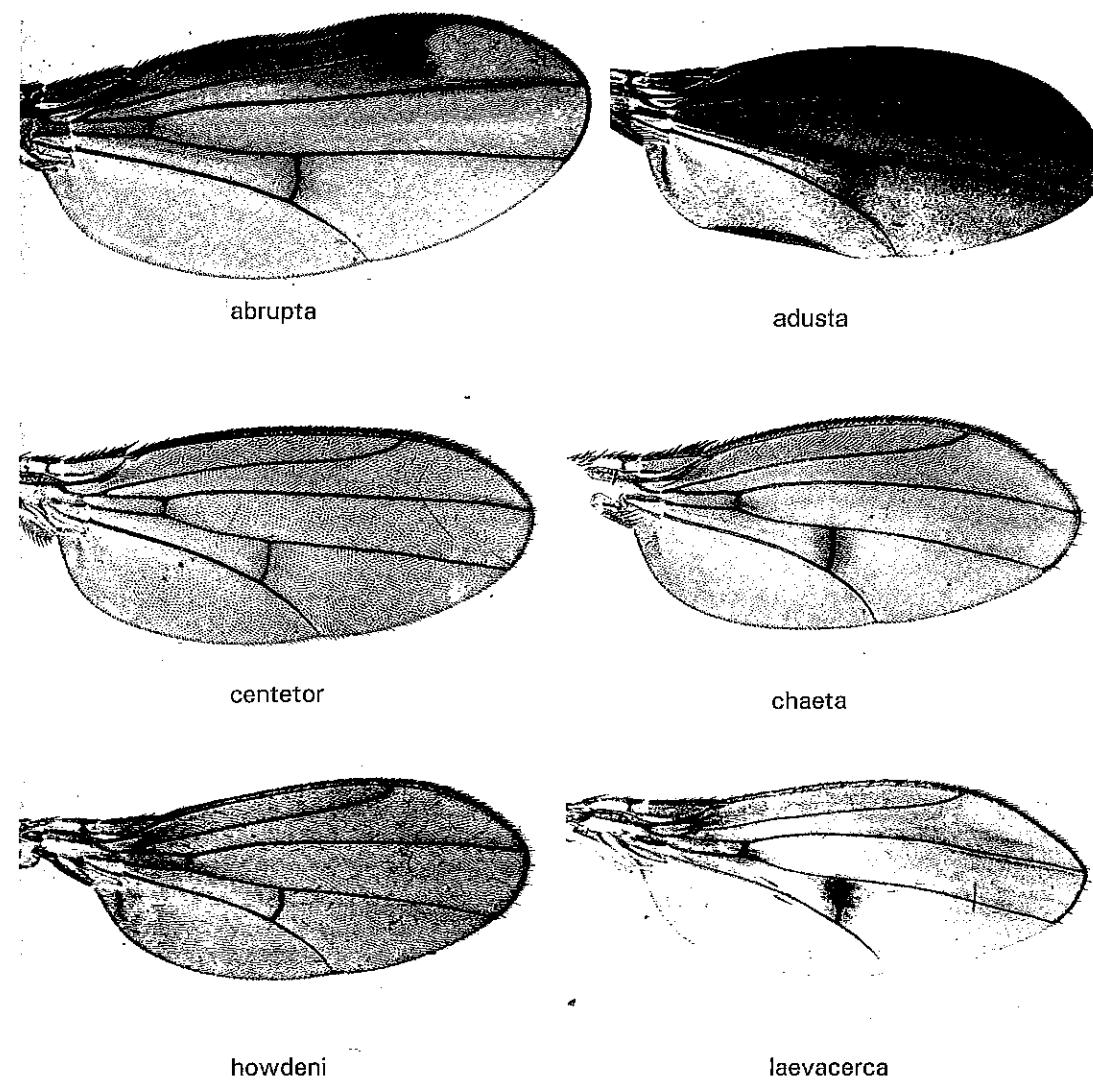
ETYMOLOGY: From Latin *ulcer*, in reference to this being the last of 112 new species described in this study.

Fig. 50. Heads of *sororia* group species.Fig. 51. Heads of *sororia* group species (continued).



Fig. 52. Aristae of *sororia* group species.Fig. 53. Female terminalia of *sororia* group species, various views.



Fig. 54. Female terminalia of *sororia* group species (continued).Fig. 55. Wings of *sororia* group species.

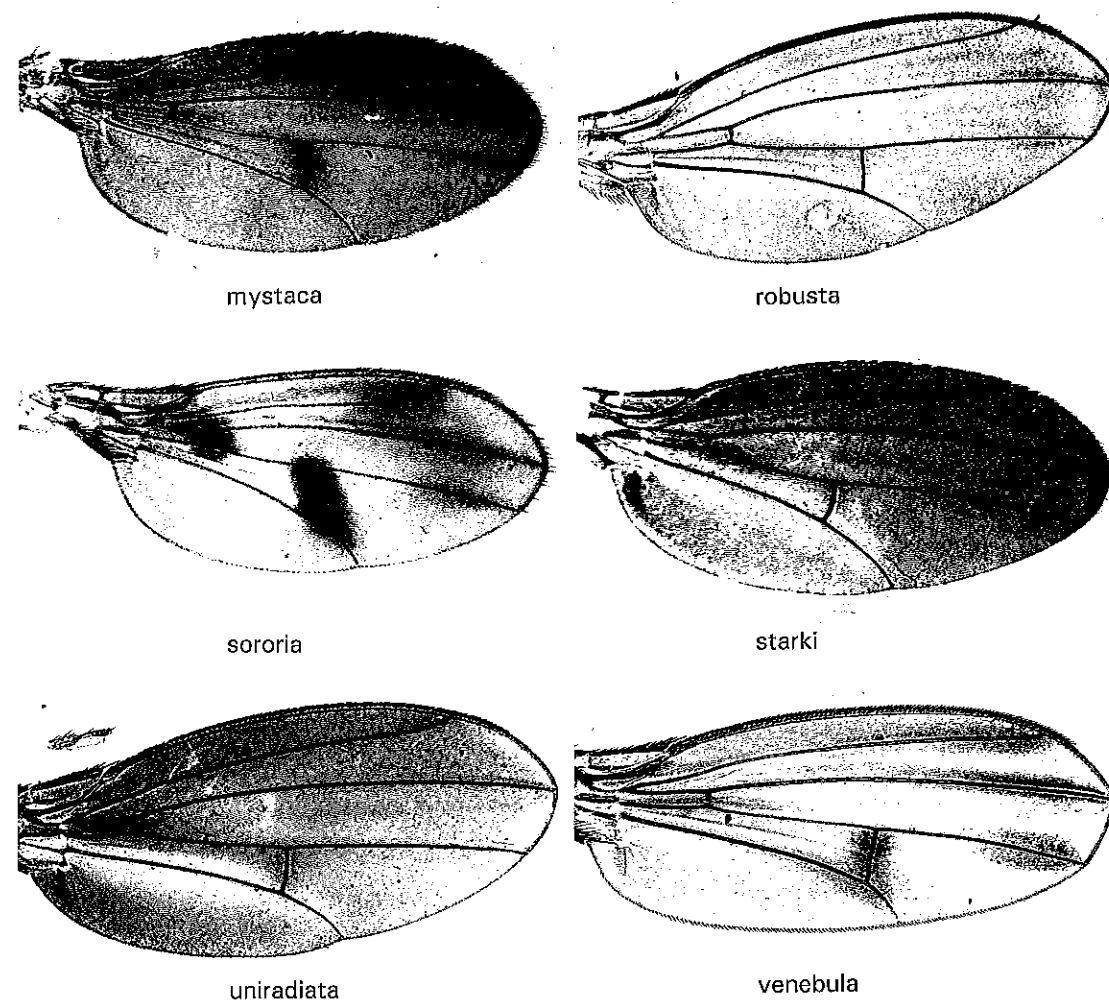


Fig. 56. Wings of *sororia* group species.



Fig. 57. Male terminalia of *C. abeja*.

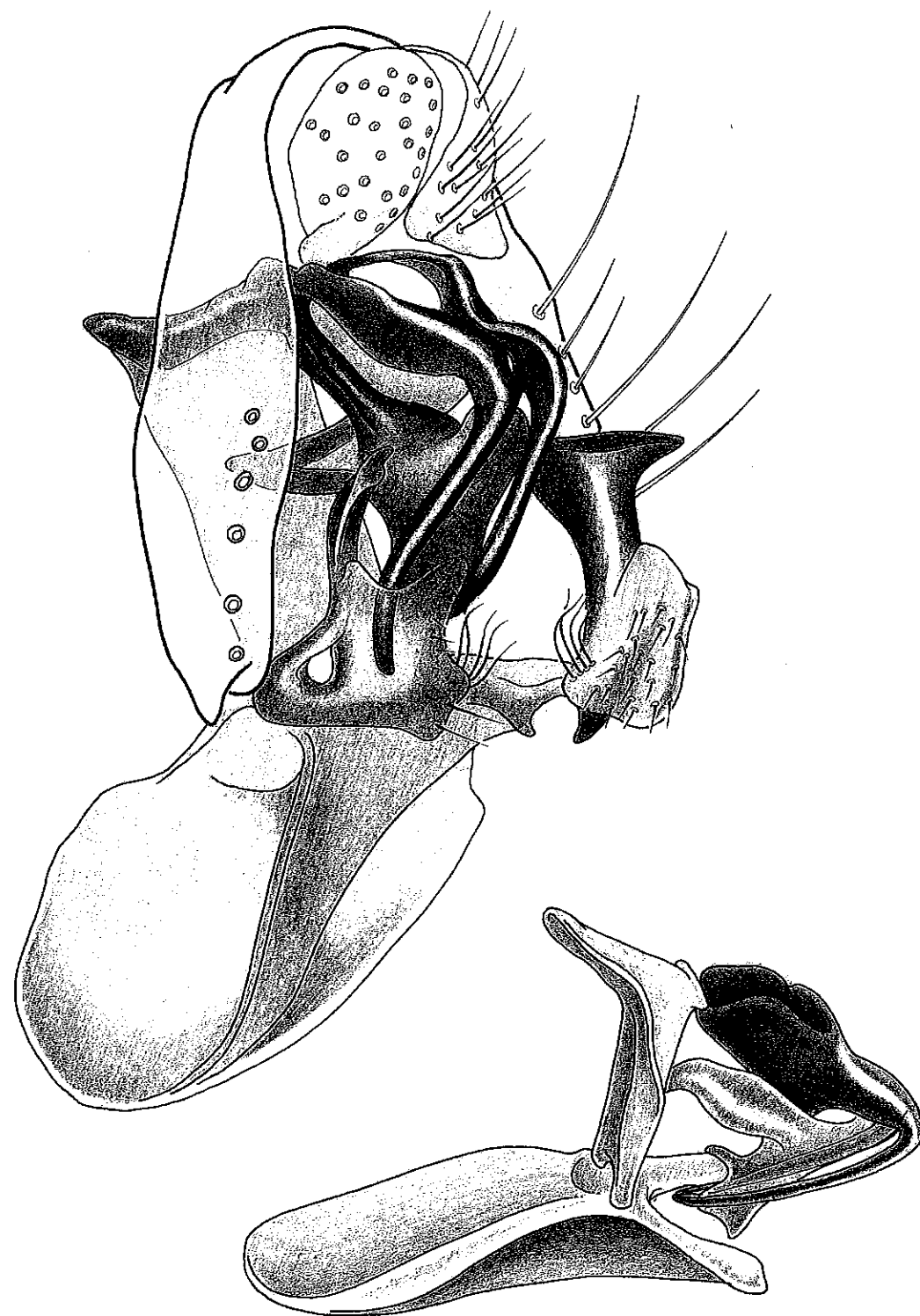


Fig. 58. Male terminalia of *C. abrupta*.

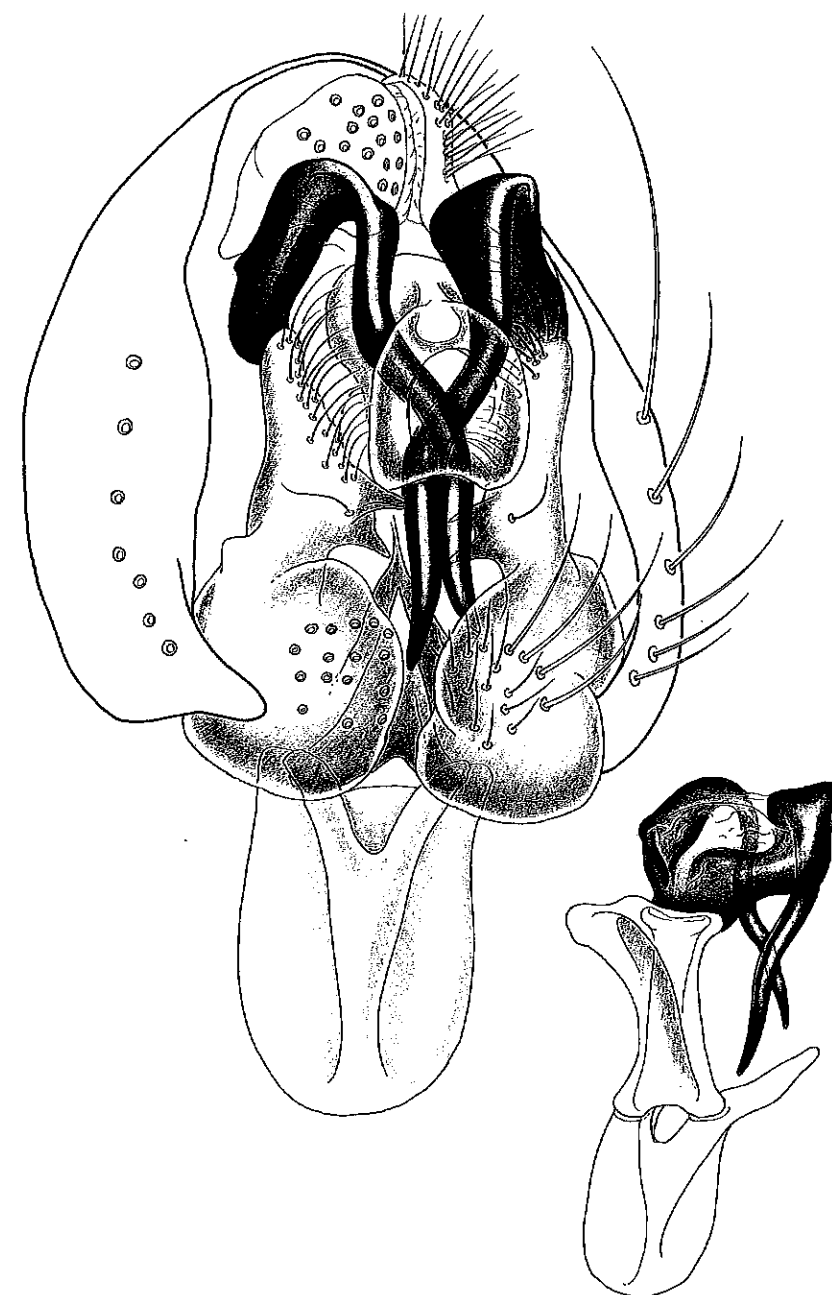


Fig. 59. Male terminalia of *C. adusta*.



Fig. 60. Male terminalia of *C. centetor*.

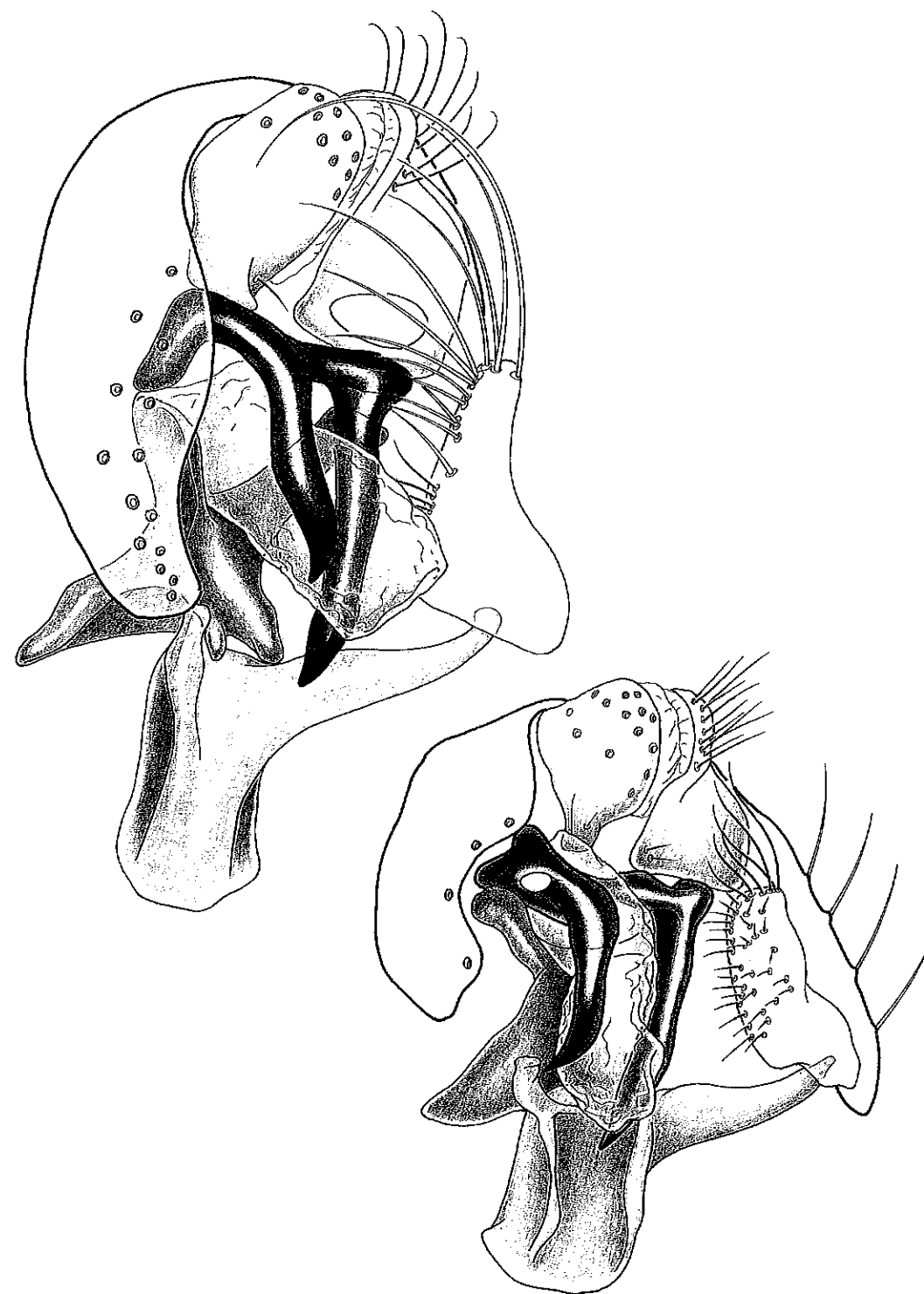


Fig. 61. Male terminalia of *C. chaeta* (above) and *C. hermani* (below).

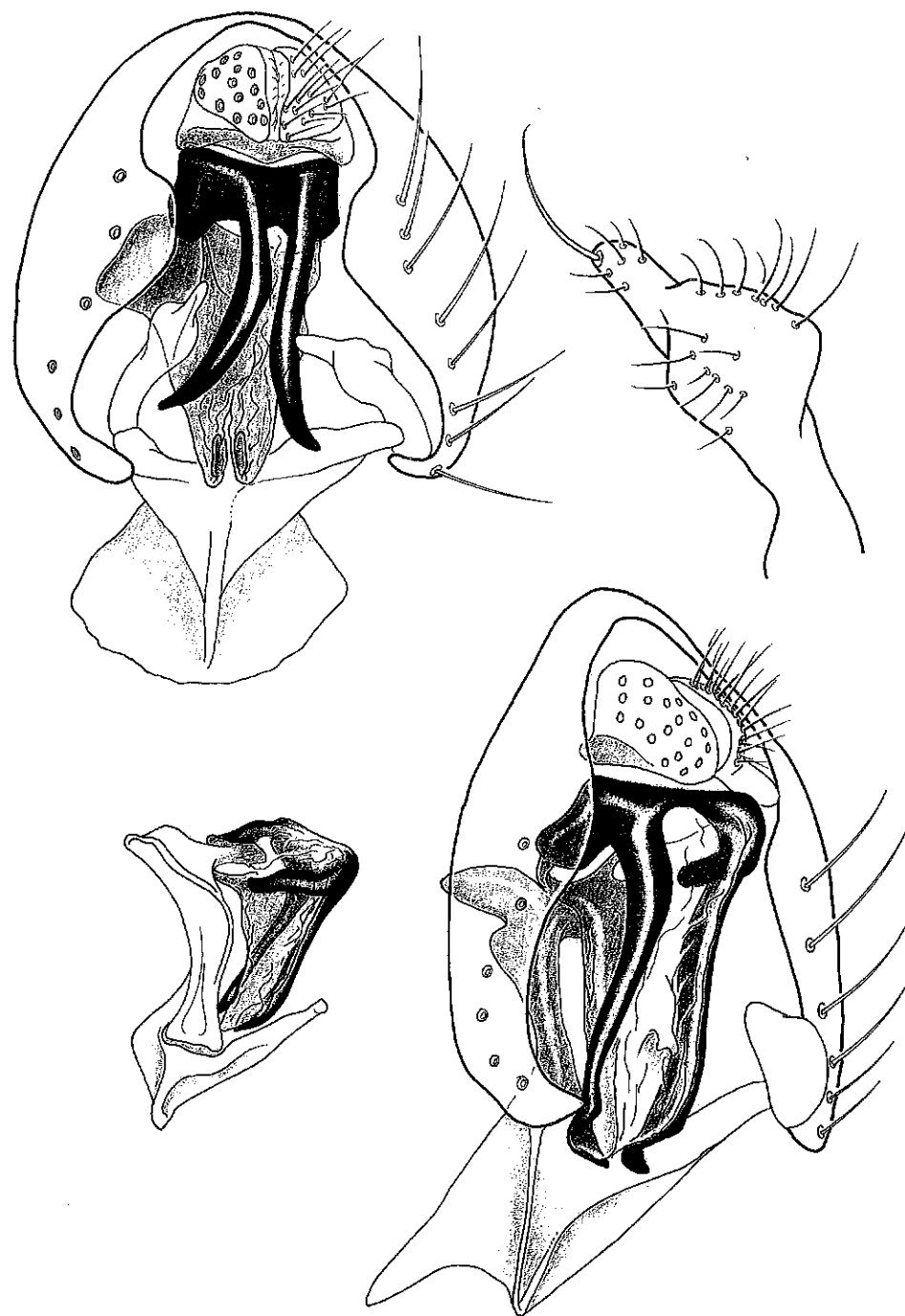


Fig. 62. Male terminalia of *C. howdeni* (above) and *C. labidia* (below).

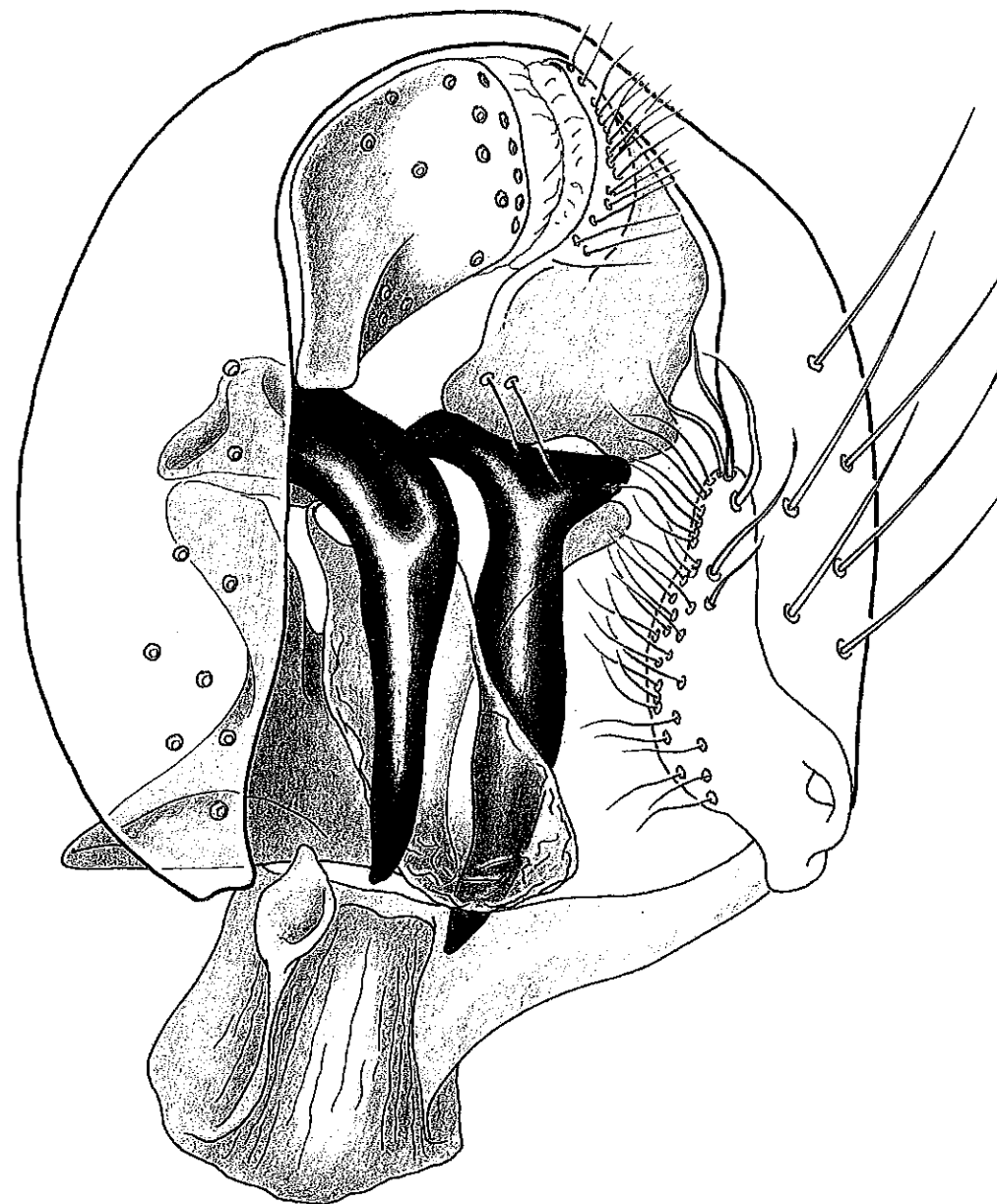


Fig. 63. Male terminalia of *C. laevacerca*.

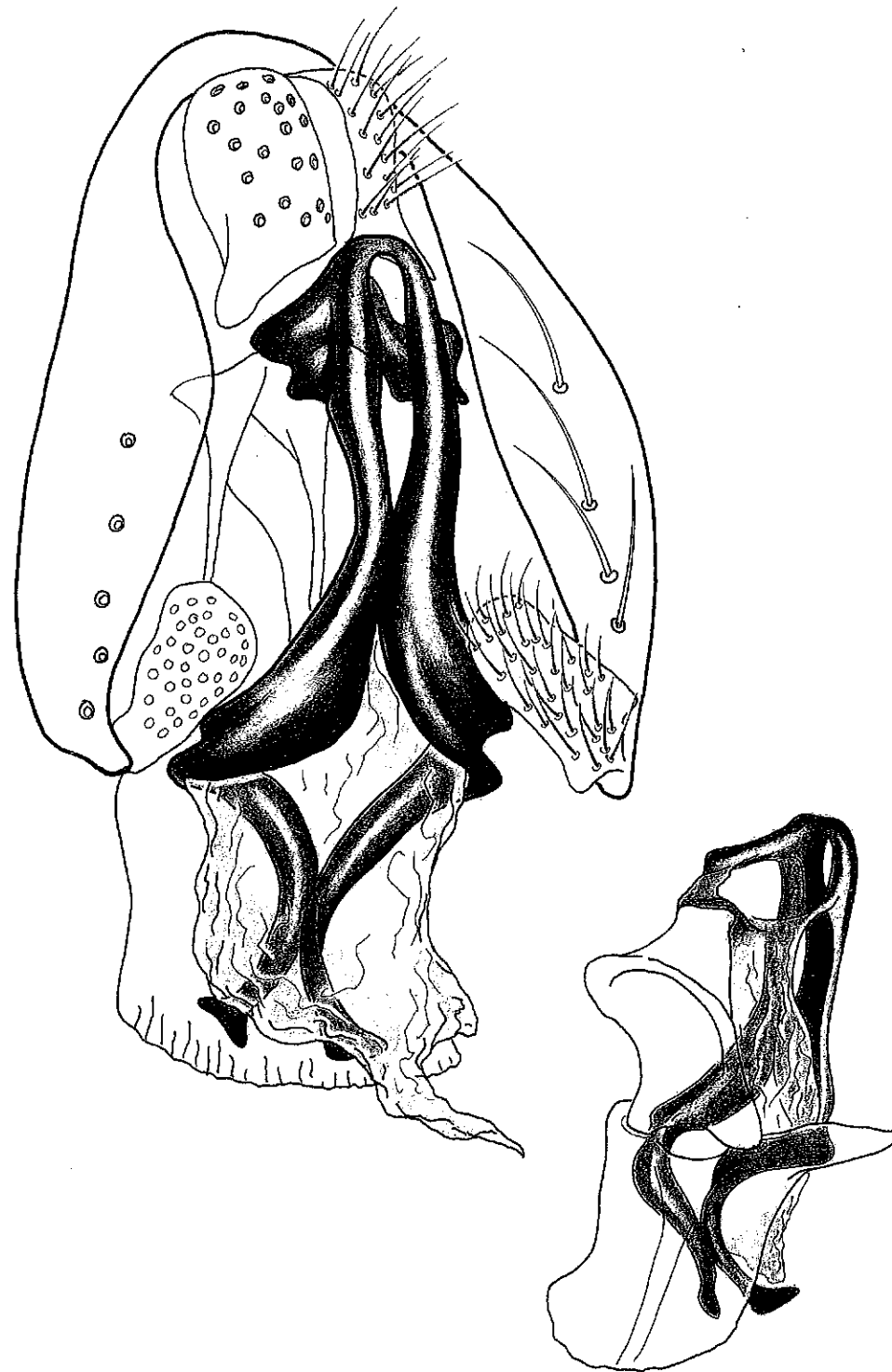


Fig. 64. Male terminalia of *C. mystaca*.

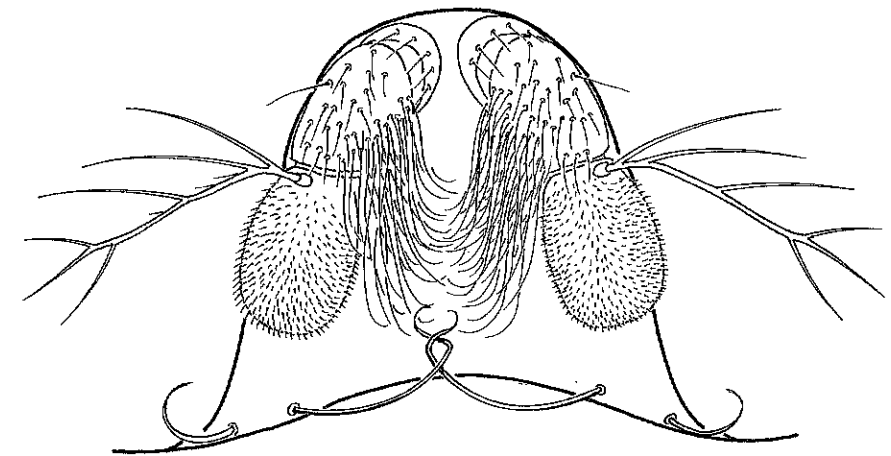
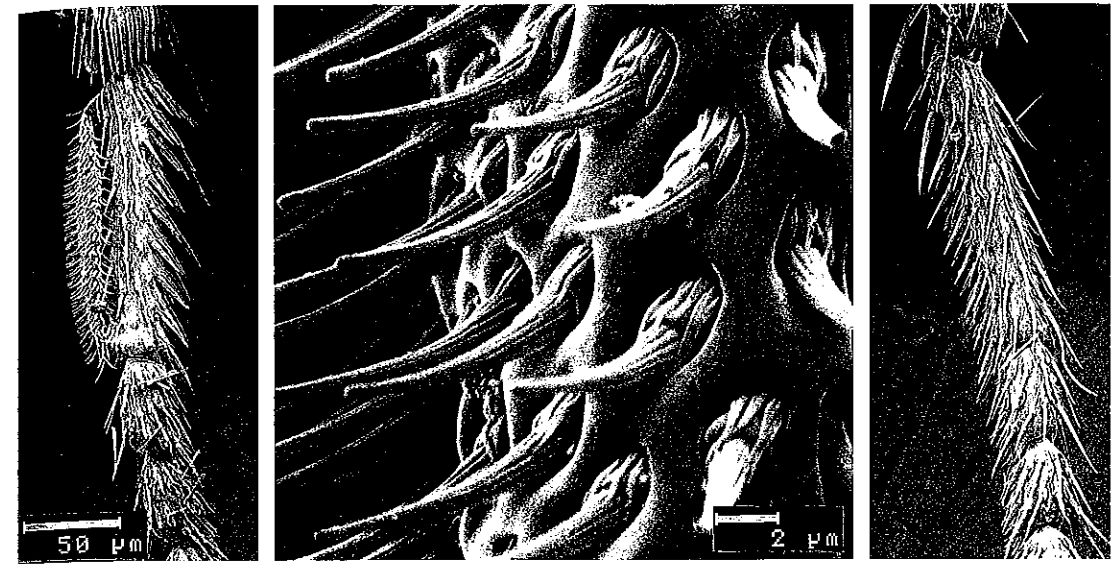


Fig. 65. Scanning electron micrographs of fore basitarsus of *C. propenicula*: left and middle (detail), male; right, female. Below: Face of *C. mystaca*, showing odd, twisted vibrissae.



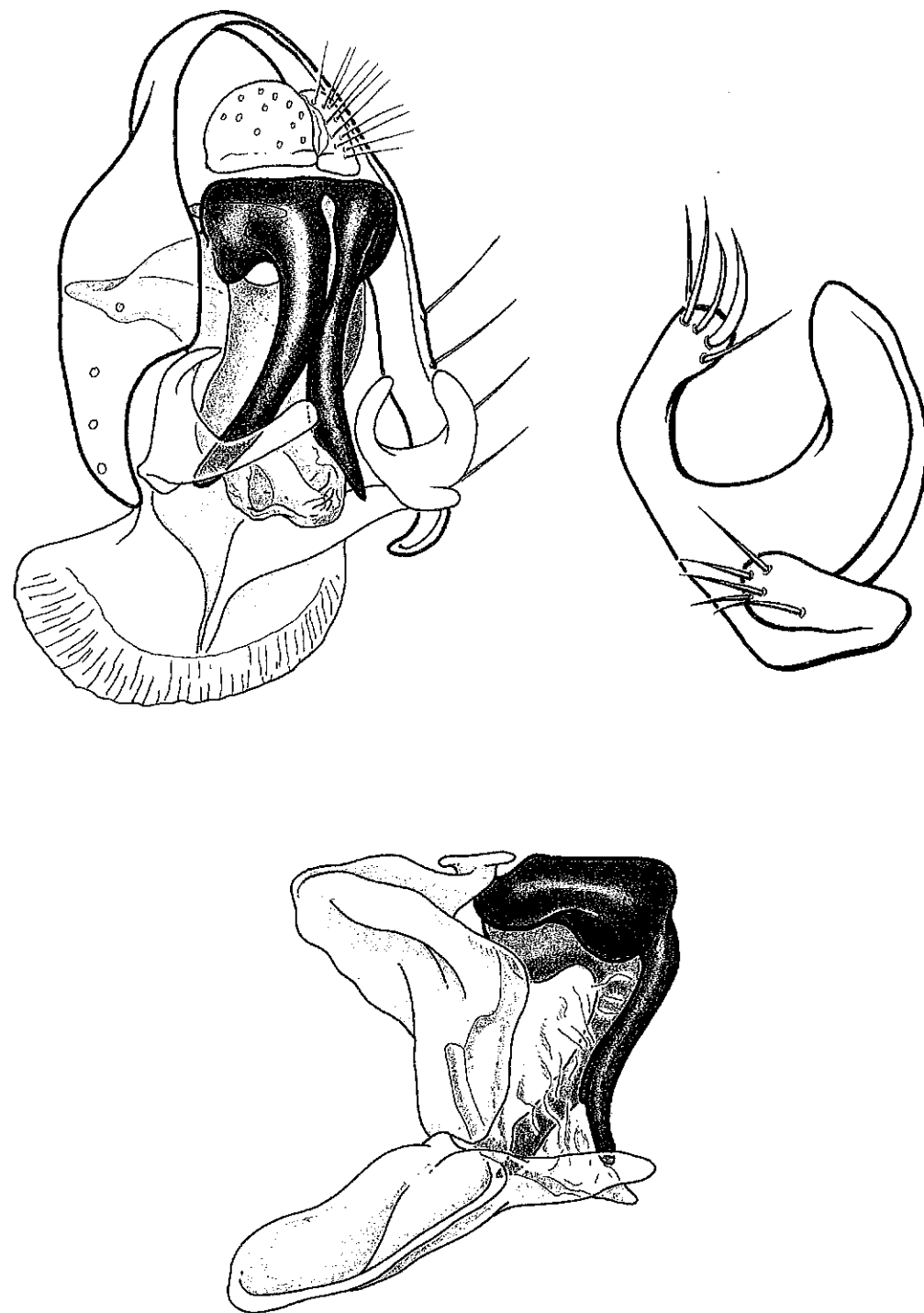


Fig. 66. Male terminalia of *C. obscura*.

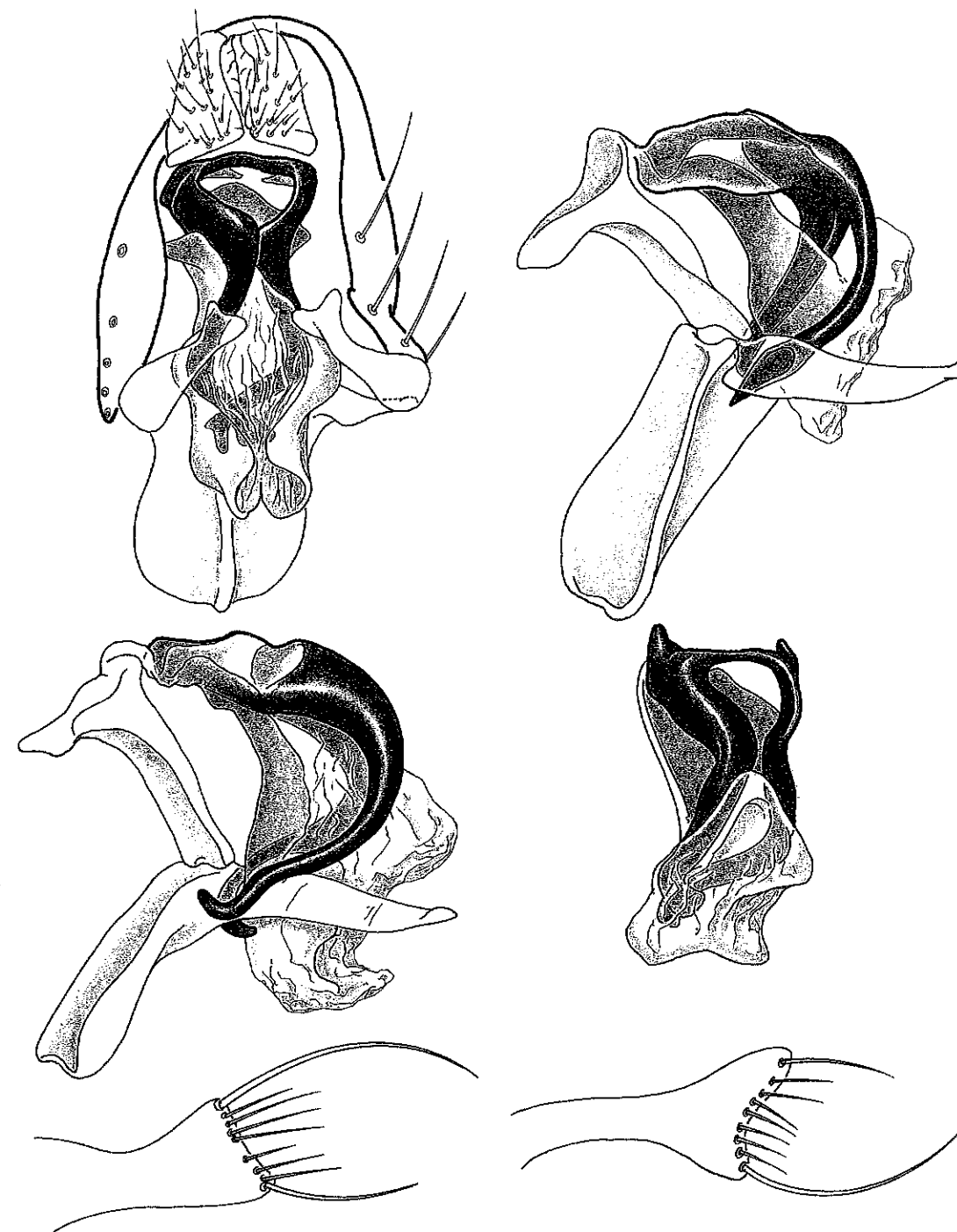


Fig. 67. Male terminalia of *C. propenacula* showing variation in internal structures and surstyli. Left, specimen from Mexico; right, from Peru.



Fig. 68. Male terminalia of *C. psychotria*.



Fig. 69. Male terminalia of *C. robusta*.

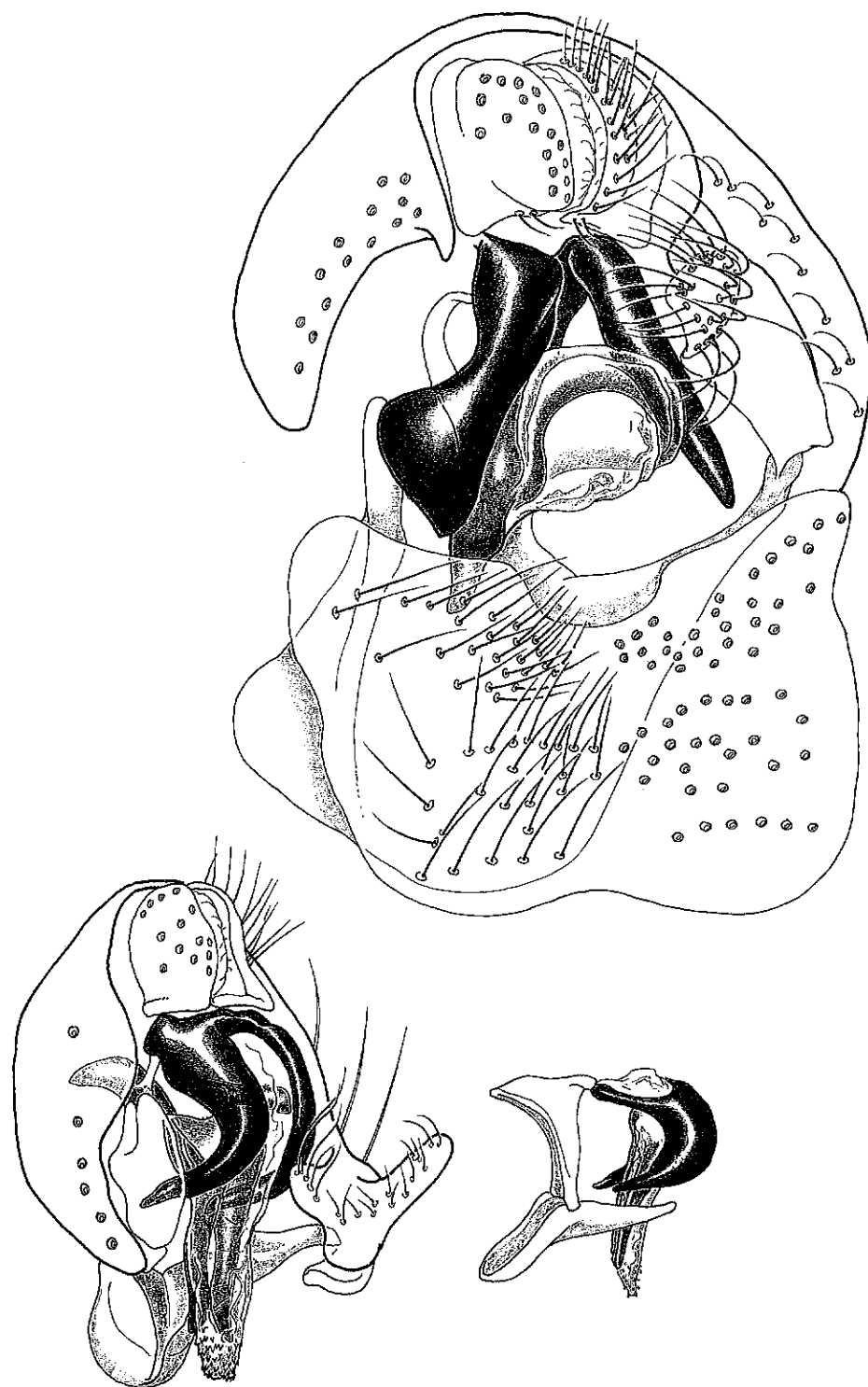


Fig. 70. Male terminalia of *C. sororia* (above) and *sepia* (below).



Fig. 71. Male terminalia of *C. starki*.

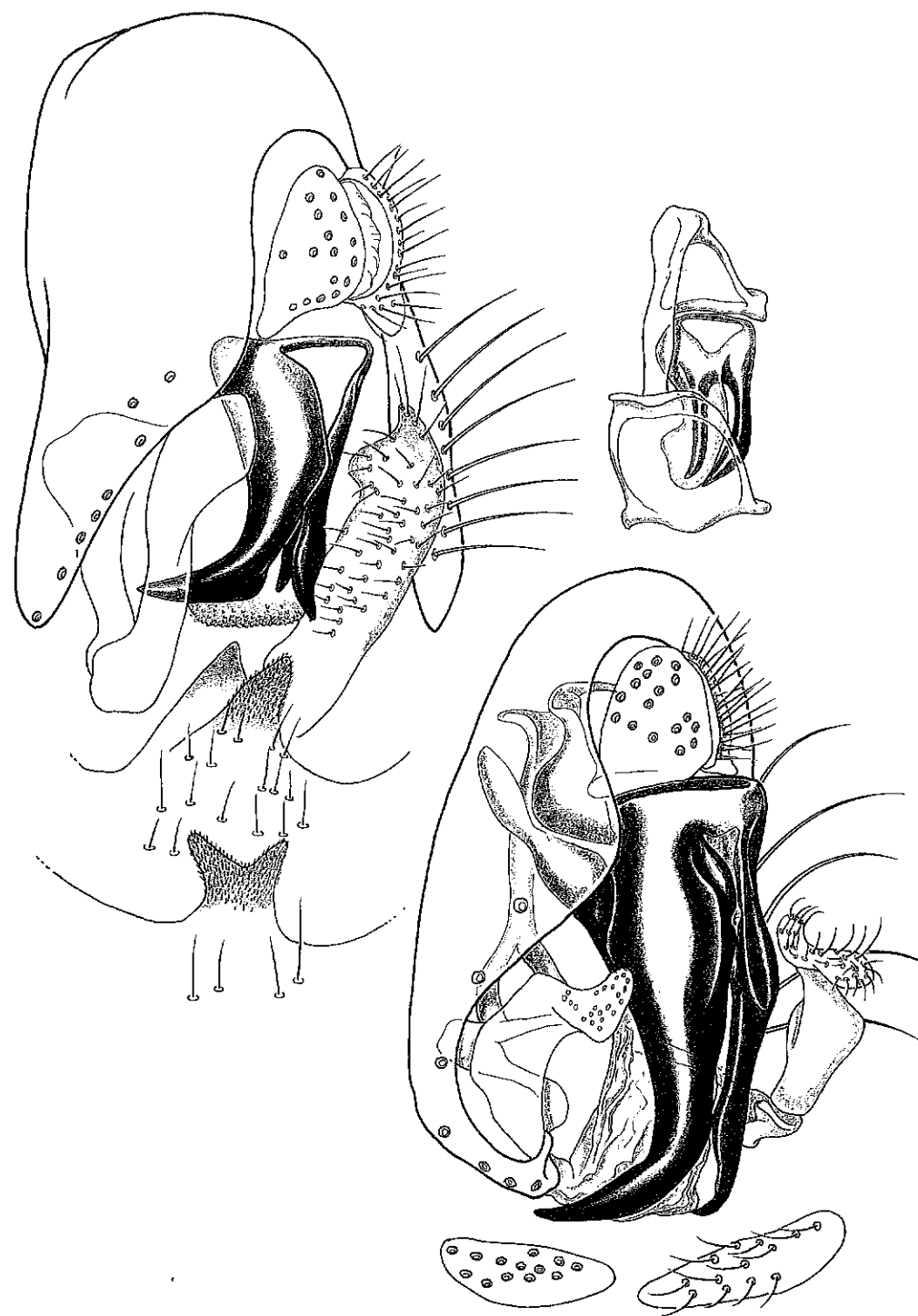


Fig. 72. Male terminalia of *C. sternospina* (above) and undescribed species (below).

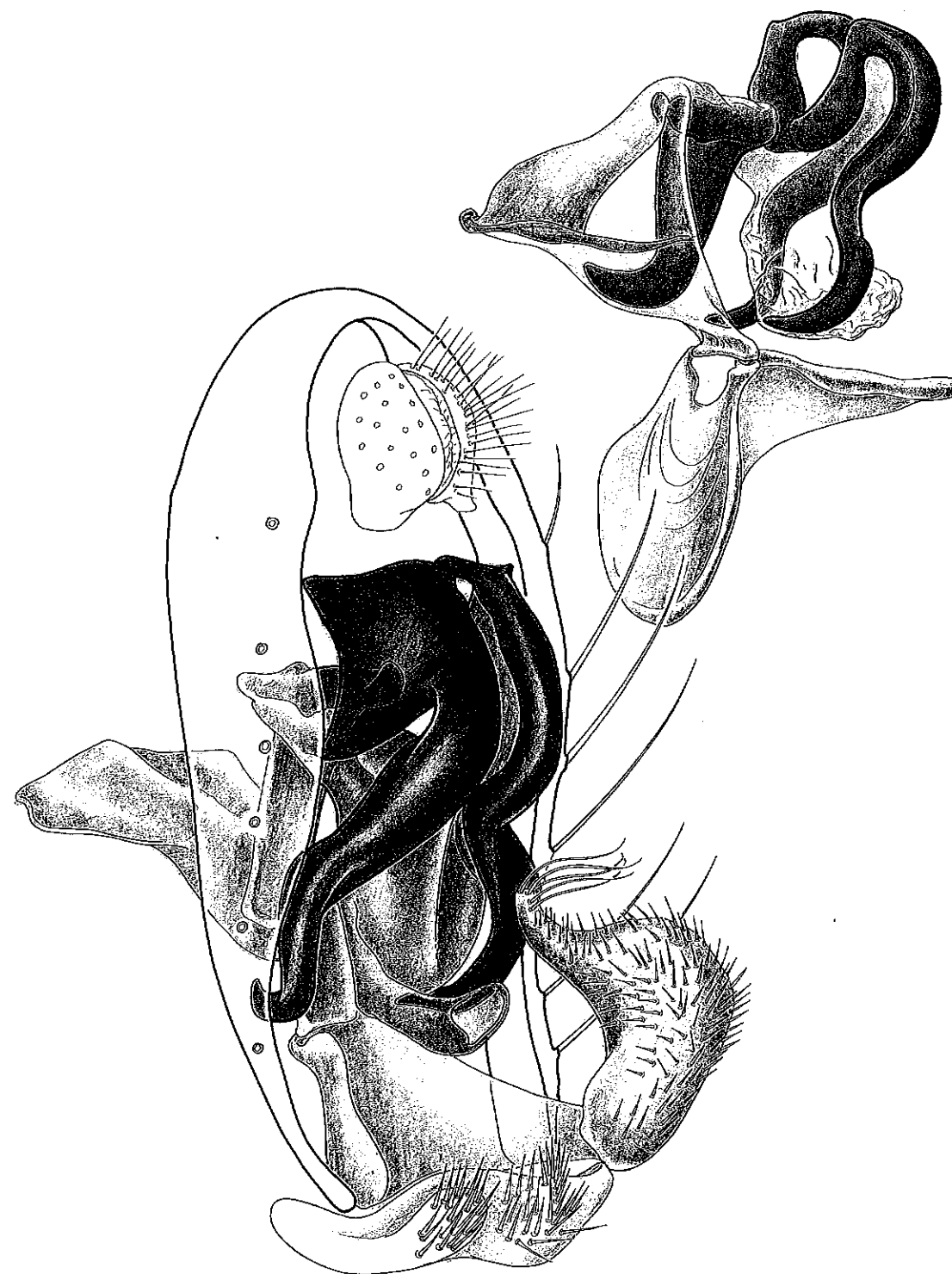


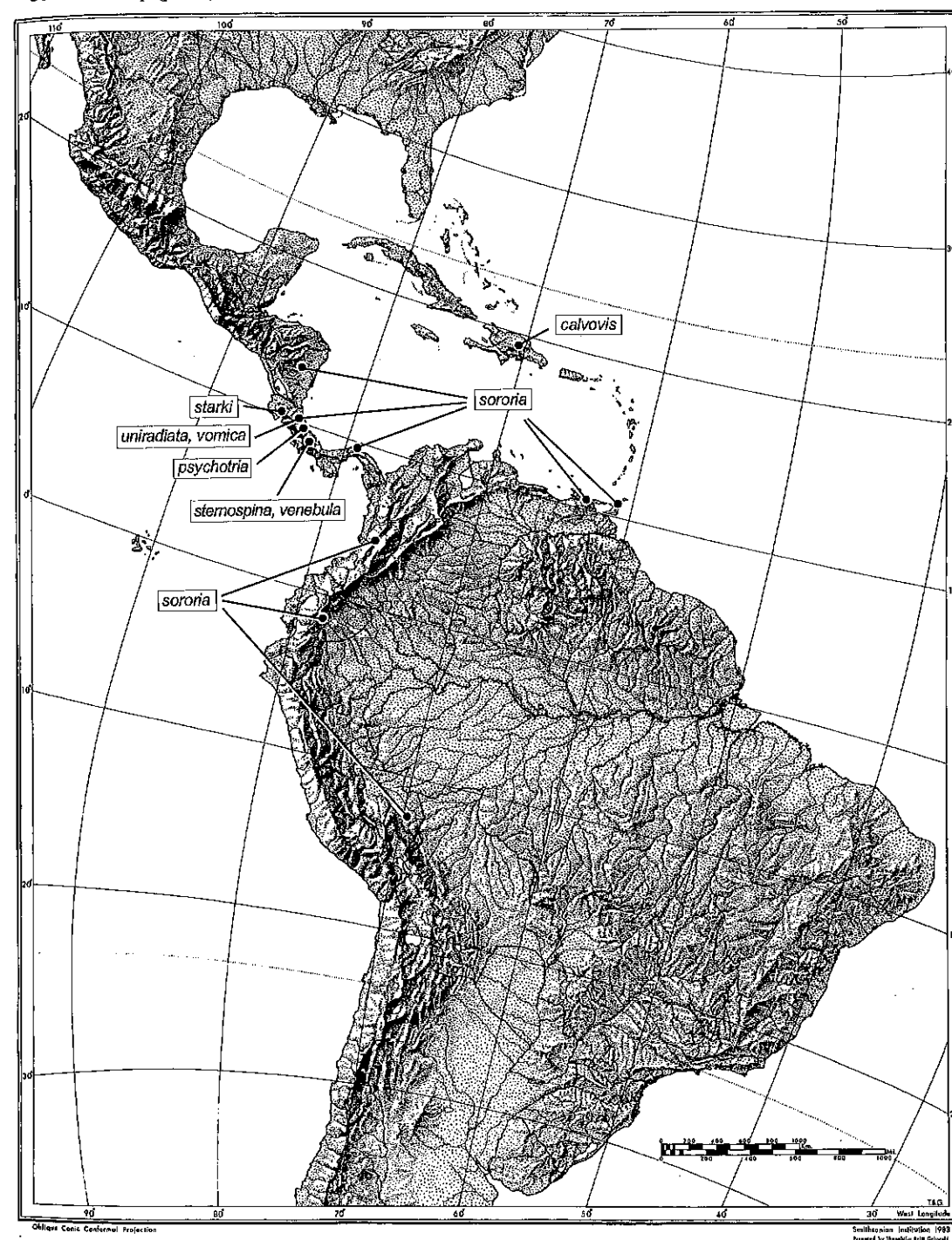
Fig. 73. Male terminalia of *C. uniradiata*.

Fig. 74. Male terminalia of *C. venebula*.Fig. 75. Male terminalia of *C. vomica*.

## Sororia Group (part 1)

Fig. 76. Distribution of *sororia* group species.

## Sororia Group (part 2)

Fig. 77. Distribution of *sororia* group species (continued).



## DIKRA SPECIES GROUP

DIAGNOSIS: A distinctively monophyletic group based on the single, median, heavily sclerotized structure lying between the surstyli. This structure is either fused paraphyses or the aedeagus (probably the latter). All but 3 species have a distiphallus with a bifid apex.

Normally, the name of the species group would be provided by the name of the constituent species that was described first, in this case *C. infumata* (Duda, 1925). Given some ambiguity in the placement of *C. infumata* (see below), we have decided to name the group for a species that is more reliably typical.

*Cladochaeta carinata*, new species

Figures 78, 80–82

DIAGNOSIS: Mostly brown; face with low, incomplete carina; wing lightly and evenly dusky; postocellar setae very small; distiphallus with short, inverted U-shaped prongs and numerous fine pits just proximal to prongs; surstylus with broad base, tapered to narrow apical lobe with row of 4 long, fine setae at apex.

DESCRIPTION: HEAD: Length in lateral view moderate (HL/HD = 0.78 [HT]). Eyes virtually bare, without fine interfacetal setulae; lower hind margin slightly indented. Pedicel and flagellomere I brown; arista with 4 dorsal branches and 8–9 minute medial ones, ventral branch closer to d-3 than to d-4, terminal fork of moderate to large size. Frontal vittae dark brown dorsally (with slight bluish pruinescence in oblique view), graded to ochre near ptilinal suture; frontal-orbital plates entirely yellow to having dorsal half dark brown. Frons with 5–6 interfrontal setulae. Frontal-orbital setae: anterior reclinate immediately lateral to proclinate; posterior reclinate much closer to proclinate than to inner vertical. Postocellars very small. Face of moderate width (FW/HW = 0.33), with narrow, low carina on dorsal half; dorsal half light, ventral half dark brown. Cheeks light brown and slightly shallow (CD/ED = 0.11 [N = 5]). Genal space of moderate depth. Proboscis and palps brown, with labellum slightly more heavily sclerotized than normal.

THORAX: Notum and scutellum brown; pleuron slightly darker. Anterior dorsocentrals about one-half the size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to anterior dorsocentrals. Acrostichals in 4 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars parallel, closer to notum than to posterior scutellars; post. scutellars slightly cruciate. Postpronotal lobe with 1 large and 1 slightly smaller seta. Legs brown (middle and hind legs slightly lighter); forefemur with 1 long, fine preapical seta on dorsolateral surface and row of 3 stouter setae in middle of ventrolateral surface. Halter light yellow. Wing slightly and evenly infuscate, but without any clouds of diffuse, darker infuscation. Apex of vein  $R_{2+3}$  virtually straight, gradually meeting costal vein (not turned abruptly costad). Veins  $R_{4+5}$  and M parallel slightly divergent. Crossvein dm-cu slightly curved. Wing tip rounded.

ABDOMEN: Most tergites evenly dark brown; tergite 1 lighter. Female terminalia: Dorsal part of penultimate tergite interrupted medially; apical tergite sclerotized, narrow. Apical sternite long, bulbous, sclerotized, with ringlike strip on anterior surface; lobate halves bearing setulae. Small, unsclerotized sclerite beneath sternite. Male genitalia: Cercus without ventral lobe, with flat ventral margin. Epandrium height ca. 1.5× width of epandrium. Ventrolateral halves of epandrium (epandrial lobes) tapered and narrow, with row of 4 large setae. Aedeagus sclerotized, hooked. Distiphallus with large apical prong, width of notch in prong about half the width of distiphallus; "neck" of distiphallus with even covering of fine pits (each with a minute microtrichia). Aedeagal apodeme with anterodorsal portion, deep, scoop-shaped; basal portion flared. Surstylus with apex narrowed into a lobe, bearing 5 long, thin, curved setae; ca. 25 smaller stiff setae on mesal surface and 3 setae of intermediate size on basal part of lateral surface. Hypandrium and gonopods lightly sclerotized. Hypandrium with simple, rounded anterior margin, shallow keel along entire ventral surface. Apical sternite simple, with ca. 18 short, stiff setulae.

TYPES: Holotype, Male: TRINIDAD: Ari-

ma: Blanchisseuse Rd., 2000 ft, 3–9/I/82, Morton S. Adams. Genitalia not dissected. Paratypes: 4♂ (1 dissected, no. 76), 1♀ (dissected, no. 78), with same label data as holotype (all in the AMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: In reference to the low, thin facial carina.

*Cladochaeta dejecta*, new species

Figures 78, 79, 83

DIAGNOSIS: Dorsal half of thorax brown (pleura darker), with yellowish area on anterior edge of notum; proclinate orbital setae minute; wing dusky brown, with darker infuscation on costal edge; arista with 3 dorsal and 1 ventral branch; male genitalia distinctive: each epandrial lobe with small flange on posterior margin; aedeagus sclerotized, erect, with articulated apical portion.

DESCRIPTION: HEAD: In lateral view rather high and short. Eyes completely bare; lower hind margin with barely an indentation. Pedicel light brown, flagellomere I slightly darker; arista with 3 dorsal branches and 1 ventral branch between d-3 and apical fork. Frons mostly ochre, slightly darker (brownish) on posterodorsal half; ocellar triangle dark black-brown. Frontal-orbital setae: Anterior reclinate minute, barely distinguishable from frontal-orbital setulae, immediately lateral to proclinate; posterior reclinate much closer to proclinate than to inner vertical. Postocellars about half the size of ocellar setae. Face flat, light brown, slightly narrow (FW/HW = 0.31 [N = 2]). Cheeks light yellow; very shallow (CD/ED = 0.08 [HT]). Genal space shallow. Proboscis mostly yellow, palps light brown.

THORAX: Notum and scutellum light brown; area from just above notopleural edge and pleuron (to dorsal margin of katapisternum) dark brown; katapisternum yellow. Anterior dorsocentrals about half the size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior and posterior scutellars convergent. Postpronotal lobe with 1 large seta, smaller ventral one.

Legs entirely light yellow; forefemur with 1 long seta near middle of dorsolateral surface, 2 setae on apical half of ventrolateral surface. Halter light brown. Wing with dusky infuscation, darker on costal edge. Apex of vein  $R_{2+3}$  turned slightly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip rounded.

ABDOMEN: Tergites evenly light brown. Female terminalia unknown. Male genitalia: Cercus slightly distended ventrally, but without distinct ventral lobe. Epandrial lobes narrow; each with distinctive, small flange on apical third of posterior edge; flange with 1 small, stiff setae (epandrium otherwise devoid of setae); ventral apex of epandrial lobe hooked posteriad. Aedeagus basically tubular, erect, sclerotized; apical third with dorsal surface sclerotized (ventral portion membranous?), articulated with basal two-thirds of aedeagus; basal portion of aedeagus with heavily sclerotized medial spine on apical margin of ventral surface. Small pair of narrow sclerites anterior to aedeagus, apparently the paraphyses. Surstyli almost spherical, with numerous fine, stiff setae on lateral surface. Hypandrium simple, relatively long, with rounded anterior margin, ventral keel shallow. Apical sternite not examined.

TYPE: Holotype, Male: DOMINICAN REPUBLIC: *La Vega Province*: 7.2 mi S Constanza, on road to San José de Ocoa, 5000 ft, 29/VII/91, Grimaldi, Stark, & Herman (not dissected). Paratype: Male, with same data as holotype (dissected, no. 272) (both specimens in AMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: Another word with the base similar to *erecta*, the species with which it apparently shares a close relationship.

*Cladochaeta dikra*, new species

Figures 78–80, 84

DIAGNOSIS: Notum yellow, pleura mostly dark brown; arista with 3 dorsal branches and large terminal fork, no ventral branch; anterior reclinate seta minute; distiphallus with pair of long, apical prongs and minute pits proximal to prongs; surstylus with broad, rounded base and narrow apical lobe with row of 4 long, curved setae.

DESCRIPTION: HEAD: Length in lateral view moderate (HL/HD = 0.69 [HT]). Eyes completely bare, without fine interfacetal setulae; lower hind margin flat, but not indented. Pedicel and flagellomere I light brown; arista with 3 dorsal branches and 5–6 minute medial ones, no ventral branch; branches of terminal fork long, equal in length at least to dorsal branches. Frontal vittae ochre, slightly shining; ocellar triangle dark black-brown to tan; frontal-orbital plates entirely yellow. Frons with 8–10 fine interfrontal setulae. Frontal-orbital setae: Anterior reclinate minute, slightly posterolateral to proclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars about one-third the size of ocellar setae. Face virtually flat, light brown, and of moderate width (FW/HW = 0.33 [N = 5]). Cheeks yellowish brown and of shallow depth (CD/ED = 0.08). Genal space quite deep. Proboscis and palps light brown.

THORAX: Notum and scutellum ochre, contrasting with dark brown pleuron (anterior half of katepisternum yellow). Anterior dorsocentrals about one-half the size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to anterior dorsocentrals. Acrostichals in 4 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars closer to notum than to posterior scutellars; post. scutellars slightly cruciate. Postpronotal lobe with 1 large and 1 slightly smaller seta. Legs yellow; forefemur with 1 long, fine seta on apical third of dorsolateral surface and 2 setae on apical half of ventrolateral surface. Halter light yellow. Wing very slightly and evenly infuscate, but without clouds of diffuse, darker infuscation, even on x-veins. Apex of vein  $R_{2+3}$  gradually meeting costal vein (not turned abruptly costad). Veins  $R_{4+5}$  and M virtually parallel. Crossvein dm-cu slightly oblique to vein M. Wing tip rounded.

ABDOMEN: Tergites dark, evenly brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe, with flat ventral margin. Epandrium height 1.3× width of epandrium. Ventrolateral halves of epandrium tapered and lobelike, apical half bent slightly out; each lobe with row of 5 setae. Aedeagus strongly arched. Distiphallus with apical knob at base and ca. 60 fine pits on

surface; with long, thin, slightly curved prongs. Aedeagus strongly sclerotized, especially distiphallus. Aedeagal apodeme sclerotized, with anterodorsal portion T-shaped where it articulates with base of aedeagus. Most of surstylus dish-shaped, with broad, concave middle area; small, thin apical lobe present, bearing 4 long, curved setae. Hypandrium and gonopods lightly sclerotized. Hypandrium with slightly angular (vs. rounded) anterior margin, with shallow but broad keel on ventral surface. Gonopods long, rodlike, not laterally flattened, articulated with bases of ventral lobe of epandrium. Apical sternite sclerotized; U-shaped, with 3 fine, stiff setulae on inner margin of of arms; setae pointed inward.

TYPES: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 900 m, sweeping in forest, III/91, D. Grimaldi. Paratypes: 4 (♂ + ♀), with same label data as holotype (all in AMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Greek *dikros* (forked or cloven), in reference to the distiphallus.

DISCUSSION: This species appears closely related to *pseudikra* based on the following features: distiphallus with very long prongs (length equal to basal part of phallus), apical sternite U-shaped (this feature also occurs in *dominitica*). There is a larger grouping of species that is defined by an aedeagus having the distal end with 2 prongs; this includes the 3 species mentioned above, as well as *carinata*, *janzeni*, *onyx*, and *tica*.

#### *Cladochaeta dominitica*, new species

Figures 81, 85

DIAGNOSIS: Body mostly light to dark brown, pleuron darker than notum; arista with just 2 dorsal branches (no ventral one); postpronotal lobe with 1 large seta; wing evenly dusky; aedeagus abruptly bent at 90° angle in middle (in lateral view); surstylus with large, broad base and long, narrow apical lobe bearing 4 small, spiculelike setae at apex.

DESCRIPTION: Head in lateral view rather long. Eyes completely bare, without fine interfacetal setulae; lower hind margin flat, without emargination. Pedicel and flagello-

mere I brown; arista with just 2 dorsal branches and 6–8 minute medial ones, no ventral branch; branches of terminal fork long, slightly shorter than dorsal branches. Frontal vittae dark brown above, light brown on lower half; ocellar triangle dark black-brown; frontal-orbital plates entirely light brown. Frons with 8 fine interfrontal setulae. Frontal-orbital setae: anterior reclinate small, about one-third the size of other orbitals, almost directly lateral to proclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars about one-third the size of ocellar setae. Face virtually flat, light brown, and of moderate width (FW/HW = 0.31 [N = 3]). Cheeks light yellow and of moderate depth (CD/ED = 0.11). Genal space deep. Proboscis and palps yellowish.

THORAX: Notum and scutellum light brown; pleuron contrastingly dark brown, including most of katepisternum. Anterior dorsocentrals about one-half the size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars parallel, much closer to notum than to posterior scutellars; post. scutellars cruciate for about one-third their length. Postpronotal lobe with 1 large seta. Legs yellow, forelegs slightly darker; forefemur with 1 long, fine seta near middle of dorsolateral surface and 2 setae on apical half of ventrolateral surface. Halter tan. Wing evenly dusky, but without clouds of diffuse, darker infuscation, even on x-veins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, virtually straight. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu straight, perpendicular to vein M. Wing tip rounded.

ABDOMEN: Tergites uniformly dark brown; slightly and diffusely lighter in middle of anterior tergites. Female terminalia reduced; penultimate tergite incomplete dorsally; apical tergite small, sclerotized, barely encircling dorsal three-quarters of epi-/hypoproct. No sclerotized structures between epi-/hypoproct and sternite; entirely membranous. Male genitalia: Similar to *C. tica*, except *dominitica* has the following features: aedeagus very sharply bent at 90° angle in middle, apical half pointed straight inward, with tips

of apical fork extended slightly beyond up-right portion of aedeagal apodeme. Dorsal part of aedeagal apodeme projected more anteriorly (inward) than in *tica*. Surstylus also with long, thin basal-medial lobe, but lobe is thinner, longer, and more curved, with 4 spiculelike setae at apex instead of 3 long, stiff setae. Large lobe of surstylus with row of 4 long, thin setae on dorsal margin (not broad, scalelike, and hooked) and 1 long preapical seta on mesal surface. Ventral keel on hypandrium shallower than in *tica*.

TYPES: Holotype, Male: HISPANIOLA (DOMINICAN REPUBLIC): *Pedernales Prov.*: 20 km NE Pedernales, 1500 m, II/92, "Las Abejas," isolated montane deciduous forest, D. Grimaldi & J. Stark (not dissected; in AMNH). Paratypes: 1♂ (dissected, no. 266), 1♀, same labels as holotype, in AMNH.

OTHER MATERIAL EXAMINED: Known only from the type series.

Etymology: Combined form of Dominican (in reference to country of type locality) and *tica*, the latter being the species of *Cladochaeta* that is its closest known relative.

#### *Cladochaeta erecta*, new species

Figures 78, 79, 86

DIAGNOSIS: Body entirely yellowish, wing hyaline; arista with 1 ventral and 4 dorsal branches; male genitalia highly modified: aedeagus large, erect, with pair of flanges on proximal half of ventrolateral surfaces; surstyli hatchet-shaped, with row of 3 sharp, stiff setae on "handle."

DESCRIPTION: Head in lateral view rather short (HL/HD = 0.68 [HT]). Eyes with very fine, short, sparse interfacetal setulae; lower hind margin rounded, not indented. Pedicel light brown; flagellomere I slightly darker brown; arista with 4 dorsal branches and 6 minute medial ones; ventral branch closer to d-3 than to d-4; branches of terminal fork long, slightly shorter than dorsal branches. Frons mostly yellow, ocellar triangle dark black-brown. Frontal-orbital setae: Anterior reclinate small, about one-third the size of other orbitals, directly lateral to proclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars about one-third the size of ocellar setae. Face flat,

yellow, and of moderate width (FW/HW = 0.31). Cheeks light yellow and rather shallow (CD/ED = 0.11 [HT]). Genal space shallow. Proboscis and palps yellowish.

THORAX: Notum, scutellum, and pleuron yellowish. Anterior dorsocentrals ca. 0.6× size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars parallel, much closer to notum than to posterior scutellars; post. scutellars slightly cruciate. Postpronotal lobe with 1 large seta. Legs light yellow; forefemur with 1 long seta in middle of dorsolateral surface and 2 setae on apical half of ventrolateral surface. Halter yellow. Wing completely hyaline, without even light diffuse infuscation. Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Tergites light brown, with lighter yellow areas in middle of anterior ones. Female terminalia unknown. Male genitalia: Cercus with entire ventral portion distended into long thin ventral lobe; height of cercus 2.5× width. Epandrium height 1.8× width of epandrium. Ventrolateral halves of epandrium (epandrial lobes) long, with apices flattened and slightly L-shaped; each lobe with row of 8 long, stiff setae. Aedeagus extremely long, erect, with slightly bulbous and membranous apex having proximal portion sclerotized. Basal half of aedeagus with pair of flanges along ventral surface; small, heavily sclerotized hook on ventral surface of base, and small pair of flat, sclerotized, slightly concave lobes flanking hook, each with small point at tip. Aedeagal apodeme with anterodorsal portion large, flat, lobate; ventral arms thin and tubular, articulated with hypandrium. Surstyli ax-shaped, width flared from based to apex, with thick lobe at apex projected posteriad. Apical surface of surstylus without setae; posterior margin of surstylus with row of 3 stout, stiff, sharp setae projected posteriad. Hypandrium and gonopods very slightly sclerotized. Hypandrium simple, with broad anterior margin, keel on ventral surface that becomes deeper posteriorly.

Apical sternite divided into 2 small setulose sclerites.

TYPE: Holotype, Male: ECUADOR: *Napo*: Coca, Napo River, 25–30/IV/65, 250 m, L. Peña (in CNC) (genitalia dissected, no. 107). The specimen is quite greasy, obscuring some hues of the original colors, but otherwise in very good condition.

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From Latin *erectus* (upright), in reference to the large erect aedeagus.

DISCUSSION: This species is doubtfully placed in this group because of the highly modified male genitalia, the shape of the head and eye (in lateral view), a completely yellow body (instead of being somewhat brown, especially on pleuron), and the completely hyaline wing.

*Cladochaeta glans*, new species

Figures 78–80, 87

DIAGNOSIS: Body mostly yellowish; wing with costal infuscation; arista with 3 dorsal branches on basal half, ventral one between d-3 and apical fork; male genitalia with sclerotized, hooded, and bulbous aedeagus.

DESCRIPTION: Head in lateral view short (HL/HD = 0.68 [HT]). Eyes with very fine, short, sparse interfacetal setulae; lower hind margin very slightly indented, almost completely rounded. Pedicel light brown; flagellomere I slightly darker brown; arista with 3 dorsal branches on basal half, 7 minute medial ones, ventral branch nearly midway between d-3 and terminal fork; branches of terminal fork slightly shorter than dorsal branches. Frons mostly light brown, ocellar triangle dark black-brown. Frontal-orbital setae: Anterior reclinate about one-third the size of other orbitals, directly lateral to proclinate or slightly posterolateral; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars slightly cruciate, about one-fourth the size of ocellar setae. Face flat, yellow, and of moderate width (FW/HW = 0.31). Cheeks light yellow and of moderate depth (CD/ED = 0.12 [HT]). Genal space shallow. Proboscis and palps yellowish.

THORAX: Notum, scutellum, and pleuron mostly yellowish; pleuron with slightly

brownish infuscation (but obscured by greasy specimen). Anterior dorsocentrals ca. 0.6× size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals slightly enlarged. Anterior scutellars divergent, much closer to notum than to posterior scutellars; post. scutellars cruciate for about one-third their length. Postpronotal lobe with 2 large setae. Legs light yellow; forefemur with 1 long seta in middle of dorsolateral surface, 2 setae on apical half of ventrolateral surface; midtibia with row of 9–10 evenly spaced, short, stiff setae. Halter light brown. Wing evenly and lightly fuscous, with clouds of diffuse darker infuscation on costal edge extended to slightly past vein  $R_{2+3}$  and to wing apex; small cloud over x-vein dm-cu (not over r-m). Vein  $R_{2+3}$  slightly curved; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip slightly pointed.

ABDOMEN: Tergites dark brown. Female terminalia unknown. Male genitalia: Cercus with thin ventral lobe projected laterad, ventral margin flat. Epandrium height ca. 1.5× width of epandrium. Ventrolateral halves of epandrium (epandrial lobes) long, but not tapered, apex blunt; each with row of 4 setae on apical half. Aedeagus with distiphallus large, bulbous, hoodlike; heavily sclerotized with smooth surface. Distiphallus with dorsoapical part large and bulbous, tapered to 2 thin ventral flanges; bulbous portion with hoodlike covering or mantle having narrow ventral lobe. Aedeagal apodeme trough-shaped, standing upright between base of aedeagus and hypandrium. Surstylus simple, almost square in shape; apical surface flat, with ca. 30 minute fine setae on apical margin. Hypandrium and gonopods hardly sclerotized. Hypandrium with simple, rounded anterior margin, keel on ventral surface becoming deeper near posterior margin. Gonopods fairly short, laterally flattened, articulated with bases of surstyli. Apical sternites not observed.

TYPE: Holotype, Male: ECUADOR: *Loja Prov.*: Loja, 2500 m, 23–25/II/65, L. Peña (in CNC) (genitalia dissected, DAG no. 110).

Specimen is greasy, which obscures true yellow color of most of the body, but is otherwise in good condition.

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: Directly from the Latin *glans* (acorn), in reference to the hooded, bulbous distiphallus.

DISCUSSION: As for *erecta*, this species is only tentatively placed in this group because of the unusual male genitalia, but also because of the pattern of infuscation on the wings and the enlarged acrostichal setulae (which are found in several other groups).

*Cladochaeta infumata* (Duda)

Figures 78, 79, 81

*Diathoneura infumata* Duda, 1925: 179.

*Clastopteromyia infumata*: Frota-Pessoa, 1947: 216 (new combination).

*Cladochaeta infumata*: Wheeler, 1963: 55 (new combination); Wheeler and Takada, 1971: 233 (male genitalia); Wheeler, 1981: 34 (catalog); Vilela and Bächli, 1990: 10 (redescription, illustration of holotype female genitalia and wing).

DIAGNOSIS: A poorly known species based presumably only on females, apparently most similar to *C. tica*, n. sp. Females of both species with single basal branch on arista; terminal tergite glabrous, without bridge beneath epi-/hypoproct, medial lobes; apical sternite bilobed but not entirely divided; each lobe setose, connected ventrally by broad anterior plate that is also turned upward and inward. Species differ by *infumata* having apical tergite unsclerotized, medial lobes closer together, and anteroventral plate of apical sternite entire (not bifid). Also, costal and apical portions of *infumata* wing with light infuscation.

DESCRIPTION: See Vilela and Bächli (1990: 10) for a full description.

TYPES: Holotype, Female: COSTA RICA: La Suiza de Turrialba, 14/IV/21. In the HNHM (dissected by Vilela and Bächli [1990: fig. 5C, D]).

OTHER MATERIAL EXAMINED: Known only from the type females.

DISCUSSION: The single basal branch of the arista would seem to indicate placement of this species in the *nebulosa* group. However, the female terminalia in the *nebulosa* group

typically have oviscapt lobes of the apical sternite projected far more than in *infumata*, and most species of the *nebulosa* group have a complete bridge in the apical tergite beneath the proctiger. The female genitalia are, in fact, quite similar in *C. tica*, also known from Costa Rica (the 2 species are easily distinguishable externally based on wings: *tica* has a dark hyaline wing, without clouds). These 2 species also share the *nebulosa* group type of arista with a single, basal branch. However, the male genitalia of *tica* indicate that the species is definitely not in the *nebulosa* group. Discovery of the male is the only way to confirm systematic placement, but given the apparent close relationship between the 2 species, *C. infumata* can for now be placed in the *dikra* group.

Wheeler and Takada (1971) illustrated the genitalia of a species from Costa Rica that they identified as *C. infumata*. Unfortunately, the specimen(s) on which their illustrations are based cannot be located. As discussed earlier under *C. inessa* (in the *nebulosa* group), the species illustrated by Wheeler and Takada belongs in the *nebulosa* group and is highly unlikely to be *C. infumata*.

*Cladochaeta janzeni*, new species

Figures 78, 79, 88

DIAGNOSIS: Body light brown, with darker pleura; arista with 3 dorsal branches, no ventral branch; wing hyaline. Male genitalia with anterior margin of hypandrium broad and flared; surstyli simple, clavate, with short setulae; apex of distiphallus bifid; aedeagus smooth, not finely punctate.

DESCRIPTION: Head in lateral view short (HL/HD = 0.60 [HT]). Eyes virtually bare of interfacetal setulae; lower hind margin indented. Pedicel light brown; flagellomere I slightly darker brown; arista with 3 evenly-spaced dorsal branches, 5 minute medial ones, no ventral branch; branches of terminal fork slightly shorter than dorsal branches. Frons mostly tan, ocellar triangle and surrounding area dark black-brown; 10 fine interfrontal setulae present. Frontal-orbital setae: Anterior reclinate small, about one-fourth the size of other orbitals, posterolateral to reclinate; posterior reclinate midway between proclinate and inner vertical. Pos-

tocellars slightly convergent, ca.  $0.3\times$  size of ocellar setae. Face flat, light brown, slightly narrowed (FW/HW = 0.30). Cheeks light yellow, rather shallow (CD/ED = 0.10 [HT]). Genal space of moderate depth. Proboscis and palps yellowish.

THORAX: Notum and scutellum ochre; pleuron brown, with bluish pruinescence when viewed at different angles. Anterior dorsocentrals ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately in front of ant. dorsocentrals enlarged, ca.  $1.5\times$  size of other acrostichals; prescutellar acrostichals not enlarged. Anterior scutellars slightly divergent, much closer to notum than to posterior scutellars; post. scutellars lost from specimen. Postpronotal lobe with 2 large setae. Legs tan; forefemur with 1 long seta in middle of dorsolateral surface and row of 3 setae on apical half of ventrolateral surface. Halter yellow. Wing completely hyaline, without any light, diffuse infuscation. Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly curved. Wing tip slightly pointed.

ABDOMEN: Tergites evenly light brown. Female terminalia unknown. Male genitalia: Cercus with small lobe on anteroventral corner with flat, heavily sclerotized ventral margin. Epandrium height ca.  $1.3\times$  width. Ventrolateral halves of epandrium (epandrial lobes) long, tapered, each with row of 4–5 setae. Aedeagus heavily sclerotized; curved, pointed ventrad. Distiphallus with deeply pronged apex; without fine pits. Base of aedeagus funnel-shaped. Aedeagal apodeme standing upright between base of aedeagus and articulation with hypandrium; aedeagal articulation flanged; composed of 2 thin rod-like structures and a thin median rod with tiny distal knob but no articulation. Surstyli simple, lobate, with slightly concave mesal surface; apical margins with ca. 20 fine setae. Hypandrium and gonopods hardly sclerotized. Hypandrium flared, with rounded anterior margin, shallow keel on ventral surface. Gonopods deep, laterally flattened, articulated with bases of surstyli. Apical sternites not observed.

TYPE: Holotype, Male: COSTA RICA: Guanacaste: Cerro El Hacha, 300 m, V–IX/87, D. Janzen (in AMNH) (dissected, no. 88).

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: Patronym in honor of Daniel Janzen, Neotropical biologist extraordinaire.

*Cladochaeta onyx*, new species

Figures 78, 89

DIAGNOSIS: Body mostly yellowish, wing completely hyaline; face and front wide; anterior reclinate orbital seta minute; surstylus unique, with large broad base having 4 long, bent, scalelike setae and long, thin apical lobe bearing 4 flat knobs.

DESCRIPTION: HEAD: Length in lateral view moderate (HL/HD = 0.71 [HT]). Eyes completely bare of interfacetal setulae; lower hind margin rounded, not indented. Pedicel light brown; flagellomere I slightly darker brown; arista damaged in only known specimen, apparently with 1 basal dorsal branch, an apical dorsal branch (d-2) and apical fork, and a ventral branch just proximal to d-2. Frons mostly tan, ocellar triangle dark black-brown; 8–10 long, fine interfrontal setulae. Frontal-orbital setae: Anterior reclinate minute, barely distinguishable from frontal-orbital setulae, lateral and slightly posterior to reclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars slightly convergent, about half the size of ocellar setae. Face broad, flat, light brown, and narrow (FW/HW = 0.28). Cheeks light yellow and slightly shallow (CD/ED = 0.10 [HT]). Genal space shallow. Proboscis and palps yellowish.

THORAX: Notum and scutellum ochre; pleuron with some light brown areas. Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately in front of ant. dorsocentrals and scutellum not enlarged. Scutellar setae damaged in specimen. Postpronotal lobe with 1 stout seta and 1 thinner, ventral seta. Legs tan; forefemur with row of 4 long setae on dorsolateral surface, row of 3 setae on ventrolateral surface. Halter yellow. Wing com-

pletely hyaline, without even light, diffuse infuscation. Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Female terminalia unknown. Male genitalia: Cercus without ventral lobe, ventral margin flat. Epandrium height ca.  $1.5\times$  the width. Ventrolateral halves of epandrium (epandrial lobes) long and slightly tapered, each with row of 4 setae. Aedeagus heavily sclerotized; with thin, heavily sclerotized "collar" proximal to apex about one-third the length of aedeagus; "collar" incomplete on dorsal surface. Aedeagus tubular, curved anteriorly, with apical prongs. Surstyli very distinctive: apex with long, thin lobe terminated in club bearing 4 scraperlike structures; median surface with row of 4–5 small setae; basal lobe of surstylus with 4 long, rhamphate, scalelike setae. Hypandrium and gonopods hardly sclerotized. Apical sternite slightly U-shaped, with distal parts of arms having small group fine setulae.

TYPE: Holotype, Male: VENEZUELA: Aragua: Rancho Grande, Parque Nacional Henry Pittier, 1100 m, 4/III/67, M. E. Irwin (in CAS) (dissected, no. 136). The type is not in good condition: missing are right arista, branches from left one; left dorsocentrals and some pleural and 2 scutellar setae; left wing, left midleg, and most of left hind leg.

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From Greek for talon or claw, in reference to the clawlike structure on a lobe of the surstylus.

*Cladochaeta pseudikra*, new species

Figures 78, 90

DIAGNOSIS: Body ochre with slightly darker, brown pleura; wing hyaline; frontal orbital seta minute; male genitalia similar to *dikra*, with distinctions as described below.

DESCRIPTION: HEAD: Long in lateral view (HL/HD = 0.85 [HT]). Eyes completely bare of interfacetal setulae; lower hind margin indented. Pedicel light brown; flagellomere I slightly darker brown; arista lost in only known specimen. Frons golden, reflective on anterior half, light brown on posterior half,



ocellar triangle dark black-brown; 11 short, fine interfrontal setulae. Frontal-orbital setae: Anterior reclinate minute, barely distinguishable from frontal-orbital setulae, lateral and slightly posterior to reclinate; posterior reclinate midway between proclinate and inner vertical. Postocellars convergent, ca.  $0.3\times$  size of ocellar setae. Face of moderate width (FW/HW = 0.28), flat, brown. Cheeks light yellow and of moderate depth (CD/ED = 0.11 [HT]). Genal space fairly deep. Proboscis and palps tan.

THORAX: Notum and scutellum ochre; pleuron light brown with some bluish pruinescence when viewed at various angles. Anterior dorsocentrals about half the size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately in front of ant. dorsocentrals and scutellum not enlarged. All but one scutellar seta lost. Postpronotal lobe with 1 stout seta and 1 smaller, ventral seta. Legs yellowish; forefemur with long setae on dorsolateral surface, row of 3 setae on ventrolateral surface. Halter yellow. Wing completely hyaline, no infuscation even on x-veins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu straight, perpendicular to vein M. Wing tip rounded.

ABDOMEN: Female terminalia unknown. Male genitalia very similar to that of *C. dikra*, except that this species has the following characteristics: posterior margin of epandrium without concavity; ventral keel on hypandrium narrow; distiphallus longer and thinner, without fine pits on dorsal half; surstylus without small, thin apical lobe but with large, curved subapical setae and row of 11–12 small, blunt, scalelike setae in middle part of medial surface.

TYPES: Holotype, Male: COLOMBIA: Sierra Nevada Mts., Campano, above Santa Marta, 5000 ft, VIII/56, W. B. Heed, M. Wasserman, H. L. Carson, & H. Hoenigsberg (dissected, DAG no. 237) (in AMNH). Lost from the specimen are the arista, some orbital and thoracic setae, and the right wing; however, the specimen is otherwise in good condition. Most of abdomen with genitalia are in a vial pinned with the specimen.

OTHER MATERIAL EXAMINED: Known only from the holotype male.

ETYMOLOGY: From *pseudo* (false), and *dikra*, in reference to its very close relationship with *Cladochaeta dikra*.

*Cladochaeta santana*, new species

Figures 78, 91

DIAGNOSIS: Body mostly ochre, wings hyaline; arista with 4 dorsal branches, d-4 very small; aedeagus short, with pronged distiphallus; prongs sclerotized, with membranous portion in middle; surstylus distinctive, as described below.

DESCRIPTION: Head length in lateral view moderate (HL/HD = 0.72 [HT]). Eyes completely bare of interfacetal setulae; lower hind margin rounded, without indentation. Pedicel light brown; flagellomere I slightly darker brown. Arista with 3 larger dorsal branches on basal half, much smaller dorsal branch (d-4); small apical fork, no ventral branch. Posterior half of frons brown with bluish pruinescence; anterior half ochre; ocellar triangle dark black-brown; 8 long, fine interfrontal setulae. Frontal-orbital setae: anterior reclinate very small, slightly longer than frontal-orbital setulae, posterolateral to reclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars parallel, fairly large, about half the size of ocellar setae. Face of moderate width (HW/FW = 0.30), flat, and tan. Cheeks light yellow and fairly deep (CD/ED = 0.13 [HT]). Genal space fairly deep. Proboscis and palps tan.

THORAX: Notum and scutellum ochre; pleuron mostly ochre with some light brown areas. Anterior dorsocentrals ca.  $0.7\times$  the size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 8 uneven rows; ones immediately in front of ant. dorsocentrals barely larger than other acrostichals; prescutellars not enlarged. Anterior scutellar setae parallel, apicals barely cruciate. Postpronotal lobe with 1 stout seta and 1 smaller ventral seta. Legs yellowish; forelegs missing on type. Halter yellow. Wing completely hyaline, even x-veins without infuscation. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly cos-

tad. Veins  $R_{4+5}$  and M virtually parallel. Crossvein dm-cu very slightly bent, perpendicular to vein M. Wing tip slightly pointed.

ABDOMEN: Female terminalia unknown. Male genitalia: Cercus without thin ventral lobe or ventral margin of cercus; anterolateral corners slightly expanded. Epandrium slightly taller than wide, height ca.  $1.2\times$  width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, with row of 6 stiff long setae. Aedeagus short, with pronged distiphallus, prongs sclerotized; membranous portion in middle. Aedeagal apodeme with ventral fork; tall and narrow. Hypandrium with flat anterior margin. Surstyli simple and lobate, not sclerotized, with small ventral lobe at base. Basal lobe of surstylus with row of 5 long, scalelike setae; bulbous part with ca. 10–12 sharp, sickle-shaped setae on medial surface, several smaller setae. Apical sternites not examined.

TYPES: Holotype, Male: EL SALVADOR: Volcan Santa Ana, W. B. Heed, XI/53, 5670 ft (in the AMNH) (Dissected, no. 240).

OTHER MATERIAL EXAMINED: Known only from the holotype male.

ETYMOLOGY: A slightly abbreviated version of the name of the type locality.

*Cladochaeta tica*, new species

Figures 78–81, 92

DIAGNOSIS: Arista with only 1 dorsal branch, at base; no apical fork. Body mostly yellowish/ochre, with pleura mostly to barely with some light brown; tergites brown to yellowish, with apical one dark brown. Male genitalia with aedeagus typical of *dikra* group; surstylus bilobed, with row of 4 long scalelike setae between lobes and 2–3 short, stout "teeth" at apex of thinner lobe.

DESCRIPTION: HEAD: Length in lateral view moderate (HL/HD = 0.72 [HT]). Eyes completely bare of interfacetal setulae; lower hind margin with indentation. Pedicel ochre; flagellomere I light brown. Arista convergent with that of *nebulosa* group; only 1 dorsal branch, at base; no apical fork or ventral branch; vestiges of 1 or 2 dorsal branches sometimes apparent. Frons mostly ochre;

ocellar triangle yellow to light brown; ca. 8 fine interfrontal setulae. Frontal-orbital setae: Anterior reclinate very small, slightly longer than frontal-orbital setulae, lateral and sometimes also slightly posterior to reclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellars slightly convergent, fairly large; ca.  $0.4\times$  size of ocellar setae. Face flat, tan, and narrow (FW/HW = 0.28 [N = 20]). Cheeks light yellow and shallow (CD/ED = 0.11). Genal space fairly deep. Proboscis and palps tan.

THORAX: Notum and scutellum ochre; pleuron light brown, with anterior half of katepisternum yellow. Anterior dorsocentrals ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; prescutellars and ones immediately in front of ant. dorsocentrals not enlarged. Anterior scutellar setae parallel, apicals parallel to barely cruciate. Postpronotal lobe with 1 stout seta. Legs yellowish; forefemur with 1 long dorsolateral seta, row of 4 long ventrolateral setae. Halter yellow. Wing evenly dusky to hyaline, without infuscation. Apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M almost perfectly parallel. X-vein dm-cu straight. Wing tip rounded.

ABDOMEN: Tergites light brown to yellowish, with apical one (and epandrium in males) dark brown; terminal tergites especially with light medial stripe. Female terminalia: Apical tergite sclerotized, not completely surrounding epi/hypoproct. Most of terminalia membranous, trussed ventrally by sclerite curled anterodorsad, bearing pair of narrow arms on anterior margin. Male genitalia: Cercus without thin ventral lobe; ventral margin of cercus flat. Epandrium taller than wide, height ca.  $1.8\times$  width. Ventrolateral halves of epandrium (epandrial lobes) long and narrow, slightly tapered apically, with row of 6 stiff, long setae. Aedeagus bulbous and heavily sclerotized; bent inward at middle; distiphallus deeply pronged, surface without minute pits. Aedeagal apodeme a typically long, narrow sclerite upright between base of aedeagus and bases of gonopods. Hypandrium oval-shaped, with shallow

ventral keel; arms of gonopods deep, slightly tapered apically. Surstyli clawlike; with apex produced into 2 thin, widely separated lobes; dorsal lobe with 2 stout, sharp, toothlike setae, ventral lobe with ca. 10 short, fine setae; space between lobes with 4 large, scalelike setae, posterior ones very sharply hooked. Apical sternites not examined.

**TYPES:** Holotype, Male: COSTA RICA: *Guanacaste*: Cerro El Hacha, 300 m, V-IX/87, D. H. Janzen, ex: Malaise trap in understory, park loc. 17-52 (not dissected) (in AMNH). Paratypes: 13♂ + ♀, with same label data as holotype (INBio and AMNH). One male (no. 48), 1 female (no. 49) dissected.

**OTHER MATERIAL EXAMINED:** PANAMA: *Canal Zone*: Colón, VII/79, canopy fogging, E. M. Broadhead (1♂, no. 152) (AMNH).

**DISCUSSION:** This species shares with *C. minuta* (Duda) the presence of long, scalelike setae on the surstylus. Otherwise, the shapes of the surstyli and aedeagus are considerably different in the 2 species, as is the fact that *tica* has a highly reduced arista and is nearly twice the size of *minuta*.

**ETYMOLOGY:** In reference to a colloquial term where in Costa Ricans refer to themselves as "ticas," as well as to the Costa Rican locality of this species.

*Cladochaeta vivipara*, new species

Figures 78, 80, 81, 92

**DIAGNOSIS:** Small species (ThL = 0.62 mm); body yellowish, with light brown pleural areas; wing dusky; eyes with short, dense, fine setulae; antennal pedicel with 2-3 long setae on ventromedial margin; anterior reclinate orbital seta small, anterolateral to proclinate; male genitalia reduced (as described below); surstylus simple, crescentic.

**DESCRIPTION:** **HEAD:** Length in lateral view moderate (HL/HD = 0.73 [HT]). Eyes with short, dense, fine setulae; lower hind margin with slight indentation; genal area large, making eye appear relatively small in lateral view. Pedicel ochre, with 2 very long and 1 shorter setae on ventromedial margin; flagellomere I light brown. Arista with 3 evenly spaced dorsal branches; apical fork with moderate-sized branches; no ventral branch-

es. Frons with frontal vittae golden, reflective; ocellar triangle yellow to light brown; ca. 8 minute interfrontal setulae. Frons relatively short and wide. Frontal-orbital setae: Anterior reclinate small, slightly longer than frontal-orbital setulae, lateral and slightly anterior to reclinate; posterior reclinate much closer to proclinate than to inner vertical. Postocellars parallel to slightly convergent; widely spaced; fine, ca. 0.4× size of ocellar setae. Face flat, tan, and broad (FW/HW = 0.34 [N = 8]). Cheeks light yellow and relatively shallow (CD/ED = 0.15). Proboscis and palps tan.

**THORAX:** Notum and scutellum yellow to ochre; pleuron light brown, with anterior half of katapisternum yellow. Anterior dorsocentrals ca. 0.8× size of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; prescutellars and ones immediately in front of ant. dorsocentrals not enlarged. Anterior scutellar setae parallel, apicals cruciate for ca. 0.2× their length. Postpronotal lobe with 1 stout seta. Legs yellowish; forefemur with 1 long dorsolateral seta near middle; 2 longer ventrolateral setae, one near middle very long. Halter yellow. Wing lightly dusky, but without clouds of darker, diffuse infuscation. Vein  $R_{2+3}$  very slightly curved, almost straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip rounded.

**ABDOMEN:** Tergites mostly dark, evenly brown. Female terminalia simple: Apical tergite an inverted U-shaped sclerite, half surrounding epi-/hypoproct. Apical sternite sclerotized, bilobed, with pair of outer, posterior surfaces bearing ca. 5 minute setulae. Sternite curled under, having pair of small internal sclerites. Male genitalia highly reduced. Cercus without ventral lobe, ventral margin flat. Epandrium rather short, height about equal to width. Ventrolateral halves of epandrium (epandrial lobes) not especially long or tapered, medial margin of apex slightly concave and accommodating surstylus; each lobe with row of 5-6 setae. Aedeagus heavily sclerotized, scoop-shaped; base wider than apex, with thin strip at base forming collar (incomplete on posterior surface).

Aedeagal apodeme sclerotized, triangular. Surstyli simple, crescentic lobes, with ca. 10 fine setulae on mesal margin. Hypandrium small, without keel; gonopods sclerotized, forming simple U-shaped sclerite with rod-like arms articulated with surstyli. Apical sternite simple, slightly sclerotized, without setulae.

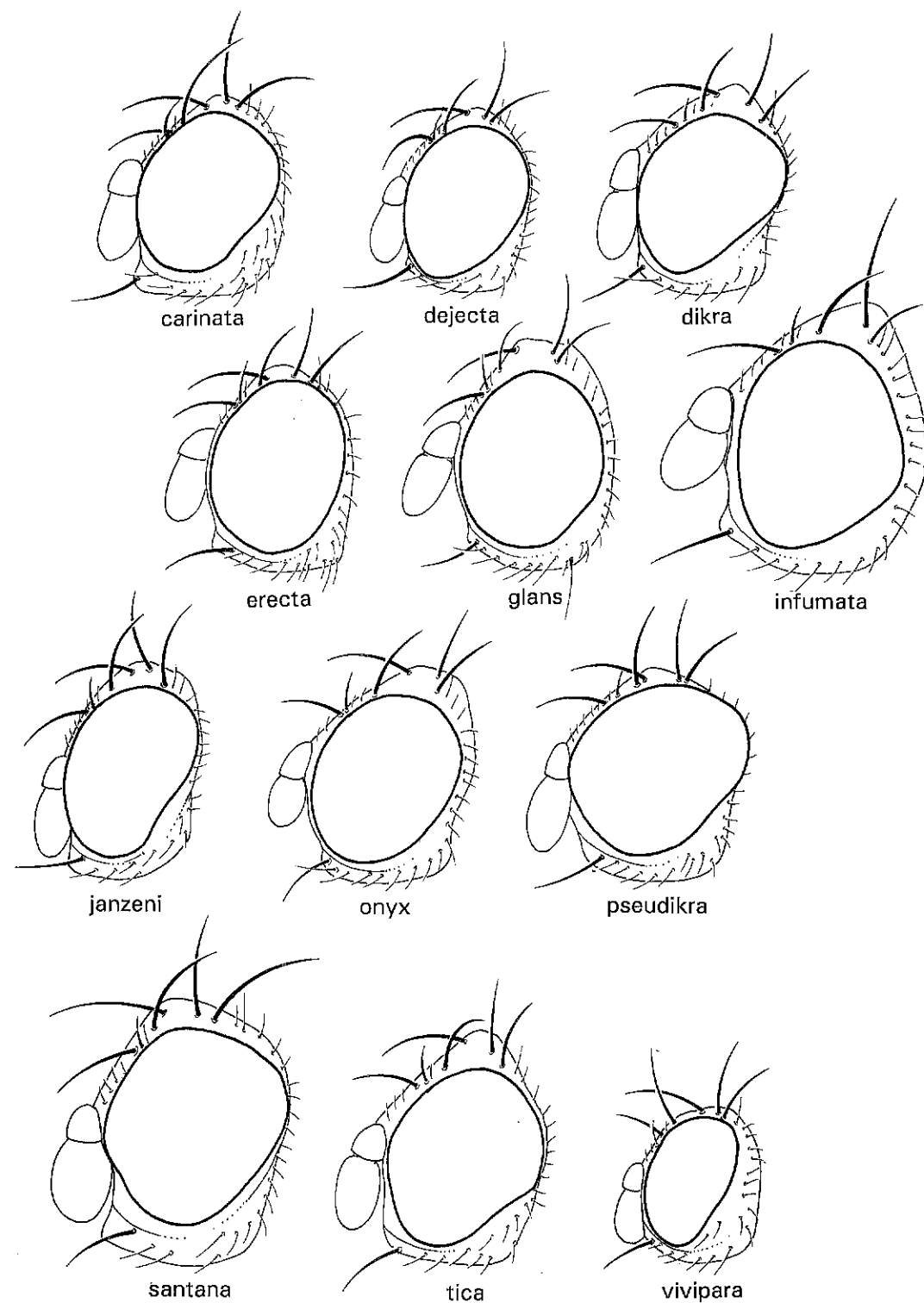
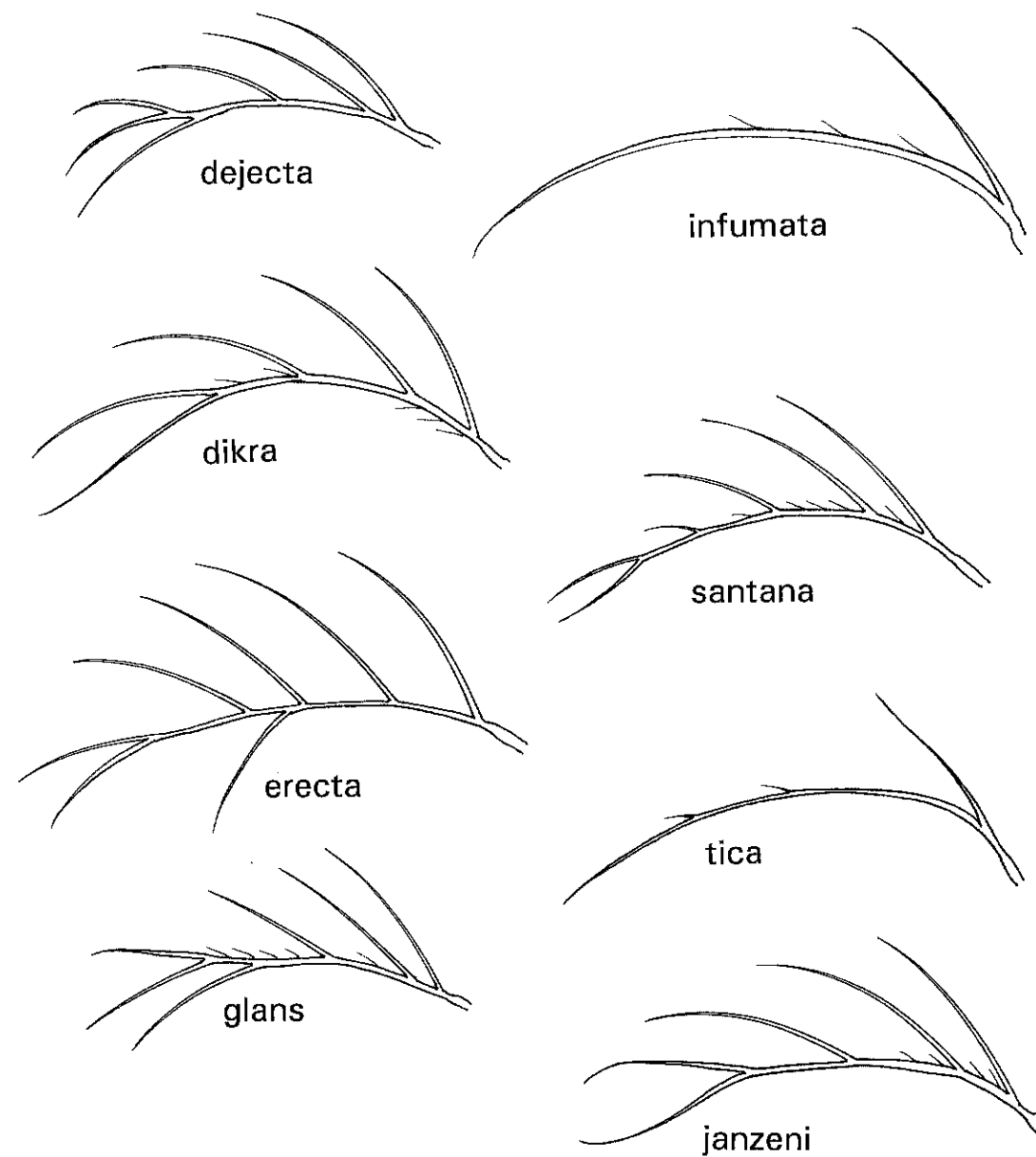
**TYPES:** Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi. Paratypes: 6 (♂ + ♀), same label data as holotype (all in AMNH).

**OTHER MATERIAL EXAMINED:** PANAMA: *Chiriqui*: Boquete, VIII/58, W. B. Heed, M. Wasserman (1♂, no. 246) (AMNH).

**ETYMOLOGY:** From Latin *viviparus* (bearing active, living young), in reference to reproduction in this species.

**DISCUSSION:** One female from Las Alturas, Costa Rica, has a very large egg protruding from the posterior opening. This indicates at least that some individuals lay eggs and others lay larvae, but the possibility remains that an individual female could be facultatively ovoviviparous.



Fig. 78. Heads of *dikra* group species.Fig. 79. Aristae of *dikra* group species.

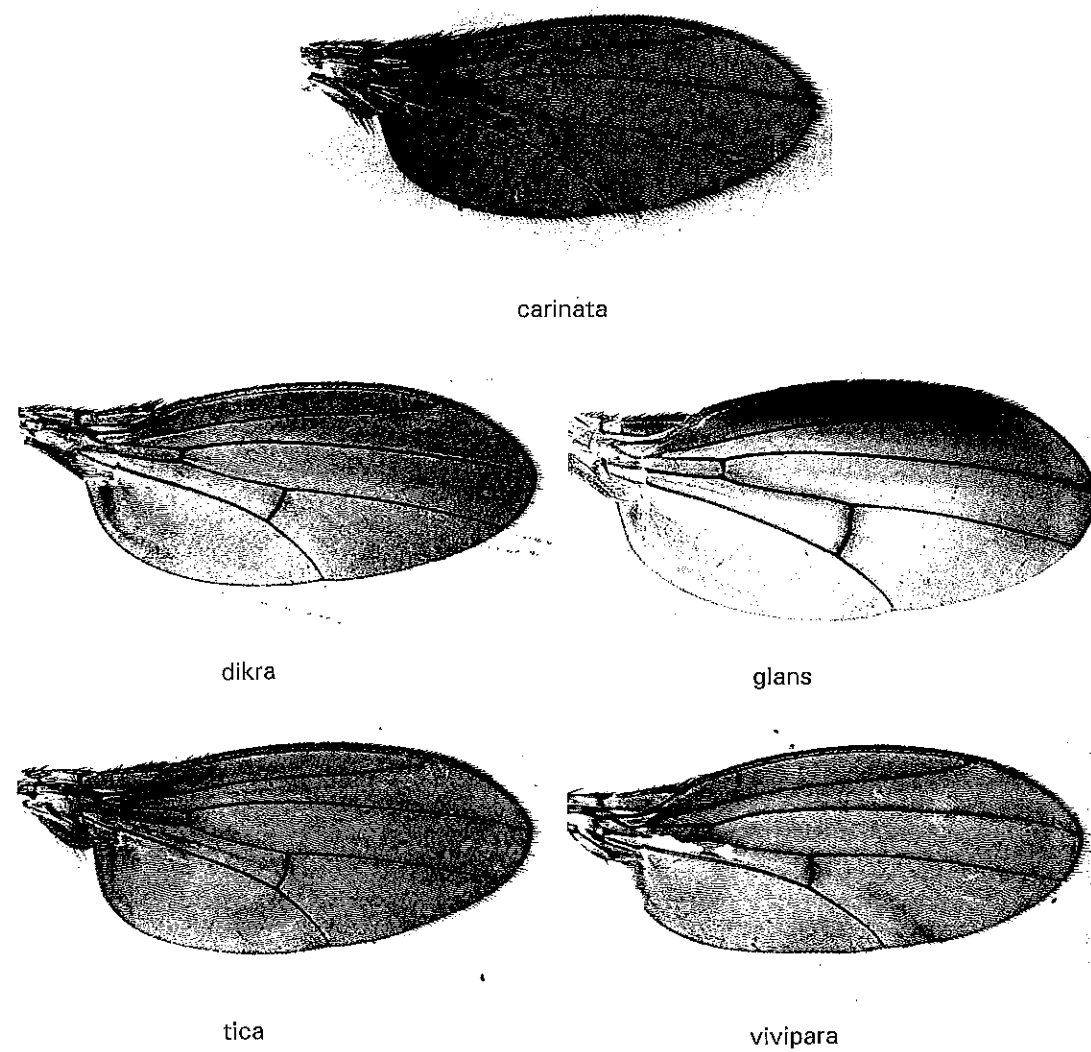
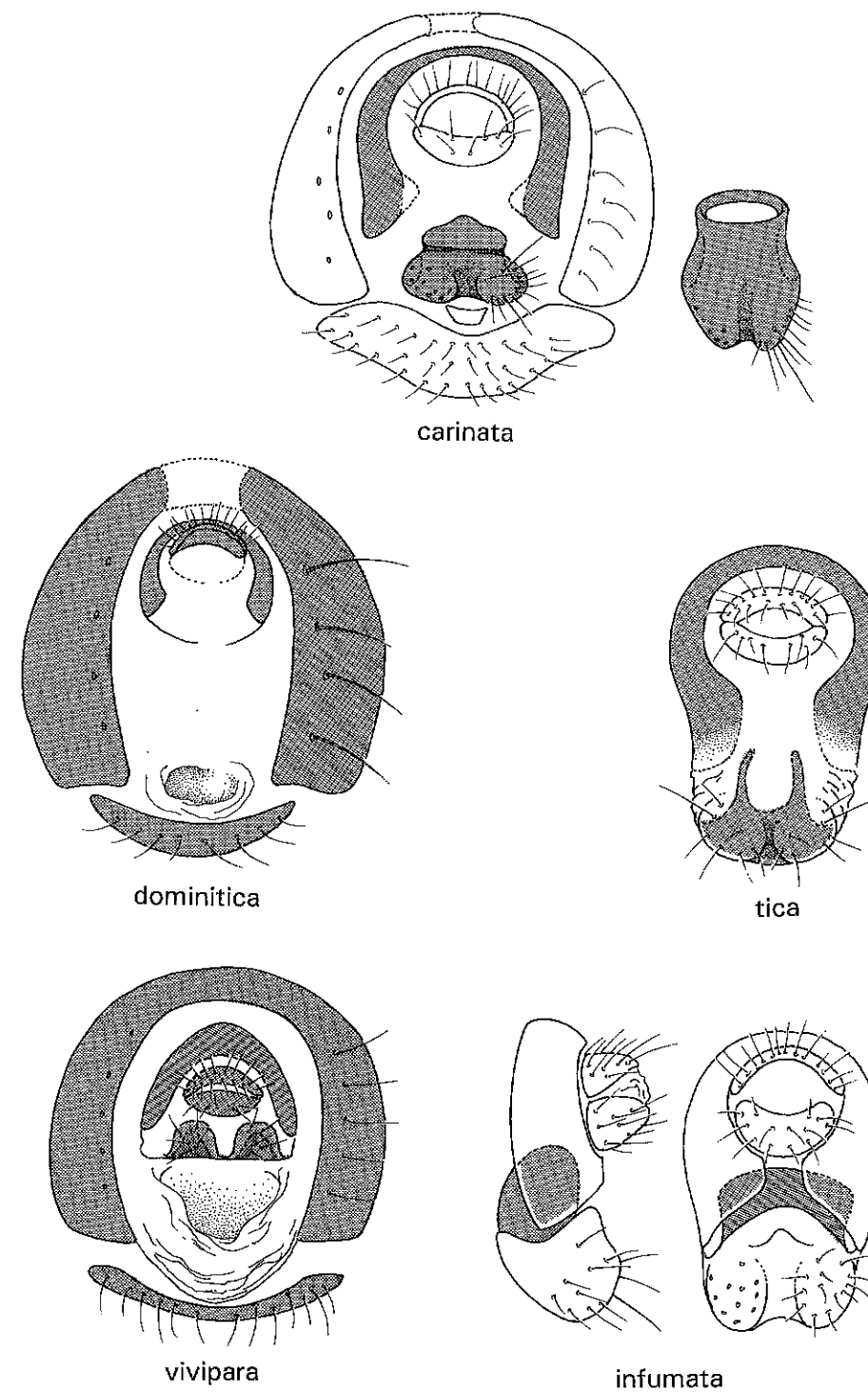
Fig. 80. Wings of *dikra* group species.Fig. 81. Female terminalia of *dikra* group species. Posterior and other views.



Fig. 82. Male terminalia of *C. carinata*.

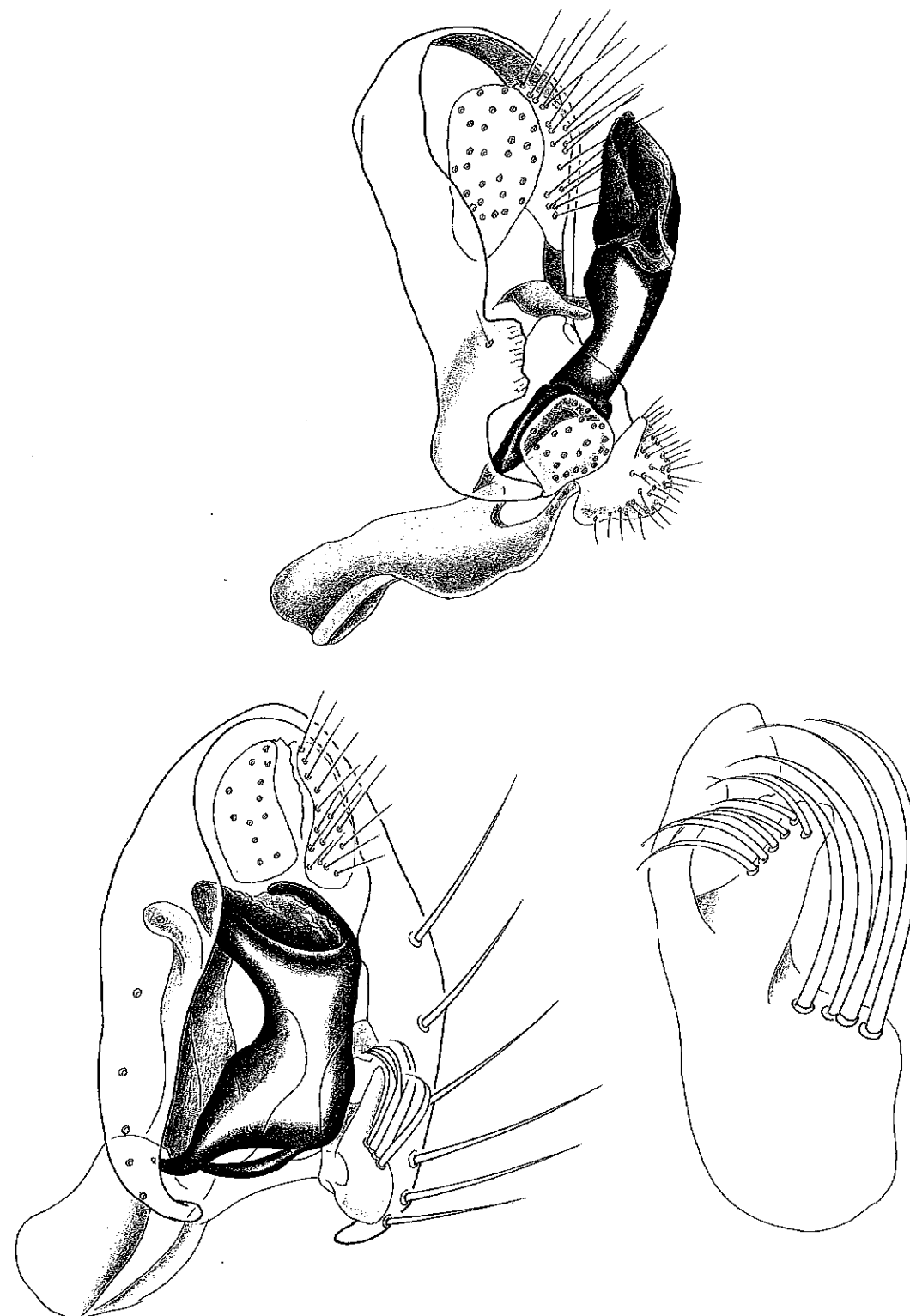


Fig. 83. Male terminalia of *C. dejecta* (above) and undescribed species near *dominiticalonyx* (below).

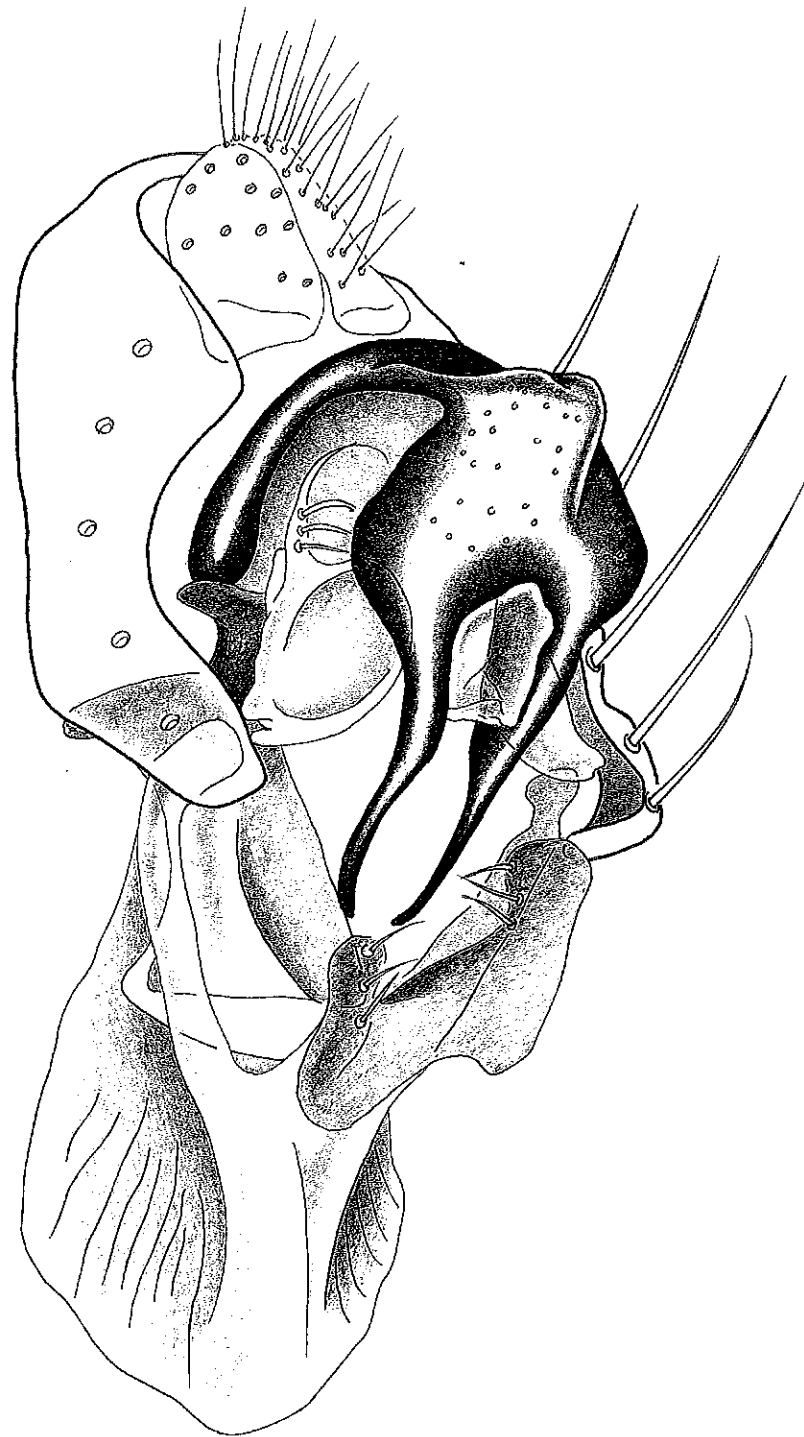


Fig. 84. Male terminalia of *C. dikra*.

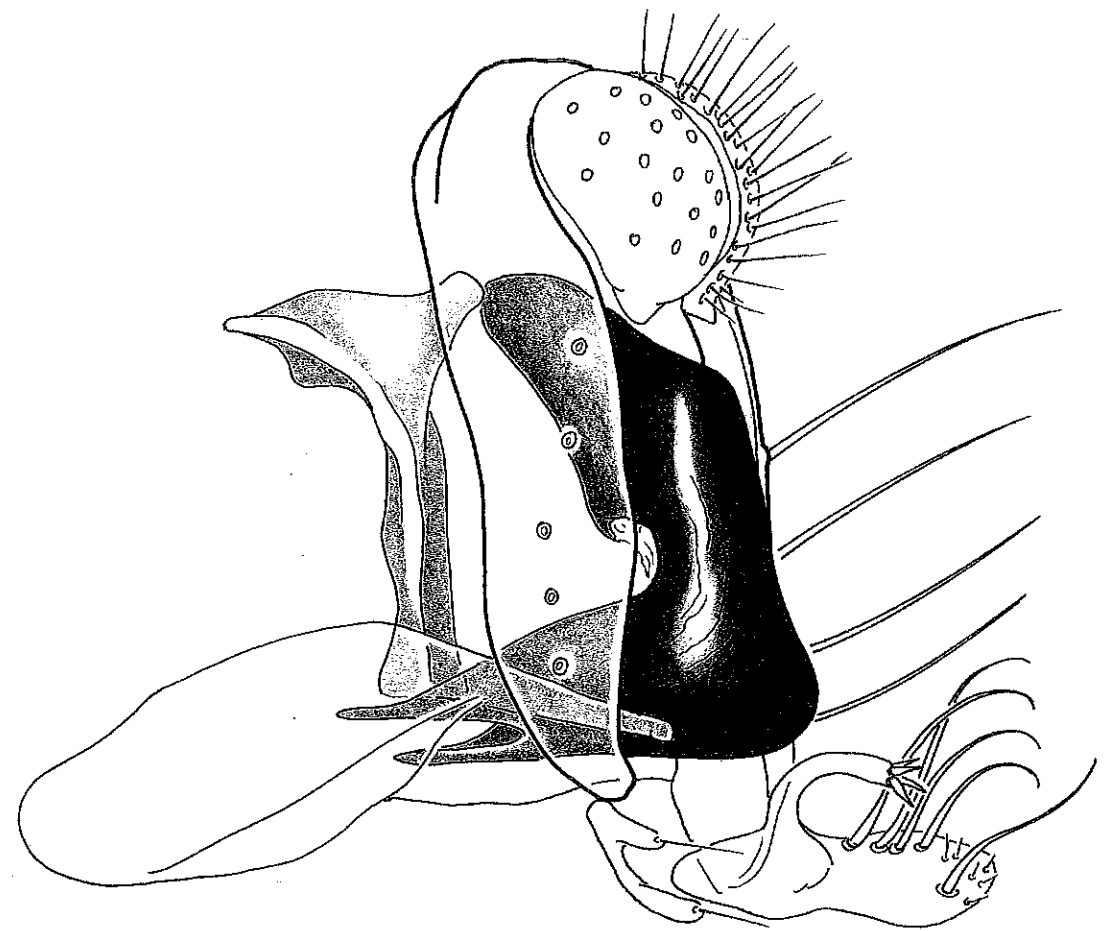


Fig. 85. Male terminalia of *C. dominitica*.

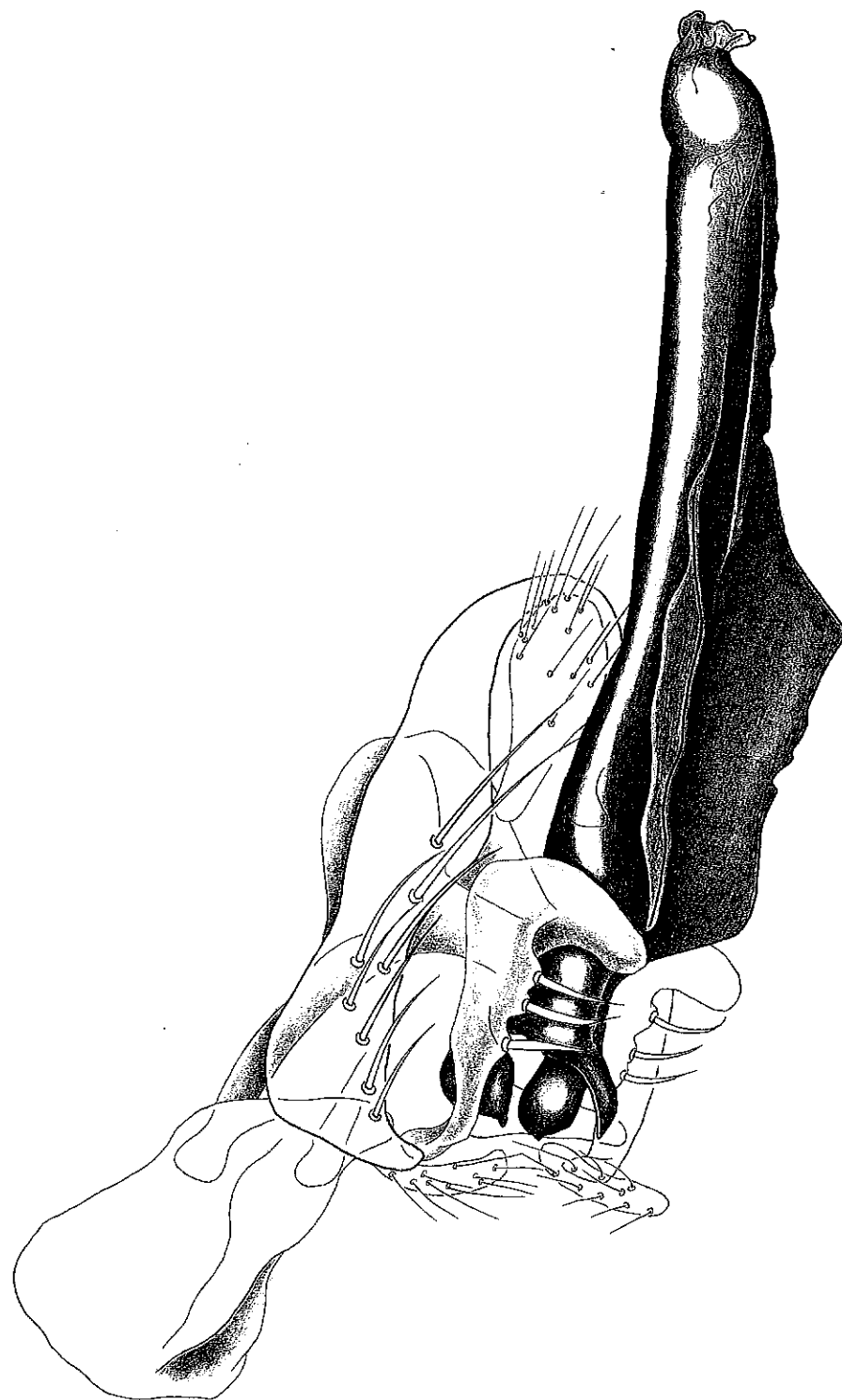


Fig. 86. Male terminalia of *C. erecta*.

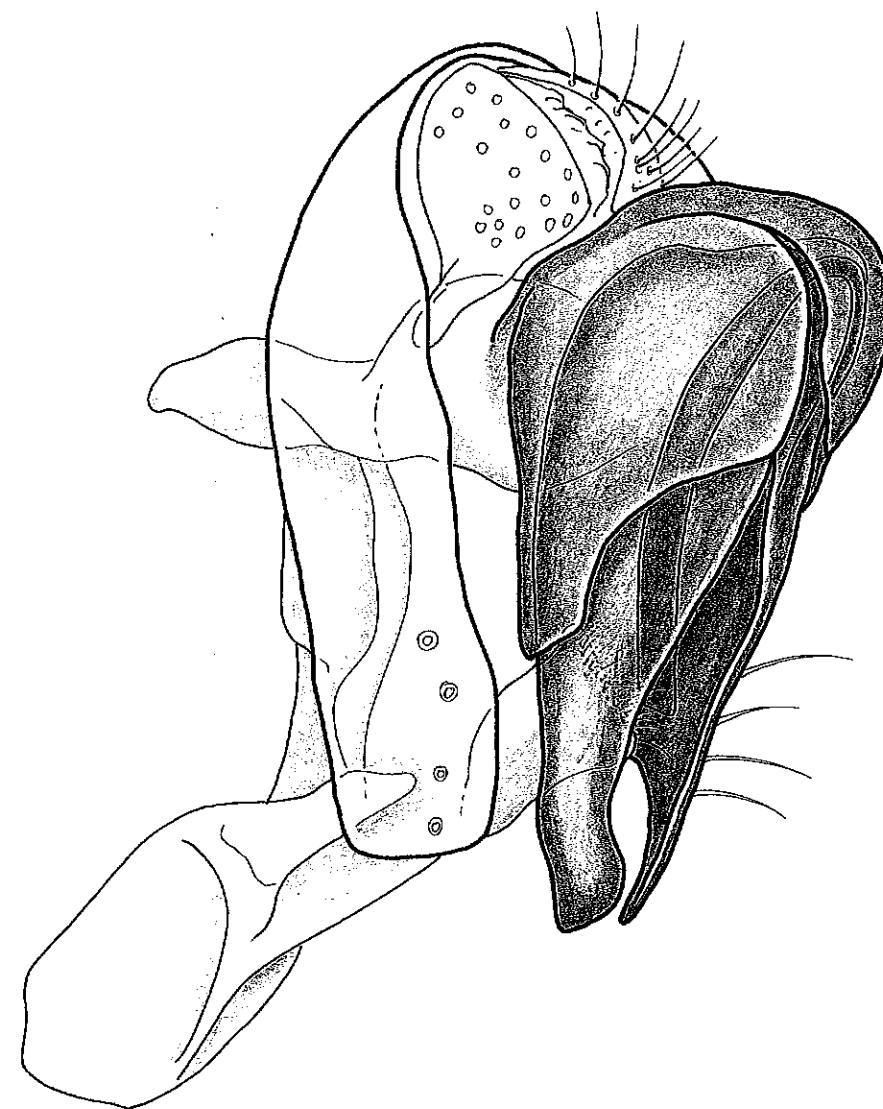


Fig. 87. Male terminalia of *C. glans*.

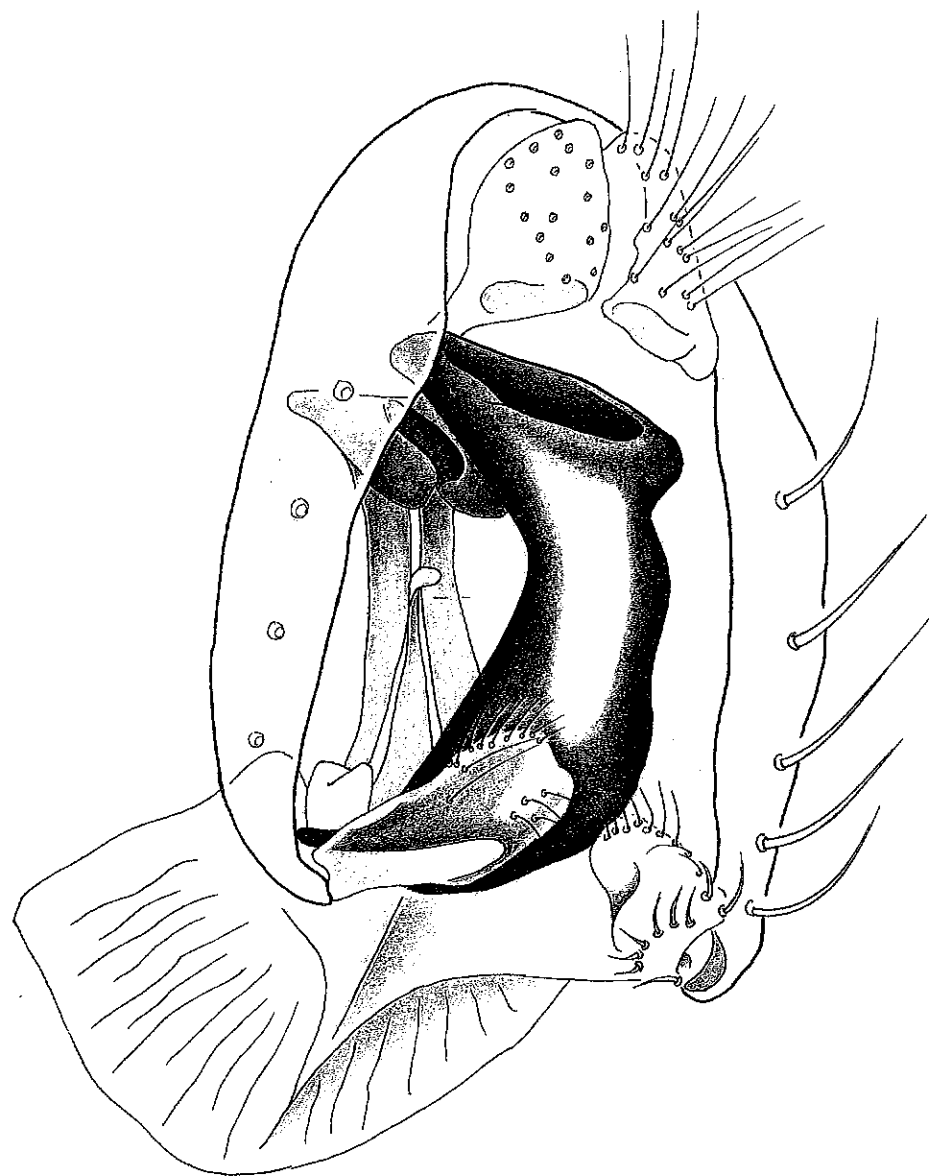


Fig. 88. Male terminalia of *C. janzeni*.

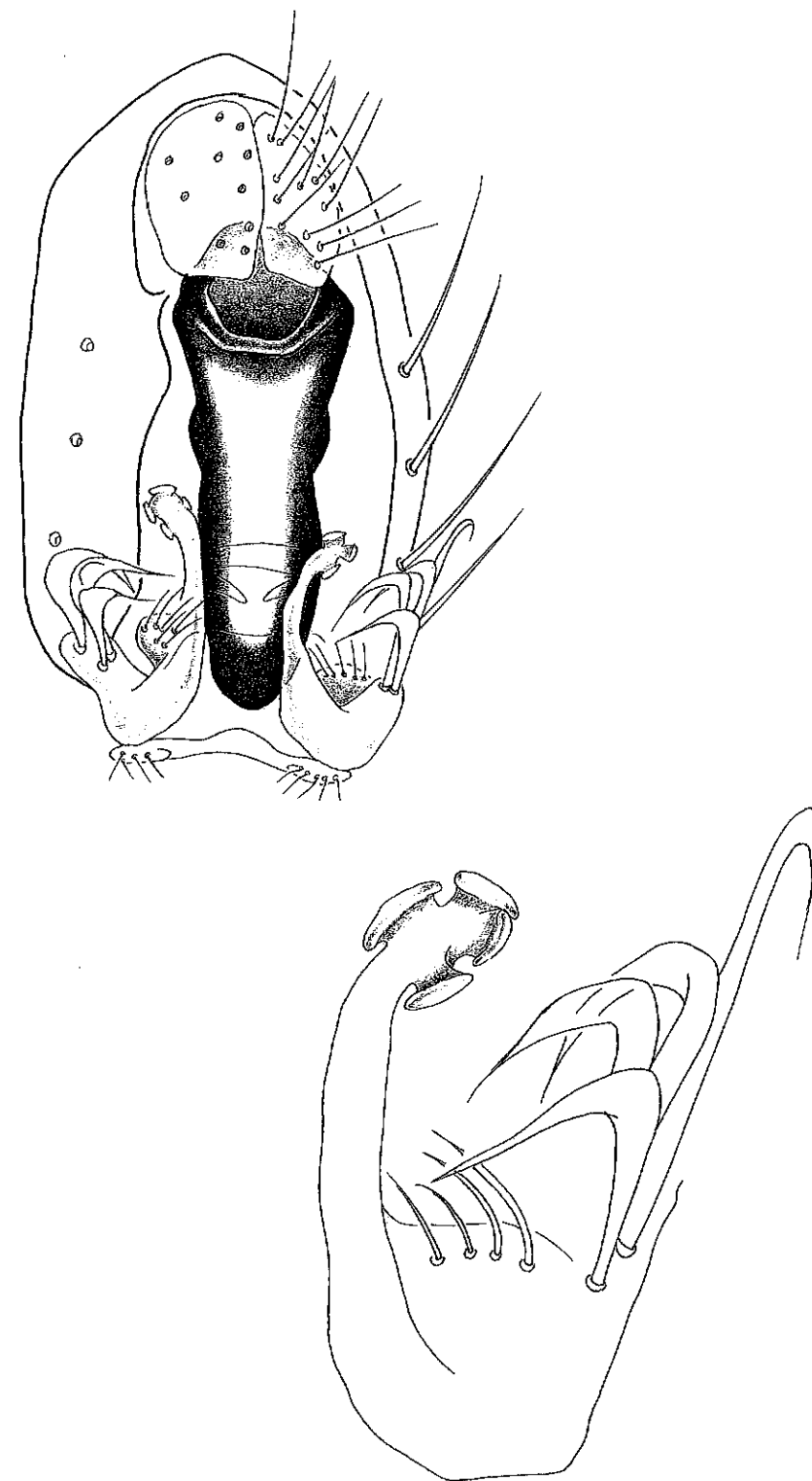


Fig. 89. Male terminalia of *C. onyx*.





Fig. 90. Male terminalia of *C. pseudikra*.

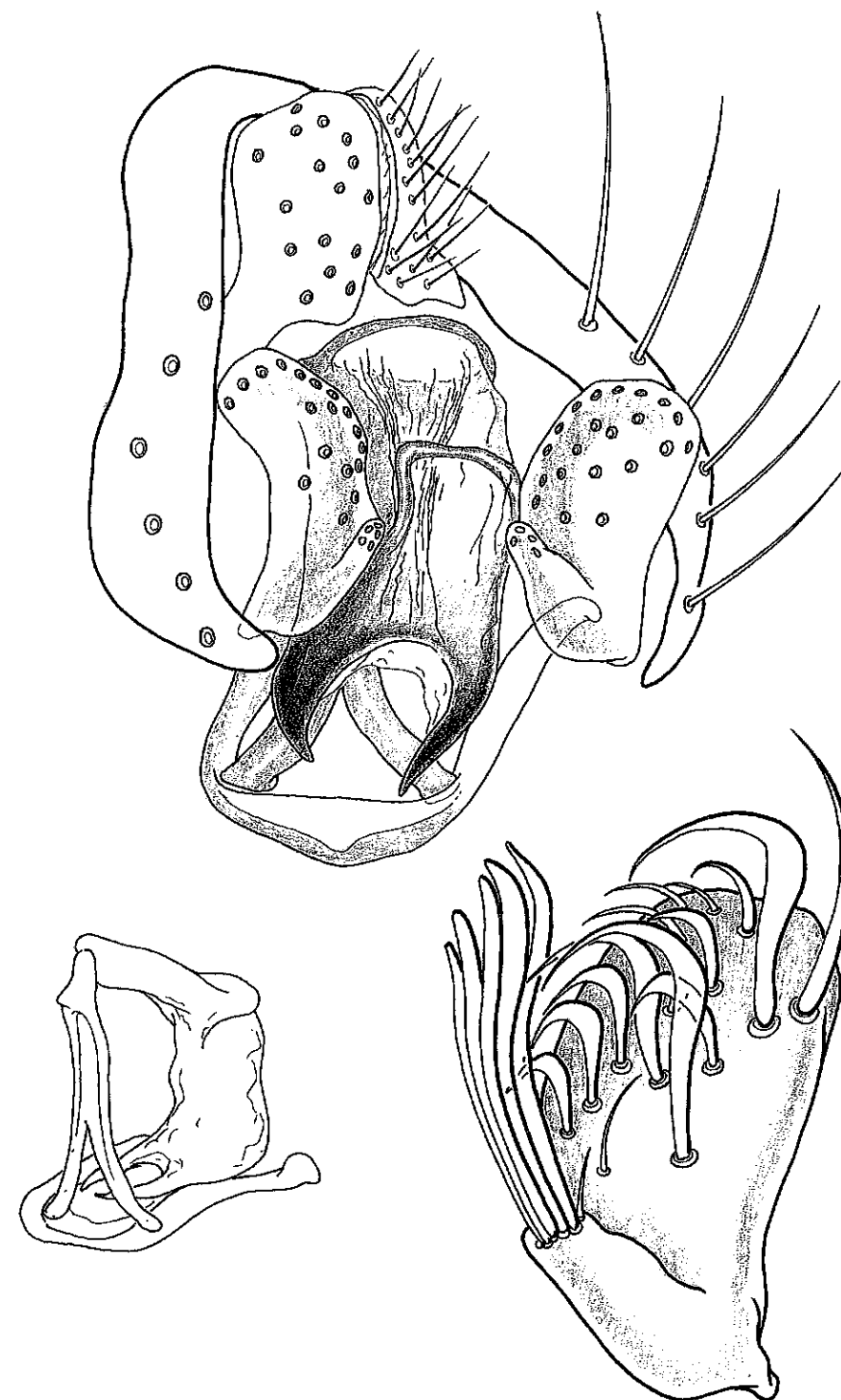


Fig. 91. Male terminalia of *C. santana*.

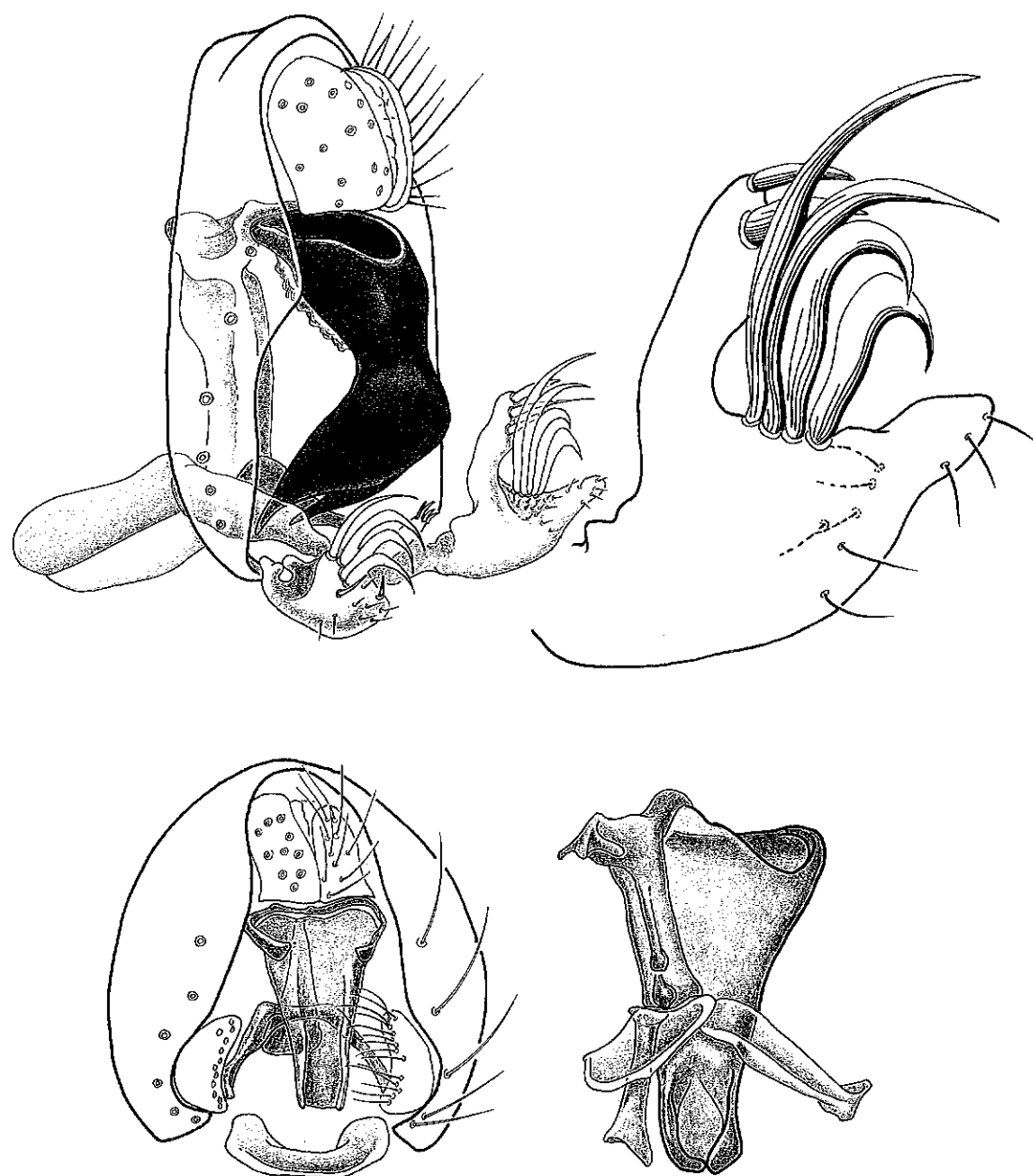


Fig. 92. Male terminalia of *C. tica* (above) and *vivipara* (below).



Fig. 93. Distribution of *dikra* group species.

## DIMINUTA SPECIES GROUP

**DIAGNOSIS:** Generally very small species; cheek usually deep; arista with 1 ventral branch; female terminalia with apical sternite deeply bilobed, sometimes with lobes separated; paraphyses apparently lost; instead, aedeagus a large, heavily sclerotized, often conical tube; aedeagal apodeme often large, scoop-shaped, and sclerotized.

*Cladochaeta abbrevifusca*, new species

Figures 94–97

**DIAGNOSIS:** Very closely related to *C. devriesi* based on male genitalia. Thorax mostly yellow; externally distinguished from *devriesi* and other species based on dark infuscation on costal edge of wing, with apical edge abrupt, not diffuse; arista with 1 ventral and 3 dorsal branches. Male genitalia differ from *devriesi* based on *abbrevifusca* having broader base of aedeagus, tip of aedeagus of slightly different shape; surstyli with finer and more setulae; surstyli with longer apical lobe; ventral margin of cercus with lightly sclerotized strip, as well as several other features.

**DESCRIPTION: HEAD:** Length relative to head moderate (HL/HD = 0.76 [HT]). Eyes with sparse, fine pile; lower hind margin with very slight indentation seen in lateral view. Antenna with pedicel and flagellomere I light brown; arista with 1 ventral and 3 dorsal branches; ventral branch between d-3 and apical fork; branches of apical fork slightly shorter than d-3. Front with frontal vittae golden, shiny; 7–8 minute interfrontal setulae. Frontal-orbital setae: Proclinate orbitals ca. 0.7× length of posterior reclinate; anterior reclinate orbitals small, ca. 0.3× size of proclinate, immediately lateral to proclinate. Face light yellow, almost whitish, flat, and of moderate width (FW/HW = 0.32 [N = 6]). Cheeks shallow (CD/ED = 0.08). Proboscis and palp yellow.

**THORAX:** Notum, scutellum, and postnotum ochre to yellow; pleura slightly darker. Anterior dorsocentrals ca. 0.7× length of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 even rows; acrostichal setula immediately anterior to ant. dorsocentral seta enlarged, ca. 1.5× length of other

acrostichals and slightly thicker; prescutellar acrostichals not enlarged. Anterior scutellars parallel; posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta, ventral one slightly smaller. Legs entirely light yellow; forefemur with ventrolateral row of 3 larger setae; 1 larger dorsolateral seta. Wing lightly fuscous with darker, diffuse clouds of infuscation on costal edge over apical half of vein  $R_{2+3}$  and small cloud over dm-cu. Distal edge of cloud over vein  $R_{2+3}$  abruptly ended near apex of  $R_{2+3}$ . Vein  $R_{2+3}$  slightly curved; apex of  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight, but oblique to, not perpendicular to, vein  $CuA_1$ . Wing tip slightly pointed, not rounded. Halter light brown.

**ABDOMEN:** All tergites dark brown to black. Female terminalia with moderate sclerotization. Apical tergite an inverted U-shaped sclerite, more sclerotized than penultimate tergite. Apical sclerite bilobed, irregularly U-shaped; mostly separated but connected by anterior bridge. Pointed, roughly triangular sclerite lies between lobes of apical sternite. Male genitalia: Cercus with ventrolateral margin pointed, lying partly under epandrium; sclerotized strip on ventral margin of cercus, slightly detached from cercus. Epandrium height about equal to width. Ventrolateral halves of epandrium sharply narrowed to points at apices. Posteroventral margins of epandrium each with row of ca. 7 setae. Aedeagus heavily sclerotized, smooth; funnel-shaped, except for subapical slit and apex; apex pronged, with one prong overlying the other. Dorsal, basal part of aedeagus ca. 4.5× with width of apex. Aedeagus ca. 0.85× length of epandrium. Aedeagal apodeme scoop shaped. Apical surface of surstylus a narrow triangle in posterior view, with long dorsal lobe; apical surface with ca. 50 fine setulae. Apex of long dorsal lobe on surstylus with 3–4 long, fine setulae. Hypandrium and gonopods lightly sclerotized. Hypandrium with quadrate, smooth anterior margin and deep ventral keel. Gonopods deep, laterally flattened, with ventral keel. Apical sternites not examined.

**TYPES:** Holotype, Male: COLOMBIA: Medellín, coffee finca, 5000 ft, XI/55, W. B. Heed (not dissected). Paratypes: COLOMBIA: 50 km W Bogota, VII/60, W. B. Heed

& H. L. Carson (2♂, UT slide no. 263; 1♀) (all in AMNH).

**OTHER MATERIAL EXAMINED:** BOLIVIA: Coroico, IV/58, M. Wasserman (1♂, UT slide no. 265) (AMNH). VENEZUELA: Caripe, X–XI/56, M. Wasserman (1♂, UT slide no. 262) (AMNH).

**ETYMOLOGY:** In reference to the abbreviated, terminal margin of the patch of infuscation on the wing.

*Cladochaeta arthrostyla*, new species

Figures 94, 96, 98

**DIAGNOSIS:** Head broad, frons mostly velvety blue-black; cheek very deep; most of thorax and part of pleura dark brown; wings hyaline; male genitalia very distinctive; aedeagus sclerotized, long, pendulent, with tip curved up; surstylus unique, 2-segmented, distal segment with numerous, fine plumose hairs, each with 3 branches. Female terminalia distinctive, as described below.

**DESCRIPTION: HEAD:** Relatively short and long, with a long sloping front. Eyes with sparse, fine, very short pile; lower hind margin of eye with slight indentation seen in lateral view. Antenna with pedicel ochre medially, brown laterally; flagellomere I brown; arista with 3 dorsal branches and 1 ventral one (perhaps the ventral branch of apical fork). Frons long, sloping, quite wide; posterodorsal two-thirds blue-black, velvety; anterior third ochre yellow (entirely blue-black in the female specimen). Frontal-orbital setae: Proclinate orbitals approximately equal in size to posterior reclinate; anterior reclinate orbitals very small, ca. 0.2× size of proclinate (and about twice the size of frontal-orbital setulae), immediately lateral to proclinate. Ocellar setae slightly shorter than orbitals; postocellars small, ca. 0.4× length of ocellar setae. Dorsal half of face light brown (dark brown in female), ventral half whitish (silvery in female), slightly protruding. Face of moderate width (FW/HW = 0.32 [N = 2]). Cheeks deep, white (silvery in female) (CD/ED = 0.17). Proboscis and palp light yellow; gena and postociput dark brown.

**THORAX:** Notum, scutellum, and postnotum dark brown; pleura mostly dark brown, except for katepisternum (mostly ochre) (en-

tirely dark in female). Anterior dorsocentrals ca. 0.6× length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows; acrostichal setula immediately anterior to ant. dorsocentral seta, and prescutellar acrostichals not enlarged. Anterior scutellars parallel; posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta, no trace of ventral one. Legs entirely light yellow in male (brown in female); forefemur with ventrolateral row of 3 larger setae; 3 larger dorsolateral setae. Wing hyaline, without even diffuse clouds of infuscation on x-veins. Vein  $R_{2+3}$  straight; apex of  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel, but both gently curved. Crossvein dm-cu straight. Wing tip slightly pointed, not rounded. Halter light yellow in male, contrasting with dark brown thorax and tergites (entirely light brown in female).

**ABDOMEN:** All tergites black-brown. Female terminalia reduced, but distinctive; apical tergite very thin, without bridge beneath epi-/hypoproct; apical sternite completely divided into pair of widely separated narrow lobes (apices of each with ca. 10 minute setulae); narrow, tongue-like sclerite lies vertically between sternal and tergal lobes; most parts of terminalia sclerotized. Male genitalia: Cercus with ventrolateral margin flat. Ventrolateral halves of epandrium long, narrow, gradually tapered apicad, each with row of ca. 12 short, stiff setae. Aedeagus heavily sclerotized, smooth (slightly wrinkled); long and pendulous, extends from ventral margin of cercus to ventral margin of epandrium; tip is curved up. Aedeagal apodeme lightly sclerotized, funnel-shaped. Surstylus 2-segmented; basal lobe with numerous fine setulae and small medial lobe; apical lobe slightly larger, with numerous fine setae that are 3-branched. Hypandrium and gonopods lightly sclerotized. Hypandrium with squared anterior margin and deep ventral keel. Gonopods deep, laterally flattened. Apical sternites not examined.

**TYPES:** Holotype, Male: COSTA RICA: San José, Zurqui de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 283). Paratype: Female, same data as holotype (dissected, no. 284). Both specimens in the AMNH.

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: from *arthro* (jointed) and *styli*, in reference to the 2-segmented surstyli.

DISCUSSION: On the basis of the very unusual feature of 3-branched setae on the surstylus, this species would apparently be closely related to *C. dolichofrons*. Male genitalia of the 2 species are quite similar overall. *C. dolichofrons* is known only from Trinidad.

*Cladochaeta devriesi*, new species

Figures 94, 99

DIAGNOSIS: Distinctive for the dark brown body, with areas of light blue-green pruinescence (frons, parts of pleura); face and anterior third of frons yellowish; wing hyaline; male genitalia with aedeagus heavily sclerotized, having subapical hole and apical cleft.

DESCRIPTION: HEAD: Rather long relative to depth (HL/HD = 0.78 [HT]). Eyes with dense, short, fine pile; lower hind margin with slight indentation seen in lateral view. Antenna with pedicel ochre and flagellomere I light brown; arista with 1 ventral and 3 dorsal branches; ventral branch between d-3 and apical fork; dorsal branch of apical fork about half the length of d-3. Posterior two-thirds of front black brown, with blue-green pruinescence (best seen at face-on view); anterior third of front ochre. Frontal-orbital setae: Proclinate orbitals ca. 0.8× length of posterior reclinate; anterior reclinate orbitals very thin and small, ca. 0.4× size of proclinate, immediately lateral to proclinate. Face yellow, flat, and of moderate width (FW/HW = 0.34). Anterior half of cheeks yellow; posterior half and gena black-brown; cheeks quite deep (CD/ED = 0.18). Proboscis and palp light brown.

THORAX: Notum, scutellum, postnotum, and pleura dark brown; slight areas of blue-green pruinescence on anterior part of katepisternum and anepimeron. Anterior dorsocentrals ca. 0.7× length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars parallel; posterior scutellars damaged in type. Postpronotal lobe setae damaged. All femora of legs light brown (forefemora slightly darker), tibia and tarsi yellowish; forefemur with

2 larger ventrolateral setae; 1 larger dorso-lateral seta. Wing completely hyaline, without even light, diffuse infuscation on cross-veins. Vein  $R_{2+3}$  slightly curved; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter light brown.

ABDOMEN: All tergites black-brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe; with flat ventral margin. Epandrium height ca. 1.5× width of epandrium. Ventrolateral halves of epandrium tapered ventrad to points. Posteroventral margins of epandrium each with row of ca. 8 setae. Aedeagus sclerotized, smooth; tubular, except for subapical hole and apex; apex slightly curved, pointed, cleft. Aedeagal apodeme with anterodorsal portion as a broad, fanlike sclerite with irregular anterior margin. Surstyli with broad apex, slightly concave; apical surface with ca. 35 fine, stiff setulae. Hypandrium and gonopods lightly sclerotized. Hypandrium with finely irregular anterior margin and shallow keel on ventral surface. Gonopods deep, laterally flattened, articulated with bases of surstyli. Apical sternites not examined.

TYPES: Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi. Genitalia dissected (no. 124) (in the AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: Named to honor Phil DeVries, close friend and colleague, who was of great help during fieldwork in Costa Rica. He also established the field station at Las Alturas, where 14 new species of *Cladochaeta* were discovered.

*Cladochaeta diminuta*, new species

Figures 94–96, 100

DIAGNOSIS: The smallest species in the genus (ThL = 0.41–0.52 mm). Notum yellow, pleura with diffuse brown and light yellow areas; male genitalia with short, lightly sclerotized, scoopshaped aedeagus.

DESCRIPTION: HEAD: Moderate length (HL/HD = 0.73). Eyes with dense, short, fine pile; lower hind margin with slight indentation seen in lateral view. Antenna with ped-

icel ochre and flagellomere I light brown; arista with 1 ventral and 3 dorsal branches (ventral branch between d-3 and apical fork), apical fork very small. Frons mostly yellowish, with frontal vittae shiny, golden; slight blue-green pruinescence on posterior half of frontal-orbital plates. Frontal-orbital setae: Proclinate orbitals ca. 0.9× length of posterior reclinate; anterior reclinate orbitals minute, ca. 0.2× size of proclinate (barely distinguishable from orbital setulae), immediately lateral to proclinate; post. reclinate closer to ipsilateral proclinate than to inner vertical. Face light brown and fairly wide (FW/HW = 0.34 [N = 16]), with very slight carina. Cheeks yellow and fairly deep (CD/ED = 0.14). Proboscis and palp yellowish.

THORAX: Notum ochre; scutellum and postnotum light brown; pleura mostly brown, with katepisternum light and with light area at base of wing. Anterior dorsocentrals ca. 0.9× length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 uneven rows. Anterior scutellars parallel; posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta; ventral seta much smaller. All legs light yellow; forefemur with 2 larger ventrolateral setae and 1 larger dorsolateral seta. Wing hyaline, without any clouds of diffuse infuscation. Vein  $R_{2+3}$  virtually straight; apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly curved. Wing tip rounded. Halter yellowish to tan.

ABDOMEN: All tergites dark brown. Female terminalia with moderate sclerotization; simple. Apical tergite an inverted U-shaped sclerite, with bridge beneath epi-/hypoproct; epi-/hypoprocts broad. Apical sternite U-shaped, narrowed apically, with ca. 15 fine setulae on lateral lobes; not connected to tergite. Male genitalia: Cercus without ventral lobe; ventral margin distinctly flattened. Epandrium height slightly greater than width. Ventrolateral halves of epandrium tapered ventrad to points. Posteroventral margins of epandrium each with row of 4–5 fine, long setae. Aedeagus sclerotized (especially at tip), short; open and flared at base, abruptly tapered at apex; scoop-shaped. Aedeagal apodeme tall, dorsally scoop-shaped. Gono-

pods long and thin, connected to bases of surstyli. Surstyli clavate, with broad apical surface bearing ca. 40 microtrichiae and ca. 10 setulae ventrally. Hypandrium short, without ventral keel. Apical sternites not examined.

TYPES: Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi. Paratypes: 15 (♂ + ♀), same label data as holotype. Genitalia dissected (nos. 120, 121) (in the AMNH, some paratypes in INBio).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Latin *minutus* (tiny), in reference to the small body size.

*Cladochaeta dolichofrons*, new species

Figures 94, 101

DIAGNOSIS: Externally distinctive for the relatively long head, flat frons, and deep cheek. Arista with only 2 dorsal branches at base and small terminal fork; postocellar setae minute. Male genitalia with aedeagus sclerotized, tubular, and curved; surstylus with distal (medial) surface broad and flat, bearing group of ca. 40 setae, some of which have trifurcate apices.

DESCRIPTION: HEAD: Very long (HL/HD = 1.02 [HT]). Eyes completely bare; lower hind margin without slight indentation. Antenna with pedicel yellow and flagellomere I light brown; arista with only 2 relatively short dorsal branches at base and small apical fork. Head nearly triangular in dorsal view; posterior end widest. Frons light brown but gradually lightened toward ptillinal suture; ocellar triangle with slight blue-green pruinescence, best seen in anterior view. Frontal-orbital setae: Proclinate orbitals nearly equal in length to posterior reclinate; anterior reclinate orbitals minute, ca. 0.2× size of proclinate, very fine (barely distinguishable from orbital setulae), immediately lateral to proclinate; post. reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae minute. Face light yellow, even whitish; flat; quite narrow for group (FW/HW = 0.30). Cheeks whitish, with silvery pruinescence, especially when viewed anteriorly; very deep (CD/ED = 0.23). Subvibrissal setae quite long, ca. 0.8× length of vi-



brissa, but thinner. Proboscis and palp very light yellowish.

THORAX: Notum, scutellum, postnotum, and pleura brown; katapisternum yellowish. Anterior dorsocentrals ca.  $0.9\times$  length of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars parallel; posterior scutellars cruciate for  $0.3\times$  their length. Postpronotal lobe with 1 large seta; ventral seta much smaller. All legs light yellow; forefemur with 2 larger ventrolateral setae; row of 3 larger dorsolateral setae. Wing completely hyaline, with no infuscation. Vein  $R_{2+3}$  virtually straight, even at apex. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter yellowish.

ABDOMEN: All tergites dark brown. Female terminalia unknown. Male genitalia: Cercus barely with lobe on anteroventral margin. Epandrium height ca.  $1.5\times$  width. Ventrolateral halves of epandrium tapered ventrad. Posteroventral margins of epandrium each with row of 6–7 setae. Aedeagus lightly sclerotized, tubular, smooth, with pointed apex; curved inward and then outward; no apparent cleft. Aedeagal apodeme with concave anterodorsal portion; longer, thin portion connecting base of aedeagus to gonopods. Surstyli flared apicad, with broad, almost flat apical surface having group of ca. 40 fine setulae, some of which have trifurcate tips. Gonopods short, broad, laterally flattened. Hypandrium short, broad, without ventral keel. Apical sternite not examined.

TYPES: Holotype, Male: TRINIDAD: *Arima*: Blanchisseuse Rd., 2000 ft, 3–9/1/82, Morton S. Adams. Genitalia dissected (no. 75) (AMNH).

OTHER MATERIAL EXAMINED: Known only from the type specimen.

ETYMOLOGY: From Latin *dolicho* (long) and *frons* (front), in reference to the long, sloping front of the head.

*Cladochaeta fasciata*, new species

Figures 94–96, 100

DIAGNOSIS: Easily recognized externally based on velvety black frons with thin, silvery stripe across anterior edge of frons (possibly only in males); face and parafacial plates dark brown, oral margin white; body

otherwise entirely dark brown, halter light yellow. Male genitalia with aedeagus heavily sclerotized, tubular, apex slightly flattened and twisted; aedeagal apodeme with ventral sclerite bearing narrow lateral flanges.

DESCRIPTION: HEAD: Moderate length (HL/HD = 0.75). Eyes with dense, short, fine setulae; lower hind margin without slight indentation. Antenna with pedicel and flagellomere I dark brown; arista with 1 ventral branch, 3 dorsal branches, and large apical fork; ventral branch between d-3 and apical fork. Frons velvety black, with thin silvery stripe across frons just posterior to margin of ptilinal suture; frontal orbital plates slightly shiny. Frontal-orbital setae: Procline orbitals nearly equal in length to posterior reclines; anterior reclinate orbitals minute, ca.  $0.2\times$  size of proclines, very fine (barely distinguishable from orbital setulae), immediately lateral to proclines; post. reclinate much closer to ipsilateral procline than to inner vertical. Dorsal two-thirds of face dark brown, oral margin white; face flat and quite wide (FW/HW = 0.35 [N = 6]). Cheeks yellowish in lateral view, with silvery pruinescence under eye when viewed anteriorly; cheeks deep (CD/ED = 0.19). Gena dark brown; proboscis and palp dark brown.

THORAX: Notum, scutellum, postnotum, and pleura dark brown, even katapisternum. Anterior dorsocentrals ca.  $0.6\times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 even rows. Anterior scutellars slightly convergent; posterior scutellars cruciate for  $0.3\times$  their length. Postpronotal lobe with 1 large seta; ventral seta much smaller. All legs brown; forefemur with row of 3 larger ventrolateral setae and 1 larger dorsolateral seta. Wing mostly lightly infuscate, with diffuse hyaline areas surrounding basal segments of veins  $R_{4+5}$ , M, and  $CuA_1$ . Vein  $R_{2+3}$  very slightly curved, almost straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M very slightly divergent. Crossvein dm-cu slightly curved. Wing tip slightly pointed, not rounded. Halter light yellow.

ABDOMEN: All tergites dark brown. Female terminalia heavily sclerotized. Penultimate tergite broad, with narrow dorsal notch. Api-

cal tergite without setae; without bridge beneath epi-/hypoproct; lateral lobes slightly bent. Apical sternite roughly triangular, bilobed, separated except for narrow anterior bridge. Apices of lateral lobes of sternite with setulae. Small, lightly sclerotized, roughly triangular sclerite lies between kinked parts of apical tergite. Male genitalia: Cercus with very slight lobe on anteroventral margin; ventral surface slightly arched (not flat). Epandrium height about twice the width. Ventrolateral halves of epandrium abruptly tapered ventrad to points. Posteroventral margins of epandrium each with row of 5 setae. Aedeagus strongly sclerotized, tubular, with asymmetric lobes at base; apex flattened, irregular, and slightly twisted. Aedeagal apodeme with ventral sclerite bearing narrow lateral flanges. Surstyli small, simple, with ca. 30 fine, stiff setulae on apical surface. Hypandrium rounded, without ventral keel; gonopods deep. Apical sternites not observed.

TYPES: Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi. Paratypes: 6♂ + ♀, same label data as holotype. Genitalia dissected (no. 125A) (in the AMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Latin for banded or striped, in reference to the coloration of the face.

*Cladochaeta pequenita*, new species

Figures 94, 96, 102

DIAGNOSIS: Recognized partly by its diminutive size (ThL = 0.45 mm); wings hyaline, body light brown; arista with 1 ventral and 3 dorsal branches. Epandrium (male) very broad, with heavily sclerotized aedeagus having 3 lobes; surstyli irregular in shape; female terminalia as described below.

DESCRIPTION: HEAD: Moderate depth and width in lateral view. Eyes completely bare; lower hind margin with slight indentation. Antenna with pedicel and flagellomere I light brown; arista with 1 ventral branch, 3 dorsal branches, and small apical fork; ventral branch between d-3 and apical fork. Frons light brown to bronze colored. Frontal-orbital setae: Procline orbitals equal in size to pos-

terior reclines; anterior reclinate orbitals minute, barely distinguishable from frontal-orbital setulae, immediately lateral to proclines; post. reclinate closer to ipsilateral procline than to inner vertical. Postocellar setae minute, no more than  $0.3\times$  size of ocellars; ocellar seta equal in size to frontal-orbital setae. Face rather high, wide (FW/HW = 0.34 [N = 3]), light brown, slightly receding. Cheeks of moderate depth (CD/ED = 0.12). Proboscis and palp light yellow.

THORAX: Entire thorax light brown; dorsal half of pleura slightly darker brown (katapisternum tan). Anterior dorsocentrals small, about one-half the length of posterior dorsocentrals but only slightly thinner; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 4 even rows. Anterior scutellar setae slightly convergent; posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta; ventral seta not present. All legs light yellow; forefemur with 2 larger ventrolateral setae and 1 larger dorsolateral seta. Wing completely hyaline, without clouds even on x-veins. Vein  $R_{2+3}$  virtually straight; apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M very slightly divergent. Crossvein dm-cu straight. Wing tip rounded. Halter tan.

ABDOMEN: Tergites dark brown. Female terminalia similar to *arthrostyla*, except that *pequenita* has terminal tergite broader, with dorsal portion heavily sclerotized; broader epi-/hypoproct; obvious absence of thin, intercalary sclerite (complete division of apical sternite and shape of the 2 lobes is very similar between the 2 species). Male genitalia: Cercus without ventral lobe; ventral margin flat. Epandrium broad, with ventrolateral halves thick and apex tapered to point; each half with row of ca. 6 setae. Aedeagus heavily sclerotized, with 3 lobes: short posterior lobe with an apical hole; slightly longer, flat median lobe pointed downward; and inner (anterior) lobe pointed and hooked upward at apex. Lobes connected to broad, funnel-like base; funnel opening directly beneath cerci. Aedeagal apodeme lightly sclerotized, with broad, flat, lateral "wings" and dorsomedial keel. Surstyli very irregular in shape, with broad base and some twisted flat lobes; setae present only on medial surface of medial lobe.



Hypandrium short, with anterior margin quadrate; gonopods very broad and stout. Apical sternites not examined.

**TYPES:** Holotype, Male: COSTA RICA: *Heredia*: Estacion Biologica Finca La Selva, 150 m, X/92, P. Hanson, Malaise trap (dissected, no. 303). Paratypes: 2♀, same data as holotype (1 dissected, DAG no. 306). All in the AMNH.

**OTHER MATERIAL EXAMINED:** Known only from the 3 type specimens.

**ETYMOLOGY:** Taken directly from the Spanish feminine adjective for tiny.

*Cladochaeta verdifrons*, new species

Figures 94, 95, 103

**DIAGNOSIS:** Frons and face light brown with bluish-green pruinescence; face with shallow carina; body mostly light brown. Male genitalia very distinctive: aedeagus a heavily sclerotized, irregular tube with broad lobe on posterior surface of base; anterodorsal sclerite of aedeagal apodeme large, hoodlike; surstylus with irregular apex and 2 short spines at apex of a thin, medial lobe.

**DESCRIPTION:** **HEAD:** Relatively long (HL/HD = 0.83). Eyes completely bare; lower hind margin with slight indentation. Antenna with pedicel ochre and flagellomere I light brown; arista with 1 ventral branch, 3 dorsal branches, and small apical fork; ventral branch nearly opposite branch d-3. Frons light brown in dorsal view, with blue-green pruinescence when viewed from front. Frontal-orbital setae: Proclinate orbitals equal in size to posterior reclinate; anterior reclinate orbitals small, ca. 0.3× size of proclinate and finer, immediately lateral to proclinate; post. reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae small but not minute. Face light brown with bluish pruinescence; slight carina; rather high and narrow for group (FW/HW = 0.30 [N = 2]). Cheeks slightly deep (CD/ED = 0.15). Proboscis and palp light yellow.

**THORAX:** Entire thorax light brown, including pleura; anterior part of pleura with bluish-green pruinescence. Anterior dorsocentrals ca. 0.6× length of posterior dorsocentrals and thinner; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 even rows. Anterior scutellar setae parallel; posterior scutellars slightly cruciate.

Postpronotal lobe with 1 large seta; ventral seta shorter and thinner. All legs ochre; forefemur with 2 larger ventrolateral setae and 2 larger dorsolateral setae. Wing very lightly infuscate, but without clouds of darker, diffuse infuscation. Vein  $R_{2+3}$  virtually straight; apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M very slightly divergent. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light yellow.

**ABDOMEN:** Tergites dark brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe; ventral margin flat. Epandrium slightly higher than wide; anterolateral margins slightly and finely scalloped. Ventrolateral halves of epandrium broad, with small apically tapered lobe. Posteroventral margins of epandrium each with row of ca. 10 setae. Aedeagus heavily sclerotized, tubular, but with broad lobe on posterior surface at base; apex with subapical hole and short, bifurcate, tapered tip; anterior surface with heavily sclerotized keel on basal half. Aedeagal apodeme with anterodorsal sclerite very large, hoodlike, sclerotized. Surstyli with irregularly shaped apical lobes, consisting of dorsal lobe with group of ca. 15 minute papillae; small lateral lobe with ca. 8 small setulae; thin, long medial lobe with 2 short spines at apex and 4 setae at base; small basal-medial lobe with ca. 4 minute papillae; 2 larger setae on lateral surface of surstylus. Hypandrium ovoid, with slight ventral keel; gonopods lightly sclerotized, deep, and laterally flattened. Apical sternites not examined.

**TYPES:** Holotype, Male: TRINIDAD: *Arima*: Blanchisseuse Rd., 2000 ft, 3-9/1/82, Morton S. Adams. Genitalia not dissected. Paratype: 1♂ (dissected, no. 77), with same label data as holotype (both specimens in the AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the 2 type specimens.

**ETYMOLOGY:** From Latin *viridis* (green) and *frons* (front), in reference to the greenish reflective microtomentum on the face and front.

**DISCUSSION:** Three species appear closely related: *fasciata*, *dolichofrons*, and *verdifrons*. The relationship is based on body coloration (mostly brown, including the scutum and pleura [*devriesi* is also similar]), cheeks very deep, and completely bare eyes. In addition, *verdifrons* and *fasciata* each have acrostichal setulae in 4 rows (as does *diminuta*).

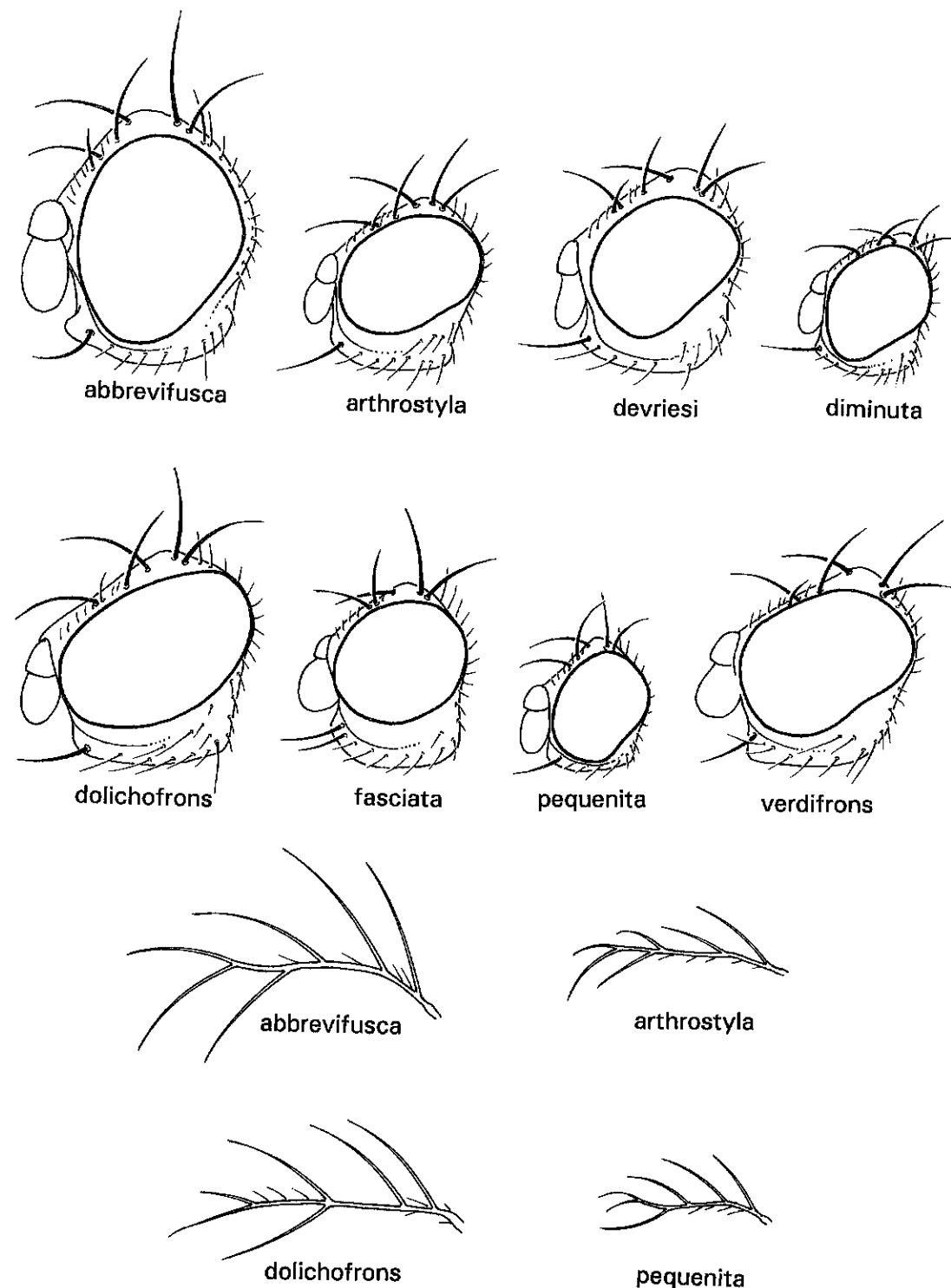
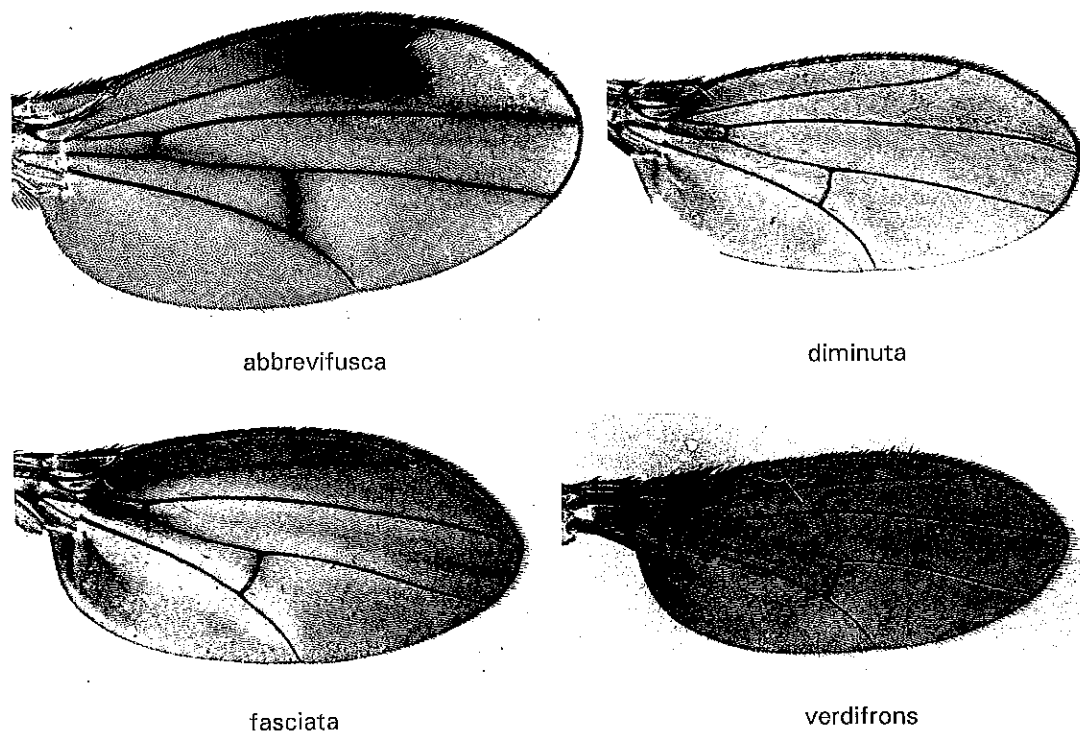
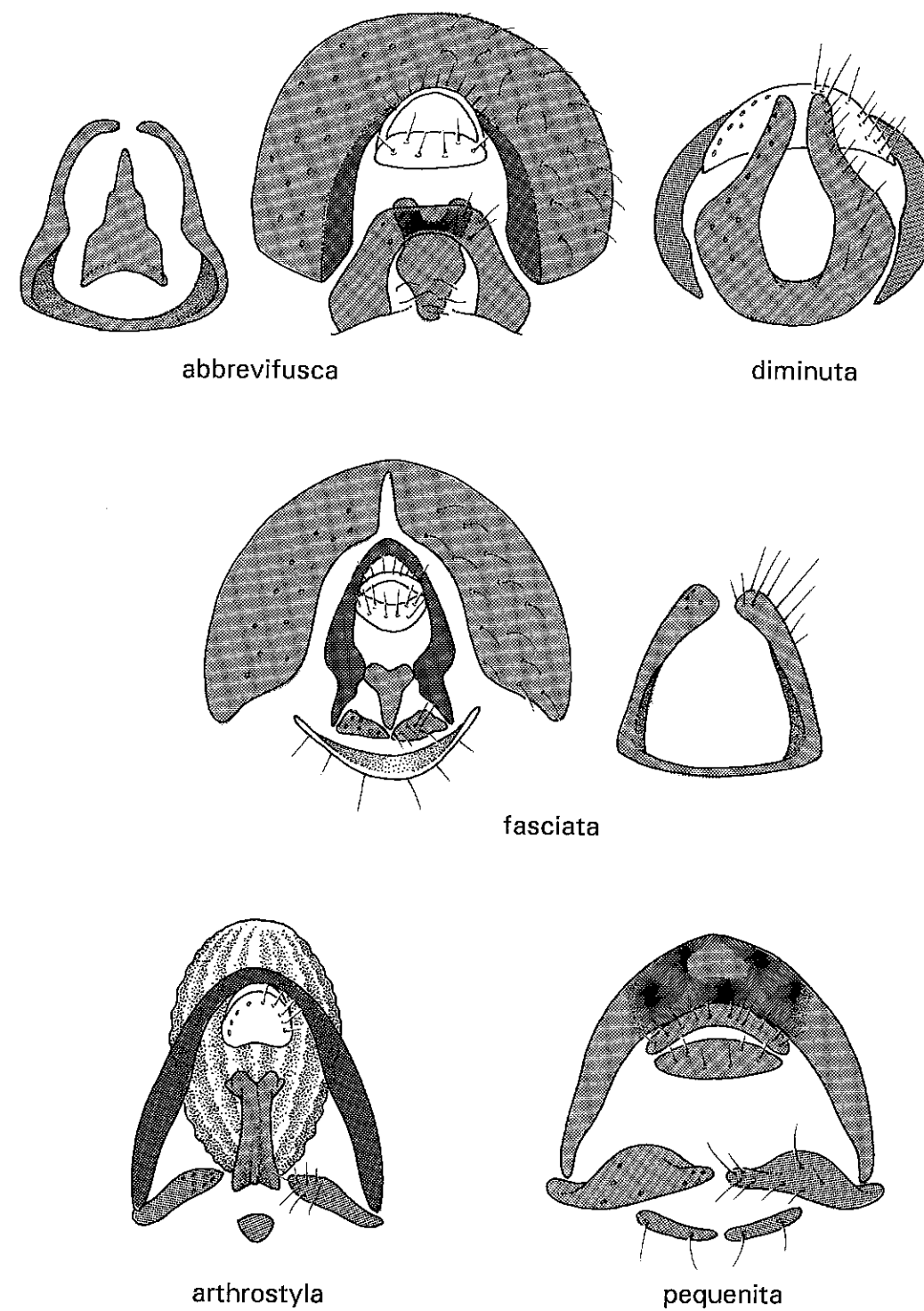


Fig. 94. Heads and arista of *diminuta* group species.

Fig. 95. Wings of *diminuta* group species.Fig. 96. Female terminalia of *diminuta* group species (most are posterior views, some ventral).

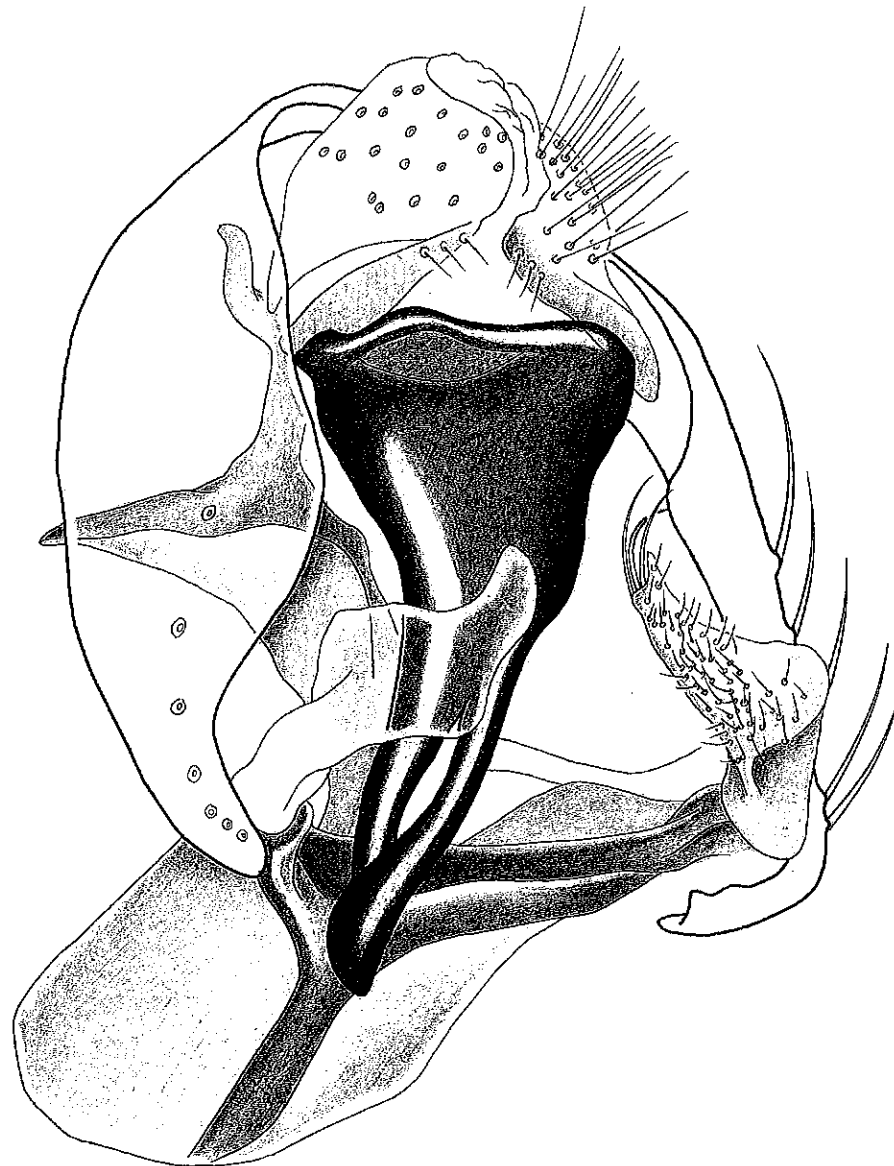


Fig. 97. Male terminalia of *C. abbrevifusca*.

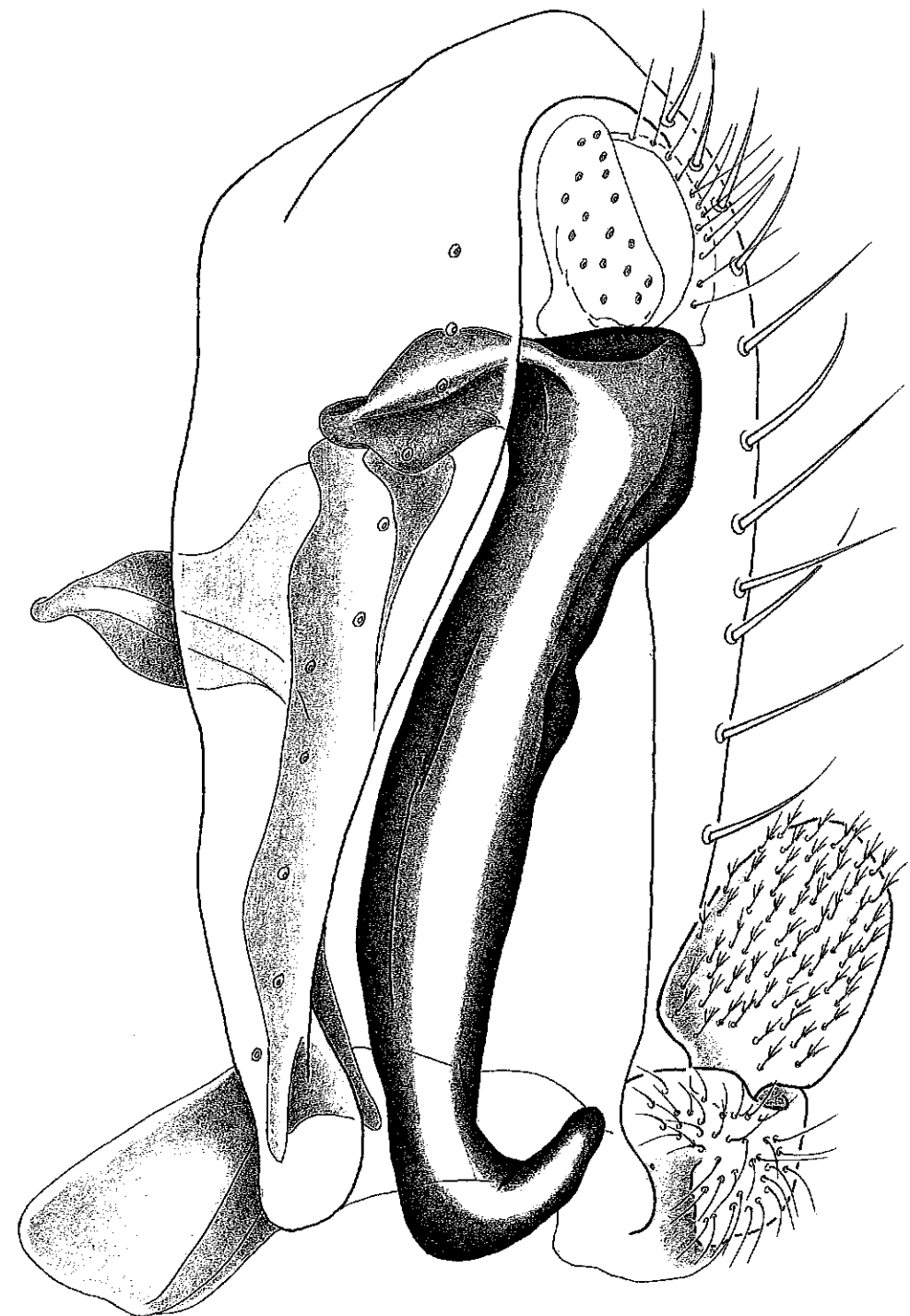


Fig. 98. Male terminalia of *C. arthrostyla*.

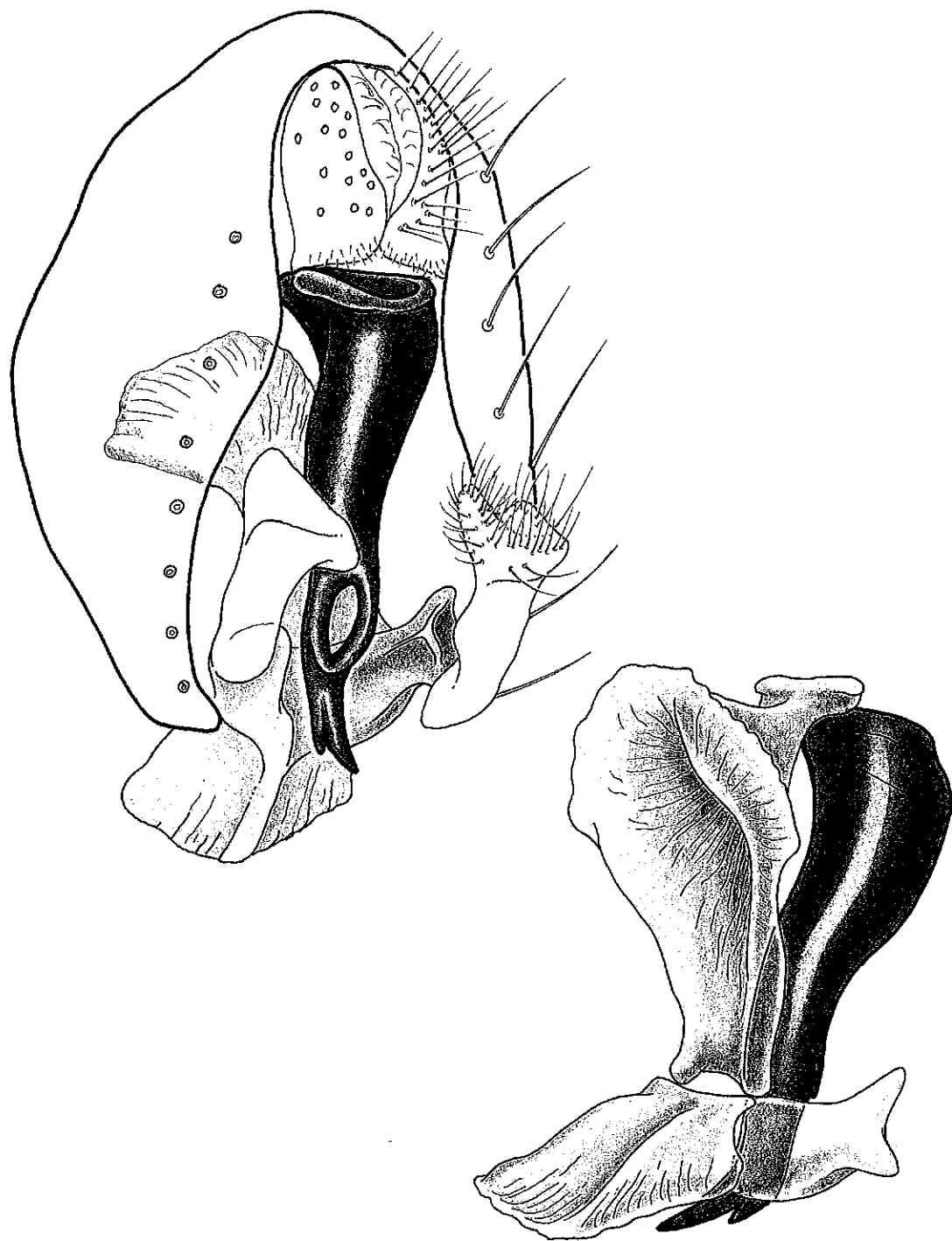


Fig. 99. Male terminalia of *C. devriesi*.

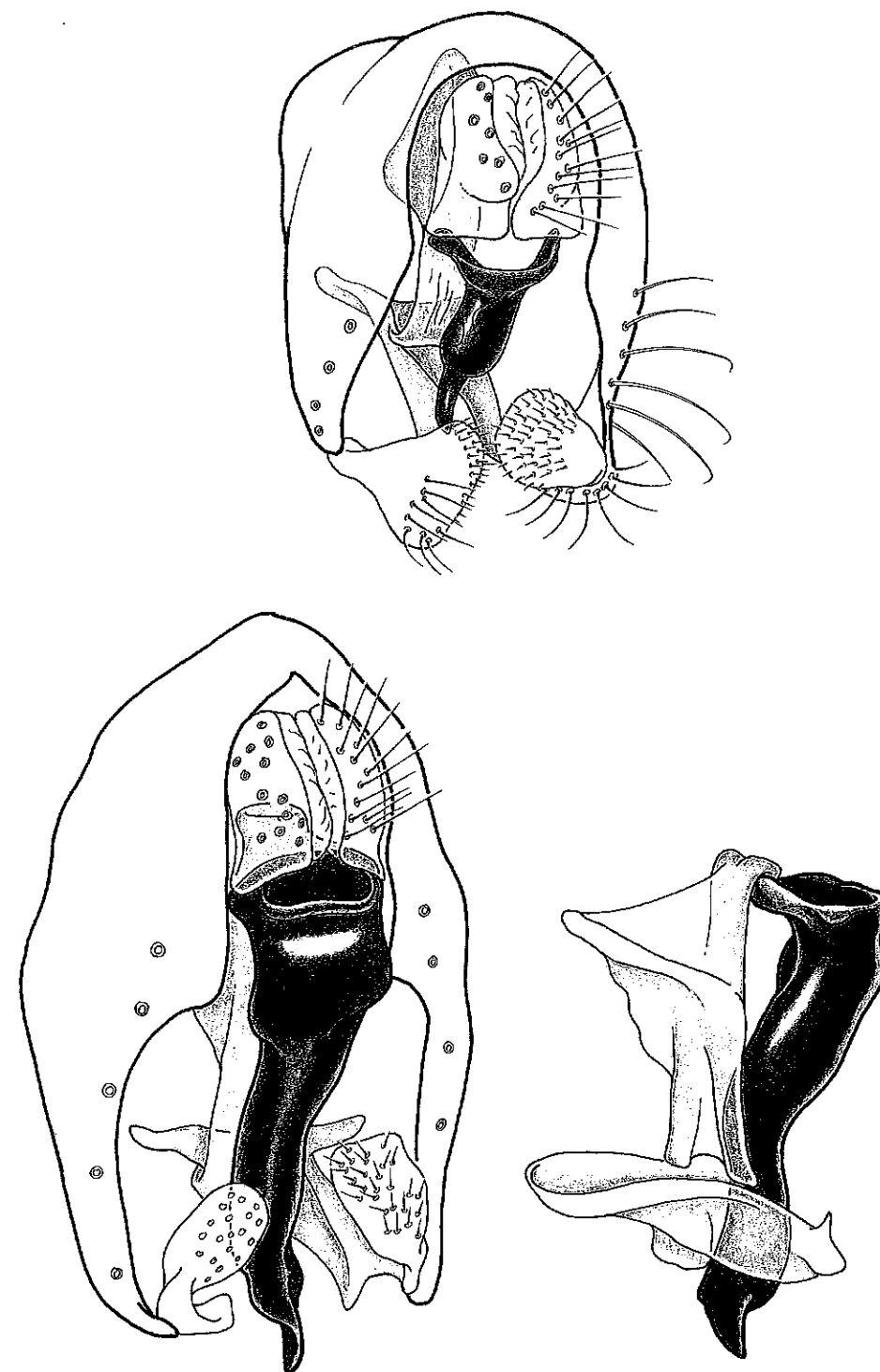


Fig. 100. Male terminalia of *C. diminuta* (above) and *C. fasciata* (below).

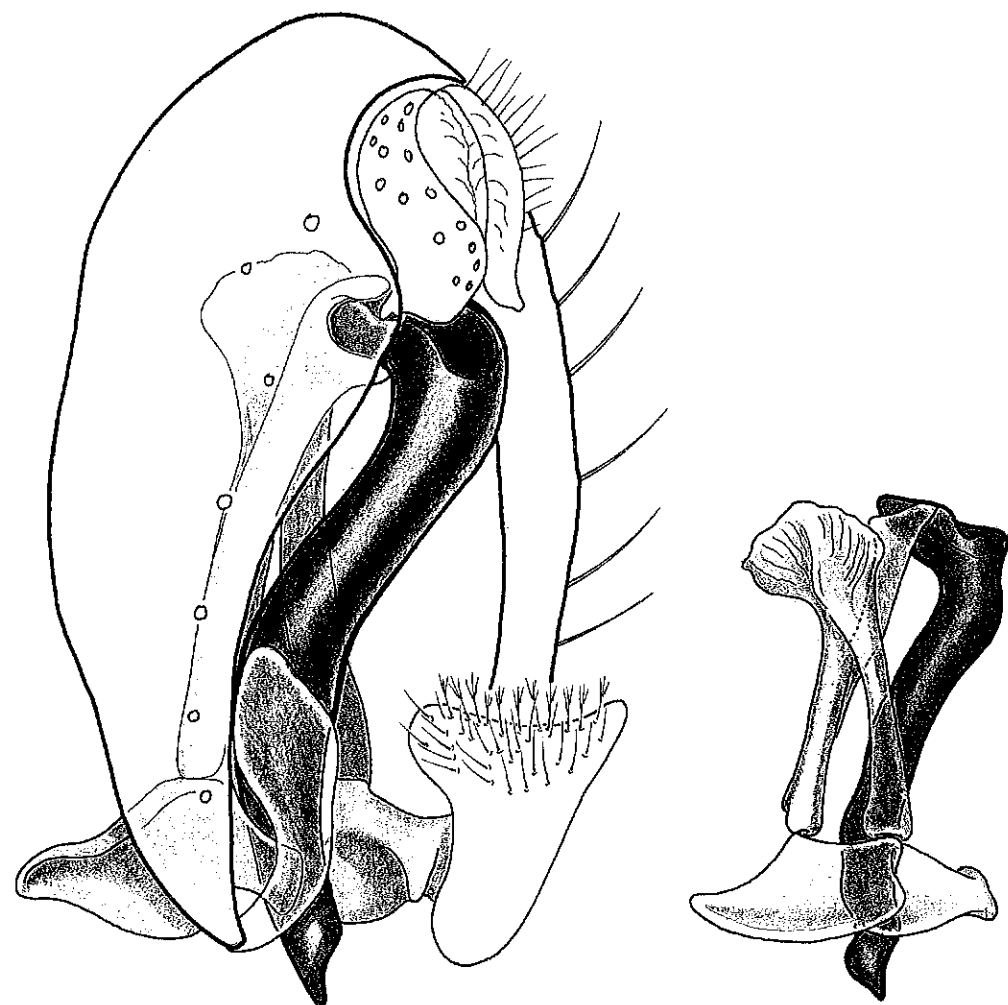


Fig. 101. Male terminalia of *C. dolichofrons*.

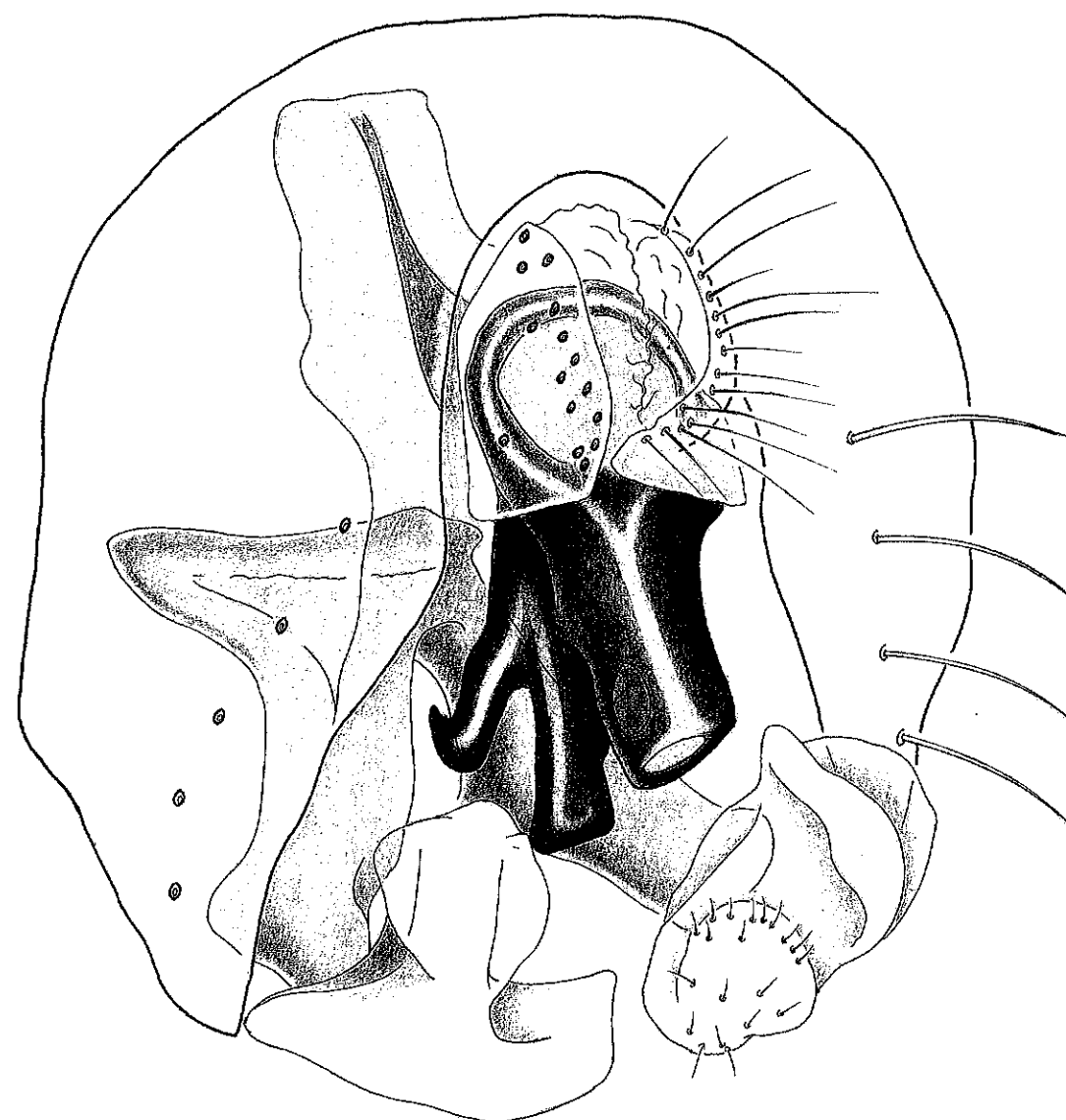
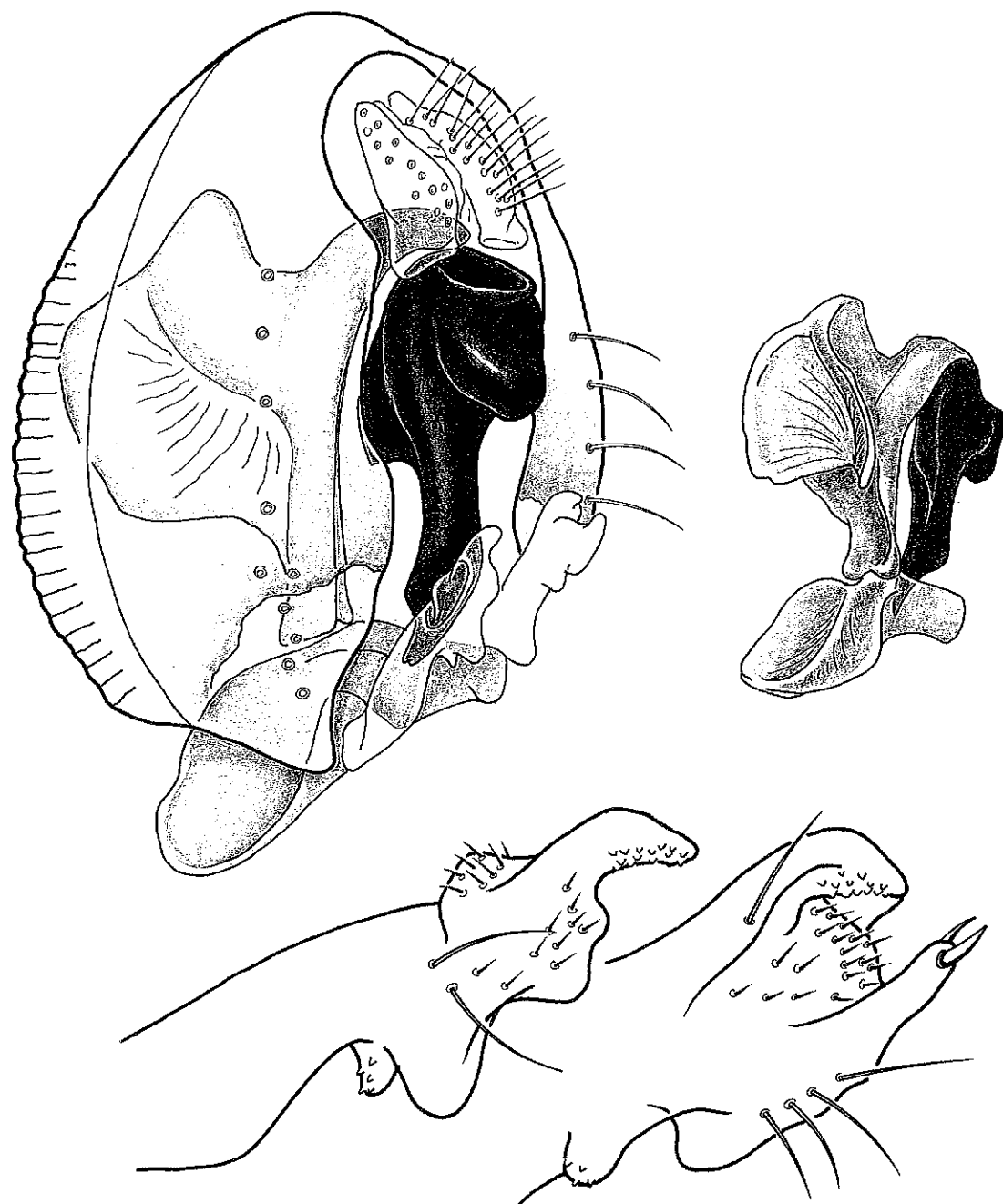


Fig. 102. Male terminalia of *C. pequenita*.

Fig. 103. Male terminalia of *C. verdifrons*.

## Diminuta Group

Fig. 104. Distribution of *diminuta* group species.



## UNCA SPECIES GROUP

DIAGNOSIS: A monophyletic group defined by the large, sclerotized median structure that is usually hooked. It is either the aedeagus with a bifurcate apex or the paraphyses fused at the base. If the former, the group is probably closely related to the *diminuta* group in sharing the loss of paraphyses. Except for *pseudunca*, the aedeagal apodeme is not nearly so large and sclerotized as in the *diminuta* group.

*Cladochaeta fuscora*, new species

Figures 105, 108

DIAGNOSIS: Externally distinctive for the light frontal vittae, bordered by dark brown frontal orbital plates, ocellar triangle, and face; notum deep yellow, with dark brown pleura; forefemur and tibia dark brown; other femora and tibiae light brown. Male genitalia most similar to *C. tubula* and best distinguished on the following bases: aedeagus in *fuscora* stouter, shorter, and slightly wrinkled; cercus with small lobe in anteroventral corner; aedeagal apodeme without distinctive pedestal-like sclerite connected to dorsal part of aedeagus.

DESCRIPTION: HEAD: Relatively high, HL/HD = 0.67 [HT]. Eyes virtually bare of fine pile, with slight indentation on lower hind margin. Antenna with pedicel ochre and flagellomere I light brown. Arista with 3 long (basally) and 1 shorter dorsal branch; 1 ventral branch between d-3 and d-4. Frontal vittae velvety bronze; frontal orbital plates and ocellar triangle black brown, with a light blue-green pruinescence. Frontal-orbital setae: proclinate ca. 0.7× size of posterior reclinate; anterior reclinate tiny, ca. 0.3× length and thickness of proclinate, very close and posterolateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae fine, slightly convergent. Face flat, relatively high and broad (FW/HW = 0.42); dark brown, with light blue-green pruinescence. Cheeks tan to light yellow; contrasting with dark brown area ventral to parafacial suture; cheeks relatively deep (CD/ED = 0.23). Proboscis yellow, palp light brown.

THORAX: Notum mostly deep yellow; scutellum with some yellow but mostly light

brown. Pleura and forecoxa dark brown, with diffuse blue-green pruinescence (most obvious when viewed anteriorly). Anterior dorsocentrals lost on the only 2 specimens; posterior dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Most scutellar setae lost on both specimens. Postpronotal lobe with 2 large setae. Legs: Forefemur and tibia dark brown (tip of femur and base of tibia light); middle and hind femur light brown; all tarsi light yellow. Ventrolateral surface of forefemur with 2 larger setae preapically and 1 seta dorsolaterally. Wing lightly and evenly fuscous, but without clouds of darker diffuse infuscation even over crossveins. Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed, not rounded. Halter light yellow.

ABDOMEN: Tergites evenly dark brown. Female terminalia unknown. Male genitalia: Cercus with small lobe on anteroventral margin. Epandrium height about twice the width; width approximately equal throughout. Posteroventral margins of epandrium each with row of 10–13 setae. Aedeagus not heavily sclerotized, mostly just where margins of infolded posterior halves touch; slightly wrinkled; posterior surface cleft for entire length, with V-shaped opening on proximal (dorsal) end. Flat U-shaped sclerite connected from base of aedeagus to aedeagal apodeme. Aedeagal apodeme with spatulate anterior arm; posteroventral arm trough-shaped; connected to bases of gonopods. Gonopods broad, laterally flattened. Surstyli relatively simple; without separate lobes, but apical surface narrower than in *tubula*; ca. 30 setulae on apical and adaxial surfaces. Hypandrium small, simple. Apical sternite divided into 2 small remnants, 1 each beneath surstyli, with 10–12 setulae each.

TYPES: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi (genitalia not dissected). Paratype: 1♂ with same label data as holotype (genitalia dissected, no. 128) (both specimens in the AMNH).

OTHER MATERIAL EXAMINED: Known only from 2 type specimens.

ETYMOLOGY: From Latin *fuscus* (dark) and

*ora* (mouth), in reference to the color of the oral margin.

*Cladochaeta hadrunca*, new species

Figures 105, 109

DIAGNOSIS: Entire body brown, including legs (pleura very dark brown); arista with 1 ventral and 4 dorsal branches; wing slightly infuscate; paraphyses (male) heavily sclerotized, mostly fused (except apical third); gonopods with pair of triangular sclerites on dorsal edge; surstyli roughly triangular, with small apical tooth.

DESCRIPTION: HEAD: Relatively high in lateral view, frons of moderate length. Eyes with fine, short, dense pile; slight indentation on lower hind margin. Antenna with pedicel brown, and flagellomere I darker. Arista with 4 large dorsal branches; 1 ventral branch slightly closer to d-4 than to terminal fork. Frontal vittae light brown, without pruinescence; ocellar triangle black brown; frontal orbital plates same color as frontal vittae. Interfrontal setulae short, stout, with 6 present. Frontal-orbital setae stout, black: proclinate ca. 0.8× size of posterior reclinate; anterior reclinate small, 0.4× size of proclinate, ca. 2× size of frontal-orbital setulae, immediately lateral to proclinate. Posterior reclinate midway between ipsilateral proclinate and inner vertical. Postocellar setae 0.4× size of ocellar setae. Face flat, dark brown, and of moderate width (FW/HW = 0.32 [N = 2]). Cheeks ochre and shallow (CD/ED = 0.08). Labium and palps brown.

THORAX: Entire thorax, including legs and coxae, brown (tarsi lighter in male, female with entire legs lighter); pleura and postnotum darker brown. Anterior dorsocentrals ca. 0.7× size of post. dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 uneven rows; acrostichal immediately anterior to ant. dorsocentral enlarged, about twice the size of other acrostichals. Anterior scutellar setae parallel; post. scutellars convergent. Postpronotal lobe with 1 large dorsal seta and smaller ventral one. Fore femur with 1 larger dorsomedial seta and 2 larger ventrolateral setae; hind femora apparently without distinctly larger setae on apical half. Wing very lightly dusky, slightly darker on costal edge.

Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, hardly turned costad. Veins  $R_{4+5}$  and M parallel, but both slightly curved. Crossvein dm-cu straight. Wing tip slightly pointed. Halter white, contrasting with brown body.

ABDOMEN: Tergites dark, black brown. Female terminalia unknown. Male genitalia: Cercus with flat ventral margin; ventral lobe not present. Epandrium with very narrow lobes; height of epandrium ca. 1.5× width; thickness of epandrial lobes approximately equal throughout. Each epandrial lobe with row of 8 fine setae. Paraphyses heavily sclerotized, mostly fused, strongly hooked down and then inward, with apical third unfused and slightly asymmetrical; dorsal surface of paraphyses funnel-shaped. Aedeagus membranous, protrudes slightly from between unfused portion of paraphyses. Aedeagal apodeme lightly sclerotized, narrow; tall and upright. Hypandrium rounded, gonopods stout. Pair of roughly triangular sclerites on dorsal edge of gonopods, slightly more sclerotized than aedeagal apodeme and hypandrium. Surstyli broad, with apical "tooth," lightly sclerotized; 3–4 long, stiff setae on mesal surface and numerous microtrichia on apical half of lateral surface. Apical sternites not examined.

TYPES: Holotype, Male: COSTA RICA: San José, Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 286). Paratype: Female, same data as holotype (dissected, no. 287) (both specimens in AMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: Another combination of words derived from the *unca* suffix, which pertains to the species group.

*Cladochaeta obunca*, new species

Figures 105, 107, 110

DIAGNOSIS: Thorax and head almost entirely yellow, pleura sometimes with very faint brown, diffuse vitta; postocellar setae relatively long and fine; inner surface of pedicel with 2 long, fine setae; male genitalia with aedeagus heavily sclerotized, developed into a hook pointed inward; surstylus clavate, with many fine, short setulae.

**DESCRIPTION: HEAD:** Moderate depth and width (HL/HD = 0.84 [HT]). Eyes with very fine, sparse pile; no slight indentation on lower hind margin. Antenna with pedicel ochre, having 2 long, fine setae on medial surface; flagellomere I light brown. Arista with 3–4 dorsal branches of moderate length; 1 ventral branch between d-3 and d-4, almost opposite d-3. Frontal vittae bronze, mildly reflective; frontal orbital plates and ocellar triangle dull yellowish. Frontal-orbital setae: Proclinate ca.  $0.8\times$  size of posterior reclinate; anterior reclinate small and fine, ca.  $0.3\times$  length and thickness of proclinate, immediately lateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae relatively long, fine, parallel. Face flat, relatively high, yellowish, and of moderate width (FW/HW = 0.31 [N = 9]). Cheeks yellow and of moderate depth (CD/ED = 0.11). Proboscis and palp yellow.

**THORAX:** Notum, scutellum, postnotum, and pleura mostly yellow, with very diffuse slightly darker areas, sometimes with faint brown vitta in middle of pleura. Anterior dorsocentrals ca.  $0.6\times$  size of post. dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellar setae parallel; post. scutellars cruciate for ca.  $0.2\times$  their length. Postpronotal lobe with 2 large setae. Legs entirely light yellow. Ventrolateral surface of forefemur with 2–3 long setae on distal half; 1 long preapical seta dorsolaterally. Hind femur with row of 4–5 setae on distal half of ventral surface; lengths about half the width of femur. Wing hyaline, not even lightly fuscous. Vein  $R_{2+3}$  slightly curved; apex of vein  $R_{2+3}$  gradually meeting costal vein. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter light yellow.

**ABDOMEN:** Tergites evenly light brown. Female terminalia mostly sclerotized, except for pair of small, lateral lobes on apical tergite. Apical tergite with small pair of medial lobes, but no bridge formed beneath epi-/hypoproct. Apical tergite without setae. Apical sternite bilobed but not separated medially, fused to tergite. Male genitalia: Cercus with small lobe on lateroventral margin. Epandrium height about twice the width; thick-

ness of epandrium similar throughout. Epandrial lobes each with row of 4 setae. Aedeagus heavily sclerotized, smooth, with lightly sclerotized basal ring and strongly hooked apical part (apex sharp and pointed anteriorly). Aedeagal apodeme barely sclerotized; with small dorsal hood connected to anteroventral corner of aedeagus; long, thin ventral portion connecting aedeagus to hypandrium and having ventral furrow. Gonopods long and thin. Surstyli simple and lobate; base with short, narrow arm, bulbous part with ca. 45 fine setulae scattered on mesal surface. Hypandrium with narrow median keel. Apical sternites not studied.

**TYPES:** Holotype, Male: EL SALVADOR: Volcan Santa Ana, 5670 ft, XI/53, W. B. Heed (not dissected). Paratypes: Same data (1♂, no. 254; 3♀) (all in AMNH).

**OTHER MATERIAL EXAMINED:** EL SALVADOR: San Salvador, X/53 (1♂, no. 256; 2♀). MEXICO: Vera Cruz, Fortin de las Flores, VI/64, light trap, F. S. Blanton (1♂, no. 173) (NMNH).

**ETYMOLOGY:** From Latin *obuncus* (bent in, hooked), in reference to the shape and position of the aedeagus.

#### *Cladochaeta pseudunca*, new species

Figures 105–107, 111

**DIAGNOSIS:** Externally very distinctive for the black, pollinose frontal orbital plates (rest of the head is much lighter); arista with just 1 large dorsal branch (at base) and small apical fork; cheeks very deep. Thorax entirely brown, legs yellow; wings hyaline. Male genitalia distinctive: paraphyses heavily sclerotized, hooked, but not symmetrical; surstylus large, with long dorsal and ventral lobes, concave; concave surface with numerous fine setulae; dorsolateral part with ca. 8–10 long, fine setae.

**DESCRIPTION: HEAD:** Relatively long (HL/HD = 0.84 [HT]), with long sloping frons. Eyes with very fine, sparse pile; without slight indentation on lower hind margin. Antenna with pedicel and flagellomere I light brown. Arista with 1 large dorsal branch at base, small terminal fork, no ventral branch. Frontal vittae black, with sparse bluish pruinescence, margin near ptilinal suture light yellowish; frontal orbital plates and ocellar

triangle shiny, brown. Frontal-orbital setae: Proclinate ca.  $0.8\times$  size of posterior reclinate; anterior reclinate minute, indistinguishable from frontal orbital setulae. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae fine, of moderate length, directed posteriorly, convergent. Face flat, relatively wide (FW/HW = 0.31 [N = 11]); oral margin light yellow, dorsal half light brown. Cheeks light yellow and very deep (CD/ED = 0.22). Proboscis yellow, palp light brown.

**THORAX:** Notum, scutellum, postnotum, and pleura brown. Anterior dorsocentrals ca.  $0.7\times$  size of post. dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows; acrostichal immediately anterior to ant. dorsocentral slightly enlarged. Anterior scutellar setae slightly convergent; post. scutellars cruciate for ca.  $0.3\times$  their length. Postpronotal lobe with 1 large dorsal seta and 1 smaller ventral one. Legs entirely yellow-ochre; forefemur with 2 long, fine setae on ventrolateral surface and 1 long seta on dorsolateral surface. Hind femur with row of 3 longer setae (lengths equal to width of femur), 1 shorter seta proximally. Wing completely hyaline, without any infuscation. Vein  $R_{2+3}$  virtually straight; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel until distal half of M, then slightly divergent. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter white.

**ABDOMEN:** Tergites dark black-brown. Female terminalia heavily sclerotized. Apical tergite surrounding epi-/hypoproct, with narrow dorsal bridge; deep ventral portion with ca. 20 fine setulae, pair of lateral depressions and slightly asymmetrical spur on ventral margin. Apical sternite unmodified, a simple sclerotized plate. Male genitalia: Cercus with very small lobe on ventral margin. Epandrium height ca.  $5\times$  width; thickness of epandrial lobes approximately equal throughout, with apex pointed and hooked posteriorly. Each epandrial lobe with row of 6 long, stiff setae. Aedeagus membranous, lying between and behind (anterior to) what are probably the paraphyses; apparently with membranous connection to base of paraphyses. Paraphyses(?) heavily sclerotized, slightly asymmet-

rical; left one strongly curved and hooked (almost curled  $270^\circ$ ), right one much less curved; deep dorsal part connecting the 2 halves. Aedeagal apodeme lightly sclerotized, large, and broad; upright, partly forming inner wall of epandrium. Surstyli large, crescentic, with long, thin ventral lobe (without setae/setulae); broad, concave median portion (with ca. 50 short, fine setulae); dorsal lobe with dense microtrichia on mesal surface and ca. 8 long, curved setae in row on lateral surface. Apical sternites not examined.

**TYPES:** Holotype, Male: PANAMA, *Chiriqui*: Guadalupe, Arriba, 1/VIII–4/IX/84, 2100 ft, H. Wolda (not dissected). Paratypes: Same data (4♂, no. 232; 6♀, no. 233) (AMNH).

**OTHER MATERIAL EXAMINED:** Known only from type series.

**ETYMOLOGY:** In reference to the relationships of the species in the *unca* species group.

#### *Cladochaeta tubula*, new species

Figures 105, 112

**DIAGNOSIS:** Externally distinctive for the white face and flagellomere I of the antenna, with rest of body mostly yellowish. Arista with 1 ventral and 4 dorsal branches. Aedeagus simple, straight, almost tubular, with cleft along apical half of posterior surface.

**DESCRIPTION: HEAD:** Moderate depth and length. Eyes virtually bare of fine pile, with slight indentation on lower hind margin. Antenna with pedicel light yellow; flagellomere I white, matching white color of face. Arista with 4 dorsal branches, 1 long ventral branch between d-3 and d-4; terminal fork with short dorsal branch. Entire front light yellowish; ocellar triangle shiny, light brown. Frontal-orbital setae: proclinate ca.  $0.8\times$  size of posterior reclinate; anterior reclinate small, ca.  $0.3\times$  size of proclinate. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, convergent. Face flat, relatively high, white, and fairly wide (FW/HW = 0.33). Cheeks light yellow to white and deep (CD/ED = 0.17). Proboscis yellow, palp white.

**THORAX:** Notum, scutellum, and postnotum yellow. Pleura very diffuse, light brown; an-

terior half of katepisternum with light blue-green pruinescence. Anterior dorsocentrals ca.  $0.6\times$  size of post. dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellar setae parallel; post. scutellars cruciate for ca.  $0.2\times$  their length. Postpronotal lobe with 1 large dorsal seta, with ventral one about half its size. Legs entirely light yellow; forefemur with 2 or 3 long, fine setae on ventrolateral surface; 1 long seta on dorsolateral surface. Hind femur without longer setae on ventral surface. Wing mostly hyaline, with very slight, diffuse infuscation over costal edge. Vein  $R_{2+3}$  slightly curved; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites light brown. Female terminalia unknown. Male genitalia: Cercus without ventral lobe. Epandrium height about twice the width. Thickness of dorsal and ventral portions of epandrium approximately equal. Posteroventral margins of epandrium each with row of 7 setae of equal lengths. Aedeagus simple, tubular; aligned dorsoventrally at rest; apex slightly curved anteriorly; with median cleft on apical half of posterior surface; most heavily sclerotized surrounding cleft. Simple U-shaped sclerite arched between proximal (dorsal) end of aedeagus and aedeagal apodeme. Aedeagal apodeme with pedestal articulated with U-shaped sclerite; slightly flanged anteriorly; end connected to gonopods flattened; lightly sclerotized. Surstyli simple without distinct lobes; 30–35 fine, short setulae on adaxial and apical surfaces. Hypandrium simple, barely sclerotized; relatively short, length about half that of aedeagus; without keel on ventral surface. Two small setose sclerites present, one beneath each surstylus (remnants of apical sternites). Preapical sternite with 16–18 setae per half.

TYPE: Holotype, Male: TRINIDAD: *Arima*: Blanchisseuse Rd., 2000 ft, 3–9/I/82, Morton S. Adams. Genitalia dissected (no. 85) (in the AMNH.)

OTHER MATERIAL EXAMINED: Known only from the type specimen.

ETYMOLOGY: In reference to the tubular shape of the aedeagus.

*Cladochaeta unca*, new species

Figures 105, 106, 113

DIAGNOSIS: Entire frons evenly tan; arista with 1 ventral and 4 dorsal branches; notum and scutellum yellow, pleura with light brown areas, foreleg with brown femur and tibia. Surstyli with hooked posterodorsal lobe bearing tuft of 5–6 setulae. Gonopods and aedeagal apodeme elongate and thin. Aedeagus extremely modified: very large, strongly hooked and heavily sclerotized, with apical half cleft along posterior surface. Known only from southwestern Costa Rica.

DESCRIPTION: HEAD: Relatively high (HL/HD = 0.62 [HT]). Eyes with dense, fine, short pile; slight indentation on lower hind margin. Antenna with pedicel ochre; flagellomere I with light yellow base, apical two-thirds light brown. Arista with 4 dorsal branches, 1 long ventral branch between d-3 and d-4 (sometimes almost opposite d-3); terminal fork with short dorsal branch. Entire front evenly tan, ocellar triangle slightly darker. Frontal-orbital setae: Proclinate ca.  $0.6\times$  size of posterior reclinate; anterior reclinate small, ca.  $0.3\times$  size of proclinate, directly lateral to proclinate and even slightly anterior. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae relatively large, slightly convergent. Face flat, relatively high, and of moderate width (FW/HW = 0.32); evenly tan. Cheeks light yellow and shallow (CD/ED = 0.08). Proboscis yellow, palp light brown.

THORAX: Notum, scutellum, and postnotum yellow. Pleura with very diffuse, light brown areas in middle and dorsal half of katepisternum. Anterior dorsocentrals ca.  $0.6\times$  size of post. dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 uneven rows; acrostichal seta immediately anterior to ant. dorsocentral slightly enlarged. Anterior scutellar setae parallel; post. scutellars slightly convergent. Postpronotal lobe with 1 large dorsal seta, ventral one ca.  $0.6\times$  its size. Forefemur and tibia brown, tarsi yellow; middle and hind femora and tibiae lighter brown, tarsi yellow. Forefemur with 2 long setae on ven-

trolateral surface and 1 long, fine seta on dorsolateral surface. Hind femur with 4 longer setae on ventral surface, lengths about half the width of femur. Wing very slightly infusate, but without clouds of diffuse, darker infuscation. Vein  $R_{2+3}$  very slightly curved; apex of  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly curved. Wing tip slightly pointed. Halter white.

ABDOMEN: Tergites light brown. Female terminalia unknown. Male genitalia: Cercus with small lobe on lateroventral margin. Epandrium height about twice the width; thickness of epandrium similar throughout. Posteroventral margins of epandrium each with row of 8–9 setae. Aedeagus strongly hooked; heavily sclerotized, particularly toward apex; smooth; apical half with cleft on posterior surface. Aedeagal apodeme barely sclerotized, with small dorsal flange connected to anteroventral corner of aedeagus; long, thin ventral portion connecting aedeagus to hypandrium and having ventral furrow. Gonopods articulated with posterior margin of hypandrium and surstyli; long and thin. Surstyli with elaborate shape: base with tooth-shaped lobe on dorsal surface; dorsoapical lobe present, hook-shaped, with tuft of 5–6 setulae; larger, posteromedian lobe with 13–15 fine, short setulae. Hypandrium slightly hourglass-shaped, with deep median keel and median lobe projected posteriorly. Apical sternites not studied.

TYPES: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi (genitalia dissected, DAG no. 132). Paratype: 1♂, with same label data as holotype (genitalia not dissected) (both specimens in the AMNH).

OTHER MATERIAL EXAMINED: Known only from the type specimens.

ETYMOLOGY: From Latin *uncus* (hook or barb), in reference to the hooked aedeagus.

DISCUSSION: *Cladochaeta unca* and *C. pseudunca* appear closely related based on the distiphallus (with cleft on posterior surface of apical half), color of the body (dark brown, especially pleura), and epandrium (lobes tall, narrow, and of uniform width from top to bottom).

OSTIA SPECIES GROUP

Monophyly defined on basis of arista with 2–3 short dorsal branches (no ventral branch); paraphyses flanking aedeagus, bases of paraphyses broad (with or without ostia); cerci broad, with numerous short setulae; epandrium glabrous and shiny. Only 2 species in the group, both from Central America.

*Cladochaeta glapica*, new species

Figures 106, 107, 114

DIAGNOSIS: Face with slight carina; arista with 3 short dorsal branches (including apical fork); male foretarsi with ca. 12 pairs setae, lengths ca.  $1.5\times$  width of tarsomeres; epandrium (male) black, glabrous (devoid of fine microtrichia), very shiny; aedeagus spade-shaped, closely flanked by heavily sclerotized paraphyses.

DESCRIPTION: HEAD: Rather deep (HL/HD = 0.71 [holotype]). Eyes with very sparse, short setulae; hind margin with slight indentation. Antenna with pedicel and flagellomere I light brown; arista with 3 dorsal branches (including large terminal fork). Frontal vittae shiny, golden; 6–7 interorbital setulae. Frontal-orbital setae: Proclinate and posterior reclinate orbitals approximately of equal lengths; anterior reclinate about one-fourth the size, immediately lateral to proclinate; posterior reclinate slightly closer to proclinate than to inner vertical. Face light brown (including oral margin), of moderate width (FW/HW = 0.31 [N = 6]), short, with slight carina. Cheeks of moderate depth (CD/ED = 0.12). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum ochre; notopleural area with small, diffuse areas of brown; ventral part of pleuron yellowish. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars slightly convergent; posterior scutellars cruciate for about one-fourth their length. Two large postpronotal lobe setae. Legs entirely yellow; forefemur with ventrolateral row of 4 long setae and 2 dorsolateral setae; foretarsi of male with ca. 12 pairs large setae, lengths ca.  $1.5\times$  width of tarsal segments. Wing entirely hyaline, except for very light, small clouds of infusca-

tion over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  turned slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M parallel, not even slightly divergent. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites I-V brown, tergite VI most yellow. Epandrium (tVIII, male) black, glabrous, very shiny. Female terminalia with moderate sclerotization, very reduced; apical tergite fused to apical sternite ventrally, forming an almost complete ring around epi-/hypoproct (with small ventral gap). Tergo-sternal ring with ca. 11 setulae near ventral margin. Small sclerite (not a sternite) just beneath tergo-sternal gap. Male genitalia: Cercus without thin ventral lobe; ventral margin flat, with dense fine setulae pointed downward; cercus almost triangular in posterior view. Epandrium almost round, height only ca.  $1.1 \times$  width. Ventrolateral halves (epandrial lobes) of epandrium with only 2 long, stiff setae. Aedeagus lightly sclerotized, lying between entire paraphyses; distiphallus extended beyond paraphyses. Middle of aedeagus trough-shaped; apex flat, slightly square-shaped, with slightly protruding points on lateroapical corners. Paraphyses heavily sclerotized, symmetrical, somewhat fang-shaped, with broad base (lightly sclerotized) and slightly curved, tapered apices (broad, flat sclerites flanking bases of paraphyses?). Aedeagal apodeme of moderate width, somewhat scoop-shaped. Gonopods triangular in lateral view. Hypandrium ovoid, with shallow ventral keel. Surstyli unsclerotized; simple lobes, without thin neck; apical surface with ca. 45 long, fine setae.

TYPES: Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi (not dissected). Paratypes: 5 ( $\delta + \eta$ ) same label data as holotype, (dissected: 1  $\eta$ , no. 118; 1  $\delta$ , no. 117). All in AMNH.

OTHER MATERIAL EXAMINED: PANAMA: Chiriqui, Boquete, VIII/58, W. B. Heed & M. Wasserman (2  $\delta$ , no. 221) (AMNH).

ETYMOLOGY: From Latin *glabra* (hairless, smooth) and apical, in reference to the black, shiny terminal tergite (epandrium) in the male.

*Cladochaeta ostia*, new species

Figures 106, 115

DIAGNOSIS: Arista with 3 short dorsal branches (excluding short terminal fork), no ventral branch; head and front relatively long in lateral view; hind femur of male with brush of ca. 35 long, fine setae; epandrium (male) black and shiny; aedeagus and paraphyses each with a distinctive large "window."

DESCRIPTION: HEAD: Rather shallow in lateral view, but quite long ( $HL/HD = 0.89$  [HT]); relatively wide. Eyes with very sparse, short setulae; hind margin without slight indentation. Antenna with pedicel and flagellomere I brown; arista with 3 short dorsal branches, excluding small terminal fork. Frons relatively wide; pruinulent blue when viewed from front; frontal vittae light brown and velvety when viewed from above; 7-8 interorbital setulae. Frontal-orbital setae: Proclinate and posterior reclinate orbitals approximately of equal lengths; anterior reclinate ca.  $0.2 \times$  their size, immediately lateral and slightly posterior to proclinate; posterior reclinate closer to proclinate than to inner vertical. Face light brown (with slightly darker oral margin), tall, and of moderate width ( $FW/HW = 0.33$ ), without any carina. Cheeks yellow and fairly deep ( $CD/ED = 0.23$ ). Proboscis and palps yellow.

THORAX: Notum, scutellum, and postnotum ochre in color; notopleural area down to dorsal margin of katapisternum with diffuse area of light brown; most of katapisternum yellowish. Anterior dorsocentrals ca.  $0.8 \times$  length of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Positions of scutellars distorted in only known specimen. One large postpronotal lobe seta, ventral one much smaller (ca.  $0.3 \times$  the size). Legs entirely yellow; forefemur with 3 long ventrolateral setae and 1 dorso-lateral seta; hind femur of male with brush of ca. 35 long, fine setae (female unknown; this is presumably a sexual dimorphism). Wing with very light, diffuse infuscation over tip and costal edge; with very slight clouds over x-veins r-m and dm-cu. Apex of vein  $R_{2+3}$  gradually meeting costal vein, almost straight; not turned costad. Veins  $R_{4+5}$

and M parallel, not even slightly parallel. Crossvein dm-cu straight. Wing tip rounded, not slightly pointed. Halter light yellow.

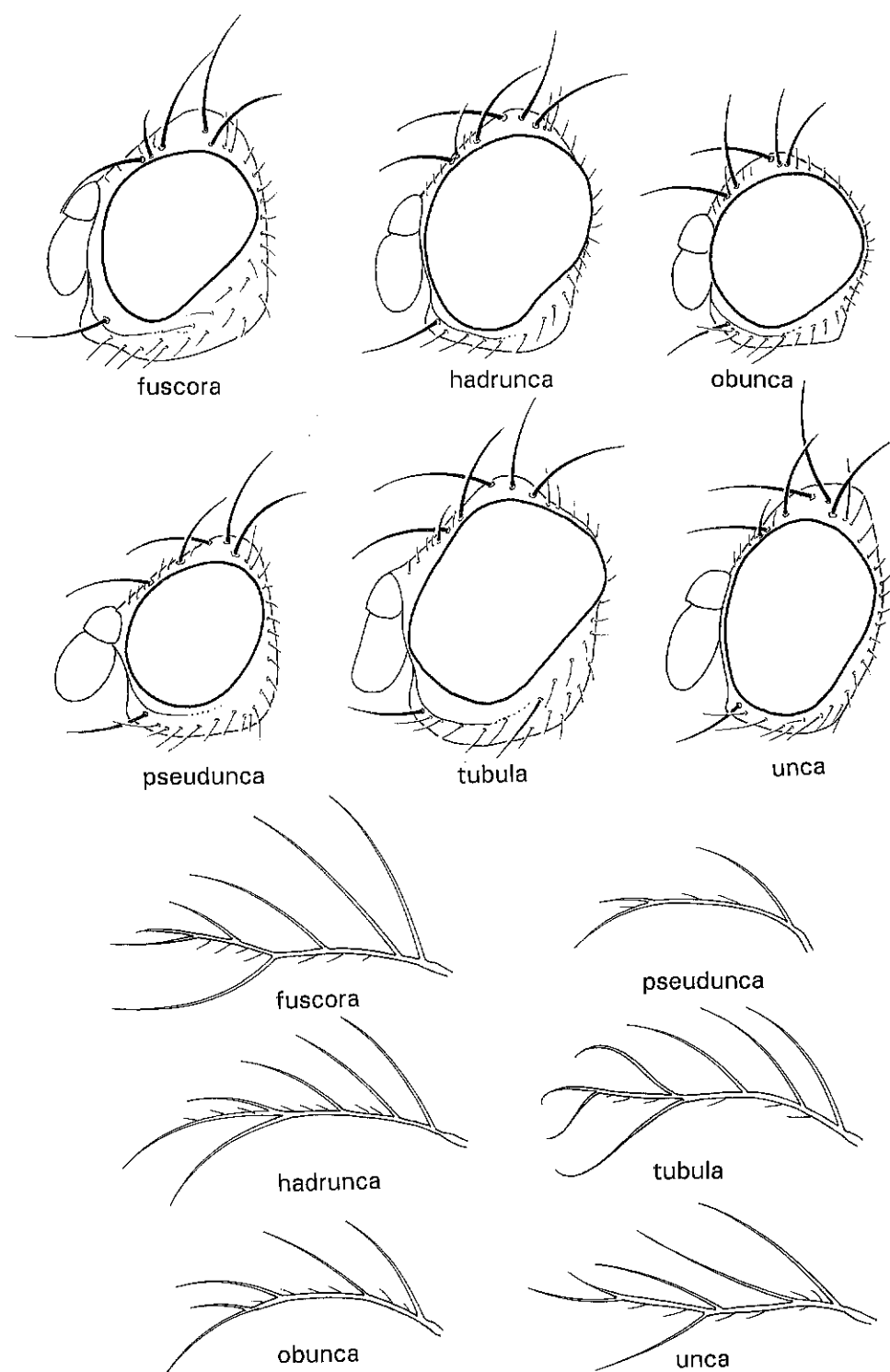
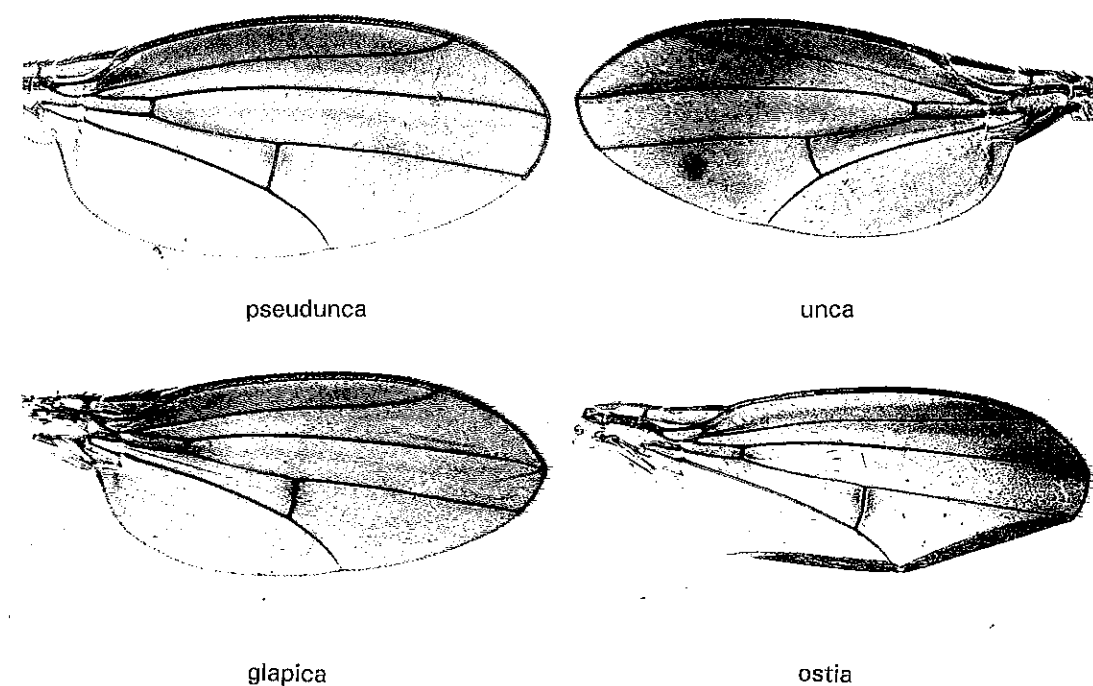
ABDOMEN: Tergites light brown, except epandrium (male tVIII), which is glabrous, black, and shiny (devoid of microtrichia). Female terminalia unknown. Male genitalia: Cercus with anteroventral corner formed into lobe; ventromedial corner expanded slightly inward; window near medial margin of cercus. Each cercus with irregular row of setae on mesal margin, scattered setae laterad; group of 4 setae on ventromesal corner. Epandrium nearly round in posterior view, height about equal to width, excluding broad flanges on dorsal part of anterior margin of epandrium. Ventrolateral halves (epandrial lobes) of epandrium with row of 9-10 fine, curved setae; apices of lobes extended beyond surstyli, nearly touching ventrally, with subapical patch of 6 fine setulae. Aedeagus a sclerotized oval, about one-half the length of paraphyses; membranous portion not ob-

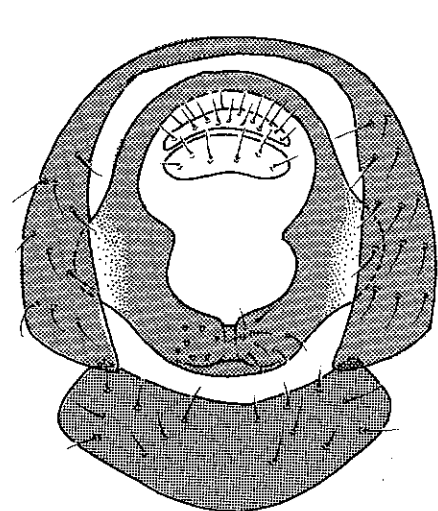
served. Paraphyses heavily sclerotized, bases with large "window," ventral lobe; sclerotized strip connecting bases of paraphyses internally, apices of strip articulating in window of paraphysis bases. Aedeagal apodeme scoop-shaped. Hypandrium with anterior margin not rounded, apex pointed; ventral keel deep. Gonopods lightly sclerotized, deep. Surstyli unsclerotized; large, broad, with broad base and middle of mesal margin concave, forming dorsal and ventral lobes. Dorsal lobe of surstylus with microtrichia; ventral lobe with row of ca. 15 fine setae on dorsal margin.

TYPE: Holotype, Male: MEXICO: *Chiapas*: 6500 ft, 20 mi N Bochil, Yerba Buena, 24/VI/69, W. R. M. Mason (in CNC) (dissected, no. 98).

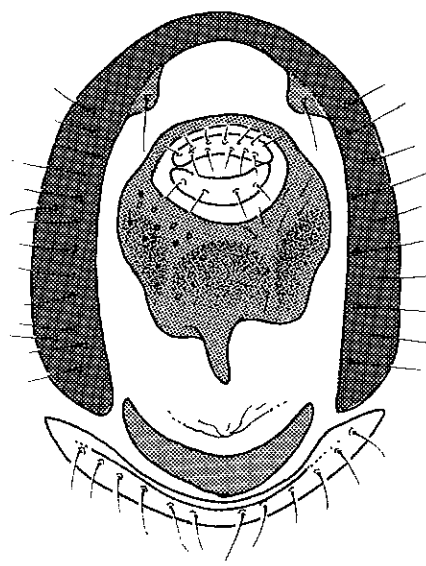
OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: From Latin *ostium* (hole, door), in reference to the ostia in the paraphyses and aedeagus of the male genitalia.

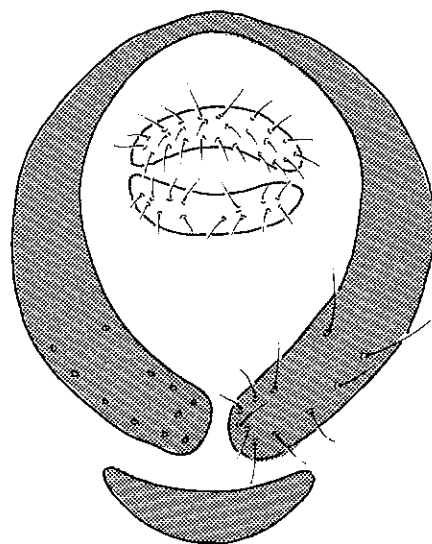
Fig. 105. Heads and arista of *unca* and *ostia* group species.Fig. 106. Wings of *unca* and *ostia* group species.



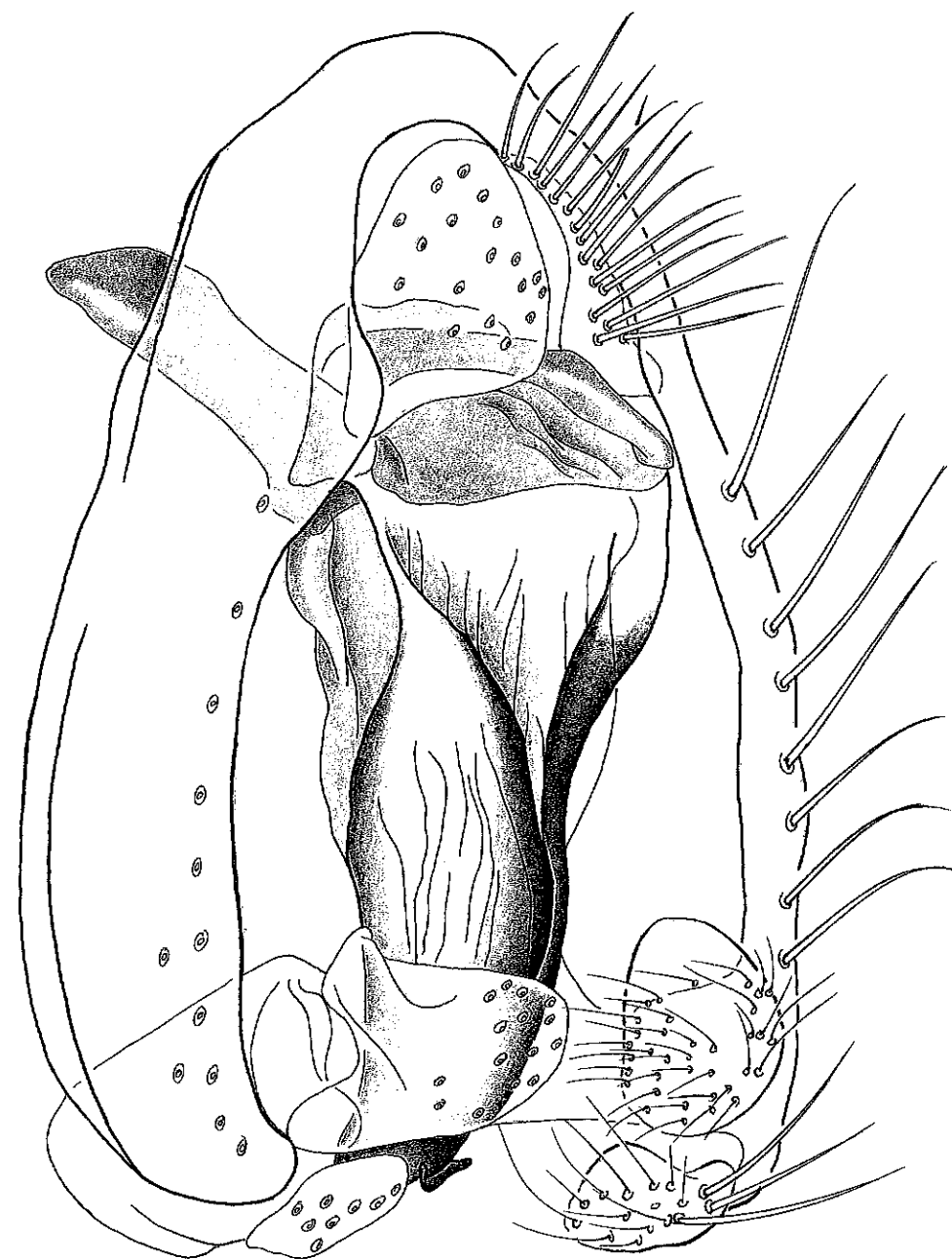
obunca



pseudunca



glapica

Fig. 107. Female terminalia of *unca* and *ostia* group species (posterior views).Fig. 108. Male terminalia of *C. fuscicornis*.



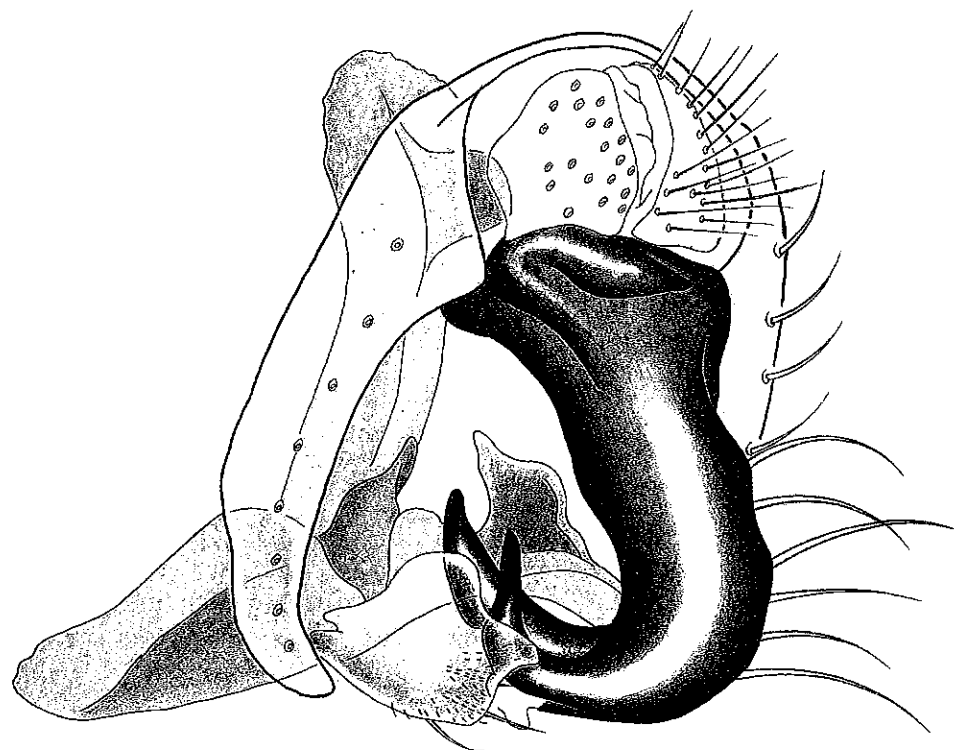


Fig. 109. Male terminalia of *C. hadrunca*.

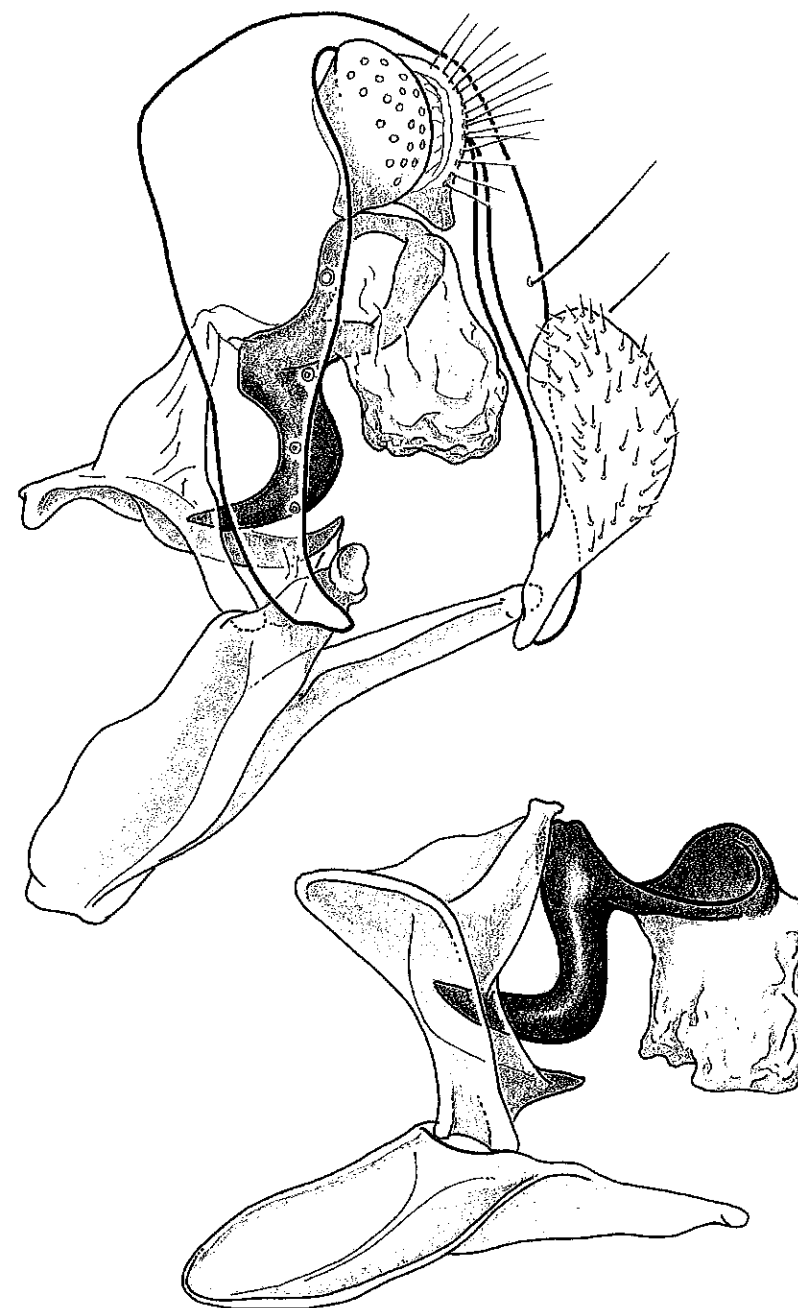


Fig. 110. Male terminalia of *C. obunca*.



Fig. 111. Male terminalia of *C. pseudunca*.

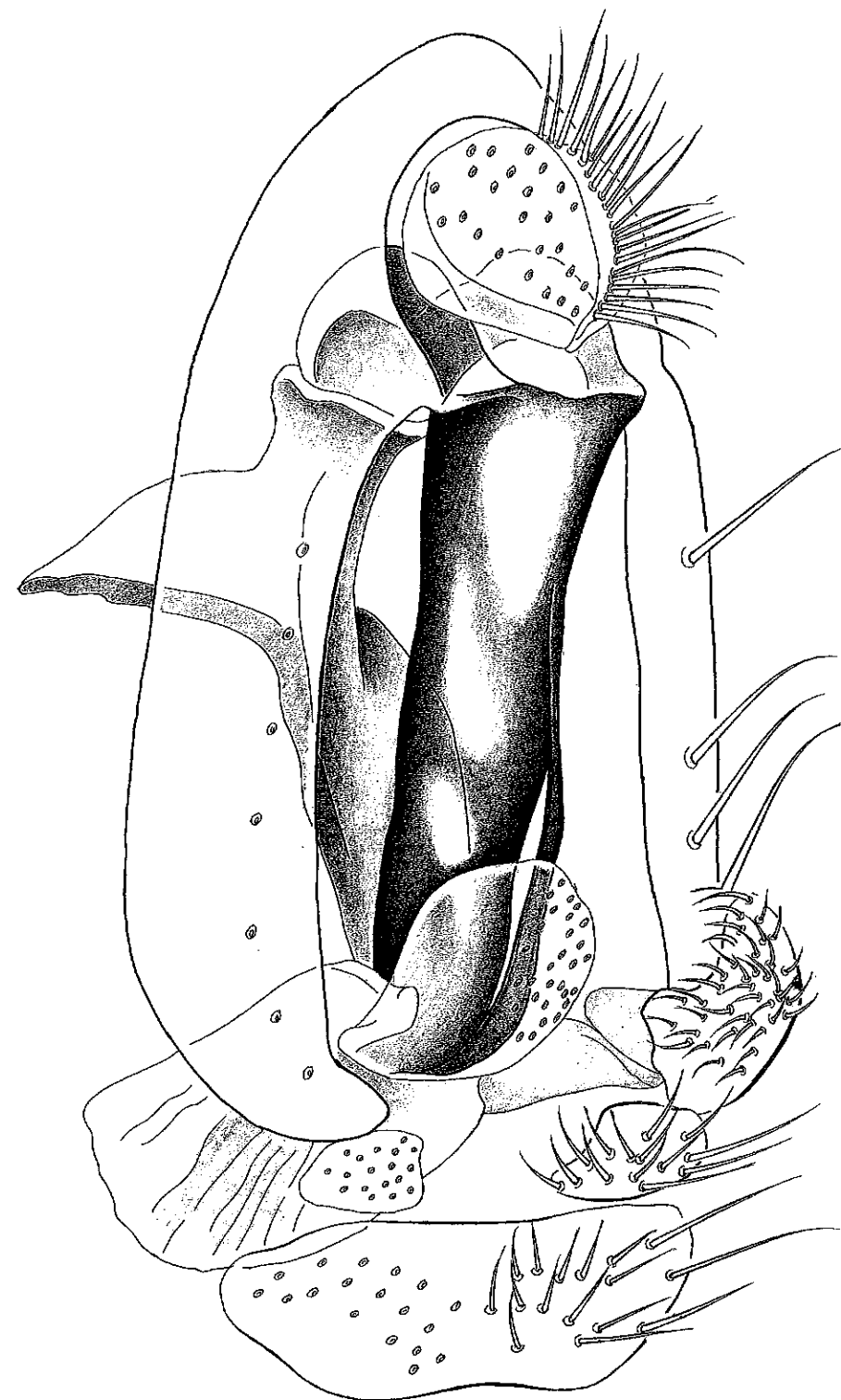


Fig. 112. Male terminalia of *C. tubula*.

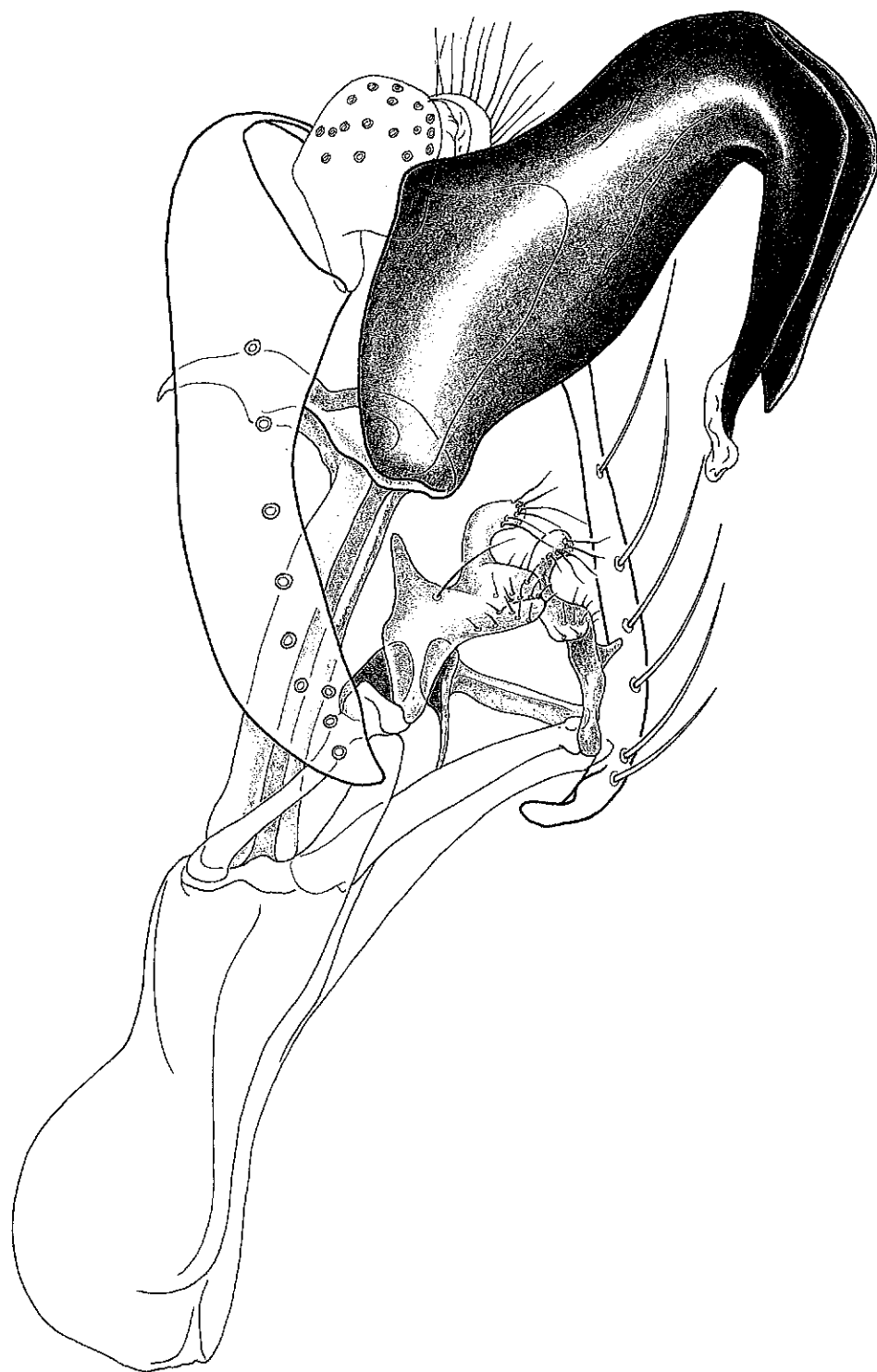


Fig. 113. Male terminalia of *C. unca*.

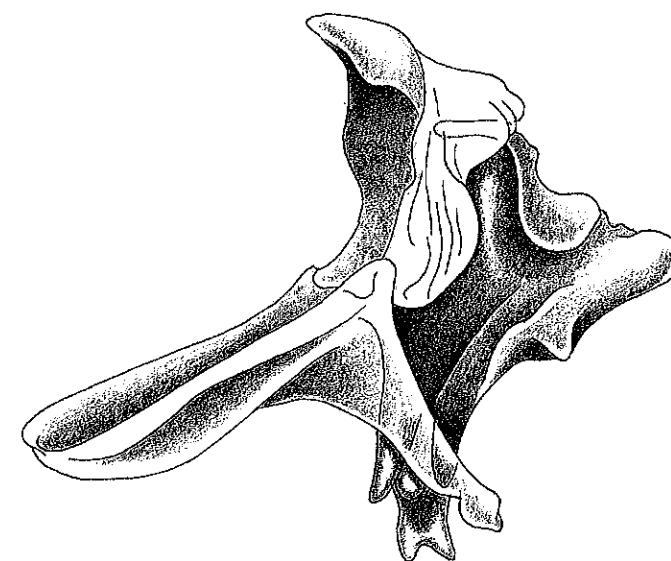
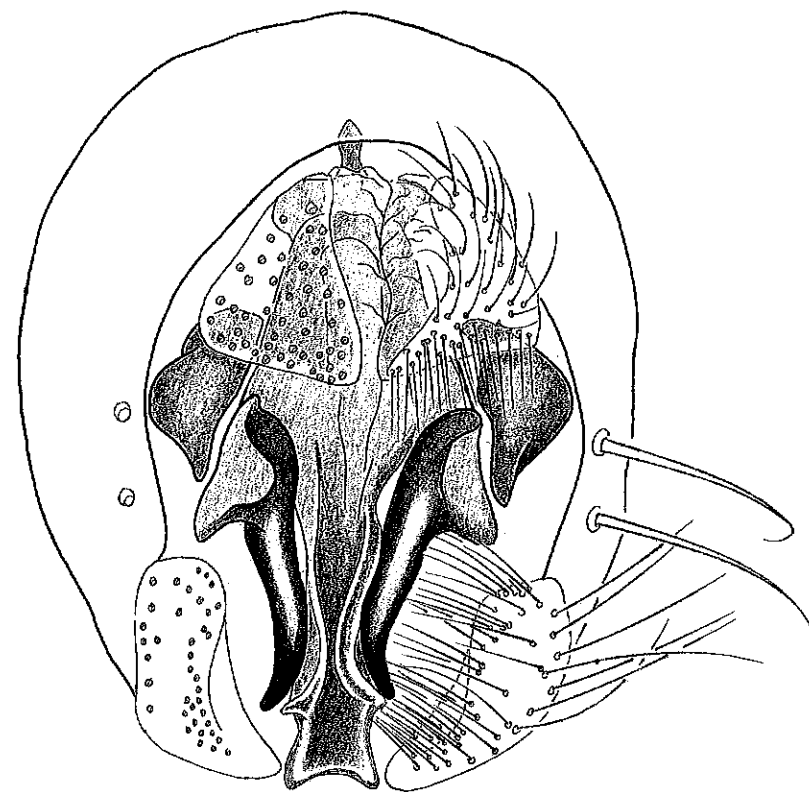


Fig. 114. Male terminalia of *C. glapica*.



Fig. 115. Male terminalia of *C. ostia*.

Tripunctata & Unca Groups

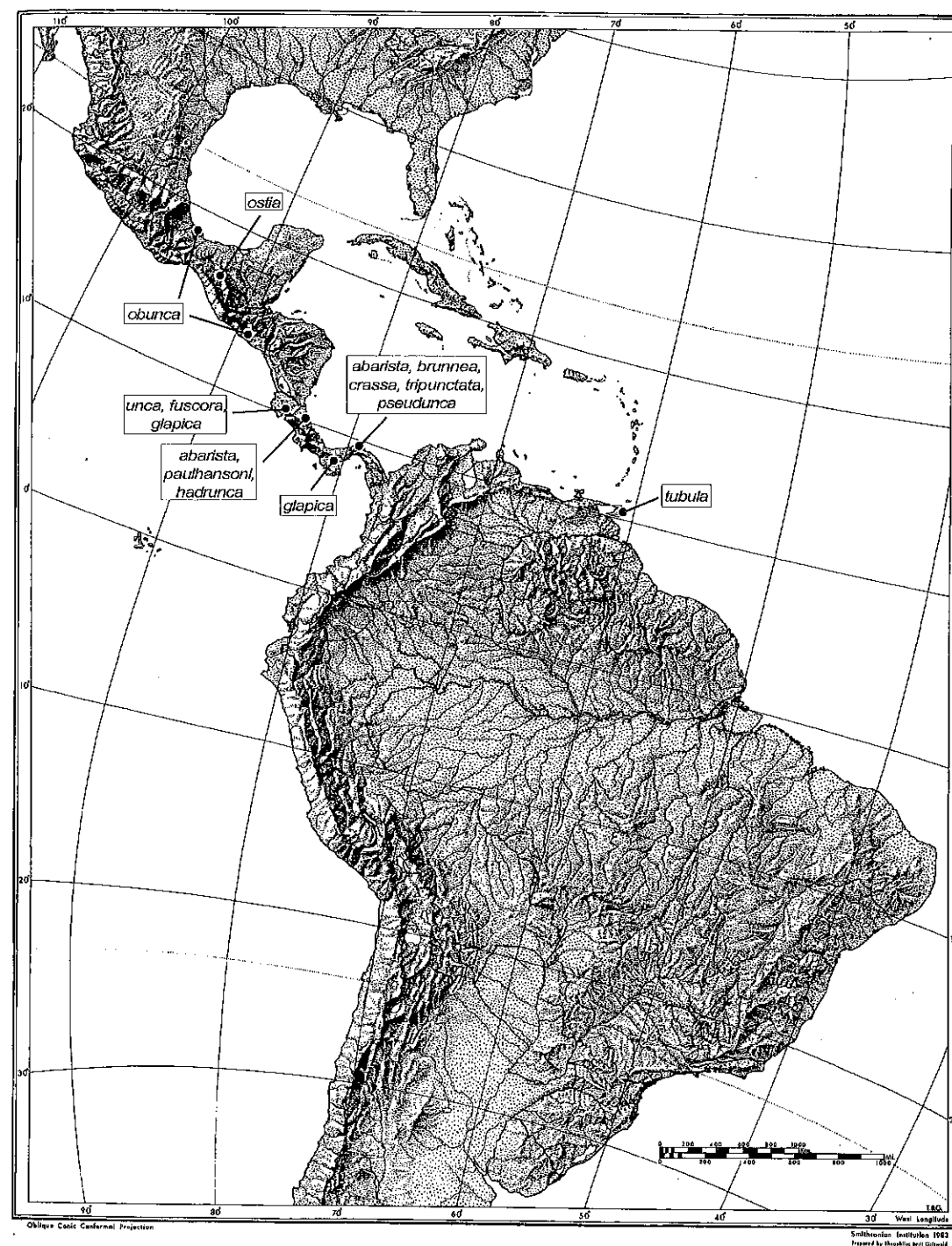


Fig. 116. Distribution of *tripunctata* and *unca* group species.

## SIMPLEX SPECIES GROUP

Monophyly of group defined by presence of 3 dorsal branches of arista (plus 1 ventral branch); loss of anterior reclinate orbital seta; distinctive male genitalia, as follows: epandrium wide, often with numerous scattered setae; cerci narrow, usually fused ventrally; surstyli simple, often triangular or scoop-shaped, with few setae; hypandrium very short, hypandrium and gonopods forming simple U-shaped sclerite.

*Cladochaeta akantha*, new species

Figures 117–121

DIAGNOSIS: Arista with 3 dorsal branches; anterior reclinate orbital seta lost/indistinguishable from setulae on frontal orbital plate; oral margin of face with dark brown stripe; dorsal half of pleuron with dark brown stripe; wing evenly dusky; male genitalia with distiphallus bearing 1 small and 3 large pairs of heavily sclerotized spines at apex; epandrial lobe with ca. 30 scattered setae.

DESCRIPTION: HEAD: Slightly long in lateral view. Eyes virtually bare, with very sparse, fine interfacetal setulae; lower hind margin of eye with slight indentation. Pedicel mostly ochre, with some dark brown; flagellomere I dark brown; arista with 3 dorsal branches, ventral one slightly closer to d-3 than to base of terminal fork. Frontal vittae shiny, golden; frontal orbital plates light yellow. Frons rather narrow, with 6–8 interfrontal setulae, close to ptilinal suture. Frontal-orbital setae: Anterior reclinate lost/indistinguishable from setulae on frontal orbital plates; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellar setae minute; ocellar setae short, ca.  $0.7 \times$  length of orbitals. Face narrow (FW/HW = 0.28 [N = 15]), flat; mostly light yellow with dark brown stripe along oral margin. Cheeks light yellow and very shallow (CD/ED = 0.08). Genal space shallow. Proboscis yellow, palps light brown.

THORAX: Notum and scutellum ochre; pleuron with dark brown stripe from beneath base of halter to near prothoracic spiracle; katapisternum light yellow. Anterior dorsocentrals about half the size of posterior dorsocentrals. Posterior dorsocentrals closer to scutellum than to anterior dorsocentrals, or midway between them. Acrostichals in 6 un-

even rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars slightly cruciate. Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 2 long, fine preapical setae on dorsolateral surface; row of 3 setae on ventrolateral surface. Halter light yellow. Wing slightly and evenly dusky, but without clouds of diffuse infuscation except over x-vein r-m. Apex of vein  $R_{2+3}$  gradually meeting costal vein, but vein slightly sinuate. Veins  $R_{4+5}$  and M parallel, not divergent, but both rather strongly curved. Crossvein dm-cu straight. Wing tip slightly pointed, not round.

ABDOMEN: Tergites evenly dark brown. Female terminalia sclerotized, broad. Apical tergite with ca. 6 setae on lateral lobe; without bridge beneath epi-/hypoproct; lateral lobes bent in middle. Apical sternite bilobed and separated in middle, forming 2 broad paramedian lobes, each with ca. 12 setulae. Sternite lobes apparently fused laterally to tergite. Small sclerite present and dorsomedial to sternite lobes. Male genitalia: Cerci narrow and long, with ventral lobe. Epandrial lobe very broad in middle, length only ca.  $1.5 \times$  width; irregular arrangement of 28–30 stiff, short setae. Aedeagus with distiphallus mostly membranous; articulated basally with broad, flat, scoop-shaped hypandrium. Distiphallus with apex bulbous, irregular shape; adorned with 8 black spines: ventral pair largest, pointed posteriad; medial pair one-half the size; dorsolateral pair short, pointed dorsad; dorsal pair minute. Aedeagal apodeme a broad, flat strip with triangular keel on posterior surface. Surstyli roughly an elongate triangle in lateral view, with row of 8 stiff, fine setulae on dorsomesal surface; heavily sclerotized.

TYPES: Holotype, Male: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi (genitalia not dissected). Paratypes: 18 ( $\delta + \eta$ ), with same label data as holotype (1 $\delta$ , no. 115, and 1 $\eta$ , no. 116, dissected).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From the Greek for thorn or spine, in reference to heavily sclerotized teeth on the aedeagus.

*Cladochaeta bispina*, new species

Figures 117, 118, 122

DIAGNOSIS: Arista with 3 dorsal branches; oral margin of face with dark brown stripe; anterior reclinate seta lost or highly reduced; pleuron with thin brown stripe; notopleural area with incomplete or complete thin brown stripe; male genitalia unsclerotized, with (apparently) distiphallus having 7 small sclerotized pegs; epandrial lobe with ca. 20 scattered setae.

DESCRIPTION: HEAD: Length relatively high in lateral view. Eyes virtually bare of interfacetal setulae; lower hind margin of eye with slight indentation. Pedicel light yellow, flagellomere I light brown; arista with 3 evenly spaced dorsal branches and small terminal fork, ventral branch slightly closer to base of terminal fork than to d-3. Frontal vittae shiny, golden; frontal orbital plates light yellow. Frons of moderate width, with 5–6 interfrontal setulae close to ptilinal suture. Frontal-orbital setae: Anterior reclinate lost/indistinguishable from setulae on frontal-orbital plates; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellar setae small; ocellar setae ca.  $0.85 \times$  length of orbitals. Face of moderate width (FW/HW = 0.31 [N = 2]), flat; mostly light yellow with dark brown stripe along oral margin. Cheeks light yellow and very shallow (CD/ED = 0.09). Genal space shallow. Proboscis yellow, palps light brown.

THORAX: Notum and scutellum ochre; pleuron with narrow brown stripe from beneath base of halter to prothorax; postpronotal lobe and notopleural edge light brown (extended into thin stripe in female paratype); katapisternum and area just above light yellow. Anterior dorsocentrals ca.  $0.6 \times$  size of posterior dorsocentrals. Posterior dorsocentrals midway between scutellum and anterior dorsocentrals. Acrostichals in 6 even rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars slightly cruciate. Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 2 setae on ventrolateral surface. Halter light yellow. Wing very lightly, evenly fuscous without any clouds even on

x-veins. Vein  $R_{2+3}$  virtually straight, apex gradually meeting costal vein. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly bent. Wing tip slightly pointed.

ABDOMEN: Tergites evenly light brown. Female terminalia unknown (only female paratype not dissected). Male genitalia very lightly sclerotized or not at all. Cerci very small, without ventral lobe. Epandrium only slightly higher than wide, almost round in posterior view; apical half of posteromesal margins flaplike. Each ventrolateral half of epandrium (epandrial lobes) with ca. 25 scattered setae, not in any rows; smallest setae ventrally, largest setae dorsally. Aedeagus membranous, slightly bulbous, tapered at apex, with 2 stout, heavily sclerotized pegs in middle, 2 minute ones dorsal to these, and 3 minute ones ventral to these; secondary lobe projected ventrad and just anterior to aedeagus, with lobe long and thin. Aedeagal apodeme short, hourglass-shaped, with short broad keel on anterior surface. Surstylus simple, with rounded apex, flat; apical margin with row of ca. 10 fine, short setulae. Hypandrium very short; hypandrium and gonopods forming simple "U." Apical sternites not examined.

TYPE: Holotype, Male: PANAMA: Bocas del Toro, Almirante, 28/X/52, F. S. Blanton (dissected, no. 253). Paratype: PANAMA, *Canal Zone*: Ft. Sherman, Mojanga Swamp, 21/VII/52, F. S. Blanton (1 $\eta$ ) (both in NMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: In reference to the 2 most conspicuous black spines (with 5 minute ones) on an otherwise almost completely membranous distiphallus.

*Cladochaeta chelifera*, new species

Figures 117–120, 123

DIAGNOSIS: Face with oral margin dark brown; arista with 3 dorsal branches; anterior reclinate orbital seta lost; ocellar setae about half the size of orbitals; postocellars minute; dorsal half of pleuron brown; male genitalia similar to *akantha* except that in *chelifera* the dorsal lobe is strongly arched and its spines arranged differently and slightly longer, sur-

styli not tapered apically as in *akantha*. Epandrial lobe with ca. 20 scattered setae.

DESCRIPTION: HEAD: Length moderate in lateral view (HL/HD = 0.73). Eyes virtually bare, with very sparse, fine interfacetal setulae; lower hind margin of eye with very slight indentation. Pedicel ochre with some light brown areas dorsally, flagellomere I dark brown; arista with 3 dorsal branches, ventral one closer to d-3 than to base of terminal fork, or midway between them. Frontal vittae shiny, golden; frontal orbital plates light yellow. Frons of moderate width, rather long and sloping, with 6-8 interfrontal setulae close to ptilinal suture. Frontal orbital setae: Anterior reclinate lost/indistinguishable from setulae on frontal orbital plates; posterior reclinate about midway between proclinate and inner vertical. Postocellar setae minute; ocellar setae small and thin, about half the length of orbitals. Face of moderate width (FW/HW = 0.30), flat; mostly light yellow with thin brown stripe on oral margin. Cheeks light yellow and very shallow (CD/ED = 0.08). Genal space shallow. Proboscis yellow, palps light brown.

THORAX: Scutellum and notum (to notopleural edge) ochre; dorsal half of pleuron brown (sometimes with light spot beneath postpronotal lobe); katapisternum light yellow. Anterior dorsocentrals about half the length and width of posterior dorsocentrals. Posterior dorsocentrals about midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars slightly cruciate. Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 2 long, fine preapical setae on dorsolateral surface; row of 3 setae on ventrolateral surface. Hind femora of male slightly stouter than in female. Halter light brown. Wing lightly and evenly dusky, without dark clouds even on x-veins. Apex of vein  $R_{2+3}$  turned very slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M parallel, slightly curved. Crossvein dm-cu straight. Wing tip rounded.

ABDOMEN: Tergites evenly light brown. Female terminalia very simple, sclerotized. Apical tergite a narrow, inverted U-shaped

sclerite, without setae. Apical sternite bilobed, completely divided, very broad, each lobe with ca. 10 fine setae; sternite lobes not fused laterally to tergite. Male genitalia: Cerci quite small, with small ventral lobe. Epandrial lobe very broad in middle, length only ca.  $1.8\times$  width (medial margins almost touching), with irregular arrangement of 20 stiff, short setae. Aedeagus with distiphallus mostly membranous; articulated basally with broad, scoop-shaped endophallus, which has sides folded  $45^\circ$ . Distiphallus with apex slightly trough-shaped; adorned with 8 black spines, all pointed laterad: ventral pair largest; next pair shorter and thinner; next pair short and stout; dorsal pair smallest and isolated from other 3 pairs. Aedeagal apodeme broad, concave, H-shaped. Surstyli long and flat, with row of 3-5 stiff, fine setulae on dorsomesal surface in middle; apical third heavily sclerotized. Apex of surstylus with ventral point. Hypandrium very short, with large gonopods broadest apically.

TYPES: Holotype, Male: DOMINICA (West Indies): S. Chiltern Est., 2/II/65, W. W. Wirth (not dissected). Paratypes: DOMINICA: Clarke Hall, 11-20/III/65 (1♂; 4♀, no. 186); Fond Figue Road, 3/II/65 (4♂, no. 185; 1♀); Manets Gutter, 7/III/65 (1♂) (1♂, 1♀ in AMNH; all others, including holotype, in NMNH).

OTHER MATERIAL EXAMINED: COSTA RICA: *Heredia*: Estacion Biologica Finca La Selva, 50 m, X/92, Malaise trap (in AMNH), dissected (no. 303).

ETYMOLOGY: Form Latin *chela* (claw), for the clawlike structure of the male genitalia as seen in *akantha*.

DISCUSSION: Closely related to *akantha* based on oral margin of face with dark brown stripe; pleura with dark brown, longitudinal stripe; epandrial lobe with numerous (>20) setae; aedeagus with spinose, dorsal lobe, and spines stout and long; ocellar setae small (half the size of frontal-orbitals). *C. vittata* has the first 4 of these characters.

#### *Cladochaeta inornata*, new species

Figures 117, 118, 124

DIAGNOSIS: Arista with 1 ventral and 3 dorsal branches; anterior reclinate orbital seta completely lost; wing fuscous, without dark

spots even on crossveins. Distinguished from other species of the group by the very large lobes ventral to cerci in males, bearing 13 spines each, and by simple, lobate surstyli with 3-4 blunt, sclerotized teeth on apex.

DESCRIPTION: HEAD: Moderate length and depth. Eyes completely bare; lower hind margin of eye without even slight emargination. Pedicel ochre medially, light brown laterally; flagellomere I darker brown; arista with 3 dorsal branches, ventral branch midway between d-3 and small terminal fork. Frontal vittae shiny, golden; frontal orbital plates matte. Frons of moderate length and width, with 9 interfrontal setulae near ptilinal suture. Frontal orbital setae: Anterior reclinate minute, indistinguishable from setulae on frontal orbital plates, or apparently entirely lost; posterior reclinate slightly closer to proclinate than to inner vertical; proclinate and post. reclinate orbitals about equal in size. Postocellar setae minute, slightly larger than setulae on frons; ocellar setae ca.  $0.6\times$  length of orbitals and slightly thinner. Face flat and of moderate width (FW/HW = 0.31); light tannish with oral margin whitish. Cheeks whitish and fairly shallow (CD/ED = 0.08). Genal space shallow. Proboscis and palps yellowish.

THORAX: Scutellum, notum, and postnotum ochre; diffuse brown stripe on ventral side of notopleural edge; pleura mostly yellow, with diffuse brown stripe running through center of anepisternum and anepimeron; katapisternum entirely light yellow. Anterior dorsocentrals small, about half the length and width of posterior dorsocentrals. Posterior dorsocentrals midway between anterior dorsocentrals and scutellum. Acrostichals in 6 fairly even rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars slightly cruciate. Postpronotal lobe with 1 stout seta, a much smaller seta ( $0.4\times$  the length) dorsally. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; row of 3 setae on ventrolateral surface. No distinctive setae on other legs. Halter with stem light brown, knob yellow. Wing evenly and lightly fuscous, without dark clouds even on x-veins. Apex of vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M parallel, slightly

curved. Crossvein dm-cu slightly curved and slightly oblique to  $R_{4+5}$ . Wing tip rounded, not slightly pointed as in several other species of the group (*akantha*, *neosimplex*, *simplex*).

ABDOMEN: Tergites evenly light brown; female terminalia unknown. Male genitalia with cerci unmodified, without ventral/lateral flanges. Two very large, pendulous lobes ventral to cerci, connected basally to a sclerite surrounding cercus; sclerite possibly connected to (and an extension of) cercus (doubtfully epandrial in origin). Pendulous lobes adorned with 13 heavily sclerotized spines: one on posterior edge, midway along length of lobe; most on apex of lobe, generally shorter than more anterior spine. Internal portions of genitalia (paraphyses, aedeagus, aedeagal apodeme, hypandrium) lost in dissection. Surstyli short, simple lobes with apex having 3-4 blunt sclerotized teeth.

TYPE: Holotype: Male: COSTA RICA: *San José*: Zurqui de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 315) (in AMNH).

OTHER MATERIAL EXAMINED: Known only from the type specimen.

ETYMOLOGY: Unadorned, in reference to all aspects of the external features with exception of the spinose cercal lobes.

DISCUSSION: In lieu of the internal parts of the male genitalia, the species identity of this fly is certain based on the elaborate spined lobes ventral to the cercus.

#### *Cladochaeta longistyla*, new species

Figures 117, 118, 122

DIAGNOSIS: Eyes large, completely bare; anterior reclinate orbital setae minute, postocellar setae very small; wing entirely hyaline; male genitalia most similar to *C. neosimplex*, but differs by *longistyla* having no fine setulae on ventral lobe of cercus, fewer setae on epandrium, surstyli longer and thinner, and small lobe behind aedeagus absent.

DESCRIPTION: HEAD: Rather high in lateral view. Eyes quite large relative to head, completely bare; lower hind margin of eye with very slight indentation. Pedicel ochre, flagellomere I brown; arista with 3 dorsal branches, ventral one about midway between d-3 and base of terminal fork. Frontal vittae



shiny, dull gold; frontal lunule yellow. Frons with ca. 6 interfrontal setulae, close to ptilinal suture. Frontal orbital setae: Anterior reclinate minute, barely distinguishable from fine frontal-orbitals in row anterior to it, other orbitals quite long; posterior reclinate much closer to proclinate than to inner vertical; proclinate slightly shorter than post. reclinate. Postocellar setae very small, about one-fourth the size of ocellars; ocellar setae equal in size to frontal-orbitals. Face of moderate depth and width (FW/HW = 0.32 [N = 2]), flat, tan. Cheeks light yellow and very shallow (CD/ED = 0.07). Genal space shallow. Proboscis and palps yellow.

THORAX: Mostly light brown, but obscured by greasy body. Anterior dorsocentrals about half the length and width of posterior dorsocentrals. Posterior dorsocentrals about midway between scutellum and anterior dorsocentrals. Acrostichals in 6 even rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; just the very tips of post. scutellars cruciate. Postpronotal lobe with 1 large seta; ventral seta much shorter and finer. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 2 setae on ventrolateral surface. Halter tan. Wing very light and evenly dusky, without clouds of diffuse infuscation, even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel, not divergent. Crossvein dm-cu slightly curved. Wing tip very slightly pointed.

ABDOMEN: Tergites dark brown. Female terminalia unknown. Male genitalia: Cerci narrow, with pair of thin, fused ventral lobes, devoid of setulae. Both epandrial lobes very broad; each with 5–6 stiff, short setae. Aedeagus short, narrow, with membranous, trough-shaped distiphallus slightly longer than cerci. Aedeagal apodeme small, hardly sclerotized. Surstyli sclerotized, especially apical half, with long, thin, upturned apices and blunt tip; pair of very fine, stiff setae at base but none apically. Hypandrium very short, gonopods paddle-shaped.

TYPES: Holotype, Male: NICARAGUA: El Recreo, VI/54, W. B. Heed (dissected, DAG no. 226). Other than having a greasy body, the specimen is mostly intact (sans abdomen,

with dissected genitalia). Paratype: Male, NICARAGUA: Bluefields, VI/54, W. B. Heed (dissected, no. 223). The body of the paratype is mostly gone, with just the head, wings, and legs remaining on the point (genitalia in small capsule beneath point). Both specimens in AMNH.

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: In reference to the elongate surstyli.

#### *Cladochaeta neosimplex*, new species

Figures 117–119, 125

DIAGNOSIS: Body evenly tan, wing very slightly dusky; male genitalia most similar to *yanomama* except that in *neosimplex* aedeagus with end of distiphallus bulbous, epandrial lobe with more setae (15 vs. 10 in *yanomama*), and gonopods stouter in *neosimplex*.

DESCRIPTION: HEAD: Shape almost round in lateral view (HL/HD = 0.82 [HT]). Eyes large relative to head, completely bare; lower hind margin of eye almost completely rounded. Pedicel ochre, flagellomere I brown; arista with 3 dorsal branches, ventral one about midway between d-3 and base of terminal fork. Frontal vittae shiny, golden; frontal orbital plates dull, light yellow. Frons with 3–4 interfrontal setulae, close to ptilinal suture. Frontal orbital setae: anterior reclinate lost, other orbitals quite long; posterior reclinate much closer to proclinate than to inner vertical. Postocellar setae small; ocellar setae equal in size to frontal-orbitals. Face rather narrow (FW/HW = 0.31 [N = 2]) and flat; entirely light yellow, oral margin not brown. Cheeks light yellow and shallow (CD/ED = 0.09). Genal space shallow. Proboscis and palps yellow.

THORAX: Scutellum, notum, and pleuron tannish. Anterior dorsocentrals about half the length and width of posterior dorsocentrals. Posterior dorsocentrals about midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars cruciate for ca. 0.3× their length. Postpronotal lobe with 1 large seta. Legs entirely light yellow; fore-

femur with 1 long, fine preapical setae on dorsolateral surface; row of 3 setae on ventrolateral surface. Halter tan. Wing evenly dusky, without clouds of diffuse infuscation, even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, almost straight, not turned costad. Veins  $R_{4+5}$  and M parallel, not divergent, but both curved. Crossvein dm-cu straight. Wing tip very slightly pointed, almost rounded.

ABDOMEN: Tergites evenly light brown; epandrium (male) darker, more shiny. Female terminalia unknown. Male genitalia: Cerci narrow and long, with long, fused ventral lobe bearing 5 short setulae. Epandrial lobe very broad in middle, length twice the width; 16–18 stiff, short setae irregularly arranged. Aedeagus very short, with membranous distiphallus; distiphallus narrow, troughlike; slightly longer than cerci. Aedeagal apodeme narrow, scoop-shaped, lightly sclerotized, with ventral end having slight median notch. Surstyli sclerotized; long, broad, scoop-shaped, apices rounded; mesal surface with 3–4 stiff, erect setae; apical third with row of 5 short setulae. Hypandrium very short; gonopods short, very deep.

TYPES: Holotype, Male: TRINIDAD: Arima: Blanchisseuse Rd., 2000 ft, 3–9/I/82, Morton S. Adams. Genitalia not dissected. Paratype: Male, same data as holotype. Genitalia dissected (DAG no. 79). Both in the AMNH.

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: "New" *simplex*, in reference to its species group placement.

#### *Cladochaeta peruviana* (Duda)

*Diathoneura peruviana* Duda, 1927: 96; Vilela and Bächli, 1990: 35.

*Cladochaeta peruviana* (Duda), NEW COMBINATION.

DIAGNOSIS: Most closely related and similar to *telescopica*, n. sp. (from Trinidad) on basis of triangular surstyli and shape of cerci. Surstylus in *peruviana*, however, is more evenly triangular; aedeagus is slightly longer, and distiphallus is of slightly different shape.

DESCRIPTION: Redescription provided by Vilela and Bächli (1990). Male genitalia: Cerci narrow and long; without distinct ven-

tral lobe, ventral portions fused. Epandrial lobe very broad in middle, length only twice the width. Median margins separated by distance about equal to width of cerci; each lobe with 11–12 stiff setae of intermediate length, irregularly arranged. Distiphallus membranous, short; clavate in lateral view. Surstyli sclerotized, roughly triangular in lateral view, but without angles pointed; mesal surface with 12 scattered setulae. Hypandrium very short, U-shaped, with deep gonopods.

TYPES: Holotype, Male: PERU: "Meshag. 14/9/.03, Urubambafl." In the Staatliches Museum für Tierkunde, Dresden, Germany. Genitalia dissected and illustrated by Vilela and Bächli (1990).

OTHER MATERIAL EXAMINED: Known only from the holotype male.

DISCUSSION: There is no doubt as to the placement of this species in *Cladochaeta*, for the male genitalia share several distinctive features with the *simplex* group. (The possibility that the *simplex* group species are in *Diathoneura* is easily dismissed based not only on the male genitalia, but also because of the one ventral branch of the arista and the fact that the females are known for 2 species [*akantha* and *telescopica*]. These females possess the primitive oviscapt without pegs, which excludes them from *Diathoneura*.)

#### *Cladochaeta similex*, new species

Figures 117, 118, 126

DIAGNOSIS: Wings lightly and evenly dusky, costal half slightly darker; arista with 1 ventral and 3 dorsal branches; anterior dorsocentral setae quite small, about half the size of posterior dorsocentrals; cheek very shallow (e.g., one-half the depth of *simplex*); distinguished best from most similar species (e.g., *simplex*, *neosimplex*, *longistyla*) on basis of size and shape of aedeagus and surstyli (discussed below).

DESCRIPTION: HEAD: High and short in lateral view. Eyes quite large, completely bare; lower hind margin of eye without indentation, even a slight one. Pedicel ochre, flagellomere I slightly darker brown. Arista with 3 dorsal branches, ventral one about midway between d-3 and base of terminal fork; branches of terminal fork almost as long as

other branches. Frons quite narrow, with frontal vittae dull ochre. Frons with ca. 5 interfrontal setulae, close to ptilinal suture. Frontal orbital setae: Anterior reclinate minute, indistinguishable from frontal-orbital setulae anterior to it. Other orbital setae long; posterior reclinate closer to proclinate than to inner vertical. Postocellar setae minute, about one-fourth the size of ocellars; ocellar setae slightly longer than frontal-orbitals. Face rather high and narrow ( $0.30 [N = 2]$ ), flat, and tan. Cheeks light yellow and very shallow ( $CD/ED = 0.06$ ). Genal space shallow. Proboscis and palps yellow.

THORAX: Thorax (including pleura) entirely and evenly yellowish tan. Anterior dorsocentrals quite small, about half the length of posterior dorsocentrals. Posterior dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 very uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars convergent, rather short (ca.  $0.6 \times$  length of ant. scutellars). Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 3 setae on ventrolateral surface. Halter tan. Wing lightly dusky, with costal half slightly darker; no clouds of infuscation on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein; vein  $R_{2+3}$  almost straight, apex not turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip very slightly pointed.

ABDOMEN: Tergites light, even brown. Female terminalia unknown. Male genitalia very similar to *simplex*, with differences as follows: distiphallus much smaller, especially more narrow and not baglike. The surstylus is slightly different, with *simplex* having the middle part thicker and with 5 (vs. 3) long, stiff setae; the apex is not as long and thin as in *simplex*.

TYPES: Holotype, Male: PANAMA: Canal Zone: Colón, VII/79, canopy fogging, E. M. Broadhead (dissected, no. 154). Paratype: Male, NICARAGUA: El Recreo, VI/54, W. B. Heed (dissected, no. 243). Both specimens in AMNH.

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: In reference to its morpho-

logically cryptic similarity to *simplex* and other species in this group.

*Cladochaeta simplex*, new species

Figures 117–120, 127

DIAGNOSIS: Wings lightly and evenly dusky; arista with 1 ventral and 3 dorsal branches; distinguished best from most similar species on basis of bulbous distiphallus and long, tapered surstyli, each with 2 fine, stiff setae on mesal surface.

DESCRIPTION: HEAD: Rather high and short in lateral view ( $HL/HD = 0.74 [HT]$ ). Eyes completely bare; lower hind margin of eye with very slight indentation. Pedicel ochre, flagellomere I brown; arista with 3 dorsal branches, ventral one about midway between d-3 and base of terminal fork; branches of terminal fork almost as large as other branches. Frontal vittae shiny, golden; frontal orbital plates dull, light yellow. Frons with 3–4 interfrontal setulae, close to ptilinal suture. Frontal orbital setae: Anterior reclinate lost, other orbitals long; posterior reclinate much closer to proclinate than to inner vertical. Postocellar setae minute; ocellar setae slightly longer than frontal-orbitals. Face high, narrow ( $FW/HW = 0.29 [N = 6]$ ), and flat; entirely light yellow. Cheeks light yellow and very shallow ( $CD/ED = 0.07$ ). Genal space shallow. Proboscis and palps yellow.

THORAX: Scutellum, notum, and pleuron entirely and evenly tannish. Anterior dorsocentrals ca.  $0.7 \times$  length of posterior dorsocentrals. Posterior dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars barely cruciate. Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 2 setae on ventrolateral surface. Halter tan. Wing evenly and lightly dusky; without clouds of diffuse infuscation even over crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein; vein  $R_{2+3}$  almost straight, apex not turned costad. Veins  $R_{4+5}$  and M parallel, not slightly divergent, but both curved. Crossvein dm-cu straight. Wing tip very slightly pointed.

ABDOMEN: Tergites light, even brown. Female terminalia mostly sclerotized. Very similar to *chelifera* except that *simplex* has ca. 10 fine setulae dorsally on apical tergite; setae on sternite lobes slightly longer, and lobes connected (but apparently not fused) laterally to tergite. Male genitalia: Cerci narrow and long, with ventral lobe bearing 9–10 short setulae on lateral surface. Epandrial lobe very broad in middle, length twice the width, with row of 9 stiff setae of intermediate length. Aedeagus very short, with membranous distiphallus; distiphallus baglike, with large central opening. Aedeagal apodeme narrow, unsclerotized. Surstyli long, narrow, with scoop-shaped ends and sharp apices; mesal surface with 3 stiff, erect setae; apical third of surstylus heavily sclerotized. Hypandrium very short, with large gonopods.

TYPES: Holotype, Male: TRINIDAD: Arima: Blanchisseuse Rd., 2000 ft, 3–9/I/82, Morton S. Adams. Genitalia not dissected. Paratypes: 2♂ (1 dissected, no. 80), 3♀, with same label data as holotype.

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From Latin for simple and unadorned, in reference to the simple male genitalia.

*Cladochaeta telescopica*, new species

Figures 117–120, 128

DIAGNOSIS: Easily distinguished from other species in the group on the basis of wings: x-veins with clouds, costal edge and wing tip infuscate. Also, male genitalia with distinctively triangular, toothlike surstyli; hypandrium U-shaped; distiphallus small.

DESCRIPTION: HEAD: Rather high and short in lateral view ( $HL/HD = 0.71$ ). Eyes completely bare; lower hind margin of eye not indented, rather flat. Pedicel ochre, flagellomere I light brown; arista with 2–3 dorsal branches, ventral one opposite d-2 and d-3 or between it and terminal fork; branches of terminal fork long. Frontal vittae shiny, golden; frontal orbital plates dull light yellow. Frons quite narrow, with 9–10 interfrontal setulae close to ptilinal suture. Frontal orbital setae: Anterior reclinate lost, other orbitals

long; posterior reclinate much closer to proclinate than to inner vertical. Postocellar setae minute; ocellar setae slightly longer than frontal-orbitals. Face high and slightly narrow ( $FW/HW = 0.29 [N = 7]$ ) and flat; entirely light yellow. Cheeks light yellow and very shallow ( $CD/ED = 0.07$ ). Genal space shallow. Proboscis and palps yellow.

THORAX: Scutellum, notum, and pleuron entirely and evenly tannish yellow. Anterior dorsocentrals ca.  $0.6 \times$  length of posterior dorsocentrals. Posterior dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars convergent, post. scutellars strongly so. Postpronotal lobe with 2 large setae. Legs entirely light yellow; forefemur with 3 long, fine preapical setae on dorsolateral surface; 1 seta on ventrolateral surface. Wing with clouds of diffuse infuscation over crossveins and on costal edge and wing tip. Apex of vein  $R_{2+3}$  gradually meeting costal vein; vein  $R_{2+3}$  almost straight. Veins  $R_{4+5}$  and M parallel, not slightly divergent, but M slightly curved. Crossvein dm-cu slanted slightly toward wing edge. Wing tip very slightly pointed.

ABDOMEN: Tergites evenly light brown, epandrium (male) darker and shiny. Female terminalia distinctive: last 2 segments with tergites and sternites long and telescoping, having scattered setae on posterior margin of sclerites. Posterior and penultimate tergites divided medially into 2 sclerotized, lateral rods. Larviparous. Male genitalia: Cerci narrow and long; without distinct ventral lobe. Epandrial lobe very broad in middle, length only  $1.7 \times$  width, nearly touching in middle; each lobe with 8 stiff setae of intermediate length, irregularly arranged. Aedeagus very short, with membranous distiphallus; distiphallus somewhat trough-shaped. Aedeagal apodeme broad, H-shaped. Surstyli sclerotized, roughly triangular in lateral view, with 3 points; ventromedial point sharp, dorsal point with 1 minute setula; row of 4 small setulae in middle. Hypandrium very short, U-shaped, with short, thick gonopods.

TYPES: Holotype, Male: TRINIDAD: Arima: Blanchisseuse Rd., 2000 ft, 3–9/I/82,

Morton S. Adams. Genitalia not dissected. Paratypes: 1♂ (dissected, no. 81b), 3♀ (1 dissected, no. 82, contained larva), with same label data as holotype. All in the AMNH.

OTHER MATERIAL EXAMINED: VENEZUELA: *Bolívar*: Guaiquinima Tepui, camp I, 63°30'W, 55°5'N, 1150 m, 24–28/II/90, D. Grimaldi (1♂, 1♀, both dissected, nos. 142, 143, respectively) (in the AMNH).

ETYMOLOGY: In reference to the telescoping female terminalia.

*Cladochaeta trauma*, new species

Figures 117, 118, 120, 129

DIAGNOSIS: Postocellar setae minute, ocellar setae small (ca. 0.6× size of frontal-orbital setae); anterior reclinate setae minute; frons long and sloping; oral margin with dark brown stripe; thorax mostly yellow, with diffuse brown stripe on notopleural edge and darker, thin stripe in middle of pleura; anterior dorsocentrals about half the size of posterior ones; male and female genitalia very distinctive within genus, as described below.

DESCRIPTION: HEAD: Rather long in lateral view, with front long and sloping. Eyes completely bare; lower hind margin of eye with very slight indentation, barely perceptible. Pedicel ochre medially, light brown laterally; flagellomere I dark brown; arista with 3 dorsal branches, ventral one closest to base of terminal fork. Frontal vittae shiny, golden; frontal orbital plates lighter, yellow. Frons of moderate width, rather long and sloping, with 6–8 interfrontal setulae near ptilinal suture. Frontal orbital setae: Anterior reclinate minute, indistinguishable from setulae on frontal orbital plates; posterior reclinate about midway between proclinate and inner vertical; proclinate and post. reclinate orbitals about equal in size. Postocellar setae minute; ocellar setae small and thin, ca. 0.6× length of orbitals. Face of moderate width (FW/HW = 0.33) and flat; light yellow with dark brown stripe just dorsal to oral margin. Cheeks light yellow and shallow (CD/ED = 0.09). Genal space shallow. Proboscis yellow, palps mostly yellow with tips light brown.

THORAX: Scutellum and notum ochre; postnotum ochre; diffuse brown stripe along no-

topleural edge; pleura mostly yellow, with thin, dark brown stripe running along entire length; katapisternum entirely light yellow. Anterior dorsocentrals small, about half the length and width of posterior dorsocentrals. Posterior dorsocentrals slightly closer to anterior dorsocentrals than to scutellum. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars almost parallel; post. scutellars slightly cruciate. Postpronotal lobe with 1 stout seta, other seta indistinguishable from setulae. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 2–3 setae on ventrolateral surface. Halter with stem light brown, apical half of knob yellow. Wing hyaline, without dark clouds even on x-veins. Apex of vein  $R_{2+3}$  turned very slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M parallel, slightly curved. Crossvein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Tergites evenly light brown; epandrium (male) darker and shinier than others. Female terminalia without tergal bridge beneath epi-/hypoproct; apical sternite heavily sclerotized and completely separated into pair of broad lateral lobes, each with ca. 20 fine setulae near apex; small ventral sclerite and narrow medial sclerite having trifid apex between sternal lobes. Male genitalia very distinctive: Cerci quite small, with small flat flange on lateral edge of both halves; ventral lobes (presumably of cerci) apparently monstrously developed into membranous sac bearing 6 heavily sclerotized spines (2 ventral ones largest, 4 dorsal ones ca. 0.2–0.3× the size). Epandrial lobe very broad in middle, with irregular arrangement of numerous stiff, short setae, ca. 30 per lobe. Aedeagus sclerotized, with distiphallus trowel-shaped, having pointed tip and small preapical flanges. Surstyli unique in genus: Long, thin (pointed at apex), curved dorso-medially, and slightly cruciate (resembling tusks), with row of ca. 7 stiff, fine setulae on mesal margin at base; tip is heavily sclerotized. Hypandrium very short, with very long gonopods.

TYPES: Holotype, Male: COSTA RICA: *San José*: Zurquí de Moravia, 1600 m, VII/

92, P. Hanson, Malaise trap (not dissected). Paratypes: 1♂ (dissected, no. 293), 4♀ (1 dissected, no. 292), with same data as holotype. All in the AMNH.

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Named in reference to the imposing appearance of the spines on the male genitalia.

*Cladochaeta vapidia*, new species

Figures 117–119, 130

DIAGNOSIS: Distinctive from other species in the group for the light brownish body color (evenly yellow in others, and with brown pleural stripe in some); male genitalia hardly sclerotized, even surstyli; surstylus lobate and with numerous fine setae at apex, not pointed and sclerotized; known only from the Dominican Republic.

DESCRIPTION: HEAD: Rather high and short in lateral view (HL/HD = 0.69 [HT]). Eyes completely bare; lower hind margin of eye very slightly indented. Pedicel light brown, flagellomere I darker brown; arista with 3 dorsal branches, ventral one midway between d-3 and terminal fork; branches of terminal fork of moderate length. Frontal vittae shiny, golden; frontal orbital plates dull, ochre. Frons of moderate width, with 4 interfrontal setulae. Frontal orbital setae: Anterior reclinate lost, other orbitals long; posterior reclinate slightly closer to proclinate than to inner vertical. Postocellar setae minute; ocellar setae about same size as post. reclinate setae. Face of moderate width (FW/HW = 0.34), flat, and light yellowish white. Cheeks of moderate depth (CD/ED = 0.08). Genal space shallow. Proboscis and palps yellow.

THORAX: Scutellum, notum, and pleuron entirely and evenly light brown, except for light yellow on ventral part of katapisternum; bluish pruinescence (when viewed at anterior angle) on anterior part of katapisternum. Anterior dorsocentrals ca. 0.6× length of posterior dorsocentrals. Posterior dorsocentrals about midway between scutellum and anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior

scutellars parallel, post. scutellars slightly convergent. Postpronotal lobe with 1 large seta. Legs entirely light yellow; forefemur with 1 long, fine preapical seta on dorsolateral surface; 3 setae on ventrolateral surface. Wing entirely hyaline, without clouds of dark infuscation even on x-veins. Apex of vein  $R_{2+3}$  turned very slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly bent. Wing tip slightly pointed.

ABDOMEN: Female terminalia unknown. Male genitalia: Cerci not narrow and long; slight ventral lobe bearing 1 long seta. Epandrial lobe very narrow in middle, length 5× width, with row of only 3 stiff, short setae in middle. Distiphallus narrow, troughlike; slightly longer than cerci. Surstyli unsclerotized, with broad apical lobe, ventrolaterally flattened, apex of lobe with ca. 20 setulae, base with 1 seta. Hypandrium very short, gonopods of standard length and width.

TYPE: Holotype, Male: DOMINICAN REPUBLIC: La Vega, 24 km E El Rio, 3/VIII/78, L. B. O'Brien (in NMNH) (genitalia dissected, no. 141).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Latin *vapidus* (dull, stale), in reference to the dull, yellow, undistinguished habitus and simple male genitalia.

*Cladochaeta vittata*, new species

Figures 117, 131

DIAGNOSIS: The dark, even stripe along the midline of the pleuron is a distinctive external feature of this species, as is the long, flat head. Male genitalia very distinctive, with membranous sac bearing 2 pairs small, sclerotized spines; sac flanked by 2 pairs of very large sclerotized spines. Cerci and epandrium also distinctive, as described below.

DESCRIPTION: HEAD: Quite long and flat in lateral view (HL/HD = 1.02 [HT]). Eyes completely bare; lower hind margin of eye barely indented. Pedicel light brown, flagellomere I darker brown; aristae badly damaged in only specimen, apparently with 3 dorsal branches and 1 ventral branch. Frontal vittae shiny, golden; frontal orbital plates dull yellow. Frons broad, with 10 interfrontal

setulae. Frontal orbital setae: Anterior reclinate lost, other orbitals long; posterior reclinate midway between proclinate and inner vertical. Postocellar setae minute; ocellar setae small, ca.  $0.6\times$  size of orbitals. Face wide of moderate width ( $FW/HW = 0.31$ ), flat; light yellowish white with dark brown stripe along oral margin. Cheeks shallow ( $CD/ED = 0.08$ ). Genal space shallow. Proboscis yellow, palps light brown.

THORAX: Scutellum and notum mostly yellowish, with faint diffuse brown on notopleural edge; pleuron mostly yellow, except for dark brown stripe in middle of pleuron along entire length. Anterior dorsocentrals about half the length of posterior dorsocentrals. Posterior dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Anterior scutellars parallel, post. scutellars slightly convergent. Postpronotal lobe with 1 large seta. Legs badly damaged. Wing entirely hyaline, without any infuscation, even faint clouds over x-veins r-m and dm-cu. Vein  $R_{2+3}$  almost straight, apex gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Female terminalia unknown. Male genitalia: Cerci with long ventral lobe bearing dense microtrichia. Epandrial lobe not very broad in middle, length ca.  $4\times$  width (medial margins slightly convex); each lobe with irregular arrangement of 26–28 stiff, short setae, row of 5 setae near medial margin largest. Aedeagus with distiphallus having a membranous bag (about equal in size to cerci); ventral half of bag with fine, membranous spicules. Membranous bag with 2 pairs of black spines: ventral pair closer together, one-half the size of dorsal pair. Base of distiphallus "bag" with pair of long, sharp, sclerotized spines pointed downward; length equal to that of bag. Base of aedeagus with pair of sclerotized rods on each side, apices articulated with distiphallus "bag" and pointed downward. Aedeagal apodeme triangular in lateral view; posterior end with rectangular opening. Surstyli short, broad,

and flat, with ca. 8 tiny scattered setulae; apical tip curled inward; apical third heavily sclerotized. Hypandrium very short (with gonopods?).

TYPE: Holotype, Male: PANAMA: *Chiriqui*: Boquete, VIII/58, W. B. Heed & M. Wasserman (dissected, no. 252) (in AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype specimen.

ETYMOLOGY: In reference to the pleural vitta, or stripe.

*Cladochaeta yanomama*, new species

Figures 117–119, 130

DIAGNOSIS: Wings evenly dusky; male genitalia similar to *neosimplex*, with differences as noted under diagnosis of that species.

DESCRIPTION: HEAD: Short and tall in lateral view ( $HL/HD = 0.69$  [HT]). Eyes completely bare; lower hind margin of eye slightly indented. Pedicel yellow, flagellomere I light brown; aristae with 3 dorsal branches and 1 ventral branch (slightly closer to d-3 than to terminal fork); branches of terminal fork relatively long. Frontal vittae shiny, golden on dorsal half (anterior half dull yellow); frontal orbital plates dull yellow. Frons of moderate width, with 7 interfrontal setulae. Frontal orbital setae: Anterior reclinate lost, other orbitals long; posterior reclinate much closer to proclinate than to inner vertical. Postocellar setae minute; ocellar setae same size as orbitals. Face narrow ( $FW/HW = 0.25$ ), flat, and light yellow. Cheeks shallow ( $CD/ED = 0.07$ ). Genal space shallow. Proboscis yellow, palps yellow.

THORAX: Scutellum, notum, and pleuron entirely and evenly yellowish. Anterior dorsocentrals about half the length of posterior dorsocentrals. Posterior dorsocentrals slightly closer to scutellum than to anterior dorsocentrals. Acrostichals in 6 uneven rows; ones immediately anterior to scutellum and ant. dorsocentrals not enlarged. Scutellar setae damaged. Postpronotal lobe with 1 large seta. Forefemur with 1 preapical seta dorsolaterally and with row of 3 setae ventrolaterally. Wing evenly and lightly dusky, but without clouds of darker infuscation even over x-veins. Apex of vein  $R_{2+3}$  gradually

meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed.

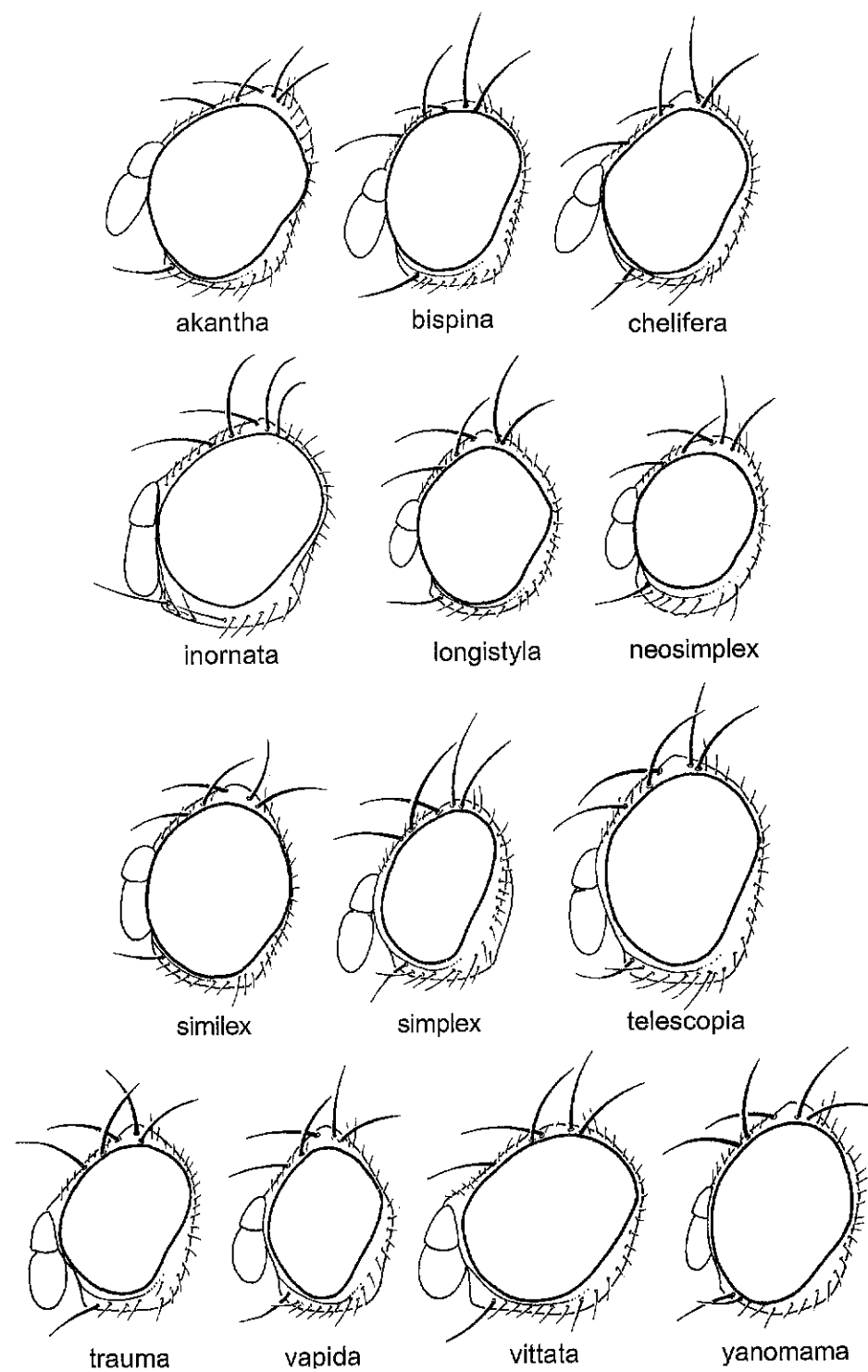
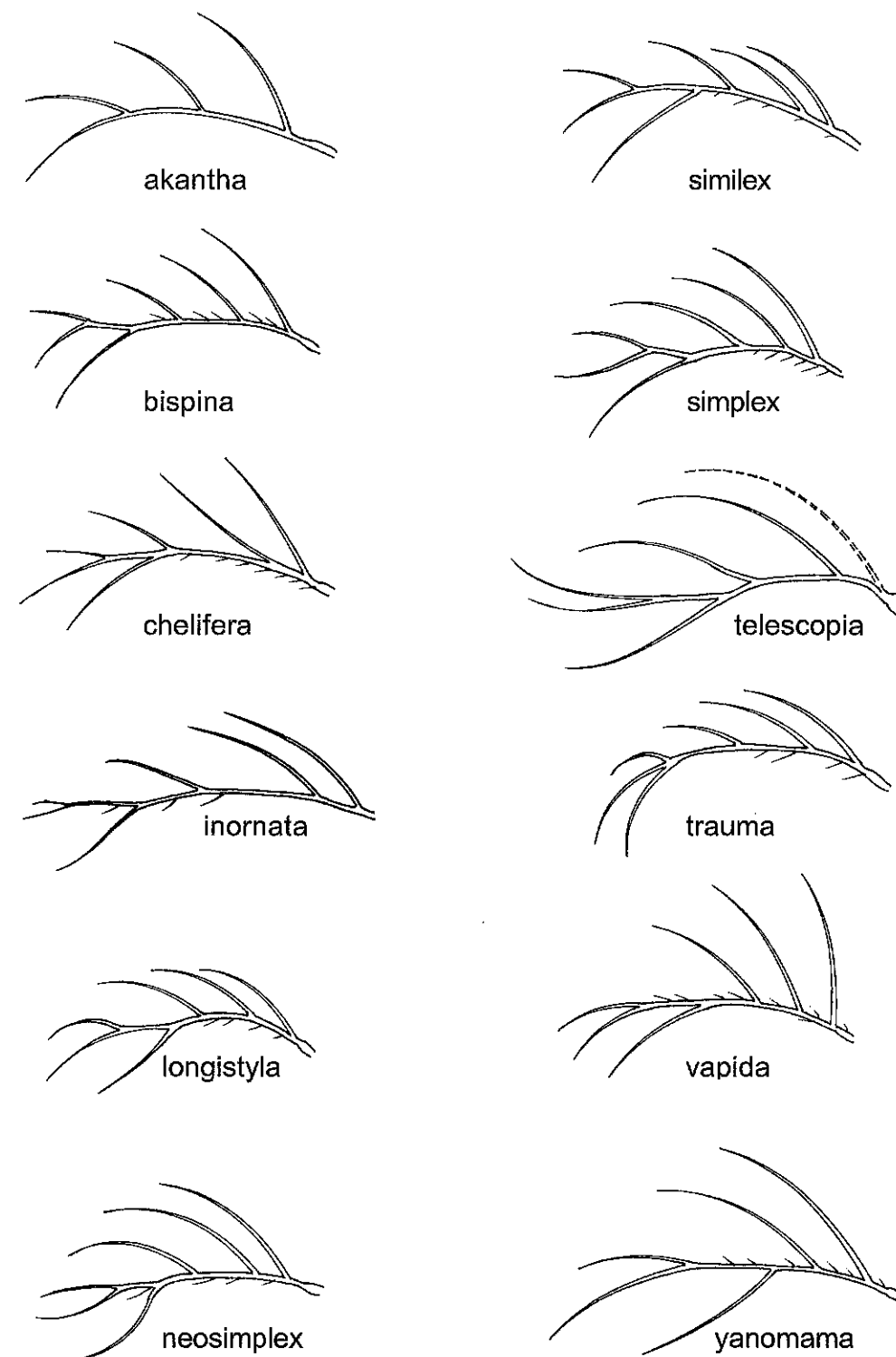
ABDOMEN: Female terminalia unknown. Male genitalia: cerci rather small, with distinct, small ventral lobe. Epandrial lobe broad in middle, length only  $2.5\times$  width; each lobe with irregular row of 8–9 stiff, short setae. Aedeagus short, with membranous distiphallus; distiphallus somewhat bulbous, with large central opening. Aedeagal apodeme broad, flat, upright. Surstyli sclerotized (especially at ends); broad in lateral

view, dorsal margin with hump in middle; mesal surface with 10 fine, scattered setulae. Hypandrium very short, U-shaped, with deep gonopods very far apart.

TYPE: Holotype. Male: VENEZUELA: *Amazonas*: Rio Mavaca Camp,  $65^{\circ}06'W$ ,  $2^{\circ}2'N$ , 150 m, 16–27/III/89, Phipps-FUDECI Expedition by AMNH, D. A. Grimaldi (in AMNH) (genitalia dissected, no. 133).

OTHER MATERIAL EXAMINED: Known only from holotype.

ETYMOLOGY: Named for the indigenous people of the type locality.

Fig. 117. Heads of *simplex* group species.Fig. 118. Aristae of *simplex* group species.



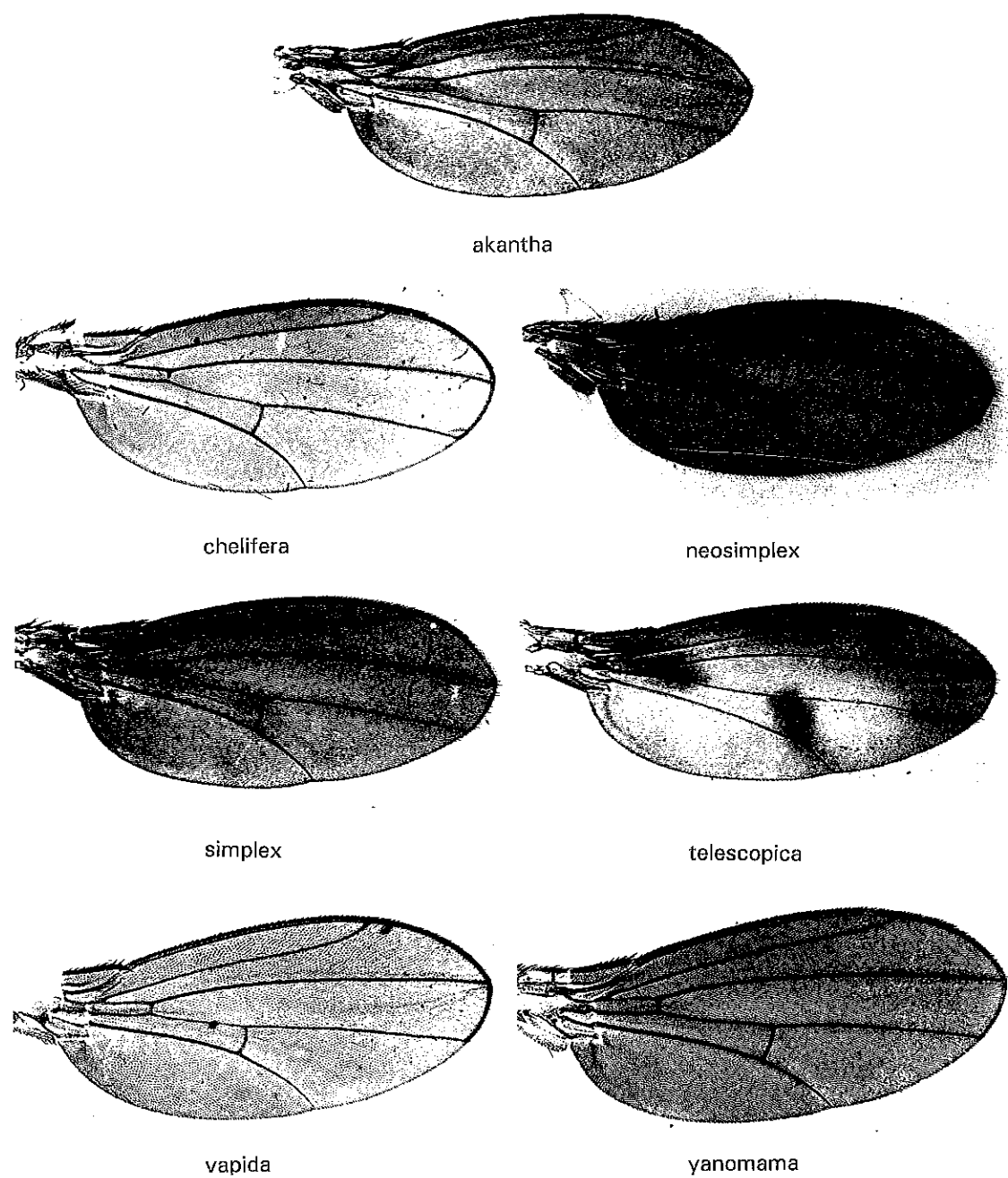


Fig. 119. Wings of *simplex* group species.

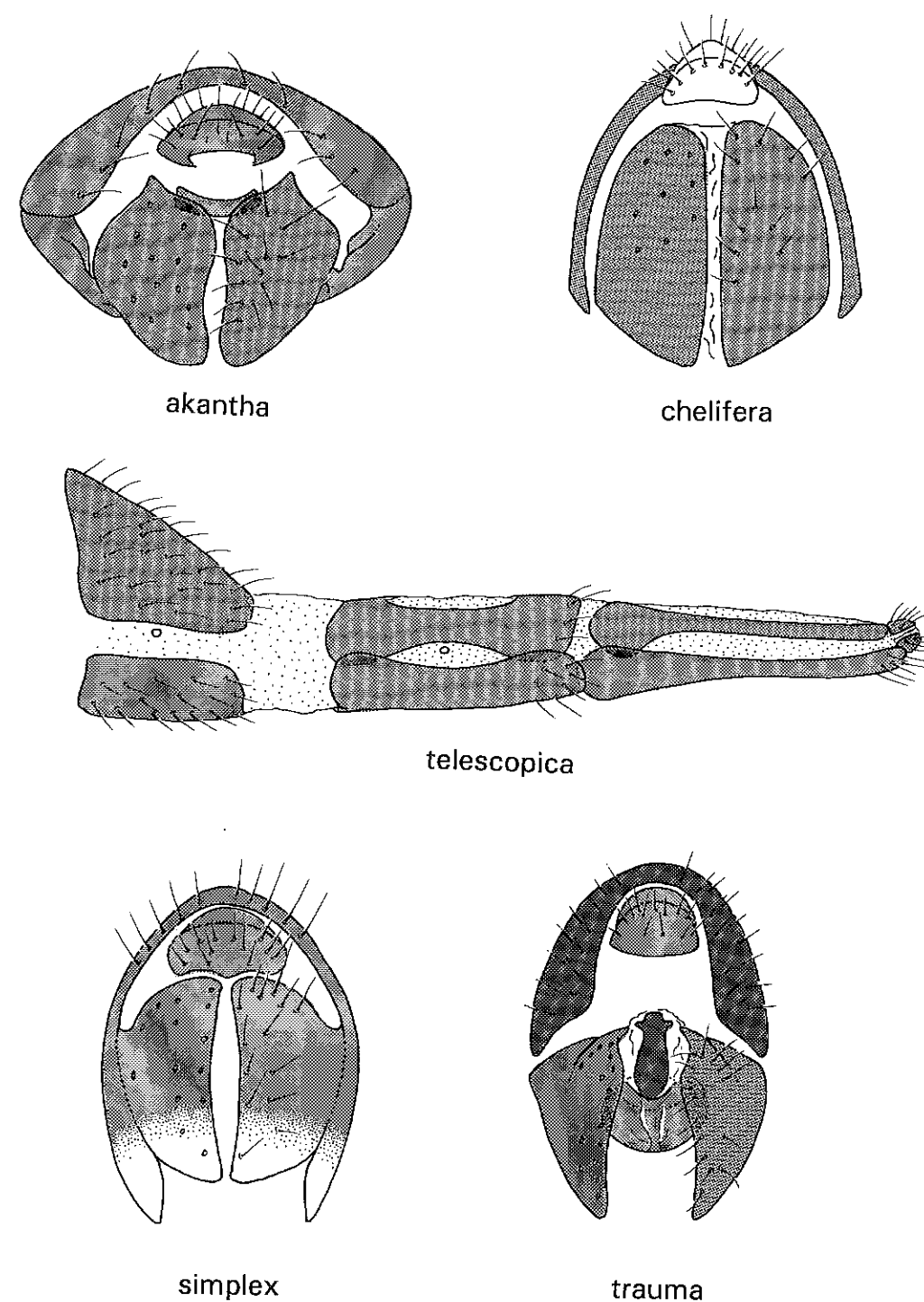


Fig. 120. Female terminalia of *simplex* group species, posterior views (*telescopica* is lateral).





Fig. 121. Male terminalia of *C. akantha*.

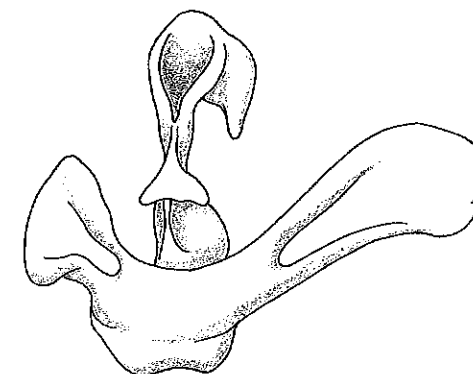
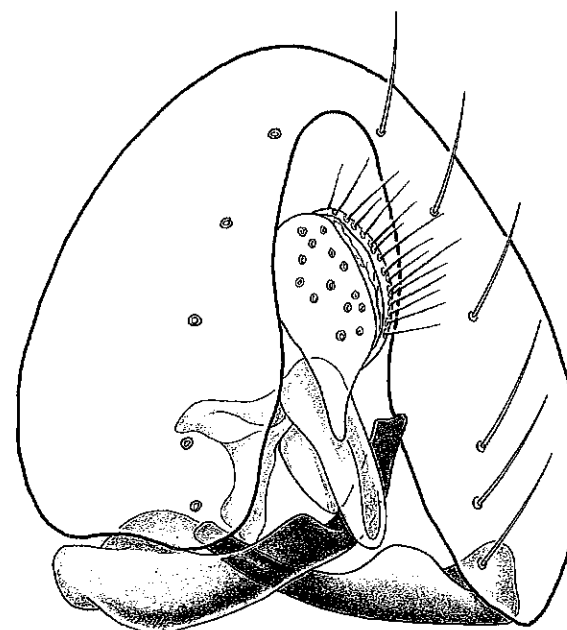
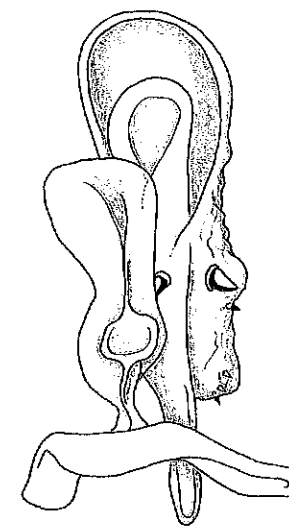
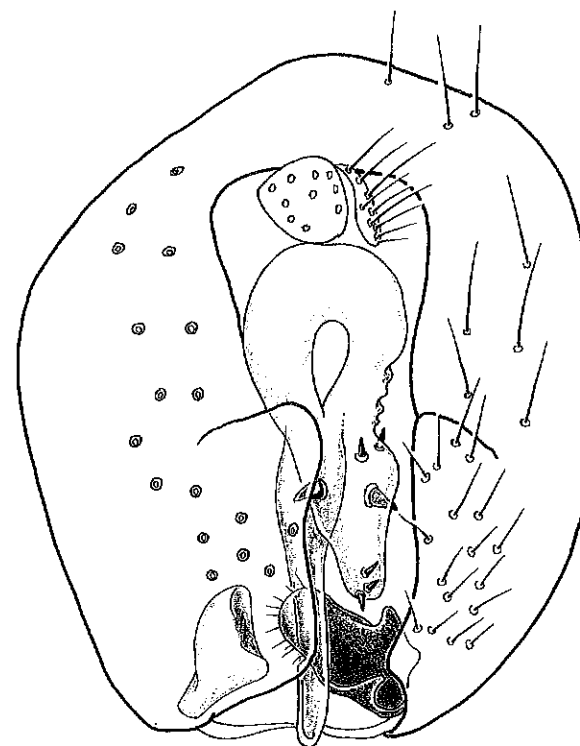


Fig. 122. Male terminalia of *C. bispina* (above) and *C. longistyla* (below).



Fig. 123. Male terminalia of *C. chelifera*.

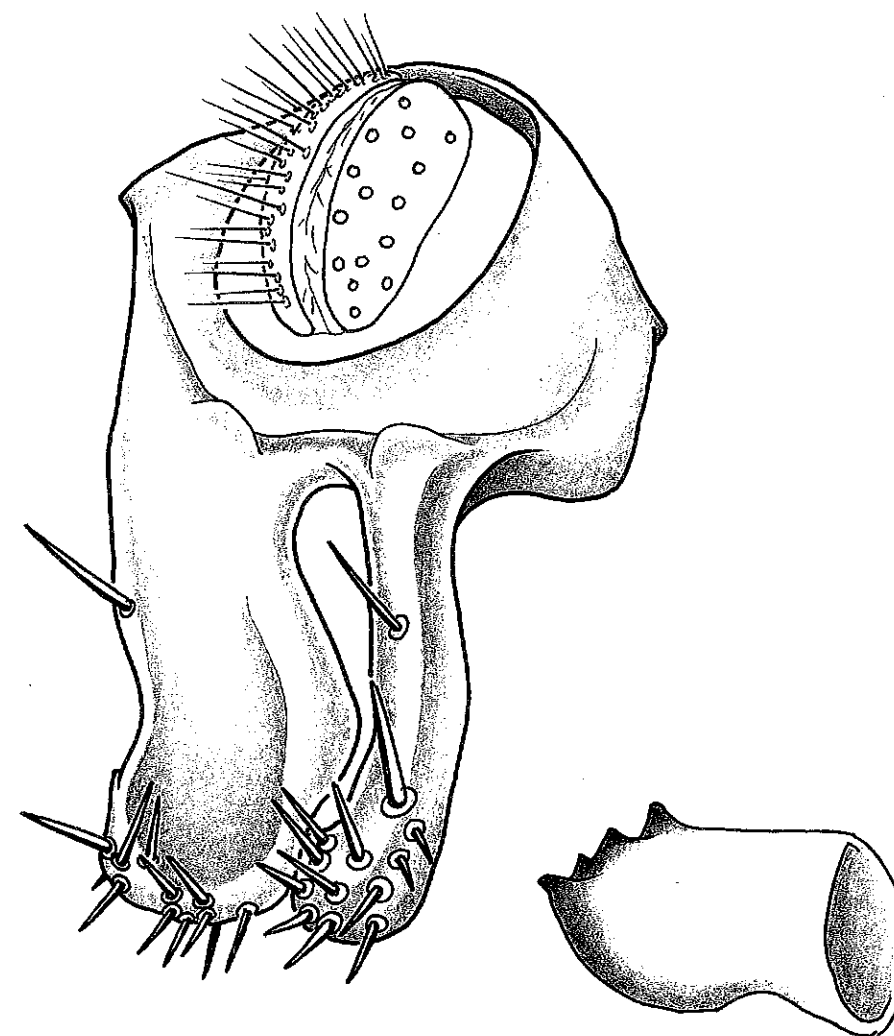


Fig. 124. Male terminalia of *C. inornata*, epandrium with lobes only, plus surstylus.

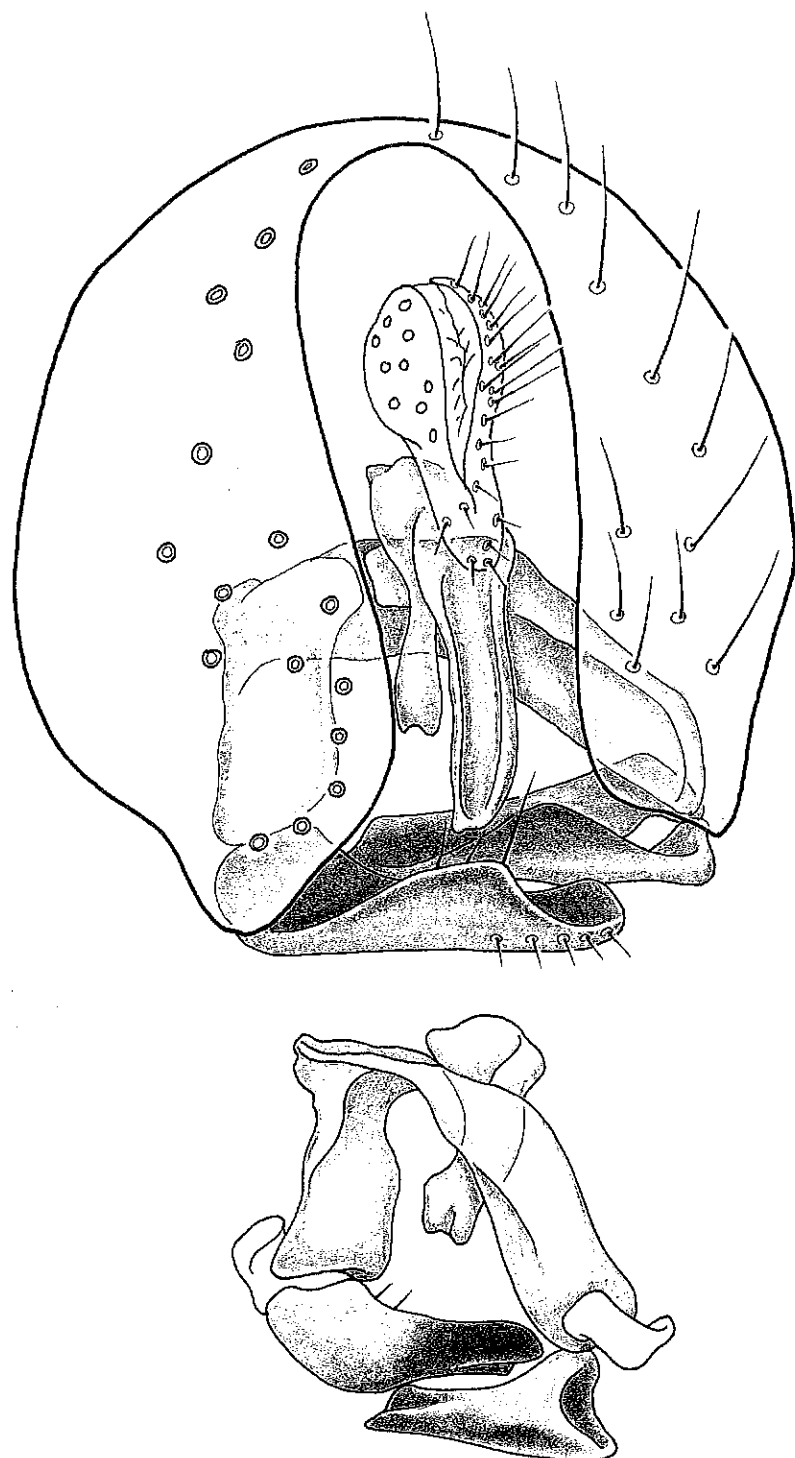


Fig. 125. Male terminalia of *C. neosimplex*.

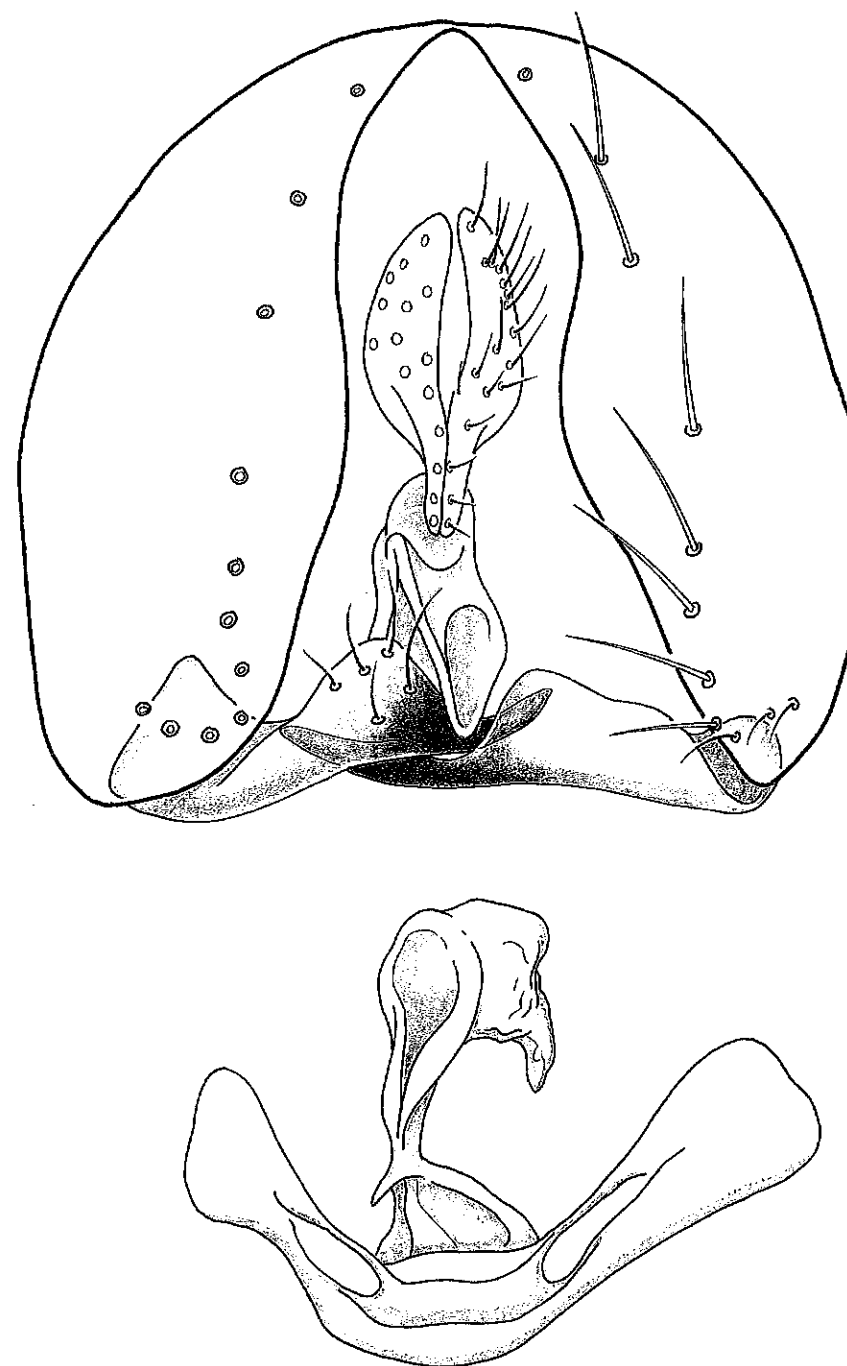


Fig. 126. Male terminalia of *C. similex*.

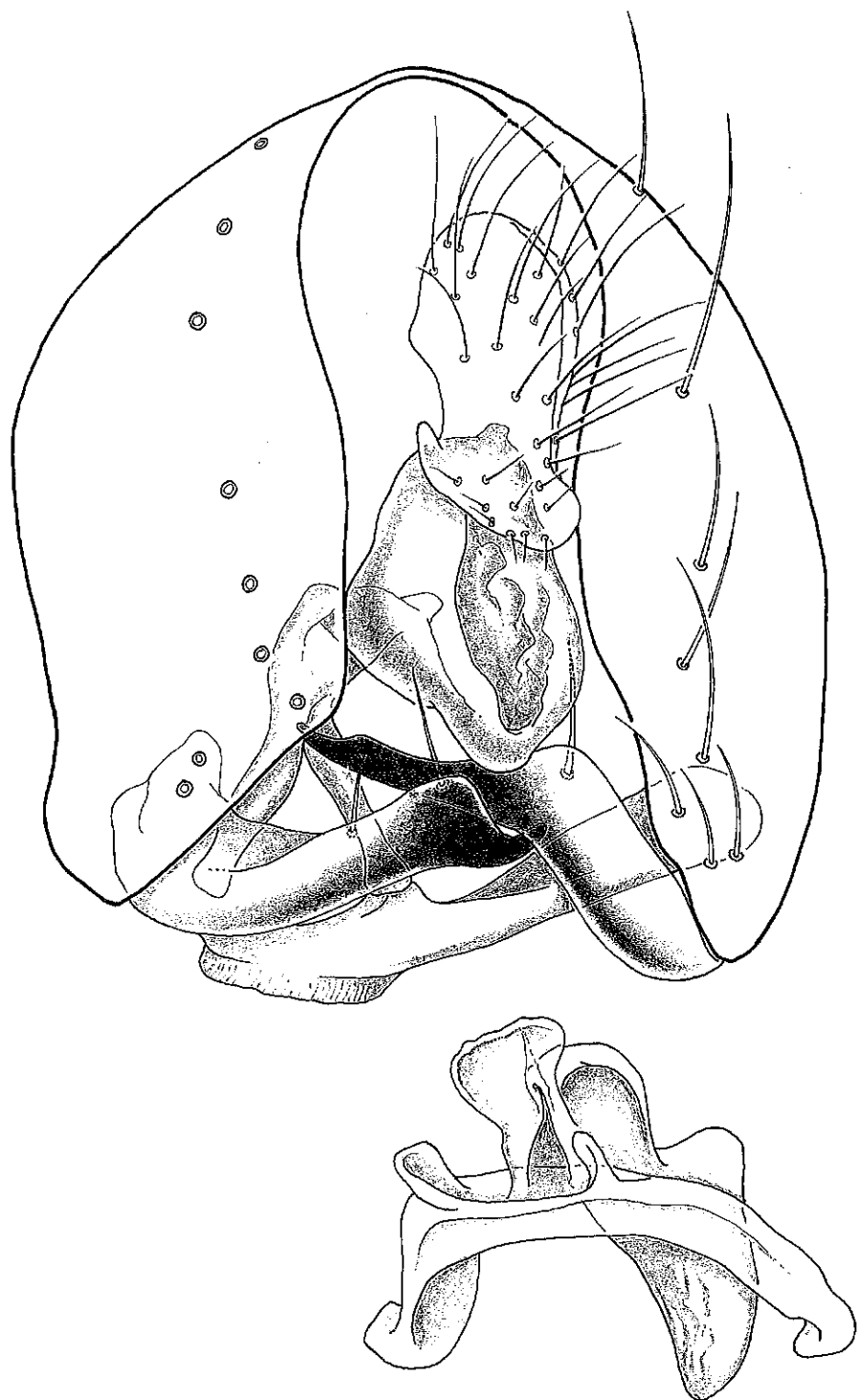


Fig. 127. Male terminalia of *C. simplex*.

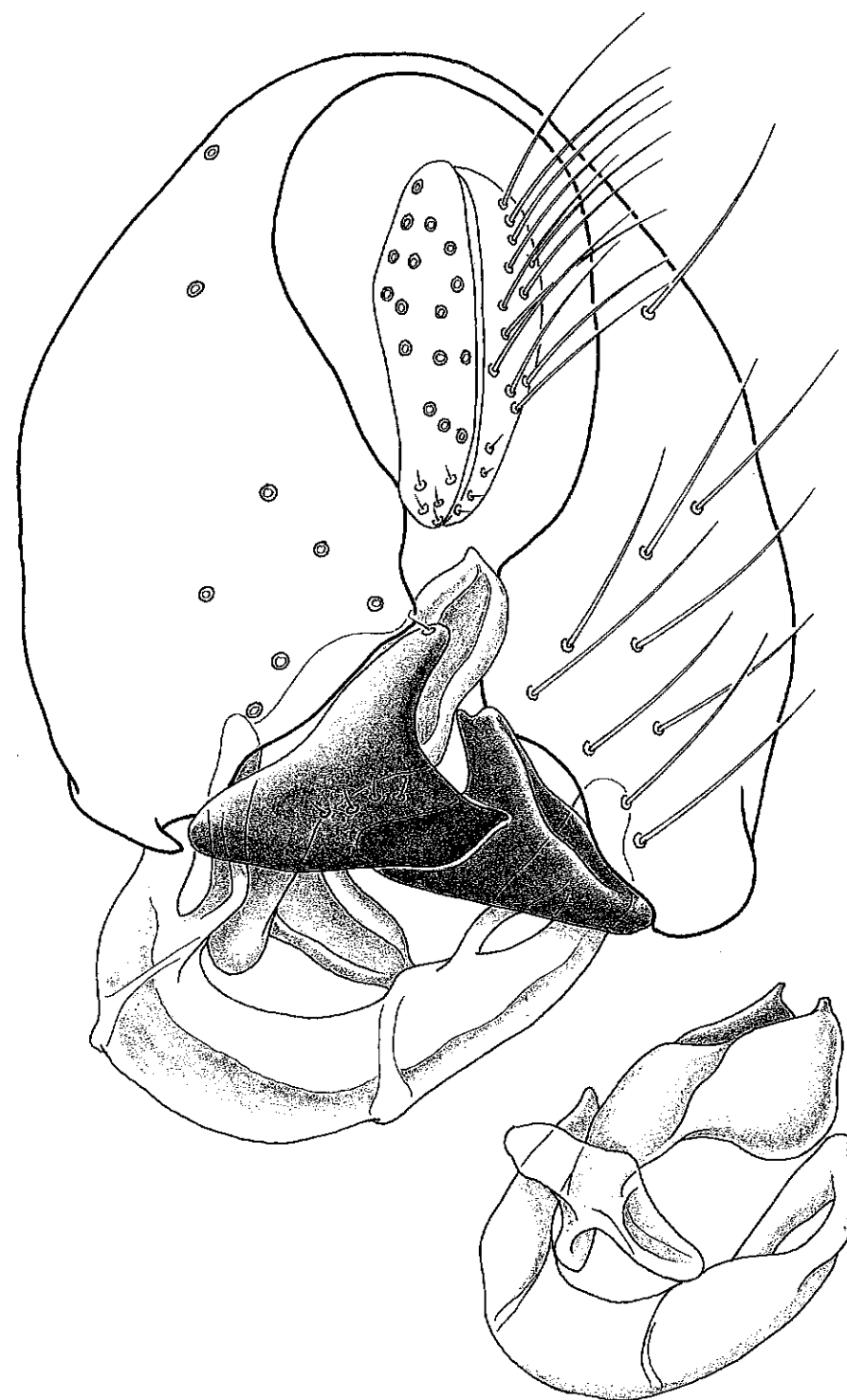


Fig. 128. Male terminalia of *C. telescopica*.



Fig. 129. Male terminalia of *C. trauma*.

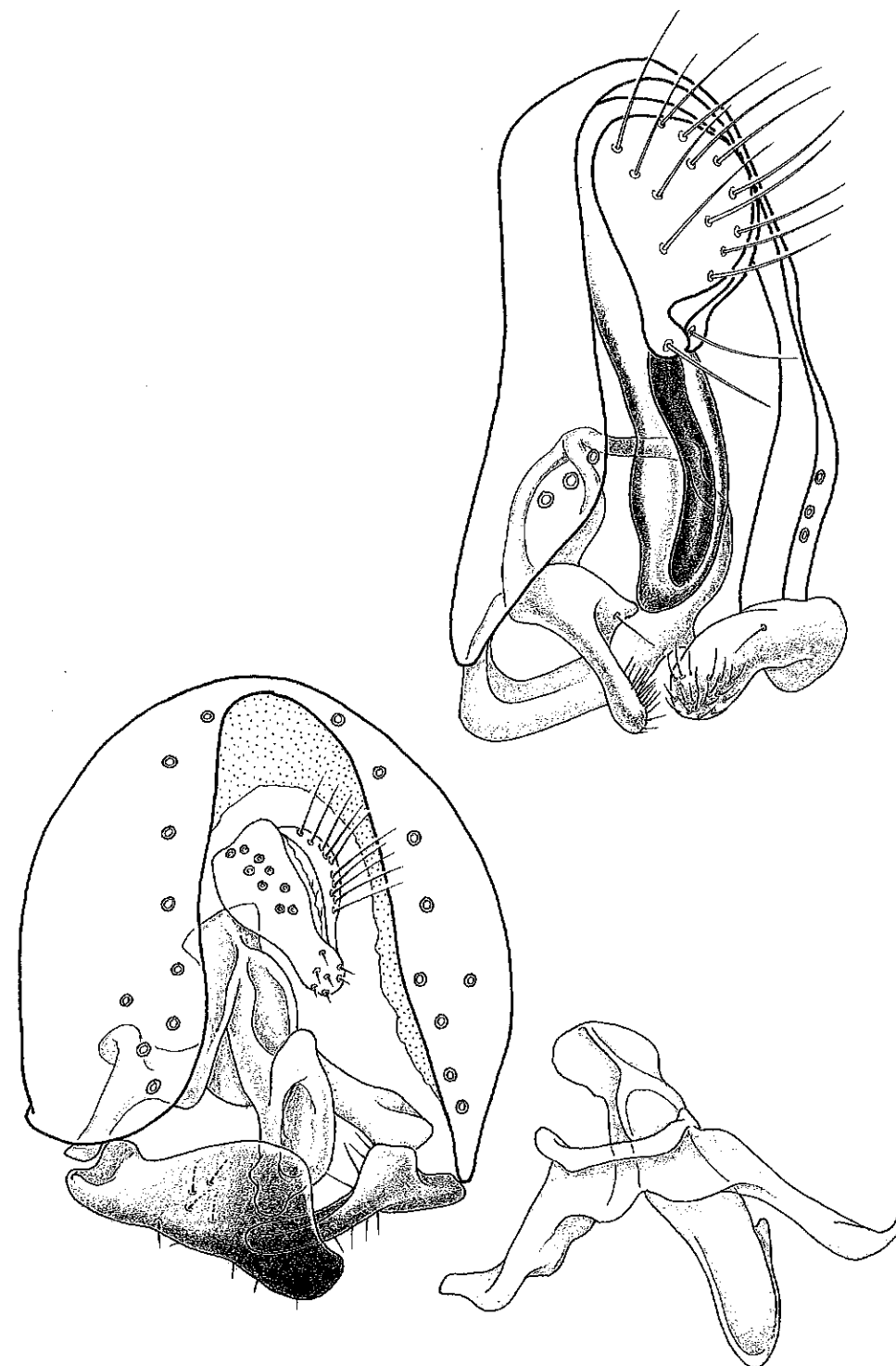


Fig. 130. Male terminalia of *C. vapida* (above) and *C. yanomama* (below).

Fig. 131. Male terminalia of *C. vittata*.

## Simplex Group

Fig. 132. Distribution of *simplex* group species.



## ARMATA SPECIES GROUP

DIAGNOSIS: Distinctly monophyletic based on the intricate modifications of the male genitalia, in particular an aedeagal-paraphysal complex that is heavily sclerotized and has hooked spines.

*Cladochaeta albifrons*, new species

Figures 133, 135

DIAGNOSIS: Externally distinctive based on front of head that is white, pollinose; flagellomere I almost white, arista reduced to 2 short dorsal branches (with very short dorsal branch on apical fork); anterior reclinate orbital seta minute, posterolateral to proclinate; wings hyaline, body almost entirely yellow; male genitalia with heavily sclerotized, complex paraphyses forming 6 spines, as described below. Known only from a single male from central Costa Rica.

DESCRIPTION: HEAD: Rather short in lateral view. Eyes with short, very fine, sparse pilosity; lower hind margin of eye with slight indentation. Antenna with pedicel yellow, flagellomere I almost white. Arista with 2 short dorsal branches, very short apical branch, no ventral branches. Front mostly pollinose white, more yellowish when viewed dorsally; ocellar triangle yellow, not dark; postociput yellow, not dark brown. Frontal-orbital setae: Proclinate orbitals same size as posterior reclines; anterior reclinate orbitals minute, no larger than interfrontal and frontal-orbital setulae, posterior and slightly lateral to proclines. Posterior reclinate midway between ipsilateral proclinate and inner vertical. Face short, fairly broad (FW/HW = 0.35), tan, and without carina. Cheeks fairly shallow (CD/ED = 0.11 [HT]). Proboscis and palps yellow.

THORAX: Entire thorax yellow, even pleura. Dorsocentral and scutellar setae damaged and mostly lost in type specimen. Acrostichals in 6 uneven rows. Postpronotal lobe with 1 large seta (ventral one small and fine, ca. 0.3× size of dorsal one). Legs entirely light yellow; forefemur unobservable. Wing entirely hyaline, without clouds of diffuse infuscation even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Wings too twisted to deter-

mine if veins  $R_{4+5}$  and M are parallel. Crossvein dm-cu straight. Wing tip slightly pointed. Halter tan.

ABDOMEN: Tergites dark brown. Female terminalia unknown. Male genitalia: Cercus with ventral margin flat. Epandrium higher than wide; height ca. 1.5× the width. Ventrolateral halves of epandrium (epandrial lobes) very narrow, each with row of 5 long, fine setae. Aedeagus typically heavily sclerotized and twisted into sharp points. Paraphyses very heavily sclerotized, asymmetrical; connected dorsally by thin bridge. Right paraphysis with 2 lobes, both projected ventrad. Left paraphysis complex, with dorsal pair of lobes closely adpressed, projected posteriad; ventral lobes projected ventrad; most of inner lobe spatulate, possibly the aedeagus. Aedeagal apodeme narrow, spatulate, lightly sclerotized. Surstyli barely sclerotized; without narrow stem, with long basal lobe (having row of ca. 5 fine setulae at apex), a broad median lobe with a smaller, thin dorsal lobe; inner edge of median lobe with row of ca. 10 fine, stiff setulae. Hypandrium with rounded anterior margin, shallow ventral keel. Gonopods well developed. Apical sternites not examined.

TYPES: Holotype, Male: COSTA RICA: *San José*: Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 281) (in the AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: In reference to its most distinctive external feature, a white (*alba*) front (*frons*).

*Cladochaeta amblyharpa*, new species

Figures 133, 134, 136, 145

DIAGNOSIS: Ocellar triangle with bluish pruinescence; arista with 3 dorsal branches (no ventral ones); pleura mostly brown, with lighter notum; paraphyses very heavily sclerotized, with left one hooked upward, tip of right paraphysis with blunt end; ventral lobe of epandrium with row of 3 large, lanceolate, scalelike setae.

DESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.86 [HT]). Eyes with short, dense pilosity; lower

hind margin of eye with slight indentation. Antenna with pedicel brown; flagellomere I mostly brown, with yellow spot on inside surface at dorsal edge. Arista with 3 short dorsal branches, very short apical branch, no ventral branches. Front bronze to light brown; ocellar triangle darker, but with bluish pruinescence when head is viewed from front. Frontal-orbital setae: Proclinate orbitals ca. 0.8× length of posterior reclines; anterior reclinate orbitals ca. 0.3× width and length of proclines, immediately lateral to proclines (sometimes also slightly posterior to them). Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Face short, fairly broad (FW/HW = 0.33 [N = 20]), tan, and without carina. Cheeks fairly deep (CD/ED = 0.13). Proboscis yellow, palps light brown.

THORAX: Notum, scutellum, and postnotum ochre. Most of pleura brown, ventral half of katepisternum yellow. Anterior dorsocentrals ca. 0.7× length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars parallel; posterior scutellars cruciate for ca. 0.3× their length to just barely cruciate. Postpronotal lobe with 1 large seta (ventral one small, about half the size of dorsal one). Legs entirely light yellow; forefemur with ventrolateral row of 4 very long setae; dorsolateral row with 1 preapical and 1 subbasal seta, smaller ones between them. Wing entirely hyaline, without clouds of diffuse infuscation even on crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites light brown; last 2 tergites lighter and yellowish in males. Female terminalia moderately sclerotized; apical tergite setose, not connected beneath epi-/hypoproct; peaked dorsally. Apical sternite completely divided into pair of small, roughly triangular setose lobes lying near ventral tip of lateral tergal lobes. Penultimate tergite and sternite connected laterally (but not fused), forming ring around tergite and sternite.

Male genitalia: Cercus with lateroventral corner projected into a thin lobe; apex slightly beneath epandrium. Epandrium much higher than wide; height ca. 1.8× width. Ventrolateral halves of epandrium (epandrial lobes) very narrow; each with row of 6 long, broad, scalelike setae (3 dorsalmost setae ca. 2× larger than 3 ventral ones). Paraphyses very heavily sclerotized, asymmetrical; connected by thin dorsal bridge. Left paraphysis projected posteriad with apex turned sharply upward; strongly hooked. Right paraphysis complex, with lobe in middle projected posteriad, larger ventral lobe with flat apical knob; smaller lobe projected inside, also with flat apical knob. Aedeagal apodeme much broader dorsally, scoop-shaped. Surstyli without narrow stem, almost L-shaped, with large dorsal lobe and small medial lobe ventrally; ca. 25 fine setulae along mesal surface. Hypandrium with rounded anterior margin, shallow ventral keel. Apical sternites not examined.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-4/IX/84, 2100 m, H. Wolda (not dissected). Paratypes: Same data (8♂, no. 247; 17♀) (all in AMNH).

OTHER MATERIAL EXAMINED: Known only from type series.

ETYMOLOGY: From Greek *amblys* (blunt) and Latin *harpago* (grappling hook), in reference to the blunt tip of the right paraphysis.

*Cladochaeta armata* (Frota-Pessoa)

Figures 133, 134, 137, 138, 145

*Cladochaeta armata* Frota-Pessoa, 1947: 195.  
*Cladochaeta armata*: Wheeler, 1981: 34 (new combination); Vilela and Bächli, 1990: 7.

DIAGNOSIS: The male of this species is very easily distinguished from other males by the unique setation of the middle and hind legs, as given in the description. Genitalia of male with paraphysis forked. Females are not distinctive and are best identified by association with males in series.

REDESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.71). Eyes with short, dense pilosity; lower hind margin of eye with very slight indentation. Antenna with pedicel light brown; flagello-

mere I darker brown. Arista with 3 short dorsal branches, very short apical branch; 1 ventral branch, closer to d-3 than apical branch, or almost opposite d-3. Front light brown; ocellar triangle about same color as rest of front. Frontal-orbital setae: Proclinate orbitals approx. equal in length to posterior reclinate; anterior reclinate orbitals completely lost (no vestiges remain). Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Face broad (FW/HW = 0.33 [N = 9]), flat, tan, and without carina. Cheeks of moderate depth (CD/ED = 0.11). Proboscis yellow, palps yellow.

THORAX: Notum, scutellum, and postnotum ochre. Most of pleura light brown, ventral half of katepisternum yellow. Anterior dorsocentrals ca. 0.8× length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars parallel; posterior scutellars barely touching to very slightly cruciate. Postpronotal lobe with 1 large seta (ventral one small, ca. 0.6× size of dorsal one). Legs entirely yellow. Male: Mid-tibia apically with row of 5 curved short setae; a pair of longer, straight setae just proximal to these (1 on each side); 1 very long (ca. 4× width of tibia) seta more proximal yet to these, on lateral surface; 4 slightly curved setae in row near middle of tibia, lengths 2–3× width of tibia. Hind leg: Femur with ventral row of 8 slightly curved setae; tibia with 2 rows of conspicuous setae on ventral and dorsal surfaces. Ventral row with 5 setae and dorsal row with 9 longer setae; lengths of dorsal setae ca. 2.5× width of tibia. Wing slightly and evenly dusky, but without clouds of diffuse infuscation even over x-veins. Vein  $R_{2+3}$  virtually straight; apex gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M very slightly divergent, almost parallel but both curved. Crossvein dm-cu slightly bent. Wing tip rounded. Halter light yellow.

ABDOMEN: Tergites light brown. Female terminalia: Apical tergite sclerotized, without setae, not connected beneath epi-/hypoproct. Apical sternite bilobed, completely separated; each lobe bulbous, with small, flat lateral lobe, each with ca. 8 setulae. A broad, shal-

low, roughly triangular sclerite lies ventromedial to sternal lobes. Male genitalia: Cercus with ventral margin nearly flat, slight ventrolateral lobes. Epandrium height ca. 1.3× width. Lobes of epandrium each with vertical row of 10 setae. Paraphyses heavily sclerotized, elaborate: each one with 2-pronged apex, basally with broad flange. Aedeagus membranous; supported by lightly sclerotized, flat lateral rods. Aedeagal apodeme flat, with shallow dorsal keel. Hypandrium oval, with shallow ventral keel and well-developed gonopods. Surstyli apically bilobed, with group of ca. 10 short, fine setae on smaller, proximal lobe; ca. 8 longer, curved setae on apical lobe.

TYPES: Holotype, Male: BRAZIL: *Sao Paulo*: Campos-do-Jordao, 1600 m, II/45. In the Museu Nacional, Rio de Janeiro, Brazil. I did not examine this specimen or the paratypes, but relied on the accuracy of Frota-Pessoa's leg and genitalia illustrations. Paratypes (1, an allotype): Same label data as holotype (1♀, 1♂), also in the Museu Nacional, and 1♂ in the Laboratorio de Helminologia do Instituto Oswaldo Cruz (Frota-Pessoa, 1947).

MATERIAL EXAMINED: BRAZIL: *Nova Teutonia*: 27°11'S, 52°23'W, 300–500 m, Fritz Plaumann, XI/58 (2♀, 1 dissected, DAG 96); IX/58 (2♀); VII/59 (1♀); VIII/58 (1♀); VIII/62 (2♀); IX/62 (1♂, dissected, no. 95). All in the CNC, except 2 females placed in the AMNH.

ETYMOLOGY: The species was originally named in reference to the very spiny hind legs of the male.

DISCUSSION: It is quite possible that the male uses the combs of enlarged setae on the middle and hind legs to brush against the abdomen of females during copulation and/or mounting. This species is known only from the small series that we examined, as well as the holotype and a paratype male.

*Cladochaeta hamula*, new species

Figures 133, 139

DIAGNOSIS: A small species that is quite indistinct externally: arista with 3 short dorsal branches and large terminal fork; cheek deep (CD/ED = 0.19). Identified best on ba-

sis of external and internal male genitalia: paraphyses heavily sclerotized, left one much larger and triangular; aedeagus mostly membranous and bulbous, with hooked process.

DESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.75). Eyes with short, dense pilosity; lower hind margin of eye with very slight indentation. Antenna with pedicel light brown; flagellomere I darker brown. Arista with 3 short dorsal branches, rather large apical branch; no ventral branches. Frontal vittae shiny, golden; frontal-orbital plates approximately of same color; ocellar triangle small, with slight bluish pruinescence. Frontal-orbital setae: Proclinate orbitals ca. 0.7× length of posterior reclinate; anterior reclinate orbitals very small, ca. 0.3× size of proclinate, immediately lateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Face broad (FW/HW = 0.36 [N = 3]), flat, and tan, without carina. Cheeks quite deep (CD/ED = 0.13). Proboscis yellow, palps yellow.

THORAX: Notum, scutellum, and postnotum ochre. Most of pleura light brown, including most of katepisternum. Anterior dorsocentrals ca. 0.6× length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars parallel; posterior scutellars with apices barely touching. Postpronotal lobe with 1 large seta. Legs entirely yellow; forefemur with 1 long dorsolateral seta and 2 dorsoventral setae. Wing entirely hyaline, without clouds even on x-veins. Vein  $R_{2+3}$  virtually straight; apex gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly bent. Wing tip slightly pointed.

ABDOMEN: Tergites dark brown. Female terminalia unknown. Male genitalia: Cercus with ventral margin narrowed, but not elongate. Epandrium barely higher than wide; ventrolateral halves of epandrium (epandrial lobes) splayed, not especially narrow; each with row of 6 long, fine setae. Aedeagus membranous, slightly sclerotized, with long, thin apical spine sharply hooked to the left. Paraphyses heavily sclerotized, asymmetrical

and irregular; connected dorsally by broad bridge; both are stout lobes covering dorsal half of aedeagus; 2 small sclerites flank the sides of the aedeagal sac. Aedeagal apodeme small, lightly sclerotized, rectangular. Surstyli without narrow stem, almost L-shaped, with longer apical lobe having ca. 20 fine setae on ventral margin and 20 on base. Hypandrium and gonopods not observed. Apical sternite small, round, with dense microtrichia.

TYPES: Holotype, Male: EL SALVADOR: Cerro Monte Cristo, 7000 ft, II/54, W. B. Heed (not dissected). Paratypes: Same data (3♂, nos. 222, 257) (AMNH).

OTHER MATERIAL EXAMINED: Known only from the type specimens.

ETYMOLOGY: From the Latin *hamus* (hook), in reference to the acutely hooked spine at the apex of the aedeagus.

*Cladochaeta paravolsella*, new species

Figures 133, 140

DIAGNOSIS: Head very distinct: front is white, pollinose, and shiny (perhaps just a male character; female is unknown). Arista with 3 short dorsal branches, no ventral branch; wing hyaline. Male genitalia most similar to *C. amblyharpa*, but distinct as described below.

DESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.86 [HT]). Eyes almost completely bare; lower hind margin of eye with slight indentation. Antenna with pedicel and flagellomere I light brown. Arista with 3 short dorsal branches and very short apical branch, no ventral branches. Front (of male only?; females unknown) white, pollinose, and reflective, particularly at frontal view. Ocellar triangle slightly darker, but with light bluish pruinescence around edge. Frontal-orbital setae: Proclinate orbitals ca. 0.8× length of posterior reclinate; anterior reclinate orbitals ca. 0.3× width and length of proclinate, immediately lateral to proclinate. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Face short, fairly wide (FW/HW = 0.34), and tan, without carina. Cheeks fairly deep (CD/ED = 0.15). Proboscis and palps whitish.

THORAX: Notum, scutellum, and postnotum ochre. Most of pleura and notopleural area light brown, katapisternum yellow. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars slightly convergent; posterior scutellars cruciate for ca.  $0.2\times$  their length. Postpronotal lobe with 1 large seta (ventral one small, ca.  $0.4\times$  size of dorsal one). Legs entirely light yellow; forefemur with 2 long ventrolateral setae and 1 preapical seta dorsolaterally. Wing entirely hyaline, without clouds of diffuse infuscation even over crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel, slightly curved. Crossvein dm-cu straight. Wing tip slightly pointed. Halter light yellow.

ABDOMEN: Tergites light brown. Female terminalia unknown. Male genitalia: Cercus with lateroventral corner projected slightly into a small lobe, apex not reaching margin of epandrium. Epandrium higher than wide; height ca.  $1.5\times$  width. Ventrolateral halves of epandrium (epandrial lobes) narrow; each with row of 7 long, thin, stiff setae. Paraphyses very heavily sclerotized, asymmetrical; connected by thin dorsal bridge. Left paraphysis with basal part of arm projected downward, then apical part turned posteriad but paraphysis not hooked. Right paraphysis complex, with lobe in middle projected posteriad (apical tip bent slightly upward); large cup-shaped ventral portion with lobe projected downward; ventral lobe without knob at apex (apex tapered to point); smaller lobe projected inside. Aedeagal apodeme unsclerotized; broad, troughlike. Surstyli without narrow stem, with large dorsal lobe and small medial lobe at base; medial lobe sclerotized, apex pointed; ca. 25 fine setulae along mesal surface. Hypandrium with rounded anterior margin, shallow ventral keel, gonopods short. Apical sternites not examined.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-4/IX/84, 2100 m, H. Wolda (dissected, no. 228) (AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype.

ETYMOLOGY: From Greek *para* (beside, near) and *volSELLa*, a specific epithet for another species in the group.

*Cladochaeta tricerabops*, new species

Figures 133, 134, 141

DIAGNOSIS: Anterior reclinate orbital seta lost; arista with 1 ventral and 4 dorsal branches; pleura mostly brown; wing hyaline; male genitalia distinctive for the 3 sharp, heavily sclerotized prongs surrounding aedeagus, as described below; hypandrium and aedeagal apodeme sclerotized.

DESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.68). Eyes with very short, fine, dense pile; lower hind margin of eye with very slight indentation. Antenna with pedicel and flagellomere I brown. Arista with 4 dorsal branches of intermediate length, an apical branch (half the length of dorsal branches), one ventral branch between d-3 and d-4. Front shiny, golden, some specimens with bluish pruinescence when head viewed from front. Four fine, short interorbital setulae present. Frontal-orbital setae: Proclinate orbitals equal in size to posterior reclimates; anterior reclinate orbitals completely lost. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Face of moderate depth and fairly wide (FW/HW = 0.33 [N = 7]), tan to light brown, completely flat. Cheeks of moderate depth (CD/ED = 0.11). Proboscis yellow, palps light brown.

THORAX: Notum, scutellum, and postnotum ochre to light brown. Most of pleura brown, darker than notum, including katapisternum. Anterior dorsocentrals ca.  $0.6\times$  length of posterior dorsocentrals; post. dorsocentrals approximately midway between scutellum and ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars slightly convergent; posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta (ventral one small, about half the size of dorsal one). Legs entirely light yellow; forefemur with 2 long ventrolateral setae and 1 preapical seta dorsolaterally. Wing entirely hyaline, without even small clouds of infuscation over crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned abruptly costad. Veins

$R_{4+5}$  and M parallel. Crossvein dm-cu slightly bent in middle. Wing tip rounded. Halter light yellow.

ABDOMEN: Tergites dark brown. Female terminalia very reduced to simple apical tergite, an inverted U-shaped sclerite, without setae. Apical sternite bilobed, completely divided into pair of almost spherical lobes articulating with ventral tips of lateral lobes of apical tergite.

Male genitalia: Most of genitalia heavily sclerotized, including epandrium, hypandrium, aedeagal apodeme, paraphyses, and part of aedeagus. Cercus without narrow ventral lobe, ventrolateral corner pointed; ventral margin without sclerotized strip. Epandrium higher than wide; height ca.  $1.3\times$  width. Ventrolateral halves of epandrium each with row of 5 long, stiff setae (longest one dorsally; smallest one ventrally); ventral half of posterior margin slightly concave. Distiphallus (mostly obscure) small, with membranous base; apical knob with 2 ventral, sclerotized spines. Paraphyses forming 3 sharp spines with bases on circular collar; 2 dorsal ones with bases very close, spines nearly straight and pointing posteroventrad; ventral one medial to dorsal ones, ca.  $0.6\times$  length, and with tip curved. Aedeagal apodeme broad, paddle-shaped, with keel-like dorsal apodeme articulating with base of paraphysis collar. Surstyli simple, clavate, very lightly sclerotized. Apex of surstylus with row of ca. 12 fine setae on margin. Hypandrium nearly oval, with fairly deep ventral keel. Gonopods laterally thin and deep, long. Apical sternites not studied.

TYPES: Holotype, Male: DOMINICA (West Indies): Fond Figue Road, 3/II/65, W. W. Wirth, rain forest (not dissected). Paratypes: DOMINICA: S. Chiltern Est., 2/II/65 (2♀, no. 184); Fond Figue Road, 3♂, 1♀ (no. 183) (1♂, 1♀ in AMNH; all others and holotype in NMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: From the Greek *keras* (horn), or "three horns," in reference to the 3 largest prongs of the male genitalia, like the horns of *Triceratops*.

*Cladochaeta volsella*, new species

Figures 133, 142, 145

DIAGNOSIS: Arista with 4 short dorsal branches, very short apical branch; wing hyaline; male genitalia with distinctive surstyli and paraphyses, as described below.

DESCRIPTION: HEAD: Length and height moderate in lateral view (HL/HD = 0.77 [HT]). Eyes with very short, fine, dense pile; lower hind margin of eye with very slight indentation. Antenna with pedicel and flagellomere I light brown (flagellomere I slightly darker). Arista with 4 short dorsal branches and very short apical branch, no ventral branches. Front shiny, golden when viewed above; lightly pollinose blue viewed anteriorly. Ten fine, rather long interorbital setulae present. Frontal-orbital setae: Proclinate orbitals ca.  $0.8\times$  length of posterior reclimates; anterior reclinate orbitals minute, ca.  $0.2\times$  width and length of proclimates, immediately lateral to proclimates. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Face of moderate depth and fairly wide (FW/HW = 0.32 [N = 4]), tan, and completely flat. Cheeks of moderate depth (CD/ED = 0.14 [HT]). Proboscis and palps yellowish.

THORAX: Notum, scutellum, and postnotum ochre. Most of pleura yellowish, with slight brownish infuscation surrounding postpronotal lobe. Anterior dorsocentrals ca.  $0.6\times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars slightly divergent to parallel; posterior scutellars cruciate for  $0.2-0.3\times$  their length. Postpronotal lobe with 1 large seta (ventral one small, ca.  $0.4\times$  size of dorsal one). Legs entirely light yellow; forefemur with row of 4 long ventrolateral setae and 1 preapical seta dorsolaterally. Wing entirely hyaline, without any diffuse infuscation even over crossveins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel, not slightly divergent. Crossvein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Tergites light brown. Female terminalia unknown. Male genitalia: Ventrolateral corner of cercus with small lobe, ex-

tended to posterior edge of epandrium. Epandrium much higher than wide; height ca. 2× width. Ventrolateral halves of epandrium (epandrial lobes) narrow; each with row of 5 long, stiff setae. Paraphyses very heavily sclerotized, asymmetrical; connected by thin dorsal bridge. Left paraphysis with apical part hooked upward, with smaller spine in middle. Right paraphysis with broader base, apex narrow and acutely hooked downward. Aedeagal apodeme unsclerotized; broad, troughlike. Surstyli broad, slightly triangular, with pointed apex; ca. 25 fine setulae mostly on mesal surface. Hypandrium large, with

rounded anterior margin, shallow ventral keel. Apical sternites not examined.

**TYPES:** Holotype, Male: MEXICO: *Chiapas*: 7000 ft, 20 mi N Bochil, Y. Buena, cloud forest, 10/VI/69, Mason (not dissected). Paratypes: 2♂ (1 dissected, no. 99), with same label data as holotype (in CNC).

**OTHER MATERIAL EXAMINED:** PANAMA: *Chiriqui*: Chiriqui Viejo R., El Volcan, 5280 ft, 22/VII/66, A. Broce, light trap (1♂, no. 176) (NMNH).

**ETYMOLOGY:** Directly from Latin for pin-cers, in reference to the paraphyses of the male genitalia.

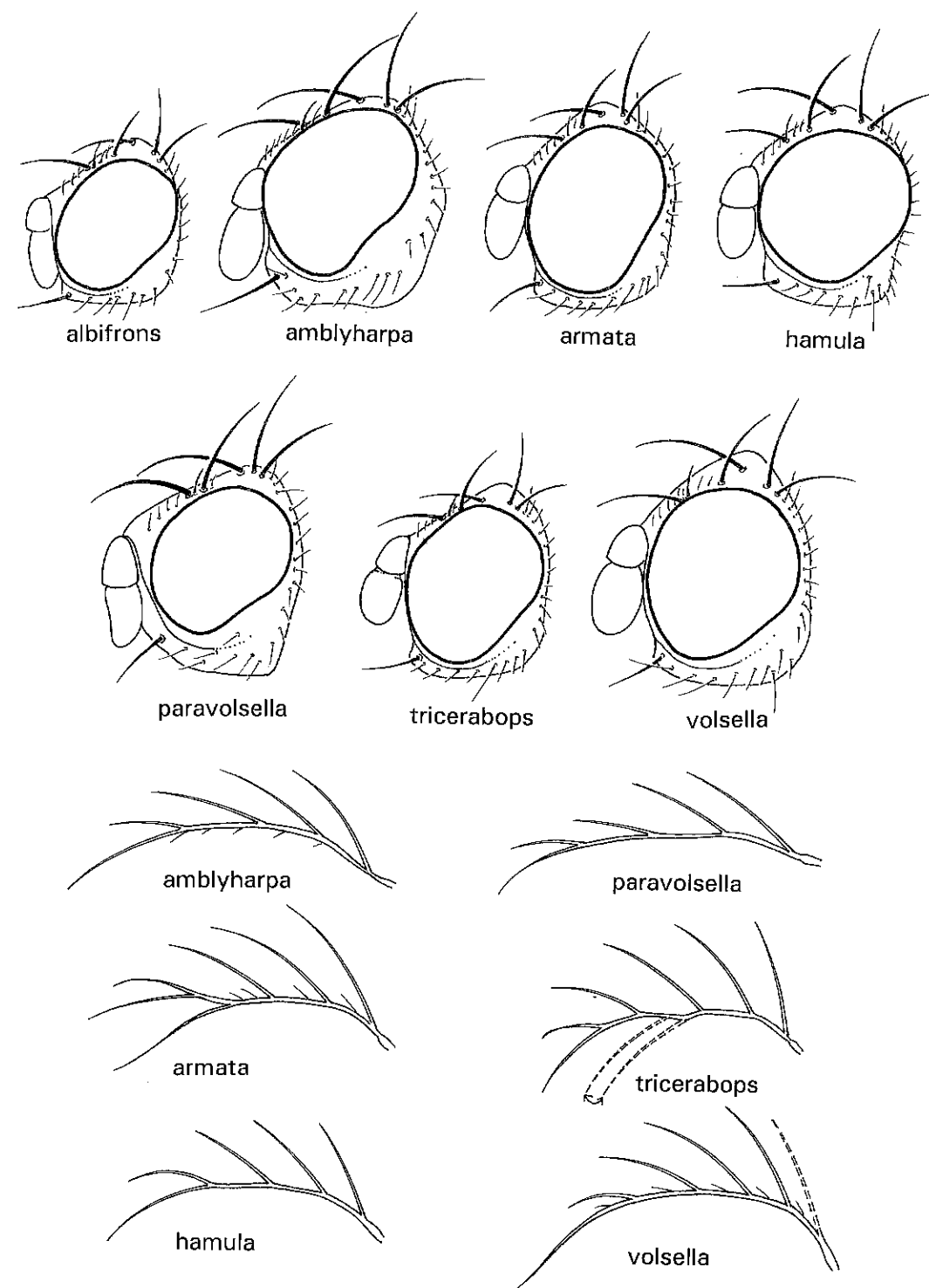


Fig. 133. Heads and aristae of *armata* group species.

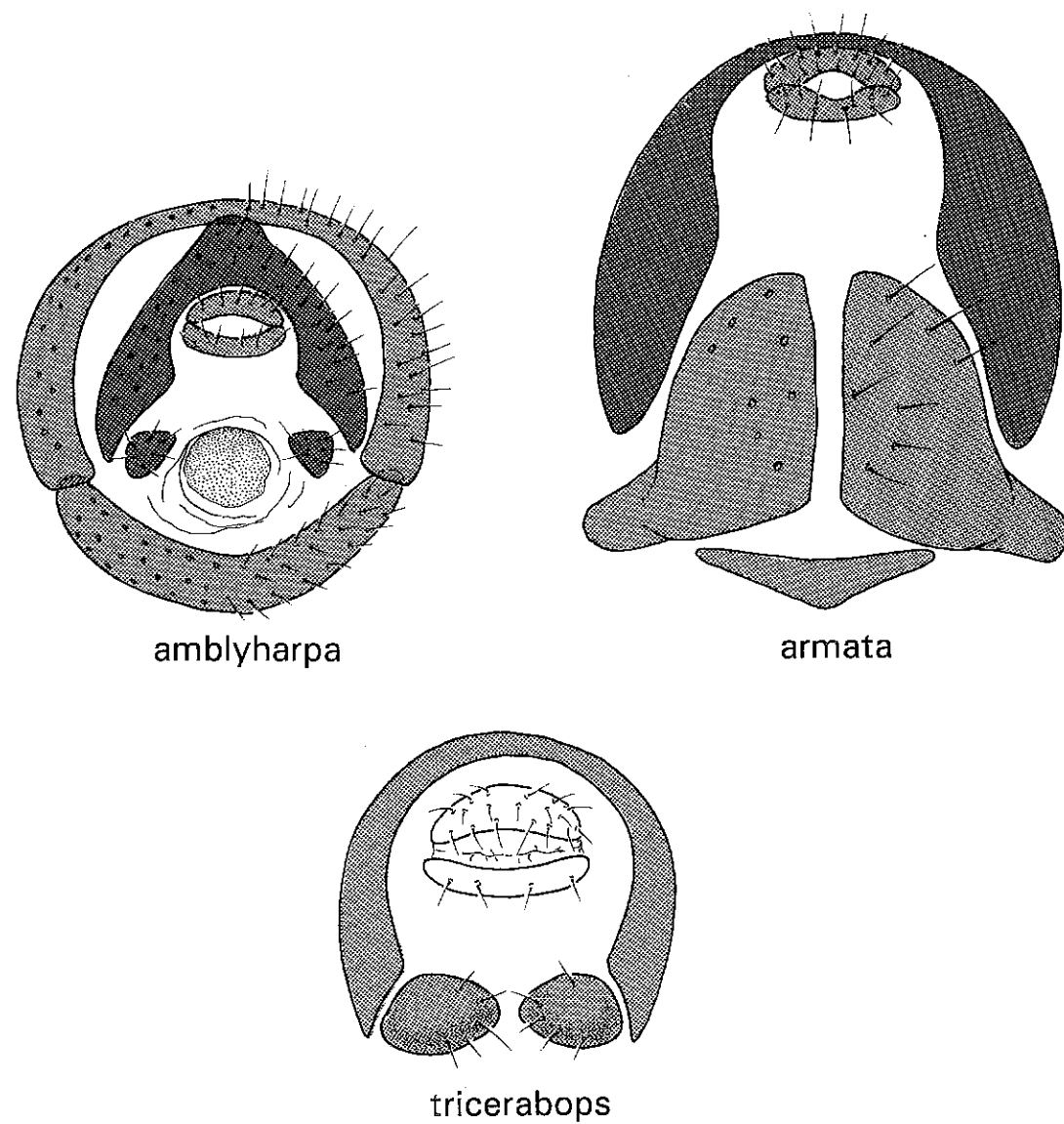


Fig. 134. Female terminalia of *armata* group species (posterior view).

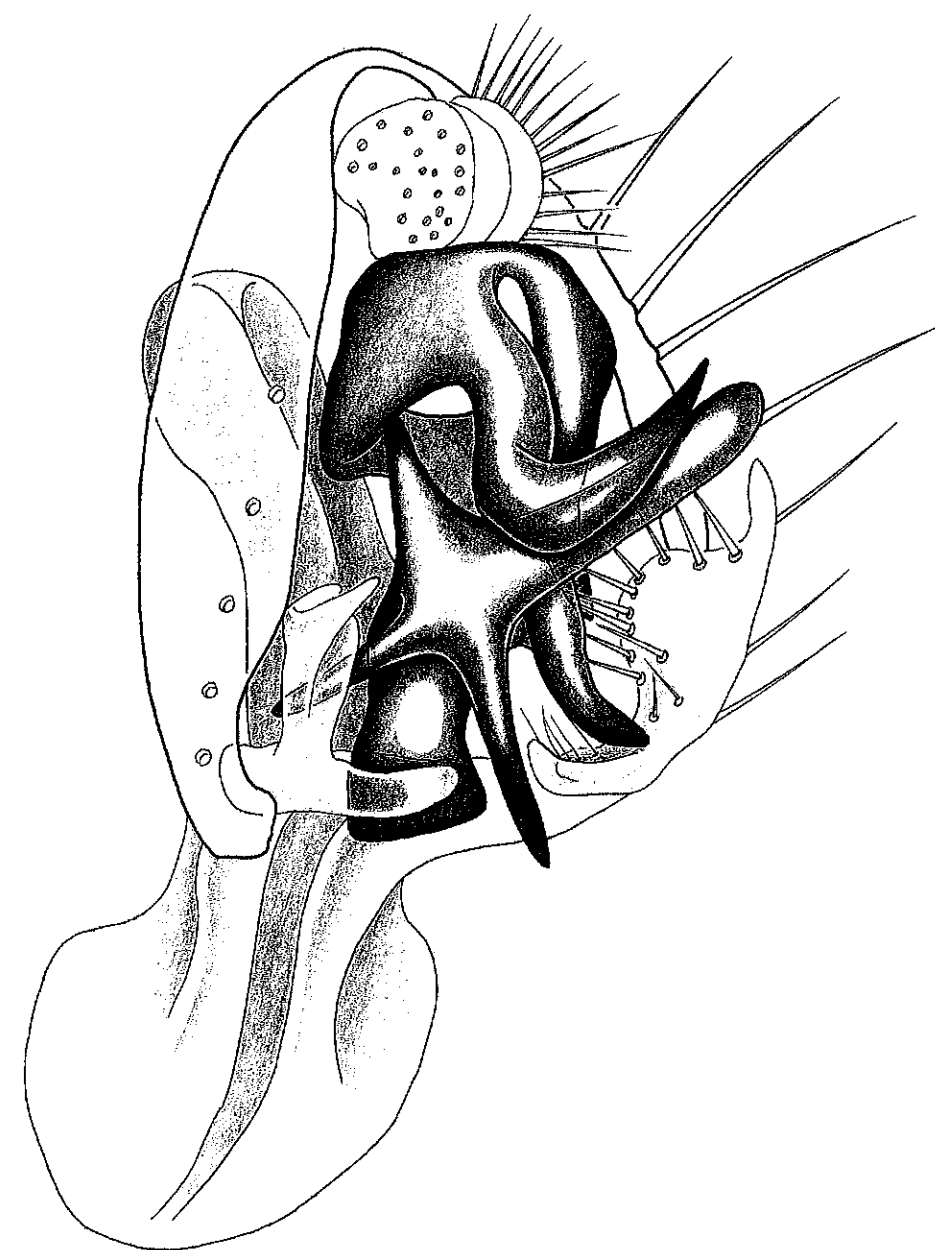


Fig. 135. Male terminalia of *C. albifrons*.



Fig. 136. Male terminalia of *C. amblyharpa*.



Fig. 137. Male terminalia of *C. armata*.



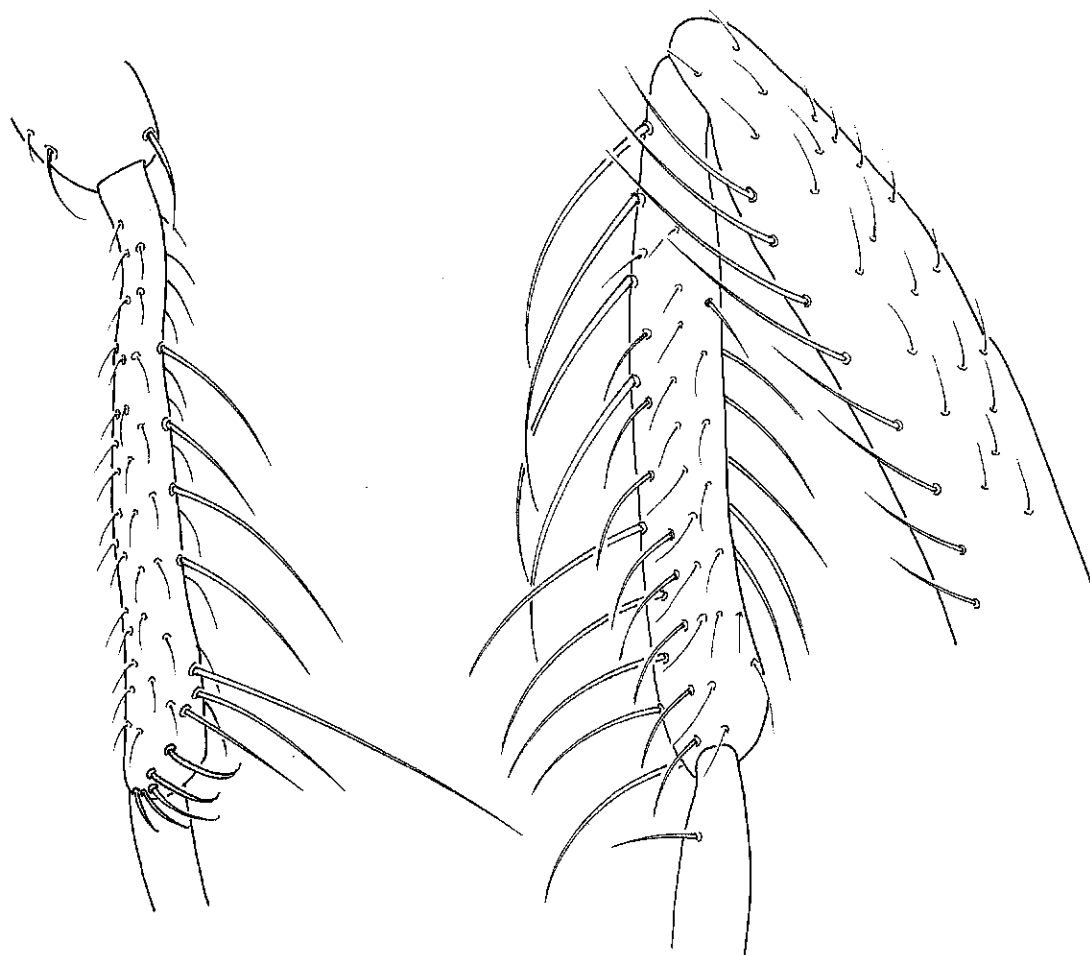


Fig. 138. Tibiae of *C. armata*. Left, left midleg (lateral view). Right, right hindleg (lateral view).

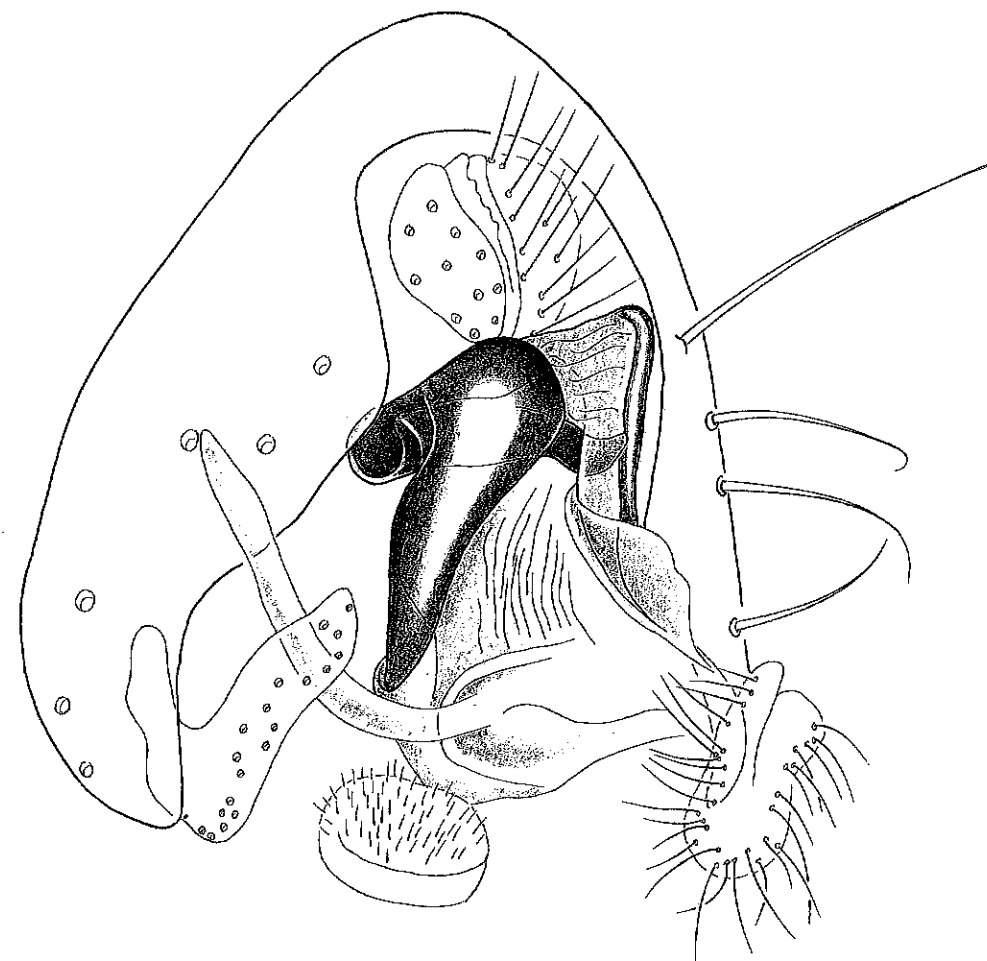


Fig. 139. Male terminalia of *C. hamula*.

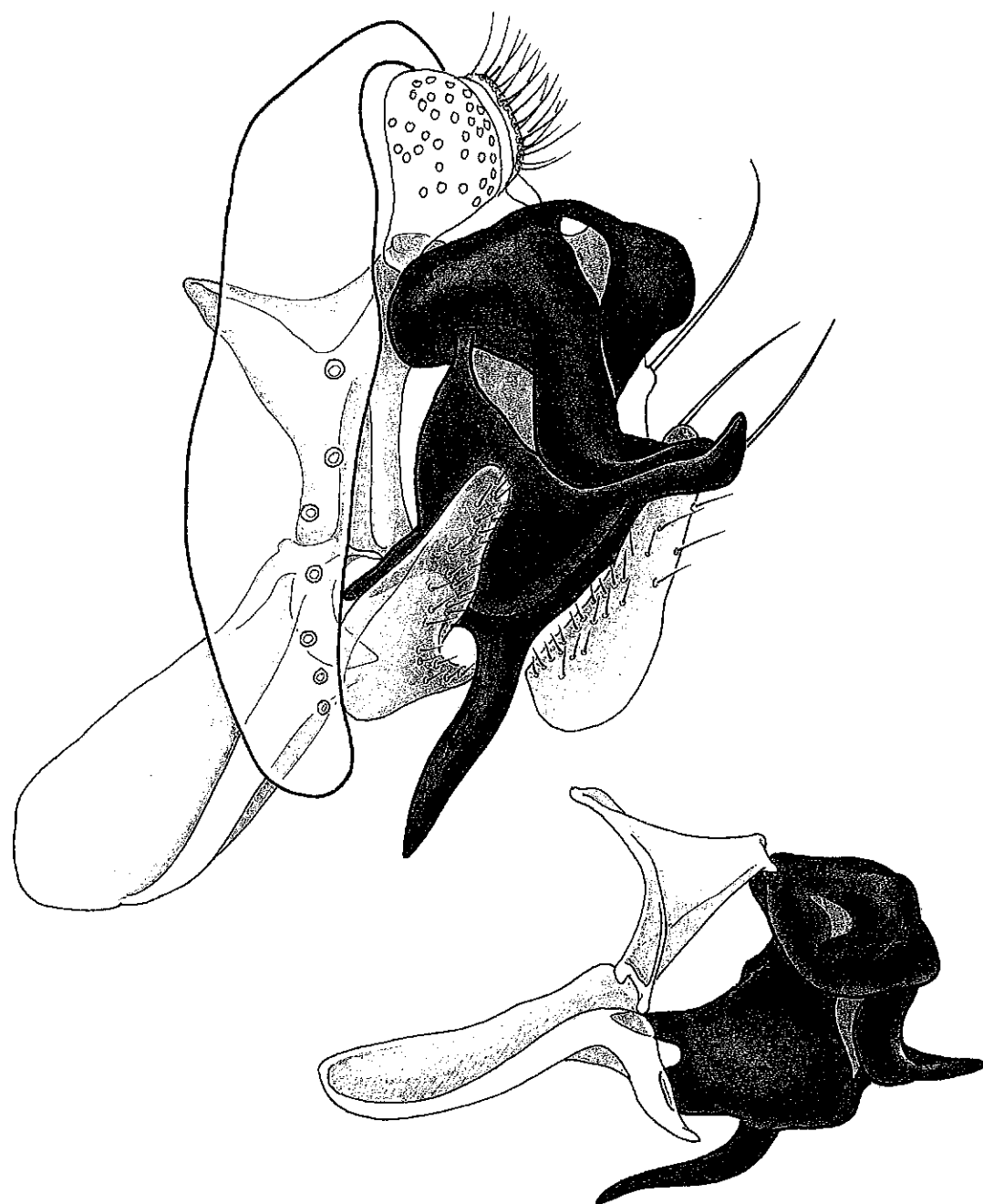


Fig. 140. Male terminalia of *C. paravolsella*.

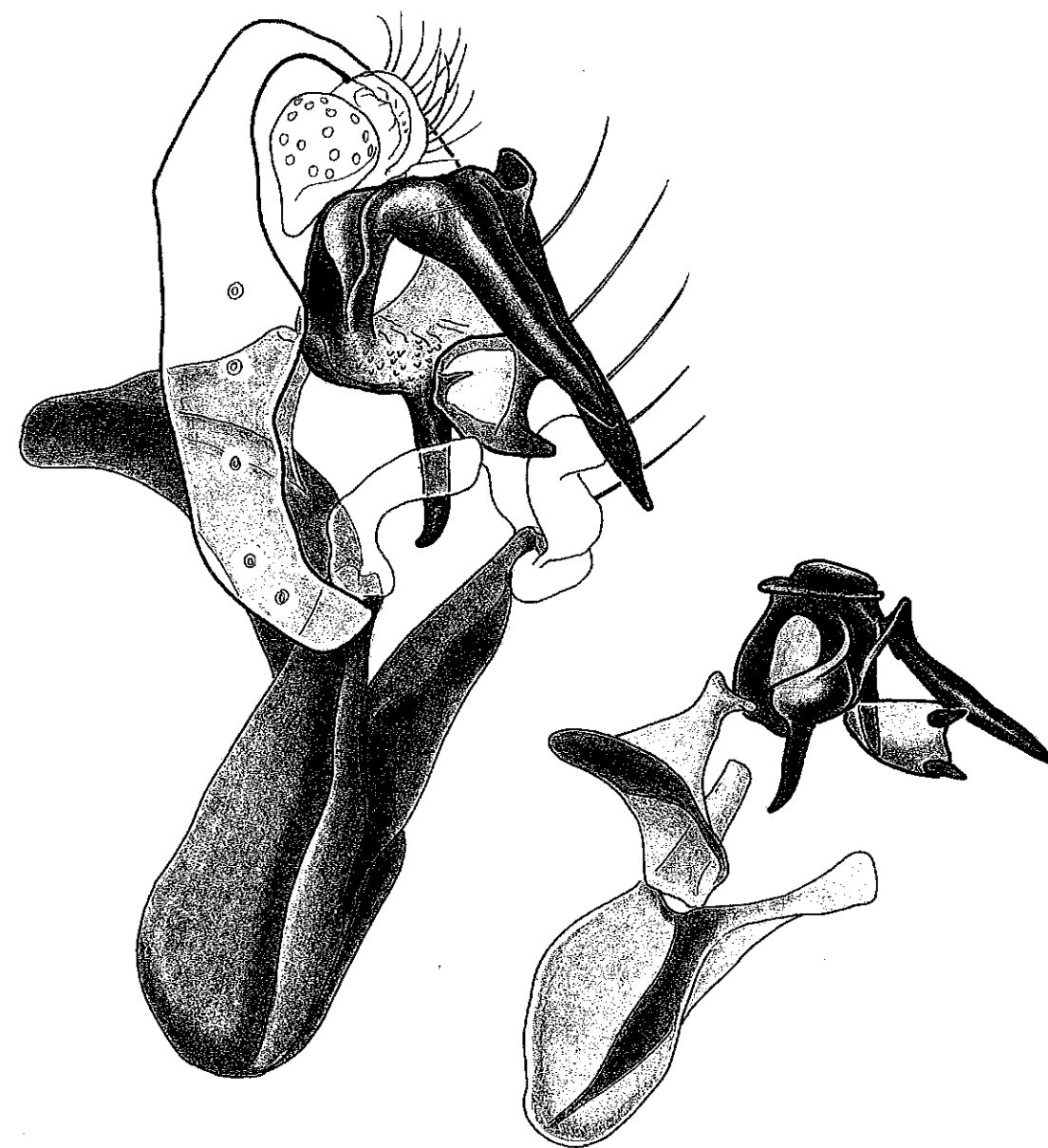


Fig. 141. Male terminalia of *C. tricerabops*.



Fig. 142. Male terminalia of *C. volsella*.



Fig. 143. Distribution of *armata* group species.

## TRIPUNCTATA SPECIES GROUP

Monophyly defined by presence of a reduced arista (3 or fewer short dorsal branches, no ventral one), 3 spots on wing (over both crossveins, usually at tip of  $R_{2+3}$  [this one can be very slight]); and distinctive male genitalia: epandrial lobe with patch of numerous setae in middle, not in a row; paraphyses heavily sclerotized and strongly hooked. Female genitalia (4 of 5 known species) simple, usually with pair of apical lobes that point mediad or even meet medially (these lobes apparently fused in *C. paulhansoni*).

*Cladochaeta abarista*, new species

Figures 144, 145–147

DIAGNOSIS: Arista reduced, dorsally with only 1 large branch at base and 2 minute ones distad (no ventral ones); thorax (including pleura) almost entirely yellow; large dark clouds over both x-veins and apex of vein  $R_{2+3}$ ; male genitalia with numerous fine setulae on epandrium and cerci, aedeagus sharp and hooked, apical sternite small and heavily sclerotized; female genitalia most distinctive for small, heavily sclerotized, spherical apical sternite (visible in undissected, critical point dried, and pinned specimens).

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine, sparse pile; lower hind margin of eye without indentation, or very slight one. Antenna with pedicel and flagellomere I light brown (flagellomere I can be dark brown). Arista reduced; always with 1 large dorsal branch at base and 2 minute dorsal branches; no ventral branches. Front shiny, golden to light brown, with 7–10 well-developed interorbital setulae. Frontal-orbital setae: Proclinate orbitals ca.  $0.7\times$  length of posterior reclinate orbitals; anterior reclinate orbitals minute, ca.  $0.2\times$  width and length of proclinate (just slightly larger than interfrontals), immediately lateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca.  $0.3\times$  size of verticals. Face rather high and of moderate width (FW/HW =  $0.31$  [N = 14]), tan, and completely flat. Cheeks of moderate depth (CD/ED =  $0.11$ ). Proboscis and palps yellowish.

THORAX: Notum, scutellum, postnotum, and pleura ochre; pleura sometimes with diffuse, light brown infuscation. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars slightly divergent to parallel; posterior scutellars convergent, but not touching or cruciate. Postpronotal lobe with 1 large seta, ventral one ca.  $0.3\times$  size of dorsal one. Legs entirely light yellow; forefemur with row of 3 long ventrolateral setae, with 3 setae dorsolaterally. Halter yellow to light brown. Wing with 3 large dark clouds of infuscation on x-veins and over apex of  $R_{2+3}$ , with no other infuscation on costal edge. Infuscation very light and diffuse on apices of  $R_{4+5}$  and M, barely connected along margin of wing tip. Cloud on x-veins dm-cu largest (extended past  $CuA_1$  and  $R_{4+5}$ ), cloud on apex of  $R_{2+3}$  smallest. Apex of vein  $R_{2+3}$  turned slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly bent. Wing tip rounded.

ABDOMEN: All tergites dark brown. Female terminalia simple; no ventral bridge present beneath epi-/hypoproct; pair of unsclerotized lobes projected mediad, each with ca. 8 minute setulae, with 1 longer; small, heavily sclerotized apical sternite with spherical end and short anterolateral arms between and ventral to lobes. Male genitalia: Cercus with long ventral lobe having broad mesal surface; each surface with dense (ca. 45), fine, stiff setae that cover part of lobe. Epandrium about as high as wide. Ventrolateral halves of epandrium with ca. 40 scattered setae; 7–8 lateralmost setae largest, arranged in row, others on mesal surface, which is turned inward. Mesal surface of epandrial lobe projected into lobe. Aedeagus sclerotized, hook-shaped, with apex sharply pointed and projecting posteriad. Paraphyses sclerotized; small, hooked flaps above base of aedeagus. Anterodorsal portion of aedeagal apodeme broad, fanlike, lightly sclerotized. Surstyli unsclerotized; without narrow neck; simple, crescentic, with ca. 30 fine setae on mesal and lateral surfaces. Hypandrium rounded, with shallow ventral keel anteriorly, much deeper posteriorly. Gonopods slightly twisted. Apical sternite small, heavily sclerotized

and with dense microtrichia; projected posteriad to almost between and in front of surstyli.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Boquete, VIII/58, W. B. Heed & M. W. Wasserman (not dissected). Paratypes: Same data (3♂, no. 249; 2♀) (all in AMNH).

OTHER MATERIAL EXAMINED: COSTA RICA: *Cartago*: La Cangreja, 1950 m, VI–VII/92, P. Hanson, Malaise trap, 1♀ (AMNH). *San José*: Zurqui de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (1♂ dissected, no. 278), 6♀ (1 dissected, no. 277) (AMNH and UCR). PANAMA: *Chiriqui*, David, 2200 ft, 24/VII/64, A. Broce, light trap (1♂, no. 208; 2♀, no. 209) (NMNH).

ETYMOLOGY: From *ab* (from aberrant) and *arista*, in reference to the highly reduced arista resembling members of the *nebulosa* group.

*Cladochaeta brunnea*, new species

Figures 144, 145, 146, 148

DIAGNOSIS: Thorax (except legs) mostly dark brown, including ocellar triangle and adjacent area; arista slightly reduced, with 2 short dorsal branches, minute apical fork, no ventral branches. Male genitalia distinctive: epandrial lobes thin, with group of ca. 12 short, stiff setae on each; aedeagus bulbous, having flat, spatulate ventral lobe with 6 long spicules on anterior edge; female terminalia simple, unsclerotized, with pair of lobes touching medially.

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine, sparse pile (hardly visible); lower hind margin of eye with very slight indentation. Antenna with pedicel ochre and flagellomere I light brown. Arista slightly reduced, with 2 short dorsal branches, small apical fork, no ventral branches. Front with dorsal/posterior half dark, black-brown (with bluish pruinescence when viewed from front); anterior half ochre, dull, with ca. 6 fine interorbital setulae. Frontal-orbital setae: Proclinate orbitals only slightly shorter than posterior reclinate; anterior reclinate orbitals small, ca.  $0.3\times$  width and length of proclinate (slightly larger than interfrontals), immediately lateral and slightly posterior to proclinate. Posterior reclinate slightly closer

to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca.  $0.3\times$  size of verticals. Face rather high and narrow for group (FW/HW =  $0.30$  [N = 2]), tan, and completely flat. Cheeks light yellow and fairly deep (CD/ED =  $0.14$ ). Proboscis and palps yellowish.

THORAX: Notum, scutellum, postnotum, and pleura dark brown. Anterior dorsocentrals ca.  $0.6\times$  length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars slightly divergent to parallel; posterior scutellars parallel. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow; forefemur with 2 long ventrolateral setae, with 1 seta dorsolaterally. Hind femur of male with even row of 5 stiff setae on apical half (2–3 in female), lengths of setae slightly shorter than width of femur. Halter yellow. Wing mostly hyaline, with spots of dark infuscation over x-veins and apex of  $R_{2+3}$  (no infuscation on costal edge). Cloud on x-vein dm-cu largest (extended to past  $CuA$ ); cloud at apex of  $R_{2+3}$  smallest. Apex of vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly kinked in middle. Wing tip rounded.

ABDOMEN: Tergites dark brown. Female terminalia simple, unsclerotized; with bridge beneath epi-/hypoproct and pair of lateral lobes meeting medially; lobes each with row of 4 fine setulae at apex. Male genitalia: Cercus without long, thin ventral lobe; ventrolateral corner slightly elongate, tip beneath edge of epandrium. Epandrium only slightly higher than wide. Ventrolateral halves of epandrium (epandrial lobes) not tapered, of uniform width throughout; each half with 10–12 short, stiff setae arranged in 2 irregular rows. Aedeagus entirely membranous and very distinctive: left portion a “bag,” right portion flat with apical lip and posterior edge with row of ca. 8 sharp, scalelike spicules. Aedeagal apodeme small. Paraphyses the most sclerotized portions of genitalia (but only slightly sclerotized); left paraphysis a thin lobe, about one-half the length of aedeagal bag; right paraphysis complex, folded and twisted on dorsal part of aedeagal bag. Surstyli unsclerotized; simple, clavate; apex with ca. 45 fine setulae. Hypandrium with

rounded anterior margin, ventral keel very shallow; gonopods very long. Apical sternites not examined.

TYPES: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-4/IX/84, 2100 m, H. Wolda (dissected, no. 230). Paratype: Same data (1♀, no. 231) (both in AMNH).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens and possibly a female specimen: COSTA RICA: *Cartago*: La Cangreja, 1950 m, VI-VII/92, P. Hanson, Malaise trap. The body of this specimen is not dark brown.

ETYMOLOGY: In reference to the dark brown body color.

*Cladochaeta crassa*, new species

Figures 4, 144, 149

DIAGNOSIS: Males are easily distinguished from other species with 3 dark spots on wing (over x-veins and near tip of  $M_{1+2}$ ) by the enlarged hind femur with a long, curved tibia; dense, fine setae occur on ventral surface of hind coxa and most sternites; arista reduced to 2 small dorsal branches (and small apical fork). Male genitalia as described below. Female unknown.

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine, dense pile; lower hind margin of eye without even slight indentation. Antenna with pedicel and flagellomere I mostly ochre, also with some light brown. Arista reduced, with 2 short dorsal branches on basal half; apical fork very small, with minute dorsal branch; no ventral branches. Front mostly ochre, with ocellar triangle and periphery dark brown; 11 fine interorbital setulae present. Frontal-orbital setae: Proclinate orbitals about the same length as posterior reclinate; anterior reclinate orbitals small, ca.  $0.3\times$  width and length of proclinate (slightly larger than interfrontals), immediately lateral to proclinate. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate size, ca.  $0.4\times$  size of verticals. Face of moderate depth and width ( $FW/HW = 0.33$ ), tan, and completely flat. Cheeks light yellow and of moderate depth ( $CD/ED = 0.11$ ). Proboscis and palps yellowish.

THORAX: Notum ochre, with 3 diffuse, light brown longitudinal vittae; scutellum ochre; postnotum dark brown; pleura mostly dark brown, with ventral half of katapisternum yellow. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals much closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars slightly divergent; posterior scutellars damaged in type specimen. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow; forefemur with 2 long ventrolateral setae and row of 3 setae dorsolaterally. Hind femur enlarged (presumably just of the male), with just fine, yellow setae ventrally (no stiff, longer setae on apical half). Dense, long, fine setae occur on ventral surface of hind coxa. Halter yellow. Wing mostly hyaline, with spots of dark brown infuscation over x-veins and preapically on M; very slight cloud of infuscation at apex of  $R_{2+3}$ ; no infuscation on costal edge. Cloud on x-vein dm-cu largest (extended to past CuA); cloud on M smallest. Apex of vein  $R_{2+3}$  virtually straight, not turned abruptly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu virtually straight. Wing tip slightly pointed.

ABDOMEN: Tergites dark brown; male with most sternites having dense, fine brushes of setae. Female terminalia unknown. Male genitalia: Cercus with thin ventrolateral lobe; ventromedial margin with row of ca. 8-10 fine, short, stiff setulae. Epandrium much higher than wide; height about twice the width. Ventrolateral halves of epandrium each with cluster of ca. 25 fine, stiff setae near middle on posterior margin, not arranged in rows. Aedeagus membranous, protruding beneath lower part of paraphysis, to almost beneath gonopods; apex with opposing "hooks" pointed posteriad. Paraphyses very heavily sclerotized; fused for most of their lengths; very strongly curved inward, curved ca.  $270^\circ$ ; with 2 small spines pointed downward. Aedeagal apodeme lightly sclerotized, with broad, fanlike anterior portion. Hypandrium with rounded anterior margin and shallow ventral keel. Gonopods shallow and long; slightly sclerotized. Surstyli unsclerotized, simple and clavate, with broad apex having ca. 50 fine, curved setae on apical margin and on mesal surface. Apical sternites with highly modified setation; posterior 3 sternites each with 2 paramedian patches of setae. Posterior sternite with paramedian patches of 17-25 fine, short setulae pointed posteriad; 2 similar setulae lateral to these patches. Penultimate sternite with paramedian patches of 35-40 similar setulae pointed posteromedial, with 4-7 similar setae lateral to patches. Antepenultimate sternite with paramedian patches of 65-70 long, fine, curved, erect setae forming dense, golden pile in dried specimen.

TYPE: Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII-14/IX/84, 2100 m, H. Wolda (dissected, no. 269) (in AMNH).

OTHER MATERIAL EXAMINED: Known only from the holotype male.

ETYMOLOGY: In reference to the crassate hind femora, which is one of the several distinct features of this species.

*Cladochaeta paulhansonii*, new species

Figures 144, 146, 150

DIAGNOSIS: Arista with 3 short dorsal branches (no ventral ones); acrostichals in 4 rows; pleura mostly yellow, with small areas of brown infuscation; male genitalia most diagnostic: paraphyses fused dorsally, with pair of large ventral spines (not symmetrical) and 3 smaller spines pointed inward.

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine, dense pile; lower hind margin of eye with slight indentation. Antenna with pedicel and flagellomere I mostly brown, some small areas of ochre. Arista reduced, with 3 short, evenly spaced dorsal branches on basal half; apical fork small, with minute dorsal branch; no ventral branches. Front with anterior half bronze, posterior half dark brown when viewed from front (front entirely bronze when viewed dorsally); 4 rather long interorbital setulae on front, several others on ptilinal suture. Frontal-orbital setae: Proclinate orbitals about the same length as posterior reclinate; anterior reclinate orbitals minute, ca.  $0.2\times$  width and length of proclinate (same size as interfrontals), immediately lateral and slightly posterior to proclinate. Posterior reclinate about midway between ipsilateral proclinate and inner vertical. Post-

cellar setae of moderate size, ca.  $0.4\times$  size of verticals. Face slightly shortened and of moderate width ( $FW/HW = 0.32$  [ $N = 6$ ]); tan to light brown, completely flat. Cheeks light yellow and rather shallow ( $CD/ED = 0.11$ ). Proboscis and palps yellowish.

THORAX: Notum ochre; scutellum ochre, but postnotum dark brown; pleura mostly yellowish, with some light brown infuscation on dorsal half; katapisternum entirely yellow. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 rows. Anterior and posterior scutellars parallel. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow; forefemur with 2 long ventrolateral seta and 1 seta dorsolaterally. Ventral surface of hind femur with setae barely enlarged from all others on femur. Halter tan. Wing mostly hyaline, with spots of dark brown infuscation over x-veins; apex of  $R_{2+3}$  with very slight cloud of infuscation; no infuscation on costal edge. Cloud on x-vein dm-cu largest (extended to past CuA). Apex of vein  $R_{2+3}$  turned slightly costad. Veins  $R_{4+5}$  and M virtually parallel. Crossvein dm-cu slightly bent. Wing tip slightly pointed.

ABDOMEN: Tergites dark brown. Female terminalia hardly sclerotized; tergite largely fused beneath epi-/hypoproct (lateral, setose lobes seen in other species of group apparently fused, with only small medial excavation ventrally and floor of each lobe turned inward). Male genitalia: Cercus without ventrolateral lobe. Epandrium higher than wide; height ca.  $1.5\times$  width. Ventrolateral halves of epandrium each with cluster of ca. 22 fine setae near middle on posterior margin, not arranged in rows. Aedeagus membranous, protruding beneath lower part of paraphysis, extended slightly beneath gonopods. Paraphyses very heavily sclerotized, curved inward; with 5 spines (posterior one largest, pointed ventrally; group of 3 anterior ones pointed inward). Aedeagal apodeme sclerotized, with troughshaped anterior portion. Hypandrium sclerotized, with rounded anterior margin and shallow ventral keel. Gonopods sclerotized, shallow, and long. Surstyli unsclerotized, apex with dorsal corner slightly dis-



tended; apex broad, having ca. 50 fine, curved setae. Apical sternites unmodified.

**TYPES:** Holotype, Male: COSTA RICA: *San José*: Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 289) (in AMNH). Paratypes: 5♀, same data as holotype (1 dissected, no. 288).

**OTHER MATERIAL EXAMINED:** Known only from the type series.

**ETYMOLOGY:** It is a pleasure to name this species for Paul Hanson, professor at the University of Costa Rica, San José, for his generosity in allowing the senior author to sort through his many Malaise trap samples from Costa Rica, and for his hospitality.

*Cladochaeta ranhyae*, new species

Figures 144, 145, 151

**DIAGNOSIS:** Based on male genitalia, closely related to *C. brunnea*. Wings of *brunnea* and *ranhyae* very similar. Best distinguished from other species in group by arista with single large dorsal branch (at base), very small other dorsal branch; very light body color (*brunnea* has a brown body); genitalia most similar to *brunnea* but distinguished on basis of epandrial setulae, shape and setation of surstyli, and structure of aedeagus and paraphyses.

**DESCRIPTION:** HEAD: Slightly higher than long (HL/HD = 0.89 [HT]). Eyes with very short, fine, sparse pile (hardly visible); lower hind margin of eye with very slight emargination. Antenna with pedicel yellow and flagellomere I virtually white. Arista highly reduced, with 1 long dorsal branch (at base) and very small dorsal branch (near middle); no small apical fork or ventral branches. Front light yellow, with ca. 8 fine interfrontal setulae. Frontal-orbital setae: Proclinate orbitals barely shorter than posterior reclines; anterior reclinate orbitals minute, ca. 0.3× thickness and length of proclines (slightly larger than interfrontals), immediately lateral to slightly posterolateral to proclines. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca. 0.3× size of verticals. Face completely flat; short, at same level as apices of flagellomere I (FW/HW = 0.36). Cheeks light yellow and slightly shallow (CD/ED = 0.12). Proboscis and palps light yellow.

**THORAX:** Notum, scutellum, and postnotum ochre; pleura lighter. Posterior dorsocentrals slightly closer to scutellum than to ant. dorsocentrals; relative lengths not comparable (post. dorsocentrals lost in type specimen). Acrostichals in 6 even rows. Postpronotal lobe with 1 large seta, ventral one minute. Legs entirely light yellow; foretibia with erect, preapical seta. Hind femur slightly crassate, without row of stiff setae on ventral surface. Halter whitish. Wing mostly hyaline, with spots of dark infuscation over x-veins and (much lighter) over apex of  $R_{2+3}$ . Cloud on x-vein dm-cu largest (extended to past CuA); cloud at apex of  $R_{2+3}$  smallest. Apex of vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M parallel. Wing tip rounded, with 3 stiff, fine setulae on margin between apices of veins M and  $R_{4+5}$ , with lengths of setulae twice that of other marginal setulae.

**ABDOMEN:** Tergites light brown. Female terminalia unknown. Male genitalia: Cercus without long, thin ventral lobe, but with lateral and ventral flat rim more sclerotized than rest of cercus. Epandrium only slightly higher than wide; very narrow dorsally, thickest medially, with ventral lobe thin and curved. Each ventrolateral lobe of epandrium with 16–18 short fine setulae in middle (tightly grouped), not in rows. Aedeagus sclerotized (but not as much as paraphyses), complex: left portion S-shaped, with pointed apex and a central groove. Right half of aedeagus flat, very irregular in overall shape, with ventral portion divided into 3 curved, sharp lobes. Paraphyses the most sclerotized portions of genitalia; left paraphysis smaller than right one; right paraphysis in lateral view long, extended anteriorly to aedeagal apodeme. Aedeagal apodeme large, trident in lateral view. Surstyli lightly sclerotized; simple, roughly triangular in lateral (broadest) view; distal edge with row of ca. 15–18 fine setulae. Hypandrium with very broad, flat anterior margin, ventral keel very shallow, almost nonexistent; gonopods long. Apical sternites with dense, fine pilosity.

**TYPES:** Holotype, male: COSTA RICA: *San José Prov.*: Zurquí de Moravia, 1600 m, VII/92, Paul Hanson, Malaise trap (dissected, no. 313) (in AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the type specimen.

**ETYMOLOGY:** Pronounced ron-hee'-ae, for Ranhy Bang, for her friendship and mutual interest in drosophilids.

*Cladochaeta tripunctata*, new species

Figures 144, 145, 146, 152

**DIAGNOSIS:** Arista with 2 short dorsal branches; pleura mostly dark brown; male genitalia with aedeagal apodeme, gonopods, and hypandrium sclerotized; paraphyses heavily sclerotized, strongly hooked, complicated; surstylus with comb of fine setae on apical edge.

**DESCRIPTION:** HEAD: Length and height moderate in lateral view. Eyes with very short, fine, dense pile; lower hind margin of eye with slight indentation. Antenna with pedicel and flagellomere I light brown, some small areas of ochre (mostly on mesal surface). Arista reduced, with 2 short dorsal branches (one at base, other at approximately midpoint); apical fork largely absent, dorsal branch very minute; no ventral branch. Front with area near ptilinal suture yellow, becoming dark brown posteriorly (almost matte black in some specimens); ca. 8 rather long interorbital setulae. Frontal-orbital setae: Proclinate orbitals about the same length as posterior reclines; anterior reclinate orbitals minute, ca. 0.3× width and length of proclines (same size as interfrontals), immediately lateral (sometimes also slightly posterior) to proclines. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate size, ca. 0.4× size of verticals. Face of moderate depth and width (FW/HW = 0.32 [N = 13]), yellowish, and completely flat. Cheeks light yellow and of moderate depth (CD/ED = 0.12). Proboscis and palps yellowish.

**THORAX:** Notum mostly ochre, with diffuse brown median vitta; scutellum almost entirely brown; postnotum dark brown; pleura mostly dark brown, with ventral half of katapisternum yellow. Anterior dorsocentrals ca. 0.8× length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Anterior scutellars parallel, posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta, ventral one minute.

Legs entirely light yellow; forefemur with 2–3 long ventrolateral seta (1 preapical, others at about midpoint) and 1 seta dorsolaterally. Ventral surface of hind femur with setae not enlarged. Halter tan. Wing membrane mostly hyaline, with 3 clouds of dark infuscation. Largest cloud over x-vein dm-cu (extended past CuA<sub>1</sub>), smallest one preapically on vein M (distance from wing tip about the diameter of cloud). Infuscation very light, diffuse on costal edge, especially at apex of vein  $R_{2+3}$ . Vein  $R_{2+3}$  very slightly turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed.

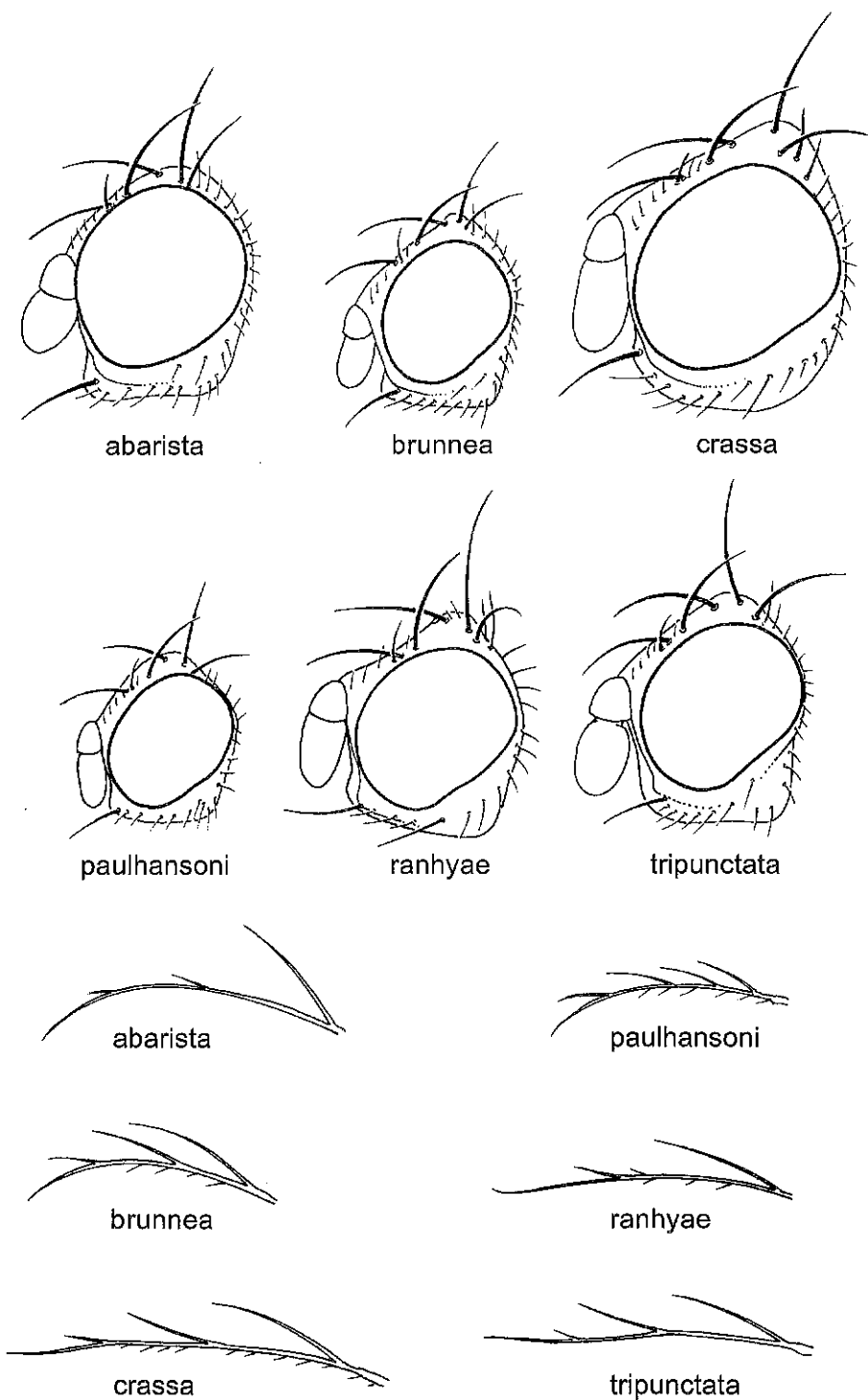
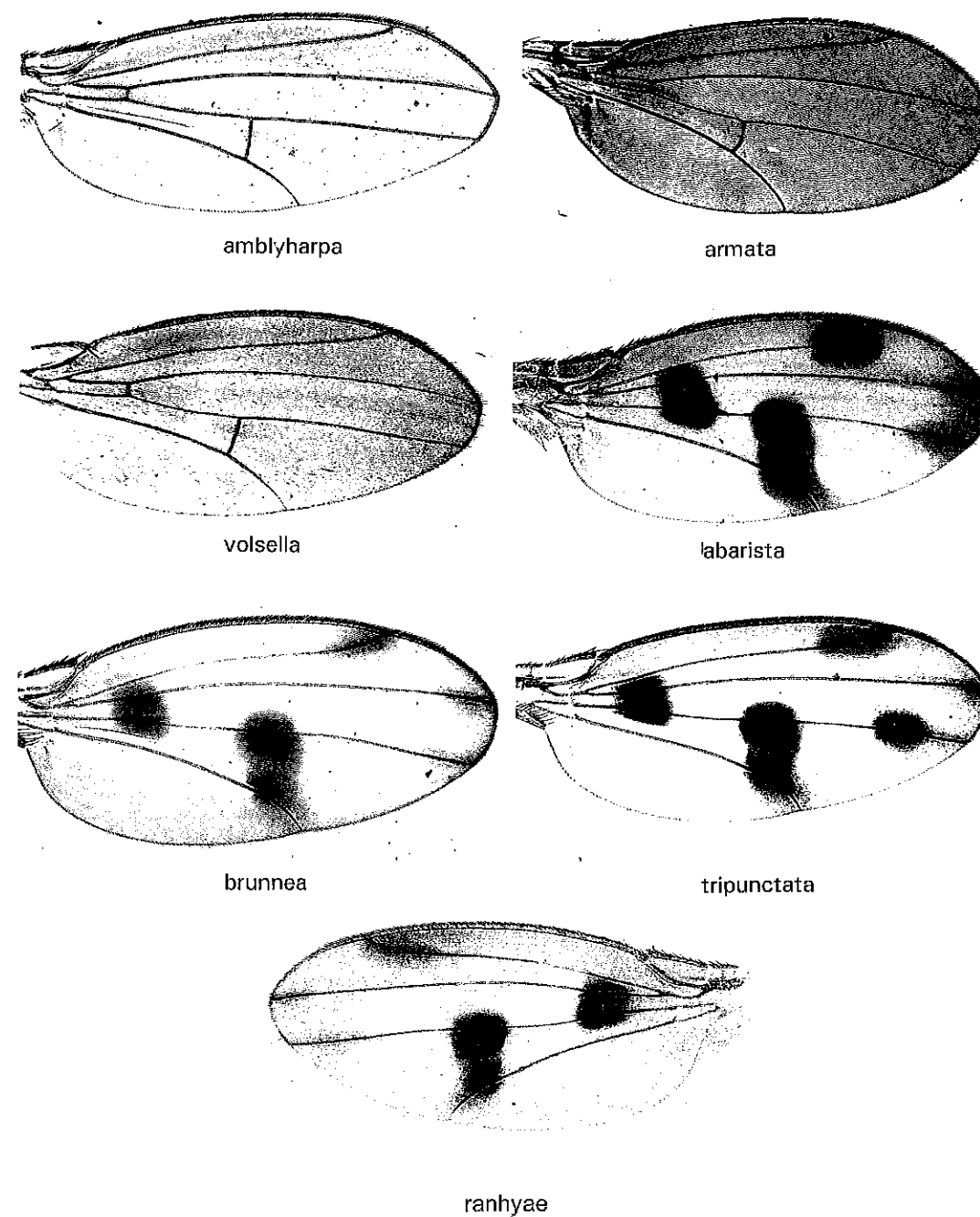
**ABDOMEN:** Tergites dark brown. Female terminalia virtually unsclerotized; apical tergite without bridge beneath epi-/hypoproct, but with pair of lateral lobes touching medially (each lobe with 4–5 fine setae); lobes projected (in lateral view), as for oviscapt of higher drosophilines, but without pegs. Male genitalia: Cercus with ventrolateral corner slightly elongate. Epandrium much higher than wide; height ca. 1.9× width. Ventrolateral halves of epandrium each with cluster of ca. 25 fine, stiff setae near middle on posterior margin, not arranged in rows. Aedeagus sclerotized, membranous portion not identified; with 2 small, ventrally directed spines situated below paraphyses. Paraphyses very heavily sclerotized; fused for most of their lengths; very strongly curved inward, curved ca. 270°. Aedeagal apodeme sclerotized, with broad, fanlike anterior portion. Hypandrium with rounded anterior margin and centralized ventral keel. Gonopods laterally flattened, deep, long; slightly sclerotized. Surstyli unsclerotized, with broad apex having ca. 25 fine, curved setae on apical margin and ca. 15 finer setulae on mesal surface. Surstyli connected by narrow, sclerotized strip, folded into inverted "V". Apical sternites not examined.

**TYPES:** Holotype, Male: PANAMA: *Chiriqui*: Guadalupe, Arriba, 1/VIII–4/IX/84, 2100 m, H. Wolda (dissected, no. 234). Paratypes: Same data (12♀, no. 235) (AMNH).

**OTHER MATERIAL EXAMINED:** Known only from the type series.

**ETYMOLOGY:** Named in reference to the 3 spots along longitudinal vein M.



Fig. 144. Heads and aristae of *tripunctata* group species.Fig. 145. Wings of *armata* group and *tripunctata* group species.

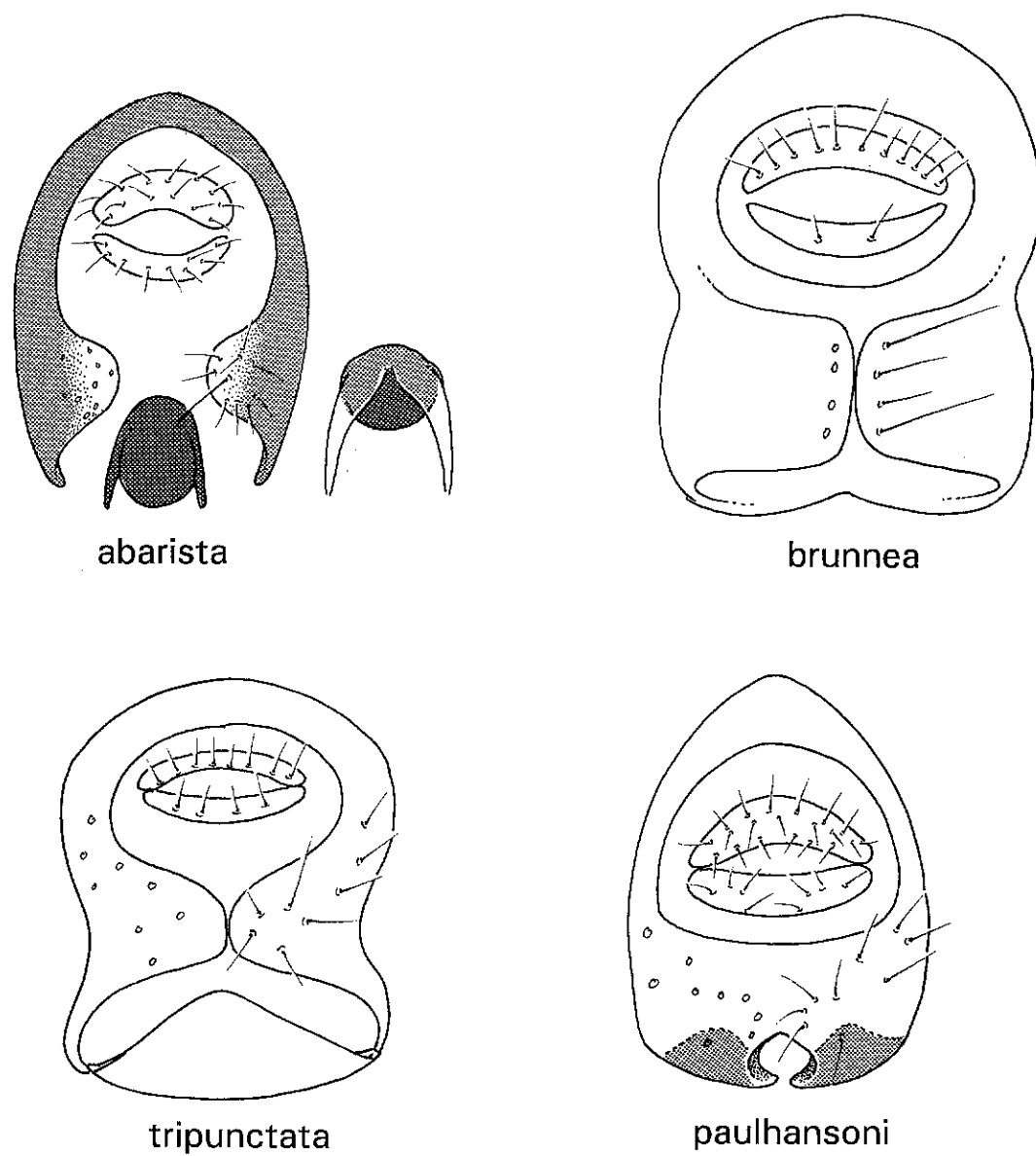


Fig. 146. Female terminalia of *tripunctata* group species (posterior view).

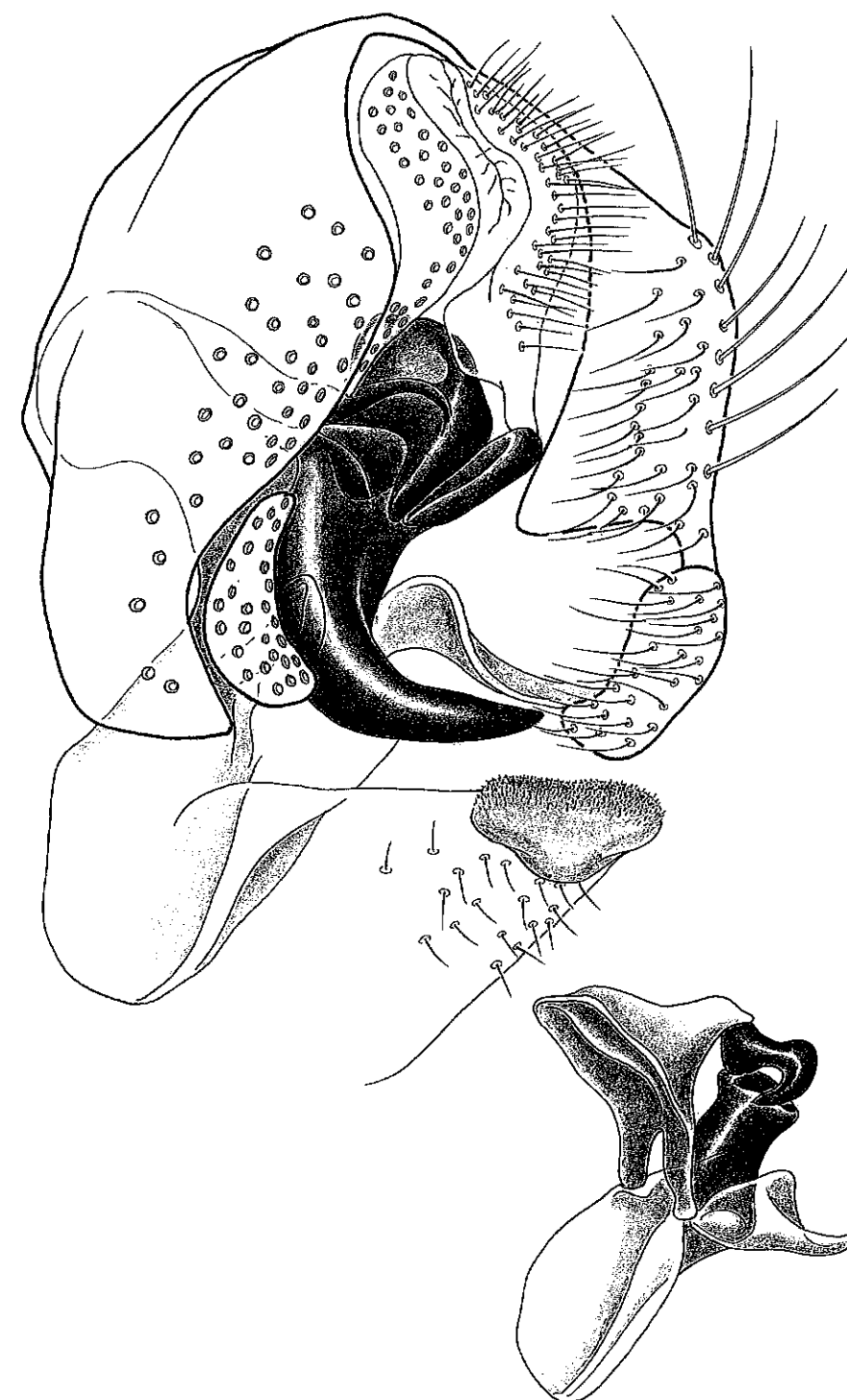
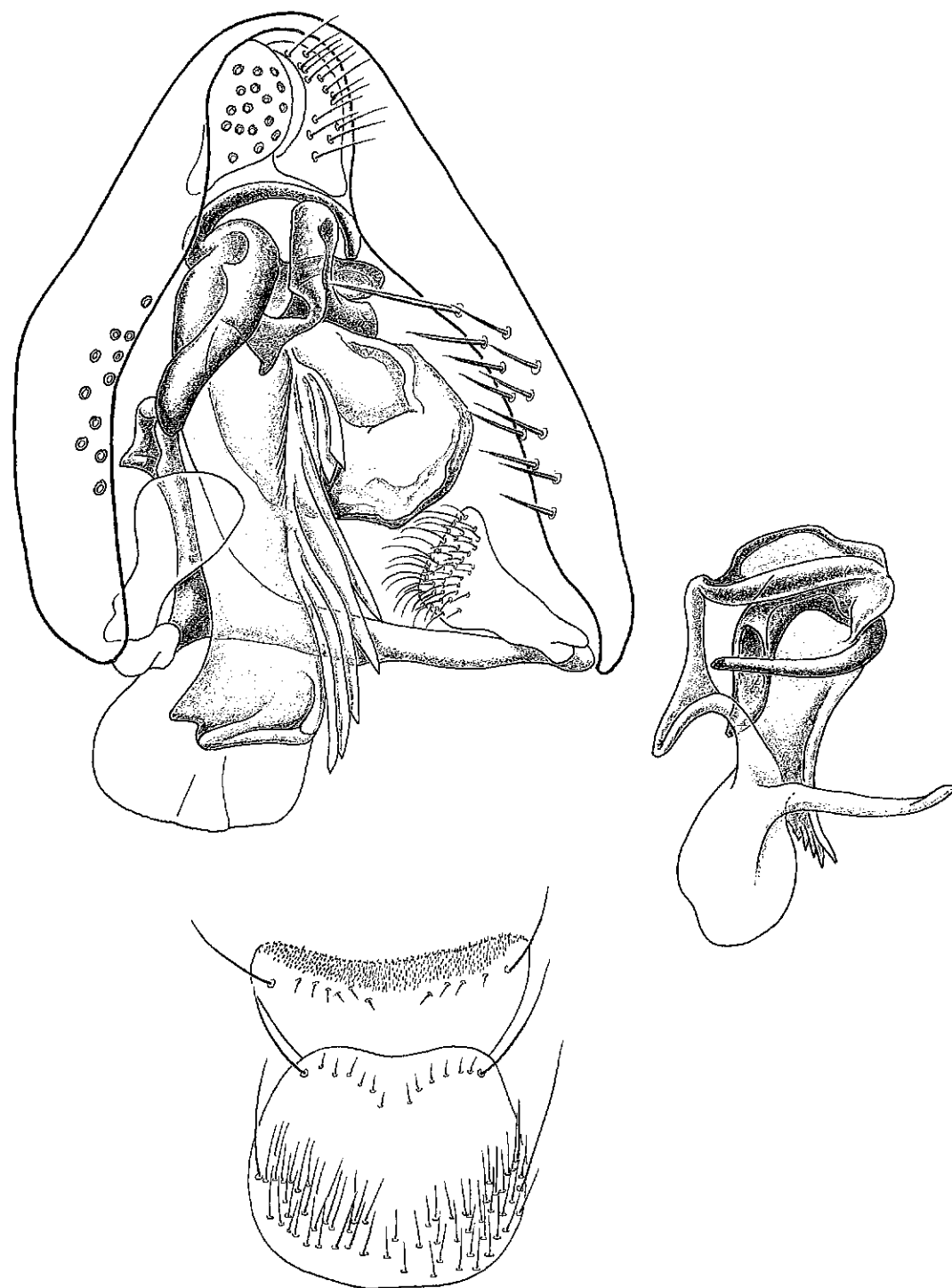


Fig. 147. Male terminalia of *C. abarista*.

Fig. 148. Male terminalia of *C. brunnea*.Fig. 149. Male terminalia of *C. crassa*.

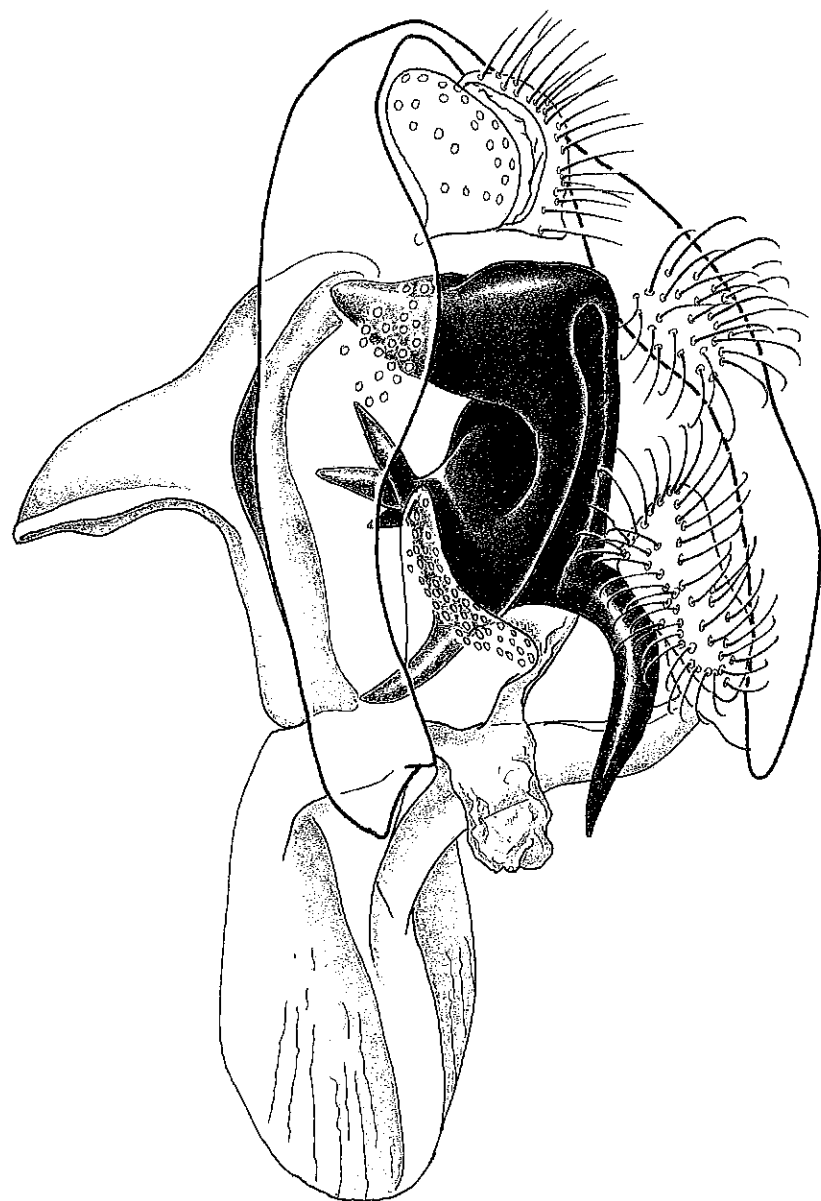


Fig. 150. Male terminalia of *C. paulhansoni*.

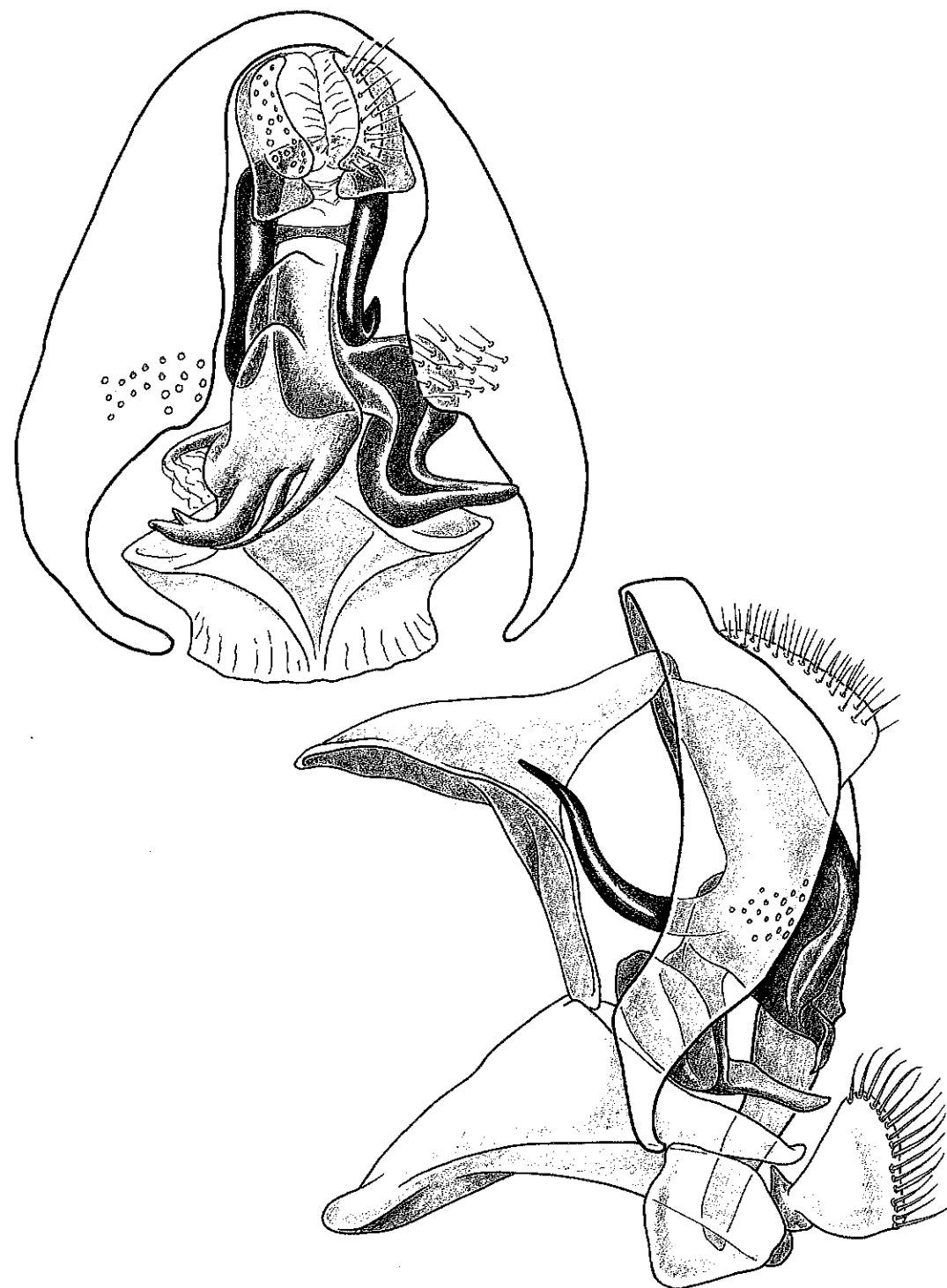


Fig. 151. Male terminalia of *C. ranhyae*.

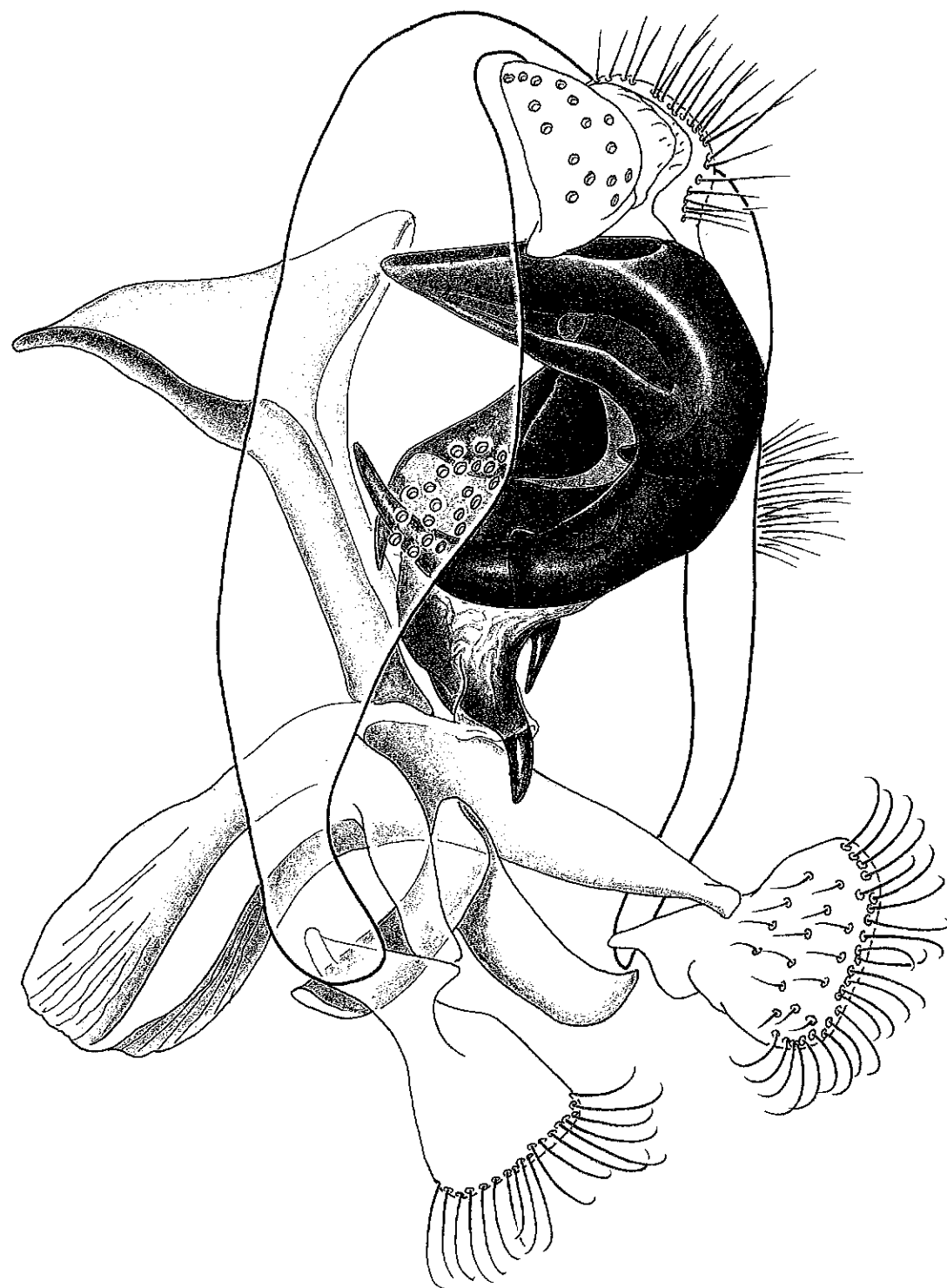


Fig. 152. Male terminalia of *C. tripunctata*.

### BOMPLANDI SPECIES GROUP

**DIAGNOSIS:** Defined on basis of very distinctive apomorphies. Wing with dark clouds over both crossveins, over apex of vein  $R_{2+3}$ , preapically over  $R_{4+5}$  and M; crossvein dm-cu sigmoidal. Male genitalia extravagant: epandrial lobes with extremely large setae, developed into 2 pairs of long, stiff "spikes" in 2 species (*bomplandi*, *ptyelophila*) and into brushes in another species (*spectabilis*); aedeagus large, heavily sclerotized, paraphyses small or vestigial; surstyli small, base with row of 3–4 stiff setulae. Female terminalia rather simple, but with pair of or fused ventral lobes.

#### *Cladochaeta bomplandi* (Malloch)

Figures 3, 153, 154, 158

*Diathoneura bomplandi* Malloch, 1934: 438; Wheeler, 1981: 35.

*Clastopteromyia bomplandi*: Frota-Pessoa, 1947: 198; Wheeler, 1957: 107.

*Cladochaeta bomplandi*: Vilela and Bächli, 1990: 8 (new combination, fig. of terminalia).

**DIAGNOSIS:** Distinguished externally by the head (in lateral view) tall and narrow in profile; wing most distinctive (but very similar to *C. taeniatipennis*; see below) by having preapical band, cloud over x-vein m-cu and small cloud over vein r-m (*taeniatipennis* with thin strip of infuscation on costal edge; *bomplandi* hyaline in this area). Male has 7 pairs of bizarre, huge, spinelike setae on last 3 tergites, lengths slightly longer than abdomen. Female terminalia distinctive (as described below), and several undescribed species exist in other parts of South America based on morphology of terminalia of various isolated females (unassociated with males).

**DESCRIPTION:** Provided by Vilela and Bächli (1990) based on type specimens, supplemented as follows: face wide (FW/HW = 0.33 [N = 6]), cheek shallow (CD/ED = 0.05). Wing: Dark, diffuse clouds of infuscation over x-veins and as a preapical band. No infuscation present on costal edge and apex of wing. Preapical band irregular, extended from apex of vein  $R_{2+3}$  to vein M. Cloud on dm-cu extended past  $CuA_1$ . Apex of vein  $R_{2+3}$  gradually meeting costal vein, turned only very slightly costad. Veins  $R_{4+5}$

and M parallel for most of their lengths, but slightly divergent apically. Crossvein dm-cu slightly kinked in middle; oblique to vein  $CuA_1$ , not perpendicular. Wing tip slightly pointed.

**ABDOMEN:** Tergites dark brown. Female terminalia with apical tergite sclerotized, glabrous; a thin, arched strip; without bridge beneath epi-/hypoproct. Apical sternite very small, roughly oval, with fine setulae; median sulcus invaginated into large, internal apodeme; thin, smaller apodeme on ventral margin of sternite. Male terminalia with bizarre modification of the last 3 tergites (including epandrium): tergites bearing 14 long, stiff, thick, black bristles projected straight backward; lengths slightly longer than length of abdomen. tVI with 2 such bristles on each side in posterolateral corner; arranged in row along posterior margin, bases separated from each other by distances slightly less than diameter of bristle bases. tVII with 1 stouter bristle on each side, also in posterolateral corner. Epandrium with stoutest bristles of the 3 segments, 2 on each ventral lobe, with bases at about the same level as the distiphallus. Sternites VI, VII, and VIII with fine setulae divided medially, forming 2 groups each on a lateral lobe. Setulae on last sternite short. Cercus without thin ventral lobe; ventral margin almost flat; cerci long, tapered, forming a cone, with numerous very short setae. Ventrolateral halves of epandrium each with pair of extremely long, thick bristles (described above) and group of ca. 18 short, stiff setae, not arranged in rows; portion of epandrial lobe bearing setae raised and rounded, heavily sclerotized. Aedeagus very heavily sclerotized; simple, clavate; distiphallus unadorned. Surstyli small, apices flattened and with dense microtrichia; bases with 2–3 short, stiff setulae. Gonopods heavily sclerotized, short, with dorsal flange.

**TYPES:** Holotype, Female: ARGENTINA, Misiones, Terr. F. & M. Edwards, BM. 1927–63, Bompland. 13–14/I/27. Paratype: 1♀, same data as holotype (dissected by Vilela and Bächli), both in BMNH.

**OTHER MATERIAL EXAMINED:** BRAZIL: Nova Teutonia, Fritz Plaumann, 1♂, 4♀ (AMNH).

**DISCUSSION:** This is the only known male of the species, which is an exceptionally in-

triguing specimen. We thought that this specimen had to be dissected in order to reveal internal details of the genitalia. Maceration left the huge spinelike setae still articulated to the tergites. Identity of the species was based on comparisons of the females in the series with the type female, which is from Argentina (about 200 km distant from the Brazil specimens), which agree very closely.

*Cladochaeta ptyelophila* Tsacas

*Cladochaeta ptyelophila* Tsacas, in Tsacas and Couturier, 1993: 85.

DIAGNOSIS: Very similar in wing pattern and genitalic morphology to *C. bomplandi*, both of which possess 2 pairs of large, spikelike setae on the epandrial lobes. Distinguished from *bomplandi* by spikes having blunt, rounded apices (sharp and pointed in *bomplandi*); surstylus more clavate (hook-shaped in *bomplandi*), with dense brush of apical setulae having longer setulae; aedeagus with distiphallus longer, having apical, nipple-shaped tip (simple and rounded in *bomplandi*).

TYPE: Holotype, Male: ECUADOR: *Oriente Prov.*: San Pablo de Kantesiya (0°16'S, 76°28'W), 200 m, IV/85, reared from larvae on nymphs of *Cephus erythrocephalus* (Cercopidae) feeding on *Manihot esculenta* ("manioc"). Paratypes: 1♂, 3♀, same data as holotype. All types in the Natural History Museum, Paris.

DISCUSSION: We relied on the excellent description and illustrations provided by Tsacas and Couturier (1993) to make the comparisons provided in the diagnosis. Female terminalia described by Tsacas and Couturier (1993) differ from one of the specimen described above ("*bomplandi*" sp. A) as well as specimens from Ecuador (Napo Prov.). Thus, at least 3 *bomplandi* group species occur in Ecuador. Observations on the spittlebug association of *ptyelophila* are discussed later in this monograph.

*Cladochaeta spectabilis*, new species

Figures 153, 155–157

DIAGNOSIS: Immediately recognizable as males by the elaborate male terminalia, particularly the 2 pairs of brushes comprised of

long, thick, black setae located on ventrolateral lobes of tergite VII and the epandrium. Wing with 2 small, incomplete, spurious crossveins on  $R_{2+3}$  and  $R_{4+5}$  at same level as dm-cu crossvein (development is variable); this feature presumably present in females.

DESCRIPTION: HEAD: Relatively high (HD/HL = 1.59). Frons light brown and of moderate width; with 8 fine interfrontal setulae. Frontal orbital setae: Proclinate  $0.8 \times$  length of posterior reclinate, post. reclinate strongly curved, ant. reclinate upright and rather long,  $0.6 \times$  length of proclinate; ant. reclinate anterolateral to proclinate. Antenna with pedicel light brown, mesal surface with 2 long, fine setae on ventral margin; flagellomere I darker brown. Arista with 1 ventral and 4–5 dorsal branches, plus smaller apical fork; ventral branch between d-3 and d-4; additional dorsal branch opposite ventral branch. Face lighter than frons, with very slight carina, virtually flat; relatively deep and of moderate width (FW/HW = 0.31). Cheeks lighter than frons and of moderate depth (CD/ED = 0.08). Proboscis light colored, with light brown palps.

THORAX: Notum, scutellum, postnotum, and dorsal half of pleura light brown; rest is ochre. Notum broad dorsally, with 8 irregular rows acrostichals; acrostichals anterior to dorsocentrals and to scutellum not enlarged. Anterior dorsocentrals  $0.6 \times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Anterior scutellar setae convergent; posterior scutellars cruciate for  $0.4 \times$  their length. Legs lighter than notum; fore femur with ventrolateral row of 3 longer setae, dorsolaterally with 2 setae (1 much longer than other); mid-femur with ventral, preapical seta; hind femur with ventral row of 4 setae on distal half. Mid tibia with apical comb of 4 short, black setae on ventral surface. Wing: Dark, rather discrete clouds of infuscation over x-veins and as either a preapical band (specimen no. 327) or divided into 3 oblong spots on or near apices of main longitudinal veins. No infuscation present on costal edge and apex of wing. Apex of vein  $R_{2+3}$  gradually meeting costal vein, turned only very slightly costad. Veins  $R_{4+5}$  and M parallel for most of their lengths, but slightly divergent apically. Crossvein dm-cu slightly

sinusoidal, virtually perpendicular to vein  $CuA_1$ . Small, incomplete spurious veins connected to veins  $R_{2+3}$  and  $R_{4+5}$  at same level as crossvein dm-cu; development highly variable from barely noticeable to distinctly present (lengths only twice the width of longitudinal veins); spurious x-veins variable between wings on same fly. Wing tip rounded.

ABDOMEN: Tergites dark brown. Female terminalia unknown. Male terminalia extremely elaborate, with 2 pairs of apical "brushes" developed from very long, modified setae. Abdomen dorsoventrally broad, rather flat. Genitalia very large, invaginated in sternal pocket extended anteriorly to sternite 3. Cerci laterally flattened, rather elongate and projected ventrad. Pair of long, thin, lateroapical lobes present, probably developed from tergite VI and/or VII (definitely not derived from epandrium [tIX]); each lobe with 5 very long, whiplike setae on apex and 3 shorter setae on lateral surface. Epandrium very small, striplike; largely hidden in non-macerated specimen by hoodlike, membranous tergite VII; dorsal surface tVII with 2 pairs of long, stiff setae. Anterior ends of epandrial lobes connected to and articulating with pair of heavily sclerotized ventral lobes (derivatives of epandrium). Sclerotized epandrial lobes with 4–5 thick, long, whiplike setae on apex; pair of small hook-shaped surstyli just medial to these lobes. Surstylus with base having row of 4 short, stiff setulae on mesal surface. Paraphyses long, thin, lightly sclerotized, flanking aedeagus; anterior ends curved ventrad. Aedeagus large, heavily sclerotized, with flat, median lobe and pair of lateral flanges on anterior end. Membrane surrounding cavity that houses genitalia is densely setulose.

TYPES: Holotype, Male: ECUADOR: *Napo*: Jondachi, 7200 ft, 20/V/91, G. Onore, on/with spittlebug nymphs of *Sphodroscorta* sp. (det. by K. G. A. Hamilton) (not dissected). Paratype: 1♂, same data as holotype (dissected, no. 327). Both specimens are in the CNC, Ottawa.

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: In reference to the spectacular male sexual features.

DISCUSSION: Description and discussion of

the spittlebug association is given later in this monograph.

Additional Undescribed Species

At least 3 (perhaps 4) other species closely related to *bomplandi* exist based on females unassociated with males from Ecuador, Peru, and El Salvador, being quite distant from the type locality. All have the charactersitic wing pattern and sclerotized internal apodeme of the apical sternite. One specimen from Peru (Cuzco: Quincemil, 1–15/XI/62, L. Pena coll.; 700 m, in CNC) is very similar to *bomplandi*, except that the Peruvian specimen has the sternal apodeme not as long, is apically tapered and not curled; and has no small, thin ventral apodeme. See figure 158 for female terminalia. The apparently undescribed species are listed below.

sp. A: One female from ECUADOR: *Napo*: Coca, Napo River, V/65, 250 m, L. Peña (coll.) (in CNC) (DAG dissection no. 106). Apical tergite glabrous, almost entirely circular (nearly meeting ventrally); epiproct large, curved around laterally, nearly meeting ventrally; hypoproct apparently lost; apical sternite small, with pair of thin, lateral flanges; median internal apodeme narrow and bifurcate on apical half.

sp. B: Two females from PERU: *Madre de Dios*: Manu N.P., Pakitza, 12°7'S, 70°58'W, 250 m, 9–23/IX/88, A. Friedberg (in NMNH) (1 dissected, DAG no. 150). Differs from *bomplandi* principally by having long and thin apical sternite, with 4 fine, stiff setulae apically and with a low, keel-like flange dorsally.

sp. C: One female from EL SALVADOR: San Salvador, VI/54, W. B. Heed (in AMNH) (dissected, DAG no. 149). Differs from *bomplandi* by having the preapical wing band incomplete, and with distinctly different terminalia: penultimate tergite very narrow, epiproct strongly arched, hypoproct short, stout; apical sternite similar to *bomplandi*, except that apodeme is much broader in lateral view.

SPECIES INCERTAE SEDIS

The following 10 described species, as well as several undescribed ones, are not placed in species groups because either the males are unknown or the males are so au-



tapomorphic that no characters could be found to place them into a group.

*Cladochaeta antalba*, new species

Figures 159, 160

**DIAGNOSIS:** Externally distinctive for the creamy white flagellomere I, which contrasts with the yellow-brown pedicel and bronze front; arista with 1 long ventral and 3 dorsal branches; proclinate orbital seta and posterior reclinate orbital very close together; notum and pleura dark brown, contrasting with light yellow halter and coxae; wings hyaline; known only from females from 2 montane forest sites in Costa Rica.

**DESCRIPTION:** **HEAD:** Relatively high in lateral view; broad dorsally. Eyes with very short, fine, sparse pile (virtually bare); lower hind margin of eye with slight indentation. Antenna with pedicel yellow on medial surface, light brown on lateral surface; flagellomere I creamy white. Arista with 3 long dorsal branches; ventral branch long, between d-3 and apical fork. Front evenly bronze or bronze with posterodorsal surface brown; ocellar triangle dark brown; front with 3-4 fine interorbital setulae. Frontal-orbital setae: Proclinate orbitals slightly smaller than posterior reclines; anterior reclinate orbitals minute, about twice the size of frontal-orbital setulae, immediately lateral to proclines (sometimes also slightly anterior to proclinate). Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca.  $0.3\times$  size of ocellars. Face relatively wide ( $FW/HW = 0.33$  [ $N = 2$ ]), ochre (darker than flagellomere I), completely flat. Anterior half of cheeks light yellow, posterior half grading to dark brown gena; cheek deep ( $CD/ED = 0.18$ ). Proboscis and palps yellowish.

**THORAX:** Entire thorax dark brown, contrasting with light yellow to whitish halter and coxae. Anterior dorsocentrals ca.  $0.8\times$  length of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 4 even rows. Anterior scutellars convergent, posterior scutellars cruciate for ca.  $0.3\times$  their length. Postpronotal lobe with 1 large seta, ventral one minute. Legs mostly yellowish, with apical half of femora and all of tibiae

with slight infuscation; forefemur with 3 long ventrolateral setae, dorsolaterally with 1 seta near middle and shorter seta near base. Ventral surface of hind femur with setae not enlarged. Halter yellowish white. Wing entirely hyaline, without any clouds of diffuse infuscation even on x-veins. Vein  $R_{2+3}$  virtually straight, apex gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight. Wing tip slightly pointed.

**ABDOMEN:** Tergites dark brown, penultimate tergite divided by light median area. Female terminalia: Apical tergite very narrow, sclerotized, without bridge beneath epi-/hypoproct. Apical sternite completely divided into pair of quadrate lobes lying at apices of tergite; each lobe with ca. 8 fine setulae on dorsal half; dorsal and ventral halves of lobes apparently articulated. Male genitalia unknown.

**TYPE:** Holotype, Female: COSTA RICA: *Puntarenas*: Las Alturas, 20 km NE San Vito, 2500 m, sweeping in forest, III/91, D. Grimaldi (genitalia dissected, no. 131) (in AMNH).

**OTHER MATERIAL EXAMINED:** COSTA RICA: *San José*: Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap, 1♀ (not dissected, in AMNH). This specimen is not made a paratype since we hesitate to assign paratype status to specimens from other than the type locality.

**ETYMOLOGY:** From antenna and the Latin *albus* (white), in reference to the distinctively white antennae in this species.

*Cladochaeta aquila*, new species

Figures 153, 159, 161

**DIAGNOSIS:** Small, entirely dark brown species with fuscous wings (no spots or clouds), arista with 3 short dorsal branches (no ventral branches). Best distinguished on basis of genitalia: epandrium tall and narrow; surstyli very long and thin, adpressed to inner margins of epandrial lobes; aedeagus tall, trough-shaped, with hook-shaped apex at ventral end; paraphyses small, lightly sclerotized.

**DESCRIPTION:** A small species ( $ThL = 0.54$  mm). Entire body, including head, face, antennae, and all of thorax, dark brown; legs

lighter. **HEAD:** Length and height moderate in lateral view ( $HL/HD = 0.87$ ). Eyes with very short, sparse pile, barely noticeable; lower hind margin of eye with very slight emargination. Arista with 3 dorsal branches, 1 at base of trunk; smallest one is preapical; no small apical fork present. Frons of moderate width, dark and velvety; frontal orbital plates slightly shiny. Frontal-orbital setae: Proclines same size as posterior reclines; anterior reclines minute, barely larger than frontal-orbital setulae, slightly posterolateral to proclines. Posterior reclinate closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca.  $0.3\times$  size of ocellars. Face of moderate depth and width ( $FW/HW = 0.33$ ), flat. Cheeks dark brown and of moderate depth ( $CD/ED = 0.15$ ). Proboscis and palps light brown.

**THORAX:** Dorsocentrals not observed (lost from unique specimen), sizes not discerned; posterior dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Postpronotal lobe with 1 large seta. Forefemur without long ventrolateral setae. Ventral surface of hind femur with setae not enlarged. Halter lighter brown than thorax. Wing entirely and evenly fuscous, without dark clouds even on crossveins. Apex of vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu straight, perpendicular to  $R_{4+5}$ . Wing tip rounded, not slightly pointed. Margin of wing tip with 4 fine, longer setulae between apices of veins  $R_{4+5}$  and M.

**ABDOMEN:** Tergites brown. Female terminalia unknown. Male genitalia: Cercus unmodified, with simple ventral margin. Epandrium tall and narrow, height  $1.7\times$  width. Ventrolateral lobes each with 8 setae, with 4 dorsalmost ones largest. Aedeagus erect, trough-shaped, moderately sclerotized; dorsally asymmetrical, left side with lobe extended to slightly past dorsal bridge; ventral end with hook-shaped apex (seen in lateral view). Paraphyses small, weakly sclerotized, flanking aedeagus at dorsal end. Aedeagal apodeme long and thin, with keel-like portion connected anteriorly to bases of paraphyses; narrow ventral arm articulating with base of hypandrium (this ventral portion not divided into 2 arms). Surstyli lightly sclerotized; very long and thin, somewhat foot-

shaped, with numerous fine setulae on mesal surface of apical half. Hypandrium lightly sclerotized, without large ventral keel(s).

**TYPES:** Holotype, Male: COSTA RICA: *Cartago*: La Cangreja, 1950 m, VI-VII/92, P. Hanson, Malaise trap (dissected, no. 323).

**OTHER MATERIAL EXAMINED:** Known only from the holotype.

**ETYMOLOGY:** Derived from *brown*, in reference to the body coloration.

*Cladochaeta bilinea*, new species

Figures 159, 160

**DIAGNOSIS:** Externally distinctive for the pair of diffuse yellow vittae on the dark brown notum (faded toward scutellum); arista with 4 long dorsal branches and 1 ventral one; postocellar setae minute, ca.  $0.2\times$  size of ocellars; face yellow, contrasting with dark antennae; female terminalia as described below. Known only from 3 females from the La Selva Biological Station, eastern Costa Rica.

**DESCRIPTION:** **HEAD:** Moderate depth and width in lateral view. Eyes completely bare; lower hind margin of eye with slight indentation. Antenna with pedicel and flagellomere I light brown. Arista with 3 long dorsal branches; ventral branch long, between d-3 and d-4. Front brown, lighter near frontal-orbital plates; ocellar triangle dark brown; front with very few (2-3) fine interorbital setulae. Frontal-orbital setae: Proclinate orbitals slightly smaller than posterior reclines; anterior reclinate orbitals minute, barely distinguishable from frontal-orbital setulae, immediately lateral to proclines. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae minute, ca.  $0.2\times$  size of ocellars. Face large, relatively wide and high ( $FW/HW = 0.31$  [ $N = 3$ ]), yellow (contrasting with dark antenna), and completely flat. Cheeks mostly light yellow and shallow ( $CD/ED = 0.09$ ). Proboscis yellow, palps light brown.

**THORAX:** Most of thorax (including pleura) dark brown, with pair of diffuse yellow, paramedian vittae on notum, gradually faded posteriad. Dark thorax contrasting with light yellow to whitish halter and fore- and hind-coxae. Anterior dorsocentrals ca.  $0.7\times$  length of posterior dorsocentrals; post. dorsocentrals

closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars convergent, posterior scutellars convergent or barely cruciate. Postpronotal lobe with 1 large seta, smaller ventral one. Legs light brown; forefemur with 2 long ventrolateral setae, with 2 setae (1 near middle and shorter seta near base) dorsolaterally. Ventral surface of hind femur with setae not enlarged. Halter yellowish white. Wing entirely hyaline, without any clouds of diffuse infuscation even on x-veins. Apex of vein  $R_{2+3}$  gradually meeting costal vein, not turned costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly bent. Wing tip rounded.

ABDOMEN: Tergites dark brown, penultimate tergite divided by light median area. Female terminalia: Apical tergite very narrow, glabrous, with small dorsal flange, sclerotized, without bridge beneath epi/hypoproct. Apical sternite almost completely divided into pair of lobes lying at apices of tergite (connected by thin anterior bridge); lobes protrudent, each with ca. 10 fine setulae apically. Male genitalia unknown.

TYPES: Holotype, Female: COSTA RICA: *Heredia*: Estacion Biologica Finca La Selva, 150 m, X/92, P. Hanson, Malaise trap (not dissected). Paratypes: 2♀, same data as holotype (1 dissected, no. 308) (all in AMNH).

OTHER MATERIAL EXAMINED: Known only from type series.

ETYMOLOGY: In reference to the diffuse pair of yellow vittae on the notum (i.e., "two-lined").

*Cladochaeta calvovis*, new species

Figures 153, 159, 160, 162

DIAGNOSIS: Arista with 3 short dorsal branches, apical fork apparently with branches as long or longer than branch d-1; wing dusky, with large dark cloud surrounding apical two-thirds of vein  $R_{2+3}$ ; female terminalia as described below. Male genitalia distinctive: paraphyses heavily sclerotized, with pair of thin outer lobes connected anteriorly to broad ventral floor that is tapered apicad; aedeagus membranous; aedeagal apodeme shaped like a thin furcula. Known only from the Cordillera Septentrional of the Dominican Republic.

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine, dense pile; lower hind margin of eye with slight indentation. Antenna with pedicel brown and flagellomere I slightly darker. Arista with 3 short dorsal branches; apical fork either very large (its branches as long as branch d-1), or dorsal branch of apical fork absent, with 1 ventral branch on arista. Front rather narrow; frontal vittae dark bronze, somewhat shiny, with 6 stout interorbital setulae; ocellar triangle black-brown. Frontal-orbital setae: Proclinate orbitals slightly shorter than posterior reclinate; anterior reclinate orbitals small, twice the size of frontal-orbital setulae, immediately lateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae of moderate size, ca.  $0.7\times$  size of ocellars. Face of moderate width (FW/HW = 0.32), yellowish, slightly receding. Cheeks light yellow and fairly shallow (CD/ED = 0.10). Proboscis and palps yellowish.

THORAX: Thorax mostly ochre with very slight, diffuse brown areas near notopleural edge. Dorsocentrals ca.  $0.6\times$  length of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellars parallel, posterior scutellars slightly cruciate. Postpronotal lobe with 1 large seta, ventral one about half the size. Legs entirely light yellow; forefemur with 2 long ventrolateral setae (1 preapical, other at about midpoint) and 1 seta dorsolaterally. Ventral surface of hind femur with setae not enlarged. Halter light yellow. Wing membrane slightly dusky, with dark clouds over much of costal edge, especially surrounding apical two-thirds of vein  $R_{2+3}$ . X-veins with barely any clouds. Vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly bent. Wing tip rounded.

ABDOMEN: Tergites dark brown. Female terminalia lightly sclerotized; apical tergite glabrous, with narrow bridge beneath epi/hypoproct and small, pointed, lateral lobes extended slightly beyond bridge. Apical sternite almost entirely divided, with deep ventromedial cleft dividing sternite into pair of bulbous lobes, each with 4 minute apical se-

tae. Male genitalia: Cercus without thin ventral lobe; ventral margin flat, with lightly sclerotized strip. Epandrium very thin, dorsal portion merely a thin strip; height ca.  $1.3\times$  width. Epandrial lobe with 5–6 setae in irregular row; middle seta twice the size of other setae. Apex of epandrial lobe with concave posterior margin. Aedeagus a diaphanous, membranous "bag" lying between apices of paraphyses. Aedeagal apodeme very thin, shaped like a bird furcula ("wish-bone"), having pair of long thin ventral arms and short stem. Surstyli unsclerotized, very simple lobes, without thin stem or neck; ca. 10 very fine, short setulae at apex. Hypandrium lightly sclerotized, ventral keel of moderate depth; gonopods of moderate length.

TYPES: Holotype, Male: HISPANIOLA: DOMINICAN REPUBLIC: La Vega, 9 km SE Constanza, near Valle Nuevo; 18-50N, 70-42W; 1930 m., 17/VIII/90, J. E. Rawlins & S. Thompson (not dissected, in CMNH). Paratypes: 3♂ (no. 265), 3♀, with same label data as holotype (1♂, 1♀ in AMNH, others in CMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: from the Latin *ovis* (sheep) and *calvaria* (skull), in reference to the shape of the paraphyses of the male genitalia, which vaguely resemble the skull of a sheep.

*Cladochaeta nigranus*, new species

Figures 159, 160

DIAGNOSIS: Distinguished externally by the brown face and front; an ochre notum with brown pleura; arista with 1 ventral branch, 4 dorsal branches, and (in females) large, thick, H-shaped sclerite formed at least partially by fusion of apical sternites. Known only from a series of females from the La Selva Biological Station, eastern Costa Rica.

DESCRIPTION: HEAD: Moderate depth and width in lateral view. Eyes with very short, fine, dense pile; lower hind margin of eye with very slight indentation. Antenna (pedicel and flagellomere I) entirely dark brown, about same color as the face. Arista with 4 long dorsal branches; 1 ventral branch, between d-3 and d-4. Front unicolorous dark brown, including ocellar triangle, with 7–8

fine interorbital setulae. Frontal-orbital setae: Proclinate orbitals about same size as posterior reclinate; anterior reclinate orbitals ca.  $0.3\times$  size of proclinate, lateral and slightly posterior to proclinate. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae relatively large, ca.  $0.3\times$  size of ocellars. Face relatively high, of moderate width (FW/HW = 0.33 [N = 7]), dark brown, slightly receding. Cheeks ochre, shallow (CD/ED = 0.10); gena dark brown. Palps light brown; proboscis yellow.

THORAX: Notum, scutellum, and postnotum ochre; pleura mostly brown, except for small diffuse areas of yellow on dorsal and ventral edges of katepisternum. Anterior dorsocentral setae  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 even rows. Anterior scutellar setae parallel, posterior scutellar setae convergent. Postpronotal lobe with 1 large seta, no trace of minute ventral one. Legs yellowish and with brownish infuscation; forefemur with 1 long ventrolateral setae, dorsolaterally with 2 setae (1 near middle, other at base). Ventral surface of hind femur with row of 3 setae at apex, lengths slightly less than width of femur. Halter tan. Wing entirely dusky, but without darker clouds of infuscation even on x-veins. Apex of vein  $R_{2+3}$  straight, not turned costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly kinked in middle. Wing tip slightly pointed.

ABDOMEN: Tergites dark brown. Female terminalia with apical tergite very small: a thin, barely arched sclerite lying over epi/hypoproct. Posterior end of abdomen with conspicuous, heavily sclerotized, thickly H-shaped sclerite, formed at least partially by fusion of the apical sternite. In middle of sclerite is small, semicircular flap with numerous and irregular small fenestrae on margin. Membranous bags lie at tips of ventral arms of sclerite. Male genitalia unknown.

TYPES: Holotype, Female: COSTA RICA: *Heredia*: Estacion Biologica Finca La Selva, 150 m, X/92, P. Hanson, Malaise trap (not dissected) (in AMNH). Paratypes: 7♀, same data as holotype (2 dissected, nos. 301, 302) (in AMNH and UCR).

OTHER MATERIAL EXAMINED: Known only from the small type series.

ETYMOLOGY: In reference to the very heavily sclerotized, dark posterior sclerite.

*Cladochaeta pleurvitta*, new species

Figures 159, 160

DIAGNOSIS: Distinguished externally by the 1 long ventral and 3 dorsal branches on the arista; flagellomere I dark brown, with medial surface having ca. 5 irregular, creamy spots; face yellow, with oral margin dark brown; palps brown; anterior reclinate setae completely absent; pleura with dark vitta (notum ochre, ventral pleura creamy); female terminalia distinctive (described below). Known only from 3 females from eastern Costa Rica.

DESCRIPTION: HEAD: Relatively high and short in lateral view. Eyes bare, completely devoid of fine pile; lower hind margin of eye without slight indentation. Pedicel dark brown on lateral surface, ochre on medial surface; flagellomere I darker brown, ca. 5 irregular, creamy white spots on medial surface. Arista with 3 long dorsal branches; 1 long ventral branch between d-3 and d-4; apical fork with long branches. Front unicolorous ochre, with dark brown to black ocellar triangle; front with sparse interorbital setulae, ca. 3-4 present. Frontal-orbital setae: Proclinate orbitals about same size as posterior reclinate orbitals; anterior reclinate orbitals apparently completely lost. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae relatively small, ca.  $0.2\times$  size of ocellars. Face relatively high and of moderate width (FW/HW =  $0.33$  [N = 3]), yellow, with dark brown oral margin. Cheeks light yellow, shallow (CD/ED =  $0.09$ ); gena yellow. Palps brown; proboscis yellow.

THORAX: Notum and postnotum ochre, scutellum slightly darker; brown infuscation on notopleural edge and slightly darker on dorsal half of postpronotal lobe. Pleura mostly creamy yellow, except for dark brown vitta through middle. Anterior dorsocentral setae ca.  $0.6\times$  size of posterior dorsocentrals; post. dorsocentrals midway between scutellum and ant. dorsocentrals. Acrostichals in 6 uneven rows. Scutellar setae damaged in specimens

(positions cannot be determined). Postpronotal lobe with 1 large seta, no trace of minute ventral one. Legs entirely light yellow; forefemur with 3 long ventrolateral setae, dorsolaterally with 1 seta. Ventral surface of hind femur without enlarged setae at apex. Halter knob yellow, stem brown. Wing entirely dusky, without darker clouds of infuscation on x-veins. Apex of vein  $R_{2+3}$  straight, not turned costad. Veins  $R_{4+5}$  and M slightly divergent. Crossvein dm-cu slightly kinked in middle. Wing tip slightly pointed.

ABDOMEN: Most tergites dark brown, except for penultimate and apical ones, which are yellow. Female terminalia with apical tergite highly reduced to small, barely curved sclerite (apices not extending laterally beyond epi-/hypoproct). Apical sternite very large, divided into pair of conspicuous, bulbous lobes (joined dorsally by very narrow bridge); each lobe with ca. 20 fine setulae. Small, heavily sclerotized, triangular sclerite ventromedial to sternal lobes. Sclerotized, thin, forked sclerite medial and anterior (internal) to lobes; in lateral view this sclerite roughly L-shaped and broad.

TYPES: Holotype, Female: COSTA RICA: *Heredia*: Estacion Biologica Finca La Selva, 150 m, X/92, P. Hanson, Malaise trap (not dissected). Paratypes: 2♀, same data as holotype (1 dissected, no. 309) (all in AMNH).

OTHER MATERIAL EXAMINED: Known only from the small type series.

ETYMOLOGY: In reference to the dark brown vitta on the pleura.

*Cladochaeta polia*, new species

Figures 153, 159, 160

DIAGNOSIS: A large, externally distinctive species of the genus, based on the entirely dark gray, pollinose thorax and abdomen (halter white, legs yellow); wing lightly and evenly dusky, but without clouds; arista with just 2 dorsal branches (apical fork apparently lost); female terminalia as described below. Known only from 2 females from Volcan Turrialba, eastern Costa Rica (ca. 9000 ft).

DESCRIPTION: HEAD: Moderate depth and width in lateral view; broad dorsally. Eyes with very short, fine, dense pile; lower hind margin of eye without even a slight indentation. Antenna (pedicel and flagellomere I)

entirely dark gray, much darker than face. Arista with 2 long dorsal branches (1 at base, 1 slightly past midpoint); no ventral branch; apical fork apparently lost. Front dark gray, almost velvety, including ocellar triangle; front with 5-6 fine interorbital setulae on ptilinal suture. Frontal-orbital setae: Proclinate orbitals  $0.8\times$  size of posterior reclinate orbitals; anterior reclinate orbitals minute, only slightly larger than frontal-orbital setulae, immediately lateral to proclinate. Posterior reclinate much closer to ipsilateral proclinate than to inner vertical. Postocellar setae relatively large, about half the size of ocellars. Face wide (FW/HW =  $0.36$  [N = 2]), gray, completely flat. Cheeks ochre, gena dark brown; cheek deep (CD/ED =  $0.19$ ). Proboscis and palps light brown.

THORAX: Entire thorax dark gray, with small, diffuse areas of ochre at bases of dorsocentral setae. Anterior dorsocentral setae ca.  $0.7\times$  size of posterior dorsocentrals; post. dorsocentrals slightly closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 uneven rows. Positions of scutellar setae damaged in both known specimens. Postpronotal lobe with 1 large seta, no trace of minute ventral one. Legs entirely yellowish, forefemur with 2 long ventrolateral setae, dorsolaterally with 1 seta near middle. Ventral surface of hind femur with setae not enlarged. Halter yellowish white, contrasting with darker body. Wing entirely dusky, but without darker clouds of infuscation even on x-veins. Apex of vein  $R_{2+3}$  turned very slightly costad, not meeting costal vein gradually. Veins  $R_{4+5}$  and M parallel. Crossvein dm-cu slightly kinked in middle. Wing tip rounded.

ABDOMEN: Tergites entirely dark gray, pollinose. Female terminalia with apical tergite ventrally broad, setose; connected ventrally, but with median notch on ventral margin, and small lobe inside notch; small, glabrous plate beneath tergal notch (not the apical sternite); apical sternite not entirely divided, but with deep median notch on posterior edge. Male genitalia unknown.

TYPES: Holotype, Female: COSTA RICA: *Cartago*: W. slope Volcan Turrialba, 3000 m, swept at forest edge, 14/III/91, Grimaldi & Stark (in AMNH) (genitalia not dissected).

Paratype: 1♀, with same label data as holotype (genitalia dissected, no. 151).

OTHER MATERIAL EXAMINED: Known only from the 2 type specimens.

ETYMOLOGY: From Greek *polios* (ash-gray) in reference to the distinctive body coloration.

*Cladochaeta taeniatipennis* (Duda),

New Combination

Figure 160

*Diathoneura taeniatipennis* Duda, 1925: 172. Vilela and Bächli (1990: 40) (redescription of type specimen, illustration of type genitalia).

*Clastopteromyia taeniatipennis*: Frota-Pessoa, 1947: 218 (new combination).

DIAGNOSIS: Unique among *Cladochaeta* for the 2 ventral branches of the arista (dorsally with 4 branches). Apparently related to *Cladochaeta bomplandi* based on the following wing characteristics: presence of a light subapical band, a cloud over the posterior crossvein, a slight cloud over the anterior crossvein, and a unique cross vein dm-cu slanted, with the cubital end more distal than the medial end; *taeniatipennis* with slightly more costal infuscation. Diffuse brown vitta running along pleura; female terminalia with tVIII thin, strongly arched around epi-/hypoproct; a thin sclerotized plate curled under epi-/hypoproct and then inward and upward. Known only from 2 females from eastern Costa Rica.

Despite the fact that the female terminalia of this species certainly are those of *Cladochaeta* (such as lacking a spermathecal capsule), Vilela and Bächli hesitated to transfer the species to *Cladochaeta* since the male was unknown and this species was the type species of *Diathoneura*.

TYPES: Lectotype, female: COSTA RICA: Suiza de Turrialba, 5/V/21, designated by Bächli, 1983 (in Vilela and Bächli, 1990). Paralectotype: 1♀, same data as lectotype, dissected by Vilela and Bächli (1990: fig. 37A, B).

*Cladochaeta travassosi* (Frota-Pessoa)

*Clastopteromyia travassosi* Frota-Pessoa, 1947: 214.

DIAGNOSIS: Indeterminate (see below).

TYPES: Holotype, Male: BRAZIL: Rio de

Janeiro, Corcovado, V/46. The holotype was not examined, but it and a paratype female are reported to be in the Museu Nacional, Rio de Janeiro (specimen nos. 81, 82).

DISCUSSION: Frota-Pessoa indicated that this species was closely related to *C. minuta*, but in lieu of examining the original specimens of this species there is some uncertainty as to the appropriate generic placement. On the one hand, Frota-Pessoa's description indicates *travassosi* to be in *Cladochaeta* by lacking teeth (dentes) on the oviscapt; however, he only indicated that there are 6–7 arisal branches (ramos), without specifying how many ventral branches there are, if any. The way in which the male genitalia have been illustrated makes it possible to determine only that the surstylus appears to be also without "teeth" (prensisetae) and is triangular with a sclerotized tip. These are features of some *Cladochaeta*, such as *C. peruviana*.

*Cladochaeta zurquia*, new species

Figures 159, 160, 162

DIAGNOSIS: Distinctive externally, with arista bearing just one large dorsal branch (basally), but not to be confused with *nebulosa* group species; thorax mostly ochre, with narrow brown stripe running along middle of pleura; wing dusky, with slightly darker costal edge; male genitalia very distinctive (with features not easily accommodated within any of the species groups): paraphyses stout, short, heavily sclerotized, forming "hood" over narrow, projected aedeagus; gonopods short, deep, triangular.

DESCRIPTION: HEAD: Length and height moderate in lateral view. Eyes with very short, fine pile; lower hind margin of eye barely with indentation. Antenna with pedicel ochre on medial surface, brown on lateral surface, flagellomere I slightly darker brown. Arista highly reduced, with 1 long dorsal branch, at base of trunk; preapical, dorsal branch minute; even small medial branches highly reduced. Front broad; frontal vittae bronze, shiny, with 10 minute interorbital setulae; frontal orbital plates yellow; ocellar triangle same color as frontal vittae. Frontal-orbital setae: Proclimates same size as posterior reclimates; anterior reclimates minute,

barely larger than frontal-orbital setulae, immediately lateral to proclimates. Posterior reclinate slightly closer to ipsilateral proclinate than to inner vertical. Postocellar setae small, ca.  $0.3\times$  size of ocellars. Face of moderate depth and width ( $FW/HW = 0.31$  [ $N = 2$ ]), light brown, flat. Cheeks light yellow and fairly shallow ( $CD/ED = 0.12$ ). Proboscis and palps yellowish.

THORAX: Thorax mostly ochre, with diffuse, thin, light brown vitta running longitudinally through middle of pleura. Anterior dorsocentrals ca.  $0.8\times$  length of posterior dorsocentrals; post. dorsocentrals closer to scutellum than to ant. dorsocentrals. Acrostichals in 6 even rows; acrostichal immediately anterior to ant. dorsocentral slightly enlarged. Anterior scutellars parallel, posterior scutellars slightly convergent. Postpronotal lobe with 1 large seta, ventral one ca.  $0.3\times$  the size. Legs entirely light yellow; forefemur with 3 long ventrolateral setae; dorso-laterally with 1 seta. Ventral surface of hind femur with setae not enlarged. Halter light yellow. Wing membrane slightly dusky, with darker cloud over most of vein  $R_{2+3}$ . X-veins with barely any clouds. Apex of vein  $R_{2+3}$  turned very slightly costad. Veins  $R_{4+5}$  and M parallel, but both slightly curved. Cross-vein dm-cu straight. Wing tip slightly pointed.

ABDOMEN: Tergites with some yellow, especially on anterior half, brown on medial portions and especially lateral corners. Female terminalia lightly sclerotized; apical tergite glabrous, without bridge beneath epi-/hypoproct. Apical sternite completely divided into pair of small, roughly triangular sclerites, each with 6 fine setae. Small, heavily sclerotized sclerite beneath and between sternal lobes. Male genitalia: Cercus long and thin, ventral margin flat. Epandrium rather broad, each lobe with row of ca. 10 setae. Aedeagus lightly sclerotized, narrow, projected posteriad, and lying between and just beneath paraphyses. Paraphyses heavily sclerotized; thick, stout lobes with small apical points turned slightly laterad; base of paraphyses connected by thin bridge to aedeagal apodeme. Surstyli unsclerotized, long, thin lobes, with numerous fine setulae on me-

sal and ventral surface. Hypandrium lightly sclerotized, with 2 ventral keels attached to short, triangular gonopods.

TYPES: Holotype, Male: COSTA RICA: San José: Zurquí de Moravia, 1600 m, VII/92, P. Hanson, Malaise trap (dissected, no. 296). Paratype: 1♀, same data as holotype (dissected, no. 295) (both specimens in AMNH).

OTHER MATERIAL EXAMINED: Known only from the type series.

ETYMOLOGY: Taken directly from the type locality.

Undescribed Species

A female specimen in the Hungarian Natural History Museum is from the type series of *C. minuta* (originally designated by Duda) from Turrialba, Costa Rica. Vilela and Bächli (1990) reported that the female specimen does not belong to *minuta*, with which we agree. We have seen a similar female specimen from Guanacaste, Costa Rica. Vilela and Bächli designated the Turrialba specimen as a paralectotype of *minuta*, even though they recognized it as a separate species.

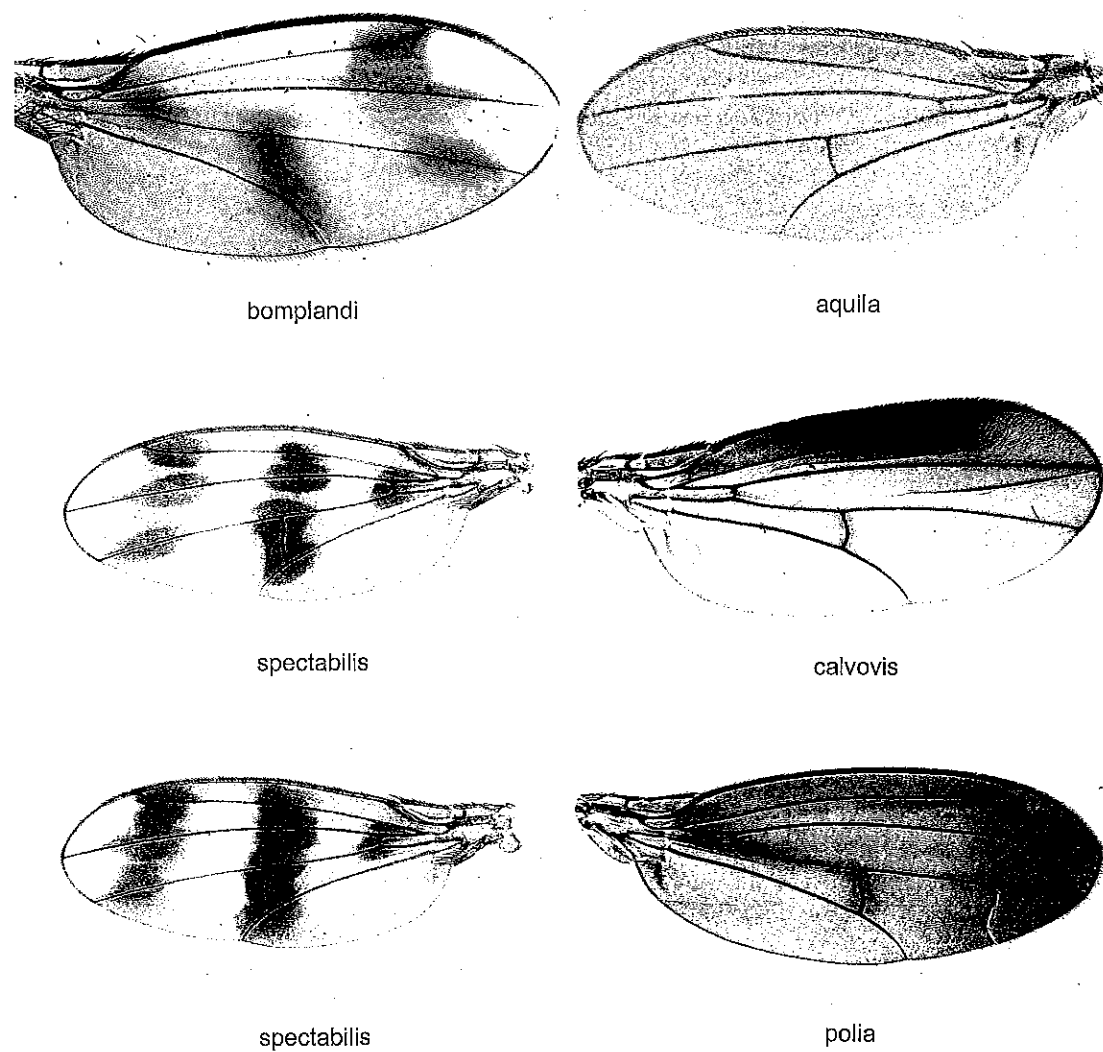


Fig. 153. Wings of *bomplandi* group and unplaced species. Wings from 2 *C. spectabilis* specimens show variation in pigmentation and development of spurious veins on the radial veins.

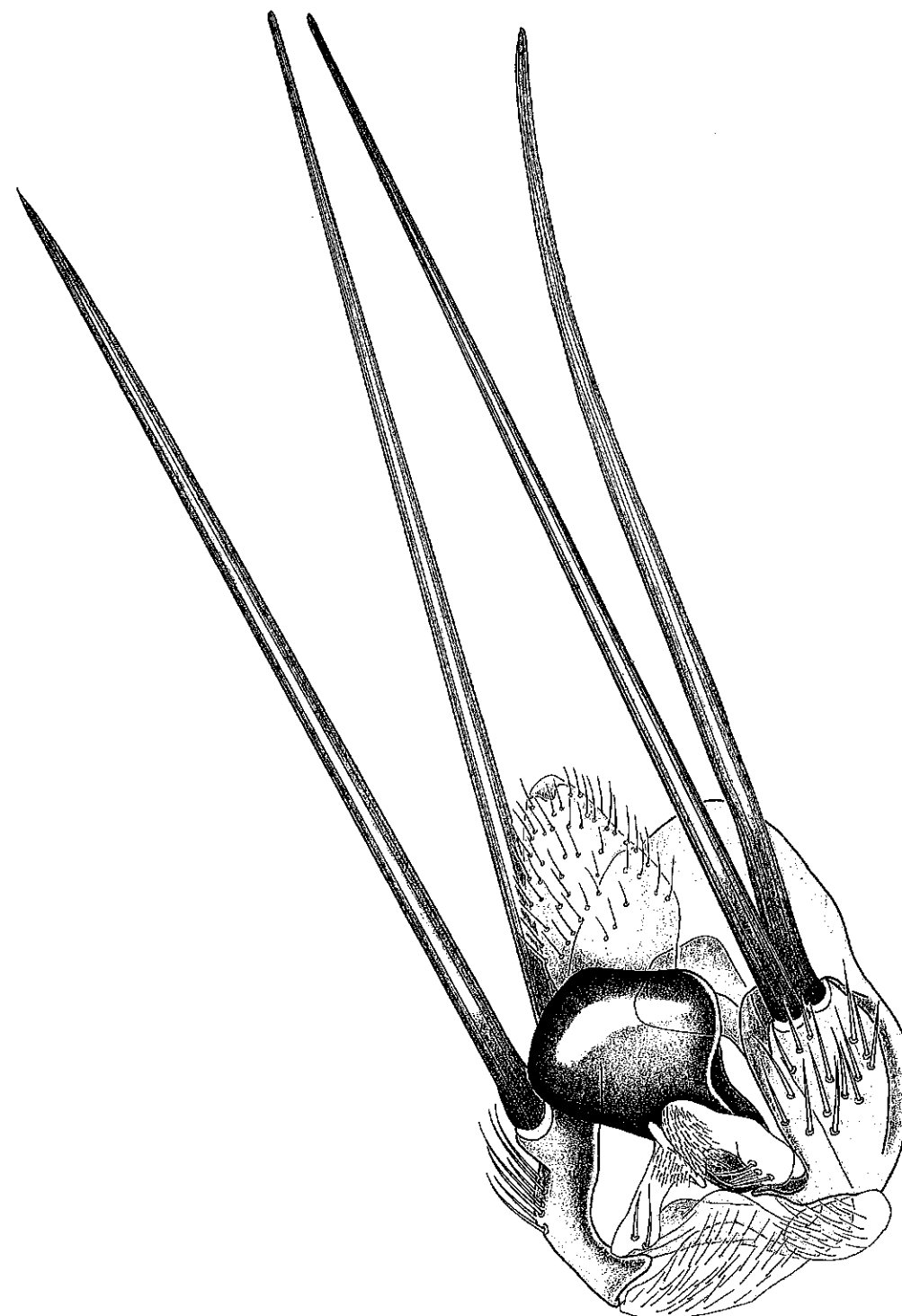


Fig. 154. Male terminalia of *C. bomplandi*.

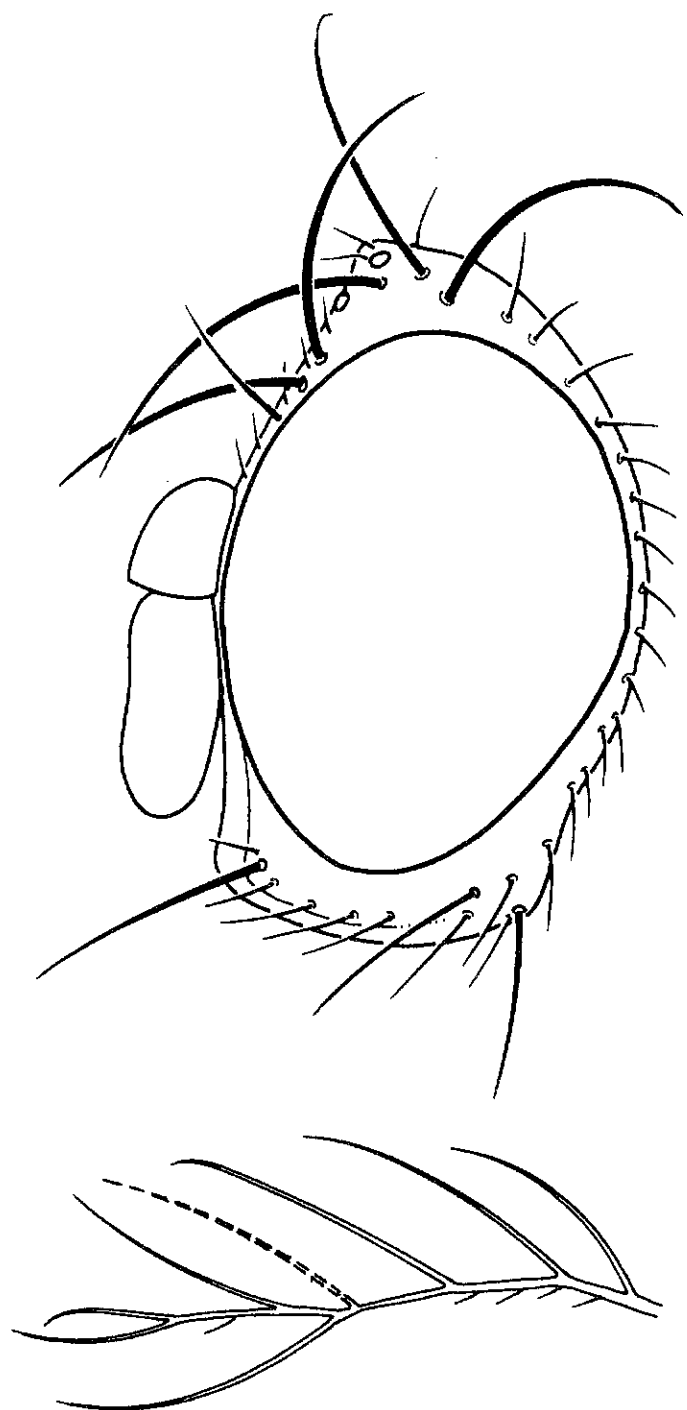


Fig. 155. Head and arista of *C. spectabilis*.

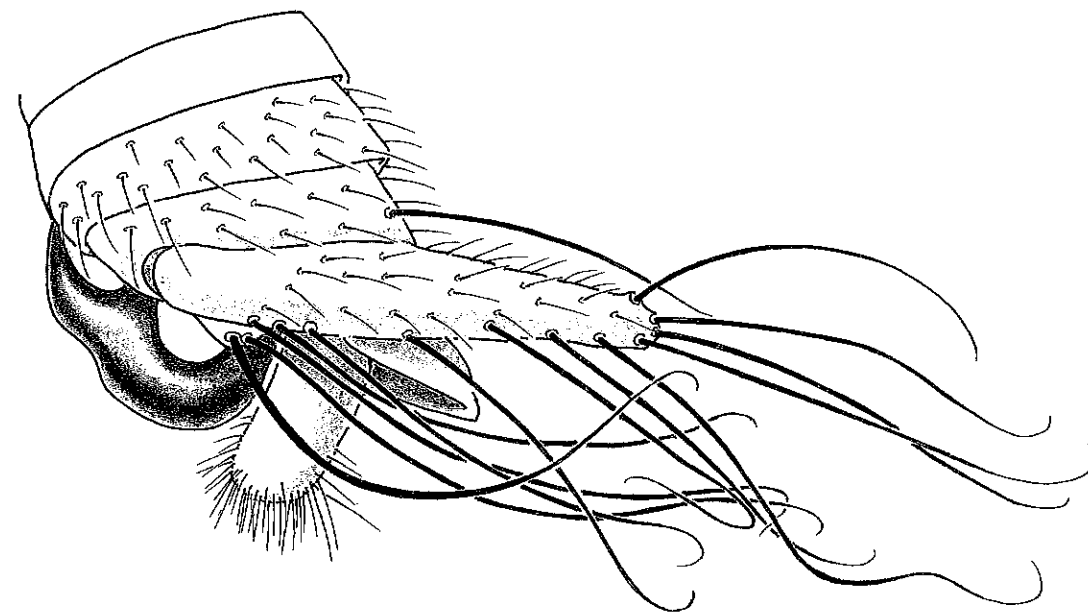


Fig. 156. Male terminalia of *C. spectabilis*, lateral view.



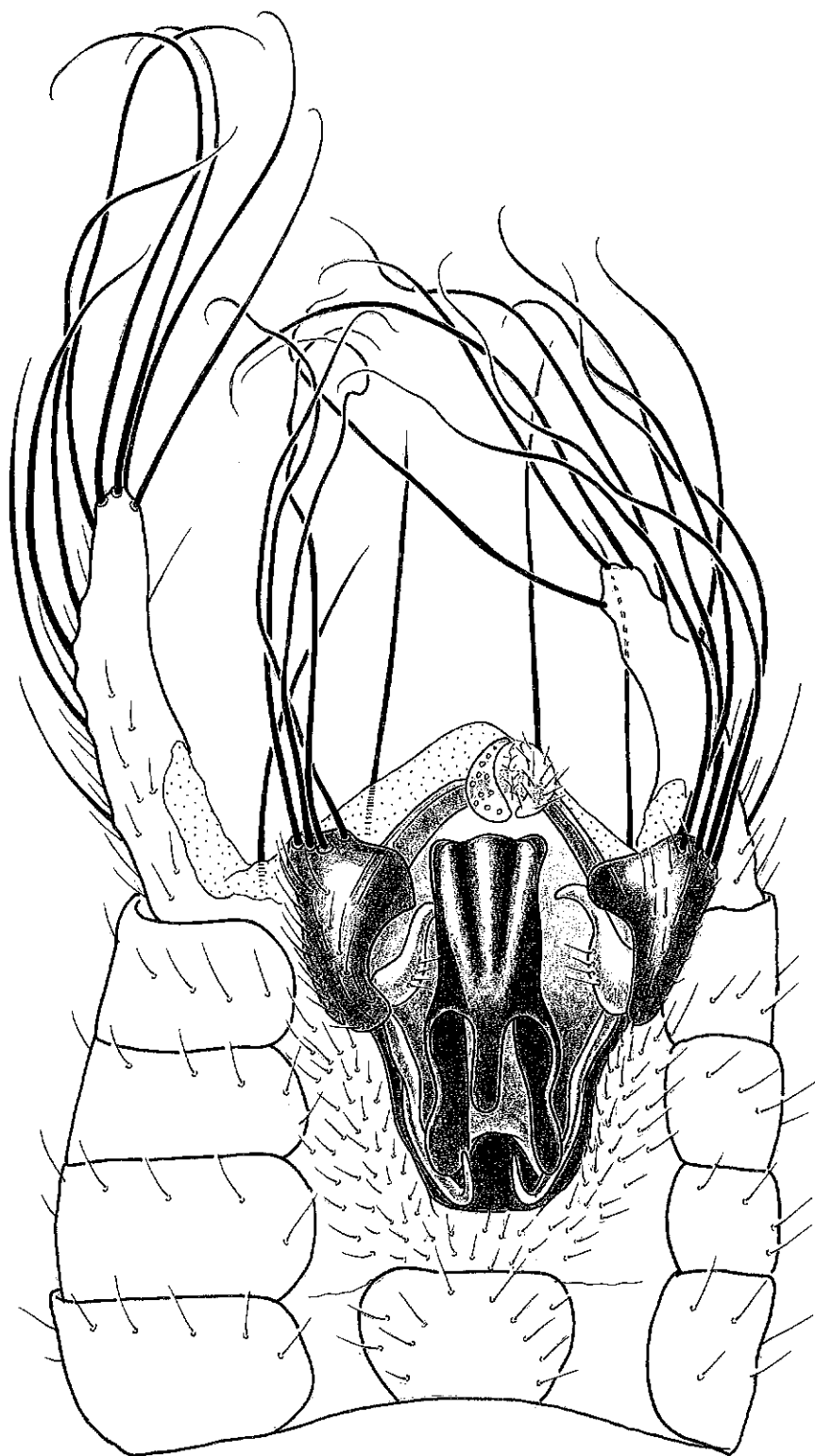


Fig. 157. Male terminalia of *C. spectabilis*, ventral view.

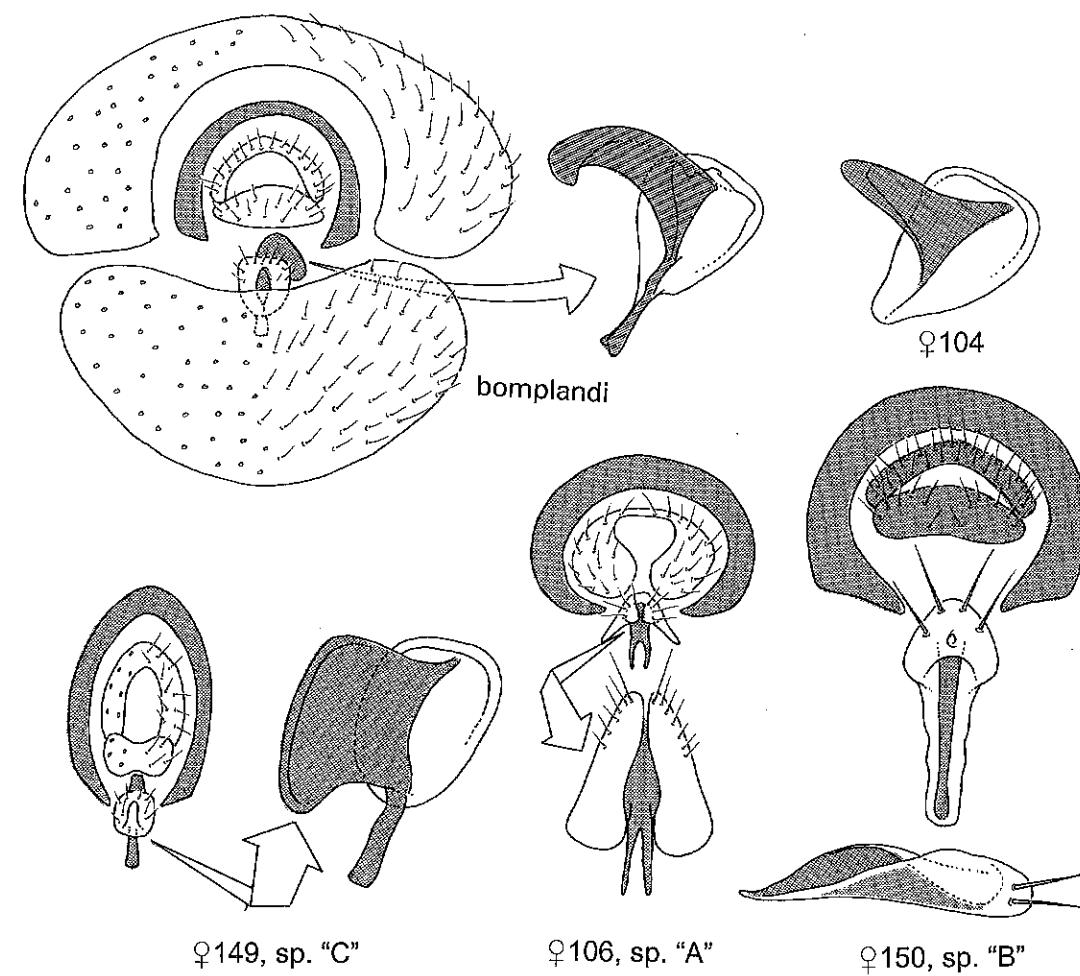


Fig. 158. Female terminalia of *C. bomplandi* and undescribed *bomplandi*-group species.

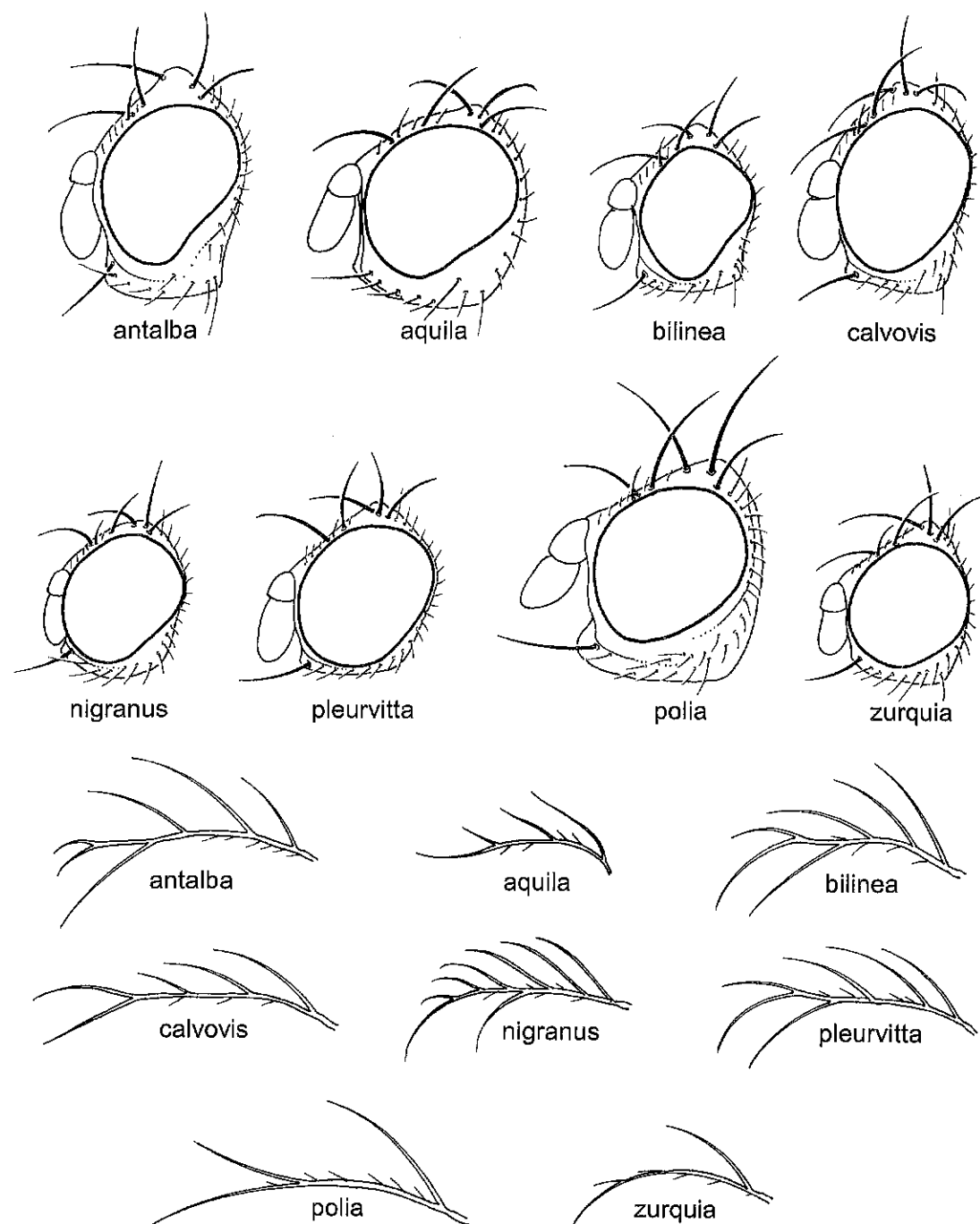


Fig. 159. Heads and arista of unplaced species.

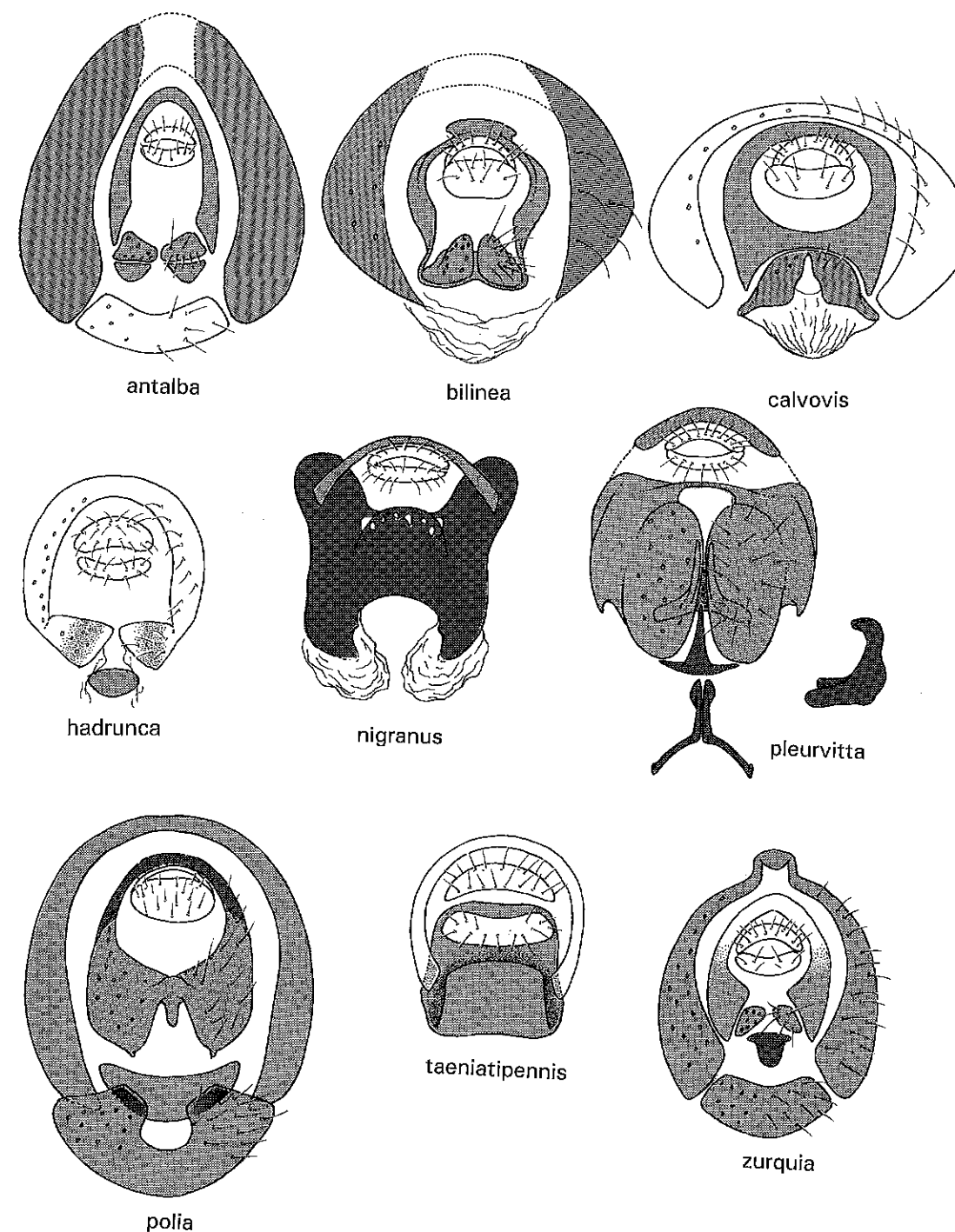


Fig. 160. Female terminalia of unplaced species (posterior views).

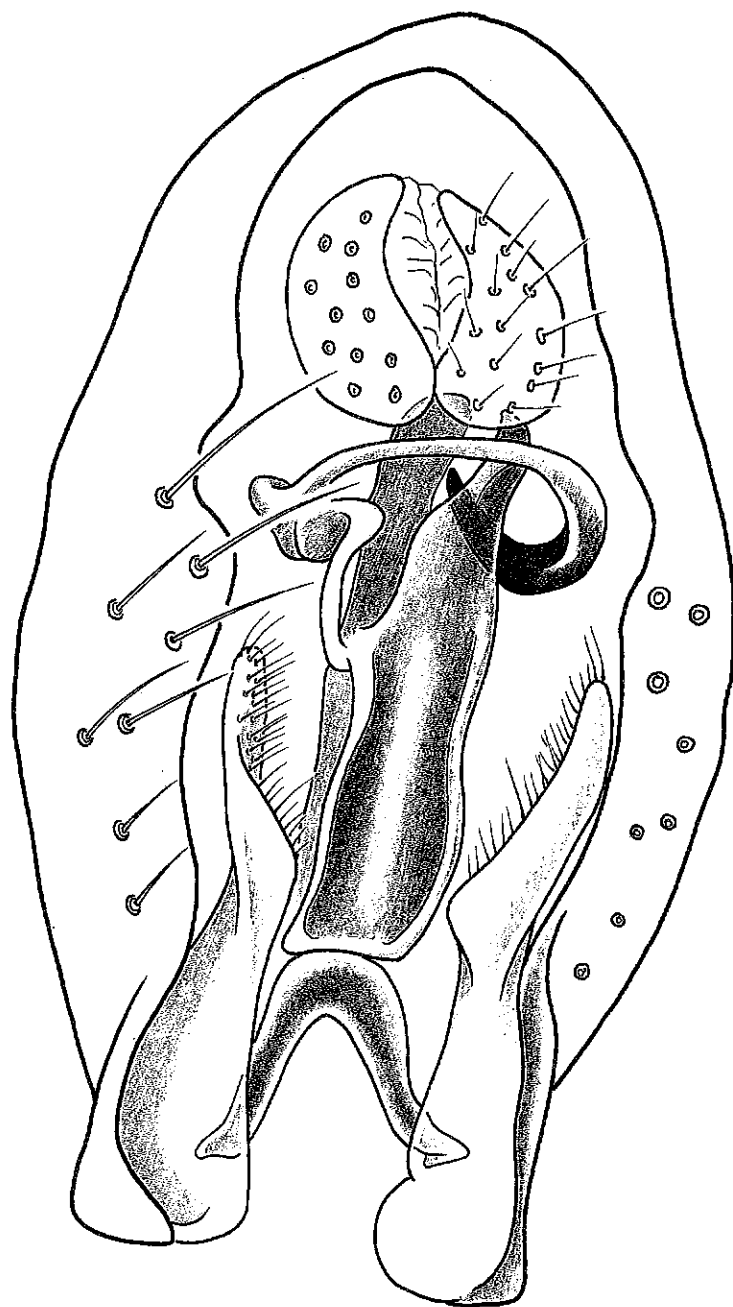


Fig. 161. Male terminalia of *C. aquila*.

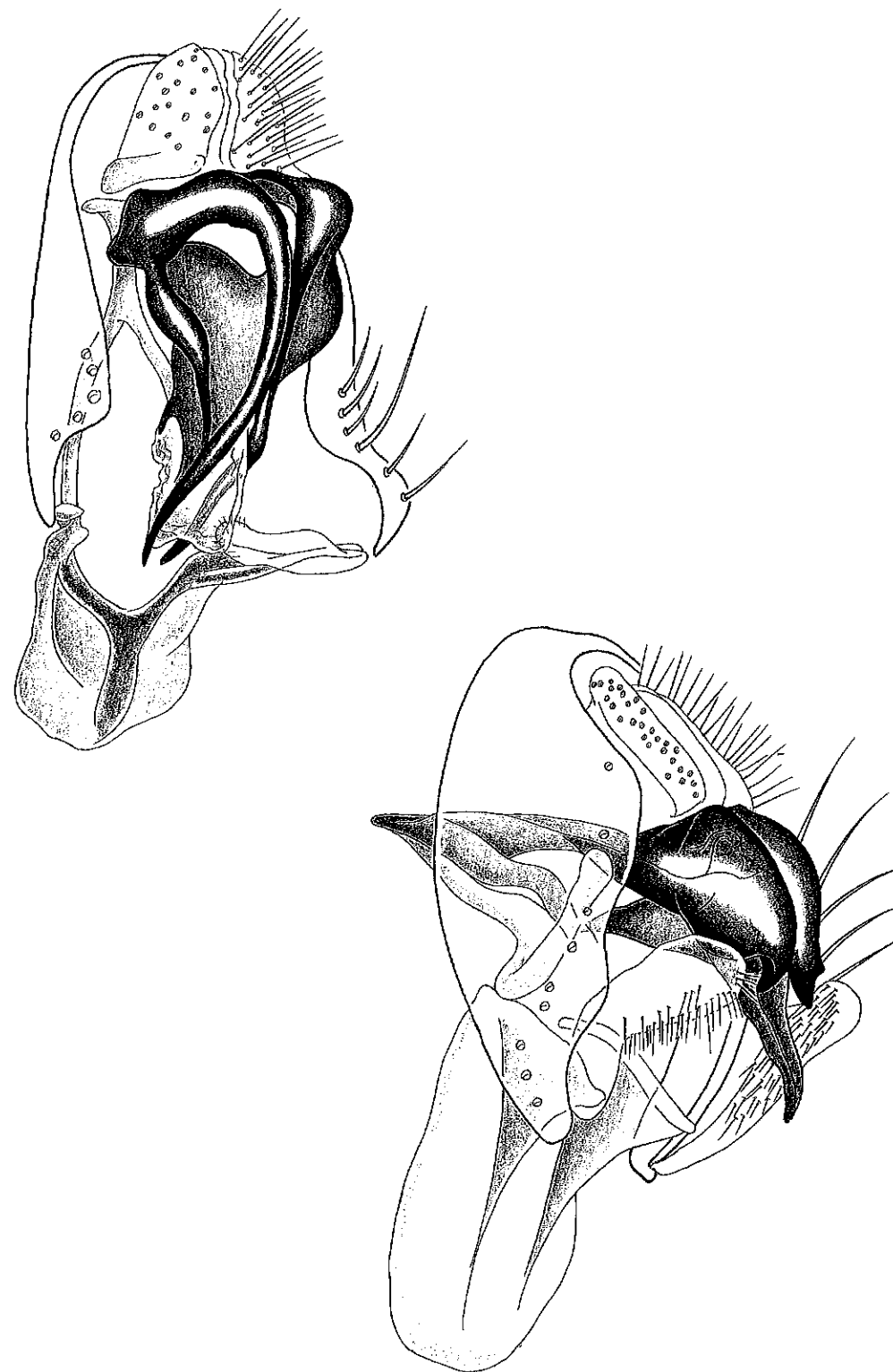


Fig. 162. Male terminalia of *C. calvovis* (above) and *C. zurquia* (below).

## Bomplandi Group &amp; Unplaced Species

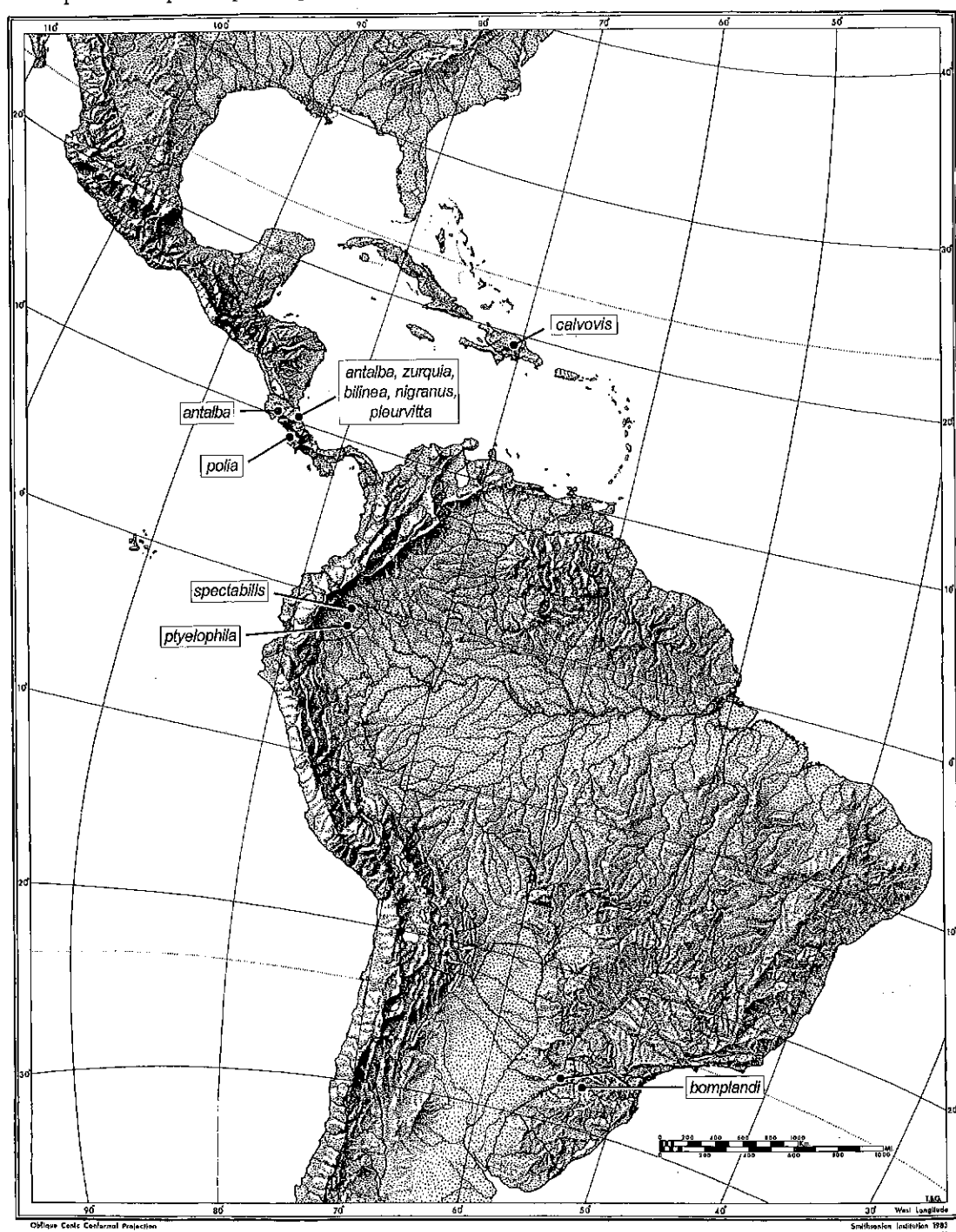


Fig. 163. Distribution of bomplandi group and unplaced species.

## LIFE HISTORY AND SPECIES DIVERSITY

Incredibly, the unusual larvae of *Cladochaeta* have never been described in any detail. Additionally, with the exception of work by Thompson and Mohd-Saleh (1995), there has been little organized study addressing the question of parasitism by *Cladochaeta* larvae. Here, we present a synopsis of all life history information known thus far for the genus, including a discussion on the parasitism debate.

IMMATURES  
VIVIPARITY

Eggs were rarely seen in the pinned specimens that were dissected for this study. Only the egg of *Cladochaeta dikra* was examined in detail, which came from pinned dissected specimens. The egg had 14 (7 pairs) short filaments surrounding an oval operculum area. It was slightly asymmetrical bilaterally, with irregular longitudinal furrows (fig. 164). Fourteen filaments are the highest number yet recorded for the Drosophilidae, but a large number of filaments is a feature that is consistent with other primitive genera of drosophilines (sensu Grimaldi, 1990). For example, *Chymomyza* and *Scaptodrosophila* have between 6 and 10 (3–5 pairs) short to long filaments, which is distinct from the 2 pairs of filaments seen in the ground plan of more recently derived drosophilines such as *Drosophila*.

Females of 5 species harbored first-instar larvae in their abdomens; the species were all collected in March 1991 by Grimaldi at Las Alturas, Costa Rica, and are *antalba*, *fasciata*, *glapica*, *telescopica*, and *vivipara* (see records of specimens). For *Drosophila melanogaster* it is known that if females with mature eggs are starved and not provided with an oviposition substrate, they apparently will hatch a first-instar larva "in utero" (personal obs.). This suggests that viviparity could develop facultatively rather easily. Viviparity in *Cladochaeta*, however, was found in species belonging to several species groups (placement of *C. antalba* is uncertain without males), suggesting that the trait is rather widespread and therefore perhaps not facultative. Viviparity has not been found in

other *Cladochaeta* species where many females have been dissected, such as *C. inversa* and *C. genuinus*. It is possible that viviparity is peculiar to the specimens collected at Las Alturas and is related to seasonality and scarcity of hosts, although there is nothing to suggest this.

Viviparity occurs rarely and sporadically in the Drosophilidae. It is known for *Amiota* (*Sinophthalmus*) *picta* Coquillett (facultatively), *Diathoneura cruciata* Duda (Vilela and Bächli, 1990), *Colocasiomyia*, and *Engiscaptomyza*. In *Colocasiomyia*, the habit is known in *C. diconica* only (Yafuso and Okada, 1990), for oviposition is reported in a number of other species: *xanthogaster*, *heterodonta* (Yafuso and Okada, 1990), *sulawesiana* (Okada and Yafuso, 1989), and *C. pistilicola* and *C. stamenicola* (Carson and Okada, 1980). Kambyzellis and Heed (1971) reported viviparity in *Engiscaptomyza undulata* and *E. nasalis* from Hawaii. According to Michael Kambyzellis (personal commun., 1992), the habit occurs in *E. crassifemur*, as well as in *Exalloscaptomyza*, also from Hawaii. One ecological pattern that can be discerned in the sporadic occurrence of viviparity is an association with flowers, since the breeding sites of *Colocasiomyia* are in the inflorescences of aroids, and *Exalloscaptomyza* breed in morning glory (*Ipomoea*) flowers. However, this is a tenuous conclusion, since the breeding sites of *Amiota picta*, *Diathoneura cruciata*, and *Engiscaptomyza* are unknown. Viviparity in *Diathoneura cruciata* is of particular interest, since this is the sister genus to *Cladochaeta* (Grimaldi, 1990; see also previous discussions). Occurrence of the trait throughout *Diathoneura* will be impossible to assess without numerous dissections and a revision of this speciose genus.

## LARVAL MORPHOLOGY

**FIRST INSTARS:** In utero first-instar larvae of *Cladochaeta* were always found with their anterior end pointed anteriorad in the female abdomen (also reported for *D. cruciata* [Vilela and Bächli, 1990]) (fig. 164). The single larva always found for some females occu-

pied a length approximately one-half the abdomen. The larvae had telescoping posterior spiracles that were inverted. Larvae for 4 of the species were examined for details of the cephalopharyngeal skeleton (CS) and creeping welts (fig. 164). Two of the 4 species had simple nonserrate mandibles (*vivipara* and *antalba*). *Cladochaeta glapica* had 4 rounded teeth posterior to the apical hook; *C. fasciata* had very small serrations. In comparison to the rest of the CS, the mandibles of these first instars were relatively larger than in third instars of *C. inversa* and *C. floridana* (described below). Only the mandibles and anterior portion of the CS were sclerotized. A few oral lamellae were found in *C. glapica*; the other 3 species examined had none. Larvae of all species had creeping welts on 6 segments, as do mature instars of other species. Both *C. glapica* and *C. antalba* first instars had ca. 12 creeping welt spinules on a ventromedial "proleg" posterior to creeping welt 6, which is a structure not seen in third instars of at least *inversa* and *floridana*. All species had very minute sparse spinules on creeping welt 1. In *C. antalba* and *C. vivipara*, creeping welts 2-6 were interrupted medially, with the spinules in each welt arranged in 2 ovals (fig. 164). Each oval had 2 anterior rows of spinules pointed anteriorly and 2 posterior rows pointed posteriorly. The anterior and posterior rows each had a row of larger spinules toward the center of the oval. The medial separation of the creeping welts in *C. antalba* and *C. vivipara* are possibly an early developmental stage toward the extreme separation of the welts into prolegs with "crochets," as seen in mature larvae of *C. inversa* and *C. floridana*. If hosts of *C. antalba* and *C. vivipara* are ever found, perhaps the third-instar larvae will have these proleg structures. It would be extremely interesting to study first instars of *C. inversa* in order to trace the development of the creeping welts and the mandibles (e.g., are they serrate?).

**THIRD INSTARS** (figs. 165-167, 172): Third-instar larvae of 3 species were studied with SEM and compound light microscopy: *C. inversa* (from New York and Ohio), *C. floridana* (from Bermuda), and a species (perhaps *dracula*) from the Southwestern Research Station, Portal, Arizona, collected by

Tom Eisner on cercopids feeding on the composite *Grindelia aphanactis* (see Host Table, below). Below is a description of common attributes, with differences peculiar to each species also noted.

**Description:** Amphipneustic, typical of Muscomorpha. Anterior spiracles with 3 filaments each. Head much smaller (relative to thoracic segment 1) than in saprophagous species. Antenna and maxillary palp complex typical of all drosophilids; apparently highly conserved. Labial lobe lost. Oral cavity small, round. Triangular lobe just lateral to maxillary palp, with small sensilla near apex. Oral lamellae ("oral ridges" sensu Teskey [1981]) reduced to 3 transverse rows with long, thin fringes anterior to oral cavity (not developed lateral to oral cavity, nor converged into oral cavity, as in saprophagous drosophilid larvae). Figure 170 shows 5 genera of drosophilid larvae that illustrate the more numerous oral lamellae and fringes in saprophagous larvae. In *Cladochaeta* the cephalopharyngeal skeleton is reduced, with a dorsal and ventral cornu, hypopharyngeal sclerite, parastomal bar, and dental sclerite (basal to mandible), all unsclerotized (fig. 172). Pharyngeal ridges present, but without filter chambers. Mandible small, sharp, acutely hooked; no teeth in *C. inversa* and Arizona spp., with small basal-lateral tooth in *C. floridana*. Creeping welts on first 6 abdominal segments modified into prolegs, each with rosette of spinules forming a "crochet" (figs. 165-167). Each crochet with 20-25 flat, sharp, acutely hooked spinules; with 2 anterior rows pointed anteriorly, posterior ones pointed posteriorly. Pair of simple, bladderlike structures lateral to anus in *C. inversa* (fig. 167), not found in other 2 species examined. All 3 species with posterior spiracles on a telescoping trunk; trunk about twice the length of both everted spiracular tubes (figs. 165, 167). Spiracle tubes separated, highly sclerotized, eversible. Spiracular plate with 3 spiracular openings to one side in mature larva (typical of Muscomorpha) (fig. 166). Spiracular hairs reduced; not highly dissected and filamentous as in most drosophilines (cf. fig. 171), but short, scalelike, and closely adpressed to rim of spiracular plate. Three to 4 ribs present under spiracular plate, giving it an accordion-like appearance.

In the course of searching for immatures of *Cladochaeta* at the Las Alturas field station near San Vito, Costa Rica, larvae were found associated with spittlebugs, but not belonging to the family Drosophilidae. The host spittlebug was a large black and red species, *Tomaspis inca*, common at the site on *Heliconia* and found throughout Central America. Adults were not reared from the larvae, but morphology strongly indicates the larvae to be a species of ephydrine ephydrid, possibly even *Ephydra*. The larvae were never found attached to the spittlebug nymphs, but were creeping on the floor of the spittle mass. Four to 5 larvae were found in some spittle masses. Superficially, the larvae are very similar to *Cladochaeta*, suggesting preadaptation of the ephydrid larvae to living in spittle masses, as well as convergence of *Cladochaeta* larvae.

Figures 173 and 174 present the morphology of this larval commensal of *Tomaspis*. Similarities between the ephydrid larva and *Cladochaeta* are striking, in particular are the prolegs bearing crochets of 25 large spinules and several smaller ones. However, in the ephydrid there are 7 pairs of prolegs and a medioventral one posterior to pair 7 (typical of *Ephydra*). In the ephydrid larva there is a dorsomedial group of about 25 spinules at the base of the spiracular tubes, also typical of *Ephydra*. The spiracular tubes, as for *Cladochaeta*, are long, bifurcate, eversible, and have a spiracular plate with flat, scalelike spiracular hairs. The head of the ephydrid larva is distinctive for the set of 9-10 transverse rows of lamellae; the anterior 4-5 rows bear elements resembling toothed scales.

In contrast to *Cladochaeta*, the ephydrid larva is definitely saprophagous. The lamellate oral ridges are well developed, with 12-13 horizontal rows feeding into the oral cavity, and 4 vertical rows flanking these. The lamellar filaments are dense, particularly above the oral cavity. These features indicate efficient filtering ability. The cephalopharyngeal skeleton is heavily sclerotized, including the cornuas. Mandibles are serrate, with a row of 3-4 teeth on both ventral edges of each mandible, thus forming a scoop out of the ventroapical surface of the mandible (as in saprophagous forms). This larva and its habits allow important morphological

comparisons with *Cladochaeta*, as well as inferences about feeding.

## HOSTS AND PHENOLOGY

### HOSTS

Table 1 presents new data on *Cladochaeta* hosts. Neotropical and Nearctic species are included. Most of the host records concern species of *Clastoptera*, which is by far the largest among the 10 North American genera of cercopids. It is possible that the predominance of host records on this genus is due simply to the species dominance of this genus, although *Philaenus* probably has greater biomass in north temperate regions, particularly in weedy habitats. *Clastoptera* does not appear to be unique in the variety and kinds of its host plants compared to other cercopid genera, particularly since plant use can be very restricted for some cercopid species. Other genera are restricted to plants of a particular growth form (e.g., perennial herbs, shrubs, grasses). Thus, the apparent predilection of *Cladochaeta* for *Clastoptera* does not seem to be mediated by association of *Clastoptera* with any particular kind or growth form of plant host.

### NEGATIVE HOST RECORDS

We think that negative records encountered in the search of hosts (e.g., cercopids on which *Cladochaeta* has not been found) are just as important to report as are the positive host records. The extent of negative records directly bears on the confidence one has in the mono- or oligophagous nature of an insect. It is quite apparent that even though some cercopids are plentiful and readily available, they are not hosts to *Cladochaeta*. Furthermore, there could be geographical and/or seasonal variation in host use, which is very difficult to document but is suggested by some of the information given below.

Wheeler (1984) found no *Cladochaeta* on nymphs of *Clastoptera arborina* feeding on ornamental Juniper (*Juniperus chinensis*) in Pennsylvania. However, Kuenzi and Coppel (1985) reported finding larvae of a fly (probably *Cladochaeta*) on nymphs of *Clastoptera arborina* feeding on red cedar (*Juniperus virginiana*) in Wisconsin. W. A. Palmer (per-

TABLE 1  
Host Records for Species of *Cladochaeta*

Host nymph	Plant	Locality	Reference
<i>Cladochaeta paradoxa</i> (Lamb)			
<i>Clastoptera</i> sp.	<i>Casuarina</i> ? <sup>a</sup>	Trinidad	Lamb, 1918
<i>Clastoptera taeniata</i>	<i>Casuarina</i> sp.	Trinidad	Williams, 1922
<i>Cladochaeta floridana</i> (Malloch)			
<i>Clastoptera</i> sp. (undulata?)	<i>Casuarina</i> sp.	Bermuda	Hilburn, here
<i>Clastoptera</i> sp. (undulata?)	<i>Casuarina equisetifolia</i>	Florida	Wheeler, here
None mentioned	<i>Bidens pilosa</i> <sup>b</sup>	Florida	Steyskal, 1972
<i>Cladochaeta inversa</i> (Walker)			
<i>Clastoptera achatina</i>	<i>Carya glabra</i> <sup>c</sup>	Ohio	Foote, here
<i>Clastoptera hyperici</i>	<i>Hypericum prolificum</i>	Michigan	Hanna, 1969
<i>Clastoptera obtusa</i>	<i>Alnus "americana"</i> <sup>d</sup>	New York?	Baerg, 1920
	<i>Ostrya virginiana</i>	Michigan	Thompson et al., 1987
	<i>Alnus</i> sp.	New York	Valley, here
	<i>Alnus</i> sp.	Pennsylvania	Valley, here
	<i>Hamamelis virginiana</i>	Ontario	Marshall, here
<i>Clastoptera</i> sp. (prob. <i>obtusa</i> )	<i>Alnus serrulata</i>	Ohio	Foote, here
<i>Clastoptera proteus</i>	<i>Cornus</i> spp.	Illinois	Thompson et al., 1987
<i>Clastoptera</i> sp.	<i>Corylus</i> sp.	Ohio	Foote, here
<i>Cladochaeta psychotria</i> , new species			
Flower only	<i>Psychotria chiriquiensis</i>	Costa Rica	Harms, personal commun.
<i>Cladochaeta ptyelophila</i> Tsacas			
<i>Cephus erythrocephala</i>	<i>Manihot esculenta</i>	Ecuador	Tsacas and Couturier, 1993
<i>Cladochaeta spectabilis</i> , new species			
<i>Sphodroscorta</i> sp.	unknown	Ecuador	here
<i>Cladochaeta sturtevantii</i> Wheeler and Takada			
<i>Clastoptera lineaticolis</i>	unknown	California	Sturtevant, 1921
<i>Clastoptera</i> spp.	<i>Artemisia</i> sp.	California	Sturtevant, 1921
	<i>Baccharis</i> sp.	California	Sturtevant, 1921
	<i>Lepidospartum</i> sp.	California	Sturtevant, 1921
	<i>Senecio douglasii</i>	California	Sturtevant, 1921

sonal commun. to D. G.) did not find *Cladochaeta* larvae in spittle masses of *Clastoptera xanthocephala* feeding on *Baccharis* in Texas; Sturtevant, however, reared a male *Cladochaeta sturtevantii* from a cercopid on *Baccharis* in California. Jorge Santiago-Blay (personal commun. to D. G.) did not find any *Cladochaeta* larvae on nymphs of *Clastoptera lugubris* feeding on *Grindelia* in California, even though hundreds of spittle masses were examined; Eisner, however, found larvae with cercopid nymphs feeding on *Grindelia aphanactis* in southeastern Arizona. Baerg (1920) reported finding no *Cladochaeta* larvae on nymphs of *Clastoptera proteus* (on dogwood), even though the larvae were common associates of *Clastoptera obtusa* (on alder) in the immediate vicinity; Thompson et al. (1987), however, found *C. proteus* to be a host in Illinois. Baerg did not indicate where the fieldwork was done (presumably it was in Ithaca, New York). Foote (unpubl.) found that even though spittle masses of the cercopid *Aphrophora cribrata* were common on white pine (*Pinus strobus*) in Kent, Ohio, no masses harbored fly larvae; likewise, Bales and Furniss (1984) found no larvae of *Cladochaeta*

*Cladochaeta inversa* larvae on nymphs of *Clastoptera proteus* (on dogwood), even though the larvae were common associates of *Clastoptera obtusa* (on alder) in the immediate vicinity; Thompson et al. (1987), however, found *C. proteus* to be a host in Illinois. Baerg did not indicate where the fieldwork was done (presumably it was in Ithaca, New York). Foote (unpubl.) found that even though spittle masses of the cercopid *Aphrophora cribrata* were common on white pine (*Pinus strobus*) in Kent, Ohio, no masses harbored fly larvae; likewise, Bales and Furniss (1984) found no larvae of *Cladochaeta*

TABLE 1  
(Continued)

Host nymph	Plant	Locality	Reference
<i>Cladochaeta</i> spp. undetermined			
<i>paradoxa</i> ?			
<i>Clastoptera</i> spp.	<i>Flacourtia indica</i>	Trinidad	Bennett, 1965
	<i>Casuarina equisetifolia</i>	Trinidad	Bennett, 1965
<i>paradoxa</i> /"nebulosa"?			
<i>Clastoptera</i> sp. nt. <i>diminuata</i>	<i>Coffea arabica</i>	Puerto Rico	Bennett, 1965
	<i>Hibiscus rosa-sinensis</i>	Puerto Rico	Bennett, 1965
<i>Clastoptera flavidorsa</i>	<i>Casuarina equisetifolia</i>	Jamaica	Bennett, 1965
probably <i>inversa</i>			
<i>Clastoptera arborina</i>	<i>Juniperus virginiana</i> <sup>e</sup>	Wisconsin	Kuenzi and Coppel, 1985
(dracula?)			
<i>Clastoptera</i> sp.	<i>Grindelia aphanactis</i> <sup>e</sup>	Arizona	Eisner, here

<sup>a</sup> Lamb (1918) indicated the cercopid plant hosts to have been cacao trees, but in an original reprint annotated by Lamb, cacao is crossed out and "*Casuarina*" is written in. Also, Bennett (1965) cited this record as being *Clastoptera theobromae*, but there is no mention in Lamb's paper to that species.

<sup>b</sup> This record actually refers to *Cladochaeta nebulosa* (Steyskal, 1972), which does not occur in Florida (identification based on examination of voucher specimens). Steyskal made no mention of spittlebugs among the insects he reared from the *Bidens* flower heads.

<sup>c</sup> This record is based on the presence of larvae and puparia in and near the spittle masses of this species, not on rearings of adults.

<sup>d</sup> The species name *Alnus "americana"* does not appear to be valid; the species this record represents is uncertain.

<sup>e</sup> Records based solely on larvae.

associated with nymphs of the cone spittlebug, *Aphrophora canadensis*, on Mugho Pine (*Pinus mugo*) in Idaho. In Costa Rica, no *Cladochaeta* larvae were found on 4 species of *Prosapia*, one of which is very abundant in pastures (Dan Peck, personal commun.).

Availability certainly does not dictate host use in *Cladochaeta*. In May and June in New Jersey, meadow spittlebugs are extremely dense, but we have yet to find one *Cladochaeta* larva with them. For example, in 1990, 57 *Aphrophora* nymphs were examined on 55 plants of thistle, ragweed, grass, sorrel, and dandelion. Another 95 spittle masses were examined of a different *Aphrophora* species feeding on Scotch Pines (*Pinus sylvestris*) in the same field. There were an estimated 7000 spittle masses in this one field bordered by trees, and a sampling of ca. 2% of the total found no *Cladochaeta* larvae. Since these are spring spittlebugs, it may be phenology that dictates host use in the flies.

Ashburner (1981) cited Pipkin (1965,

1966) in saying that *Cladochaeta* may have a tropical niche that is much broader than just the use of spittlebug nymphs and/or their spittle. It is unclear if the larval breeding site of *Cladochaeta* are anything but inhabited spittle masses. Pipkin recorded that she occasionally captured adult *Clastopteromyia* (an old, suppressed generic name) while sweeping over fallen fruits and flowers. Her voucher collection at the AMNH and the Smithsonian Institution has been examined, and the only specimens to which she could have been referring are *Dithoneura* species (*albinota*, *opaca*, *superba* and relatives, and a few other species).

Two records do not include spittlebugs: (1) Steyskal (1972) reported breeding 5 individuals of *Cladochaeta nebulosa* out of 60 heads of *Bidens pilosa* (Compositae) collected in late November in Dunedin, south Florida. The flies emerged about 2 weeks after the dried flower heads were collected. Re-examination of Steyskal's voucher specimens in the Smithsonian Institution shows that the



TABLE 2  
Phenology of *Cladochaeta* Larvae on  
*Clastoptera* in Ohio

Date of collection	Number of nymphs	Number of larvae	Infestation rate (%)
25/VIII/83	23	9	39
26/VIII/83	21	12	57
30/VIII/83	25	15	60
5/IX/83	16	9	56
24/VIII/84	24	14	58
28/VIII/84	9	8	89
21/VI/85	2	0	0
26/VI/85	5	0	0
27/VI/85	5	0	0
8/VIII/85	13	8	62
17/VIII/85	25	21	84
10/VI/86	10	0	0

Data courtesy of Ben Foote, Kent State University.

species is actually *C. floridana* (*C. nebulosa*, as revised above, is not known to occur in Florida). It is unclear if the *Cladochaeta* larvae were feeding on the flower heads, as is assumed in the report, or if they emerged from puparia lodged in the flower heads. It is quite possible that *Cladochaeta* larvae, while feeding on spittlebugs on the *Bidens* plants, crawled into the heads to pupate. *Cladochaeta inversa* pupae are always found cemented to the edge of a twig, near the apex (sometimes even between stipules), and are usually very cryptic. (2) The other record involves several specimens of *Cladochaeta psychotria*, n. sp. which were reared from larvae feeding among the bracts of *Psychotria chiriquiensis* in Monteverde, Costa Rica (Kyle Harms, personal commun.). The larvae were apparently feeding on pollen in the bracts, which each contains about a dozen flowers; larvae were found at the base of the flowers, so it is almost certain they are not associated with spittlebugs. Clearly, not all species are spittlebug associates.

#### PHENOLOGY

The most extensive phenological data taken thus far are by Ben Foote for *Cladochaeta inversa* around the vicinity of Kent, Ohio. Table 2 shows the dates, numbers of nymphs examined and the number harboring larvae, and the number of larvae found. One to 2 larvae were found per nymph, although one

larva per nymph was most common (this was reported by Baerg [1920] for *C. inversa* larvae on *Clastoptera obtusa* as well). Numbers of larvae of each instar per spittle mass were also recorded by Foote. There was apparently no indication that more first and second instar larvae occurred per spittle mass or per nymph compared to third instars; thus, an even larval distribution is due not to cannibalism, but probably to oviposition. Female *Cladochaeta* must selectively oviposit among the available spittle masses, but it is possible that resident larvae may cannibalize eggs placed in their spittle mass.

Collections of *Cladochaeta inversa* in Ohio from the fall always produced *Cladochaeta* larvae; spring collections revealed none. It is possible that this is due to the smaller cercopid populations in the spring (or just to the diapause pattern of the fly), but presumably they would be cause-and-effect related. Even though many fewer spittle masses were censused in the spring (total of 22) versus the fall (166), it is unlikely that the absence of spring larvae is due solely to sampling bias. For example, for any one fall census the numbers of spittle masses were similar or much less than the spring total (a range of 9–25), but a range of 8–21 larvae was found in all fall censuses. Also, the number of spittle masses harboring fly larvae almost always exceeded 50% during the fall. Thompson et al. (1987) reported very low numbers of *Cladochaeta* larvae on *Clastoptera proteus* during late June and early July in Illinois and Michigan, with ca. 3% of the nymphs with larvae. They stated, however, that "almost every *C. obtusa* spittle had associated *C. inversa* pupae," but did not indicate how many spittle masses were censused. It is most likely then that *C. inversa* in Ohio and the other northern U.S. states has 2 generations per year: larvae develop in late summer to early fall; overwintering occurs as puparia or pharate adults, with probably considerable mortality; adults emerge in (middle/late?) spring; mating and oviposition take place, producing an early summer larval generation; a second, much larger population of *Cladochaeta* larvae then occurs in late summer and early fall, the offspring of the late spring, overwintered adults.

At the Black Rock Forest in Cornwall,

southern New York, 2 alders heavily infested with *Clastoptera obtusa* were examined by the senior author on 12 and 29 September 1990. These alders occurred in a small group. On 12 September, 30 out of 92 nymphs examined had fly larvae. On 29 September, 11 out of 35 nymphs examined had larvae. Both censuses revealed that about 32% of the nymphs had larvae, which is lower than that found by Foote in Ohio (table 2) for the same season. Fifty to 100% of the *Clastoptera obtusa* nymphs in Guelph, Ontario, were found with fly larvae (Steve Marshall, personal commun.).

Among 11 spittle masses of *Clastoptera* sp. (*undulata*?) sampled 6 October 1988 on *Casuarina* in Bermuda, 33 nymphs bore 8 *Cladochaeta floridana* immatures (larvae, sometimes puparia) (an infestation rate of ca. 25%). No nymph hosted more than 1 larva (D. Hilburn, personal commun.). It is interesting that Bennett and Hughes (1963) found *C. undulata* populations on Bermuda from late August to early November to be nearly 3 times higher than in the preceding months. It is highly unlikely that the larvae cause mortality in the cercopids (see below), but even if they impose reduced size and fecundity, this common association must be a considerable selection pressure for the cercopids.

#### INQUILINE OR PARASITE?

Are *Cladochaeta* larvae just inquilines, are they parasites, or sometimes one and sometimes the other? Of the slightly more than 300 nymphs examined by the senior author at the Black Rock Forest site in New York, none was ever found dead or moribund, which is an observation consistent with all those made by other investigators. If *Cladochaeta* larvae have an effect on their hosts, it is subtle, and they probably never kill their hosts. Baerg (1920) found that for only 1 nymph out of about 100 was there any visible sign of injury from an attached nymph ("bruised" along the side of the abdomen). Baerg (p. 21) concluded that the fly larva "apparently feeds on plant sap in the form of spittle produced by the *Clastoptera*." Williams (1923) came to the same conclusion, but Bennett (1965: 98) stated about Williams' work that "later, when working with

*Clastopterymyia paradoxa* in the froth of *C. taeniata* in Trinidad, [Williams] stated that this species 'undoubtedly kills some of the nymphs.' " Wheeler (1952) thought that *Cladochaeta inversa* was ectoparasitic and stated that "the larvae feed directly on the *Clastoptera* nymphs; in examining spittle masses for larvae they were invariably found lying on the abdominal dorsum of the nymph with the mouthparts inserted between two adjacent tergites, usually the third from the rear. The posterior spiracles are surrounded by a large bubble. We were never able to rear larvae to adults when the nymphs were removed from the spittle masses" (emphasis added). Our observations agree with those by Wheeler. The larvae cling so tenaciously to their host that often they could not be dislodged even when the nymph was immersed in ethanol for preservation. If the larvae were simply phoretic on the nymphs, why should they require such a lifestyle? The spittlebug nymphs hardly move from one feeding area, and feeding on spittle would not require attachment to the host. The best available evidence indicates that the larvae are not just phoretic, but are parasitic instead.

#### HOST INJURY

Bennett (1965) reported finding no evidence of integument injury (e.g., holes or tears in the intersegmental membrane, melanized spots) on *Clastoptera* nymphs hosting *Cladochaeta* larvae in Puerto Rico, Jamaica, and Trinidad. This contrasts with the situation we have found for *C. inversa* in New York. Nymphs of *Clastoptera obtusa* were examined on speckled alder (*Alnus incana*) at Black Rock Forest (BRF), Orange Co., New York, on 12 and 29 September 1990. Nymphs that had hosted fly larvae and those without larva were examined at 60X magnification for integumental injuries, and these injuries were even more closely examined under the scanning electron microscope. All the nymphal specimens were first preserved in ethanol, then critical-point dried, and point mounted. Very small melanized spots were found on some nymphs, which were easily overlooked at low magnifications. Figure 168 shows the dorsal and ventral views of *C. obtusa*; several spots were greatly magnified on

TABLE 3  
Measurements of *Clasoptera obtusa* Nymphs  
With and Without Larvae of *Cladochaeta inversa*  
(September 1990; BRF, New York)

	No. nymphs	Presence of spots		Nymphal head width (mm), mean (range)
		No. nymphs with spots	Spots per nymph, mean (range)	
With larvae				
Instar 4	8		6.8 (1-21)	0.99 (0.95-1.08)
Instar 5	22		5.1 (0-21)	1.53 (1.03-1.72)
Total		21 (75%)		
Without larvae				
Instar 4	7		4.6 (1-18)	0.97 (0.95-1.12)
Instar 5	62		1.6 (0-18)	1.59 (1.14-1.81)
Total		24 (35%)		

the dorsal surface of a *C. obtusa* abdomen. Injuries caused by the larvae are all holes, but these vary in structure. Some were holes with irregular, diffuse edges, where the integument was seemingly abraded very thin. Other holes were surrounded by irregularly shaped feeding tubes. Finely shredded regions of integument had caused other melanized spots. Mature nymphs with black spots on the dorsum (never on the ventral surface) of the abdomen were routinely found; occasionally such nymphs did not even have a larva attached to them.

At BRF, 97 fourth and fifth instar nymphs were collected, with and without fly larvae. Table 3 shows the results: 69 were found without larvae, 28 with larvae. Of the 69 nymphs without larvae, 35% of them had small melanized spots (vs. 75% of the nymphs having spots that also had larvae). Moreover, of the nymphs with spots but without larvae, there were fewer spots per nymph. These results indicate, not surprisingly, that the fly larvae cause the small melanized spots. However, why should there be any spots on nymphs found without larvae? It is possible that these nymphs at one time harbored larvae, which had since pupated.

Probably the most interesting result is that there was a significantly higher proportion of fourth instar nymphs among those found with larvae (28%) versus nymphs without larvae (10%). These data implicate the *Cladochaeta* larvae in retarding development of the nymphs. This result is not consistent with that of Thompson and Mohd-Saleh (1995), who found no significant differences among *C. obtusa* nymphs with and without *Cladochaeta* larvae. A few data on nymphal size (using head width as an index), however, suggest that larvae do not stunt nymphal growth. Size comparisons of nymphs with and without larvae made between fourth instars and between fifth instars show no significant differences.

One certainty emerges: *Cladochaeta inversa* larvae make holes in the integument of their hosts and embed their heads there. Larvae probably feed on hemolymph, and this possibly delays development of the host nymph.

At least 2 Neotropical species actually pupate on the nymphal host (fig. 169): *Cladochaeta ptyelusimya* and *C. spectabilis*, n. sp., both from Ecuador, but on different genera of spittlebugs.

#### HOST AND LARVAL SURVIVORSHIP

In an attempt to prove experimentally if *Cladochaeta* is parasitic, Bennett (1965) took eggs and various instar *Cladochaeta* larvae and supplied them with fresh spittle but without nymphs. He found that older larvae readily pupated on just spittle, but that only 2 out of 10 eggs developed to the pupal stage, and no adults emerged from these pupae. The numbers of tested larvae were not given but were apparently quite small, and the small experiment was done without replicates or a control. This is a preliminary indication that at least older larvae may not require cercopid hemolymph to pupate. However, other measures of fly development are more meaningful to study for such an experiment, since death in the pupal and pharate adult stages is a very common form of inviability in *Drosophila*, and in fact third instar larvae of many *Drosophila* species will readily form a puparium (but will not metamorphose) if

starved. It would be best to measure survivorship of larvae to the adult stage and the size of the adult, compared between sets on *Clasoptera* nymphs with and without spittle, and a set with just spittle (ideally, fertility would also be compared). Also, the fact that the older fly larvae can pupate with just spittle does not rule out deleterious effects that the larvae have on the host nymph. Thus, development time, survivorship of nymphs to the adult, and adult size should be measured for cercopid nymphs with and without *Cladochaeta* larvae. We found that nymphs readily abandoned spittle masses when probed too much while looking for larvae, so such experiments on adult survivorship and size should be done very carefully.

Foote tested whether *Cladochaeta inversa* larvae could develop solely on spittle by providing 10 second instar larvae solely with *Clasoptera obtusa* spittle. Within 1 to 3 days they wandered from the spittle, even when it was supplied fresh, and all died within 1 week. Only 1 larva had formed an undersized and inviable puparium. These results suggest that *C. inversa* larvae search for another nymph when displaced from their original one, because they cannot subsist on spittle alone.

#### LARVAL DIET

That cercopid spittle can be the major or even sole dietary component of *Cladochaeta* larvae is suggested by the comprehensive study of spittle composition by Wilson and Dorsey (1957). Cercopid spittle issues from the anus of the feeding nymph and is formed from excess sap drained from the host plant. It reduces desiccation and possibly parasitism and predation. Wilson and Dorsey reported that Licent (1912) "found that cercopid spittle contained more water (99.4 vs. 94.57%), less organic material (0.14 vs. 3.83%) and less inorganic matter (0.38 vs. 1.60%) than the associated plant sap." Wilson and Dorsey reported that the spittle masses of the meadow spittlebug (*Aphrophora* sp.) contained a few amino acids and some sugars and that the pH was basically neutral, having averaged 7.26 and ranged from 6.15

to 7.81 (N = 23). Marshall (1966) reported that not just sugars, but a mucopolysaccharide is secreted by the nymph (deriving from the malpighian tubules, the substance probably serving to reduce surface tension and stabilize the bubbles). Marshall reported that after hydrolysis of the polysaccharide, very small quantities of glucuronic acid, glucosamine, glucose, rhamnose, and proteins occurred in the spittle. With a medium of such composition it is of little surprise that Wilson and Dorsey found bacteria thriving in it (at concentrations of 18.4-108.4 million/ml of spittle [average of 59.4 million; N = 12 samples]). The bacteria were almost all Gram-negative rods, belonging to the genera *Flavobacterium* and *Achromobacter*. Bacteria and yeasts are among the foodstuffs ingested by saprophytic *Drosophila* larvae, from mycophagous to cactophilic and frugivorous species. The fact that spittle supports microorganismal growth and contains some basic ingredients for larval development is one reason why Ashburner (1981: 410) concluded that it should "provide food for the development of a drosophilid." Perhaps the easiest way to test this conclusion is to examine the gut of *Cladochaeta* larvae (Is it filled with hemolymph cells of its host?). Electrophoretic evidence presented by Thompson and Mohd-Saleh (1995) was equivocal: 1 larva among 19 appeared to have ingested tissue of its *Clasoptera* host. They interpreted this as genuinely sporadic occurrence of parasitism, but acknowledged the possibility of limitations in the technique.

#### TRANSITION TO PARASITISM

If, as Licent (1912) reported, the spittle is not as rich in nutrients as the plant sap from which it is derived, then why would *Cladochaeta* evolve a use of the spittle? Spittle may simply be in copious supply compared to, say, sap fluxes. For example, there are many acalyptate flies that breed solely in the sap fluxes of trees (*Aulacigaster* [Aulacigasteridae], *Stenomicro* [Perisclididae], *Chymomyza*, and various *Drosophila* [Drosophilidae] species), so an obligate, specialized sap flux guild has evolved that does not include *Cladochaeta*. The transition to a spittle-in-

habiting larva need not have been via sap feeding, however, as suggested by anecdotal evidence from other drosophilids.

Wheeler (1991) reared *Scaptomyza pallida* from spittle masses of the cercopid *Lepyronia coleoptrata* on the introduced weed legume crown vetch (*Coronilla varia* L.) in Pennsylvania. Larvae were found inside the spittle masses and eggs were beneath the spittle, suggesting that females were actually ovipositing in the spittle. Larvae were not attached to the nymphs but were crawling through the spittle mass. The spittle mass was serving as a refuge or larvae were feeding on debris and microorganisms in the spittle. *Lepyronia* is a widespread, abundant, polyphagous cercopid that feeds on various weeds, including Canada thistle (*Cirsium arvense* L.). *Scaptomyza pallida* larvae were also found in spittles of *L. coleoptrata* on thistle. The intriguing aspect of these rearing records is that *S. pallida* is a leafminer, typical of the entire genus, albeit this species is extremely polyphagous and is even occasionally found in rotting vegetation. In many places in North America, particularly in disturbed and weedy habitats, *S. pallida* can be by far the most abundant fly. High population densities could lead to indiscriminate oviposition and the use of all sorts of substrates in the immediate habitat, including, as in this case, spittle.

Another example of larvae dwelling (probably facultatively) in spittle masses is *Drosophila (Sophophora) azteca* (Kelson, 1964). We examined Kelson's series of 4 males and 3 females collected from California (San Francisco, Lobos Creek, 20/VII/62, W. E. Kelson), which "emerged 24/VII/62, reared from spittlebug" (specimens in CAS collection), with the spittlebug reported in the published note being *Aphrophora canadensis*. *Drosophila azteca* belongs to the *obscura* species group, which includes very abundant flies in Holarctic forests of cooler climates and higher altitudes. Some species appear very polyphagous, but the main breeding sites of all species remain largely unknown.

Lastly, Odhiambo (1958) reported having bred a species of *Leucophenga* (Drosophilidae: Steganinae) from *Ptyelus flavescens* F.

(Cercopidae) on the legume tree *Milletia* in Uganda. Séguy (1932) originally reported this habit in a fly from Madagascar, found also in association with *Ptyelus*, and which he described as *Ptyelusimyia decaryi* (this genus has now been synonymized with *Leucophenga*; unfortunately, we cannot tell if Odhiambo's specimens are a different species than Séguy's—even though Odhiambo mentioned that specimens were originally deposited in the University Texas collection, they are not there). A *Leucophenga* species, perhaps *L. decaryi*, has also been bred from *Ptyelus grossus* spittle masses in Nigeria (J. Deeming and M. C. Dike, personal commun. to D. G.). Also, a *Paraleucophenga* species (originally identified as a Campichoetidae) was reported as "commensal, parasitic, or predatory" on nymphs of the spittlebug *Hindola viridicans* in Sumatra feeding on clove (*Syzygium*) (Lomer et al., 1993). These records, plus the record of the ephydrid larva discussed earlier, indicate at least 6 independent invasions (some facultative) of spittle masses by various ephydroids, including *Cladochaeta*. The transition from being a saprophagous larva to an inquiline is apparently not a major barrier.

Perhaps the best evidence for the parasitic nature of *Cladochaeta* larvae comes from comparative morphology. Several structures adapt *Drosophila* larvae to filter the microorganisms from their decaying, liquified host medium, which are lamellate oral ridges and a system of fine canals on the floor of the pharyngeal sclerite (Dowding, 1967). Small sharp mandibles of the *Cladochaeta* larvae can be construed as evidence mostly in favor of parasitism rather than inquilinism. They are obviously used for piercing, tearing, and abrading the intersegmental membranes between abdominal tergites of the cercopid nymph, and they would be entirely ineffective in shoveling spittle into the oral cavity, wherein microorganisms would normally be strained out. Apparently the 6 pairs of pseudopods with crochetlike hooks adapt the larva for attachment to its host. The additional finding of an ephydrid species in Costa Rica (described above), with larvae that live in spittle masses, do not adhere to the host, and have a typical saprophagous oral morphology, indicates that saprophagy in spittle mas-

ses is behaviorally and morphologically distinct from what is seen in *Cladochaeta*.

Writing at a time when much less was known of *Cladochaeta* habits, Clausen (1940) mentioned that there was a curiously similar analogue to *Cladochaeta* in the Lepidoptera: the Epipyropidae. A more recent review of the biology of this bizarre group of moths is provided by Davis (1987) and Common (1990). Epipyropids also have highly modified, styletlike mandibles, which they embed in the dorsal part of their homopteran

host (generally, a fulgorid, but also on Cicadellidae and Cicadidae). They have very well-developed claws and specialized crochets for adhering to their hosts. The effect of the parasitism, too, appears relatively slight, for "the amount of body fluids abstracted is comparatively small, with only a certain degree of weakness [of the host]" (Clausen, 1940: 490). Krishnamurti (1933) concluded similarly. Early studies of epipyropids likewise assumed the larvae were feeding on waxy secretions, not hemolymph.

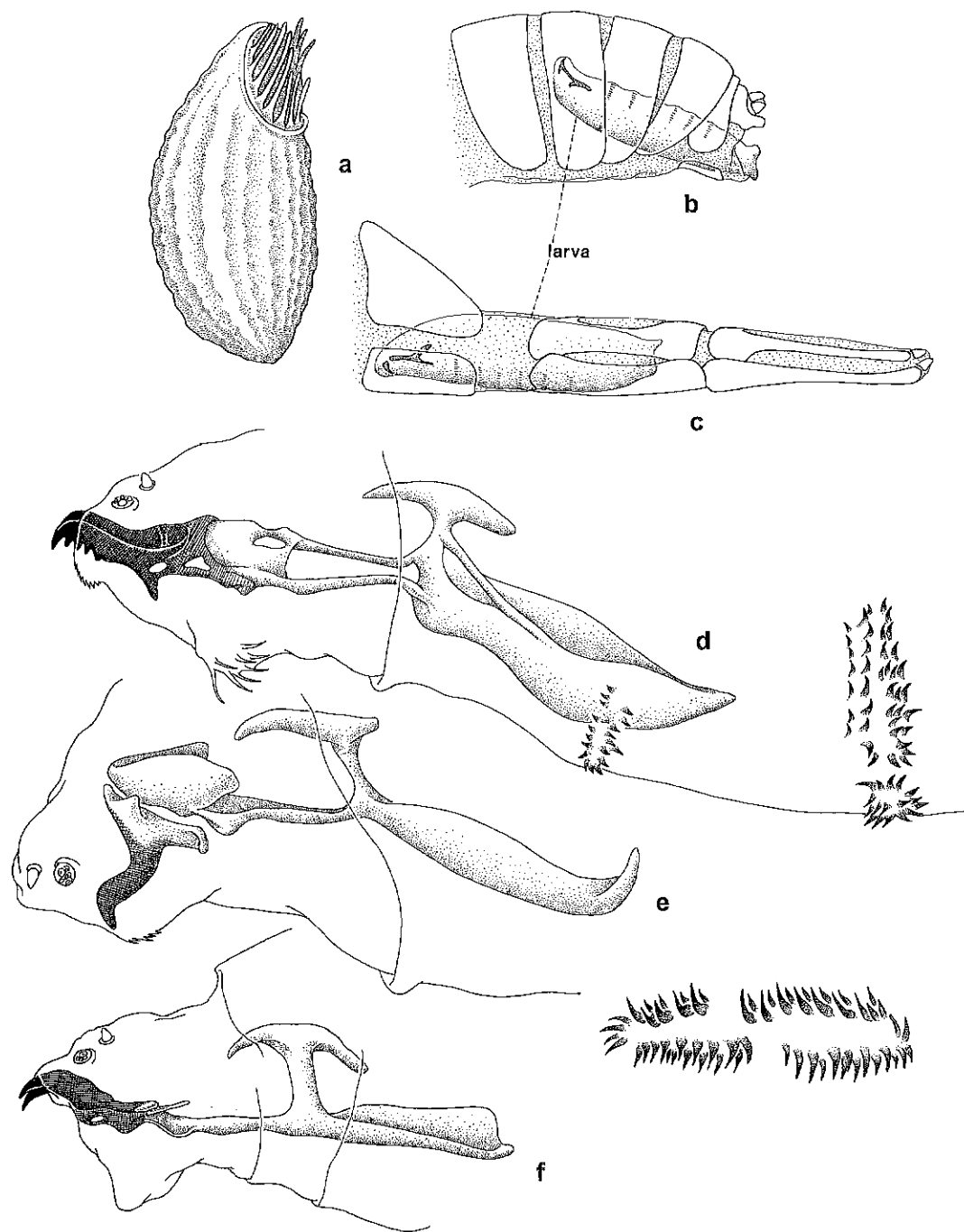


Fig. 164. Early immature stages of *Cladochaeta*, also showing viviparity. a. Egg of *Cladochaeta dikra*. b. First instar larva in abdomen of *C. vivipara*. c. First-instar larva in abdomen of *C. telescopica*. d, E. Heads (lateral view) of first in-utero first-instar larvae. d. *C. glapica*, also showing first 2 creeping welts. e. *C. vivipara*, with creeping welt 4. f. *C. antalba*.



Fig. 165. Scanning electron micrograph of third-instar larva of *Cladochaeta floridana*, lateral view. Curled repose is typical of live larva, but integument is crumpled in this preserved specimen.

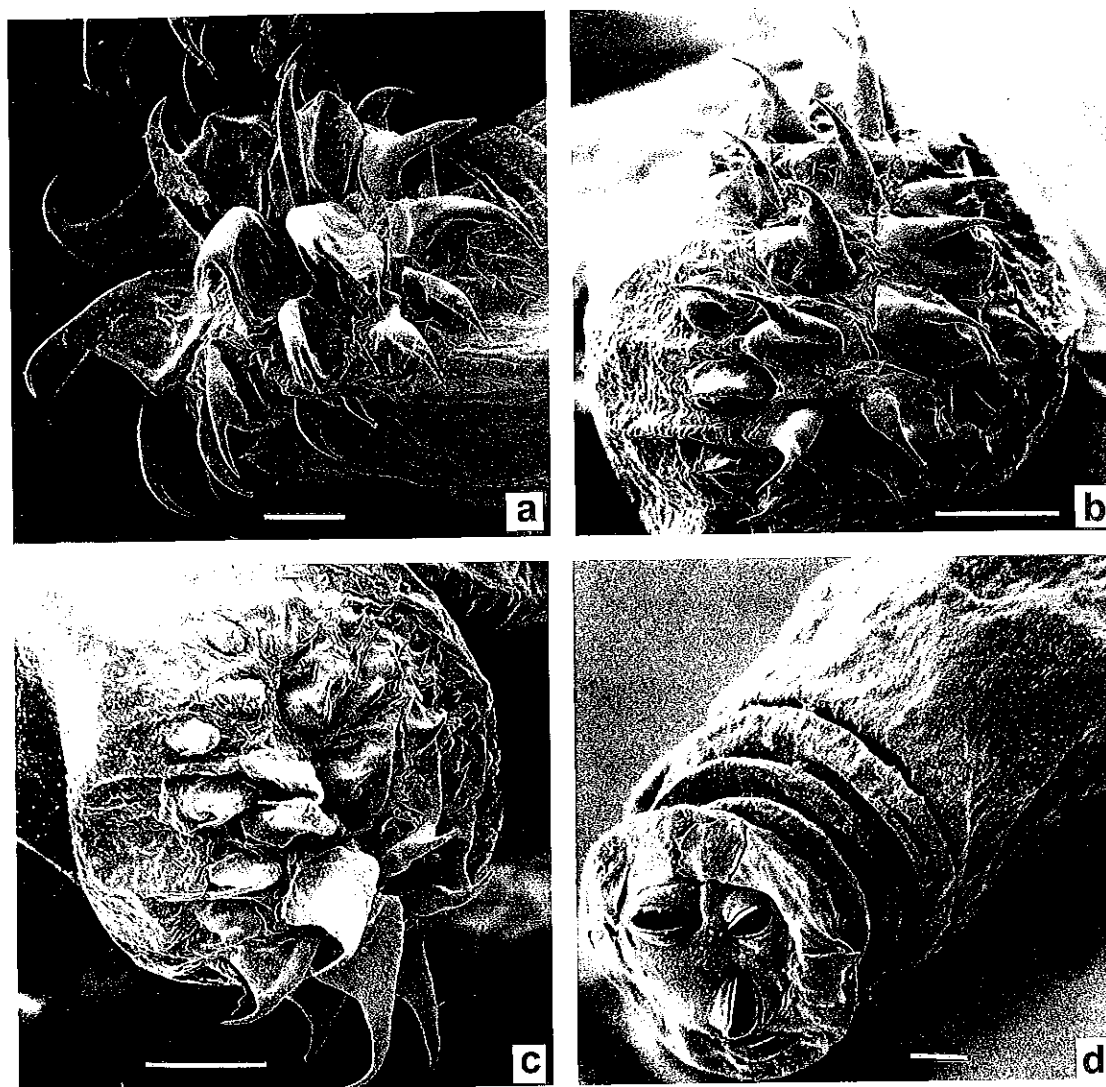


Fig. 166. Scanning electron micrograph details of *C. floridana* third-instar. a-c. Various prolegs, showing "crochets" or rosettes of creeping welt spinules. d. Apex of posterior spiracle, showing spiracular disk, openings, and leaf-like spiracular "hairs."

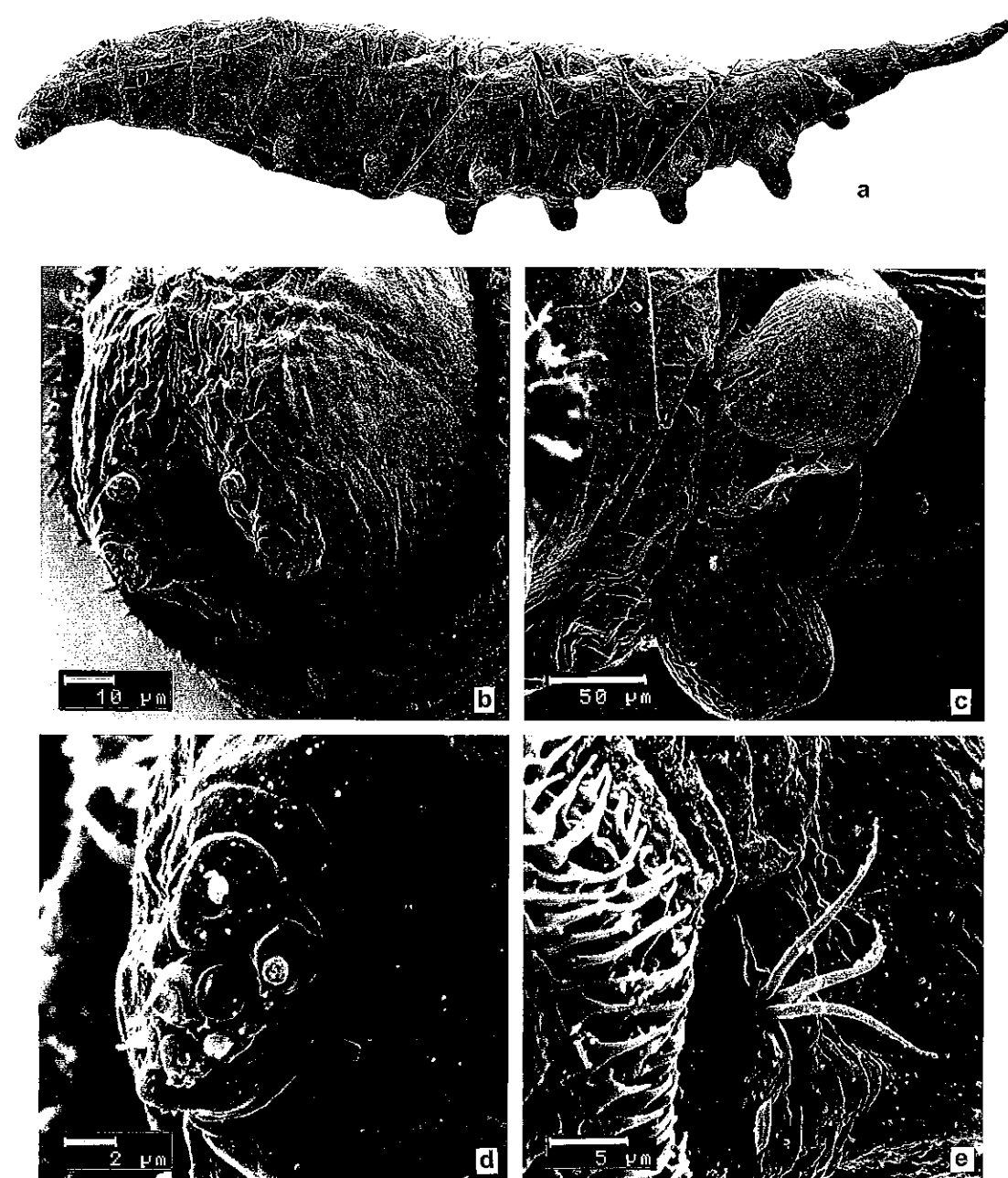


Fig. 167. Third-instar larva of *C. inversa*. a. Lateral view. b. Detail of head. c. Paranal sacs. d. Maxillary palp complex. e. Keilin's organ, thoracic segment 2.



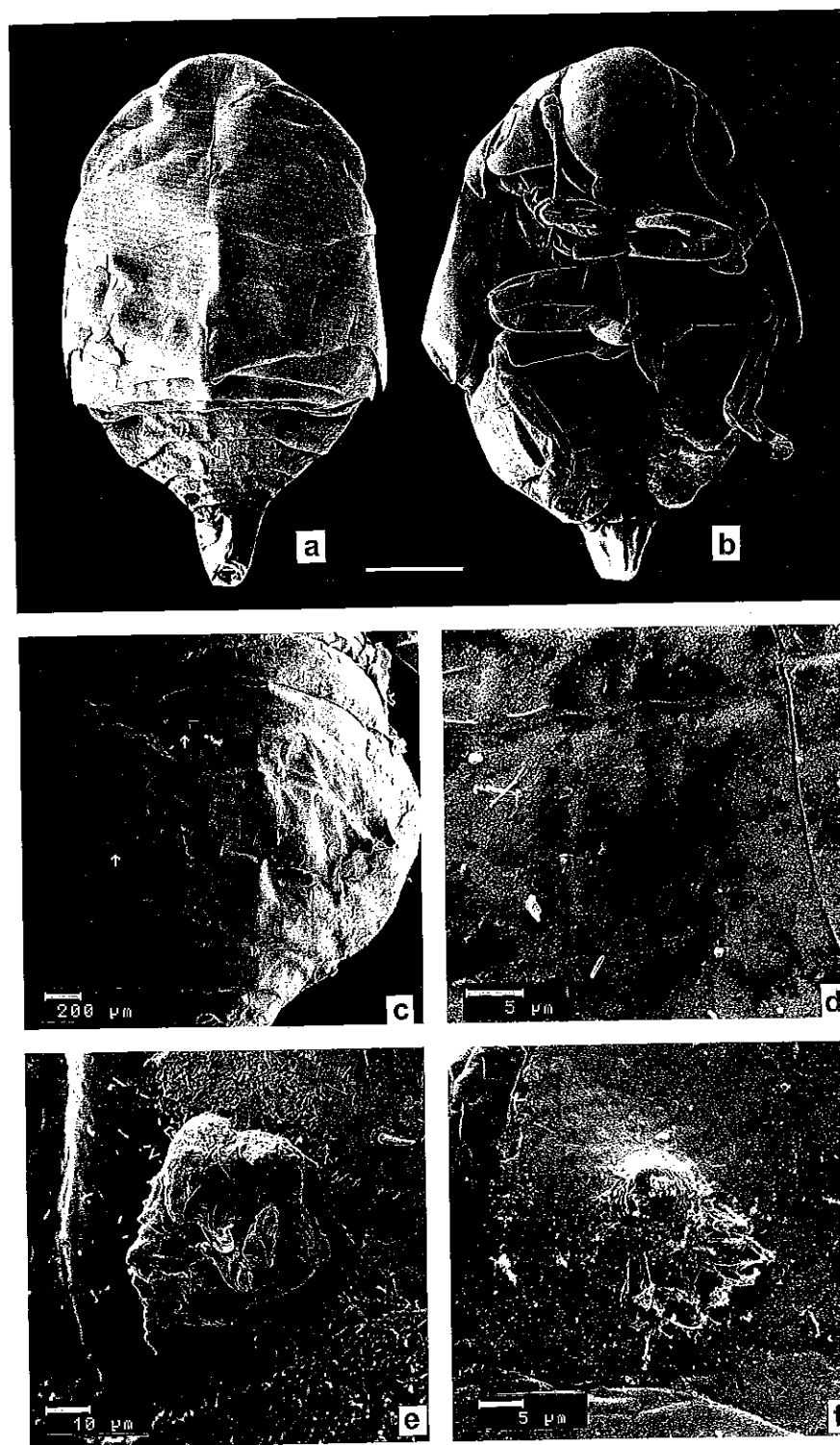


Fig. 168. *Clastoptera* hosts and injuries. a, b. *Clastoptera obtusa*, dorsal and ventral. c. *C. obtusa*, tergites. Arrows point to melanized spots that have higher magnification SEM shots. d. Detail of spot in C. e. Detail of spot in C. f. Detail of spot in C.

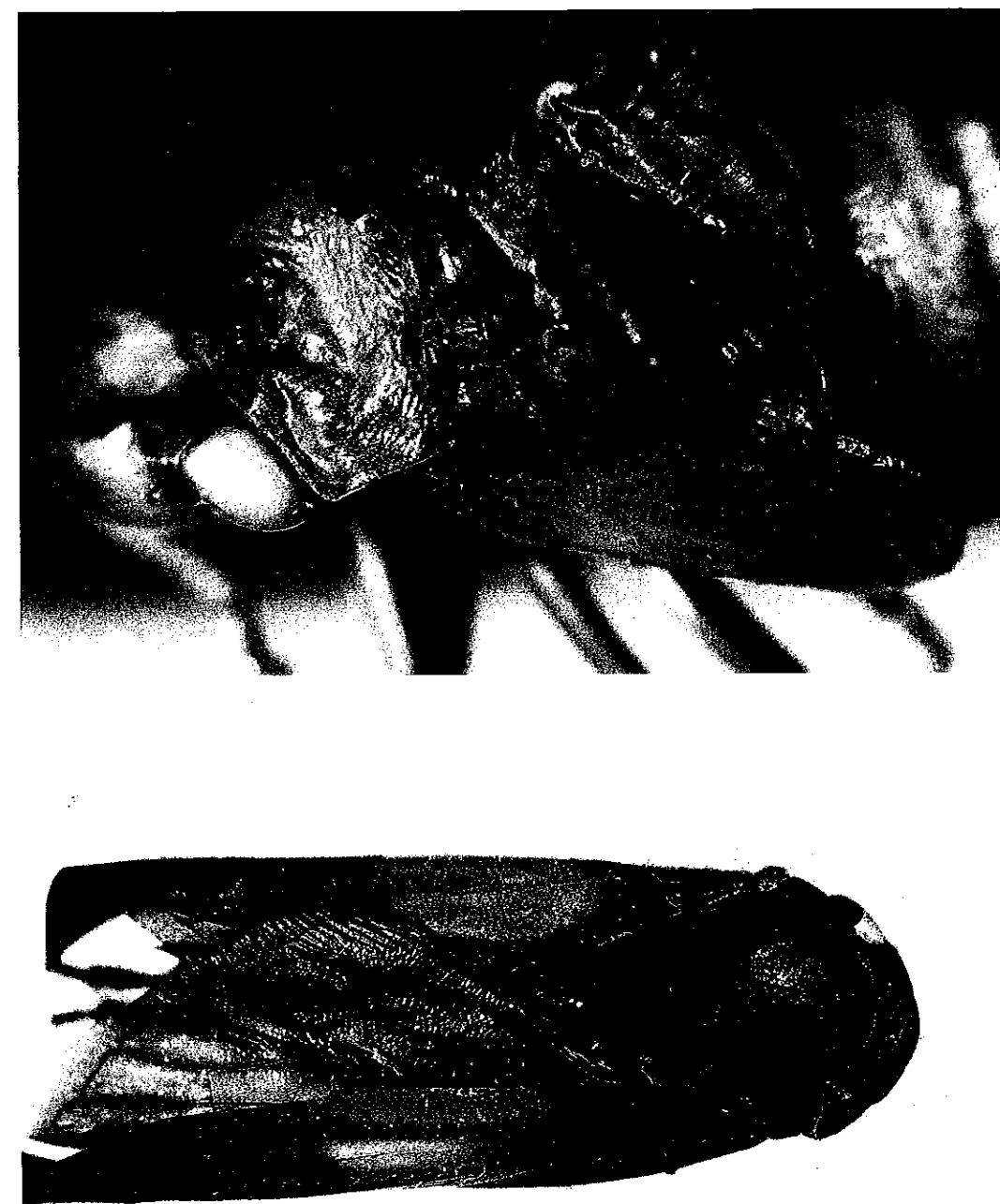


Fig. 169. Nymph and adult of *Sphodroscorta* sp. (Cercopidae) from Ecuador. The nymph (top) has 2 pupae of *Cladochaeta spectabilis* attached to the thorax just above the wing pad.



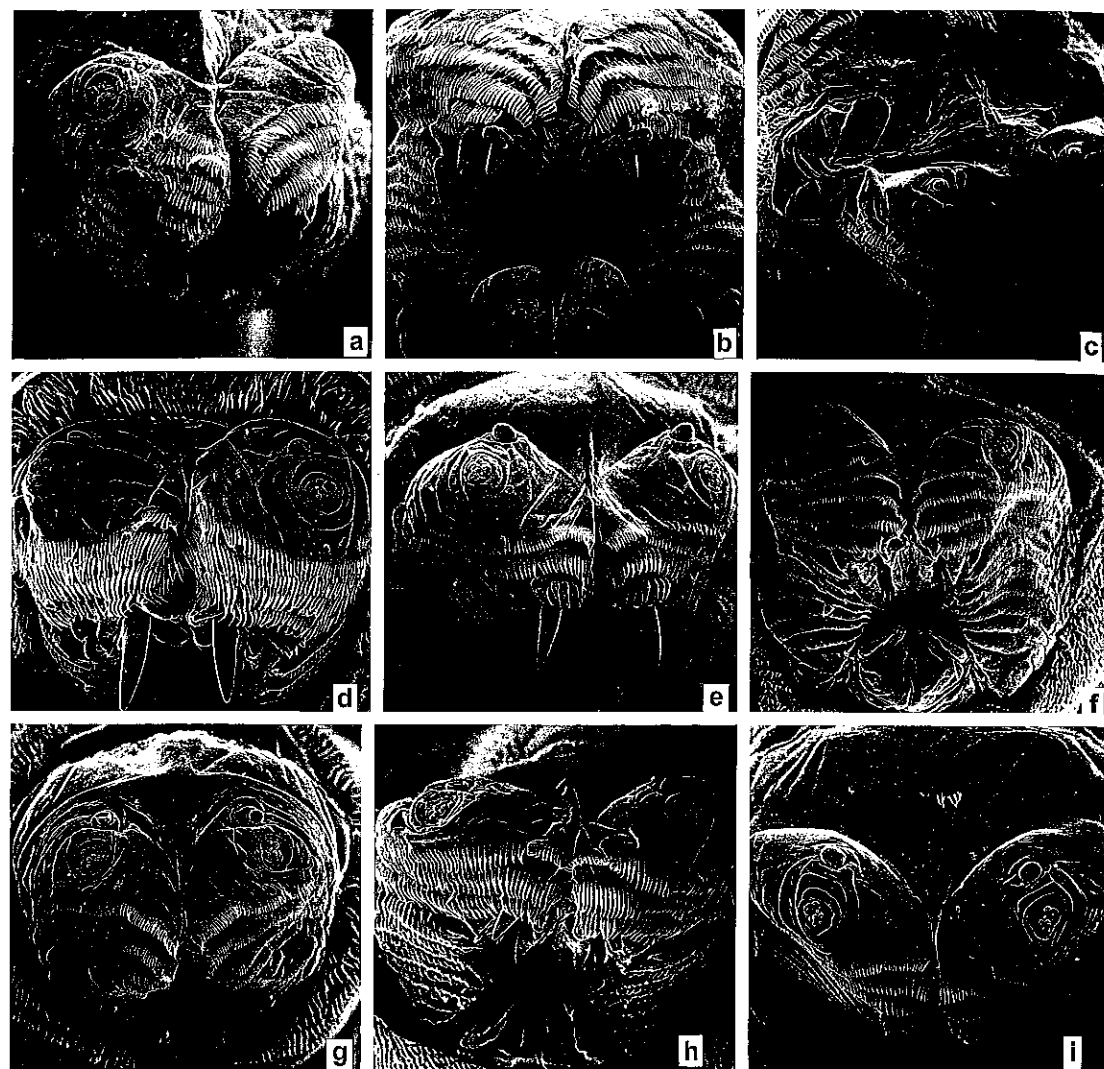


Fig. 170. Scanning electron micrographs of heads of third-instar larvae of representative saprophagous drosophilids. **a.** *Drosophila bromeliae*. **b.** *D. bromeliae* (ventral). **c.** *D. (Sophophora) melanogaster*. **d.** *D. (Drosophila) immigrans*. **e.** *Idiomyia mimica*. **f.** *Hirtodrosophila pictiventris*. **g.** *Scaptodrosophila stonei*. **h.** *Zaprionus ghesquierei*. **i.** *Chymomyza procnemis*.

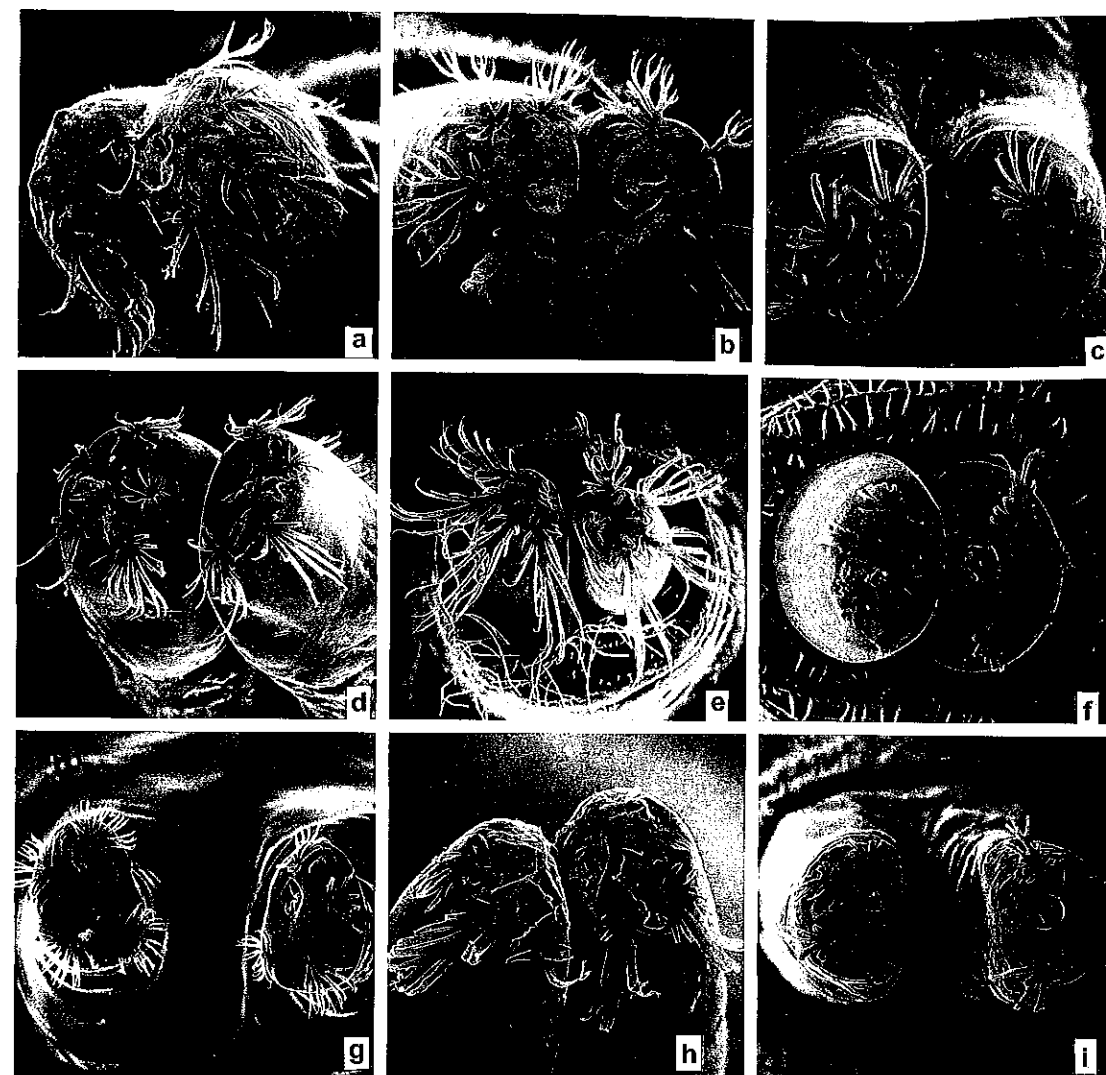


Fig. 171. Scanning electron micrographs of posterior spiracles of third-instar larvae of representative saprophagous drosophilids. **a.** *Drosophila (Dorsilopha) busckii*. **b.** *Drosophila bromeliae*, ventral view. **c.** *D. (Sophophora) melanogaster*. **d.** *Zaprionus ghesquierei*. **e.** *Scaptodrosophila stonei*. **f.** *Idiomyia mimica*. **g.** *Chymomyza procnemis*. **h.** *Hirtodrosophila pictiventris*. **i.** *Scaptomyza adusta*.

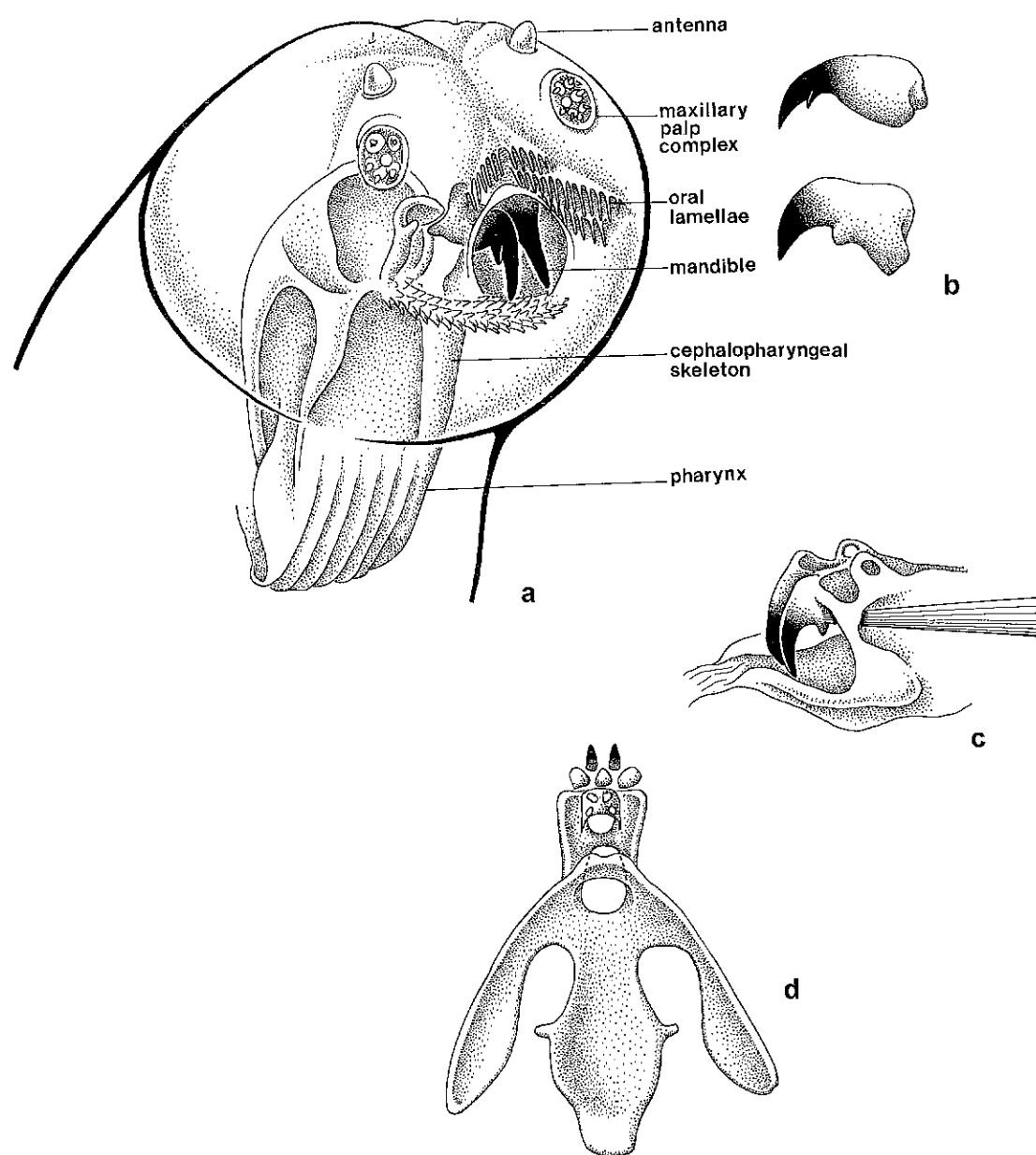


Fig. 172. Mouthparts of *Cladochaeta*. a. Head of third-instar *Cladochaeta floridana*, showing cephalopharyngeal skeleton and oral lamellae. b. Third-instar mandibles of *C. floridana* (above) and *C. inversa* (below). c. *C. inversa* mandibles situated in oral cavity, with muscle attachment. d. Cephalopharyngeal skeleton of *C. inversa*.

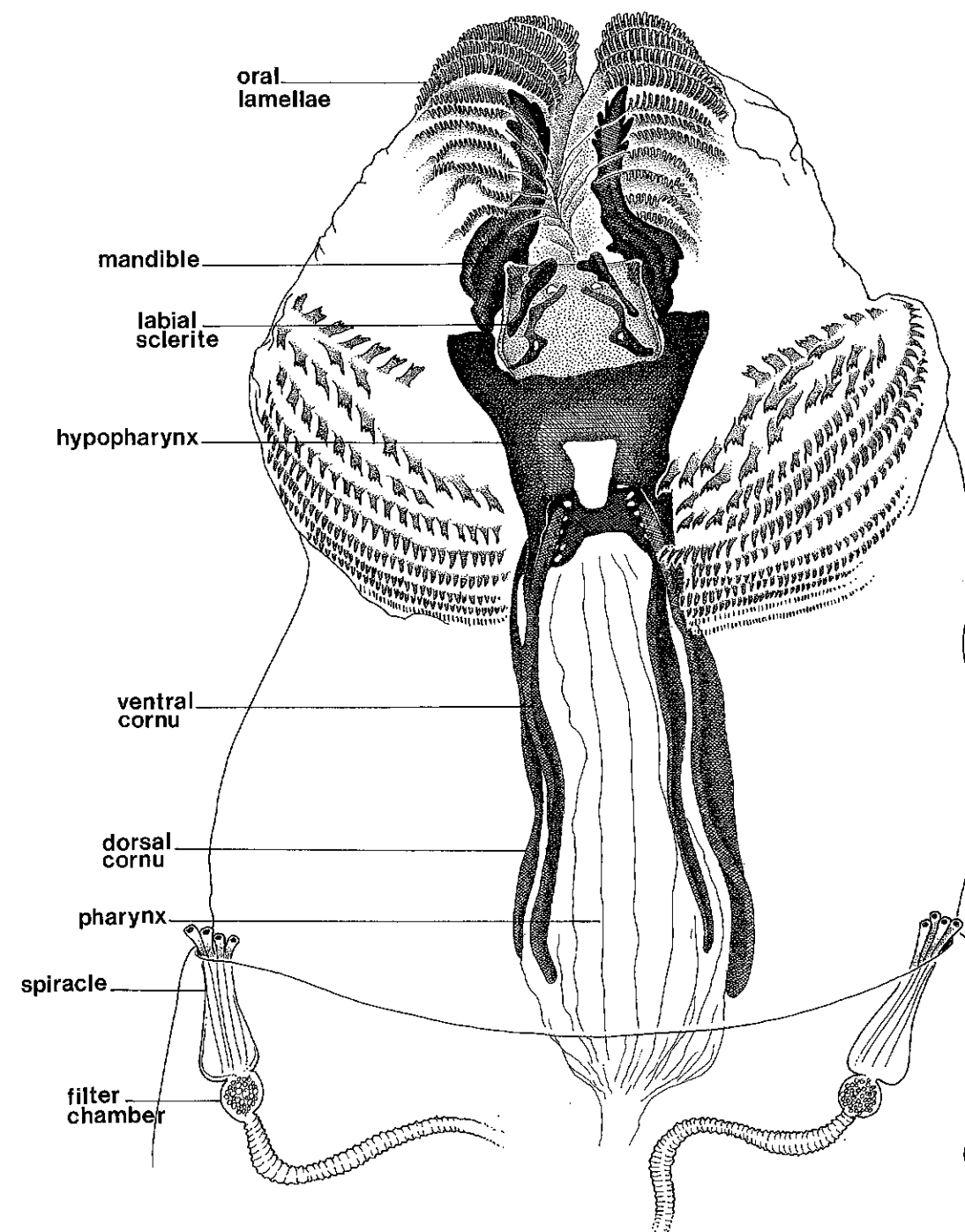


Fig. 173. Head (ventral view) of ephydrid larva from Costa Rica found in spittle masses of *Tomaspis inca*, including details of cephalopharyngeal skeleton and oral lamellae. It is a saprophagous inquiline.

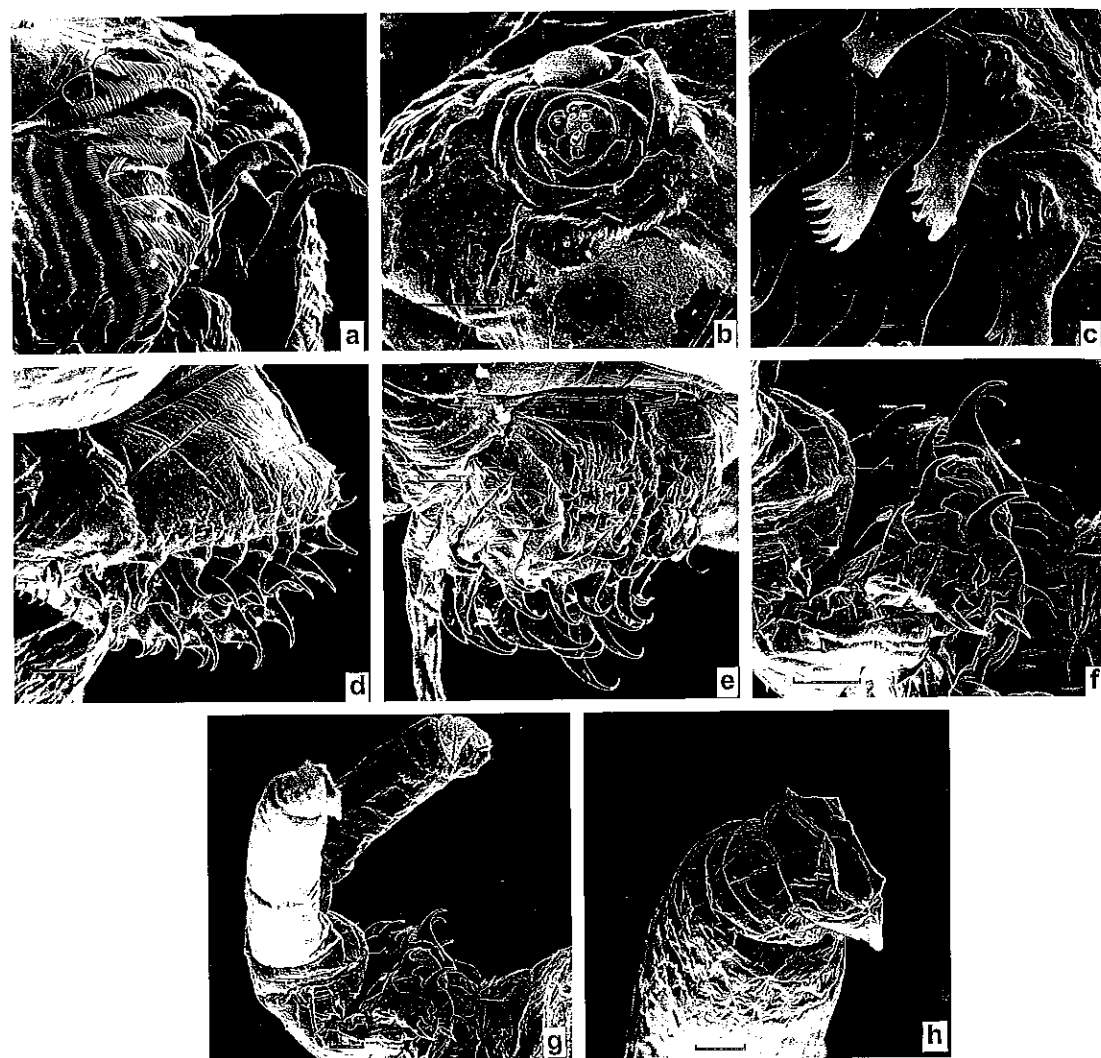


Fig. 174. Scanning electron micrographs of ephydrid larva from Costa Rica found in spittle masses of *Tomaspis inca*. a. Head, oblique anterior view. b. Maxillary palp complex. c. Cephalic creeping welt spinules. d. Second proleg. e. Posteriormost ventromedian proleg. f. Posterior group of dorsomedial spinules. g. Posterior spiracles. h. Detail, apex of posterior spiracle.

### SPECIES DIVERSITY

In a study where the species diversity of a group has become almost an order of magnitude greater than it was, the natural question arises: Just how many species of *Cladochaeta* are there? Different methods of estimating diversity have been discussed, such as species accumulation curves, as well as the estimation of complementarity and extrapolations from local richness (Colwell and Coddington, 1994; Hammond, 1994). Virtually all rigorous estimation methods depend on systematic sampling protocols: one or more constant-effort techniques applied in an area over a long period, then used in different areas. Sweep netting has proven to be too "uneven" in its success, so Malaise trapping is probably the best constant-effort technique for comparing the diversity of *Cladochaeta* at different sites (if the traps are maintained through different seasons). For this monograph, only 2 sites were systematically sampled using Malaise traps, both of them in Costa Rica and only about 50 km apart: Zurqui de Moravia, a cloud forest at 1600 m; and Estacion Biologica Finca La Selva, a low-elevation tropical rainforest. Both sites yielded 11 species each, with none in common between the 2 sites. Complementarity of these 2 nearby sites, then, is 0, which suggests vast diversity.

For *Cladochaeta*, the sampling of Central America is, in fact, far better than for South America. Brazil, for example, has only 2 *Cladochaeta* species recorded! If Central America sampling could be taken as a baseline (still obviously a gross underestimate), and if species diversity were in direct relationship to land area, one could calculate the number of species expected in South America. (In reality, species-area curves for well-known organisms usually show asymptotes, so there is a critical point where the increase in area yields disproportionately few species). The Central-South American extrapolation is useful in that only 3% of all *Cladochaeta* species are found on both continents (*hodita*, *labidia*, *sororia*, and possibly *propenicula*). This is a pattern shared with other groups of Drosophilidae, such as *Zygothrica* (Grimaldi, 1987). In the simplest calculations, given 64 species in Central

America (2,484,000 km<sup>2</sup>) and in tropical South America (14,195,000 km<sup>2</sup>), there would be 365 species expected from South America, where only 45 species are now known. This is only the roughest estimate, since species diversity of montane and lowland regions can be entirely different; also, a vast amount of South America is comprised of lowland Amazonian forest, and species of drosophilids in the Amazon Basin tend to be widespread. On the other hand, what makes an estimate of 365 species perhaps itself an underestimate is the relatively poor sampling historically throughout even Central America. Thirty-two species (28%) in the genus are only known by the holotype specimen. Costa Rica and Panama are the best surveyed tropical countries for the genus; collectively they have 35 species in 127,782 km<sup>2</sup>. If this diversity were taken as a baseline for the diversity of the rest of Central America, a simple species-area relationship would yield 645 species! Clearly, as Colwell and Coddington (1994) warn, such a wild extrapolation is "illusory," one reason being that an asymptotic function of species area is not taken into consideration. However, even if this estimate were pared to less than half, say 300 Central American species, this would result in the astronomical estimate of 1700 South American species!

Similar estimations can be developed for the Caribbean, but with probably less "illusion" since species seem to be often restricted to individual islands. Taking Hispaniola, the best sampled island (48,443 km<sup>2</sup>), as a baseline of species diversity (7 species, no doubt incomplete), the rest of the Caribbean (165,753 km<sup>2</sup>) would have 24 species. Twenty Caribbean species are now known. This estimate does not take into account insularity. If estimated on an island-by-island basis, Cuba alone (114,494 km<sup>2</sup>) would have 16 species (1 species is now known), but Puerto Rico (8,897 km<sup>2</sup>) would have only 1 species (2 species are known), and Jamaica would have 1.6 (3 are known). Clearly, the 7 species from Hispaniola is an incomplete figure. Realistically, the Caribbean probably harbors 50 species total.

Very conservatively, if there are 300 species from Central America and the Caribbe-

an, and 500 additional species from South America, the presently known diversity of

122 Nearctic and Neotropical species is a fraction (15%) of the actual diversity.

## EPILOGUE

Only 10–12 species have a host or some hosts known; the polyphagy of only *Cladochaeta inversa* on 3 species of *Clastoptera* spittlebugs is documented. Even for a species as available for study as *C. inversa*, unequivocal evidence still does not exist as to whether the larva is parasitic or not, and if so, how it feeds and what effect it has on the host. One well-documented record of *Cladochaeta* from flowers casts doubt on whether the spittlebug association is even the norm for this group. Estimates of total, undescribed species diversity are so vast that *Cladochaeta* could very likely be the most speciose genus of drosophilids in the world after *Drosophila*. Already, as a result of this study, *Clado-*

*chaeta* is the most speciose lineage of drosophilids restricted to the Western Hemisphere. Probably the only way to accurately survey species would be to intensively sample mega-diverse areas that are also very poorly sampled or totally unsampled for *Cladochaeta*. These priority areas are the highlands of central and southern Mexico; mid-elevation Andean forests of eastern Bolivia, Peru, Ecuador, Colombia, and western Venezuela; and the Atlantic coastal forest of Brazil, what little of it remains.

Nothing could be more fundamentally clear: Field exploration is the most substantial contribution needed for the systematics and biology of this fascinating group of flies.

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## Synopsis of Species Classification

<i>nebulosa</i> group	<i>sororia</i> group	<i>simplex</i> group
<i>adumbrata</i>	<i>abeja</i>	<i>akantha</i>
<i>ambidextra</i>	<i>abrupta</i>	<i>bispina</i>
<i>bupeo</i>	<i>adusta</i>	<i>chelifera</i>
<i>dominicana</i>	<i>centetor</i>	<i>inornata</i>
<i>ectopia</i>	<i>chaeta</i>	<i>longistyla</i>
<i>floridana</i>	<i>hermani</i>	<i>neosimplex</i>
<i>genuinus</i>	<i>howdeni</i>	<i>peruviana</i>
<i>hodita</i>	<i>labidia</i>	<i>similex</i>
<i>incessa</i>	<i>laevacerca</i>	<i>simplex</i>
<i>jamaicensis</i>	<i>minuta</i>	<i>telescopica</i>
<i>masneri</i>	<i>mystaca</i>	<i>trauma</i>
<i>mathisi</i>	<i>obscura</i>	<i>vapida</i>
<i>neblina</i>	<i>propenacula</i>	<i>vittata</i>
<i>nebulosa</i>	<i>psychotria</i>	<i>yanomama</i>
<i>pruinopleura</i>	<i>robusta</i>	
<i>sclerstyla</i>	<i>sepia</i>	<i>armata</i> group
<i>spira</i>	<i>sororia</i>	<i>albifrons</i>
<i>tepui</i>	<i>starki</i>	<i>amblyharpa</i>
<i>vermes</i>	<i>sternospina</i>	<i>armata</i>
<i>wirthi</i>	<i>uniradiata</i>	<i>hamula</i>
	<i>venebula</i>	<i>paravolsella</i>
	<i>vomica</i>	<i>tricerabops</i>
<i>inversa</i> group		<i>volsella</i>
<i>austrinversa</i>	<i>dikra</i> group	
<i>dracula</i>	<i>carinata</i>	<i>tripunctata</i> group
<i>florinversa</i>	<i>dejecta</i>	<i>abarista</i>
<i>heedi</i>	<i>dikra</i>	<i>brunnea</i>
<i>inversa</i>	<i>dominitica</i>	<i>crassa</i>
<i>mexinversa</i>	<i>erecta</i>	<i>paulhansoni</i>
<i>neoinversa</i>	<i>glans</i>	<i>ranhyae</i>
<i>paradoxa</i>	<i>infumata</i>	<i>tripunctata</i>
<i>reversa</i>	<i>janzeni</i>	
<i>spinacosta</i>	<i>onyx</i>	<i>bomplandi</i> group
<i>spinula</i>	<i>pseudidikra</i>	<i>bomplandi</i>
<i>sturtevanti</i>	<i>santana</i>	<i>ptyelophila</i>
<i>wilhansoni</i>	<i>tica</i>	<i>spectabilis</i>
	<i>vivipara</i>	sp. A
<i>unca</i> group		sp. B
<i>fuscara</i>	<i>diminuta</i> group	sp. C
<i>hadrunca</i>	<i>abbrevifusca</i>	
<i>bunca</i>	<i>arthrostyla</i>	<i>incertae sedis</i>
<i>pseudunca</i>	<i>devriesi</i>	<i>antalba</i>
<i>tubula</i>	<i>diminuta</i>	<i>aquila</i>
<i>unca</i>	<i>dolichofrons</i>	<i>bilinea</i>
	<i>fasciata</i>	<i>calvovis</i>
<i>ostia</i> group	<i>pequenita</i>	<i>nigranus</i>
<i>glapica</i>	<i>verdifrons</i>	<i>pleurvitta</i>
<i>ostia</i>		<i>polia</i>
		<i>taeniatipennis</i>
		<i>zurquia</i>

## APPENDIX: MEASUREMENTS

NEBULOSA GROUP															
Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$
<i>ambidextra</i>	♂	1	0.71	0.00	0.06	0.00	0.29	0.00	0.20	0.00	0.21	0.00	0.62	0.00	0.33
<i>bupeo</i>	♂	9	0.83	0.16	0.03	0.01	0.33	0.08	0.10	0.02	0.18	0.04	0.62	0.12	0.30
standard error				0.06		0.00		0.02		0.01		0.01		0.04	0.02
	♀	6	0.80	0.18	0.03	0.01	0.32	0.09	0.10	0.02	0.18	0.05	0.59	0.15	0.31
standard error				0.07		0.00		0.03		0.01		0.02		0.05	0.01
<i>dextra</i>	♂	4	0.65	0.13	0.03	0.01	0.30	0.06	0.09	0.03	0.17	0.02	0.56	0.06	0.31
	♀	2	0.86	0.07	0.03	0.01	0.36	0.08	0.09	0.05	0.22	0.01	0.67	0.04	0.34
<i>dominicana</i>	♂	4	0.82	0.22	0.04	0.01	0.34	0.09	0.11	0.04	0.18	0.04	0.63	0.13	0.29
	♀	7	0.80	0.10	0.03	0.01	0.31	0.06	0.11	0.01	0.17	0.05	0.57	0.12	0.29
standard error				0.04		0.00		0.02		0.00		0.02		0.04	0.02
<i>ectopia</i>	♂	2	0.67	0.07	0.03	0.01	0.30	0.03	0.09	0.02	0.17	0.03	0.56	0.08	0.30
	♀	1	0.76	0.00	0.03	0.00	0.33	0.00	0.08	0.00	0.19	0.00	0.59	0.00	0.32
<i>incessa</i>	♂	4	1.02	0.16	0.03	0.00	0.41	0.04	0.08	0.02	0.21	0.03	0.72	0.07	0.30
<i>floridana</i>	♂	1	0.83	0.00	0.04	0.00	0.35	0.00	0.10	0.00	0.22	0.00	0.67	0.00	0.33
	♀	8	0.77	0.21	0.03	0.01	0.33	0.07	0.09	0.04	0.20	0.07	0.62	0.18	0.33
standard error				0.07		0.00		0.03		0.01		0.02		0.06	0.01
<i>genuinus</i>	♂	12	0.71	0.11	0.03	0.01	0.33	0.07	0.09	0.03	0.18	0.03	0.59	0.10	0.31
standard error				0.03		0.00		0.02		0.01		0.01		0.03	0.01
	♀	8	0.78	0.08	0.03	0.01	0.34	0.03	0.08	0.04	0.19	0.03	0.63	0.07	0.31
standard error				0.02		0.00		0.01		0.01		0.01		0.02	0.01
<i>hodita</i>	♂	16	0.71	0.28	0.03	0.01	0.33	0.10	0.08	0.04	0.17	0.07	0.57	0.21	0.29
standard error				0.08		0.00		0.03		0.01		0.02		0.06	0.03
	♀	19	0.77	0.19	0.03	0.02	0.35	0.09	0.08	0.04	0.19	0.05	0.62	0.13	0.30
standard error				0.06		0.00		0.02		0.01		0.01		0.04	0.01
<i>jamaicensis</i>	♂	2	0.77	0.10	0.03	0.01	0.34	0.03	0.10	0.02	0.16	0.01	0.59	0.04	0.28
	♀	16	0.77	0.30	0.03	0.01	0.33	0.10	0.10	0.02	0.17	0.06	0.59	0.18	0.29
standard error				0.08		0.00		0.03		0.01		0.02		0.05	0.02
<i>masneri</i>	♂	1	0.67	0.00	0.03	0.00	0.28	0.00	0.11	0.00	0.16	0.00	0.55	0.00	0.29
	♀	1	0.90	0.00	0.03	0.00	0.39	0.00	0.07	0.00	0.20	0.00	0.66	0.00	0.30
<i>mathisi</i>	♂	1	0.86	0.00	0.04	0.00	0.33	0.00	0.13	0.00	0.24	0.00	0.68	0.00	0.36
<i>neblina</i>	♂	1	0.77	0.00	0.04	0.00	0.28	0.00	0.13	0.00	0.19	0.00	0.56	0.00	0.33
<i>nebulosa</i>	♀	5	0.77	0.15	0.03	0.01	0.35	0.04	0.09	0.03	0.20	0.02	0.61	0.05	0.33
<i>pruinopleura</i>	♂	3	0.89	0.08	0.04	0.01	0.37	0.02	0.10	0.02	0.21	0.02	0.67	0.04	0.31
<i>sclerostyla</i>	♂	1	0.86	0.00	0.05	0.00	0.34	0.00	0.13	0.00	0.19	0.00	0.65	0.00	0.30
	♀	1	0.93	0.00	0.05	0.00	0.38	0.00	0.12	0.00	0.23	0.00	0.73	0.00	0.32
<i>spira</i>	♂	2	0.74	0.05	0.04	0.00	0.30	0.01	0.13	0.00	0.23	0.00	0.63	0.01	0.36
	♀	3	0.81	0.17	0.04	0.01	0.31	0.05	0.12	0.02	0.25	0.03	0.67	0.09	0.37
<i>tepu</i>	♂	1	0.65	0.00	0.03	0.00	0.35	0.00	0.08	0.00	0.17	0.00	0.53	0.00	0.29
<i>vermes</i>	♂	1	0.86	0.00	0.04	0.00	0.33	0.00	0.11	0.00	0.18	0.00	0.63	0.00	0.29
<i>wirthi</i>	♂	2	0.75	0.01	0.03	0.01	0.36	0.01	0.08	0.02	0.18	0.01	0.60	0.04	0.30
	♀	3	0.75	0.18	0.03	0.00	0.33	0.01	0.09	0.01	0.19	0.02	0.61	0.04	0.32

Abbreviations: ThL = thorax length; CD = cheek depth; ED = eye depth; FW = face width; HW = head width

## SORORIA GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>abeja</i>	♂	1	0.87	0.00	0.04	0.00	0.39	0.00	0.10	0.00	0.24	0.00	0.71	0.00	0.34	0.00
<i>abrupta</i>	♂	2	0.72	0.02	0.05	0.02	0.33	0.03	0.15	0.07	0.18	0.01	0.61	0.00	0.29	0.02
<i>adusta</i>	♂	1	0.85	0.00	0.05	0.00	0.41	0.00	0.13	0.00	0.26	0.00	0.76	0.00	0.34	0.00
<i>centetor</i>	♂	6	0.60	0.11	0.03	0.01	0.28	0.05	0.11	0.04	0.15	0.03	0.52	0.10	0.29	0.03
standard error				0.04		0.00		0.02		0.01		0.01		0.03		0.01
	♀	5	0.66	0.09	0.03	0.01	0.29	0.04	0.10	0.02	0.17	0.02	0.57	0.05	0.30	0.02
<i>chaeta</i>	♂	8	0.63	0.09	0.03	0.01	0.29	0.04	0.09	0.03	0.15	0.03	0.51	0.11	0.29	0.06
standard error				0.03		0.00		0.02		0.01		0.01		0.03		0.02
	♀	2	0.66	0.03	0.02	0.01	0.30	0.03	0.07	0.03	0.18	0.01	0.53	0.04	0.34	0.04
<i>hermani</i>	♂	1	0.55	0.00	0.02	0.00	0.26	0.00	0.08	0.00	0.14	0.00	0.47	0.00	0.28	0.00
	♀	4	0.66	0.05	0.02	0.01	0.31	0.01	0.08	0.02	0.16	0.01	0.55	0.02	0.29	0.02
<i>howdeni</i>	♂	6	0.57	0.08	0.03	0.01	0.27	0.04	0.09	0.02	0.15	0.02	0.49	0.04	0.30	0.05
standard error				0.03		0.00		0.01		0.01		0.01		0.02		0.02
	♀	5	0.56	0.08	0.02	0.01	0.26	0.06	0.10	0.03	0.15	0.02	0.47	0.03	0.32	0.05
<i>labidia</i>	♂	3	0.50	0.10	0.02	0.00	0.26	0.07	0.09	0.01	0.16	0.01	0.47	0.04	0.34	0.02
	♀	4	0.56	0.02	0.03	0.01	0.28	0.03	0.10	0.02	0.16	0.02	0.51	0.05	0.32	0.05
<i>laevacerca</i>	♂	3	0.61	0.01	0.03	0.01	0.29	0.02	0.09	0.02	0.14	0.01	0.52	0.01	0.27	0.01
	♀	1	0.65	0.00	0.02	0.00	0.29	0.00	0.08	0.00	0.15	0.00	0.48	0.00	0.30	0.00
<i>minuta</i>	♂	1	0.55	0.00	0.03	0.00	0.27	0.00	0.09	0.00	0.15	0.00	0.48	0.00	0.32	0.00
	♀	2	0.60	0.04	0.03	0.00	0.26	0.05	0.11	0.04	0.17	0.01	0.47	0.08	0.36	0.04
<i>mystaca</i>	♂	1	0.90	0.00	0.06	0.00	0.34	0.00	0.18	0.00	0.24	0.00	0.69	0.00	0.36	0.00
<i>obscura</i>	♂	1	0.47	0.00	0.03	0.00	0.25	0.00	0.13	0.00	0.15	0.00	0.47	0.00	0.32	0.00
<i>propenicula</i>	♂	5	0.59	0.15	0.03	0.01	0.29	0.05	0.10	0.01	0.15	0.02	0.49	0.10	0.30	0.07
	♀	1	0.70	0.00	0.03	0.00	0.34	0.00	0.08	0.00	0.20	0.00	0.57	0.00	0.34	0.00
<i>psychotria</i>	♂	2	0.96	0.18	0.03	0.00	0.36	0.07	0.07	0.01	0.25	0.05	0.74	0.07	0.33	0.03
<i>robusta</i>	♂	6	1.01	0.15	0.04	0.02	0.43	0.07	0.09	0.05	0.26	0.06	0.83	0.13	0.32	0.03
standard error				0.05		0.01		0.02		0.02		0.02		0.05		0.01
	♀	3	0.92	0.05	0.04	0.03	0.42	0.07	0.09	0.06	0.25	0.06	0.81	0.10	0.31	0.04
<i>sepia</i>	♂	1	0.64	0.00	0.03	0.00	0.30	0.00	0.11	0.00	0.18	0.00	0.58	0.00	0.31	0.00
<i>sororia</i>	♂	12	0.71	0.18	0.03	0.02	0.33	0.09	0.10	0.08	0.18	0.04	0.57	0.11	0.31	0.07
standard error				0.06		0.01		0.03		0.02		0.01		0.04		0.02
	♀	9	0.75	0.19	0.03	0.02	0.33	0.11	0.11	0.09	0.19	0.04	0.59	0.14	0.32	0.05
standard error				0.06		0.01		0.03		0.03		0.01		0.05		0.02
<i>starki</i>	♂	1	0.85	0.00	0.03	0.00	0.38	0.00	0.08	0.00	0.25	0.00	0.69	0.00	0.37	0.00
	♀	3	0.81	0.12	0.03	0.01	0.38	0.07	0.07	0.02	0.23	0.05	0.65	0.09	0.35	0.04
<i>sternospina</i>	♂	3	0.68	0.08	0.05	0.01	0.29	0.04	0.16	0.03	0.21	0.02	0.58	0.04	0.36	0.01
	♀	1	0.71	0.00	0.05	0.00	0.30	0.00	0.16	0.00	0.22	0.00	0.61	0.00	0.36	0.00
<i>uniradiata</i>	♂	4	1.05	0.08	0.04	0.01	0.49	0.05	0.08	0.02	0.27	0.05	0.84	0.14	0.32	0.01
	♀	4	1.03	0.10	0.04	0.01	0.47	0.06	0.08	0.02	0.28	0.02	0.83	0.09	0.34	0.02
<i>venebula</i>	♂	2	0.96	0.04	0.05	0.00	0.37	0.00	0.13	0.00	0.22	0.07	0.71	0.11	0.31	0.05
<i>vomica</i>	♂	1	0.74	0.00	0.05	0.00	0.34	0.00	0.14	0.00	0.24	0.00	0.68	0.00	0.35	0.00
	♀	1	0.78	0.00	0.03	0.00	0.38	0.00	0.07	0.00	0.22	0.00	0.65	0.00	0.33	0.00



## INVERSA GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>austrinversa</i>	♂	2	0.97	0.04	0.06	0.01	0.43	0.02	0.13	0.01	0.23	0.01	0.69	0.03	0.33	0.00
<i>florinversa</i>	♂	4	0.87	0.10	0.06	0.01	0.44	0.05	0.13	0.03	0.21	0.05	0.70	0.07	0.30	0.06
	♀	3	0.82	0.12	0.05	0.02	0.42	0.02	0.12	0.05	0.21	0.02	0.69	0.11	0.31	0.03
<i>heedi</i>	♂	4	1.02	0.04	0.07	0.01	0.44	0.08	0.15	0.03	0.26	0.03	0.79	0.03	0.32	0.02
	♀	8	1.02	0.24	0.08	0.03	0.44	0.12	0.17	0.06	0.26	0.02	0.79	0.10	0.33	0.03
<i>inversa</i>	♂	14	0.98	0.22	0.06	0.04	0.42	0.07	0.13	0.07	0.24	0.04	0.77	0.15	0.32	0.04
standard error				0.06		0.01		0.02		0.02		0.02		0.04		0.01
	♀	10	0.94	0.10	0.06	0.02	0.42	0.13	0.14	0.05	0.24	0.06	0.75	0.22	0.32	0.04
standard error				0.07		0.01		0.03		0.01		0.02		0.06		0.01
<i>mexinversa</i>	♂	1	1.19	0.00	0.07	0.00	0.47	0.00	0.14	0.00	0.27	0.00	0.89	0.00	0.30	0.00
	♀	1	1.12	0.00	0.06	0.00	0.45	0.00	0.13	0.00	0.27	0.00	0.78	0.00	0.35	0.00
<i>neoinversa</i>	♂	2	0.94	0.02	0.06	0.00	0.41	0.00	0.14	0.00	0.23	0.02	0.74	0.02	0.32	0.03
	♀	4	0.84	0.21	0.05	0.02	0.39	0.07	0.12	0.02	0.21	0.04	0.67	0.12	0.31	0.01
<i>paradoxa</i>	♂	1	0.80	0.00	0.03	0.00	0.38	0.00	0.08	0.00	0.14	0.00	0.61	0.00	0.23	0.00
<i>reversa</i>	♂	1	0.76	0.00	0.04	0.00	0.36	0.00	0.10	0.00	0.19	0.00	0.60	0.00	0.32	0.00
<i>spinacosta</i>	♂	1	1.13	0.00	0.04	0.00	0.49	0.00	0.07	0.00	0.22	0.00	0.79	0.00	0.28	0.00
<i>spinula</i>	♂	1	0.91	0.00	0.04	0.00	0.42	0.00	0.10	0.00	0.22	0.00	0.67	0.00	0.33	0.00
<i>sturtevanti</i>	♂	10	1.06	0.38	0.07	0.04	0.43	0.10	0.17	0.05	0.27	0.10	0.81	0.26	0.34	0.02
standard error				0.13		0.01		0.03		0.02		0.03		0.08		0.01
	♀	9	0.96	0.35	0.07	0.03	0.41	0.12	0.16	0.04	0.25	0.09	0.74	0.26	0.34	0.04
standard error				0.10		0.01		0.04		0.01		0.03		0.08		0.01
<i>willhansonii</i>	♂	4	0.97	0.09	0.07	0.01	0.41	0.08	0.17	0.04	0.25	0.01	0.76	0.06	0.33	0.05
	♀	7	0.98	0.20	0.06	0.02	0.41	0.10	0.16	0.07	0.25	0.03	0.77	0.07	0.32	0.05
standard error				0.06		0.01		0.03		0.02		0.01		0.02		0.01

## BOMPLANDI GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>aquila</i>	♂	1	0.54	0.00	0.04	0.00	0.26	0.00	0.15	0.00	0.17	0.00	0.52	0.00	0.33	0.00
<i>bomplandi</i>	♂	1	1.11	0.00	0.02	0.00	0.54	0.00	0.04	0.00	0.30	0.00	0.83	0.00	0.36	0.00
	♀	5	1.09	0.18	0.03	0.01	0.50	0.07	0.06	0.01	0.27	0.05	0.88	0.26	0.30	0.03
<i>spectabilis</i>	♂	2	1.17	0.04	0.04	0.00	0.52	0.00	0.08	0.00	0.28	0.01	0.89	0.07	0.31	0.02

## UNPLACED SPECIES

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>antalba</i>	♀	2	0.72	0.09	0.06	0.01	0.31	0.02	0.18	0.05	0.23	0.01	0.68	0.01	0.33	0.02
<i>bilinea</i>	♀	3	0.64	0.19	0.03	0.01	0.31	0.06	0.09	0.00	0.19	0.05	0.61	0.11	0.31	0.03
<i>calvois</i>	♂	4	0.74	0.12	0.03	0.01	0.33	0.04	0.09	0.03	0.18	0.01	0.58	0.06	0.31	0.03
	♀	3	0.72	0.04	0.04	0.00	0.32	0.02	0.12	0.02	0.18	0.01	0.57	0.01	0.33	0.02
<i>nigranus</i>	♀	7	0.65	0.13	0.03	0.01	0.30	0.06	0.10	0.01	0.17	0.03	0.52	0.07	0.33	0.06
standard error				0.05		0.00		0.02		0.00		0.01		0.03		0.02
<i>pleurvitta</i>	♀	3	0.63	0.13	0.03	0.00	0.30	0.05	0.09	0.02	0.17	0.03	0.53	0.07	0.33	0.02
<i>polia</i>	♀	2	0.95	0.14	0.06	0.02	0.32	0.01	0.19	0.06	0.27	0.00	0.74	0.01	0.36	0.01
<i>zurquia</i>	♂	1	0.70	0.00	0.03	0.00	0.30	0.00	0.10	0.00	0.18	0.00	0.59	0.00	0.31	0.00
	♀	1	0.75	0.00	0.03	0.00	0.27	0.00	0.12	0.00	0.19	0.00	0.58	0.00	0.32	0.00

## DIKRA GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>carinata</i>	♂	3	0.68	0.07	0.03	0.01	0.34	0.02	0.10	0.02	0.21	0.02	0.63	0.06	0.33	0.01
	♀	2	0.65	0.09	0.04	0.00	0.33	0.07	0.11	0.03	0.20	0.01	0.61	0.12	0.33	0.04
<i>defecta</i>	♂	2	0.93	0.22	0.03	0.01	0.38	0.05	0.08	0.01	0.20	0.02	0.65	0.05	0.31	0.00
<i>dikra</i>	♂	4	0.75	0.04	0.04	0.00	0.32	0.03	0.13	0.02	0.21	0.01	0.66	0.04	0.32	0.02
	♀	1	0.81	0.00	0.03	0.00	0.33	0.00	0.08	0.00	0.22	0.00	0.67	0.00	0.33	0.00
<i>dominitica</i>	♂	2	0.75	0.07	0.03	0.01	0.29	0.01	0.11	0.02	0.21	0.01	0.67	0.02	0.31	0.02
	♀	1	0.69	0.00	0.03	0.00	0.30	0.00	0.11	0.00	0.21	0.00	0.68	0.00	0.31	0.00
<i>glans</i>	♂	1	0.85	0.00	0.04	0.00	0.36	0.00	0.12	0.00	0.21	0.00	0.69	0.00	0.31	0.00
<i>erecta</i>	♂	1	0.77	0.00	0.04	0.00	0.35	0.00	0.11	0.00	0.20	0.00	0.65	0.00	0.31	0.00
<i>onyx</i>	♂	1	0.86	0.00	0.04	0.00	0.34	0.00	0.12	0.00	0.21	0.00	0.75	0.00	0.28	0.00
<i>pseudikra</i>	♂	1	0.78	0.00	0.04	0.00	0.36	0.00	0.11	0.00	0.20	0.00	0.72	0.00	0.28	0.00
<i>janzeni</i>	♂	1	0.70	0.00	0.03	0.00	0.33	0.00	0.10	0.00	0.20	0.00	0.66	0.00	0.30	0.00
<i>santana</i>	♂	1	0.90	0.00	0.05	0.00	0.41	0.00	0.13	0.00	0.22	0.00	0.75	0.00	0.30	0.00
<i>tica</i>	♂	7	0.74	0.15	0.03	0.01	0.31	0.05	0.11	0.03	0.18	0.07	0.65	0.18	0.28	0.08
standard error				0.05		0.00		0.02		0.01		0.02		0.05		0.03
	♀	13	0.81	0.28	0.04	0.01	0.33	0.05	0.11	0.03	0.20	0.08	0.70	0.15	0.28	0.08
standard error				0.07		0.00		0.02		0.01		0.03		0.04		0.02
<i>vivipara</i>	♂	6	0.59	0.05	0.03	0.01	0.23	0.01	0.14	0.03	0.16	0.03	0.45	0.07	0.34	0.04
	♀	2	0.68	0.01	0.04	0.01	0.25	0.02	0.15	0.05	0.17	0.01	0.50	0.01	0.35	0.03

## DIMINUTA GROUP

GROUP																
Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>diminuta</i>	♂	6	0.44	0.03	0.03	0.01	0.24	0.23	0.14	0.10	0.14	0.02	0.41	0.04	0.35	0.03
standard error				0.01		0.00		0.08		0.03		0.01		0.02		0.01
	♀	10	0.48	0.09	0.03	0.01	0.21	0.03	0.15	0.05	0.14	0.02	0.42	0.07	0.33	0.05
standard error				0.03		0.00		0.01		0.02		0.01		0.02		0.02
<i>abbrevifusca</i>	♂	5	0.85	0.08	0.04	0.02	0.38	0.06	0.09	0.05	0.21	0.03	0.65	0.07	0.32	0.05
	♀	1	0.81	0.00	0.03	0.00	0.37	0.00	0.08	0.00	0.21	0.00	0.64	0.00	0.33	0.00
<i>arthrostyla</i>	♂	1	0.67	0.00	0.06	0.00	0.26	0.00	0.23	0.00	0.21	0.00	0.65	0.00	0.32	0.00
	♀	1	0.59	0.00	0.04	0.00	0.24	0.00	0.17	0.00	0.18	0.00	0.56	0.00	0.32	0.00
<i>devriesi</i>	♂	1	0.64	0.00	0.05	0.00	0.28	0.00	0.18	0.00	0.19	0.00	0.56	0.00	0.34	0.00
<i>dolichofrons</i>	♂	1	0.66	0.00	0.06	0.00	0.27	0.00	0.23	0.00	0.19	0.00	0.61	0.00	0.30	0.00
<i>fasciata</i>	♂	4	0.56	0.05	0.04	0.01	0.22	0.02	0.20	0.07	0.19	0.04	0.54	0.07	0.35	0.06
	♀	2	0.58	0.00	0.04	0.01	0.23	0.23	0.18	0.06	0.20	0.03	0.57	0.05	0.35	0.01
<i>pequenita</i>	♂	1	0.46	0.00	0.02	0.00	0.24	0.00	0.10	0.00	0.15	0.00	0.42	0.00	0.35	0.00
	♀	2	0.42	0.03	0.03	0.00	0.22	0.02	0.13	0.01	0.14	0.01	0.42	0.00	0.34	0.03
<i>sticula</i>	♂	1	0.72	0.00	0.03	0.00	0.30	0.00	0.09	0.00	0.19	0.00	0.59	0.00	0.32	0.00
<i>verdifrons</i>	♂	2	0.58	0.01	0.05	0.00	0.30	0.01	0.15	0.01	0.18	0.01	0.61	0.01	0.30	0.01

## SIMPLEX GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>akantha</i>	♂	8	0.64	0.16	0.03	0.01	0.34	0.08	0.08	0.02	0.16	0.05	0.56	0.12	0.29	0.05
standard error				0.06		0.00		0.03		0.01		0.01		0.05		0.02
	♀	7	0.69	0.24	0.03	0.01	0.34	0.10	0.09	0.04	0.16	0.05	0.57	0.18	0.27	0.05
standard error				0.07		0.00		0.04		0.01		0.02		0.05		0.02
<i>bispina</i>	♂	1	0.63	0.00	0.03	0.00	0.33	0.00	0.09	0.00	0.17	0.00	0.56	0.00	0.31	0.00
	♀	1	0.64	0.00	0.03	0.00	0.30	0.00	0.09	0.00	0.17	0.00	0.55	0.00	0.32	0.00
<i>chelifera</i>	♂	6	0.58	0.13	0.02	0.00	0.32	0.05	0.08	0.02	0.16	0.01	0.55	0.11	0.29	0.05
standard error				0.05		0.00		0.02		0.01		0.00		0.04		0.02
	♀	6	0.61	0.17	0.03	0.01	0.32	0.09	0.08	0.03	0.18	0.02	0.56	0.12	0.31	0.07
standard error				0.06		0.00		0.03		0.01		0.01		0.05		0.02
<i>inornata</i>	♂	1	0.79	0.00	0.03	0.00	0.35	0.00	0.08	0.00	0.21	0.00	0.69	0.00	0.31	0.00
<i>longistyla</i>	♂	2	0.71	0.00	0.02	0.00	0.33	0.02	0.07	0.01	0.17	0.00	0.55	0.05	0.32	0.03
<i>neosimplex</i>	♂	2	0.59	0.08	0.03	0.00	0.30	0.07	0.09	0.01	0.16	0.01	0.51	0.10	0.31	0.04
<i>similex</i>	♂	2	0.75	0.01	0.02	0.00	0.38	0.04	0.06	0.00	0.18	0.01	0.61	0.03	0.30	0.03
<i>simplex</i>	♂	3	0.68	0.10	0.02	0.01	0.36	0.07	0.07	0.01	0.17	0.03	0.58	0.08	0.29	0.02
	♀	3	0.68	0.18	0.02	0.01	0.33	0.07	0.07	0.03	0.16	0.03	0.55	0.13	0.30	0.03
<i>telescopia</i>	♂	3	0.76	0.03	0.03	0.00	0.41	0.03	0.07	0.00	0.18	0.01	0.59	0.09	0.30	0.03
	♀	4	0.82	0.20	0.03	0.01	0.41	0.08	0.07	0.02	0.18	0.02	0.62	0.08	0.29	0.01
<i>trauma</i>	♂	2	0.77	0.00	0.03	0.00	0.33	0.03	0.10	0.02	0.21	0.00	0.65	0.06	0.33	0.03
	♀	4	0.84	0.21	0.03	0.01	0.37	0.07	0.09	0.02	0.23	0.03	0.69	0.16	0.33	0.03
<i>vapida</i>	♂	1	0.62	0.00	0.02	0.00	0.30	0.00	0.08	0.00	0.17	0.00	0.50	0.00	0.34	0.00
<i>vittata</i>	♂	1	0.72	0.00	0.03	0.00	0.34	0.00	0.08	0.00	0.19	0.00	0.60	0.00	0.31	0.00
<i>yanomama</i>	♂	1	0.67	0.00	0.03	0.00	0.37	0.00	0.07	0.00	0.15	0.00	0.61	0.00	0.25	0.00

## TRIPUNCTATA GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>abarista</i>	♂	5	0.80	0.16	0.04	0.01	0.33	0.06	0.11	0.03	0.20	0.01	0.65	0.08	0.31	0.03
	♀	9	0.80	0.16	0.03	0.01	0.32	0.05	0.10	0.01	0.21	0.03	0.64	0.12	0.32	0.04
standard error				0.06		0.00		0.02		0.00		0.01		0.04		0.01
<i>brunnea</i>	♂	1	0.60	0.00	0.03	0.00	0.26	0.00	0.13	0.00	0.16	0.00	0.53	0.00	0.31	0.00
	♀	1	0.68	0.00	0.04	0.00	0.28	0.00	0.15	0.00	0.19	0.00	0.62	0.00	0.30	0.00
<i>crassa</i>	♂	1	0.98	0.00	0.04	0.00	0.38	0.00	0.11	0.00	0.26	0.00	0.81	0.00	0.33	0.00
<i>paulhansoni</i>	♂	1	0.65	0.00	0.03	0.00	0.26	0.00	0.11	0.00	0.18	0.00	0.53	0.00	0.33	0.00
	♀	5	0.68	0.16	0.03	0.00	0.29	0.06	0.11	0.03	0.18	0.02	0.58	0.11	0.31	0.07
<i>ranhyae</i>	♂	1	0.85	0.00	0.04	0.00	0.31	0.00	0.12	0.00	0.24	0.00	0.67	0.00	0.36	0.00
<i>tripunctata</i>	♂	1	0.76	0.00	0.05	0.00	0.31	0.00	0.15	0.00	0.22	0.00	0.66	0.00	0.33	0.00
	♀	12	0.83	0.22	0.04	0.01	0.33	0.06	0.12	0.03	0.22	0.07	0.70	0.13	0.32	0.07
standard error				0.06		0.00		0.02		0.01		0.03		0.04		0.03

## UNCA &amp; OSTIA GROUPS

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>fuscara</i>	♂	2	0.83	0.04	0.08	0.01	0.35	0.04	0.23	0.06	0.30	0.01	0.71	0.02	0.42	0.03
<i>hadrunca</i>	♂	1	0.87	0.00	0.04	0.00	0.43	0.00	0.08	0.00	0.23	0.00	0.75	0.00	0.31	0.00
	♀	1	0.79	0.00	0.03	0.00	0.39	0.00	0.09	0.00	0.22	0.00	0.68	0.00	0.33	0.00
<i>obunca</i>	♂	5	0.64	0.15	0.03	0.01	0.28	0.06	0.12	0.05	0.16	0.07	0.53	0.07	0.31	0.12
	♀	4	0.73	0.10	0.03	0.01	0.29	0.02	0.11	0.04	0.17	0.06	0.55	0.10	0.31	0.05
<i>pseudunca</i>	♂	5	0.67	0.12	0.06	0.03	0.28	0.06	0.24	0.14	0.20	0.03	0.64	0.07	0.32	0.06
	♀	6	0.75	0.13	0.06	0.03	0.30	0.07	0.19	0.07	0.20	0.02	0.67	0.08	0.31	0.02
standard error				0.04		0.01		0.03		0.02		0.01		0.03		0.01
<i>tubula</i>	♂	1	0.80	0.00	0.06	0.00	0.37	0.00	0.17	0.00	0.24	0.00	0.73	0.00	0.33	0.00
<i>unca</i>	♂	1	0.85	0.00	0.03	0.00	0.38	0.00	0.08	0.00	0.22	0.00	0.68	0.00	0.32	0.00
<i>glapica</i>	♂	4	0.62	0.04	0.04	0.02	0.28	0.02	0.13	0.09	0.17	0.04	0.53	0.05	0.33	0.05
	♀	2	0.71	0.07	0.04	0.00	0.29	0.01	0.12	0.01	0.16	0.02	0.52	0.03	0.30	0.03
<i>ostia</i>	♂	1	0.83	0.00	0.07	0.00	0.30	0.00	0.23	0.00	0.22	0.00	0.67	0.00	0.33	0.00

## ARMATA GROUP

Species	Sex	N	ThL		CD		ED		CD/ED		FW		HW		FW/HW	
			$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
<i>albifrons</i>	♂	1	0.63	0.00	0.03	0.00	0.28	0.00	0.11	0.00	0.18	0.00	0.50	0.00	0.35	0.00
<i>amblyharpa</i>	♂	10	0.73	0.20	0.04	0.03	0.31	0.10	0.14	0.07	0.20	0.04	0.61	0.15	0.32	0.05
standard error				0.01		0.01		0.03		0.02		0.01		0.04		0.01
	♀	10	0.79	0.20	0.04	0.02	0.33	0.27	0.13	0.12	0.22	0.05	0.64	0.17	0.34	0.07
standard error				0.06		0.01		0.04		0.03		0.01		0.06		0.02
<i>armata</i>	♂	1	0.66	0.00	0.05	0.00	0.29	0.00	0.16	0.00	0.18	0.00	0.58	0.00	0.30	0.00
	♀	8	0.67	0.10	0.03	0.01	0.30	0.06	0.11	0.06	0.19	0.02	0.58	0.07	0.33	0.04
standard error				0.03		0.00		0.02		0.02		0.01		0.02		0.01
<i>hamula</i>	♂	3	0.71	0.02	0.04	0.01	0.29	0.01	0.13	0.04	0.20	0.02	0.56	0.03	0.36	0.01
<i>paravolsella</i>	♂	1	0.72	0.00	0.04	0.00	0.27	0.27	0.15	0.00	0.20	0.00	0.58	0.00	0.34	0.00
<i>tricerabops</i>	♂	4	0.58	0.08	0.03	0.01	0.28	0.04	0.11	0.02	0.17	0.01	0.51	0.04	0.34	0.01
	♀	3	0.60	0.09	0.04	0.01	0.30	0.03	0.11	0.01	0.17	0.02	0.55	0.06	0.32	0.00
<i>volsella</i>	♂	4	0.74	0.14	0.04	0.01	0.30	0.04	0.13	0.03	0.20	0.00	0.59	0.10	0.33	0.02

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