

PHYLOGENETICS AND
TAXONOMY OF *ZYGOTHRICA*
(DIPTERA: DROSOPHILIDAE)

DAVID A. GRIMALDI

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 186 : ARTICLE 2 NEW YORK : 1987

Recent issues of the *Bulletin* may be purchased from the Museum. Lists of back issues of the *Bulletin*, *Novitates*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, New York 10024.

PHYLOGENETICS AND
TAXONOMY OF *ZYGOTHRICA*
(DIPTERA: DROSOPHILIDAE)

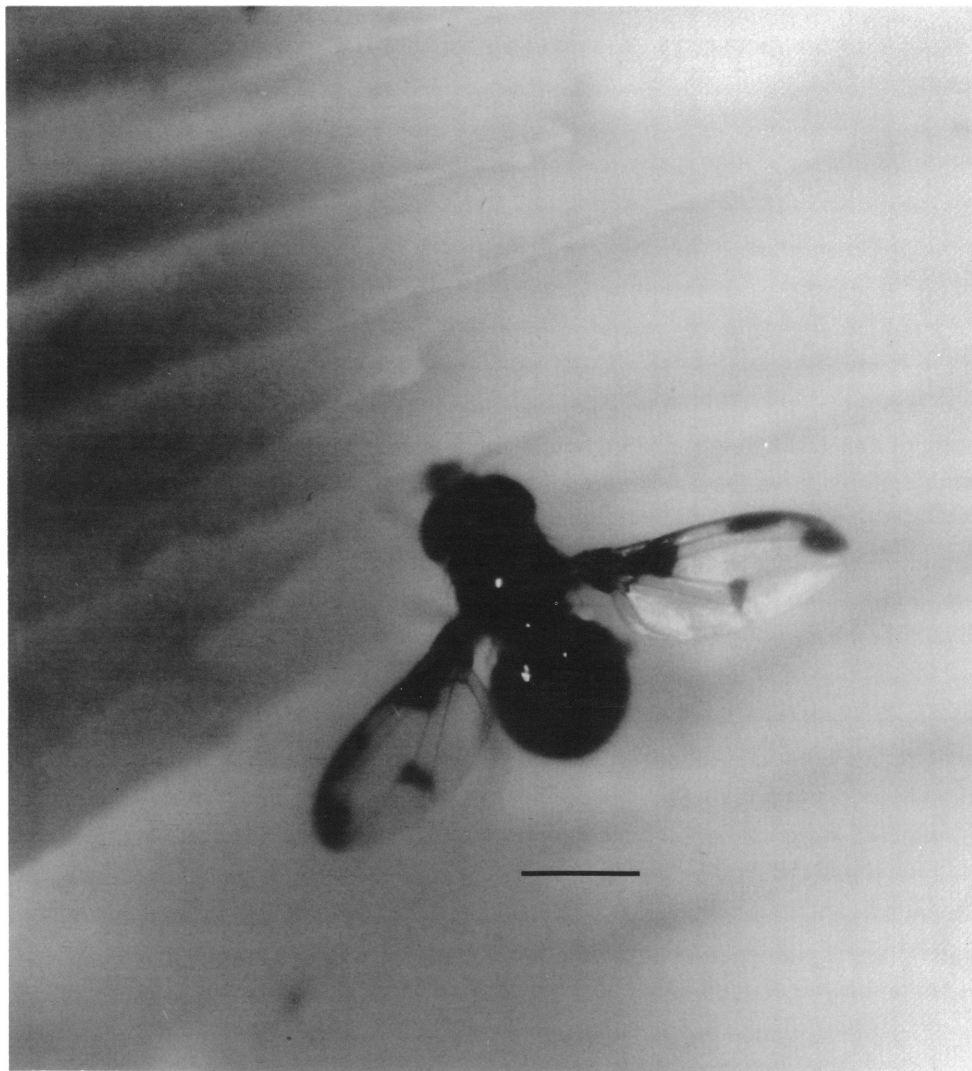
DAVID A. GRIMALDI
Assistant Curator
Department of Entomology
American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 186, article 2, pages 103–268, tables 1–7, figures 1–525

Issued September 4, 1987

Price: \$11.60 a copy



Zygothrica centralis, n. sp. male grazing between gills of a *Pleurotus* mushroom (Barro Colorado Island, Panama: Olympus 55 mm lens with autobellows and dedicated flash, D. A. Grimaldi). Scale line = 1.0 mm.

CONTENTS

Abstract	107
Introduction	107
Acknowledgments	108
Materials and Methods	109
Phylogenetic Analysis and Taxonomic Protocol	109
Adult Morphological Characters and Terminology	110
Breeding Sites	123
Immatures	126
Adult Aggregations	128
Major Phylogenetic Patterns: Morphological Characters	133
Phylogenetics: Behavioral Characters	138
General Taxonomy	147
Species Accounts	149
Key to Major Groups of Clade 1	150
Clade 1.1	151
Clade 1.2	156
<i>celsa</i> Complex	156
<i>dispar</i> Complex	165
<i>neolinea</i> Species-Group	165
<i>dispar</i> Species-Group	177
<i>dispar</i> Subgroup	178
<i>aldrichii</i> Subgroup	196
<i>caudata</i> Subgroup	247
References Cited	266

ABSTRACT

Species of the large neotropical and Indopacific genus *Zygothrica* are reclassified from Burla's (1956) species-groups, as based on cladistic character analyses and a classification reflecting relative genealogical relationships. The genus is defined by a prominent and sharp facial carina, a medially cleft oral margin, and a sclerotized proboscis with an acute joint between the mentum and submentum. *Zygothrica* is divided into five sections, and each section is variously divided into hierarchical levels. Cladistic hypotheses are based on adult morphological traits and reproductive behavioral repertoires of seven of the species. Breeding records are reviewed and immatures of three species are described. Removed from *Zygothrica* and placed into the *thoracis* species-group of *Drosophila* (*Hirtodrosophila*) are the following: *D. (H.) clypitata*, n. nov. (for *Z. clypeata* Burla, 1956), *D. (H.) strigocula*, n. comb., and *D. (H.) pleurostigmata*, n. comb.

Species accounts are given for 62 (neotropical) members of clade 1, which is a portion of the largest *Zygothrica* group. Of these, 48 are new species described as the following: *abbrevidispar*,

aliucapa, *amplialdrichi*, *andea*, *antedispar*, *anota*, *bilinefilia*, *caputrichia*, *celsa*, *centralis*, *cryptica*, *dissimulata*, *femina*, *florinjecta*, *fuscalata*, *glossusta*, *joeyesco*, *karenae*, *latipanops*, *latipaps*, *manni*, *mediogaster*, *mediovitta*, *microeristes*, *neolinea*, *nigra*, *nigropleura*, *ora*, *oviserrata*, *pallida*, *panamensis*, *panopia*, *paravitta*, *perplexa*, *peruviana*, *pictura*, *posthona*, *prensiseta*, *radialis*, *simulans*, *somatia*, *sphaerocera*, *spinathigma*, *tambopata*, *trinidada*, *vitrea*, *zonata*, and *zygia*. Provided for most of the 62 species are distribution maps and figures of various diagnostic morphological features, including wings and male and female terminalia. Synonymies are given for *Zygothrica orbitalis* (Sturt.) (which are *Z. nitidifrons* Duda, *Z. ochracella* Hendel, and *Z. parilis* Burla) and *Z. bilineata* (Williston) (synonym: *Z. gemma* Burla). *Zygothrica poeyi* of Burla is a misidentification for *Z. laevifrons* Duda. Hypotheses of supraspecific relationships within a large portion of clade 1 are discussed. Fourteen species have broad-headed ("hypercephalic") males, and the trait is hypothesized to have arisen six times among them.

INTRODUCTION

About certain bracket fungi that grow from fallen rainforest trees in Latin America can be found swarms of small flies. Some are dark, others are striped and yellow; some have patterned or spotted wings which are flagged in various ways, and most of the flies are busy fighting, feeding, courting, or being courted. They are *Zygothrica*, and the fungus is an oviposition site for some species as well as a rendezvous site for all.

So strong is the site-tenacity of *Zygothrica* that only occasionally are they found away from fungi. Standard Malaise and baited traps catch very few individuals, which may be the reason why these otherwise common but very curious drosophilids have attracted little interest. The taxonomic history of the genus is brief. *Zygothrica* was described in 1830 by the first student of neotropical flies, C. R. W. Wiedemann (1770–1840). "Thread-head," or literally "thread-yoke," aptly describes the distended and pointed eyes of *Zygothrica dispar*, the type species. Because of the wide-headed males, *Zygothrica* was described as a subgenus in *Achias* (Platystomatidae), which

is a Papuan group. Use of *Zygothrica* as a generic name in the Drosophilidae began with Loew (1873). Sturtevant (1920) provided an early account of *Zygothrica* taxonomy.

Since Wiedemann's original paper, 14 papers have dealt wholly or in part with *Zygothrica* taxonomy. The most important ones are by Duda (1927) and Burla (1956). Around the time of Duda's timely monograph on Costa Rican Drosophilidae, scattered species descriptions appeared: one *Zygothrica* (and the first known southeast Asian form) was described by Malloch (1934), and two each by Williston (1896), Hendel (1913, 1936), and Sturtevant (1920, 1921). Much later, Wheeler (1952, 1968) and Takada (1976) described three species each. Burla's monograph is the most comprehensive reference on these flies; prior to this, the only attempts at a revision of the taxonomic concept of *Zygothrica* was a brief diagnosis by Sturtevant (1920) and a division of the genus into two subgenera (*Zygothrica* and *Tanyglossa*) by Duda (1925). Besides dividing *Zygothrica* into five species-groups, Burla had expanded the definition of

Zygothrica and described 41 species based on material from southeastern Brazil. To date, 65 *Zygothrica* species have been named.

The present study was inspired by perusing several major drosophilid collections and finding many new species, particularly ones from eastern foothills of the Andes and from Central America. Since many of the new species seemed phylogenetically much more varied than the described ones, a reanalysis of the major cladistic patterns in the genus was in order. Such a phylogenetic analysis would also provide a test for the "naturalness" (correspondence with genealogy) of Burla's (1956) species-groups and Duda's (1925) subgenera. Also, the taxonomic positions of 12 *Zygothrica* species were considered ambiguous or were not discussed by Burla; these included *Z. samoaensis*, the only southeast Asian species known at the time. The description of 49 new species is probably the most substantial contribution of this study, but information on distributions is a precedent set here for the rather brief history of *Zygothrica* study. With 114 species now described, as of this report, and about 60 to be described in a subsequent paper, it is very apparent that *Zygothrica* is the most speciose lineage of neotropical Drosophilidae. It is my hope that future collecting and a continuing study of *Zygothrica* systematics will contribute much knowledge on the diversification of neotropical Drosophilidae and other insects.

ACKNOWLEDGMENTS

Specimens were borrowed from the following collections with the help of the respective curators:

AMNH	American Museum of Natural History, New York (Randall T. Schuh).
ANC	Australian National Insect Collection, Canberra (D. H. Colless).
BBM	Bernice P. Bishop Museum, Honolulu (Neal Evenhuis and Kenneth Y. Kaneshiro).
BMNH	British Museum (Natural History), London (Brian Cogan and John Chai-ney).
CAS	California Academy of Sciences, San Francisco (Paul H. Arnaud, Jr.).
CNC	Canadian National Collection, Biosystematics Research Institute, Ottawa (J. Frank McAlpine).

CUIC	Cornell University Insect Collections, Ithaca, New York (James K. Liebherr).
HNHM	Hungarian Natural History Museum, Budapest (D. Dely-Draskovitz).
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Francesca C. Val).
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (D. J. Bickel and J. M. Carpenter).
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Wayne N. Mathis).
SMT	Staatliches Museum für Tierkunde, Dresden (R. Krause).
TSM	Tokyo Science Museum, Japan (Toyohi Okada).
UT	University of Texas Collection, Austin (Marshall R. Wheeler).
ZMUS	Zoologisches Museum der Universität Zürich, Switzerland (Gerhard Bächli and Hans Burla).

Museum abbreviations serve to indicate the location of type specimens as given in the descriptions.

It is a pleasure to thank the people who have contributed in various ways to this project, which was done in partial fulfillment for the requirements of a Ph.D. degree at Cornell University. Quentin Wheeler was extremely supportive and, as chairman of my graduate committee, he assumed with diligence the persistent responsibility of funding and other logistic matters. William L. Brown never seemed perturbed by my incessant inquiries on taxonomic protocol and general advice. Marshall Wheeler and Francesca Val sent thousands of specimens from collections in their care; their efforts were an integral part of this study. Wayne Mathis graciously helped me to utilize the facilities and collection at the NMNH in the best possible ways during my visits. I am very grateful to the following readers of this work who provided thorough critiques: William L. Brown, Lee Herman, Wayne Mathis, Frank McAlpine, Frederick Rindge, Randall T. Schuh, and Quentin Wheeler.

The Harold E. Moore Fund of the Cornell University Bailey Hortorium funded my trip to southeastern Peru. A year of unimpeded research was made possible by a Griswold Fellowship provided by the Entomology De-

partment at Cornell. A NSF Doctoral Dissertation Improvement Grant funded the use of a SEM and travel to Panama and the Dominican Republic. Lastly, measurements of specimens were made possible by NSF Grant No. BSR 8315457 to Quentin D. Wheeler.

As for my wife, Karen, words cannot say in how many ways she has been of help towards the completion of this work.

MATERIALS AND METHODS

Drosophilids are best collected by sweeping over the hosts or baits and preserving the adults in 70 percent ethanol. After thoroughly dehydrating the specimens in absolute ethanol, they should be critical-point dried (see Gordh and Hall, 1979). This process leaves flies completely distended, free of grease and other residues. All the setae remain intact, and even color patterns (such as those on the eyes of some species) are very well preserved. The flies are then point-mounted.

For my drosophilid studies, genitalia are dissected by clearing the terminalia in cold 10 percent KOH overnight, rinsing once each in water and 70 percent ethanol, and then passing them to glycerine. To prepare genitalia for compound microscopy, the terminalia are then transferred to a small (ca. $2 \times 2 \times 2$ mm) piece of glycerine jelly (gelatin + glycerine) on a clean slide. The slide is heated until the jelly begins to melt, whereupon the terminalia are disarticulated under a stereoscope at $50\times$ while the mountant is still molten. Generally, separation of the hypandrium + aedeagus from the epandrium (both mounted ventral side up) is sufficient to view most details, and this dissection was done with a pair of minutens. The advantage of the glycerine jelly technique is that it allows positioning of the specimen for a proper orientation while the mountant cools and solidifies. When the mountant is solidified, a 0-thickness coverslip (to compensate for the thickness of the preparation) is applied. To store the preparation, the genitalia are scooped out with a piece of jelly and stored in a small (10×3 mm) plastic microvial with a small drop of glycerine. The vial is pinned below the data labels on the pin bearing the specimen.

Compound microscopy was done using a

Leitz Nomarski optics microscope, and a camera lucida was used to illustrate most structures. Routine stereoscopic work was done at $25\text{--}50\times$ with a Wild M-5, and a camera lucida was used here too for illustration. Critical-point dried specimens were prepared for scanning electron microscopy (SEM) by gold-palladium sputter coating at $20 \text{ \AA}$ thickness. In the SEM, specimens were examined using 10 kV beam current. Prior to critical-point drying, larvae were first prepared by immersing them in a rapidly permeating fixative (Grodowitz et al., 1982).

Types of measurements are described in the section on morphological terms. Measurements were made on camera lucida images of specimens at 25 or $50\times$ projected onto a digitizing tablet and traced with a cursor. The tablet is an electronic image analyzer (Zeiss, Inc.) capable of several measurements and functions; curve closure error at the tablet surface is ± 0.10 mm. Measurement error was due mostly to positioning of the specimen, and varied as well with the structure being measured. In general, an error of ± 0.10 mm was found to be reliable for all structures measured at $25\text{--}50\times$. Unless indicated otherwise, units of absolute measurements are in millimeters.

Types were examined as indicated in the species accounts. Specimens from paratype series were usually distributed among the AMNH, BMNH, CUIC, MZSP, and NMNH. Other particular methods (e.g., behavioral comparisons) are discussed under the appropriate sections.

PHYLOGENETIC ANALYSIS AND TAXONOMIC PROTOCOL

My procedure for delimiting species was based entirely on a morphospecies concept. Where consistent, definable gaps existed in structural characters, the intervening space constituted a species. I view a species as a reproductively isolated unit in nature, and this populational view is not inconsistent with a purely morphological approach for several reasons: (1) Morphological and any other phenotypic gaps denote reproductive isolation (i.e., gene exchange, or a blending of phenotypes, does not occur). (2) Cryptic species will undoubtedly be found in *Zygothrica* when

some other characters are used, but at present, morphology is the most comprehensive source of characters for convenient comparison in flies. Indeed, the correspondence is often close between species limits based on morphology and the limits defined by the use of chromosomal and biochemical characters.

A cladistic analysis was used to arrive at hypotheses of phylogenetic relationships. The reasoning behind the approach is very simple: if two or more species possess a derived trait, then the trait presumably arose in a recent ancestor common to them (Hennig, 1950, 1965). To assess each decision on the synapomorphic state of a character (a similar trait due to common descent), versus one which has evolved in parallel or convergently, a comparison was then made to distributions of other putative synapomorphies. To decide upon the polarity of character evolution, a taxon was compared to species not included therein (Maddison et al., 1984; Watrous and Wheeler, 1981), but generally to the most closely related, or sister, taxon. An important and often overlooked point of outgroup comparison is that character polarity can hypothetically change with taxonomic level: as the analysis becomes centered toward the species level, so too should the taxonomic rank of the outgroup change. For an analysis of highest relationships, the taxa compared to *Zygothrica* were *Diastata* (Diasatidae), *Camilla* (Camillidae), and, in the Drosophilidae, several species each of *Stegana*, *Mycodrosophila*, *Drosophila* (*Hirtodrosophila*), *D. (Drosophila)*, and *D. (Sophophora)*. Hypotheses of relative genealogical relationships have been constructed.

The classification of *Zygothrica* was constructed so as to (1) erect monophyletic groups, and (2) reflect relative genealogical

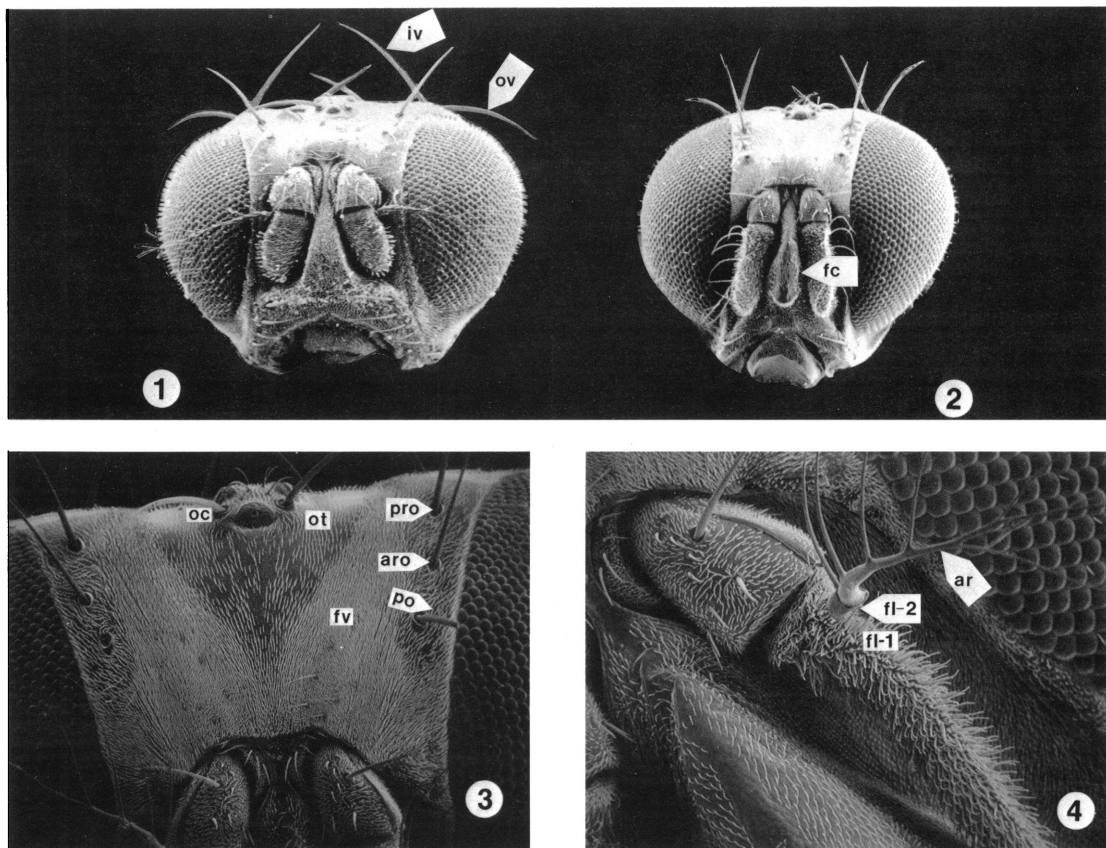
relationships as closely as possible. To facilitate use of such a classification, Hennig's enumeration technique was employed for identifying most clades. For very large groups with multiple levels of nested taxa, letters were used for some terminal lineages. With a long list of hierarchical ranks, it has been argued that purely cladistic classifications are too cumbersome to use. However, I believe that it is biologically more meaningful for comparative and evolutionary studies that a classification reflects phylogeny rather than convenience, overall similarity, or presumed adaptive significance of particular structures or species. For a speciose and phylogenetically diverse group as is *Zygothrica*, it is just difficult to provide a simple summary of the natural classification.

My format for citing taxonomic names here, and in subsequent papers, is rather unconventional. In only a few instances is the author's name included with the generic or the binomial names, specifically, as the leading entry in a listing of homonyms or as a reference prior to a diagnosis or redescription. Use of an author's name at the end of a taxonomic name is purely for reference purposes: repeated application of it, especially in a revision (where the original citations are listed anyway) is not only redundant, but misleading in that the concept of a taxon changes with the reviser. Additional apomorphies can be discovered to reveal changes in taxonomic placement or the presence of cryptic species. Indeed, Wiedemann's concept of *Zygothrica* as platystomatid flies with tapered eyes is considerably at variance with the concept presented here. Also, the ICZN (1985: 95) states: "The name of the author does not form part of the name of a taxon and its citation is optional"

ADULT MORPHOLOGICAL CHARACTERS AND TERMINOLOGY

Basic aspects of muscomorphan morphology are covered in McAlpine (1981), from which I have derived some of the terminology suitable for drosophilids and *Zygothrica*. Terms given in this section are used throughout the text and especially in the diagnoses

and descriptions. *Ground* color is the most extensive color on a sclerite that possesses a pattern. It may vary among the three main tagmata, and, for the thorax, it may vary between the (meso)notum and pleura. *Pruinescence* is the fine microtrichia on sclerite



Figs. 1, 2. *Drosophila* (*D.*) *recens* (106 $\times$) and *Zygotherica vittinubila* (92 $\times$), respectively; frontal view of heads. *fc*, facial carina; *iv*, inner vertical seta; *ov*, outer vertical seta.

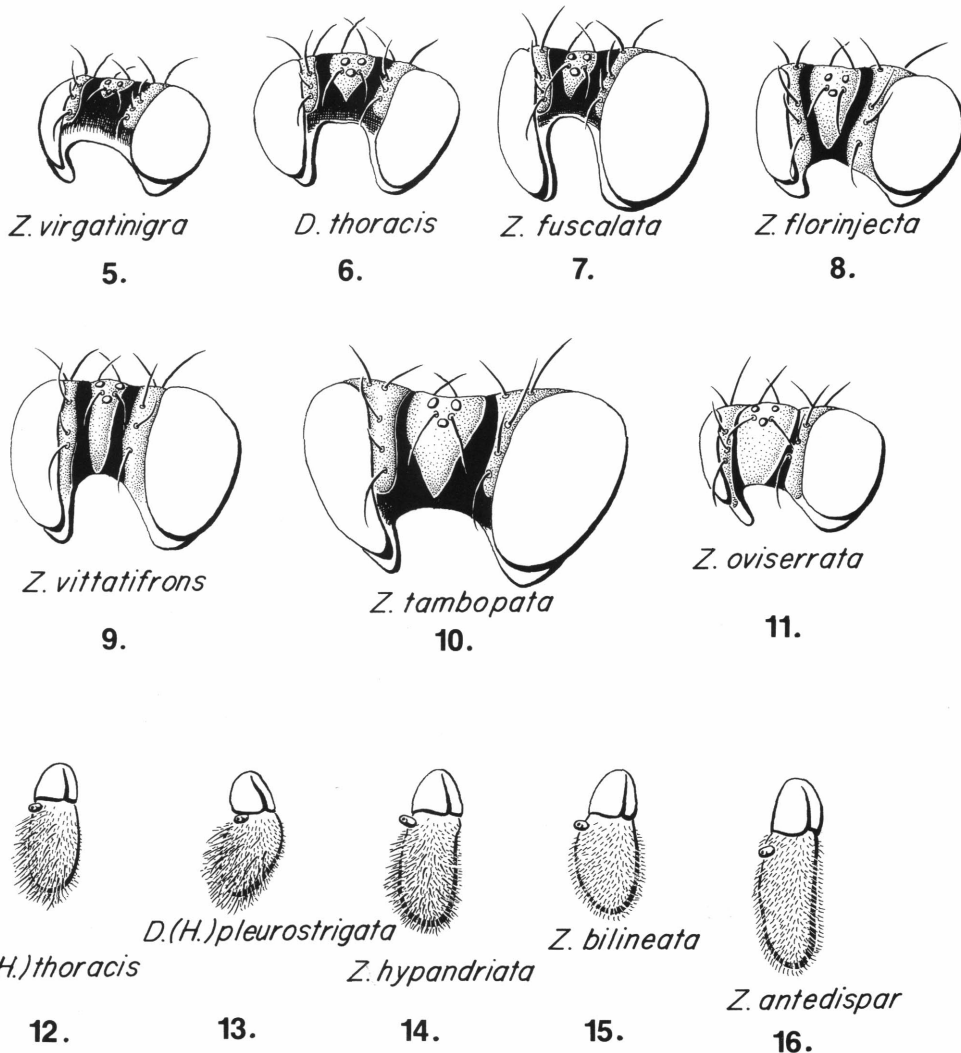
Figs. 3, 4. Anterior aspect of head of *Zygotherica pallida*, n. sp. 3. 286 $\times$, front. *aro*, anterior reclinate orbital seta; *fv*, frontal vitta; *oc*, ocellar seta; *ot*, ocellar triangle; *po*, proclinate orbital seta; *pro*, posterior reclinate orbital seta. 4. 324 $\times$, antennal base. *ar*, arista (flagellomere III); *fl-1*, *fl-2*, flagellomeres I, II.

surfaces. Sclerites with dense, matted microtrichia are *microtomentose*, and sclerites devoid of microtrichia are *glabrous* and sometimes *shiny*. A pair of setae that point mesad is *convergent*, *divergent* if pointed laterad, and *parallel* if neither. Convergent setae that cross are *cruciate*.

HEAD: The most conspicuous cranial modification is broadening, or *hypercephaly*. In unmodified forms, the head is only slightly wider than the thorax, but extremely hypercephalic males have heads up to three times wider than the thorax. Involved in hypercephaly are mostly the eyes and *frontal-orbital plates* (figs. 5–11), although the *face* and *ocellar triangle* (figs. 3, 17–24) affect the modification slightly. Eyes have varying degrees

of interfacetal setulae density, or *eye pilosity* (figs. 1, 2). Ocellar triangles vary in length and width (figs. 5–11). If the triangle is very narrow and long, it is also usually *parallel-sided* (fig. 9). In some forms with a rudimentary triangle, a *median frontal vitta* exists, which is a narrow light stripe running from the median ocellus to sometimes the *ptilinal fissure* (fig. 35). Lateral to the triangle are the microtomentose *frontal vittae* (figs. 3, 5–11). Frontal vittae may be *dull*, or *reflective* when viewed at an oblique anterior angle, and color may be white, ochre, cream, golden, and black. The frontal vittae converge anterior to the ocellar triangle in all but a few forms with very large triangles (fig. 11).

The main cephalic setae are the *proclinate*,

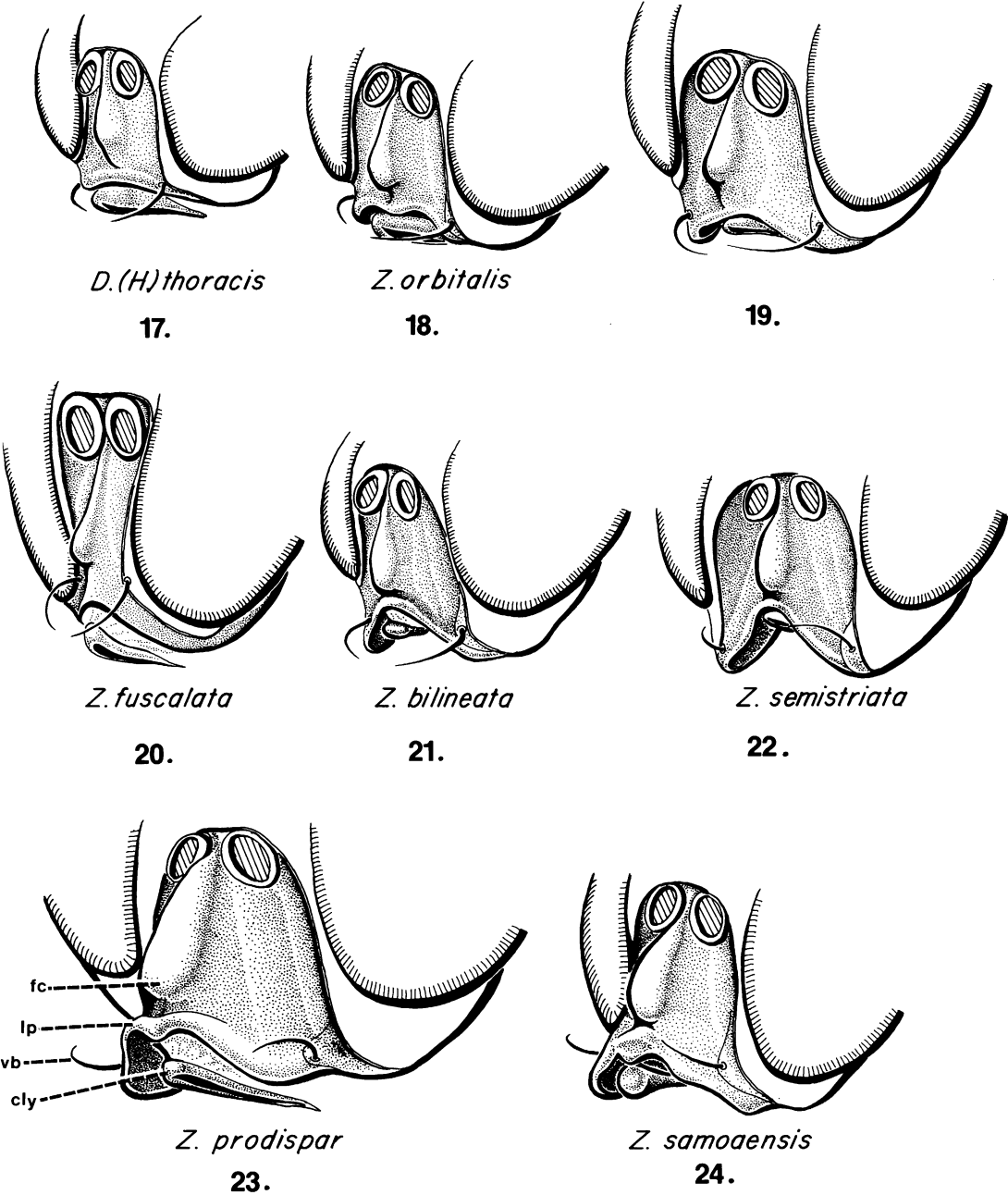


Figs. 5-11. Oblique frontal views of heads of *Drosophila* and *Zygothrica*, showing development in frontal vitta (black), frontal-orbital plates, and the ocellar triangle.

Figs. 12-16. Pedicels and flagellomeres I, II of *Drosophila* (H.) and *Zygothrica*, showing shapes and setulae development.

anterior reclinate, and posterior reclinate orbitals, the inner and outer verticals, postverticals, postocellars, ocellars, and the vibrissa (see figs. 1-3 for their positions). Setulae, as defined by zones, are the interfrontals, postoculars, and subvibrissals. If the facial carina protrudes well beyond the depth of flagellomere I, it is *pronounced* (figs. 2, 18-24; cf. figs. 1, 17). A carina with a sharp anterior margin is *acute*; one with a rounded swelling near the anterior facial margin is *bulbous* (figs.

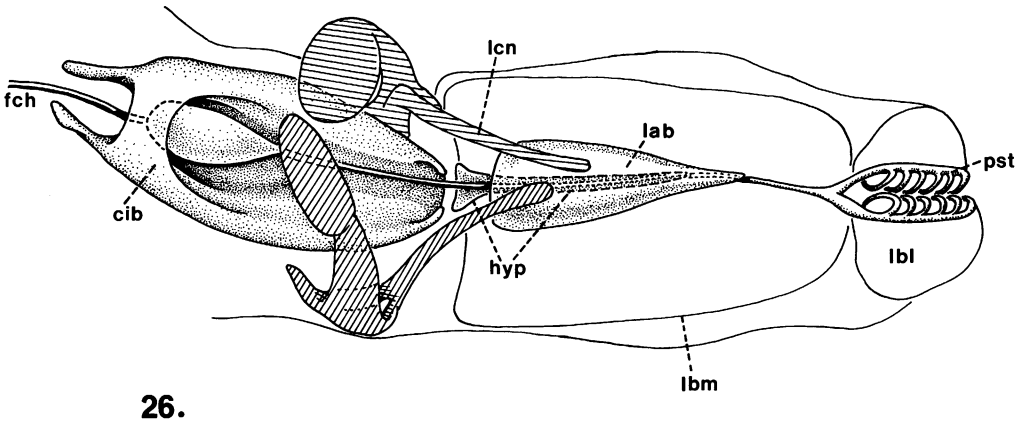
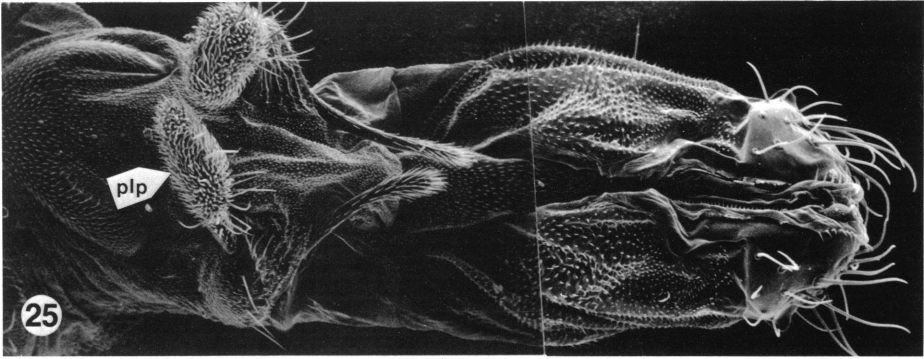
18-24). Carinae extended to the facial margin are *complete*, others are *incomplete*. If the facial margin is extended strongly anterodorsad, it is a *protuberant* face (figs. 23, 24). *Facial cleft* denotes the sharp excavation in the anterior facial margin (figs. 20-24). A face is *narrow* if the width is $1-1\frac{1}{2}\times$ the width between the lateral surfaces of the pedicels (fig. 20), but it is usually at least $2\times$ wider than this distance (figs. 17-19, 21-24). The *cheek* is the area beneath (ventral) to the eye;



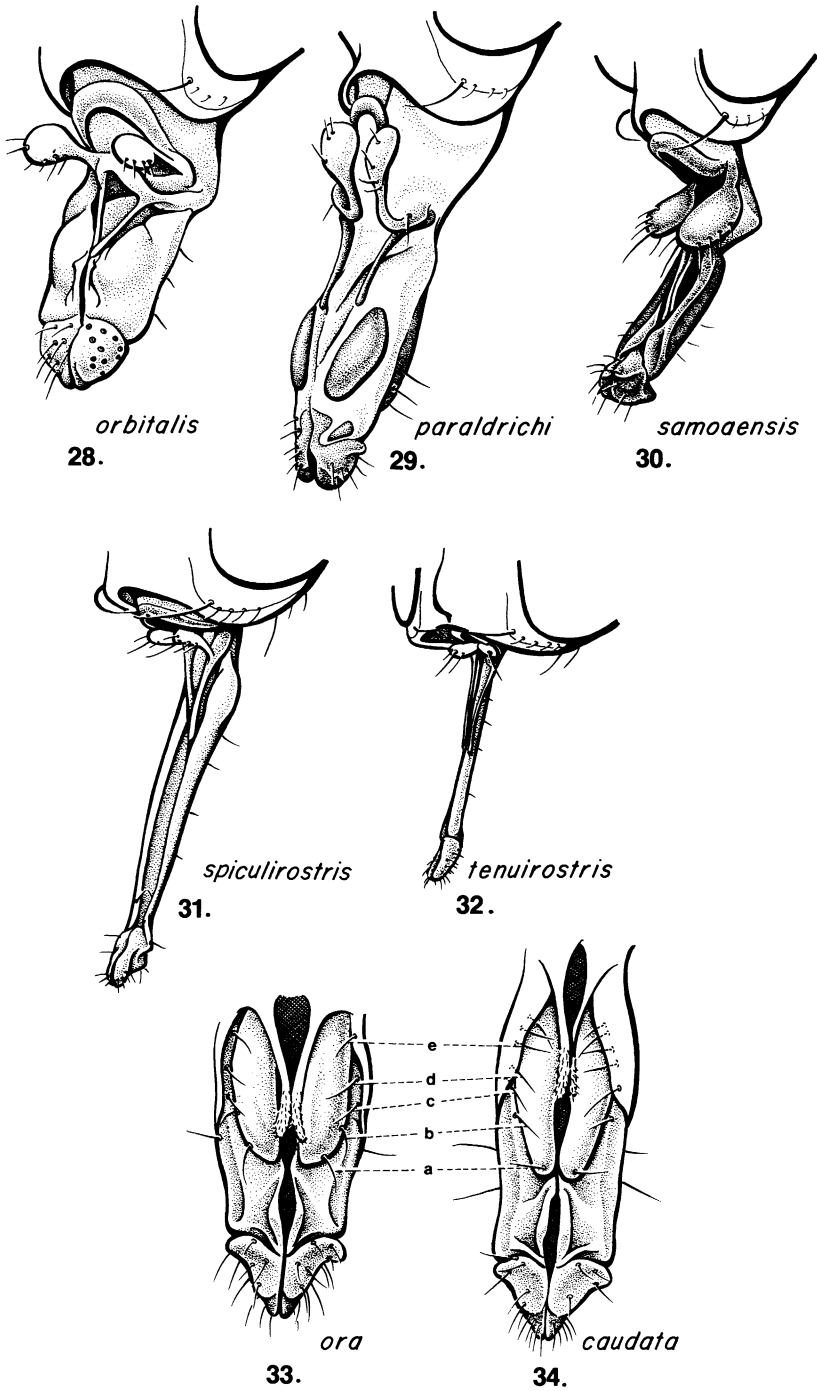
Figs. 17–24. Faces (stippled) of *Drosophila* (*Hirtodrosophila*) and *Zygothrica*. Figure 19 is an un-described species of *Zygothrica*. cly, clypeus; fc, facial carina; lp, lip; vb, vibrissa (subvibrissal setulae not shown).

that portion of the cheek which is below the frontogenal suture is the facial cheek (figs. 17–24). When the facial cheek is extended outward, it is *splayed* (figs. 23, 24).

Flagellomere I setulae may be *long* (figs. 12, 13) or *short* (figs. 14–16). Extensions of the arista (flagellomere III) are *aristal branches* (fig. 4); a count of their number, dorsal and



Figs. 25–27. Proboscis of *Zygothrica prodisspar*. 25, 26. Dorsal aspect (fig. 26 is reconstructed from cleared specimens). 27. Labellum, enlarged, ventral aspect. cib, cibarium; fch, food channel; hyp, hypopharynx; lab, labrum; lbl, labellum; lbm, labium (ventral); lcn, lacinia; plp, palps; pst, pseudotrachea.



Figs. 28–32. Proboscides and palpi of some *Zygothrica*. Heavily stippled areas are strongly sclerotized. *Zygothrica paraldrichi* proboscis is shown fully distended; *Z. tenuirostris* is the holotype. All are to the same scale.

Figs. 33, 34. Proboscides, dorsal view, of *Zygothrica ora*, n. sp. and *Z. caudata*, showing the intralabial setae (a to e plus 2 additional ones in *Z. caudata*).

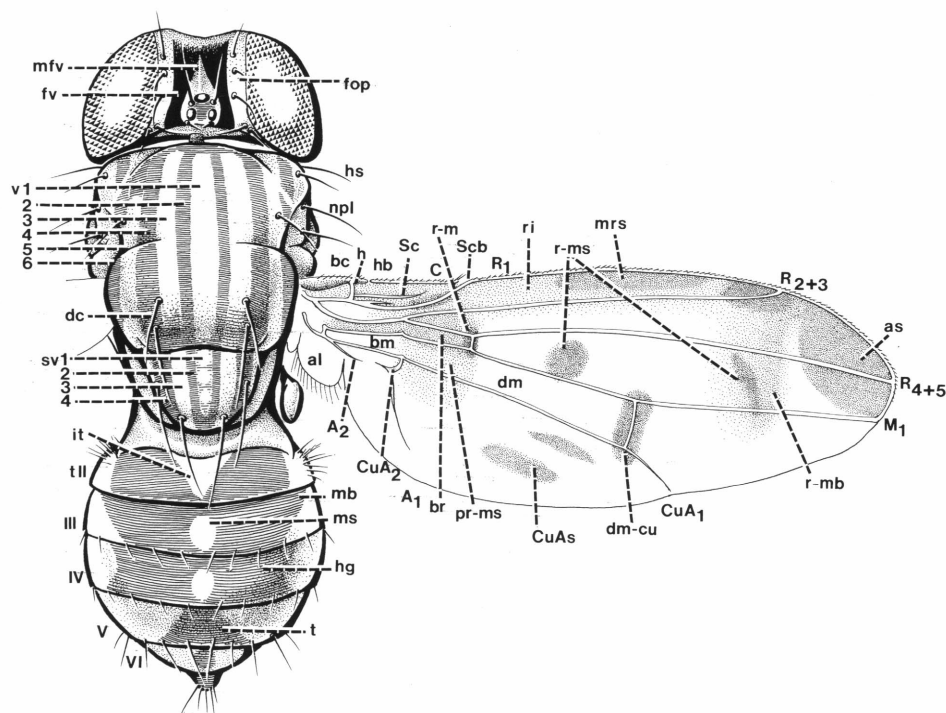
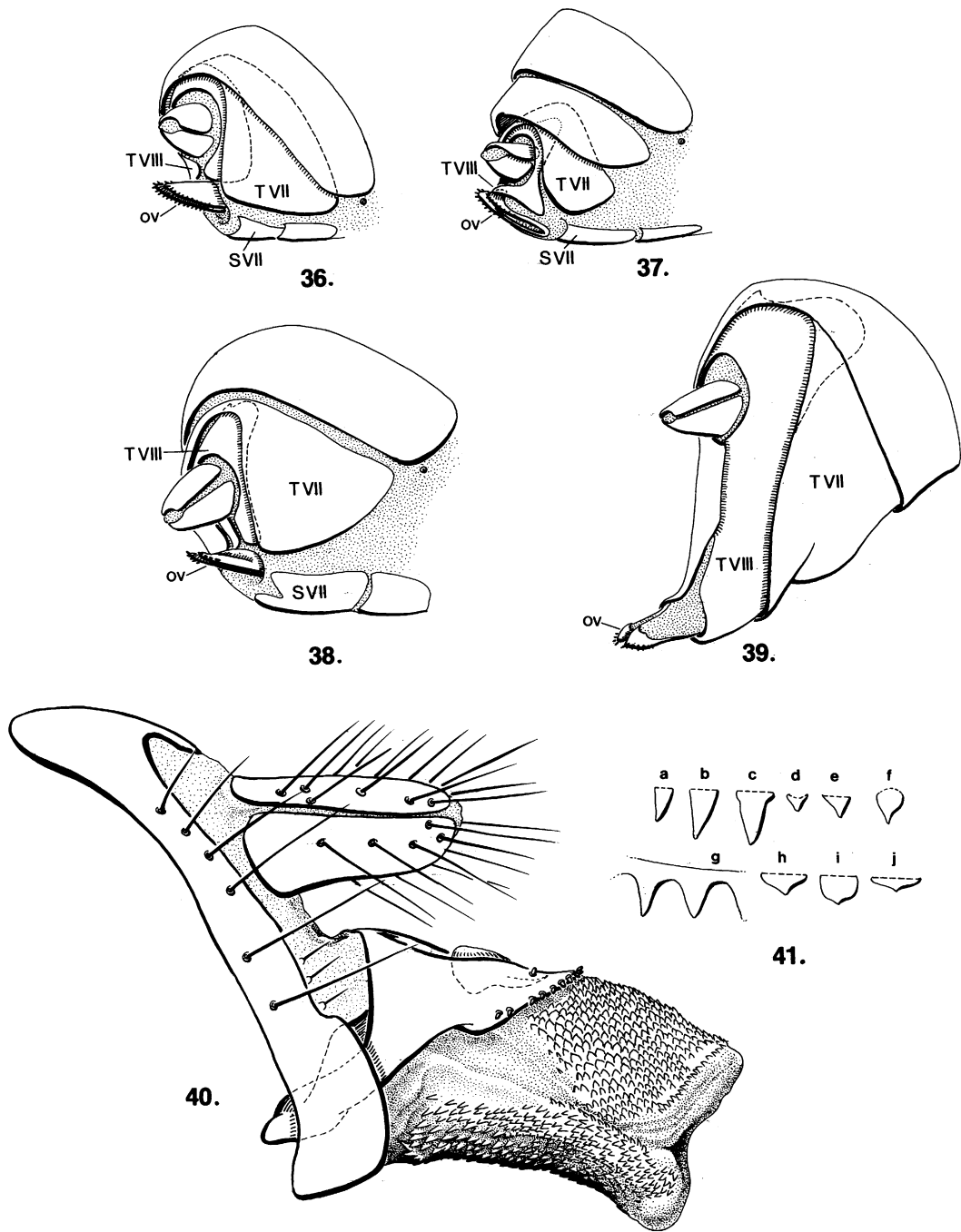


Fig. 35. Mosaic of the dorsal habitus of *Zygothrica*, showing most of the body color patterns. HEAD: **fop**, frontal-orbital plate; **fv**, frontal vitta; **mfv**, median frontal vitta. THORAX: **dc**, dorsocentral setae; **hs**, humeral seta; **npl**, notopleural seta; **sv 1-4**, scutellar vitta 1-4; **v 1-6**, (notal) vitta 1-6. WING: **al**, alula. Veins: **A₁**, **A₂**, anal; **bc**, basicostal; **C**, costa; **CuA₁**, **CuA₂**, cubitus anterior; **dm-cu**, crossvein; **h**, humeral crossvein; **R₁**, **R₂₊₃**, **R₄₊₅**, radial veins; **M₁**, medial. Cells: **br**, basiradial; **dm**, discomedial; **bm**, basal medial. Spots: **pr-ms**, proximal radial-medial spot; **ri**, radial infuscation; **mrs**, mid-radial spot; **r-ms**, radial-medial spot(s); **r-mb**, radial-medial band; **CuAs**, CuA spot(s); **as**, apical spot. Breaks: **hb**, humeral break; **Scb**, subcostal break. ABDOMEN: **hg**, hourglass (pattern); **it**, inverted triangle (pattern); **mb**, median band; **ms**, median spot; **t**, triangle; **t II-VI**, tergites.

ventral, is exclusive of the short terminal bifurcation. A proboscis that is extremely long (ca. $1\frac{1}{2} \times$ length of the head) and thin is *styli-form* (figs. 31, 32; cf. figs. 28-30). The inner surface of the labral sheath may possess sharp, straight setae pointed mediad, the *mediolabral setae* (figs. 33, 34), but this portion of the proboscis usually possesses no such setae (fig. 25). Palpi may be *broad* (fig. 30) or unmodified if the width is much less than the length (figs. 28, 29, 31, 32).

THORAX: One or two pairs of *dorsocentral setae* (fig. 35) may be present. Rows of *acrostichal setulae* are counted as they run between the anterior dorsocentrals. Two pairs of *scutellar setae* are present, which are an *anterior* and an *apical* pair. Other important thoracic setae are the *humeral* (on the humeral, or

postpronotal, lobe), *katapisternals*, *notopleurals*, and *supra-alars* (fig. 35). Color patterns vary dramatically, even among closely related species, and particularly patterns on the notum. The notum may be *unicolorous*, or with *diffuse* and/or *discrete* longitudinal stripes, or *vittae*. Where the ground notal coloration ends abruptly at the notopleural suture, this is a *distinct notopleural edge*. Vittae that run almost the entire length of the notum are *complete*; shorter vittae are *incomplete*. The median vitta is *vitta-1*, either one just lateral to it is *vitta-2*, and so on laterad to at most *vitta-6* on each side (fig. 35). *Scutellar vittae* and/or *spots* are considered separate from notal ones, but the method for naming them is the same. Pleura are usually unicolorous, but may have infuscations as specif-



Figs. 36–39. Female terminalia, posterior view. 36. *Drosophila (Drosophila) tripunctata*. 37. *Drosophila (Hirtodrosophila) thoracis*. 38. *Zygothrica vittinubila*. 39. *Z. paraldrichi*. S, sternite; T, tergite; ov, oviscape (S VIII).
Fig. 40. *Zygothrica atriangula* female terminalia, lateral view, showing everted oviprovector.
Fig. 41. Oviprovectors scales, a–j. a–b, acute; c, dentate; d–e, short acute; f, carnassate; g, pectinate; h–j, placoid (i, long placoid; j, short placoid).

ically described. Legs usually match the ground color of the pleura, but *bands* may occur on some segments. The prothoracic femora have variable numbers of setae in the *ventral row* (figs. 467–474).

Wing vein terminology is shown in figure 35, as are the following terms for markings: *apical spot*, *dm-cu* (crossvein) *spot*, *CuA spot(s)*, *radial infuscation*, *mid-radial spot*, *r-m spot(s)*, *proximal r-m spot*, *r-m band*. Wings with a distinctly rounded apex and reduced anal area are *petiolate* (figs. 127–130).

Most of the standard measurements concern thoracic structures and are the following: HEAD: *head width (HW)* = greatest distance between apical portions of eyes. THORAX: *thorax length (ThL)* = distance from anterior notal margin to apex of scutellum. WING: *costal index (C.I.)* = length of costa from subcostal break to R_{2+3} /length C from R_{2+3} to R_{4+5} (and parallel to R_{4+5}); *4-V (index)* = length of M_1 from dm-cu to apex/length M_1 from r-m to dm-cu; *wing length (W.L.)* = distance from humeral crossvein to wing apex.

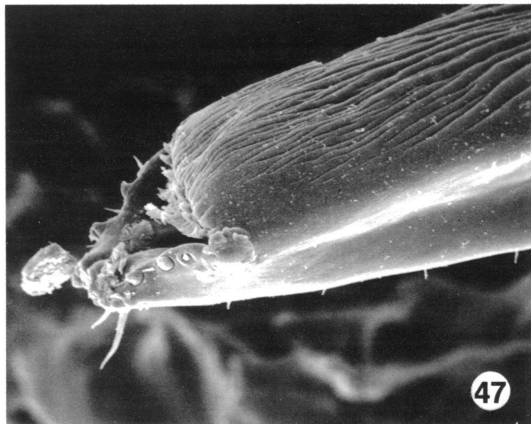
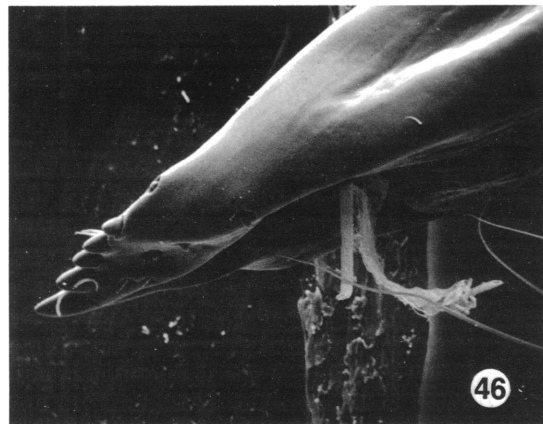
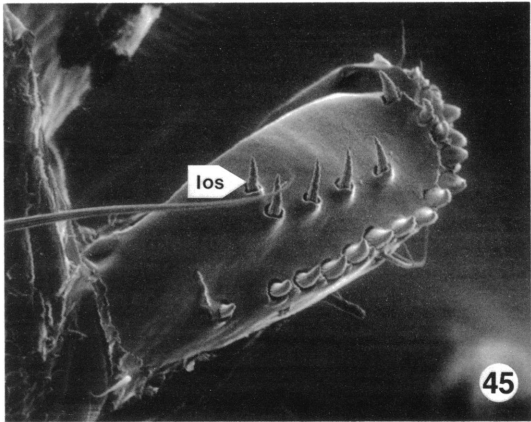
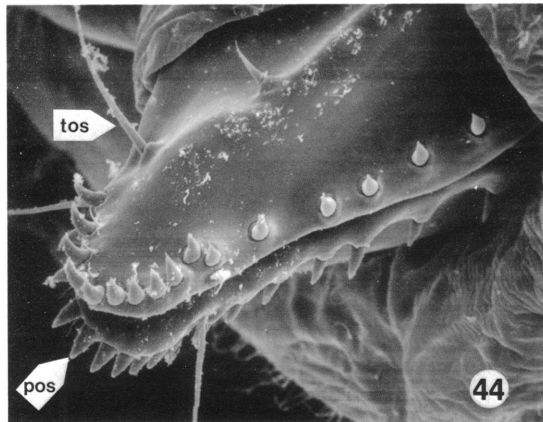
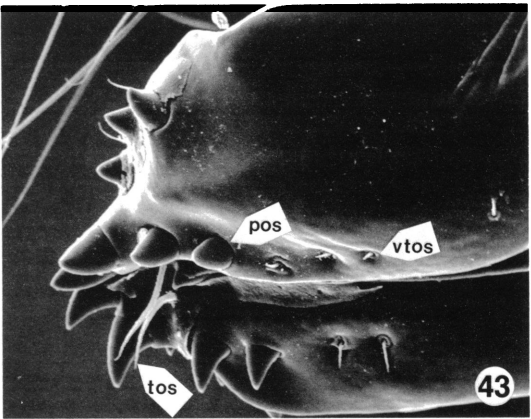
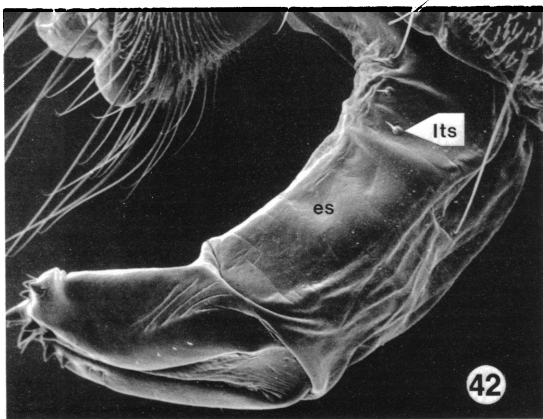
ABDOMEN: Tergites 2–9 (*t II–IX*) and *t II–VIII* are apparent in the males and females, respectively. *Sternite VIII* in females is modified into two broad lateral plates (figs. 36–40) that are joined by an *anteroventral bridge* and together form the *oviscape*. Between these two plates is an eversible, scaled membrane, the *aviprovector* (figs. 40, 51), which is actually the intersegmental membrane between S VII and S VIII that has become modified for the passage of eggs. The term was coined by Steyskal (1979) in reference to a genus of Otitidae. The lateral plates on the oviscape possess *trichoid* and *peg ovisensilla* on the apex and the ventral edge (figs. 43–50). *Sternite VII* in females may be *simple* or *bifurcate*, and with or without an *anterior ramus*. If *t VIII* in females is extended ventrad, it is *laterotergite VIII* (fig. 39). When laterotergite VIII possesses a long lateral sclerite projected posteriad (beneath membrane), the structure on each side is referred to as the *laterotergite VIII ramus*. *Cerci* that are long with parallel sides are *cylindrical*, shorter ones with a tapered apex are *conical*, and they are very often *flattened dorsoventrally*. A small dorsomedial sclerite or pair of them lying between the lateral plates of the oviscape is sometimes present, which is interpreted as a remnant of *tergite IX*. Oviprovector scale shapes vary

from *circular*, *placoid*, *triangular*, to *lanceolate* (fig. 41). Scales are usually *free* but sometimes attached to each other in rows, each row of which is a *comb* (fig. 41g). Apical scales that stand vertically and are very sharp and curved are *rhampate*. Oviscape shapes are described with respect to the dorsoventral view, and are *circular*, *oval*, *acute* (apex abruptly narrowed), *elongate* (length at least $3\times$ width), *truncate* (apical margin flat), or some combination of these (e.g., *acute elongate*). Elongate truncate oviscapes are generally referred to as *spatulate*. Peg ovisensilla on the lateral surface of the lateral oviscape plates are the *laterals* (fig. 45).

The *spermathecal capsule*, which is the sclerotized core of the *spermatheca*, is paired, and various shapes, surfaces, and degrees of sclerotization are represented. Shapes are *campanulate* (bell-shaped), *spherical*, *rectangular*, and *oblong*. The *introvert* is an inverted sleeve extended apicad into the spermathecal capsule. An *apical indentation* is sometimes found on the capsule, and a *basal collar* occasionally exists. In addition, the capsule surface may be *papillate*, *scaled*, *wrinkled*, and/or finely or coarsely *annulate* (the introvert, too, may possess annuli). In reference to the degree of sclerotization, the capsule may be *rigid*, *weak*, *intermediate*, or *membranous*.

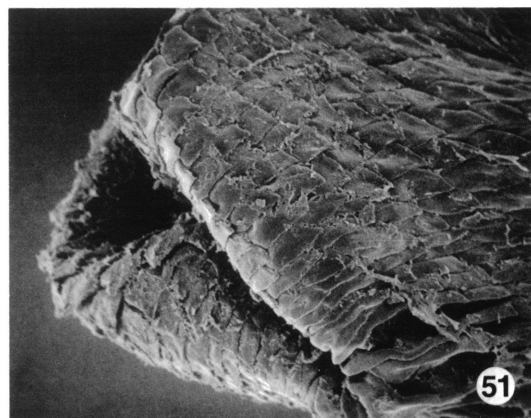
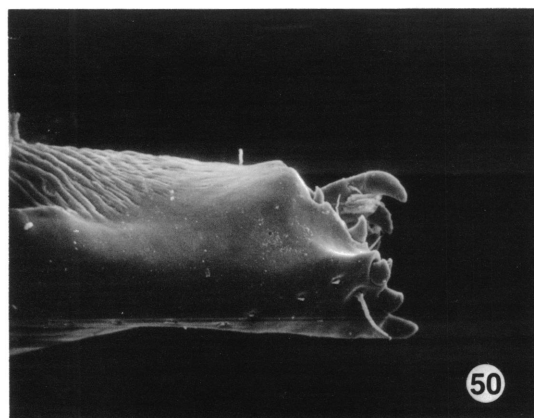
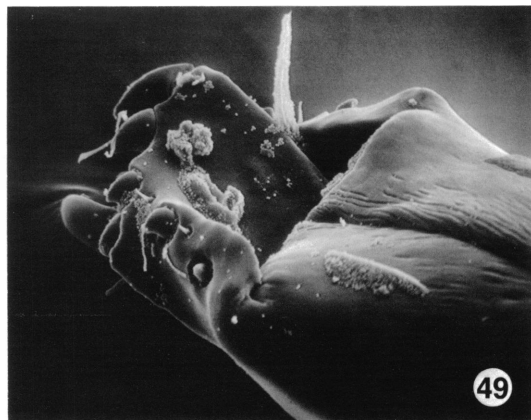
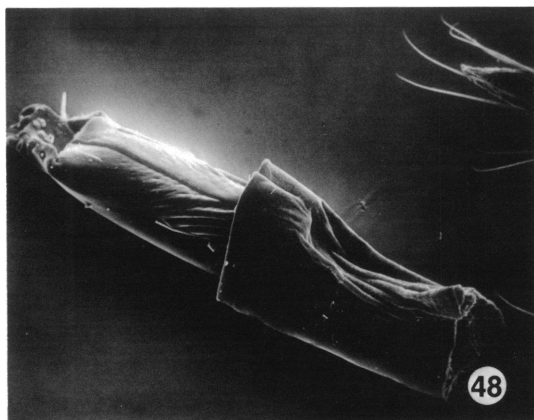
Tergites may be unicolorous, or possess the following markings (fig. 35): *median spot*, *triangle*, *inverted triangle*, *hourglass*, or *band* (a band covers most of the length and width of the tergite).

MALE TERMINALIA: Figures 52–57 show several of the apomorphic features described below. The *epandrium* is *t IX*: modifications of the basic plan are in shape and features of the ventral lobes. If the dorsal epandrial surface is at least twice the length of the ventral surface, then the epandrium is *dorsally elongate*. At the posterior end are *ventral epandrial lobes* which may be *inconspicuous* (just a swelling in the region), *adpressed* (to the anterolateral surface of the surstylus), to *pendulous* (where it hangs, and the width at the apex exceeds that at the base). One to three pairs of ventral lobes may be present; generally, anterior pairs are glabrous and thinner than the posterior pair. Setation of the ventral lobes varies in density and length; some species possess *spines* on the lobes. Posterior



Figs. 42–47. *Drosophilid* oviscapes. 42, 43. *Zygotherica orbitalis* (257×, 820×). 44. *Mycodrosophila claytonae* (980×). 45. *Zygotherica samoensis* (780×). 46. *Z. dispar* (660×). 47. *Z. vittinubila* (970×). es, eversible sheath (intersegmental membrane of S VII, S VIII); los, lateral ovisensillum (peg); Its, laterotergal ovisensillum (trichoid); pos, peg ovisensilla; tos, trichoid ovisensilla; vtos, ventral trichoid ovisensilla.

to the epandrium are the paired *cerci* and associated sclerites. In lateral view the cerci can be *lobate* (posterior end rounded and wider than base), *elongate*, or, *symplesio-*



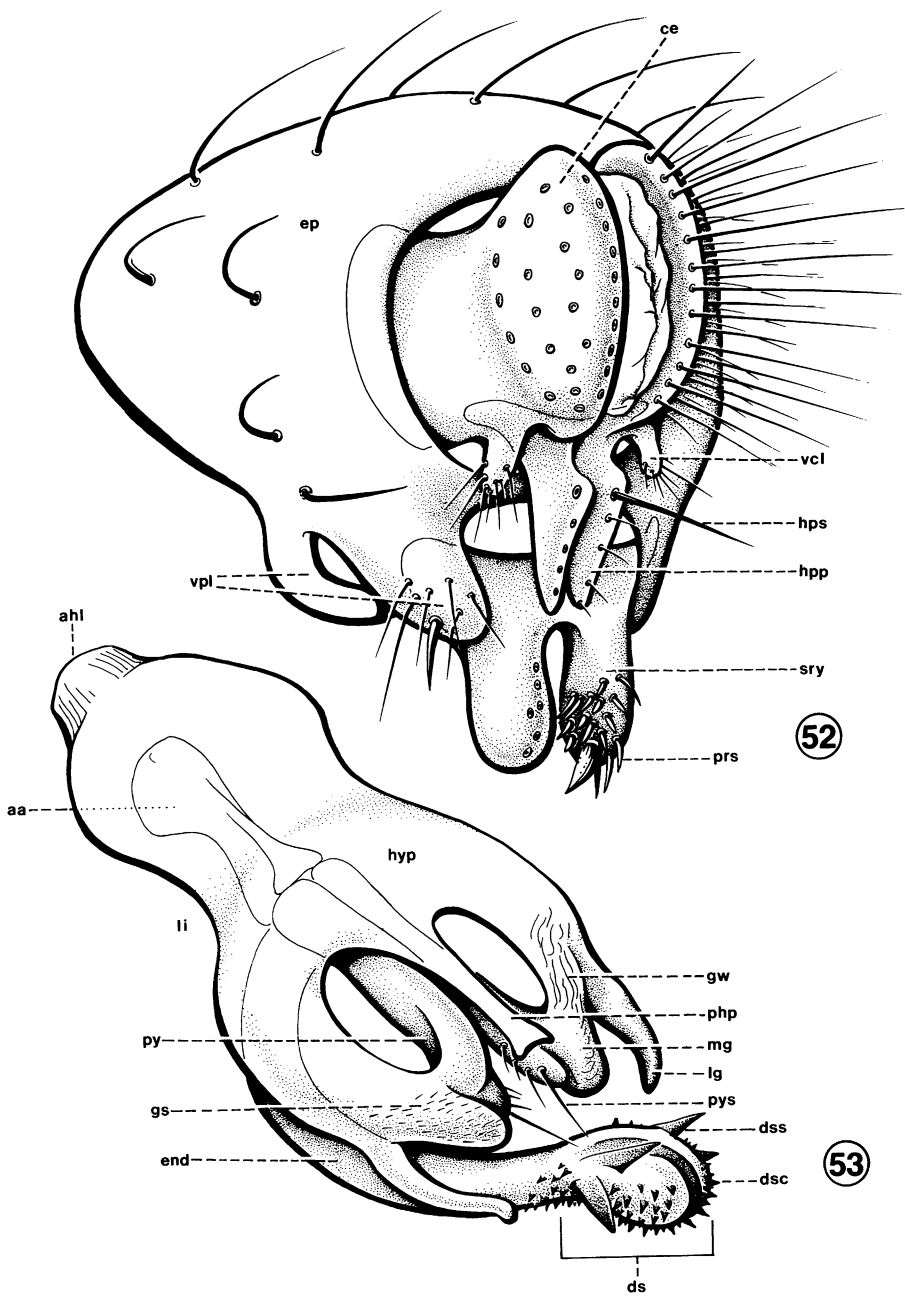
Figs. 48–51. Oviscapes of some *Zygothrica*. 48, 49, undescribed species of *Zygothrica* near *poeyi* (NICARAGUA) (293 $\times$, 1200 $\times$). 50. *Z. celsa*, n. sp., lateral view (780 $\times$). 51. *Z. aldrichii* oviprovector, showing apical aperture (1000 $\times$).

morphically, *conical*. Ventrolateral to the cerci may be a pair of *ventral cercal lobes*. A tuft of fine setulae, and sometimes stiff ones, are nearly always present in the region even if the lobes are not present. Immediately ventral to the cerci are a pair of sclerotized, pendulate plates which are triangular in lateral view, the *hypoproctal plates*. Lengths of the plates vary greatly, as defined by the distance on the surstyli to which they are extended. Setulae of variable number are present on the posterior edge of each plate, and an elongate erect *spine* may also be present.

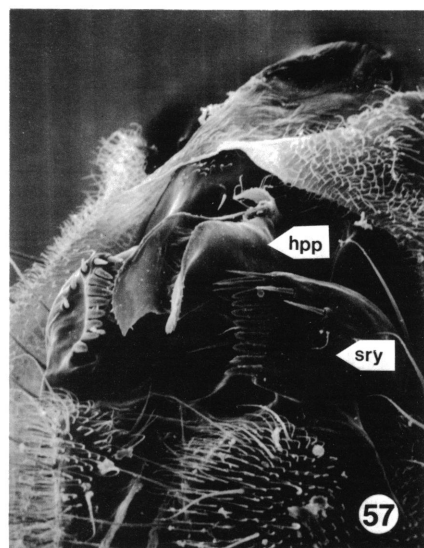
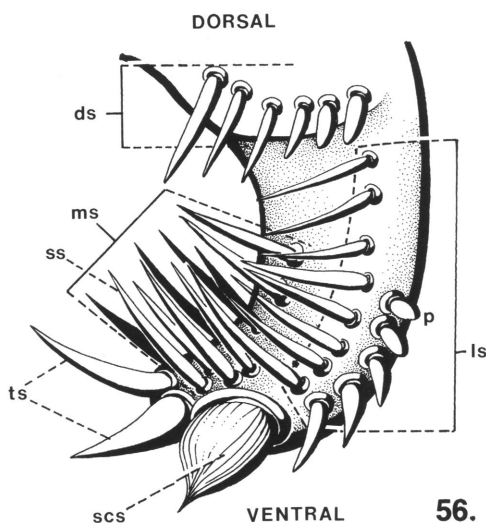
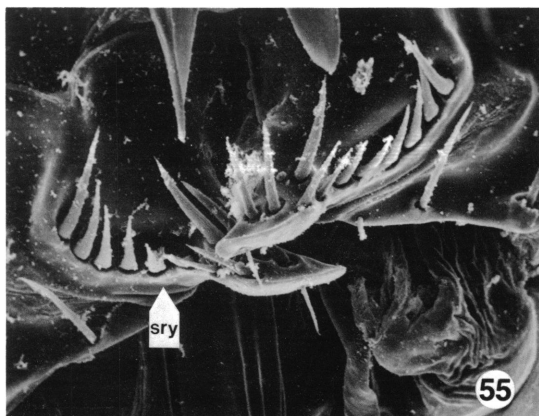
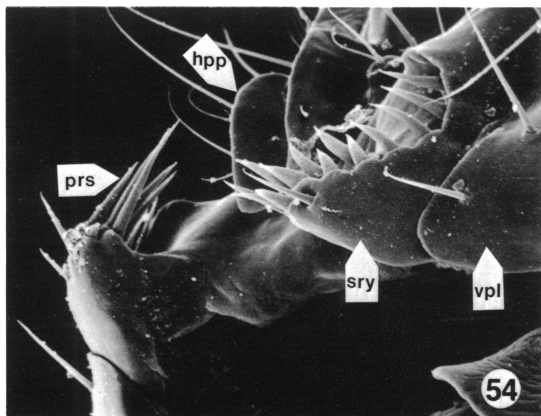
Posteroventral to the epandrium are the paired *surstyli* (*surstylus*, sing.). The pair is joined dorsally by a bridge and appears to reside on a sclerite distinct from the epandrium. The surstyler sclerite may actually be

tergite X or XI. The surstylus bears a diagnostic number and arrangement of *prensisetae* which vary in shape and size. Prensisetae are defined by their shapes (*peg*, *setiform*, *scaliform*) and positions (*laterals*, *medials*, *dorsals*, *terminals*) (fig. 56).

The *genitalia* proper are the appendages associated with the *hypandrium*, or sternite IX. Hypandria vary in size and shape; length is often defined by the distance which the anterior margin is extended past the aedeagal apodeme apex. Lateral margins of the hypandrium may be deeply *indented*; the anterior margin may be *simple*, *cleft*, *tapered*, or possess a distinct *lobe*. The *posterior margin* may be *simple*, or possess an elongate *process* (the “aedeagal guide”). The apex of the posterior hypandrial process may be



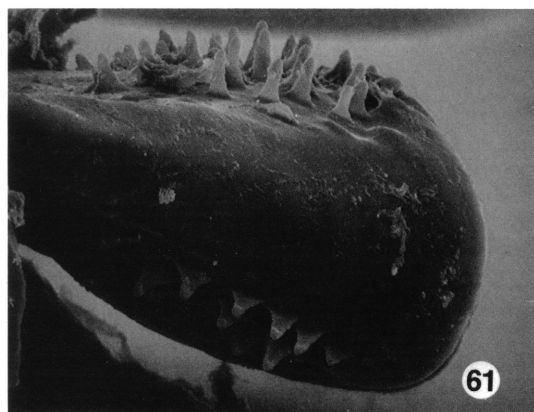
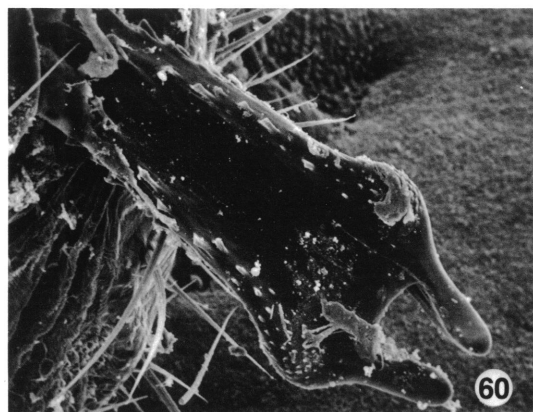
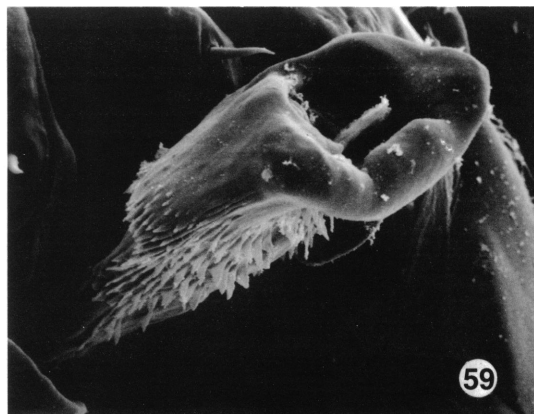
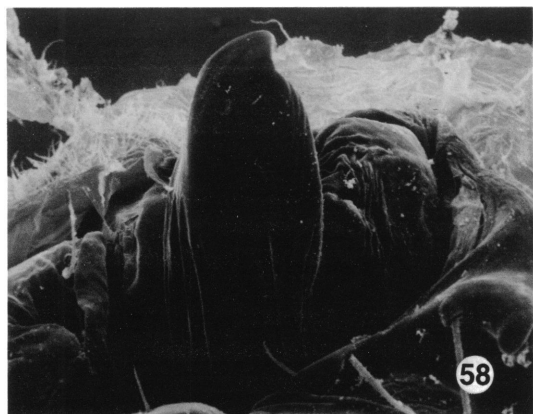
Figs. 52, 53. Male *Zygotherica* terminalia, shown as a mosaic with most of the apomorphies seen among species. 52. Epandrium (tergite IX) and associated structures, posterolateral view. **ce**, cercus; **ep**, epandrium; **hpp**, hypoproctal plate; **hps**, hypoproctal spine (and setulae); **prs**, prensisetae; **sry**, surstylus (shown here as pendulate); **vcl**, ventral cercal lobe; **vpl**, ventral epandrial lobe(s). 53. Hypandrium (sternite IX) and associated appendages, ventrolateral view. **aa**, aedeagal apodeme; **ahl**, anterior hypandrial lobe; **ds**, distiphallus; **dss**, distiphallal scales; **end**, basiphallus; **gs**, gonopod setulae; **gw**, gonopod wrinkles; **hyp**, hypandrial plate, or hypandrium; **lg**, lateral gonopod; **li**, lateral indentation (of hypandrium); **mg**, median gonopod; **php**, posterior hypandrial process; **py**, paraphysis; **pys**, paraphysial seta (and setulae).



Figs. 54–57. Details of surstyli (male). **54.** *Zygothrica dispar* (720 $\times$), posterolateral view. **55.** *Zygothrica* sp. near *poeyi* (NICARAGUA) (760 $\times$), posterior view. **57.** *Mycodrosophila claytonae* (NEW YORK) (463 $\times$), posterior view. Abbreviations are the same as in figure 52. **56.** Mosaic of *Zygothrica surstyli*, showing many apomorphic features of the prenisetae. **ds**, dorsal prenisetae; **ls**, lateral prenisetae; **ms**, medial prenisetae; **p**, peg; **scs**, scaliform preniseta; **ss**, setiform preniseta; **ts**, terminal preniseta.

rounded, bifurcate, trifurcate, or, if very pointed, lanceolate. Posterolateral portions of the hypandrium are lobate and represent the gonopods. Generally, only the fleshy, lobate pair of median gonopods is present, but a more sclerotized, slender, lateral pair can exist. The ventral surface of the median gonopods may be smooth, wrinkled, finely scaled, or possess a vestiture of very fine spicules.

Medial to the gonopods are the paraphyses (which may be homologous to the parameres of Hymenoptera and Coleoptera). The posterior apex of each paraphysis usually possesses one stout seta pointed posteriad (the paraphysial seta), and the medial surface has three to five finer, short paraphysial setulae. Articulated with the anterior end of the paraphyses and the basiphallus is the aedeagal



Figs. 58–61. *Zygothrica distiphalli*. 58. *Zygothrica* sp. near *poeyi* (NICARAGUA) (760 $\times$), ventral view; showing the glabrous surface. 59. *Z. prodisar* (940 $\times$), ventral view; showing the densely scaled surface. 60. *Z. orbitalis* (590 $\times$), dorsal view; this species possesses a lightly scaled and pronged distiphallus. 61. *Z. pallida* (1510 $\times$), lateral view; showing the densely scaled dorsal and ventral surfaces.

apodeme. The apodeme appears to vary interspecifically in size and shape, but was not used in the phylogenetic analyses because of its minute size and difficulty in providing a standard orientation.

The *aedeagus* is composed of the *basiphallus* (the shaft), and the *distiphallus* (the apical, enlarged portion, which bears the *gonopore* and usually some vestiture). If the basiphallus is elongate, it may also be *arched*

to varying degrees. *Dorsal spines* can occur on the basiphallus which vary in size, shape, and position. Structure of the distiphallus usually varies tremendously among species in shape, degree of sclerotization, size, and type and amount of vestiture. Vestiture may be *spiculate*, *scalate* (figs. 59–61), or the distiphallus can possess *spines* or be *glabrous* (fig. 58).

BREEDING SITES

Considering the species diversity of *Zygothrica*, hardly anything is known of the hosts in which they breed. All breeding records are presented in table 1. About 16 species of

Zygothrica are included in the table, and for only about 3 of them was fungus found as a larval feeding site. Even J. B. Carpenter's records of *Z. apopoeyi* and *Z. prodisar* may be

TABLE 1
Known Breeding Sites of *Zygothrica*

Species	Host	Number	Location	Ref.
<i>abbrevidispar</i> , n. sp.	<i>Dimerocostus</i> sp.	2♀, 8♂	PANAMA: Piña, Ft. Sherman Preserve	1, 2
	<i>Costus splendens</i>	1♂	PANAMA: Bocas del Toro, Almirante	1, 2
<i>aldrichii</i>	<i>Costus splendens</i>	1♀	PANAMA: Bocas del Toro, Almirante	1, 2
<i>amplialdrichi</i> , n. sp.	<i>Heliconia subulata</i>	1♀	PANAMA: Cerro Campana	1, 2
<i>andea</i> , n. sp.	<i>Heliconia</i> sp., nr. <i>latispatha</i>	2♂	PERU: Madre de Dios, Rio Tambopata	2
<i>apopoeyi</i>	"ex: fungus"	3♀, 3♂	COSTA RICA: Siquirres	2
<i>centralis</i> , n. sp.	"bred: <i>Calathea violacea</i> "	5♀, 3♂	PANAMA: Barro Colorado Island	2
<i>dispar</i>	<i>Brunfelsia excelsa</i>	— —	BRAZIL: Rio de Janeiro	3, 2
<i>florinjecta</i> , n. sp.	<i>Salvia rubescens</i>	12♀, 14♂	COLOMBIA: nr. Bogotá	4, 2
<i>laevifrons</i>	<i>Collybia</i> sp. (Tricholomataceae)	4♀, 6♂	PERU: Madre de Dios, Rio Tambopata	2
<i>neolinea</i> , n. sp.	<i>Centropogon</i> sp.	5♀, 5♂	PANAMA: Cerro Campana	1, 2
	<i>Passiflora</i> sp.	3♀, 2♂	PANAMA: Cerro Campana	
	<i>Aphelandra micans</i>	2♀	PANAMA: Cerro Campana	
<i>pallida</i> , n. sp.	<i>Dimerocostus</i> sp.	4♀, 1♂	PANAMA: Piña, Ft. Sherman Preserve	1, 2
	<i>Dimerocostus uniflorus</i>	7♀, 2♂	PANAMA: Bocas del Toro, Almirante	1, 2
<i>prodispar</i>	"bred: white toad stool"	5♀, 2♂	PANAMA: Trinidad Riv.	2
	"ex: fungus"	4♀, 3♂	COSTA RICA: La Francia	2
	"ex: fungus"	3♀, 9♂	COSTA RICA: Siquirres	2
	"bred: <i>Calathea violacea</i> "	1♂	PANAMA: Barro Colorado Island	2
<i>vittimaculosa</i>	<i>Cestrum intermedium</i>	5♀, 5♂	BRAZIL: São Paulo, Santa Isabel	5
<i>zygia</i> , n. sp.	<i>Heliconia</i> sp.	1♀	COLOMBIA: Leticia	1, 2
n. sp., nr. <i>pallidipoeyi</i>	<i>Hedychium</i> sp.	12♀, 6♂	PANAMA: Cerro Campana	1, 2
	<i>Aphelandra micans</i>	1♀	PANAMA: Cerro Campana	1, 2
sp(p).	"reared from fungus"	— —	BRAZIL: Caxias do Sul	6

References: 1. Pipkin et al., 1966; 2. Grimaldi, new record and/or from museum specimen labels; 3. Malogolowkin, 1952; 4. Heed et al., 1960; 5. Vilela, 1984, and personal commun.; 6. Cordeiro, 1952.

suspect since the specimens are labeled "ex: fungus," that may not mean reared from fungus, but caught as adults on fungus. Clearly there is a fundamental need for surveying possible breeding sites for *Zygothrica*, but it can be assumed at present that the fungal aggregation sites, where adults are so numerous, are usually not the breeding sites. How extensive the distribution of florophagy is throughout the genus is now mostly conjectural. As part of the breeding site surveys there is also a great need for proper labeling and assembling voucher collections. S. B. Pipkin bred many neotropical drosophilids from their natural hosts (see Pipkin et al., 1966), and she assembled a large voucher collection with extensive notes to accompany it. The collection was boxed and stored in the

basement of the Smithsonian Institution: recovery of it allowed me to identify the specimens that she collected and had identified as "*Zygothrica* sp." in her studies.

Flowers, principally bulky and fleshy ones, seem to be the predominant *Zygothrica* hosts. Here, larvae may feed on the reproductive parts (particularly the style) and/or petals and bracts. Ten angiosperm families are included among the florophagous records: Acanthaceae (*Aphelandra*), Campanulaceae (*Centropogon*), Labiatae (*Salvia*), Leguminosae (*Erythrina*), Liliaceae (no other identification), Marantaceae (*Calathea*, fig. 64), Musaceae (including Heliconiaceae, i.e., *Heliconia*, figs. 65–67), Passifloraceae (*Passiflora*), Solanaceae (*Brunfelsia*, *Cestrum*), and Zingiberaceae (*Costus* [fig. 63], *Dimerocostus*, and *He-*



Figs. 62–67. Habitat and hosts of some *Zygothrica* species. **62.** Canopy rain forest, Rio Tambopata Reserve, Madre de Dios, PERU. This is where some observations on behavior were made. **63.** *Costus pulverulentus* (Zingiberaceae), flowering inflorescence. A *Camponotus* ant is visiting nectaries among the bracts (Barro Colorado Island, PANAMA). **64.** *Calathea lutea* (Zingiberaceae), old inflorescence (B.C.I.). **65.** *Heliconia latispatha* (Heliconiaceae), mature inflorescence (B.C.I.). **66.** *Heliconia* sp., also with several attendant ants (Rio Tambopata). **67.** *Heliconia mariae*, a pendulous type of *Heliconia* inflorescence; this one is old and the flowers are decaying (B.C.I.). br, bract; fl, flower.

dychium). In terms of numbers of flies reared, Zingiberales (Heliconiaceae, Marantaceae, Musaceae, and Zingiberaceae) appears to be the most important host taxon. The absence of *Zygothrica* from the Afrotropics is probably not due to a lack of suitable hosts since *Strelitzia* (Musaceae s.l., in the Heliconiaceae of some workers) occurs in Africa. Lastly, in regard to a predominantly florophagous habit

in *Zygothrica* is the repeated evolution and probably functionally related trait of heavily sclerotized, narrow, and elongate oviscaptes: such an oviscape modification appears in the *Drosophila flavopilosa* species-group and in *Zapriothrica*, both of which are known to breed only in flowers. Mycophagy in *Zygothrica* represents a retention of the primitive habit seen in its sister-groups, *Mycodro-*

sophila and the subgenus *Hirtodrosophila* of *Drosophila*.

One undescribed drosophilid reported in several papers (Villa, 1980, 1985) and reviewed as part of another paper (Ashburner, 1981) is not a species of *Zygothrica* but a member of the *Drosophila* (*H.*) *thoracis* species-group. Larvae of this fly have been found in Costa Rica and Nicaragua feeding on embryos of the tree frogs, *Centrolenella*, *Agalychnis* (Centrolenellidae), and *Hyla* (Hylidae). This taxonomic conclusion is based on the following synapomorphies that the species possesses: a low, sharp carina; a posteroventral row of ovisensilla with an apical gap; a bulbous, spiculate distiphallus; an an-

terior hypandrial margin which is squared; and a broad, dark pleural band (see section under diagnosis of *Zygothrica*). The only plausible hypothesis is that the frog predator evolved from a mycophagous ancestor; such a phyletic quantum leap tempts further studies such as the ones by Villa (1985) on alternative rearing substrates for the anurophage.

Unfortunately, lab studies on *Zygothrica* will not be easy, for the flower-breeding drosophilids are difficult to culture on various standard media. Malogolowkin (1952) had no success breeding *Z. dispar* on standard banana medium, and I was able to breed only a few individuals of *Z. prodyspar* on banana media.

IMMATURES

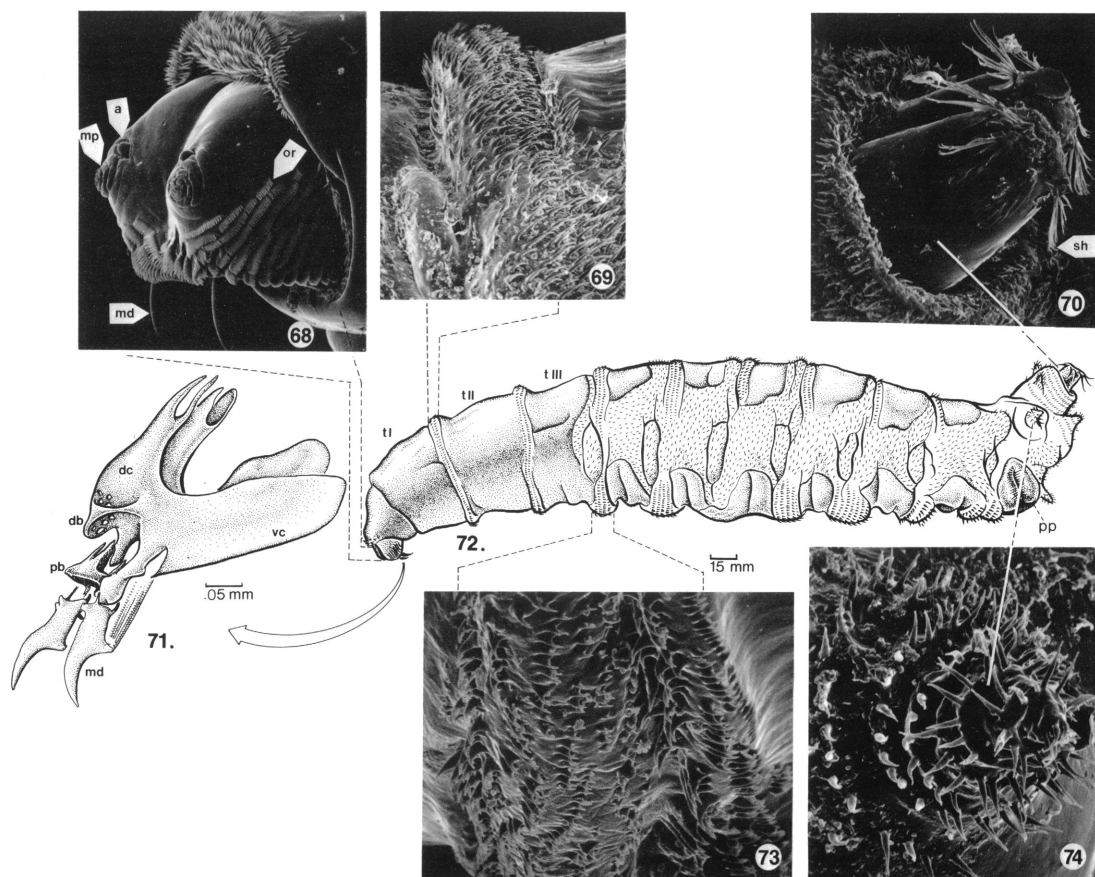
Larvae of *Zygothrica prodyspar* were obtained at Tambopata, Peru, by allowing several females to oviposit on several banana media in standard vials for *Drosophila* culture. The flies were very reluctant to lay eggs, and from the six that were found only three developed to an adult. At the same site, *Zygothrica andea* was reared from decaying *Heliconia* bracts and *Z. laevifrons* was reared from a tricholomataceous fungus. These rearings allowed me to associate the immatures of three species with adults. Malogolowkin (1952) found the immatures of *Z. dispar* in *Brunfelsia* flowers (Solanaceae), and she described the gross pupal morphology of the species.

The larva of *Zygothrica prodyspar* is unusual for the Muscomorpha (figs. 68–74), for the cephalic segment and the thoracic segments are smooth and sclerotized (fig. 72). Also, the hypopharyngeal sclerite is fused to the tentorial phragma (fig. 71; cf. fig. 88) and the dorsal cornua is bifurcate (fig. 71). In most other features, however, it is a “standard” drosophiline larva: there are 13–14 oral ridges that are finely lamellate (fig. 68; cf. figs. 89, 91); the mandibles have an even ventral margin (no serrations are present—at least in the third instar) (fig. 71; cf. figs. 87, 88); and the spinule folds (fig. 69), posterior spiracles (fig. 70; cf. fig. 86), lateral caudal tubercles (fig. 74), perianal pads, and creeping welts (fig. 73)

are unmodified. Figures 75–78 show the puparium of this species. Phylogenetically, the most important structures seen in the pupa are the anterior spiracles. Twenty-three to 25 anterior spiracular filaments are present, and their lengths are approximately equal to the length of the spiracle trunk. The spiracular filament endings are pointed and slightly hooked and possess slitted openings (fig. 77).

From the eclosed puparia of *Zygothrica laevifrons* and *Z. andea* were extracted portions of the cephalopharyngeal skeleton (the parastomal bar and hypopharyngeal sclerite could not be removed intact). *Zygothrica laevifrons* possesses the uniramous, primitive type of dorsal cornua (fig. 81), and the ventrally serrate, primitive type of mandible (fig. 80). Eight to nine filaments are on the anterior spiracles (fig. 79), which is a primitive condition, too, for this structure. *Zygothrica andea*, however, possesses a mandible having the hook with a smooth ventral edge (as in *Z. prodyspar*) but serrations are present on an oblique ventral edge (fig. 83). Also like *Z. prodyspar*, the dorsal cornua is bifurcate (fig. 84). The anterior spiracles are unusual: 35–40 filaments are present, which is the greatest number known in a drosophilid. The fine structure of the anterior spiracular filaments is the same in the three *Zygothrica*.

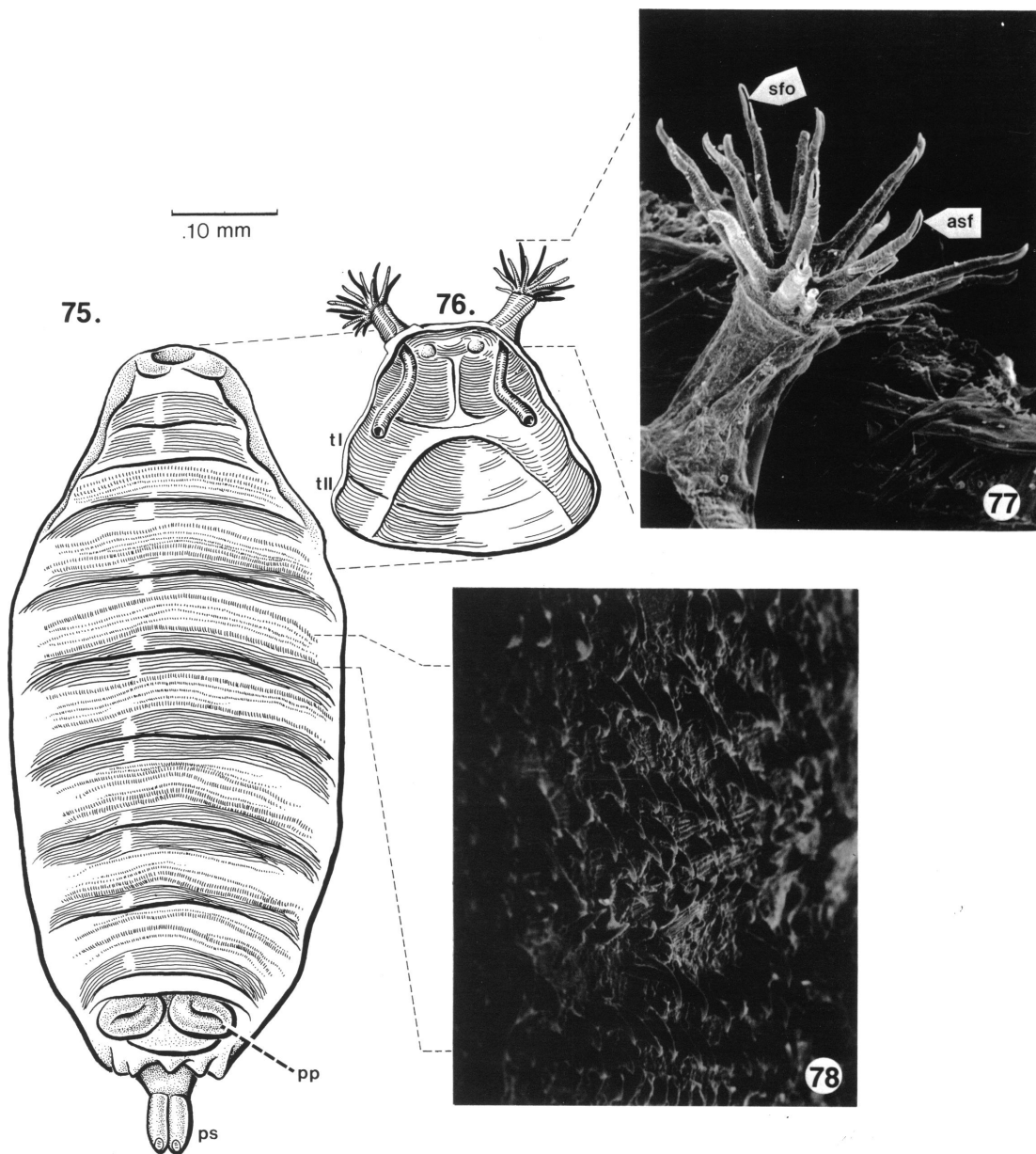
Compared to *Drosophila* (*Hirtodrosophi-*



Figs. 68–74. *Zygothrica prodispar*, instar III. 68. Cephalic segment (430×). 69. First dorsal spinule fold, lateral view (520×). 70. Posterior spiracles, lateral view (520×). 71. Cephalopharyngeal skeleton. 72. Larval habitus, left lateral aspect. 73. Creeping welt III, lateral view (960×). 74. Lateral caudal tubercle, posterior view (830×). a, antenna; db, dorsal bridge; dc, dorsal cornua; md, mandible; mp, maxillary palp; or, oral ridges; pb, parastomal bar; pp, perianal pad; sh, spiracular hairs; t I–III, thoracic segments I–III; vc, ventral cornua.

la), which generally have 5–15 anterior spiracular filaments (Okada, 1968; e.g., fig. 85), the large number of spiracular filaments seen in immatures of *Zygothrica prodispar*, *Z. dispar*, and *Z. andea* might be a synapomorphy. Synapomorphic for these three *Zygothrica* also, and for *Z. laevifrons*, may be the possession of pointed, hooked, spiracular filament openings, since *Hirtodrosophila* possess rounded filament endings and openings (fig. 85). Virtually all drosophilids have third instar larvae with ventrally serrate mandibles; so, at the generic level, I consider this state a primitive one for *Zygothrica*. It is interesting that mandibular ventral serrations have

been lost in the third instar of *Drosophila* (*H.*) *duncani* from the second instar (figs. 87, 88). Absence of serrations in instar III may be a result of mandibular peramorphosis, or accelerated development. Nevertheless, an even ventral margin on the mandibles and a bifurcate dorsal cornua can tentatively be considered as synapomorphies for *Z. prodispar* and *Z. andea*, but many more species need to be examined to determine the taxonomic level at which these are *Zygothrica* innovations. One interesting result of the larval comparisons is the discovery of the modified state of *Mycodrosophila* oral ridges (fig. 90) as being very coarsely lamellate.

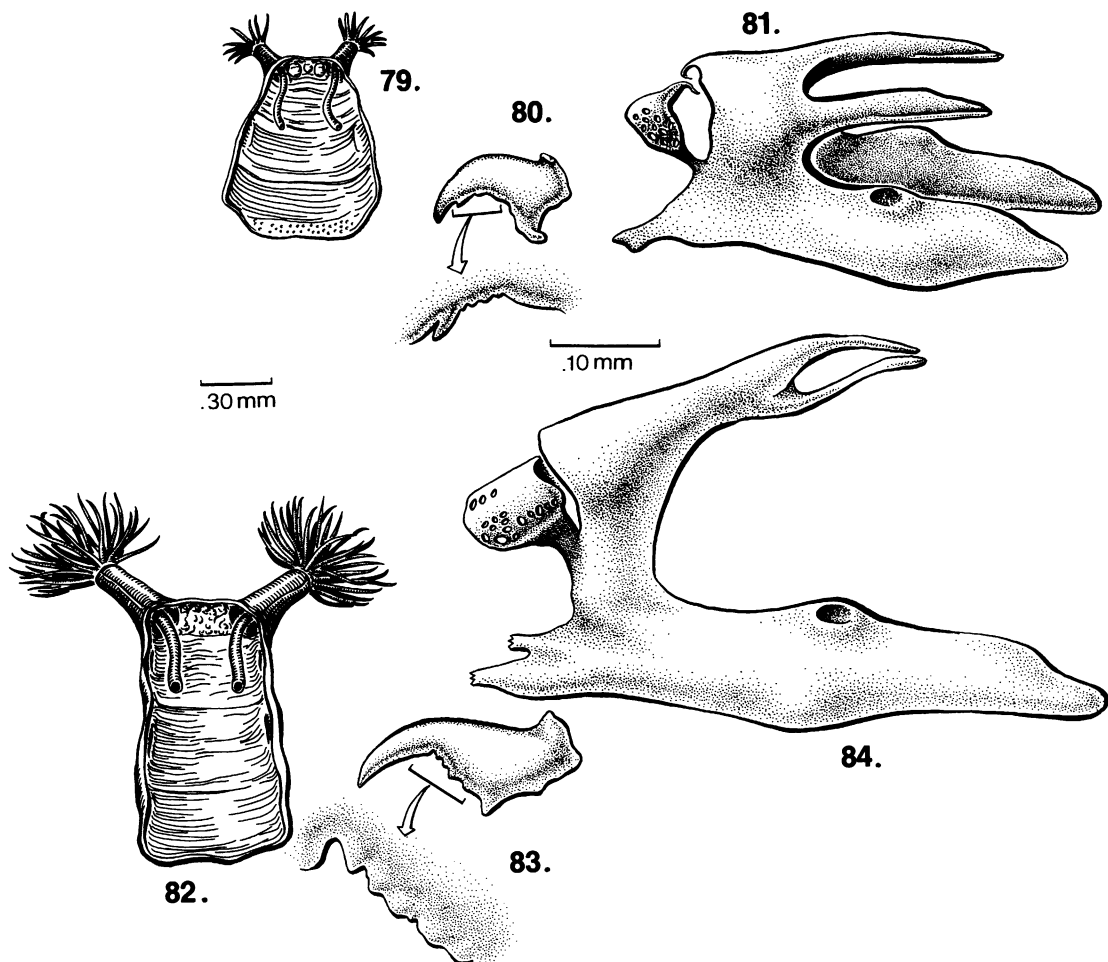


Figs. 75–78. *Zythrica prodispar* puparium. 75. Ventral habitus. 76. Dorsal eclosion sclerite (internal view), showing attached tracheae. 77. Anterior spiracle (255 $\times$). 78. Creeping welt III (1110 $\times$). asf, anterior spiracular filament; ps, posterior spiracle; sfo, spiracular filament opening. Other abbreviations as in figures 68–74.

ADULT AGGREGATIONS

METHODS: Observations were made from 19 September to 10 October 1984 at Rio Tambopata Nature Reserve, Madre de Dios,

Peru, and from 16 February to 15 March 1985 at Barro Colorado Island, Panama. The Peru site was in a mature lowland (940 m)

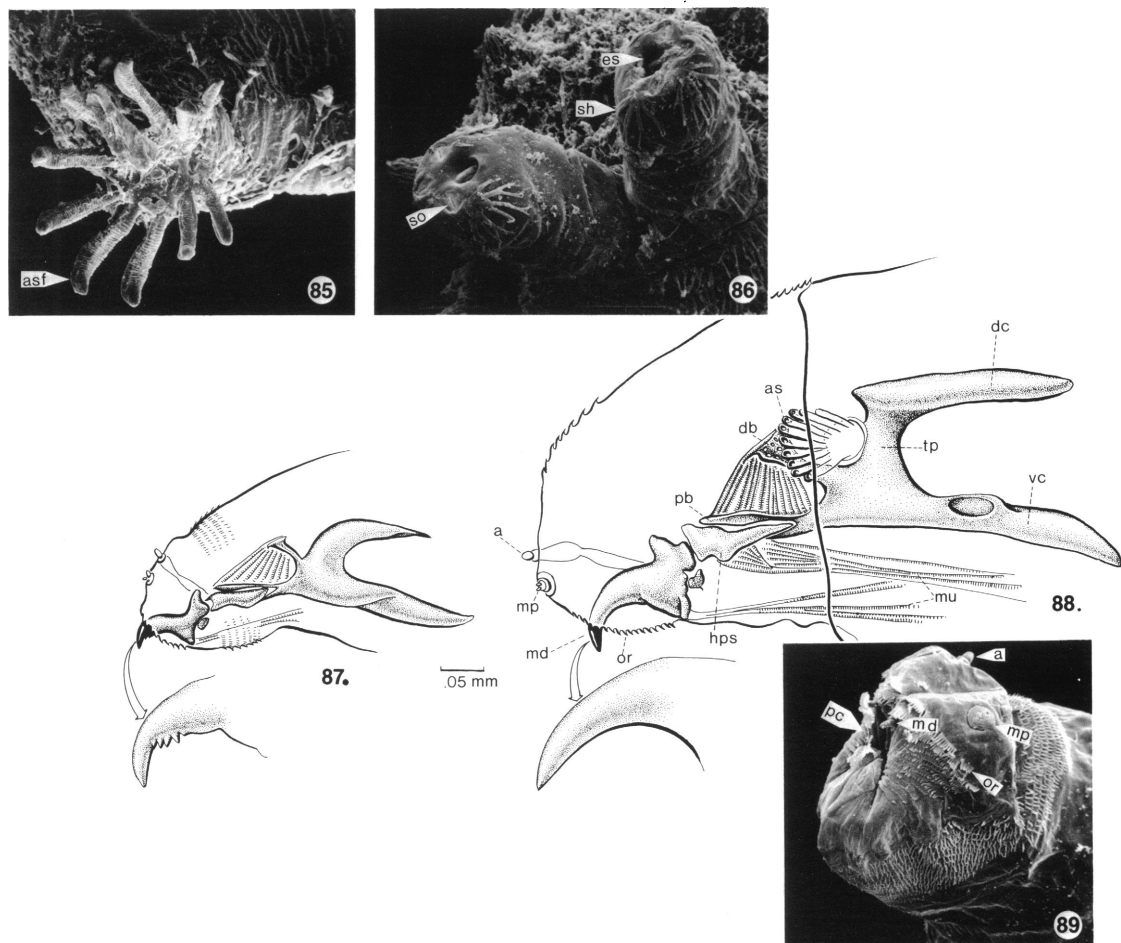


Figs. 79–84. Portions of *Zygothrica* puparia. 79–81. *Z. laevifrons*, dorsal eclosion sclerite (79), mandible with detail of ventral serration (80), and posterior portion of cephalopharyngeal skeleton. 82–84. *Z. andea*, dorsal eclosion sclerite (82), mandible with detail (83), and posterior portion of cephalopharyngeal skeleton (84).

habitat located in a southern peninsula of Amazonian inundation forest (fig. 62). Barro Colorado Island's forest is mostly old secondary tropical rain forest. Voucher specimens of fungi were prepared by first obtaining a spore print (crucial in the identification of most forms, especially polypores), and then by drying the fungus at 45°C for about two days. As someone only moderately acquainted with mycology, I have found that the two most useful references for neotropical fungus identification to be Dennis (1970) (general) and Ryvar den and Johansen (1980) (polypores). The aid of expert mycologists cannot

be underestimated, and I am very grateful to Drs. Leif Ryvar den and Thomas Lowry for their identifications of the polypores and *Auricularia*, respectively. Voucher specimens of fungi are deposited in the mycological collections at the Botanisk Institutt, Universitet Oslo, Norway (Polyporaceae), Louisiana State University, Baton Rouge (Auriculariaceae), and the Cornell University Herbarium (all forms).

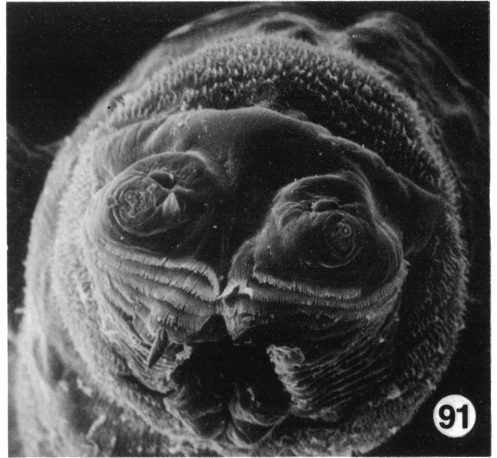
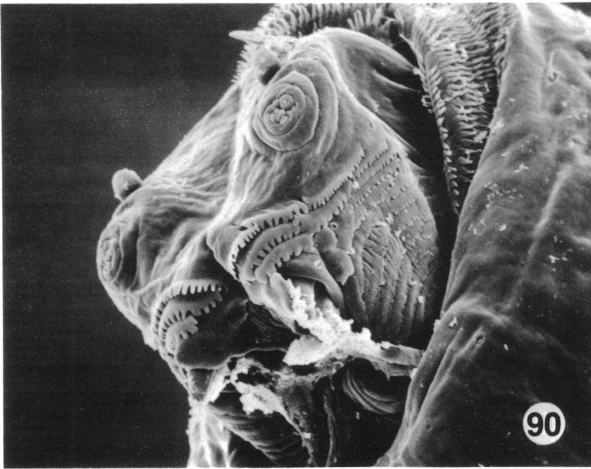
RESULTS: Two types of *Zygothrica* rendezvous sites were apparent: white, fleshy, imbricate ("bracket," or "shelf") forms of Polyporaceae and Tricholomataceae, and the



Figs. 85–89. *Drosophila (Hirtodrosophila) duncani*, portions of immature stages. **85.** Anterior spiracle, pupa, anterior view (560 $\times$). **86.** Posterior spiracle, larval instar III (560 $\times$), posterior view. **87.** Cephalopharyngeal skeleton, instar II, lateral view. The anterior portion of the mandible is enlarged to show the ventral serration (lost in instar III). **88.** Head and cephalopharyngeal skeleton, instar III. **89.** Anterior portion of cephalic segment, instar III (418 $\times$). Abbreviations are the same as in figures 68–78, plus the following: **as**, anterior spiracle; **es**, ecdysial scar; **hps**, hypopharyngeal sclerite; **mu**, muscle; **pc**, preoral cavity; **so**, spiracular opening; **tp**, tentorial phragma.

gelatinous *Auricularia* species (Auriculariaceae). In Peru, for example, 28 common polypore species were collected, which belong to the following genera: *Amuroderma*, *Antrodiella*, *Coriolopsis*, *Cymatoderma*, *Datronia*, *Gloeoporus*, *Hexagonia*, *Microporus*, *Phellinus*, *Polyporus*, *Trametes*, *Trichaptum*, and *Tyromyces*. Their texture varies considerably: *Microporus* is denser than many woods, while some others have flaccid and delicate tissue. *Polyporus tricholoma* was the only

polypore in Peru found attracting the flies. An unidentified genus of Tricholomataceae was also found to attract substantial numbers of drosophilids, and its off-white color and soft texture closely resembled that of *P. tricholoma*. *Auricularia delicata*, the only species of the genus found at the Peru site, was likewise an attractive site for *Zygothrica* (figs. 102–104). *Auricularia*, however, possess neither pores nor gills (they are Heterobasidiomycetes); and *A. delicata* is red-brown,



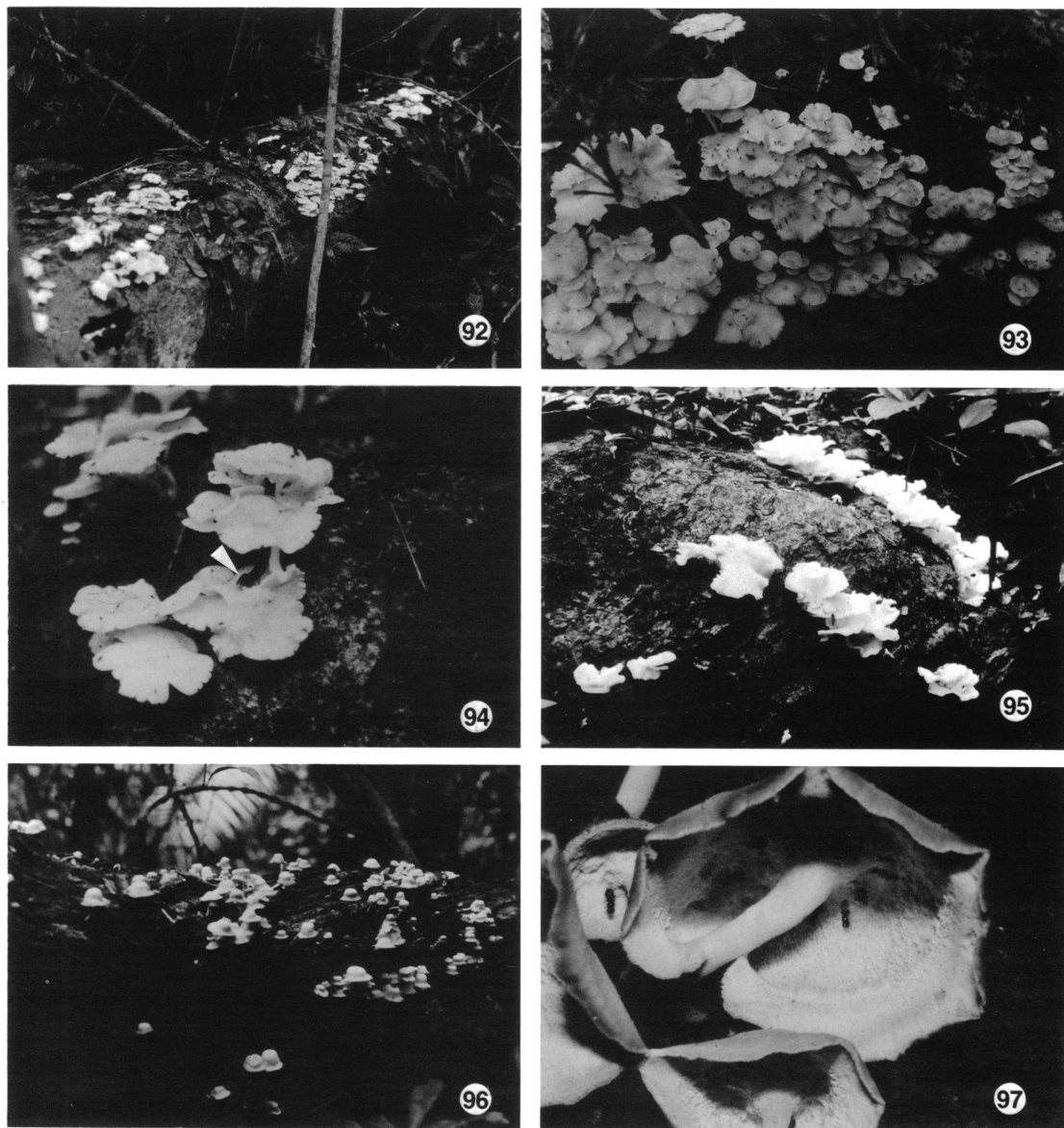
Figs. 90, 91. Anterior views of instar III cephalic segment of 2 drosophilids. **90.** *Mycodrosophila claytonae* (NEW YORK) (630 $\times$). Note the very coarse lamellae on the oral ridges compared to the ones in figures 68, 89, 91. **91.** *Drosophila (D.) putrida* (530 $\times$).

rubbery to gelatinous in texture, sweet-smelling, and the hymenial (under, or spore-producing) surface is rugose and, when the fungal bloom was found, it was producing copious beads of amber exudate and amounts of spores on which the drosophilids constantly grazed. Dissections of 10 crops each of *Zygothrica vittinubila* and *Z. tambopata* revealed that they were feeding on spores and hyphal fragments, which they probably rasped up with tiny pseudotracheal spines, and on the exudate.

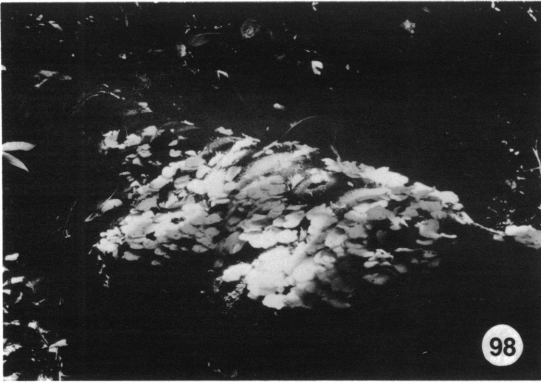
In Panama, 68 species of fungi were collected, 32 of which were Polyporaceae. Polypores that attracted clouds of *Zygothrica* and other drosophilids were *Polyporus tricholoma* and *Favolus brasiliensis* (figs. 92–94, 96–97), which are both off-white in color and fleshy. *Pleurotus* sp. was a white, imbricate Tricholomataceae that was found to be a rendezvous site for *Hirtodrosophila* and *Mycodrosophila*, but not for *Zygothrica*. *Gymnopilus* sp. (Cortinariaceae) was the most unusual mating site found. It is a stipitate, tan mushroom, and attracted in great numbers only *Zygothrica orbitalis* (fig. 105). Three *Auricularia*, *A. polytricha*, *A. fuscossuccinea*, and *A. delicata*, were found in moderate to great abundance, but only the last attracted drosophilids.

Another feature of the *Zygothrica* aggregations is the size of the sporophore blooms where they occurred. Except for the *Gymnopilus* site, where only six sporophores were found, blooms with at least 50 to generally several hundred sporophores appeared to be the most attractive sites for the flies. Thousands of flies, comprising 1–21 species of Drosophilidae, occur at the aggregation sites, and the great majority of them were always *Zygothrica*. Generally, the flies were evenly distributed on the freshest pilei, a situation probably reinforced by territoriality in some species (figs. 93, 100). Site tenacity of *Zygothrica* is quite marked, which is also probably due to territoriality: always after sweeping over a fungus bloom, most of the flies that I had missed netting had returned to the pilei within 10 seconds or so.

The dense drosophilid aggregations seemed to attract various predators. A small mantid, two individuals of a *Colostethus* sp. (Dendrobatidae: Anura) (fig. 94), a reduviid, and several Staphylinidae were seen preying on the drosophilids at the *Polyporus tricholoma* sites in Peru. The staphylinids were voracious: with darting movements they each ambushed several drosophilids in a period of about 10 minutes. This behavior was also observed in Panama.



Figs. 92–97. Adult *Zygothrica* aggregation sites. **92.** Bloom of *Polyporus tricholoma* (Polyporaceae) (Tambopata, PERU). This crop lasted 3 weeks before completely drying up, and the freshest sporophores always attracted several species of drosophilids. During a one-week period and among thousands of flies that were captured on these fungi, 9 species of *Zygothrica* and 4 other drosophilids were found here. **93.** Close-up of figure 92. Notice the fairly even distribution of mostly *Z. vittinubila* on top of the pilei. Some pilei were numbered with ink for territoriality observations. **94.** Close-up of figure 92. Arrow points to a *Colostethus* sp. (Anura: Dendrobatidae). The frog remained on the pileus for several hours while snapping up drosophilids. **95.** *Favolus brasiliensis* (Polyporaceae) (Barro Colorado Island, PANAMA). Found at this site were 10 species of drosophilids, 6 of which were *Zygothrica*. **96.** *Polyporus tricholoma* (B.C.I.) growing on a log about 2.5 m above the ground. *Zygothrica orbitalis* was the most common fly on the fungus. **97.** Close-up beneath some sporophores in figure 96. Six *Mycodrosophila nigropleura* are in the photograph; they were very inactive. *Mycodrosophila* spp. were the flies second in abundance to *Zygothrica* at this bloom of *P. tricholoma*.



Figs. 98–101. Adult *Zygothrica* aggregations (Barro Colorado Island). 98. Bloom #2 of *Favolus brasiliensis* (Polyporaceae) growing on a decaying log. 14 drosophilid species aggregated here, 10 of them *Zygothrica*. 99–101. Close-up of figure 98, showing aggregations. Some courting males are seen in figures 100 and 101.

MAJOR PHYLOGENETIC PATTERNS: MORPHOLOGICAL CHARACTERS

In table 2 are the *Zygothrica* that were examined for an analysis of higher relationships in the genus. Names followed by “n. sp.” are species described in this paper. Superscripts (1–4) in table 2 are species treated below that have several names associated with them, as determined from the examination of the holotypes.

1. *Zygothrica* “*atriangulata*”

Zygothrica atriangula: Burla, 1956: 253. This species was misidentified by Burla and will be treated in the next paper.

2. *Zygothrica bilineata*

Drosophila bilineata Williston, 1896: 409 (BMNH).
Zygothrica gemma Burla, 1956: 2249 (ZMUZ).
NEW SYNONYMY.

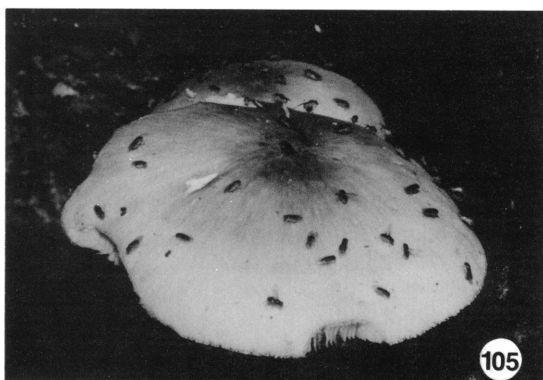
3. *Zygothrica laevifrons*

Zygothrica laevifrons Duda, 1927: 56 (SMTD).
Zygothrica poeyi: Burla, 1956: 235.

4. *Zygothrica orbitalis*

Drosophila orbitalis Sturtevant, 1916: 336 (NMNH).
Zygothrica nitidifrons Duda, 1927: 55 (SMTD).
NEW SYNONYMY.
Drosophila ochracella Hendel, 1936: 98 (NHMW).
NEW SYNONYMY.
Zygothrica parilis Burla, 1956: 220 (ZMUZ). NEW SYNONYMY.

The following list includes the character states used in the phylogenetic analysis. Those with an asterisk appear two or more times in the cladograms, and they perhaps deserve closer examination in order to test and refine



Figs. 102–107. Adult aggregation sites of some drosophilids. 102–104. *Auricularia delicata* (Tam-bopata, PERU). **102.** Bloom of about 50 sporophores growing on a decaying log. **103.** Top surfaces of some sporophores in figure 102. Note absence of flies. **104.** Hymenial (lower) surface of sporophores in figure 103, showing dense aggregation in center. 21 species of Drosophilidae were netted from the fungi over a 3 day period, 15 of which were *Zygothrica*. **105.** *Gymnopilus* sp. (Cortinariaceae) (Barro Colorado Island, PANAMA). The flies seen here are mostly *Zygothrica orbitalis*, which constantly ran about bumping into each other while flicking their wings. **106.** Eastern North America deciduous (beech-hemlock) forest (Ithaca, NEW YORK), a common habitat for mycophagous drosophilids. **107.** *Polyporus squamosus* (Polyporaceae), growing on a log in the woods in figure 106. This is an abundant, cosmopolitan basidiomycete, and is the common host of mycophagous drosophilids in the area. Two to three *Mycodrosophila* species frequent the fresh sporophores, and 5–6 *Drosophila* species (only 3–4 of which are abundant) are found on the older sporophores.

their synapomorphic definitions. The number of each synapomorphy in the list corresponds to those on the cladograms in figures 108–113.

Quotation marks denote a species to be described in a subsequent monograph on *Zygothrica*, and their use here is simply to allow easy reference for the future work. Even though in quotations, such latinized epithets may be, by strict definition of ICZN rules, valid epithets. The names are available because, should one be diligent enough, a diagnosis (Article 13i; ICZN, 1985) could be rescued from the apomorphies on the cladograms. However, no types have been designated for these undescribed species (Recommendation 73 A; ICZN, 1985). For purposes of nomenclatural stability, this publication should not serve as the official source of the species names enclosed within quotations.

- 1. Ovisensilla. A = large, peglike, heavily sclerotized (P = ovisensilla setiform).
- 2. Facial carina. A = prominent, projected to level of anterior margin of flagellomere I; very flat and broad (P = face flat, or carina a slight swelling on dorsal region of the face).
- 3. Aggregation sites. A = mycophilous, especially at imbricate polypores and tricholomataceous fungi (P = at decaying fruits and/or vegetation).
- 4. Arista. A = 1–2 ventral branches (P = 3–5 ventral branches).
- 5. Vibrissa(e). A = 1 per side, subtended by small subvibrissal setulae (P = 2 large vibrissae per side, with subvibrissal setulae gradually decreased in size).
- 6. Notum. A = in lateral view, outline rounded (P = slope of scutellum almost continuous with that of notal slope).
- 7. Subcostal breaks. A = extended and darkened into lappets (P = break point hyaline, or at least with no extensions).
- 8. Oviprovector vestiture. A = extensive scaling, covers 80–90% of the eversible portion of membrane (P = scales small, very sparse, or absent).
- 9. Proboscis. A = prognathous; sclerotized labium is not completely retracted within peristomal margin of cranium (P = labella,

TABLE 2
Species of *Zygothrica* Examined for Higher-Level Cladistic Analysis

<i>aldrichii</i>	"ordinaria"
"aliunota"	"orientalis"
<i>ampli aldrichi</i> , n. sp.	"ovifissa"
<i>antedispar</i> , n. sp.	<i>oviserrata</i> , n. sp.
<i>atriangula</i>	<i>paraptilialis</i>
"atriangulata" ¹	"parasemistriata"
<i>bilineata</i> ²	<i>perplexa</i> , n. sp.
<i>bilinefilia</i> , n. sp.	<i>peruviana</i> , n. sp.
<i>celsa</i> , n. sp.	<i>poeyi</i>
<i>circumveha</i> , n. sp.	"postidens"
"densivisua"	<i>prodispar</i>
<i>dispar</i>	<i>samoensis</i>
"dominicana"	<i>sectipoeyi</i>
<i>femina</i> , n. sp.	<i>semistriata</i>
"fjiana"	"signis"
"flavifrons"	<i>spiculirostris</i>
<i>florinjecta</i> , n. sp.	<i>subcandens</i>
<i>fuscalata</i> , n. sp.	<i>tenuirostris</i>
<i>fuscina</i>	<i>venustipoeyi</i>
"hebe"	<i>virgatalba</i>
<i>hy pandriata</i>	<i>virgatinigra</i>
"hypophallus"	<i>vittatifrons</i>
"insularis"	<i>vitticlara</i>
<i>laevifrons</i> ³	<i>vittimaculosa</i>
<i>lanceolata</i>	"vittinova"
<i>laticeps</i>	<i>vittinubila</i>
"malaysiana"	"wau"
<i>microstoma</i>	<i>zonata</i> , n. sp.
<i>orbitalis</i> ⁴	<i>zygopoeyi</i>

1–4: For explanation of these superscripts, see text.

- when proboscis is completely retracted, hidden beneath oral margin).
- 10. Proboscis. A = narrowed, length 3–4 × width; joint between mentum and distal portion of cibarium acutely angled when proboscis is retracted (P = proboscis thick, mental-cibarial joint not conspicuous).
 - 11. Flagellomere I. A = setulae, especially on apex, are elongate, 4–5 × length of ground setulae (P = even, close covering of setulae is present).
 - 12. Ovisensilla. A = gap between distal most sensilla and dorsal ones (P = row of evenly spaced ovisensilla, dorsal to ventrad).
 - 13. Face. A = oral margin with medial cleft (P = margin straight, or slightly excavated).
 - 14. Facial carina. A = prominent, with

sharp or slightly rounded edge (P = carina much smaller, or flat).

15. Ocellar triangle size. A = large, extended to beyond proclimates or to ptilinal fissure; greatest width about $3 \times$ width between outer ocelli (P = triangle small, not extended beyond anterior reclimates, much narrower).

16. Distal shape of oviscape. A = laterally flat, apically truncate; ovisensilla row on vertical edge (P = oviscape tapered apicad in lateral view; ovisensilla evenly distributed on margin).

17. Shape of facial carina. A = very narrow, width at base barely exceeds width at edge (P = carina gradually tapered toward rounded edge).

18. Width of face. A = very narrow, width about equal to distance between lateral surfaces of antennae (P = face much broader, width about $1\frac{1}{2}$ – $2 \times$ this distance).

*19. Abdominal vestiture. A = ground setulae lost, abdomen very shiny (large setae are still present) (P = ground setulae intact, or lost in some terminal tergites).

20. Wing shape. A = paddle-shaped; apex rounded, costal and anal edges gradually converged (P = costal edge relatively straight, tip with more acute curvature, anal area not reduced).

21. Ventral epandrial lobes (δ). A = pendulous, elongate, with distinct knob at apex (P = lobe simple, length less than $2 \times$ width).

22. Prensisetae (δ). A = evenly spaced comb of long, thin prensisetae (P = prensisetae varied in shape, surstylus with medial patch of prensisetae).

23. Surstylus (δ). A = elongate, projected ventrad (P = crescent-shaped lobe broadly attached to epandrium).

*24. Exterior surface of spermathecal capsule. A = papillate (P = smooth, or finely and lightly striate). a. entire capsule papillate, b. distal portion papillate.

25. Wing infuscation pattern. A = spot at apex of R_{2+3} , R_1 infuscate from beyond costal break to R_{2+3} (P = wing hyaline).

*26. Prensisetae distribution. A = 2 fields, 1 on apex, other field is dorsal and setae projected ventrad (P = no dorsal prensisetae).

*27. Exterior surface of spermathecal capsule. A = wrinkled (P = smooth/papillate), a. entirely wrinkled, b. apically.

*28. Oviprovector apex. A = with blunt,

heavily sclerotized, enlarged scale projected posteriad (P = apex smooth or scaled).

29. Anterior portion of ♀ sternite VII. A = ramus present, projected beneath S VI to usually s V, narrow (P = S VII simple, without anterior ramus).

30. Ovisensilla on medial margin of oviscape valves. A = lost (P = present).

31. Ocellar triangle size. A = extended, one side borders on ptilinal fissure or at least touches it (P = triangle apex not extended to proclimates).

32. Altitudinal distribution. A = high (≥ 2000 m) altitudes (P = lowland [≤ 1000 m] wet or tropical rain forest).

*33. Cheek depth. A = deep, height $\geq \frac{1}{3}$ height of eye (P = narrow cheek, height $\leq \frac{1}{5}$ height of eye).

*34. Oviscape length. A = elongate, length $4 \times$ or more the width (P = short, length at most $3 \times$ width).

*35. Shape of the oviscape apex. A = spaded, dorsoventrally extremely flattened: ovisensilla only on distolateral edges (P = not dorsoventrally flattened, ovisensilla usually in row on ventral edge).

*36. Facial sclerite shape. A = anterolateral corners splayed, oral margin prominent (P = oral margin not projected outward; height of facial sclerite always less than that of cheek above it).

37. Oral margin. A = possesses "lip" (P = smooth, no prominent edge on oral margin).

*38. Notal coloration. A = paramedian vittae (vitta pair-2) present, light-colored on dark ground color, incomplete (P = thorax evenly pigmented black or dark brown).

39. Frontal-orbital plates, dorsal width. A = broad, width $\geq 3 \times$ width on front (P = width 1 – $2 \times$ that of plates on front).

40. Dorsolateral region of eye. A = tapered, extremely so in males (P = eyes rounded).

41. Wing maculation. A = R_{2+3} spot, dm-cu spot, apical spot, proximal r-m band present (P = wing hyaline, or with diffuse apical infuscation).

42. Alignment of frontal vittae. A = parallel or nearly so; ocellar triangle narrow, extended to ptilinal fissure (P = vittae converge anteriad).

*43. Notal vittae. A = 1 median + 2 paramedian present; distinct, color lighter than or same as pleural ground color, bordered by

dark areas (P = 2 indistinct, incomplete, paramedians, or notum evenly pigmented).

44. Apex of wing. A = possesses discrete spot ("apical spot") between R_{2+3} and M_1 (P = wing hyaline at apex, or lightly and diffusely infusate on apex).

45. Oviprovector apex. A = with 1–3 large, ramphate scales (P = scales in this area undifferentiated).

46. Spermathecal shape. A = apex tapered (P = spermatheca campanulate, or apex rounded).

*47. Spermathecal shape. A = possesses basal collar (P = no collar).

*48. Distiphallal vestiture. A = possesses scales (P = glabrous, or spiculed).

49. Ovisensilla. A = 3 very small pegs present (P = 5 or more pegs present).

*50. Spermathecal shape. A = elongate, length $\geq 3 \times$ width (P = short, length 1–2 $\times$ width).

*51. Posterior margin of hypandrium. A = possesses median, elongate, sclerotized process extended to distiphallus (P = hypandrial margin straight, slightly excavated, or with margin slightly lobate).

*52. Terminal ovisensilla. A = very large, pointed (P = homogeneous in size).

53. Lateral margins of distiphallus. A = roughly serrate (P = smooth, or finely scaled).

54. Oviscape apex. A = short, blunt ovisensilla present (P = ovisensilla pointed, about 3–4 $\times$ size of modified ones).

55. Ventral cercal lobe (δ). A = densely setulose, lobe present (P = no lobe present, scattered setulae may be present).

56. Basiphallus length. A = elongate, greater than 3 $\times$ length of aedeagal apodeme, narrow, strongly arched (P = 1–2 $\times$ length of aedeagal apodeme).

57. Distolateral shape of oviscape. A = rounded (P = pointed or tapered).

58. Frontal region of face. A = with narrow, yellow, median vitta (P = vitta absent).

59. Palpi. A = very broad (width 5–6 $\times$ thickness, wider than proboscis), black (P = palp much narrower, yellow to ochre).

60. Setulae on ventromedial margin of male cercus. A = dense patch stiff setulae present (P = setulae sparse, fine).

61. Distribution. A = Indopacific (P = Neotropical region).

62. Halter color. A = black (P = white or yellow).

63. Color of subcosta and anterior portion of radial cells on wing. A = lightly infusate black-brown (P = hyaline).

64. Spermathecal capsule. A = vestigial; small (width $\leq 2 \times$ width spermathecal duct), membranous (P = heavily sclerotized, width $\geq 5 \times$ width spermathecal duct).

65. Proboscis. A = elongate, about equal to length of head; heavily sclerotized and melanized (P = much shorter, or, if long, not heavily sclerotized or dark).

66. Lateral portions of sternite VIII (oviscape valves). A = with 5–6 ovisensilla (P = no lateral ovisensilla present).

67. Hypandrium length. A = very short, length along median about $\frac{1}{2}$ that of basiphallus (P = hypandrium length at least equal to that of the basiphallus).

*68. Distiphallus shape. A = narrow, thinner than endophallus (P = bulbous).

69. Distiphallus. A = with dorsal knob present (P = no knob present).

*70. Oviprovector scales. A = very large, placoid (P = lanceolate or triangular in shape).

*71. Proboscis shape. A = elongate, exceeding length of head; very narrow, distal width no greater than width of palpus (P = length about $\frac{1}{2}$ – $\frac{3}{4}$ head width, proboscis considerably thicker).

72. Frontal vitta. A = densely microtomentose and reflective, covers most of frontal region of head (P = vittae lightly striate or with velvety gold or black tomentum).

73. Lateral hypandrial margins. A = deeply indented, anterior end flared out (P = lateral margins straight or slightly concave/convex).

*74. Distiphallal vestiture. A = large scales present (P = glabrous, or with many fine spicules).

75. Hypoproctal plate. A = bilobate (P = margin even, at most slightly sinuate).

76. Posteroventral epandrial lobe. A = present, long; a. setose, b. glabrous, heavily sclerotized (P = lobe closely adpressed to epandrium, broad).

77. Oviscape shape. A = broad and short, length about equal to width, dorsoventrally flat (P = length $1\frac{1}{2}$ –2 $\times$ width, oval in shape).

*78. Dorsomedial area of oviscape valves. A = sclerotized, small plates (pair) present (P = region entirely membranous).

79. Oviscape shape. A = circular or nearly

so, very flat (P = oval and with tapered distal end).

80a. Ventral epandrial lobes. A = 2 pairs present; posterior pair narrow, long, thin, heavily sclerotized (P = 1 pair present, broad and short).

80b. Spermathecal shape. A = squat, height no more than $\frac{1}{2}$ the width (P = round or campanulate, height equal to width).

81. Oviscape shape. A = broad, short, with apex abruptly narrowed (P = shape is evenly oval).

82. Medial surface of paraphyses. A = with elongate process present (P = process absent).

83. Oviprovector scale arrangement. A = pectinate, scales attached laterally into transverse rows (P = scales not attached and not in rows).

84. Oviscape apex in dorsoventral view. A = lateral margins deeply indented (P = gradual tapering of lateral margins, or acute tapering).

Eighty-seven character states ("apomorphs") were used in the phylogenetic analysis (numbers 27, 38, and 76 each have two derived states [a, b] and were counted as separate apomorphs). Of this total, 21 apomorphs (24%) are homoplasious; specifically, they appear two or more times in the cladograms. Most of the apomorphs dealing with particular regions of the body are as follows: oviscape + oviprovector (20; 6 homoplasious), male terminalia (18; 5 homoplasious), cranial sclerites (16; 2 homoplasious), spermathecae (7; 4 homoplasious), proboscis + palpi (5; 2 homoplasious). It is clear that spermathecal modifications are repeatedly evolved at a rate much faster than the other apomorphs. It is interesting that Throckmorton (1965) found a similar situation for several species-groups of *Drosophila* whose phylogenies were based on chromosomal apomorphs. This fact does not necessarily

imply that a character state which has evolved in parallel (but not convergently, since convergencies are modifications of nonhomologs) cannot also be a synapomorphy.

The cladogram in figure 108 strongly suggests that the genus *Drosophila* is paraphyletic. That is, *Drosophila* includes some species, but not all (such as those in *Zygothrica* and *Mycodrosophila*) which I have defined as possessing stout ovisensilla pegs (synapomorph 1). Throckmorton (1975) indicates that *Drosophila* is ancestral to most of the genera of the Drosophilinae. The taxonomic status of *Drosophila* and its various subgenera must be left for future study when all genera in the Drosophilidae can be compared. Relationships within *Zygothrica* are somewhat ambiguous in some cases, but definite in others (such as the existence of clades 1.1, 1.2.1.1, and 2.1). *Zygothrica* is certainly monophyletic (based on synapomorphies 10, 13, and 14), but the five earliest-branching clades are unresolved. Indeed, except for clade 2, three of these clades are each defined by only one synapomorphy. *Zygothrica orbitalis*, which is the only representative of clade 5, deserves special attention: this fly is distinctive mostly on the basis of possessing apomorphs that are found in several major *Zygothrica* clades. Its phylogenetic position is discussed in detail under the Behavior section on Phylogenetics.

In general, higher relationships in *Zygothrica* have been difficult to discern. For example, clades 4.1, 4.2, and 4.3 are unresolved and supported by 1–3 synapomorphies each, and clades 1.2.1 and 1.2.2 are each defined by one synapomorphy. Relationships among pairs and small groups of species have been much easier to discern. Besides morphology, behavior is one phenotypic level that has begun to be used for character analysis of higher-level cladogenesis in *Zygothrica*.

PHYLOGENETICS: BEHAVIORAL CHARACTERS

METHODS: Flies were watched from about 1½ ft away while they were on their fungal aggregation sites in the forest. Use of a natural setting was made so as not to disturb the

milieu of normal social stimuli among the flies. The observations were made at Barro Colorado Island, Smithsonian Tropical Research Institute, Panama, and at the Rio

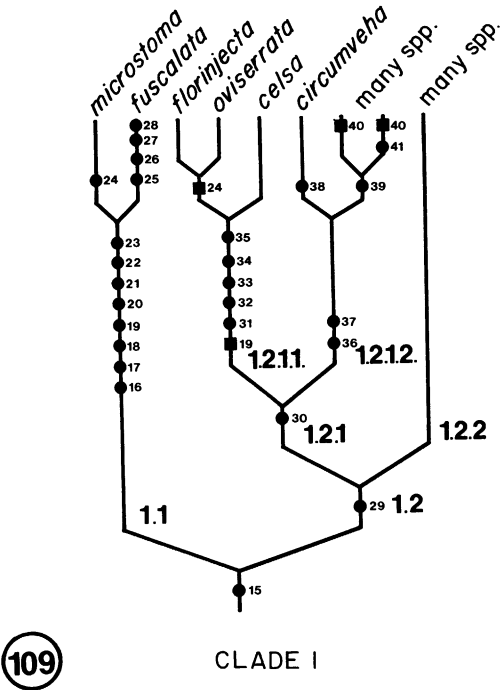
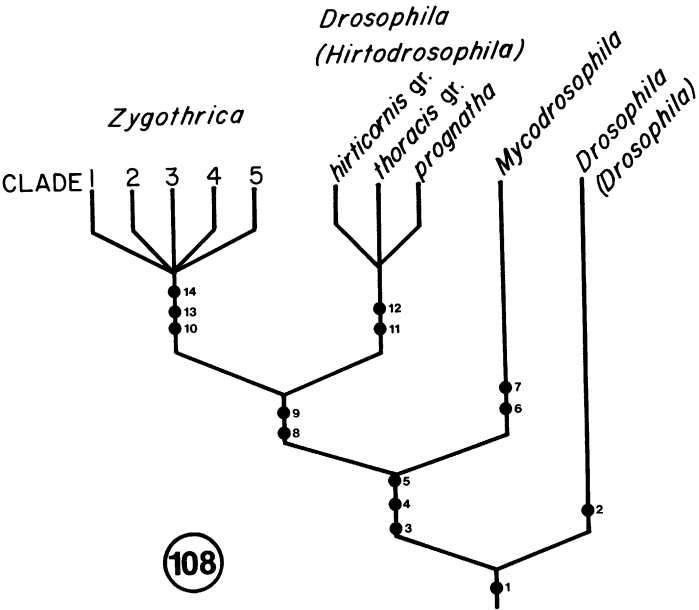
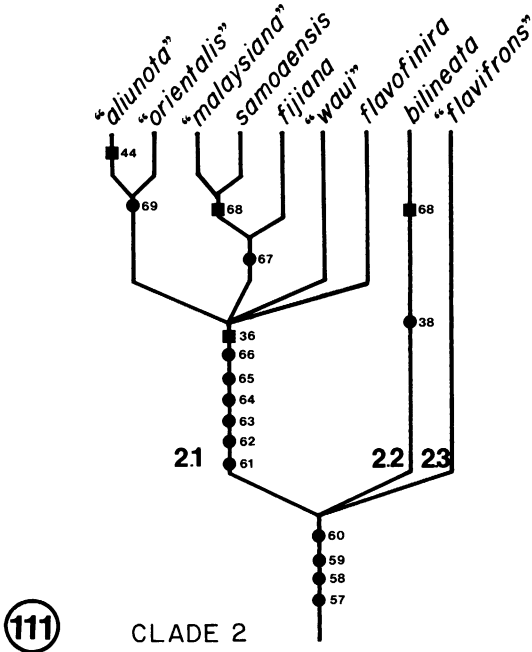
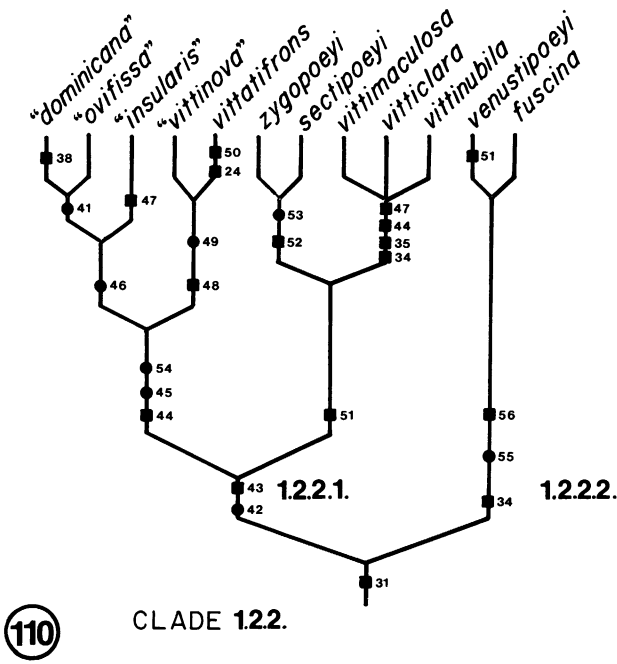
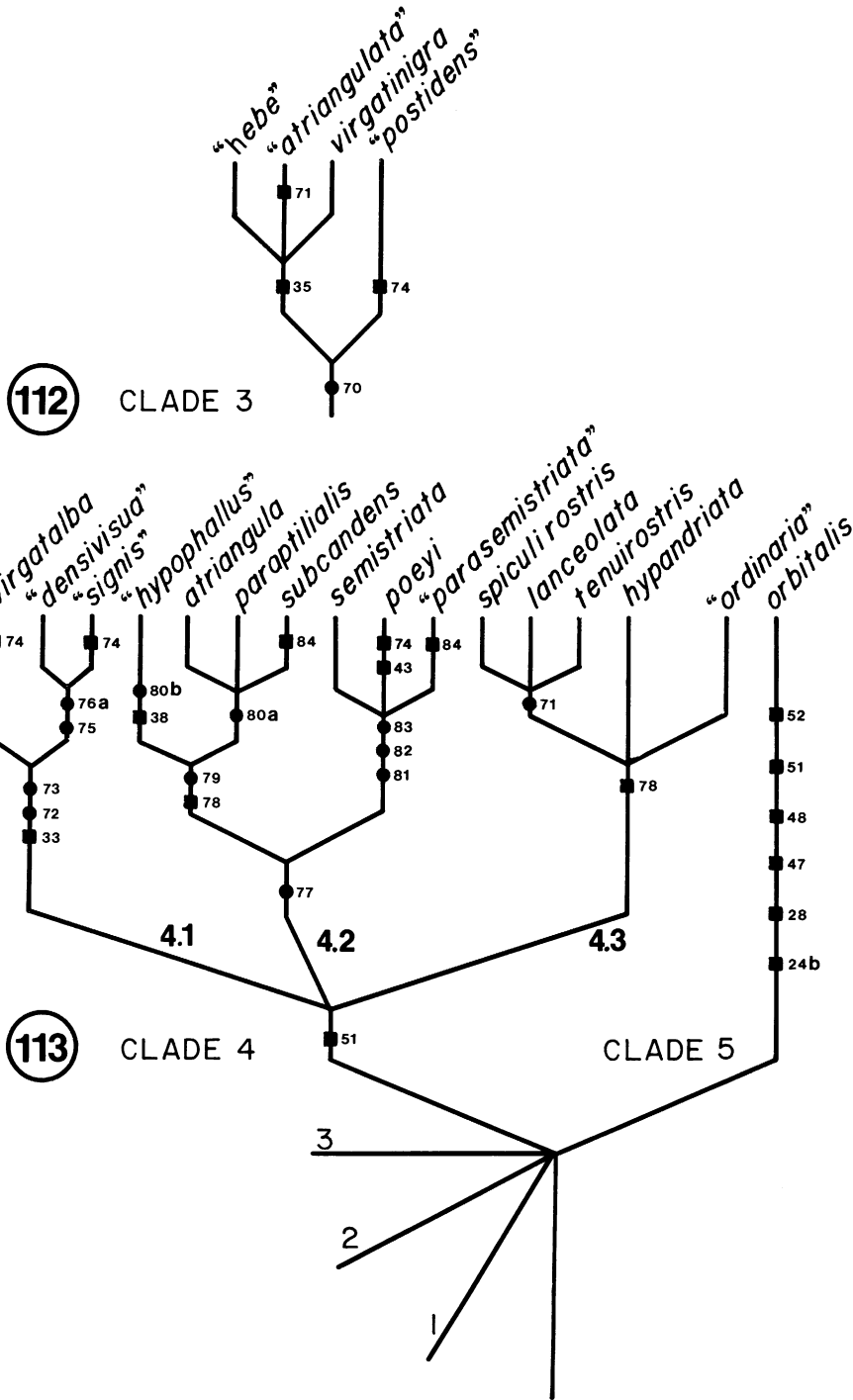


Fig. 108. Phylogenetic hypothesis of the relationships that *Zygothrica* has to other Drosophilidae. Numbers refer to synapomorphies (see text for the explanation of each). In all of the cladograms, circles are synapomorphies; squares are putative synapomorphies which occur in two or more clades and thus may be homoplasious.

Fig. 109. Major relationships within clade 1.



Figs. 110, 111. Major relationships within clade 1.2.2 and clade 2. Species in these groups will be treated in the future paper on *Zygothrica*. They are provided here mostly to present some details on the various hierarchical groups in the genus. Species epithets in quotations are undescribed species to be treated later.



Figs. 112, 113. Major relationships within clades 3, 4, and 5. As in figures 110 and 111, these species will be treated in the future paper on *Zygothrica*.

Tambopata Nature Reserve, Madre de Dios, Peru ("B.C.I." and "Tambopata," respectively, in the behavioral descriptions). Unless a courtship or sparring encounter was apparent, attention was focused on an individual fly for about 5 minutes. Behavioral sequences were continuously tape-recorded using a portable SONY with a sensitive mini-microphone pinned to my lapel. Some specimens of each species were aspirated after observation was completed so as to confirm their identity under the stereoscope. Tape-recorded data were then transcribed and certain behavioral sequences were counted and/or timed. Details of the reproductive behaviors that were observed are given in the descriptions. The order in which the descriptions are presented is phylogenetic, the most plesiotypic being first. To expedite the behavioral descriptions, repertoires were broken into elements. These elements are not necessarily taxonomic characters, since an element can occur in the context of several repertoires (e.g., wing vibrations, which are used in agonistic encounters and in courting displays by males).

RESULTS: A matrix of characters and their states is presented in table 3. A comparison was made to *Drosophila* for polarizing the evolutionary direction of character states at the genus level for *Zygothrica*. *Drosophila* (*Sophophora*) *melanogaster* was used most in this regard (for which Sturtevant [1921], Bastock and Manning [1955], Spieth [1968], Ewing [1983], and my own observations were consulted). This is because the behavior of this species is understood and characterized so well, which facilitates homologizing the elements of *D. melanogaster* with those observed in *Zygothrica*. Also used for outgroup comparison were the behaviors of several species in *Drosophila* (*Hirtodrosophila*) and in *Mycodrosophila*, as based on my own unpublished observations.

BEHAVIORAL ELEMENTS AND TERMS

Passive. Any behavioral characteristic, such as a stance, movement, or display, that occurs either in the absence of conspecifics, or without orientation to them, and that is not accompanied by aggression or courtship when a conspecific comes into view.

Bout. A sequence of actions that is marked by a stationary period before and after them which is greater than the intervals between the actions.

Semaphoring. Swaying. Slow, repetitive motions made with the wings when they are extended about 45° from each other and raised about 45° above the abdomen, then swayed from side to side. The approximate position of the wings relative to each other does not change during the swaying (fig. 114a, b).

Flicking. Wings are either alternately or synchronously extended slowly more than 90° from their resting position over the abdomen.

Scissoring. Wings are simultaneously and very rapidly extended about 90° to the longitudinal axis of the body. They are then quickly folded back to their original position over the abdomen.

Vibration. With a wing extended horizontally and parallel to the ground, generally 90° but sometimes only slightly, it is vibrated very rapidly up and down at an amplitude about equal to the width of the wing (fig. 114c, d). Duration of the vibration varies considerably among species and in different routines of the same fly.

Slashing. Males confronting each other head-on, or when one is pursuing the other, slash the forelegs and/or mesothoracic legs out quickly and strike the opponent.

Butting. Jousting. A male attacking another male may run his head into the opponent, either head-to-head or into the body. If the butting is prolonged, such that two males keep their heads pressed and engage in pushing, this constitutes *jousting*.

Pawing. The male faces lateral to or behind the female that he is courting. His foreleg(s) (either one or both) are extended and pawed over the female's head, thorax, or terminalia several times in a bout.

Side-swerving. After the male initially approaches the female from behind, he swerves his body ca. 30° to one side of her while keeping his head near the female's terminalia (fig. 114d).

Abdominal curling. Only when a male is side-swerving is the distal portion of the abdomen sometimes curled in the direction of the female's head.

Thrusting. Before copulation is terminated, the male dips backward while pivoting at

the point of coupling or intromission. The tips of the male's wings may reach close to or touch the substrate behind him (fig. 114e), and the thrusting is always repeated into a bout.

DESCRIPTIONS

Zygothrica virgatinigra. B.C.I., 3–4 Mar., 2 hours observation on *Favolus brasiliensis* bloom-2 (figs. 98–101). No passive semaphoring. ♂ confrontations always in proximity to ♀. Males usually slash head-on, one may slash opponent's posterior while it is retreating. Butting occasional. ♂ not territorial, searches pilei for mates. A ♂ would often approach to within a head's length any small, dark, and moving insect, even alleculid and staphylinid beetles. COURTSHIP: ♂ orients to ♀ by approaching to within about 3 body lengths, circles about ♀ laterally and crablike, 180–360° from point of approach. ♂ positions himself perpendicular to ♀ near her head or thorax, ♂ wings extended 45–90° from resting position; at 90° they momentarily "click" into place. About half the wing extensions are accompanied by very brief vibration. No abdominal curling during vibration. 1 wing extension every 3–6 sec (N = 4 courtships). After each bout of wing extension, ♂ swerves to close behind ♀ terminalia. 1 copulation observed (duration = 1'6"); ♂ wings folded, ♀ wings parted about 30°. No thrusting.

Zygothrica "atriangulata" (for *Z. atriangula*; Burla, 1956: see table 2 and accompanying footnote discussion). B.C.I., 2–3 Mar., 2 hours observation on *Favolus brasiliensis* bloom-2 (figs. 98–101). No passive semaphoring. 9 ♂ confrontations seen, always in proximity to ♀; ♂ not territorial, searches pilei for mates. For 7 ♂, in a period averaging 50 sec, 14 pilei were searched by any one of them. For these males, 38 approaches in total were made to other drosophilids and only 1 was to a conspecific; they too approached any small dark insects. Butting seen twice; males usually slash. COURTSHIP: brief, mean = 62 sec, N = 5 timed (9 observed). ♂ orients to ♀ as in *Z. virgatinigra*. However, no wing movements made: ♂ paws ♀ head 12–14 times per bout for 1–3 bouts/courtship. After each pawing bout, ♂ swerves to ♀ posterior and attempts mounting. Immediately before at-

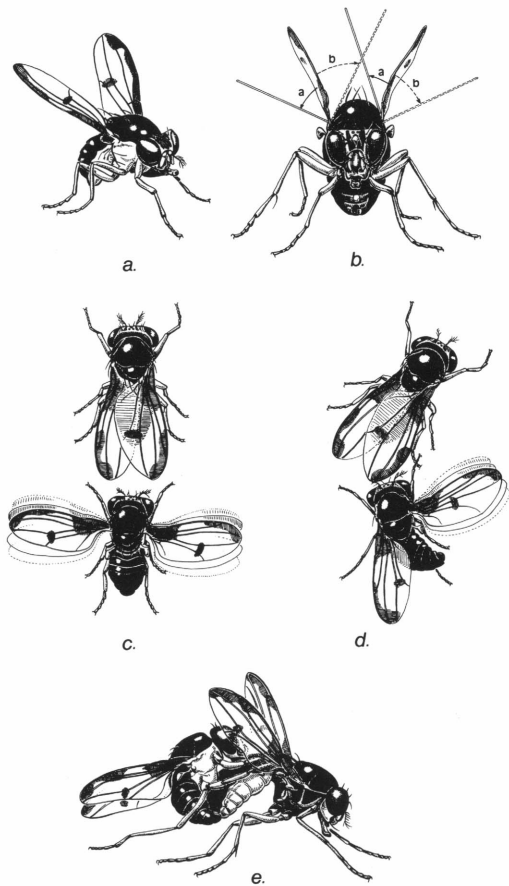


Fig. 114. Ethogram of *Zygothrica aldrichii* courtship. **a.** ♂, stance with wings held stationary. **b.** ♂, frontal view, showing the wing movements made during semaphoring. Wings are initially tilted to one side (a), then the other (b), and this is repeated at various amplitudes and speeds depending on the fly's level of excitement. **c.** Dorsal view, ♂ below approaching ♀ during initial phase of courtship. **d.** ♂ then swerves to one side of ♀, keeping the wing closest to her head outstretched while also periodically vibrating it and curling the abdomen in the same direction. The swerving is usually repeated 2–4 times. **e.** Copulation position, lateral view. Before dismounting, the ♂ dips backward while pivoting at the point of intromission, and so that the wings touch or barely touch the substrate ("thrusting"). 7–9 thrusts typically terminate copulation in *Z. aldrichii*.

tempting mount, ♂ extends wings briefly, vibrates them. ♂ jumps onto ♀ so rapidly as to appear as if striking ♀. 2 copulations seen: ♂ and ♀ wings folded, ♂ tilted far back, pivoting on point of coupling and almost facing op-

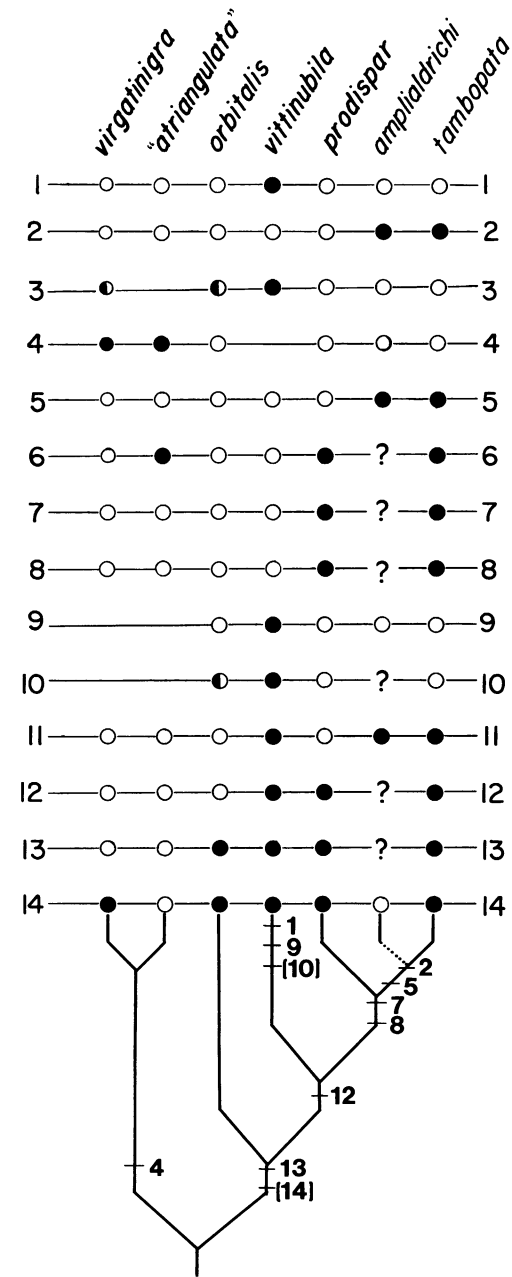


Fig. 115. Hypothesis of phylogenetic relationships for seven *Zygothrica* species based on characteristics of display, aggression, courtship, and mating. See table 3 for discussion of characters. Dark circles are apomorphies, half-filled ones are variable. Numbers below are character states that support the hypothesis, ones in parentheses appear homoplasious.

posite ♀. 10 thrusts terminated each copulation.

Zygothrica orbitalis. B.C.I., 20–24 Feb., 7 hours observation on *Polyporus tricholoma* (figs. 96, 97), *Favolus brasiliensis*, *Auricularia delicata*, and *Gymnopilus* sp. (fig. 105). No passive semaphoring. Males defend territories on top of pilei; most stand at pileus margin, facing out, females congregate beneath and on stipes. Confronting males scissor wings: wings momentarily held in place (90–120° from resting position) when extended, sometimes briefly vibrated. Aggressive ♂ wing displays repeated 2–5 ×, mean = 1.3 sec/wing extension (N = 4 ♂, timed from entire bouts). No slashing; males butt: 62 butts to body, 4 butts head-on were observed for 7 pairs of fighting males. Fighting always follows aggressive wing displays. COURTSHIP: ♂ approaches ♀ posterior to within a head's length, steps back to about ½ body length, swerves, extends wing closest to ♀ head about 90° and it momentarily "clicks" into place and is sometimes very briefly vibrated (other wing is only very slightly unfolded and motionless). 1–2 swerves per courtship; intromission attempted by jumping onto ♀ from behind. Receptive ♀ slightly elevates and spreads wings about 30°. ♂ wings folded during copulation, no thrusting. 4 copulations observed, 2 timed (40", 1'24").

Zygothrica vittinubila. Tambopata, 29–30 Sept., 10 hours observation on *Polyporus tricholoma* (figs. 92–94), Tricholomataceae sp., and *Auricularia delicata* (figs. 102–104). Passive semaphoring: ♂ extends wings alternately from folded position over abdomen to 45–90°, wings elevated ca. 45°; this is repeated about 1/sec or slower. ♂ territorial. Confronting males rush to within several body lengths of each other, wings are then rapidly scissored 2–3 × (both wings flicked forward simultaneously to almost 180° from resting position). Males then briefly butt heads, or one butts body/tail of retreator; no slashing. About half of the encounters have no apparent "victor." Retreating ♂ sometimes pursued by scissoring ♂. COURTSHIP: ♂ approaches ♀ from behind, scissors 2–3 ×, mounts; ♀ wings remain folded, moved slightly to one side of abdomen; ♂ may scissor ca. 2 × while mounted. No thrusting. Copulation time, mean 2'4" (N = 4 timed; 1'40"–3'12").

Zygothrica prodispar. Tambopata, 25–26 Sept., 11 hours observation on same fungi as *Z. vittinubila*; B.C.I., 1–7 Mar., 2 hours ob-

TABLE 3
Behavioral Characters Used for Phylogenetic Reconstruction

Character	Plesiomorphic state	Apomorphic state
1. Passive semaphoring: Flicking	absent	present
2. Passive semaphoring: Swaying	absent	present
3. ♂ courtship wing movements	vibrated	spread, no vibration
4. Courtship: ♂ orientation to ♀	briefly lateral (swerving)	always lateral
5. Passive wing position, ♂	folded over abdomen	elevated, spread
6. Copulation: termination by ♂	no thrusting	thrusting
7. Copulation: ♂ wing position	folded over abdomen	spread, elevated
8. ♂ confrontations: butting	brief, to body; or no butting	jousting
9. Courtship: ♂ orientation to ♀	side swerving	always posterior
10. ♂ confrontations: wing movements	spread, rapid vibration	scissored
11. Wing patterning	absent	present
12. ♂ confrontations: leg movements	foreleg slashing	slashing lost
13. ♂ spacing	not site tenacious	territorial
14. Courtship: ♂ leg movements	pawing at ♀	pawing lost

servation on same fungi as *Z. virgatinigra* (figs. 98–101). No passive semaphoring. ♂ territorial: darts about pileus top, usually stands at margin facing out. Opponents face each other 2–3 head lengths distant. Just before and when butting, wings extended about 90° from resting position and vibrated all during extension. Butting head-to-body much briefer than head-to-head butting. Butting for 3 ♂ tallied, about 4 min observation for each: of 85 opponents butted, 30 were to conspecific ♂, 10 to *Z. tambopata*, and 45 were to *Z. vittinubila* (at Tambopata site); 94 butts were made, 28 of them head-to-head, some were jousts. Jousts lasted 5–6 sec, 1 lasted 42 sec; occur only between conspecific males. When jousting, pair usually pushes each other back and forth, no more than 1 body length. Sometimes pair backed off briefly before resuming jousting. *Z. prodispar* was only 2% of all *Zygothrica* at the site where they were studied, so encounter frequency among males is certainly nonrandom. COURTSHIP: ♂ approaches ♀ from behind or fully lateral, both wings extended 90° and vibrated. ♂ moves to within head length of ♀ terminalia and swerves, abdomen curled, wing closest to ♀ head extended about 90° and vibrated 1–3 sec (other wing folded over abdomen). This sequence repeated 3–7×/courtship. Receptive ♀ raises and separates wings about 45°, ♂ immediately mounts, remains stationary *in copulo* (mean = 1'40", N = 4 copulations timed); dismounts after ca. 3 thrusts.

Zygothrica amplialdrichi, n. sp. B.C.I., 7–

8 Mar., 2 hours observation on *Favolus brasiliensis* (figs. 98–101). Passive ♂ semaphoring: wing swaying. Although many courtships were observed, no ♂ fighting was seen, so type of ♂ confrontation unknown but they are probably at least territorial. COURTSHIP: ♂ rushes to ♀, if ♂ faces forward or lateral to ♀, he rapidly moves crablike about her to the posterior end. If ♀ steps forward, ♂ follows close behind while probing ♀ terminalia with proboscis. Either directly behind or slightly lateral to ♀, ♂ extends wing(s) and vibrates for 1–10 sec. Swerving, with curled abdomen, occurs in ca. half the wing extensions. ♂ paws ♀ terminalia 2–3× during each wing vibration bout (wvb). 3–28 wvbs/courtship (mean = 10, N = 5 courtships tallied). No copulations were seen, but ♂ attempts mounting by inserting head below ♀ wing tips and leaping up rapidly so as to appear as if butting her.

Zygothrica tambopata, n. sp. Tambopata, 22 Sept.–5 Oct., 12 hours observation on same fungi as *Z. vittinubila* and *Z. prodispar*. Passive ♂ semaphoring: wing swaying. ♂ territorial, defends pileus or portions thereof by butting, no slashing. 4 males tallied for butting (mean = 5 min each observation period): 83 opponents butted, 89 butts occurred, 36 butts were to conspecifics. Since *Z. tambopata* were 22% of *Zygothrica* at site, and 44% encounters were intraspecific, then males must discriminate among flies. Also, 31 of the 89 butts were head-to-head, some brief jousts. Jousts occurred only between conspecific males. COURTSHIP: ♂ approaches ♀ 1–2

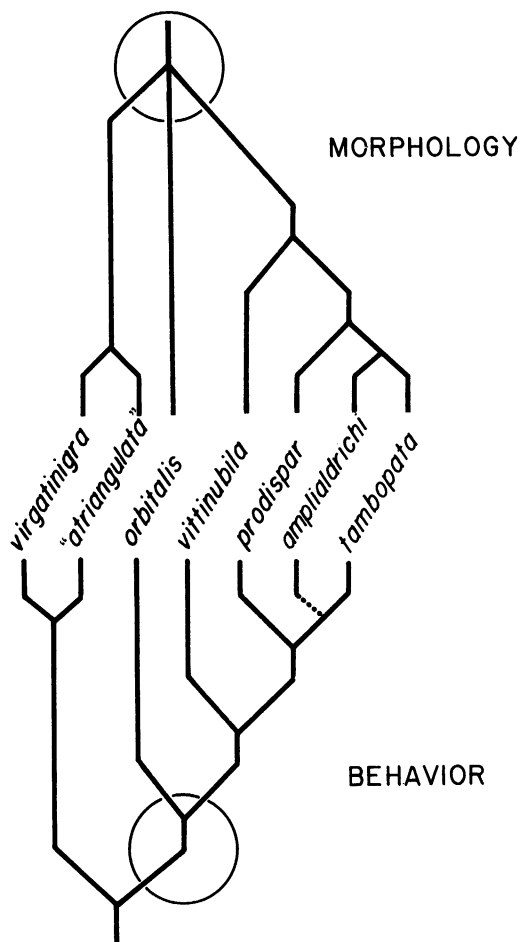


Fig. 116. Congruence between the cladogram based on behavior (below) and a reduced cladogram based on morphology of the adults (above). The topography of one is a close reflection of the other, except that behavior indicates *Z. orbitalis* to be related to the "*vittinubila*" clade (these nodes on the cladogram are circled). The behavioral apomorphy on which this hypothesis is based is territoriality.

head lengths from terminalia. 1–3 bouts, wing extension and vibration occur with abdomen curling, usually with swerving. If ♂ orientation to ♀ fully posterior, both wings extended. Receptive ♀ raises wings about 30° above abdomen, about 45° apart, ♂ immediately mounts, remains stationary until a mean of 19 (8–39, $N = 9$ copulations tallied) thrusts terminate copulation. This species shows an obvious preference for staying underneath the fungal pilei.

DISCUSSION

None of the behavioral elements and repertoires that were studied here characterize *Zygothrica*. Only the swaying manner of semaphoring may be restricted to some *Zygothrica*. Passive semaphoring has evolved at least twice in *Zygothrica*; based on the groups that were studied, the swaying and flicking manners of semaphoring are related to the type of wing patterning. "Flicking" will probably occur wherever drosophilids possess apical wing spots (e.g., *Scaptomyza adusta* and some Hawaiian *Drosophila* are known to perform this way, as are otitids and sepsids which possess such markings). If flicking appears with the evolution of apical wing spots, then this type of semaphoring has evolved at least four times in *Zygothrica* (apomorphy no. 44; figs. 110, 111, 160). "Jousting" was found to occur in two of the hypercephalic species that were studied, *Z. prodisspar* and *Z. tambopata*, and is also known in the hypercephalic species *Z. dispar* (Bristowe, 1924; H. Burla, personal commun.). Males of the Hawaiian species *Drosophila (Idiomyia) heteroneura* are hypercephalic and are known to joust (Spieth, 1985): it would be no surprise to find that the hypercephalic males of drosophilids unrelated to *Zygothrica* also behave this way (Grimaldi, ms). "Thrusting" by the male just before he terminates copulation may be a trait unique to some *Zygothrica*. There is no obvious relation between the presence of thrusting and various aedeagal apomorphs such as distiphallid shape and scaling.

"Lekking" may not be the best term to describe *Zygothrica* territoriality. Leks are male territories that are closely situated into a visual, acoustic, or pheromonal arena, and they attract females to the site based solely on the presence of males, so that no resource-defense polygamy occurs. Territories of male *Zygothrica* were often tightly packed (1–3 males per 5 cm pileus on average), but the aggregations were comprised of males and females in about equal proportions. This latter trait is no doubt due to the fact that fungi serve as sites for grazing as well as ones at which to rendezvous.

Territoriality in *Zygothrica* is considered here to be an apotypic state of male spacing behavior. This conclusion is based on the fact that the *Hirtodrosophila* species which I ob-

served on fungi with *Zygothrica* were not territorial. Presence of territoriality in other relatives of *Zygothrica*, by this hypothesis, must then be independently derived. Parsons (1977) found *D. (Hirtodrosophila) polypori* lekking beneath *Ganoderma applanatum* (Polyporaceae) sporophores in rain forests in Victoria, Australia. This cosmopolitan fungus is smokey-gray above but cream-colored underneath. *Mycodrosophila* are always found in situations similar to this (e.g., fig. 97), and the two nearctic and three neotropical species that I observed all had territorial males. Methods of male fighting differ, though, between *Zygothrica* and at least *Mycodrosophila*. Combatting male *Mycodrosophila* that I have observed back into each other and then slash with their hind and/or middle legs. Different fighting behaviors would support the view that territoriality in the three groups is independently derived. Territoriality is very likely to be the prerequisite condition for the evolution of hypercephaly, passive semaphoring, and patterned or marked wings. The attractiveness of white fungi or portions thereof for rendezvousing drosophilids is probably due to predominantly visual courtships in these flies.

Figure 115 shows the phylogenetic hypothesis for seven *Zygothrica* species, as based on just behavioral synapomorphies. Figure 116 shows the congruence between this cladogram and a reduced or collapsed cladogram derived from the more comprehensive morphological comparisons. The match of the two cladograms is very good, and, in fact, behavior has resolved a trichotomy seen at the base of the morphology cladogram that involves *Zygothrica orbitalis* (the only member of clade 5, the other four species belong to clade 1.2). The synapomorphy on which this conclusion is based is the presence of territorial males. Although *Z. fijiana* was not observed mating or courting by Takada

(1976), he did note that males defended the top of a white mushroom and were quiescent beneath the fungus. So, tentatively, clades 2 and 5 may be considered allied to clade 1.2 on the basis of territoriality. Certainly, many more species should be compared before making taxonomic changes solely on this basis. As alluded to previously, even if territoriality is independently derived in other groups of drosophilids, it does not rule out that the behavioral state is here a synapomorphy.

Throckmorton's criteria for identifying ancestral taxa are that the group be phylogenetically primitive (arise early in a tree) and possess "ancestral variability" (Throckmorton, 1962: 334). His reasoning for the latter is that "genotypes for derived characteristics must develop from a heterozygous gene pool." Behaviorally, *Z. orbitalis* repertoires were more variable than those of the other species examined (fig. 115). Also, at least six apomorphies of this species (particularly of the terminalia), appear to be shared with three lineages of *Zygothrica*, which may be the result of parallelism (independent expression of a homologous state). In this sense, *Z. orbitalis* can be described as "phylogenetically polymorphic." In applying the criterion of "ancestral variability," it is apparent that clade 5, and perhaps *Z. orbitalis* itself (which is intuitively doubtful), could be considered the best extant candidate as an ancestor to clade 1.2 or even the genus. Moreover, using the additional criterion of minimum branch lengths in constructing phylogenetic trees (e.g., Farris, 1982), making *Z. orbitalis* or clade 5 ancestral to *Zygothrica* or a portion thereof would also reduce the homoplasy index of the cladogram in figure 113. Until further evidence is more compelling to show that clade 5 has given rise to clade 1.2, the two will be separated.

GENERAL TAXONOMY

GENUS *ZYGOTHRICA*

Achias (*Zygothrica*) Wiedemann, 1830: 16. Type: *Achias* (*Zygothrica*) *dispar* Wied., 1830; by original designation.
Drosophilura Hendel, 1913: 389. Type: *Dro-*

sophilura caudata Hendel, 1913; by original designation.
Zygothrica: Sturtevant, 1920: 156.
Zygothrica (*Tanyglossa*) Duda, 1925: 189. Type: *Zygothrica* (*Tanyglossa*) *tenuirostris* Duda,

TABLE 4
Genus *Zygothrica*: Conspectus of Higher Relationships

This study	Duda (1925); Burla (1956)
Clade 1.	>Subgenus
1.1	<i>Zygothrica</i>
1.1.1 <i>fuscalata</i> sp. gr.	
1.1.2 <i>microstoma</i> sp. gr.	
1.2	
1.2.1 (unnamed)	
1.2.1.1 <i>celsa</i> complex	
1.2.1.2 <i>dispar</i> complex	> <i>dispar</i> sp. gr.
1.2.2 (unnamed)	> <i>vittatifrons</i> sp. gr.
1.2.2.1 <i>fuscina</i> complex	
1.2.2.2 <i>vittatifrons</i> complex	
Clade 2.	
2.1 <i>bilineata</i> sp. gr.	
2.2 <i>samoensis</i> sp. gr.	
Clade 3.	
3.1 <i>postidens</i> sp. gr.	
3.2 <i>atriangulata</i> sp. gr.	
Clade 4.	> <i>atriangula</i> sp. gr.
4.1 <i>virgatalba</i> sp gr.	<Subgenus
	<i>Tanyglossa</i>
4.2 <i>atriangula</i> sp. gr.	= <i>candens</i> , <i>poeyi</i> spp. gr.
4.3 <i>hypandriata</i> sp. gr.	
Clade 5.	
(<i>Zygothrica orbitalis</i>)	

Symbols: A group has the number of species in it either more than (>), less than (<), equal to (=), or otherwise related to the group to which it is most similar in the classifications of Duda and Burla.

1925. Junior homonym for *Tanyglossa* Meigen, 1803: 267 (Diptera: Tabanidae).
Zygothrica: Burla, 1956: 215.

DIAGNOSIS: Facial carina prominent, anterior edge sharp; face with oral margin medially cleft; proboscis sclerotized (especially the labellum and mentum), with an acute joint between the mentum and submentum.

COMMENTS: This is a broader definition of the genus than that given by Burla (1956), but it excludes three species discussed below. Several of the traits given by Burla as diagnostic for the genus I have found to occur in only some members: possession of an extensive ocellar triangle, a flat oviscape, and an

TABLE 5
Species in Cladograms (figs. 110-113) Arranged According to Classification in Table 4. Classification of Species in Clade 1 is Given in Table 7.

Clade 2.
2.1 <i>bilineata</i> sp. gr.
<i>bilineata</i>
" <i>flavifrons</i> "
2.2 <i>samoensis</i> sp. gr.
" <i>aliunota</i> "
<i>fijiana</i>
<i>flavofinira</i>
" <i>malaysiana</i> "
" <i>orientalis</i> "
<i>samoensis</i>
" <i>wau</i> "
Clade 3.
3.1 <i>postidens</i> sp. gr.
" <i>postidens</i> "
3.2 <i>atriangulata</i> sp. gr.
" <i>atriangulata</i> ," n. n.
" <i>hebe</i> "
<i>virgatinigra</i>
Clade 4.
4.1 <i>virgatalba</i> sp. gr.
" <i>densivisua</i> "
" <i>signis</i> "
<i>virgatalba</i>
4.2 <i>atriangula</i> sp. gr.
<i>atriangula</i>
" <i>hypophallus</i> "
<i>parapoeyi</i>
<i>paraptilialis</i>
" <i>parasemistriata</i> "
<i>poeyi</i>
<i>semistriata</i>
<i>subcandens</i>
4.3 <i>hypandriata</i> sp. gr.
<i>hypandriata</i>
<i>lanceolata</i>
" <i>ordinaria</i> "
<i>spiculirostris</i>
<i>tenuirostris</i>
Clade 5.
5.1 <i>orbitalis</i> sp. gr.
<i>orbitalis</i>

As in table 2, quotations denote the name of a species that will be described in a subsequent paper (see text).

anterior reclinate orbital seta that is midway between the other, two ipsilateral orbitals.

The species excluded from *Zygothrica* are the following:

Drosophila (Hirtodrosophila) clypitata,
nomen novum

pro *Zygothrica clypeata* Burla, 1956: 251; preoccupied by *Drosophila clypeata* Wheeler, 1968.

Drosophila (Hirto.) pleurostrigata, n. comb.
Zygothrica pleurostrigata Burla, 1956: 250.

Drosophila (Hirto.) strigocula, n. comb.
Zygothrica strigocula Burla, 1956: 251.

DISCUSSION: The above three species belong in the *Drosophila (Hirtodrosophila) thoracis* species-group since they possess dark brown pleural bands, elongate terminal setulae on flagellomere I, a large ventral epanthial lobe (♂) with a row of elongate setae, as well as being plesiomorphic with respect to the apomorphies that are diagnostic for *Zygothrica*. In addition, the distiphallus is globose and finely spiculate in *D. (H.) pleurostrigata*, but has become developed into a pronged dorsal distiphallic sclerite in the other two species.

CONSPECTUS OF HIGHER
RELATIONSHIPS

The choice of names for groups and subgroups was based on a widespread or morphologically typical representative of each. The present study divided *Zygothrica* into many more hierarchical taxa than the previous classifications of Duda (1925) and Burla (1956) (see table 4). Such a result is due primarily to a purely cladistic analysis of phylogenetic relationships and a cladistic classification, and to the fact that many more species from all portions of *Zygothrica*'s range are treated here.

Duda's only impact on classification of the genus was the proposal of subgenus *Tanyglossa* for *Z. tenuirostris*, based on the possession of an extremely narrow and elongate proboscis (fig. 32). A spiculate proboscis is also found in *Z. spiculirostris* (fig. 31). Unfortunately, the existence of *Tanyglossa* leaves

TABLE 6
Zygothrica incertae sedis

<i>apopoeyi</i>	† <i>paraptialis</i>
† <i>candens</i>	<i>parvipoeiy</i>
† <i>clavipoeiy</i>	† <i>scutellaris</i>
† <i>festiva</i>	† <i>subcandens</i>
<i>gracilipoeiy</i>	† <i>vittimarmorata</i>
<i>laevifrons</i>	† <i>vittinotalis</i>
<i>mesopoeiy</i>	<i>vittipoecila</i>
<i>ochracella</i>	† <i>vittipunctata</i>
<i>pallidipoeiy</i>	† <i>vittisecta</i>
† <i>palpipoeyi</i>	<i>vittivirgata</i>

† denotes a lack of material of one sex; the other species have either not yet been studied or require further study.

the nominal subgenus *Zygothrica* defined by a proboscis structure that is primitive at the level of the genus.

There is fairly good congruence between Burla's (1956) groupings and the ones proposed here (table 4). Having a taxon of convenient size was apparently a criterion for classification by Burla: number of species per group varied only from 6 to 12. In the present study, number of species varies widely among the major clades. Definitions of taxa, including the complexes, species-groups, and species-subgroups, are given in appropriate areas of the text where species are discussed. Table 5 provides a classification of species in clades 2–5 based on the hypotheses in figures 111–113. Species accounts of these clades will be treated in a companion paper on *Zygothrica* taxonomy, together with species of clade 1.2.2, which will also include a comprehensive synopsis on the classification of the genus as well as keys to major groups. The classification of many of the species in clade 1 is provided in table 7; most of these species are dealt with in the next section of this paper. Table 6 lists *Zygothrica* that are presently incertae sedis, either because males or females were lacking from the material which I had studied or because I have not reviewed material of some species. Incertae sedis species will be treated in the subsequent paper.

SPECIES ACCOUNTS

An asterisk (*) following the listing of a specimen or series in the Material section of

each species account indicates one or more genitalic dissections.

TABLE 7
Classification of Clade 1

Clade 1.1	<i>fuscalata</i> , n. sp. <i>microstoma</i> <i>peruviana</i> , n. sp.	<i>nealdrichi</i> <i>nigropleura</i> , n. sp. <i>pallida</i> , n. sp. <i>panamensis</i> , n. sp. <i>paraldrichi</i> <i>paravitta</i> , n. sp. <i>pilipes</i> <i>prensiseta</i> , n. sp. <i>radialis</i> , n. sp. <i>simulans</i> , n. sp. <i>somatia</i> , n. sp. <i>spinathigma</i> , n. sp. <i>tambopata</i> , n. sp. <i>trinidada</i> , n. sp. <i>zygia</i> , n. sp.
Clade 1.2		
1.2.1		
1.2.1.1, <i>celsa</i> complex	<i>celsa</i> , n. sp. <i>florinjecta</i> , n. sp. <i>oviserrata</i> , n. sp. <i>vitrea</i> , n. sp.	
1.2.1.2, <i>dispar</i> complex		
1.2.1.2.A, <i>neolinea</i> species-group	<i>bilinefilia</i> , n. sp. <i>circumveha</i> , n. sp. <i>femina</i> , n. sp. <i>neolinea</i> , n. sp. <i>perplexa</i> , n. sp. <i>zonata</i> , n. sp.	1.2.1.2.B.3, <i>caudata</i> species-subgroup <i>aliucapa</i> , n. sp. <i>caudata</i> <i>caputrichia</i> , n. sp. <i>laticeps</i> , <i>latipanops</i> , n. sp. <i>latipaps</i> , n. sp. <i>nigra</i> , n. sp. <i>ora</i> , n. sp. <i>panopia</i> , n. sp. <i>posthona</i> , n. sp.
1.2.1.2.B, <i>dispar</i> species-group		
B.1, <i>dispar</i> species-subgroup	<i>abbrevidispar</i> , n. sp. <i>antedispar</i> , n. sp. <i>dimidiata</i> <i>dispar</i> <i>dissimulata</i> , n. sp. <i>exuberans</i> <i>fascipennis</i> <i>kerteszi</i> <i>pictura</i> , n. sp. <i>prodispar</i> <i>sphaerocera</i> , n. sp.	
B.2, <i>aldrichii</i> spp.-subgroup	<i>aldrichii</i> <i>amplialdrichi</i> , n. sp. <i>andea</i> , n. sp. <i>anota</i> , n. sp. <i>centralis</i> , n. sp. <i>cryptica</i> , n. sp. <i>glossusta</i> , n. sp. <i>joeyesco</i> , n. sp. <i>karenae</i> , n. sp. <i>manni</i> , n. sp. <i>mediogaster</i> , n. sp. <i>mediovitta</i> , n. sp. <i>microeristes</i> , n. sp.	
		Clade 1.2.2
		1.2.2.1, <i>fuscina</i> complex <i>fuscina</i> <i>venustipoeiyi</i>
		1.2.2.2, <i>vittatifrons</i> complex
		1.2.2.2.A, <i>vittatifrons</i> species-group "vittinova" "insularis" "ovifissa" "dominicana" <i>vittimarginata</i> <i>vittatifrons</i>
		1.2.2.2.B, <i>vittimaculosa</i> species-group <i>vittimaculosa</i> <i>vitticlara</i> <i>vittinubila</i> <i>sectipoeiyi</i> <i>vittipunctata</i> <i>zygopoeiyi</i>

* As in tables 2 and 5, quotation marks denote the name of a species to be described in another paper.

KEY TO MAJOR GROUPS OF CLADE 1,
EXCLUSIVE OF CLADE 1.2.2

Clade is defined on the basis of synapo-
morphology 15.

1. Face very narrow with very narrow carina
(fig. 20); wings paddle shaped, with apex
of R_{2+3} almost perpendicular to C (figs.
127–130); scutellum flat and triangular
..... clade 1.1

- 1a. Face $\frac{1}{3}$ – $\frac{1}{2}$ width of head; R_{2+3} acutely joined to C; wings with prominent anal lobe . . . 2 (clade 1.2)
2. Pleura dark (δ + φ), glassy; ocellar triangle very large (figs. 8, 11); abdomen glassy (ground microtomentum lost); oviscape dorsoventrally flattened; occur at altitudes of ≥ 2000 m *Celsa* complex
- 2a. Pleura usually light, or dark only in φ ; ocellar triangle may touch ptilinal fissure, but without a side on fissure; abdomen always with microtomentum, not glassy 3 (*Dispar* complex)
3. Notum black-brown, with 2 distinct, incomplete, paramedian vittae (fig. 267d, g, e); oviscape apex dorsoventrally flattened; wing hyaline, or with diffuse/distinct apical spot (figs. 165, 170) (δ and/or φ); occur at high altitudes, ≥ 1500 m *Neolinea* species-group
- 3a. Not with all the above characteristics; ocellar triangle very large, width is $\frac{1}{2}$ or more that of the face (fig. 10); δ with inner vertical seta in line with ipsilateral orbitals 4 (*Dispar* species-group)
4. Wing with spot at apex of R_{2+3} , very light to dark and distinct (e.g., figs. 268–280), darker in φ ; vein dm-cu with spot (lost in 2 species, figs. 314–317) *Aldrichii* subgroup
- 4a. Wing hyaline or with diffuse apical infuscation in δ (3 species have elaborate patterns, figs. 206, 207, and 239) 5
- *5. Frontal vittae velvety black; medial surface of gonopod (δ) concave, smooth (e.g., figs. 233, 259); distiphallus flat, laterally flanged (e.g., figs. 236, 240); sides of oviscape tapered or parallel *Dispar* subgroup
- *5a. Frontal vittae black or yellow; setae in ventral row on profemur are stout and sharp (figs. 469–474); oviscape with slight lateral flare toward apex (e.g., figs. 486, 499, 504); surstyli (δ) small, crescentic, with short peg prensisetae (e.g., figs. 483, 496, and 501) *Caudata* subgroup

* Reliable identification may depend upon examination of genitalia.

CLADE 1.1

This is undoubtedly a monophyletic group, judging from the eight synapomorphies possessed by the three species in it. The clade is western Hylean and eastern Andean (reaches south to Peru), but also Central American and Greater Antillean. No representatives are

known from the Lesser Antilles or the Amazonian Basin. Clade 1.1 appears to be closely related to several Indopacific genera. Based on descriptions in Bock (1982) and Okada (1984), the following features may be synapomorphic with *Collessia*: a narrow carina, one pair of vibrissae, R_{2+3} meeting C abruptly, and a brown notum (but light pleura) that has distinct light notal vittae. *Mulgravea* is quite autapomorphic, as is *Collessia*, but also shares with these two genera the possession of only two rows of acrostichal setulae (seen also in *Thyreocephala* and *Lissocephala*), a wing with a very reduced anal lobe, and a narrow cheek. In addition, *Zygothrica microstoma* possesses a dark halter, as do species of *Collessia*, and *Z. fuscata* shares with *C. superba* and *C. kirishimana* the possession of an R_{2+3} , apical, and dm-cu spot on the wing. *Mulgravea* has a surstylus very similar to *Z. microstoma* and, like clade 1.1, possesses a prominent, setose, ventral cercal lobe and elongate ventral epandrial lobes. One species of *Mulgravea* (*M. minima*: N. Queensland) and three species of *Collessia* (*C. superba*: N. Queensland; *C. kirishimana* and *C. hiharai*: Japan) have been described.

Diagnostic features for species of clade 1.1 are the following: face and carina very narrow; abdomen shiny (ground setulae lost); wing paddle-shaped, with apex of R_{2+3} turned abruptly to C, most of anal lobe lost; oviscape laterally flattened, apically truncate; ventral epandrial lobes pendulous; surstyli with elongate and dorsal prensisetae. In addition, abdominal and notal ground color is light brown, the pleura are light yellow, and the notopleural suture is distinct. The scutellum is dorsally flat and triangular.

KEY TO SPECIES OF CLADE 1.1 (fig. 109)

1. Wing with pattern of diffuse brown spots on apex of R_{2+3} , on dm-cu, and on apex; halter light yellow *fuscata*, n. sp.
- 1a. Wing hyaline, halter knob dark brown . . . 2
2. Face ochre to light brown; proboscis light yellow; C.I. greater than 2.60; oviscape with 5 large ovisensilla on apical margin (figs. 120, 121); widespread (Gr. Antilles to Ecuador) *microstoma*

2a. Face, proboscis, dark brown, C.I. ca. 2.20; oviscape with 4 large apical ovisensilla; Peru
..... *peruviana*, n. sp.

Zygothrica microstoma

Figures 117–121, 129–130

Zygothrica microstoma Duda: 1925: 190.

DIAGNOSIS: Wings light brown, but hyaline and without markings; notum and tergites usually completely light brown; spermatheca papillate; oviscape with 5 large ovisensilla on apical margin; distiphallus with retrorse dorsal spine; surstyli pendulate, with medial row of setiform prensisetae.

DESCRIPTION: Since Duda described the external morphology in detail, the following is a description of the terminalia. 4–5 apical, peg ovisensilla present, evenly spaced on flat posterior margin. 5–8 smaller and ventral ovisensilla and 1 small laterosubapical ovisensillum peg present. 1 trichoid ovisensillum between first and second ventral ovisensilla pegs. Oviprovector scales not densely packed; narrow, elongate. Spermathecal capsule campanulate, with or without basal collar, finely papillate, without apical indentation. Epandrium with 2 pairs of ventral lobes: posterior pair pendulous, with apical portion triangular in posterior view, bears 8–10 setae. Surstylus elongate, broadly attached to epandrium, 13–16 setiform, evenly spaced prensisetae in medial row. Hypoproctal plate elongate, extended to middle of surstyli, with 3–4 long lateral setae. Basiphallus short, straight, slightly longer than aedeagal apodeme and slightly arched. Distiphallus with ventral pair of blunt retrorse spines and dorsomedial spine. Distiphallal apex probably eversible, possesses 4–5 minute ventral papillae.

MEASUREMENTS: N = 4♂, 3♀. ThL = 1.21 ♂ (1.12–1.25); 1.13 ♀ (1.06–1.20). HW/ThL = 0.74 ♂ (0.71–0.79); 0.77 ♀ (0.73–0.81). ThL/WL = 0.40 ♂ (0.39–0.41); 0.46 ♀ (0.41–0.49). C.I. = 2.87 (2.63–3.95); 4-V = 1.26 (1.11–1.39).

HOLOTYPE: ♂, COSTA RICA: La Suiza de Turrialba. On back of label is "1921.iv.4" (HNHM, Budapest) (type examined, genitalia not dissected). Measurements: ThL = 1.22,

HW/ThL = 0.76; ThL/WL = 0.41; C.I. = 3.74; 4-V = 1.39.

DISTRIBUTION: Central America, south to Ecuador; Greater Antilles (figs. 134, 135).

MATERIAL: COSTA RICA: La Suiza, 2♂*. ECUADOR: Chilicay: Chimborazo, VI/55, 1♂*. EL SALVADOR: San Salvador, IX/55, 1♂*; Volcan Boqueron, 4500 ft, VII/54, 1♀*; La Palma, 3200 ft, VII/54, 1♂*; Volcan Santa Ana, 5670 ft, 12/XI/53, 1♂*, 1♀. JAMAICA: Hardware Gap, 29/VII/66, 4000 ft, 1♂*, VII/58, 2♀. MEXICO: Puebla, 6 mi E Teziutlan, 17/VIII/58, 1♂*. NICARAGUA: El Recreo, VI/54, 1♂*, 1♀*. PANAMA: Chiriqui, Boquete, VI-VIII/58, 2♂*, 2♀*. PUERTO RICO: Sabana Carib., N. For., 1♂*.

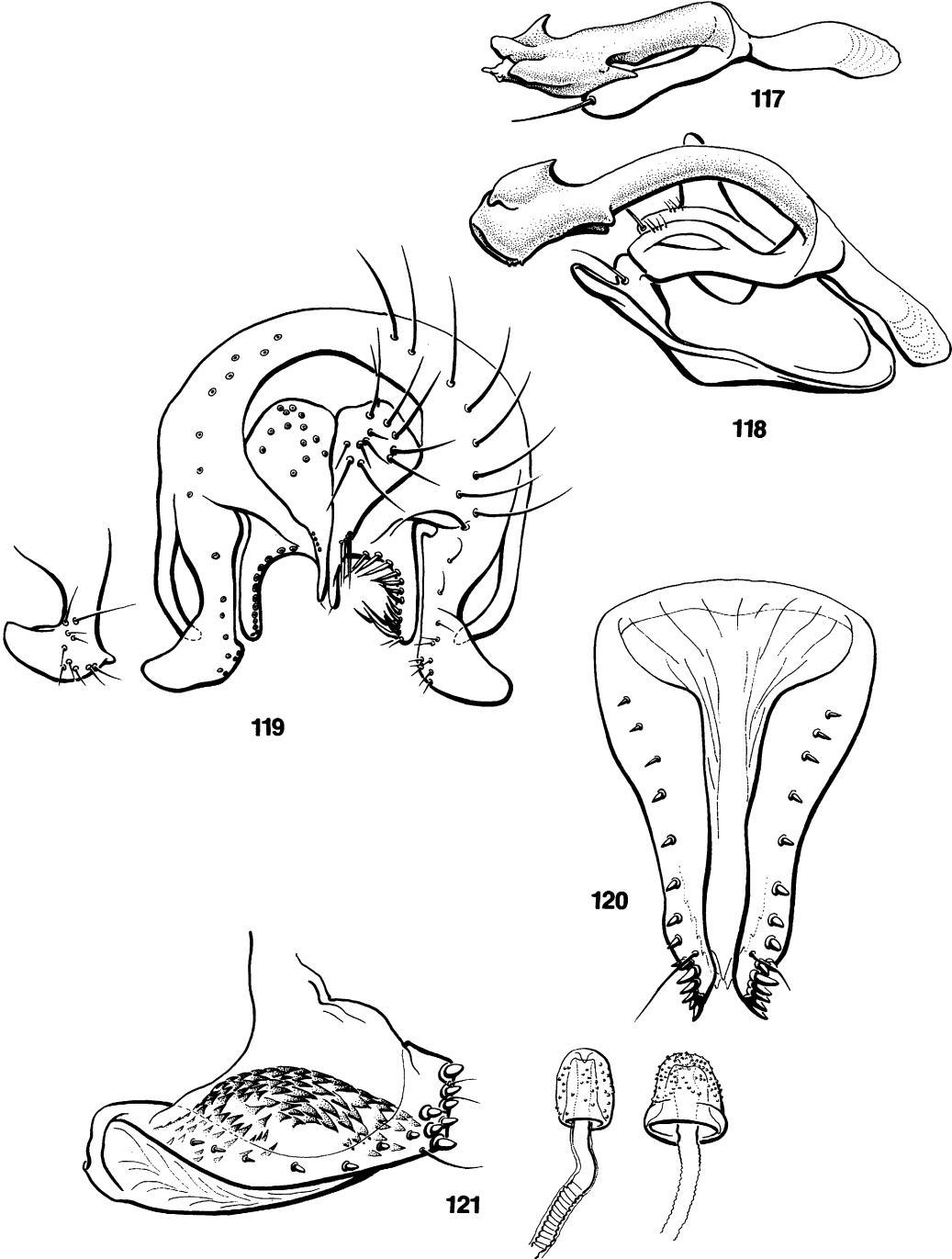
DISCUSSION: Nothing is known of its habits except that, according to label data, it does not seem to be found in lowland areas. Notal coloration varies from generally light brown with two diffuse, incomplete vittae (vitta pr. 2), to an almost black or black-brown notum.

Zygothrica fusalata, new species

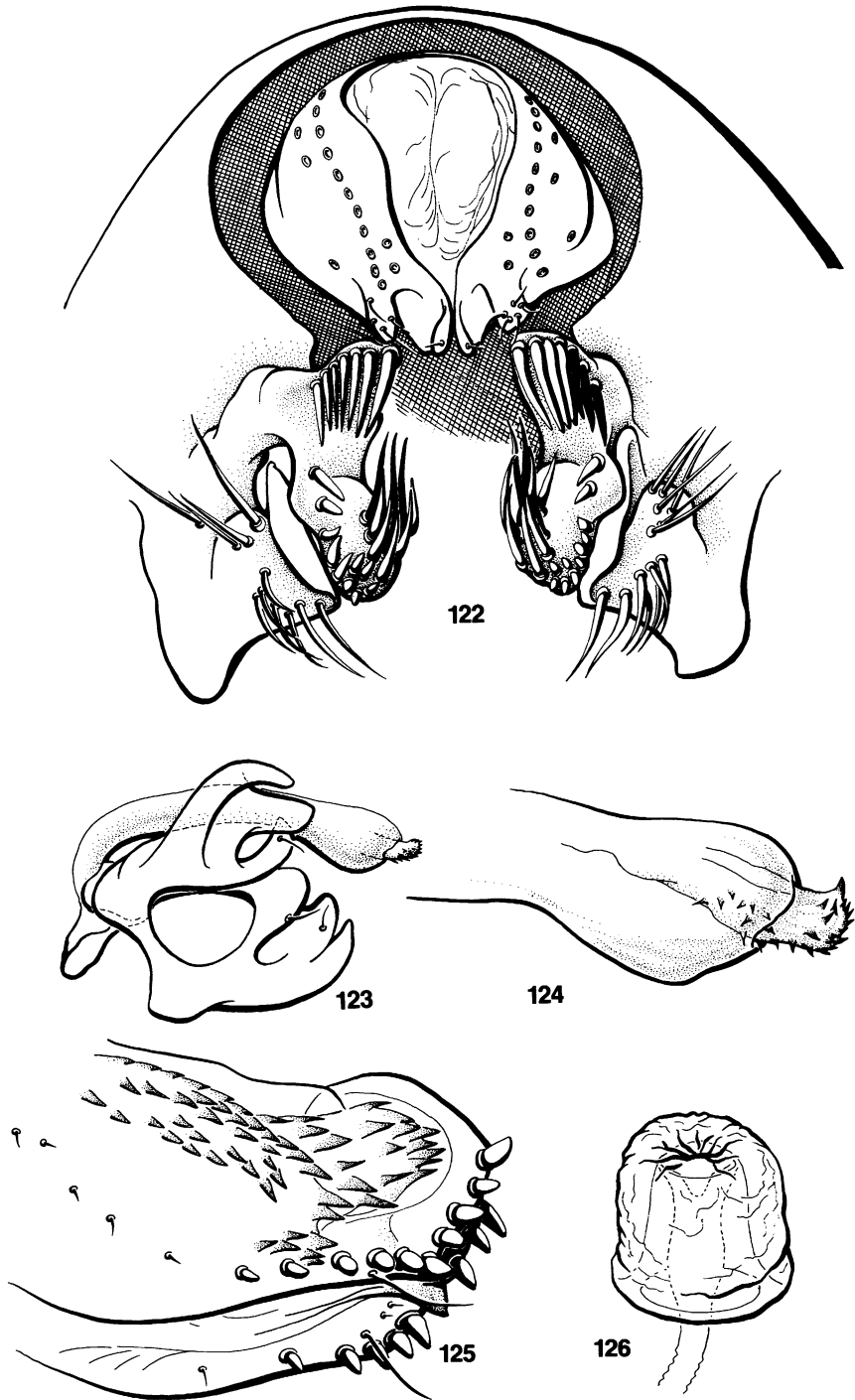
Figures 20, 122–128, 267a

DIAGNOSIS: Halter yellow; notum with diffuse, light median vitta; wing with diffuse brown R_{2+3} , dm-cu, and apical spots; spermatheca wrinkled, distiphallus with finely scaled median lobe.

DESCRIPTION: Head ground color light brown. Frontal-orbital plates $\frac{1}{2}$ width of frontal vittae. Frontal vittae light brown, shiny, finely striate. Eye setulae short, sparse. Ocellar triangle extended to ptilinal fissure, lighter than frontal vittae. Proclinate orbital setae parallel, slightly longer than posterior reclines. Anterior reclines minute, length $\frac{1}{3}$ – $\frac{1}{4}$ length of posterior reclines, slightly closer to proclines than to post. reclines. Posterior reclines slightly divergent, midway between proclinate and inner vertical seta. Ocellar setae extended past proclines. Face light brown. Carina incomplete, ended about at level of vibrissae. Cheek very narrow; facial cheek ca. $2 \times$ cheek height. Oral margin indented to just below vibrissae. Flagellomere I light brown, $2 \times$ length of pedicel, setulae very short. Arista with 5 dorsal and



Figs. 117–121. *Zygothrica microstoma*. 117. Aedeagus (lateral); Boquete, PANAMA. 118. Aedeagus + hypandrium; La Palma, EL SALVADOR. 119. Epandrium; portion of surstylus from Boquete. 120. Oviscape (ventral). 121. Oviscape (lateral); spermathecae: JAMAICA (left), EL SALVADOR (right).



Figs. 122–126. *Zygothrica fusculata*. 122. Epandrium. 123. Hypandrium + aedeagus. 124. Distiphallus. 125. Oviscape, detail of apex. 126. Spermatheca (400×).

3 ventral branches, most are longer than orbital setae. Proboscis yellow; labellum light brown, with elongate and fine setulae. Vibrissa elongate, projected strongly anteriad,

cruciate. Palpus tiny, apically triangular, dark brown, with 1 long apical seta and 10–15 stout, shorter subapical ones.

Thorax ground color brown, with diffuse yellow, median notal vitta complete. Slightly darker and diffuse vitta extended along scutellum. Pleura light yellow. Anterior scutellars divergent, apical scutellars parallel to cruciate. 2 rows acrostichals present. Leg color light yellow. Wings entirely light fuscous; present are R_{2+3} spot, crescent-shaped apical spot, and dm-cu spot. Anal edge very oblique, most of anal lobe lost.

Abdomen light brown, glassy. Posterior row tergal setae thick, particularly lateral ones. Apex of oviscapae laterally flattened, with 10 peg ovisensilla/side (5 on terminal, 5 on ventral margin) and 5 ventral trichoid ovisensilla. Scales on oviprovectore elongate, large, not all touching each other. Spermathecal capsule campanulate; surface wrinkled, no papillae; with basal collar, no apical indentation. Cerci (♀) slightly flattened. Epandrium with 2 pairs ventral lobes which project mediad. Dorsalmost pair of lobes with acute apex, ventral margin setulose; ventral pair lobate, with 2 patches elongate setae. Cerci short; ventral cercal lobes small, pendulate. Hypoproct plates narrow, extended to ventral pair epandrial lobes. Surstylus pendulous, with 25–27 prenisetae (7–8 elongate, setiform dorsally; 10–11 pegs ventrolaterally; 7–8 elongate, setiform ventromedially). Hypandrium extended to anterior margin aedeagal apodeme; anterior margin indented. Gonopods bare, 2 pairs present. Basiphallus ca. $3 \times$ length of aedeagal apodeme, slightly arched. Distiphallus membranous, clavate, with a finely scaled distal lobe that is apparently eversible.

MEASUREMENTS: $N = 3\delta, 2\eta$. ThL = 1.03 δ (0.83–1.22); 1.19 η (1.15, 1.22). HW/ThL = 0.70 δ (0.65–0.74); 0.71 η (0.47, 0.53). ThL/WL = 0.48 δ (0.44, 0.52); 0.50 η (0.53, 0.47). C.I. = 1.89 (1.80–2.01); 4-V = 1.16 (1.08–1.32).

HOLOTYPE: δ , PERU: Tingo Maria, IX/55, Th. Dobzhansky and C. Pavan (AMNH) (genitalia not dissected). ThL = 0.83; HW/ThL = 0.54; ThL/WL = 0.44; C.I. = 1.88; 4-V = 1.32.

ETYMOLOGY: Latin, “dusky wings.”

DISTRIBUTION: Eastern portions of Colombia and Peru (fig. 135).

MATERIAL: (all paratypes) COLOMBIA: Leticia, 9 km NW, VIII/60, 1 δ^* . PERU: Loreto, San Antonio, 20/VIII/65, 2 δ^* , 1 η ; Tingo Maria, IX/55, 1 η^* .

DISCUSSION: Like *Z. microstoma*, nothing is known of the habits of this species.

Zygothrica peruviana, new species

DIAGNOSIS: Wing without markings, halter brown; face and proboscis dark brown; spermatheca papillate, without basal collar; oviscapae with 3 widely spaced ovisensilla on apical margin (δ unknown); C.I. = 2.17.

DESCRIPTION: Head slightly narrower than thorax. Frontal-orbital plates ca. $\frac{1}{2}$ width of frontal vittae, light brown. Frontal vittae dark brown, velvety. Eyes dull red, with sparse setulae. Ocellar triangle light brown, extended to ptilinal fissure, greatest width ca. equal to distance between lateral surfaces of pedicels. Proclinate orbital seta ca. equal to length of posterior reclinate. Anterior reclinate seta minute, $0.3 \times$ length of other orbitals, midway between ipsilateral orbitals. Posterior reclinate slightly closer to proclinate than to inner vertical. Ocellar setae extended to ptilinal fissure. Postocellars convergent, elongate, equal to length of longest orbitals. Inner vertical seta directed anteromediad. Outer vertical seta slightly posterolateral to inner vertical. Face ochre, narrow. Carina yellow, sharp, narrow, nearly complete. Cheek and oral margin dark brown. Flagellomere I brown, $2 \times$ length of pedicel, setulae of intermediate length. Arista with 5 dorsal and 1 ventral branch. Proboscis, clypeus, palpi, dark brown.

Notal ground color brown; with diffuse brown, incomplete vitta pr.2. Scutellum brown. Pleura, legs light yellow. 4 uneven rows acrostichal setulae present. Wings hyaline; anal lobe more developed than in *Z. microstoma* and *Z. fuscilata*, anal vein ca. $2 \times$ longer than in other 2 species; joining of R_{2+3} to C more acute than in other 2 species. Halter knob light brown.

Tergal ground color dark brown, shiny but not glassy. Oviscapae laterally flattened, apically truncate, length ca. $1\frac{1}{2} \times$ width. Oviscapae with 8 peg ovisensilla/side: 3 large ones in subapical row, 3 large ones in apical row, 2 tiny ventroapical ones. Oviprovectore scales triangular, broad to long. Spermathecal cap-

sule trapezoidal in profile, surface of apex lightly papillate; no basal collar or apical indentation.

HOLOTYPE: ♀, PERU: Tingo Maria, IX/55, Th. Dobzhansky, C. Pavan (AMNH) (genitalia dissected, DAG). ThL = 1.15; HW/ThL = 0.68; ThL/WL = 0.52; C.I. = 2.17; 4-V = 1.81.

ETYMOLOGY: "From Peru."

DISTRIBUTION: Known only from the holotype (fig. 135).

COMMENTS: Because the face of this species is wider than those of *Z. microstoma* and *Z. fuscata*, and the fact that the two wing synapomorphies for the group (anal lobe reduction and R_{2+3} abruptly joined to C) are not well developed here, it is clear that *Z. peruviana* is the most primitive of the three species. This species is not included on the cladogram in figure 109.

CLADE 1.2

Figure 109

The most speciose group of *Zygothrica*, and very heterogeneous in distribution, form, and habits. Defined by synapomorphy 29.

CELSA COMPLEX, CLADE 1.2.1.1

(fig. 109)

A distinctive group, defined by synapomorphies 19 and 31–35: tergites glassy, ocellar triangle very large, cheeks high, oviscape elongate and apically flattened, pleura dark, and the species occur at high altitudes (≥ 2000 m). This group has a distribution somewhat similar to that of clade 1.1, except that only one possible representative is known from the Greater Antilles. *Zygothrica florinjecta*, n. sp. and *Z. oviserrata* appear to be sister-species, based on the possession of papillate spermathecal capsules. *Zygothrica vitrea*, n. sp. is tentatively placed in this clade even though the holotype female is a unique specimen. Actually, *Z. vitrea* may be the sister-group to clade 1.2.1.1 since it does not possess the elongate oviscape and high cheeks which are partly characteristic of the clade. However, based on the very large ocellar triangle, the dark and glassy pleura, a low (the plesiomorphic state) but sharp carina, a dorsoventrally flattened oviscape, and a glassy abdomen (ground setulae lost), plus the fact

that it was captured at 4000 ft, there is little doubt about its affinities to clade 1.2.1.1. Placing *Z. vitrea* as the sister-lineage of the *celsa*-subgroup is another example of endemism pattern A for Caribbean *Drosophilidae*, as discussed in Grimaldi (1988).

KEY TO SPECIES OF THE CELSA COMPLEX

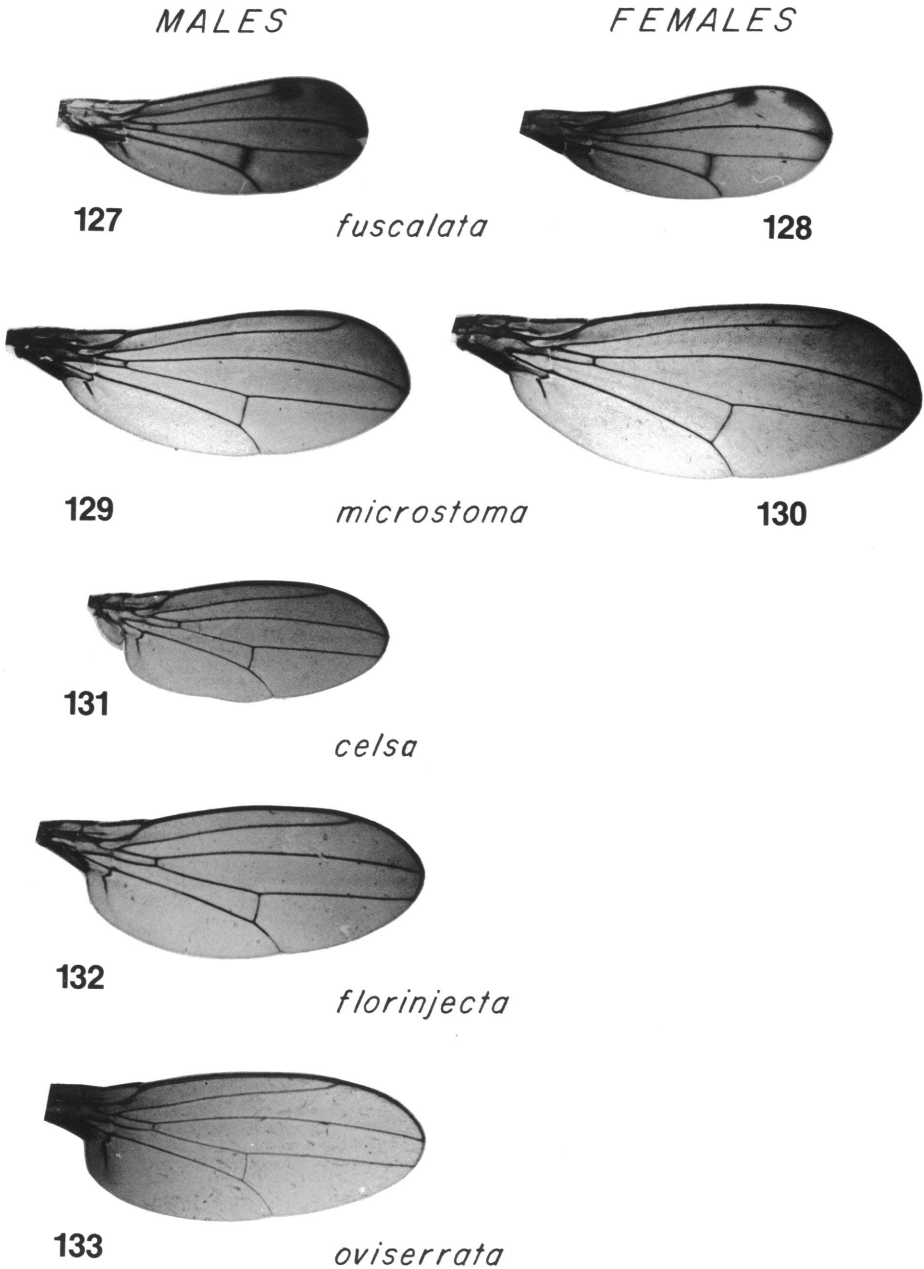
1. Body almost entirely black (including mid and hind femora), shiny in most portions; carina low, white; halteres black *oviserrata*, n. sp.
- 1a. Body at most fuscous or light black-brown; halteres light yellow 2
2. Oviscape short (slightly more than $2 \times$ width), with 3 large ovisensilla on each side of apical margin (fig. 137); C.I. ca. 2.25; Jamaica *vitrea*, n. sp.
- 2a. Oviscape long (length $2.5\text{--}5 \times$ width), with 5 or more terminal ovisensilla per side; C.I. 2.40 or more; Central America 3
3. Tergites III–V with diffuse light, median spots (fig. 267c); each side of oviscape with 5 terminal ovisensilla (fig. 143); thorax length ca. 1.00 mm ($\delta + \eta$); C.I. ca. 2.40 *celsa*, n. sp.
- 3a. Abdomen without such markings; oviscape length $4\text{--}5 \times$ width, with 15–16 small apical ovisensilla per side (figs. 155, 156); thorax length ca. 1.30 mm ($\delta + \eta$); C.I. ca. 3.20 *florinjecta*, n. sp.

Zygothrica vitrea, new species

Figures 136–138

DIAGNOSIS: Ocellar triangle broad, darker than frontal-orbital plates; integument shiny, almost entirely chocolate brown (except face, antennae, and legs, which are yellow); oviscape with 6 large terminal ovisensilla (δ unknown).

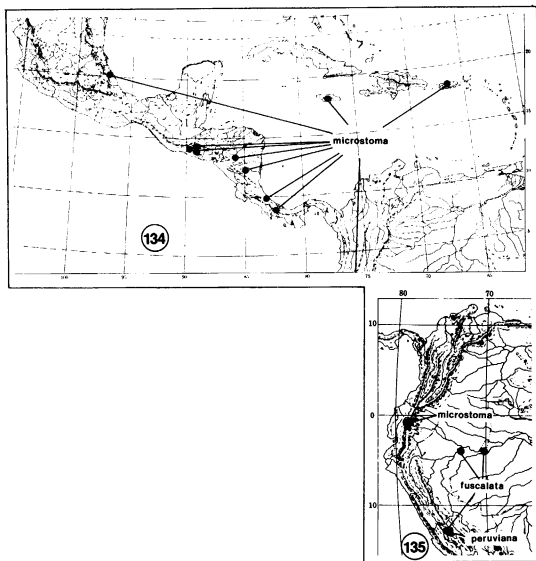
DESCRIPTION: Head mostly ochre; frontal vittae velvety black. Eyes pink, entirely bare. Ocellar triangle extended to ptilinal fissure, shiny, light brown, intraocular area dark brown. Proclimates slightly divergent, equal to length of post. reclimates; ant. reclimates ca. 0.8 length of other orbitals, closer to proclimates than to post. reclimates. Post. reclimates closer to inner verticals than to proclimates. Ocellar setae extended to slightly past anterior reclimates. Postocellars equal in length to ocellars. Inner verticals only slightly anteromedial to outer vertical. Face narrow, ca. $\frac{1}{2}$ width of vertex; yellow, with brown oral mar-



Figs. 127–133. Wings of some *Zygothrica* species in clade 1.1 (figs. 127–130) and in the *celsa* complex (clade 1.2.1.1). All wing photographs are to the same scale. Wherever the wing of one sex is not shown, that sex is either unknown, or the wing is not noticeably different from that of the opposite sex (see descriptions).

gin. Carina yellow and low, very narrow, edge sharp. Cheek shallow, $\frac{1}{10}$ height of eye. Pedicel and flagellomere I ochre, setulae short. Flagellomere I ca. $2 \times$ length of pedicel. Aris-

ta with 3 dorsal and 2 ventral branches. Clypeus same color as oral margin, palpi ochre, labellum and mentum yellow.
Notal ground color brown, shiny; markings



Figs. 134, 135. Distribution of clade 1.1.

indistinct, with incomplete vitta pr.2 slightly lighter than rest of notum. Vitta pr.4 of same color, indistinct. Scutellum, subscutellum, pleura, shiny brown. Apical scutellar setae cruciate, anterior scutellars parallel. 5 rows acrostichals present. Legs entirely yellow. Wings hyaline.

Abdomen unicolorous brown, glassy. Apex of ov scape dorsoventrally flat; ov scape length slightly more than $2 \times$ width. Ov scape with 5 large peg ovisensilla per side (2 dorsal, 3 on terminal margin). Apical oviprovectro scales large, dentate. Spermathecal capsule short ovoid; surface smooth, with small apical indentation. Cerci conical.

HOLOTYPE: ♀, JAMAICA: Hardware Gap, 4000 ft, 6/VII/66, Howden and Becker (CNC) (genitalia dissected, DAG). ThL = 0.95; HW/ThL = 0.88; ThL/WL = 0.46; C.I. = 2.24; 4-V = 1.69.

ETYMOLOGY: Latin, "glassy," in regard to the shiny integument.

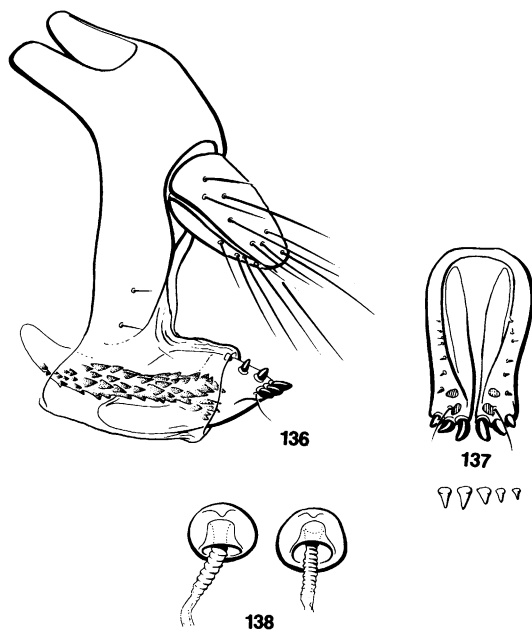
DISTRIBUTION: Jamaica, known only from the holotype (fig. 157).

DISCUSSION: This species is not included on the cladogram in figure 109 because of a lack of male specimens.

***Zygothrica celsa*, new species**

Figures 50, 131, 139–145, 267c

DIAGNOSIS: Diffuse, light median spots on tergites 3–5, diffuse dark triangular spot on

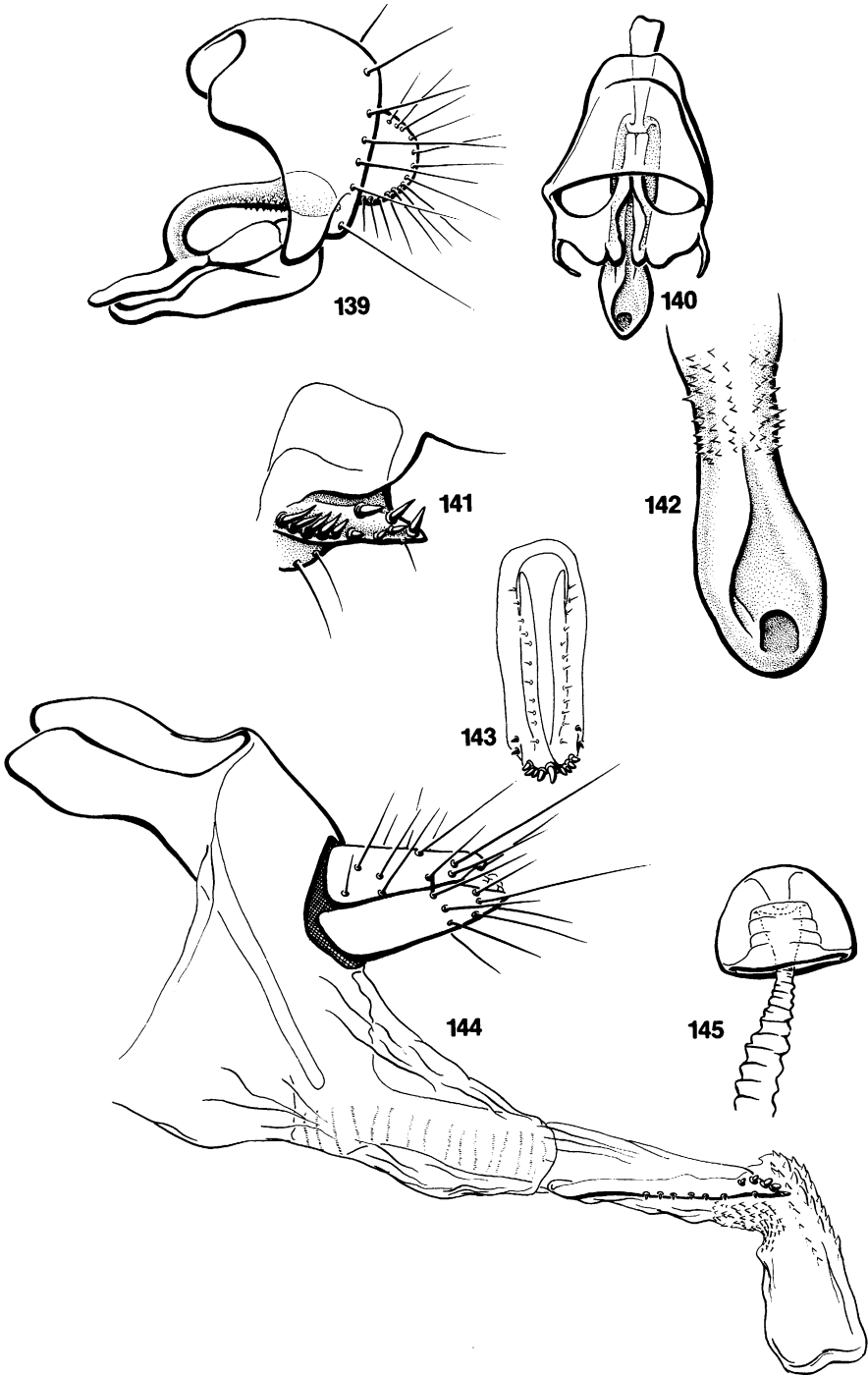


Figs. 136–138. *Zygothrica vitrea*, holotype. **136.** ♀ terminalia, including ov scape (lateral). **137.** Ov scape (ventral) + oviprovectro scales. **138.** Spermathecae.

tergites t VI, VII; distiphallid collar scaled; ov scape spaded, with 5 large, terminal ovisensilla per side.

DESCRIPTION: Head ground color light reddish-brown. Width of frontal-orbital plates less than frontal vittae. Frontal vittae black, velvety. Eye pilosity short, very sparse. Ocellar triangle extended to ptilinal fissure, light brown. Proclinate orbital seta equal to length of posterior reclinate. Anterior reclinate $\frac{3}{4}$ length of post. reclinate, slightly closer to post. reclinate than to proclinate. Posterior reclinate closer to inner vertical than to proclinate. Ocellar setae extended to anterior reclinate, slightly longer than post. reclinate. Face yellow to tan; carina prominent, complete. Cheek deep, $\frac{1}{5}$ height of eye, with brown spot just behind vibrissa. Flagellomere I light brown, length $1\frac{1}{2} \times$ pedicel, setulae short. Arista with 4 dorsal and 1 ventral branch; branches short, length ca. $\frac{1}{3}$ arista length. Proboscis yellow, palpi brown. Oral margin deeply indented, extended to level of flagellomere I apices.

Notum unicolorous black-brown; pleura slightly lighter. Scutellum and postnotum



Figs. 139–145. *Zygothrica celsa*. 139. Epandrium + genitalia (lateral). 140. Hypandrium + aedeagus (ventral). 141. Surstylus. 142. Distiphallus. 143. Oviscape (ventral). 144. ♀ terminalia (lateral). 145. Spermatheca (400×).

same color as notum. Apical scutellar setae cruciate, anterior scutellars convergent. 2 long

humeralis present, 4–5 rows acrostichals. Legs unicolorous yellow, including coxae. Distal

half of profemur with 3–4 ventrolateral setae. Halteres light yellow, wings hyaline.

Abdominal ground color dark brown; t II, III yellow, III–V with diffuse yellow, medial spots; t VI, VII, with dark brown triangle, t VIII brown. Oviscape apex dorsoventrally flat; oviscape ca. $2\frac{1}{2} \times$ longer than wide, with 5 large, terminal, peg ovisensilla and 2 smaller lateral ones, row of 11–12 tiny ovisensilla ventrally per side. Oviprovector scales not dense; large, triangular. Spermathecal capsule short, campanulate; surface smooth, with apical indentation. Cerci yellow, elongate, dorsoventrally flattened. Sternite VII deeply bifurcate, anterior ramus flanged at anterior end. Laterotergite VIII ramus elongate, sclerotized.

Epandrium with 1 pair ventral lobes, tapered. Cerci round; ventral cercal lobes small, with 4–5 setulae. Hypoproctal plates without setulae. Surstylus apically pointed, possesses 11–12 prensisetae: 5–6 setiform dorsolaterals, 3 setiform ventromedials, 2–3 tiny peg ventrolaterals. Gonopods narrow, elbowed, 1 pair present, surface bare. Basiphallus ca. $1\frac{1}{2} \times$ length of aedeagal apodeme. Aedeagus clavate. Distiphallus membranous, collar finely scaled.

MEASUREMENTS: N = 4♂, 3♀. ThL = 0.93 ♂ (0.83–0.98); 1.02 ♀ (0.97–1.08). HW/ThL = 0.73 ♂ (0.71–0.75); 0.72 ♀ (0.71–0.74). ThL/WL = 0.41 ♂ (0.39–0.42); 0.42 ♀ (0.41–0.42). C.I. = 2.37 (2.20–2.56); 4-V = 1.69 (1.58–1.79).

HOLOTYPE: ♂, MEXICO: Chiapas, San Cristobal de Las Casas, 7087 ft, 3–7/VI/69. B. V. Peterson (CNC) (genitalia not dissected). ThL = 0.94; HW/ThL = 0.72; ThL/WL = 0.42; C.I. = 2.33; 4-V = 1.58.

ETYMOLOGY: Latin, “high,” in regard to its altitudinal distribution.

DISTRIBUTION: Southern Mexico to El Salvador (fig. 157).

MATERIAL: (all are paratypes) Series of 63♂, 46♀ collected 14–27/V/69 at 7000–7200 ft in the same locality as the holotype. Others: MEXICO: Distrito Federal, Desierto Leones, III–V/65, 1♂*. EL SALVADOR: La Palma, 3200 ft, VIII/54, 1♂*.

Zygothrica oviserrata, new species

Figures 11, 133, 146–150

DIAGNOSIS: Body mostly black, shiny in some portions. A low, narrow, white carina,

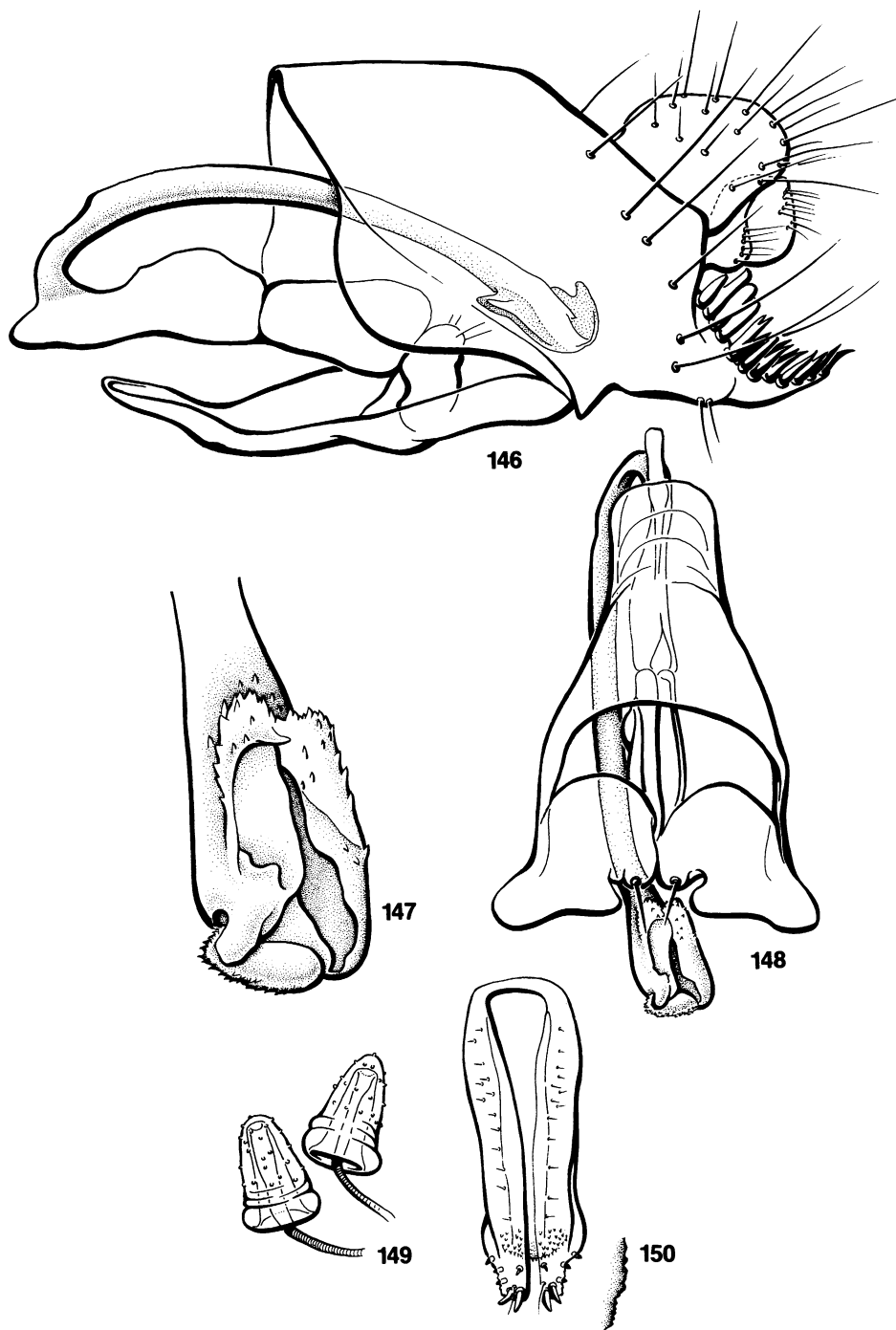
broad palpi, black halteres, dark meso- and metathoracic femora, and a black, glassy abdomen with light cerci are obvious external features. Terminalia are distinctive as described below.

DESCRIPTION: Head ground color black to black-brown, anterolateral portions of front cream. Frontal-orbital plates narrow. Frontal vittae very narrow, width less than frontal-orbital plates. Eye pilosity sparse, short. Ocellar triangle large: narrow edge bordered on ptilinal fissure; glassy, black. Proclinate orbital setae parallel, equal to length of post. reclinates. Anterior reclinates finer than other orbitals, slightly shorter in length, closest to post. reclinates. Posterior reclinates divergent, closest to inner verticals. Ocellar setae fine, extended to proclimates. Face brown laterally; carina white, with narrow edge, very low. Cheek deep, ca. $\frac{1}{3}$ depth of eye. Oral margin deeply indented, extended past level of flagellomere I apices. Flagellomere I length $3 \times$ pedicel, setulae short. Pedicel and flagellomere I dark brown. Arista with 3–4 dorsal and 1 ventral branch. Proboscis dark brown. Palpi dark brown, wide (width about equal to that of proboscis).

Ground color of notum, scutellum, postnotum, and pleura, evenly dark brown. Pleura glassy. 2 elongate humerals, 6 rows long, fine acrostichals present. Forelegs entirely yellow; mid and hind femora dark brown, apices diffuse yellow; mid and hind tibiae and tarsi yellow. Forefemur with ventral row 5 evenly spaced setae, lengths ca. equal to width of femur. Halteres black; wing hyaline.

Abdominal ground color black-brown, glassy. Oviscape flat, elongate ($3 \times$ longer than wide). Oviscape with lateral margins deeply indented apically; with uneven, fine serrations in this area. Oviscape with 5 large terminal, 1 tiny ventral peg ovisensilla per side; 10–13 fine ventral sensilla. Oviprovector scales sparse, very fine. Spermathecal capsule campanulate, apically narrowed; surface sparsely papillate; basal collar present; no apical indentation. Cerci flattened, tan to white. Sternite VII bifurcate ca. $\frac{1}{3}$ length; short, narrow anterior ramus present.

Epandrium dorsally elongate, black, glassy. Ventral epandrial lobes rudimentary. Cerci rounded, tan; ventral cercal lobes present, with row of 7–8 setulae. Hypoproctal plates small, rounded. Surstylus pointed apically, with 15–16 large, thick prensisetae arranged



Figs. 146–150. *Zygothrica oviserrata*. 146. ♂ terminalia (lateral). 147. Distiphallus (ventral). 148. Aedeagus + hypandrium (ventral). 149. Spermathecae. 150. Oviscape (ventral), with detail of lateroapical margin.

in even row. Hypandrium simple. Gonopods simple, lobate. Basiphallus elongate, ca. 3 × length of aedeagal apodemc, arched. Distiphallus complex: with finely scaled, dorsal flap; gonopore opening uneven, with small ventral, finely scaled flap.

phallus complex: with finely scaled, dorsal flap; gonopore opening uneven, with small ventral, finely scaled flap.

MEASUREMENTS: N = 3♂, 2♀. ThL = 1.27 ♂ (1.13–1.49); 1.09 ♀ (1.04, 1.13). HW/ThL = 0.68 ♂ (0.67–0.68); 0.71 ♀ (0.70, 0.72). ThL/WL = 1.27 ♂ (1.13–1.49); 1.09 ♀ (1.04, 1.13). C.I. = 2.13 (1.99–2.24); 4-V = 1.78 (1.66–1.93).

HOLOTYPE: ♂, COLOMBIA: near Bogotá, Usme-El Hato Road, VIII/60, W. B. Heed, H. L. Carson (AMNH) (genitalia dissected, DAG). ThL = 1.19; HW/ThL = 0.80; ThL/WL = 0.41; C.I. = 2.07; 4-V = 1.77.

ETYMOLOGY: Latin, "egg tooth," for serrations at the tip of the oviscape.

DISTRIBUTION: Eastern Andean slopes, El Salvador to Ecuador (figs. 157, 158).

MATERIAL: (all are paratypes) ECUADOR: Azuay, Cerro Tinajillas, 3100 m, 18–21/III/65, 1♂*; Carchi, Troya, 2950 m, 11–13/VI/65, 1♂, 1♀*. EL SALVADOR: Monte Cristo, 7–9/V/58, 1♂*.

DISCUSSION: Like most of the other members of the *celsa* group, nothing is known of the habits of *Z. oviserrata* other than its altitudinal distribution.

***Zygothrica florinjecta*, new species**

Figures 8, 132, 151–156, 267b; table 1

DIAGNOSIS: Ocellar setae parallel; face light, palpi and antennae dark brown; oviscape elongate, spaded; aedeagus simple and short; halter light yellow, notum with distinct, dark brown median vitta; pleura and femora dark brown.

DESCRIPTION: Head ground color light brown, blending to white in some areas. Frontal-orbital plates wider than frontal vittae. Frontal vittae velvety-black. Eyes dark gray-brown; with flat hind margin; interfacetal setulae sparse. Ocellar triangle extended to ptilinal fissure. Anterior reclines fine, ½ length other orbitals, midway between procclines and post. reclines. Post. reclinate closest to inner vertical. Ocellar setae parallel. Face 0.6 width of vertex, light yellow to white. Oral margin deeply indented: extended to tip of flagellomere I. Carina low, narrow, with very sharp edge. Cheek ca. ¼ height of eye, light brown to yellow. Flagellomere I gray-brown, 1½–2 × length of pedicel. Arista with 4 dorsal and 1 ventral branch. Pedicel mostly brown, with anterior yellow spot. Labellum light brown, narrow, dorsal plates sclerotized. Palpi narrow, dark brown.

Thorax ground color brown, including pleura, scutellum, and postnotum. Postpronotal lobe ochre. Notum with complete, distinct, dark brown median vitta bordered by diffuse, light brown to ochraceous vitta pr.2. Median vitta wide, about ⅓ width of notum. 7 rows acrostichal setulae present. Femora light brown, graded into light yellow of tibiae and tarsi. Forecoxae light, elongate, nearly equal to length of femora. Wings hyaline, halteres yellow.

Abdomen shiny; tergites II, III dark brown; t IV–VII ochre, t IV + V with dark lateral margins. Oviscape elongate, apex flat, terminal margins oblique; length 4½ × width. Oviscape with 15–16 peg ovisensilla/side in terminal rows; 14–16 ventral sensilla. Oviprovector scales sparse, small. Spermathecal capsule trapezoidal; surface mostly bare, apically papillate; large apical indentation present. Cerci elongate, cylindrical, ochre. Laterotergite VIII elongate: length ca. equal to oviscape. Anterior ramus S VII elongate, projected beyond anterior margin S VI.

Epandrium ochre, dorsoventrally elongate. Ventral epandrial lobes broad, with 6–7 setae. Cerci rounded, ochre; ventral cercal lobes low, triangular, with 3 setulae. Surstyli small, close together; possess 16–17 prensisetae each (6 laterals, 10–11 medials). Hypandrium simple. Gonopods simple, curved mediad. Paraphysial seta stout; 2 paraphysial setulae/side. Basiphallus short, basally trough-shaped, length 1.5–1.75 × aedeagal apodeme. Distiphallus membranous, slightly wider than basiphallus, unadorned.

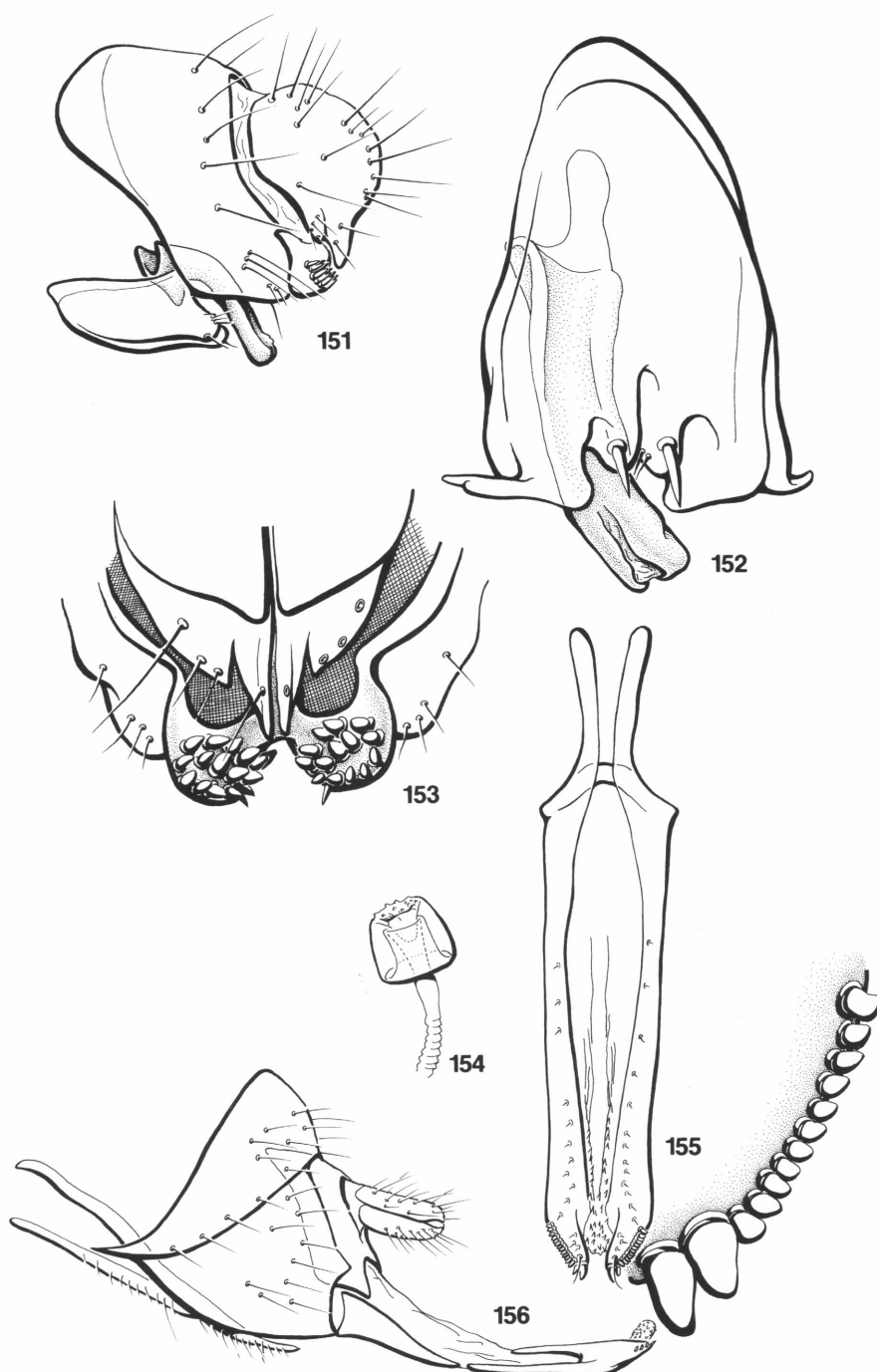
MEASUREMENTS: N = 3♂, 3♀. ThL = 1.25 ♂ (no range); 1.33 ♀ (1.31–1.37). HW/ThL = 0.63 ♂ (0.61–0.64); 0.62 ♀ (0.62–0.64). ThL/WL = 0.42 ♂ (0.41–0.43); 0.43 ♀ (0.42–0.44). C.I. = 3.17 (2.98–3.38); 4-V = 1.37 (1.28–1.41).

HOLOTYPE: ♂, COLOMBIA: 25 km W Bogotá, VII/60, W. B. Heed and H. L. Carson (AMNH) (genitalia not dissected). ThL = 1.25; HW/ThL = 0.63; ThL/WL = 0.43; C.I. = 3.13; 4-V = 1.37.

ETYMOLOGY: Latin, "flower-injector," for the type of breeding site and the form of the oviscape.

DISTRIBUTION: Colombia (fig. 157).

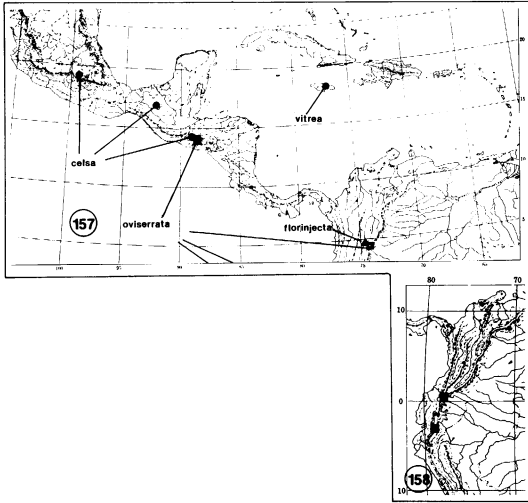
MATERIAL: (all are paratypes) 5♂, 5♀, same collection locality and date as holotype, and 8♂, 7♀, collected 50 km W Bogotá, Colombia.



Figs. 151–156. *Zygotherica florinjecta*. 151. ♂ terminalia (lateral). 152. Hypandrium + aedeagus (ventral). 153. Surstyli. 154. Spermatheca. 155. Oviscape (ventral), with detail of apical row of ovisensilla. 156. ♀ terminalia (lateral).

DISCUSSION: Based on personal communications with Dr. Hampton L. Carson, all

specimens in the above type series were reared from flowers of a *Salvia* species (Labiatae).



Figs. 157, 158. Distribution of the *celsa* species-group.

The subparamo (about 9000 ft) is presumably their habitat, and a photograph of the type locality is given in Carson (1971: 12, fig. B). Eight flower species, in the families Compositae, Labiatae, Passifloraceae, and Rosaceae were found to harbor larvae of 14–17 drosophilids in this area (Heed et al., 1960). Collections were made from 6000 to 11,000 ft in the Bogotá region, and approximately 23 drosophilid species were found breeding in 16 species of plants, but *Z. florinjecta* was restricted to the use of a *Salvia* species. The other *celsa* complex species probably have the same florophagous larval habit.

Listed below are apomorphies (numbers 85–129) used for phylogenetic reconstruction of species in *Zygothrica* clade 1.2.1.2, or the *dispar* complex. Numbering of the apomorphies continues with the prior listing used for the higher-level relationships. Here, too, an asterisk denotes the multiple occurrence of an apomorphic state. Phylogenetic hypotheses are presented in figures 159–163, and the one in figure 164 is an alternative hypothesis for some species in the *aldrichii* species-subgroup (cf. fig. 163). The cladogram in figure 164 assumes fewer repeated origins of several apomorphies; in particular, apomorphy 121 here evolved three times instead of four, and 123 arose once instead of twice, but 119 is hypothesized to have arisen once more than in the scheme in figure 163. A classification is presented in table 7 which is based

on the results in figures 159–164 and includes a tentative classification of clade 1.2.2.

85. Tergite VII (♀) shape. A = broadly triangular in lateral view (P = bandlike, as in preceding tergites).

86. Development of laterotergite VIII in ♀. A = extended ventrolaterad (P = laterotergite VIII not developed).

*87. Frontal vitta. A = velvety black (P = shiny, or microtomentose, golden-yellow, or tan).

88. Line extended from proclinate orbital seta to posterior reclinate orbital. A = pointed toward outer vertical or laterad in both sexes or in ♀ only (P = pointed toward inner vertical in both sexes).

89. Ocellar triangle width. A = dorsal portion $\frac{4}{5}$ or more width of face (P = dorsal portion $\frac{1}{2}$ or less width of face).

90. Apex of spermatheca. A = with prominent apical indentation (P = slight depression at apex, or even).

91. Distiphallal vestiture. A = gross spines present (P = scales present, or distiphallus glabrous).

*92. Apex of wing, especially in ♂. A = dark, diffuse brown spot present (P = wing completely hyaline).

93. Medial surface of gonopod. A = evenly concave, brackets distiphallus (P = lobate, simple).

94. Distiphallal shape. A = with preapical lateral flanges (P = cylindrical, tapered, or clavate).

95. Shape of distiphallus apex. A = triangular (P = bulbous or rounded).

96. Shaft of basiphallus. A = dorsoventrally flattened; wide, only slightly narrower than distiphallus (P = narrow, cylindrical).

*97. Head shape of males. A = hypercephalic: eyes and frontal-orbital plates laterally distended (head $\geq 1.75 \times$ as wide as thorax) (P = head $\leq 1.2 \times$ thorax width, eyes not tapered apicad).

*98. Ventral surface of gonopod. A = extensively and finely wrinkled (P = smooth).

99. Wing maculations. A = elaborate, involves dm-cu, wing apex, most of distal half of wing (P = wing hyaline).

100. Wing maculations. A = distal half of wing transected with bands (P = wing hyaline).

101. Postvertical setae. A = hypermorphic in ♂, lengths equal to or greater than

lengths of orbitals; very thick (P = small, inconspicuous, not apparent when head is viewed from front).

*102. Distiphallal vestiture. A = scales lost (P = erect scales present, extensive over most of distiphallus).

103. Oviscape shape (viewed dorsoventrally). A = distal half with lateral margins flared outward, then tapered distad (P = even and gradual tapering of apex, or sides parallel).

104. Prentisetiae sizes and shapes. A = most are peglike, especially medial and lateral ones (P = spinose, setose).

105. Surstylus shape. A = crescent-shaped when viewed posteriorly (P = lobate, or broadly triangular).

106. Ventral row of setae on profemur. A = stout, black, sharp (P = fine, not much differentiated from ones anterolateral on femur).

*107. Aedeagus size and shape. A = distiphallus bulbous; aedeagus very short, length ca. equal to length of aedeagal apodeme (P = length $\geq 1.5 \times$ length of aedeagal apodeme).

108. Dorsal surface of proboscis: medial surface of labral sheath. A = with 5–6 straight, black setae/side projected mediad (P = no setae present).

109. Line extended from proclinate orbital seta to posterior reclinate orbital, in δ . A = extended lateral to outer vertical seta (P = in line with outer vertical seta in δ and φ).

110. Lengths of setae in ventral row on profemur. A = elongate; lengths equal to or greater than width of femur (P = $\leq \frac{3}{4}$ femur width).

111. Apex of hind tibia, δ and φ or in φ alone. A = dark band present (P = no band).

112. Color of distal portion of of entire labium. A = dark (P = light yellow or ochre).

*113. Crossvein dm-cu. A = infuscated (P = hyaline on vein).

*114. R_{2+3} apex. A = spot present, or spot coalesced into midradial spot or radial infuscation (P = apex of wing hyaline).

115. Anterior hypandrial margin. A = distinctly and narrowly lobate (P = contour even).

116. Aedeagus. A = elongate, lanceolate, in dorsoventral view (P = bulbous distiphallus).

117. Ventral surface of gonopod. A = possesses microsetulae (spiculate) (P = glabrous).

*118. Spermathecal surface. A = scaled (P = papillate, or smooth).

*119. Length of hypoproctal plates (δ). A = elongate; extended to surstyli or past them (P = shorter, not extended past ventral margin of the epandrium).

*120. Shape of surstyli. A = pendulous: lobate and hung by base that is thinner than surstylus (P = not pendulate; broadly attached).

121. φ pleural color. A = dark, brown-black, color same as notum and tergites (P = pleura light, same color as pleura in δ).

122. Coloration of crossvein dm-cu. A = infuscation lost (see no. 113) (P = infuscated).

123. Coloration of φ mid and/or hind femora. A = dark, same color as pleura and tergites (P = not darkened).

124. R_{2+3} spot. A = elongate, extended to midradial region in δ and in φ (P = R_{2+3} spot localized at apex of vein).

125. Apical surstylar seta. A = scaliform, lanceolate (P = setiform, simple).

126. Distiphallal shape. A = apex broadly scoop-shaped: gonopore very wide (P = completely tubular, or with narrow ventral trough).

127. Coloration of φ femora. A = all are black-brown (P = only mid and hind femora dark, or all femora are light).

128. Radial infuscation on δ wing. A = extended to M_{1+2} (P = extended at most to R_{2+3}).

129. Foretarsal setae on δ . A = many erect; erect ones longer than ground setulae either slightly or by about $10 \times$ the length (P = scattered erect setae not apparently longer than decumbent, ground setulae).

DISPAR COMPLEX, CLADE 1.2.1.2

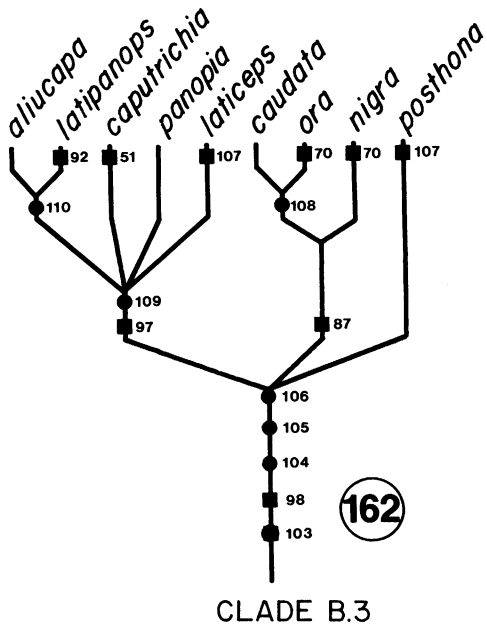
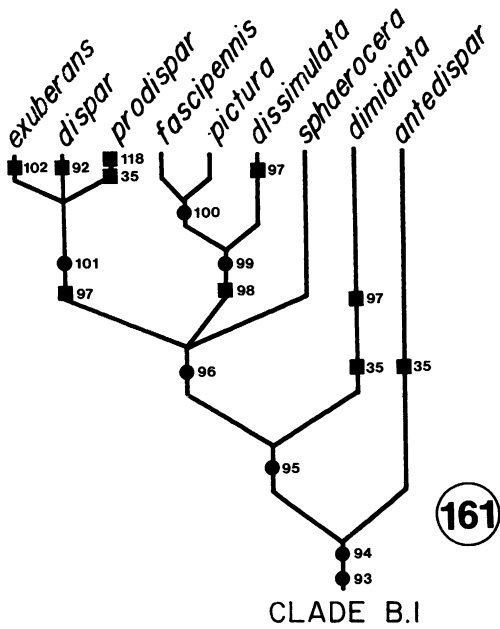
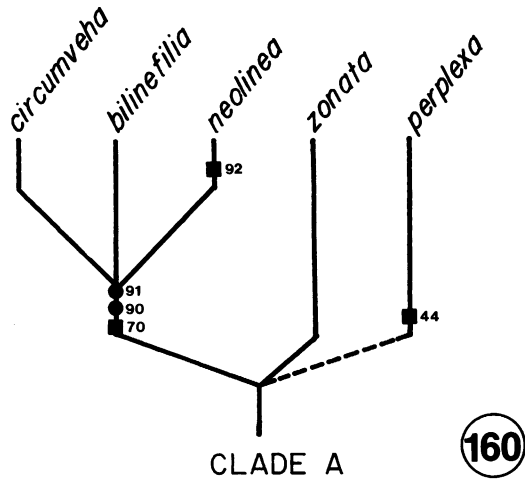
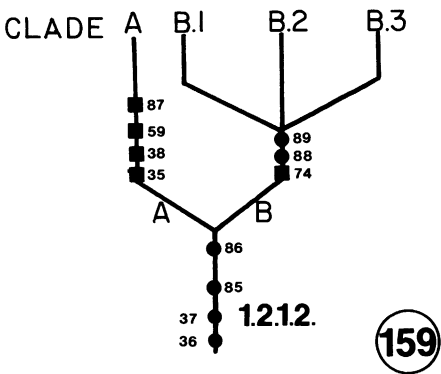
(fig. 159)

Defined by the presence of a protuberant face with the anterolateral corners splayed (apomorphy 36), a lip on the oral margin (37), a broadly triangular sternite VII in the female (85), and tergite VIII in the female has a well-developed laterotergal ramus (86).

NEOLINEA SPECIES-GROUP, CLADE 1.2.1.2.A

(fig. 160)

Contains the following species: *Zygothrica perplexa*, n. sp., *Z. zonata*, n. sp., *Z. neolinea*, n. sp., *Z. bilinefilia*, n. sp., *Z. circumveha*, n.



Figs. 159–162. Phylogenetic hypotheses for the *dispar* complex (clade 1.2.1.2). 159. Highest-level relationships. 160. *neoleia* species-group. 161. *dispar* species-subgroup. 162. *caudata* species-subgroup.

sp., and *Z. femina*, n. sp. The defining features are homoplasious, but each apomorphy is found in groups at various taxonomic levels, and they include the following: apomorphy 35 (dorsoventrally flattened oviscapex apex—seen also in clade 1.2.1.1 and in several lin-

eages of 1.2.1.2.B); 38 (presence of incomplete, light notal vitta pr.2—this trait is found in a few members of clade 1.2.1.2.B, three members of clade 2, and numerous species in 1.2.2); 59 (presence of a narrow, yellow median frontal vitta—seen also in 1.2.1.1 and

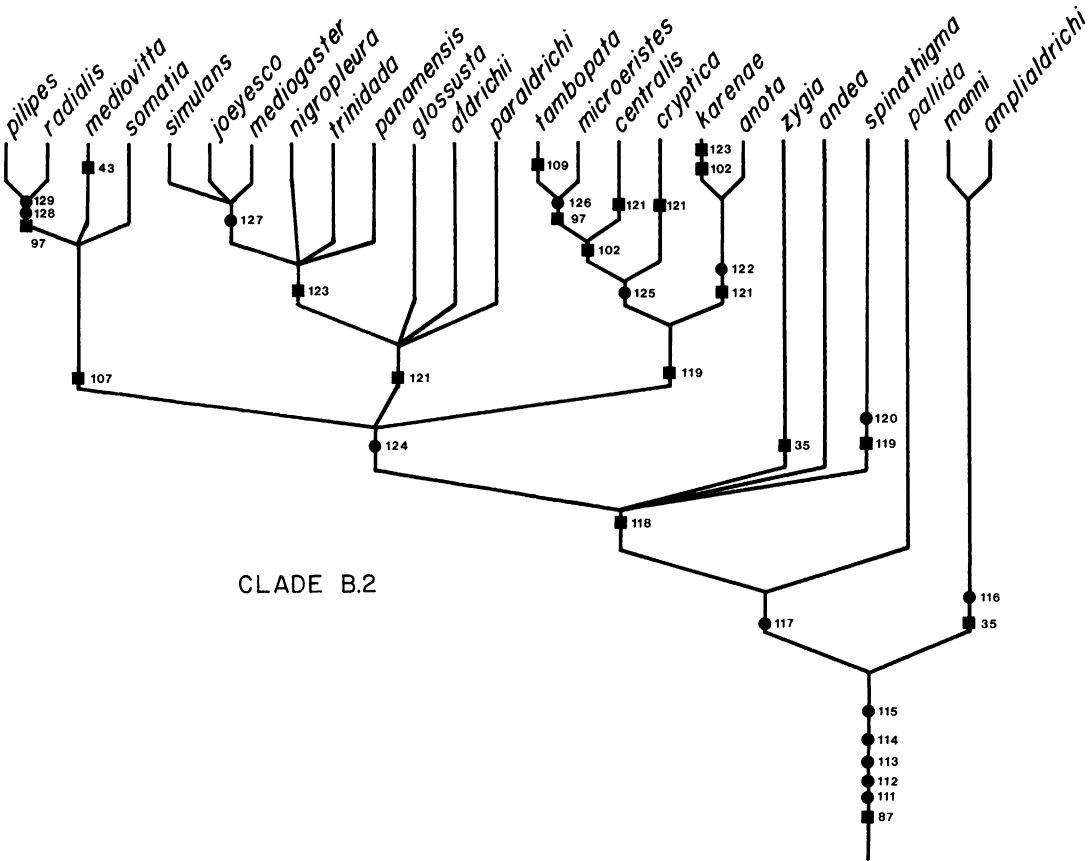


Fig. 163. Hypothesis of phylogenetic relationships for the *aldrichii* species-subgroup.

in clade 2); 87 (velvety black frontal vittae—seen again in clade 1.2.1.1, and in three species of clade 1.2.1.2.B.3). In addition, all the species have a dark brown notal ground color which usually ends abruptly at the notopleural suture, light pleura and legs, and all except *Z. perplexa* and the males of *Z. neolinea* have hyaline wings. Females are generally darker in cephalic features than are males, especially on the cheeks, the palpi, and the first flagellomeres.

The geographical and altitudinal distribution of the *neolinea* species-group is very similar to that of the *celsa* complex and to that of clade 1.1. There are three synapomorphies that define a clade for *Z. circumveha* + *Z. bilinefilia* + *Z. neolinea*: apomorphy 70 (large, placoid oviprovectors— which is also the defining state for clade 3), 90 (spermathecal apex with a prominent apical indentation), and 91 (aedeagus with 2–4 large spines).

IDENTIFICATION KEY TO SPECIES OF THE *NEOLINEA* SPECIES-GROUP

- 1. ♂ and ♀ wing with discrete apical spot (fig. 170) *perplexa*, n. sp.
- 1a. Wing hyaline, or with light, diffuse apical infuscation of ♂ 2
- *2. Oviscape tapered apicad (figs. 178, 195) .. 3
- 2a. Oviscape apex truncate, dorsoventrally flattened (e.g., figs. 184–189) 4
- 3. Apex of palp rounded; spermatheca papillate; distiphallus with 2 large ventral spines directed posteriad (figs. 192, 194)
..... *circumveha*, n. sp.
- 3a. Apex of palp with oblique ventral margin; spermatheca glabrous (♂ unknown)
..... *femina*, n. sp.
- 4. Oviscape oval in dorsolateral view (fig. 176); spermatheca ca. 2 × broader than high (fig. 177); distiphallus with 2 blunt, ventral knobs, epandrium with 2 pairs ventral lobes (figs. 172, 175) *zonata*, n. sp.
- 4a. Oviscape approximately rectangular in dor-

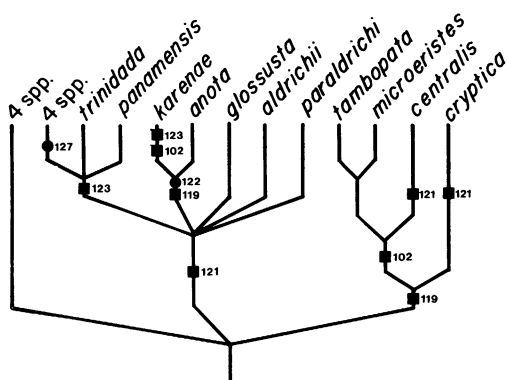


Fig. 164. Alternative phylogenetic hypothesis for some species in the *aldrichii* species-subgroup.

solateral view (figs. 184, 189); spermatheca height ca. equal to width; distiphallus with prominent spines, small ventral field of microspicules 5

5. ♂ with brush of 12–14 fine, elongate setae on apex of midtibia; midtarsi with 4–5 elongate, erect setae (fig. 182); distiphallus with 8 spines; surstylus with 18–20 prensisetae (figs. 180, 181); C.I. ca. 3.20 *neolinea*, n. sp.

- 5a. ♂ without such setae; distiphallus with 6 large spines, several smaller ones; surstylus with ca. 13 prensisetae (figs. 186, 187); C.I. ca. 2.60 *bilinefilia*, n. sp.

* Identification past this couplet requires microscopic examination of the genitalia.

Zygothrica perplexa, new species

Figure 170

DIAGNOSIS: Wing with discrete apical brown spot; apex of palp dark brown; spermatheca bare, square-oval; terminal margin of oviscapae with 8 ovisensilla/side (♂ unknown).

DESCRIPTION: Head ground color light yellow. Lunule ochre, dull. Frontal-orbital plates light yellow, shiny. Frontal vittae dark brown, velvety. Eye pilosity short, sparse. Ocellar triangle narrow, extended to proclimates, dorsal part dark brown. Proclinate orbitals equal to lengths of ant. reclinate. Anterior reclinate midway between proclimates and post. reclinate. Post. reclinate closest to inner verticals. Ocellar setae extended to anterior reclinate. Vertex lateral to inner verticals is dark brown. Face very light yellow; carina prominent, complete. Cheek with dark brown spot, extended to facial cheek. Pedicel yellow, flagellomere I light brown. Flagellomere I $2\frac{1}{2} \times$

length of pedicel; setulae short, slightly longer on apex. Arista with 4 dorsal + 2 ventral branches. Proboscis light yellow; labellum and distal portion of palp dark brown.

Notal ground color dark brown; yellow, incomplete, vitta pr.3 extended nearly to posterior dorsocentrals. Dorsal part of scutellum entirely dark brown. Pleura light yellow. Apical scutellar setae cruciate; anterior scutellars slightly convergent. 6 rows acrostichal setulae present. Legs light yellow. Wings with brown apical spot; spot extended from just before R_{4+5} to shy of R_{2+3} . Halteres yellow. Abdominal coloration and ♀ terminalia indistinguishable from that of *Z. bilinefilia*.

HOLOTYPE: ♀, PANAMA: Cerro Campana, VII/67, W. W. Wirth (NMNH) (genitalia dissected, DAG). ThL = 1.27; HW/ThL = 0.72; ThL/WL = 0.55; C.I. = 2.53; 4-V = 1.58.

ETYMOLOGY: Latin, “perplexing.” The species is almost identical in most details, including the ♀ genitalia, to *Z. bilinefilia* except for the color features given in the diagnosis and description.

DISTRIBUTION: Known only from the holotype (fig. 199).

Zygothrica zonata, new species

Figures 172–177, 267g, h

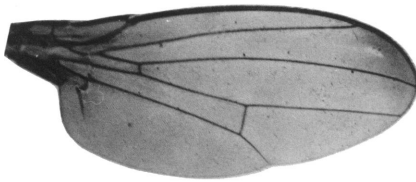
DIAGNOSIS: Proboscis with mediolabral setae a, b; incomplete yellow vitta pr.5 present; surstylus apically very narrow; aedeagus straight, with 2 ventral blunt spines; oviscapae oval.

DESCRIPTION: Frontal-orbital plates shiny. Frontal vittae light brown, dull. Eye setulae short, sparse. Ocellar triangle narrow, extended to lunule; dark dorsally, yellow anteriorly. Proclinate orbital $2 \times$ length of ant. reclinate; ant. reclinate slightly closer to proclinate than to post. reclinate, or midway between them. Ocellars extended to proclimates. Face yellow; carina pronounced and complete in ♀, incomplete in ♂. Cheek, facial cheek, dark brown in ♀, splayed; yellow, unmodified in ♂. Flagellomere I light brown, $2\frac{1}{2} \times$ length of pedicel; setulae short, distal ones longer. Arista with 4–5 dorsal and 1 ventral branch. Proboscis yellow, labellum light brown. Medi-labral setae a + b present, directed laterad. Palpi yellow, narrow.

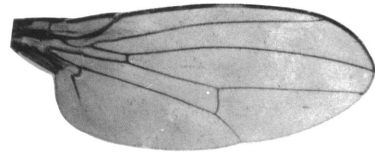
Notal ground color dark brown, not extended to notopleural suture. Distinct, in-

MALES

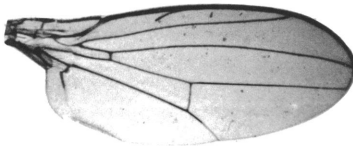
FEMALES



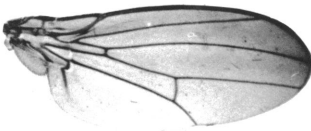
165

neolinea

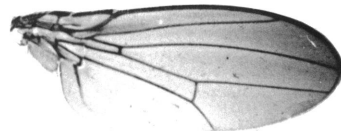
166



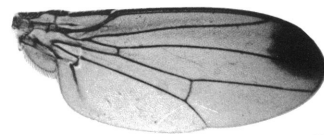
167

femina

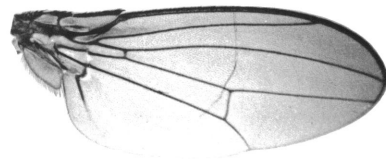
168

bilinefilia

169

*perplexa*

170

*antedispar*

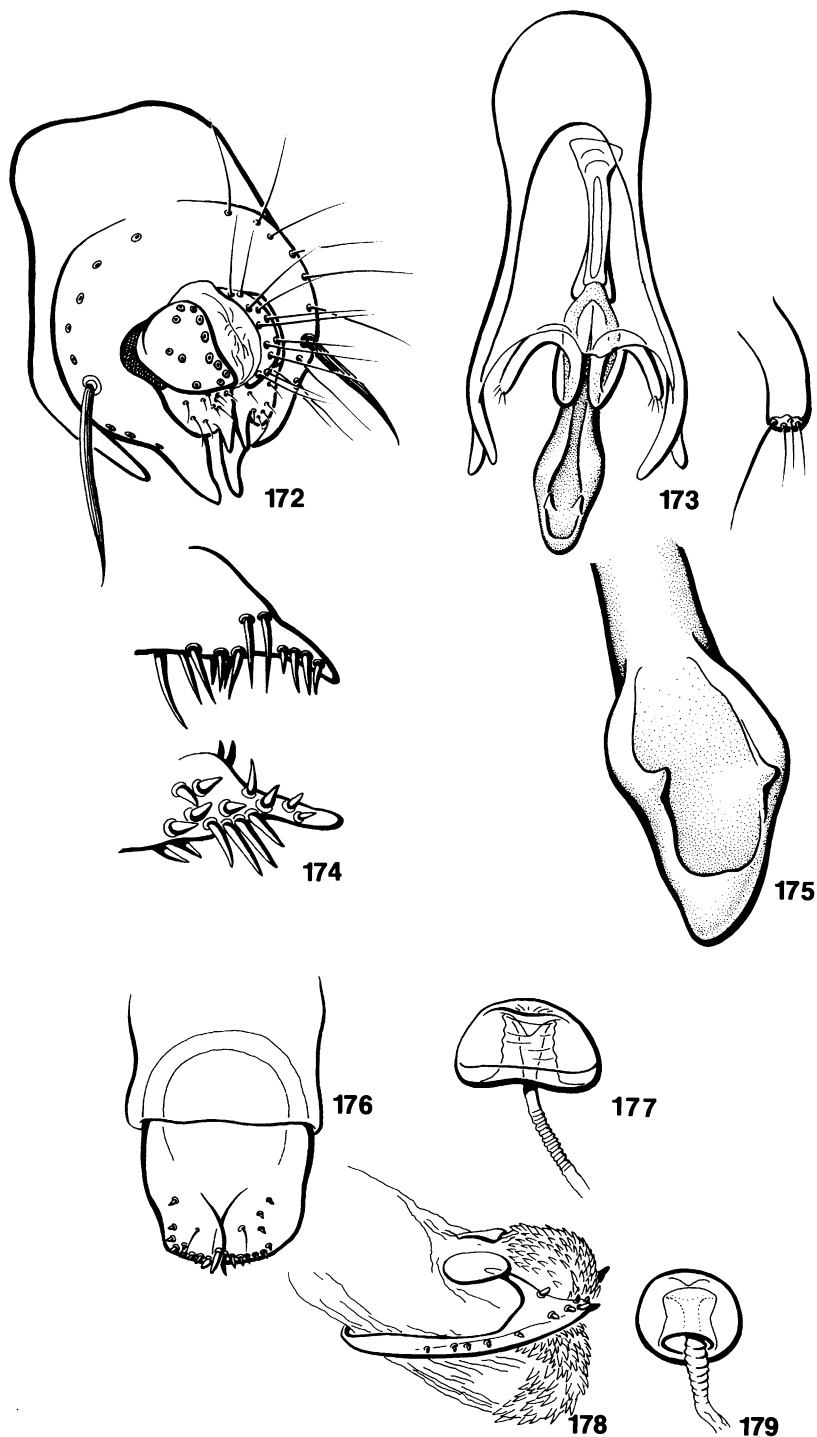
171

Figs. 165–171. Wings of some *Zygothrica* in the *neolinea* species-group (clade 1.2.1.2.A) and the *dispar* species-group (clade 1.2.1.2.B). Figure 170 is of the *Z. perplexa* holotype.

complete, yellow vitta pr.3 present, extended to post. dorsocentrals; width narrower than frontal vitta; very dark, narrow, obscure vitta-1 present. Vitta pr.5 present: incomplete, extended from posterior notal margin to ant. dorsocentrals, narrow. Apical scutellars cruciate, ant. scutellars parallel. 6 rows acrosti-

chal setulae present. Legs yellow, slightly darker than pleura. Pretarsi dark. ♂ and ♀ with 2 ventral profemoral setae. Wings hyaline; halteres light yellow.

Tergites mostly dark black-brown. ♀ with t II–V dark; t VI + VII with small yellow triangle. ♂ with t II–IV dark; V with broad tri-



Figs. 172-177. *Zygothrica zonata*. 172. Epandrium. 173. Hypandrium + aedeagus, with detail of paraphysial lobe. 174. Sursstylus, lateral (top) and medial (bottom). 175. Distiphallus (ventral). 176. Oviscape (ventral). 177. Spermatheca.

Figs. 178, 179. *Zygothrica femina*. 178. Oviscape + oviprovectro (lateral). 179. Spermatheca.

angle, VI with small triangle. Oviscape oval, slightly longer than wide, with 7–8 peg ovisensilla per side (medioapical one largest). Oviprovector scales elongate triangular. Spermathecal capsule short; surface smooth, with short apical indentation. Cerci dark brown.

Epandrium dorsally elongate, with 1 pair of narrow, elongate ventral lobes. Each lobe with 1 large scaliform seta. Cerci rounded; ventral cercal lobes small, with 6–9 setulae. Hypoproctal plates short, triangular, glabrous. Surstylus triangular, apically narrowed; possesses 13–17 prensisetae: 6 laterals (4 pegs, 2 elongate), 7–11 medials (pegs to elongate). Hypandrium elongate; posterior margin with short process. Gonopods narrow, elongate; 2 pairs present. Basiphallus shorter than aedeagal apodeme; straight. Distiphallus apically tapered; with 2 ventral blunt spines.

MEASUREMENTS: N = 4♂, 4♀. ThL = 1.10 ♂ (1.00–1.20); 1.23 ♀ (0.97–1.40). HW/ThL = 0.69 ♂ (0.66–0.73); 0.65 ♀ (0.63–0.70). ThL/WL = 0.46 ♂ (0.45–0.47); 0.45 ♀ (0.44–0.47). C.I. = 3.20 (2.72–3.49); 4-V = 1.68 (1.56–1.77).

HOLOTYPE: ♂, PANAMA: Chiriqui, 8 km W Boquete, near Quebrada Emporio, 08°48'N, 82°30'W, 2220 ft, 19/VI/73, T. L. Erwin and G. Hevel (NMNH) (genitalia dissected, DAG). ThL = 1.20; HW/ThL = 0.66; ThL/WL = 0.45; C.I. = 3.47; 4-V = 1.69.

ETYMOLOGY: Latin, "girdled," for the clear notal vittae.

DISTRIBUTION: Panama to El Salvador.

MATERIAL: (all are paratypes) EL SALVADOR: San Salvador, IX/55, 2♂*, 1♀*. PANAMA: Chiriqui, Viejo R., El Volcan, 5280 ft, 22/VII/66, 1♂*, "light trap."

***Zygothrica neolinea*, new species**

Figures 165–166, 180–184; table 1

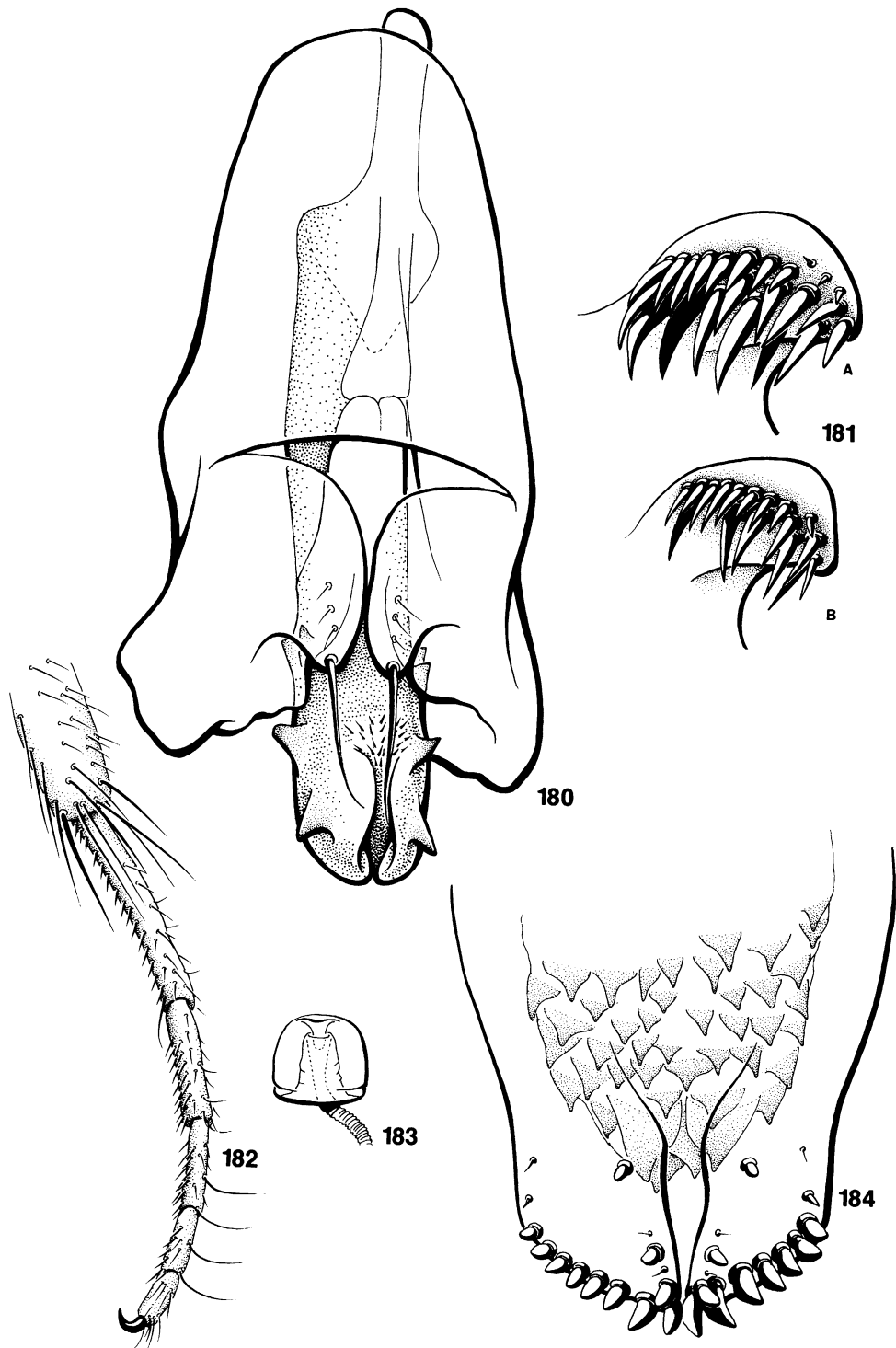
DIAGNOSIS: Genitalic characters provide the best means for distinguishing this species from other members of the *neolinea* group. In particular, for ♀: oviscape apically flat, with truncate terminal margin; spermatheca bare, dome-shaped. For ♂: midtibia with apical brush of fine, long setae, midtarsi with ca. 5 long, erect dorsal setae; genitalia as described below.

DESCRIPTION: Frontal-orbital plates yellow; frontal vittae dull, black-brown. Eyes gray-brown, interfacetal setulae sparse, short. Ocellar triangle almost extended to ptilinal fissure; median portion yellow, dorsolaterally brown. Proclinate equal to length of ant. reclinate. Ant. reclinate closer to post. reclinate than to proclinate. Post. reclinate ca. 1.5 × length other orbitals; closest to inner vertical. Ocellar setae parallel, extended past ant. reclinates. Face yellow; carina lighter, prominent, complete. Cheek deep, with light brown spot in ♂, dark brown in ♀, surrounded by yellow. Flagellomere I length 3 × pedicel, setulae short. Flagellomere I light brown, pedicel ochre. Arista with 6 dorsal and 2 ventral branches. Proboscis yellow, palpi yellow. Face protuberant, lateral facial margin slightly splayed.

Two distinct, incomplete notal vittae (pr.2) present. Vittae yellow, separated by brown vitta pr.3, equal in width to yellow vittae. Vitta pr.2 extended to between dorsocentral setae. Vitta pr.4 very indistinct, yellow, along postpronotal lobes. Pleura, legs, postnotum, light yellow. Dorsal surface of scutellum brown. 2 very long humeral setae/side, 6 rows acrostichals present. Ventral surface profemur bare. ♂ midtibia with apical brush of 12–14 elongate setae (lengths ca. 2 × tibia width); apical spur length ca. 3 × tibial width. ♂ midtarsal segments II + III with 4–5 long, erect setae. ♂ wing with diffuse, apical infuscation, ♀ wing hyaline. Halteres yellow.

Tergal ground color brown. Oviscape apex dorsoventrally flattened, length ca. 1½ × width, with 10 peg ovisensilla per side (7–8 apicals, 2 small ventrals). Oviprovector scales wide, large, placoid. Spermathecal capsule dome-shaped; surface bare; with narrow basal collar and deep apical indentation. Cerci yellow, conical.

Epandrium yellow. Ventral epandrial lobes inconspicuous, lightly setulose. Cerci rounded, yellow; ventral cercal lobes inconspicuous, lightly setulose. Hypoproctal plates broadly triangular in lateral view. Surstylus crescentric; possesses 18–20 prensisetae, all setiform, medial ones stout and curved. Hypandrium simple. Gonopods lobate, simple, 1 pair present. Basiphallus ca. 2 × length of aedeagal apodeme. Distiphallus barely wider than endophallus; with 2 pairs of blunt ven-



Figs. 180–184. *Zygothrica neolinea*. **180.** Hypandrium + aedeagus (ventral). **181.** Surstyli, both COSTA RICA. **182.** Tarsi and tibial apex of mesothoracic leg of male, showing elongate setae. **183.** Spermatheca. **184.** Distal half of oviscape, including oviprovector (dorsal).

trolateral spines, 2 pairs blunt spines anterolateral to these, and with ventromedial field of ca. 20 microspicules.

MEASUREMENTS: N = 2♂, 1♀. ThL = 1.35 (1.17–1.53). HW/ThL = 0.66 (0.64–0.69). ThL/WL = 0.48 (0.48–0.49). C.I. = 3.23 (3.06–3.44); 4-V = 1.72 (1.43–2.10).

HOLOTYPE: ♂, COSTA RICA: La Suiza de Turrialba, XI/22, P. Schild (NMNH) (genitalia dissected, DAG). ThL = 1.53; HW/ThL = 0.69; ThL/WL = 0.49; C.I. = 3.44; 4-V = 1.43.

ETYMOLOGY: Latin, "new lines," since this is yet another new species with yellow paramedian notal vittae.

DISTRIBUTION: Costa Rica, Panama.

MATERIAL: (all are paratypes) 1♂*, 1♀* with same label data as holotype. PANAMA: Cerro Campana, 5♂*, 5♀*, 3/II/63 ("ex: *Centropogon* flowers"); 2♂*, 3♀*, 2/II/63 ("ex: *Passiflora* flower"); 2♀*, 19/IX/62 ("ex: *Aphelandra micans* flower").

Zygothrica bilinefilia, new species

Figures 168–169, 185–191, 267e, f

DIAGNOSIS: Distinctive external features are the presence of discrete, incomplete, yellow notal vitta pr.2 and several more reliable genitalic features. Principally, these are a very flat oviscapex apex with a terminal row of 7–9 ovisensilla and, on the male, the surstylar and distiphallal modifications described below.

DESCRIPTION: Frontal-orbital plates yellow; frontal vittae velvety brown to black. Eyes gray-brown, pilosity short and sparse. Ocellar triangle extended to ptilinal fissure; black. Proclinate orbital equal in length to ant. reclinate. Ant. reclinate midway between post. reclinate and proclinate. Ant. reclinate midway between inner vertical and proclinate. Ocellar setae extended to ant. reclinates and proclinate. Ant. reclinate midway between inner vertical and proclinate. Ocellar setae extended to ant. reclinates. Face very light yellow; carina white, prominent, complete. Cheek with brown spot; light yellow posteriad. Flagellomere I light brown, setulae short, length ca. 2× pedicel. Arista with 5 dorsal and 2 ventral branches. Proboscis mostly yellow; labellum, distal portion of

palps light brown. Clypeus and gena light yellow. ♀ with cheek and palps more extensively and darker brown.

Postnotum, pleura, legs, light yellow. Notum with distinct incomplete, yellow vitta pr.2 extended to just past ant. dorsocentrals. Distance between vittae wider than vitta. 6 rows acrostichals present. Ventral surface of profemur with row 4–5 setae, lengths 0.5–0.7 femur width. Wings hyaline, with very light, diffuse, apical infuscation. Halteres yellow.

Tergites III, IV almost entirely brown, V with lateral portions yellow, t VI–VIII yellow (t VI in ♀ with median brown spot). Oviscapex apex dorsoventrally flat; oviscapex length more than 2× width. Oviscapex with 7–9 peg ovisensilla on terminal margin, 2 ventrally; row of 6 ventral sensilla/side. Oviprovector scales broad, large, placoid. Spermathecal capsule squared oval; surface bare; apical indentation deep. Cerci conical, yellow.

Ventral epandrial lobes indistinct, bare. Cerci rounded, yellow; ventral cercal lobes bare, rounded. Hypoproct plates broad in lateral view, extended to surstyli. Surstylus with 13 prenisetae: 5 pegs (2 laterals, 3 medials), 7 setiform (2 basomedial, 5 apicals). Hypandrium simple; anterior margin squared. Gonopods lobate, 1 pair present. Endophallus length ca. 2× aedeagal apodeme; slightly arched. Distiphallus with lateral margin turned ventromedial; with middle field of fine spicules, 2–3 blunt ventral spines (each side), 2–3 smaller ventral spines, and 1–3 spines on ventral margin of basiphallus near distiphallus.

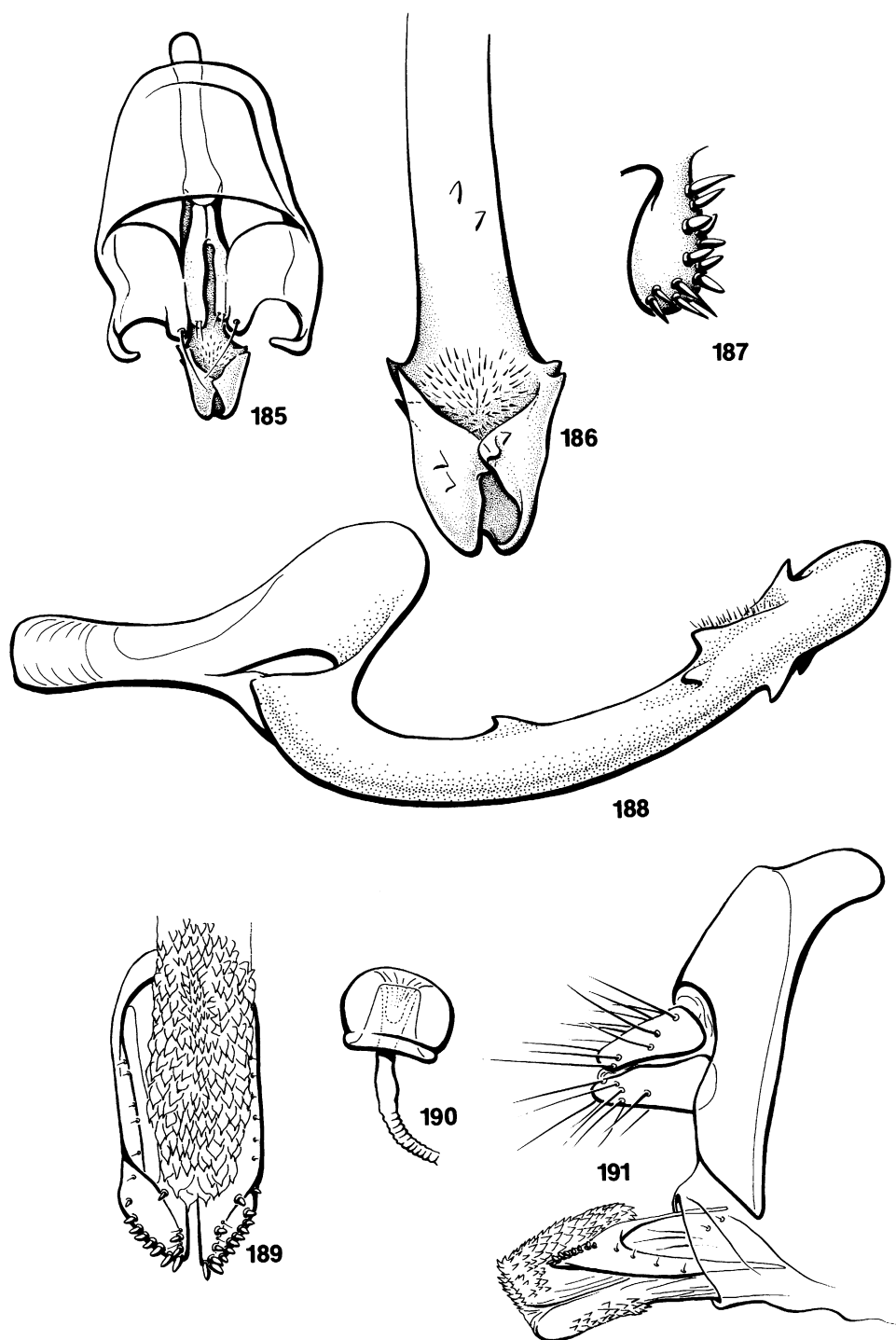
MEASUREMENTS: N = 3♂, 4♀. ThL = 1.10 ♂ (0.96–1.20); 1.14 ♀ (0.96–1.34). HW/ThL = 0.80 ♂ (0.78–0.80); 0.73 ♀ (0.69–0.75). ThL/WL = 0.53 ♂ (0.50–0.56); 0.49 ♀ (0.46–0.53). C.I. = 2.57 (2.16–2.99); 4-V = 1.72 (1.59–2.16).

HOLOTYPE: ♂, PANAMA: Cerro Campana, VII/67, W. W. Wirth (NMNH) (genitalia dissected, DAG). ThL = 1.13; HW/ThL = 0.80; ThL/WL = 0.51; C.I. = 2.59; 4-V = 1.65.

ETYMOLOGY: Latin, "two-lined daughter," for the two clear, yellow paramedian notal vittae on the dark black-brown background.

DISTRIBUTION: Panama to Bolivia (fig. 199).

MATERIAL: (all are paratypes) BOLIVIA: S. Inicua, Riv. Alto Beni, 15–18/I/76, 1100 m, 1♀*; Coroico, IV/58, 1♂*. PANAMA: Cerro



Figs. 185–191. *Zygothrica bilinefilia*. 185. Hypandrium + aedeagus (ventral). 186. Distiphallus (ventral). 187. Surstylus. 188. Aedeagus + aedeagal apodeme (lateral, dorsal side up). 189. Oviscape + oviprovectator (dorsal). 190. Spermatheca. 191. ♀ terminalia, with oviprovectator everted.

Campana, VII/67, 3♂*, 3♀*; 6/XII/60, 1♀*; El Valle, II/58, 1♀*.

Zygothrica circumveha, new species

Figures 192–197

DIAGNOSIS: Best distinguished among close congeners by the possession of 1–2 large distiphallal spines directed posteriad, a lightly papillate spermathecal capsule, and the nearly complete dark face.

DESCRIPTION: Head ground color brown. Frontal-orbital plates ochre. Frontal vittae velvety black. Eyes gray-brown, bare. Ocellar triangle shiny, brown, not fully extended to ptilinal fissure. Anterior reclinate long, slightly shorter than other orbitals; closest to proclinate. Ocellar setae parallel or nearly so. Face dark ochre to dark brown; narrow, ca. ½ width of vertex. Carina prominent, complete. Oral margin with lip. Cheek low; cheek, gena, and back of head dark brown. Flagellomere I ca. 2× length of pedicel, setulae short. Pedicel ochre, flagellomere I brown. Arista with 3–5 dorsal and 1 ventral branch. Proboscis, palpi, clypeus, brown. Oral margin of face deeply indented: extended to distal tip of flagellomere I.

Notal ground color black-brown, including scutellum and postnotum. Notal markings variable: yellow, incomplete vitta pair 2 present in some Mexican specimens of varying amount, and in Colombian, El Salvadoran specimens but not in those from Greater Antilles. Pleura light yellow to light ochre. 3 long humerals, 6 rows acrostichals present. Legs yellow. Ventral surface of profemur bare. Wings hyaline; halteres yellow.

Tergites dark brown, shiny; unicolorous in island and some mainland specimens, gradation to following pattern: dark brown triangle on t III–V, median dark spots on t VI + VII, last tergite brown. Oviscape length ca. 1.7× width; with 7 peg ovisensilla per side (4 terminal, 3 dorsal). Oviprovector scales broad, large, placoid. Spermathecal capsule campanulate, surface lightly papillate, with deep apical indentation. Cerci elongate, conical, yellow to light brown.

Epandrium with indistinct ventral lobes; 5–6 setae in region of lobe. Cerci rounded, brown; ventral cercal lobes indistinct and with 3–5 setulae. Hypoproctal plates broadly tri-

angular in lateral view, with 4–5 setulae. Surstylus lobate, with 12–13 prensisetae, all setiform: 7–8 laterals, 3 apicals, 2 small ones on distolateral edge. Hypandrium simple, apically tapered. 1 pair gonopods present, small. Basiphallus ca. 5× length of aedeagal apodeme, arched. Distiphallus with 1–2 lateral spines directed posteriad; spine on one side may be absent.

MEASUREMENTS: N = 5♂, 3♀. ThL = 1.07 ♂ (0.98–1.14); 0.98 ♀ (0.92–1.07). HW/ThL = 0.75 ♂ (0.69–0.79); 0.79 ♀ (0.74–0.85). ThL/WL = 0.45 ♂ (0.43–0.47); 0.44 ♀ (0.40–0.47). C.I. = 2.53 (2.09–3.02); 4-V = 1.62 (1.46–1.72).

HOLOTYPE: ♂, MEXICO: Sinaloa, 15 mi W El Palmito, 5000 ft, 30/VII/64, W. R. M. Mason (CNC) (genitalia dissected, DAG). ThL = 1.14; HW/ThL = 0.69; ThL/WL = 0.43; C.I. = 2.72; 4-V = 1.66.

ETYMOLOGY: Latin, “circum-navigating,” for the distribution, which is nearly circum-Caribbean.

DISTRIBUTION: Greater Antilles, Central America (fig. 198).

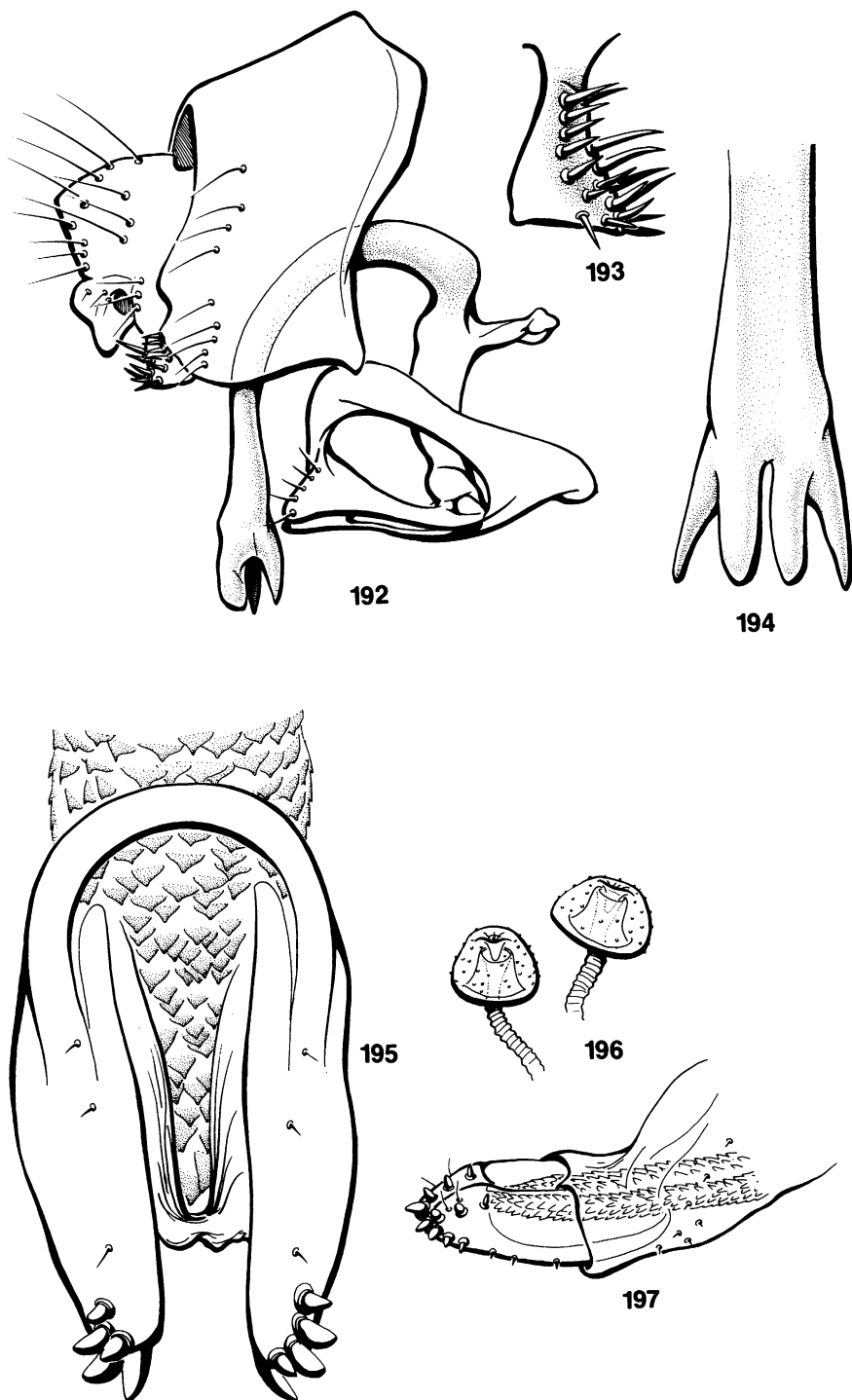
MATERIAL: (all are paratypes) COLOMBIA: El Recuerdo, Sierra Nevada de Sta. Marta, XII/55, 1♂*. EL SALVADOR: Volcan Santa Ana, 5670 ft, 11/XI/53, 1♂*. HAITI: Kenscoff, 4000 ft, II/56, 1♂*. JAMAICA: nr. Bath, II/56, 1♂, 1♀*; Hardware Gap, II/56, 1♂, VII/58, 1♂*; VII/25/66, 4000 ft, 20♂*, 2♀*. MEXICO: Sinaloa, 15 mi W El Palmito, 5000 ft, 30/VII/64, 1♂, 1♀*.

DISCUSSION: This species is morphologically quite variable in coloration of the notum and abdomen and in the distiphallus spines, as described above. Close study of additional material may distinguish if there are discrete differences between some populations, particularly the island and some mainland ones.

Zygothrica femina, new species

Figures 167, 178, 179, 267d

DIAGNOSIS: Externally, *Z. femina* can be distinguished by the brick-red eyes, a dark brown flagellomere I, presence of mediolabral setulae a + b, an elongate palp with an oblique (not rounded) ventral margin. A spherical spermathecal capsule which is bare, and an oviscape with a pair of oval, dorsal



Figs. 192–197. *Zygothrica circumveha*. 192. ♂ terminalia (lateral). 193. Surstylus. 194. Distiphallus (dorsal). 195. Oviscape and oviprovect (ventral). 196. Spermathecae. 197. Oviscape and oviprovect (lateral).

sclerites, are autapomorphies for the *neolinea* group (δ unknown).

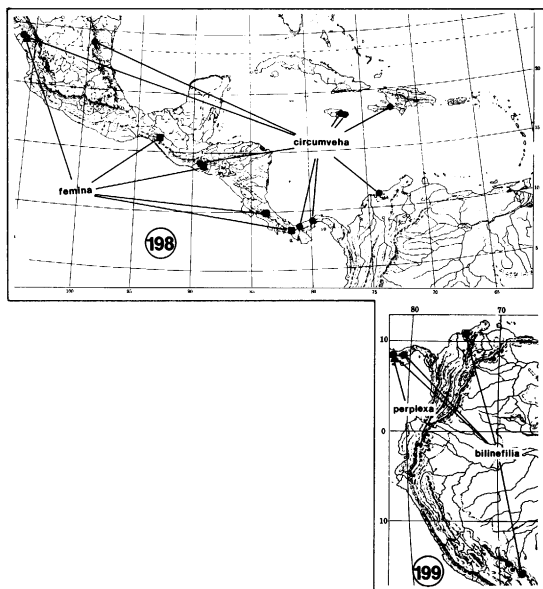
DESCRIPTION: Frontal-orbital plates yellow. Frontal vittae velvety black-brown. Eyes brick-red, with sparse, short, interfacetal setulae. Ocellar triangle extended to slightly past proclinate. Ant. reclinate ca. 0.7 length of post. reclinate, slightly closer to proclinate than to post. reclinate. Post. reclinate midway between inner vertical and proclinate. Ocellar setae extended to ant. reclinates. Face mostly yellow; ventrolateral corners dark brown, splayed. Carina light yellow, prominent, complete. Cheek deep, $\frac{1}{5}$ depth of eye, dark brown. Flagellomere I length $3 \times$ pedicel, setulae short. Flagellomere I brown; pedicel ochre, brown on base. Arista with 4–6 dorsal and 1 ventral branch. Proboscis yellow, with mediolabral setae a + b. Labellum brown; palpi narrow, ventral margin oblique, apex brown. Face protuberant.

Notal ground color dark brown, including scutellum and postnotum. Pleura and legs light yellow. Yellow notal vitta pr.2 present; incomplete, distinct. Vittae extended to slightly past ant. dorsocentrals. Yellow, narrower, indistinct vitta pr.4 present; extended across dorsal margin of postpronotal lobe to lateronotal presutural seta. 2 long humerals, 6 rows acrostichal setulae present. Profemur with ventrolateral row 4–5 short setae. Wings hyaline, halteres yellow.

Tergites II–V mostly brown; t VI–VII with brown triangles, t VII triangle ca. $\frac{1}{2}$ size of preceding one. Oviscape tapered apicad; length ca. $1\frac{1}{2} \times$ width. Oviscape with small pair of oval, dorsal sclerites. Oviscape with 7 peg ovisensilla/side: 4 apicals, 3 smaller ones on dorsal surface. Oviprovector scales dorsally lanceolate, ventrally triangular. Spermathecal capsule spherical; surface bare, apical indentation unapparent or very slight. Cerci cylindrical, yellow.

MEASUREMENTS: N = 5♀. ThL = 1.13 (0.88–1.30). HW/ThL = 0.64 (0.63–0.66). ThL/WL = 0.43 (0.40–0.46); C.I. = 3.06 (2.77–3.40); 4-V = 1.77 (1.68–1.88).

HOLOTYPE: ♀, MEXICO: Chiapas, 4 km N Union Juárez, 22/IV/83, W. N. Mathis (NMNH) (genitalia dissected, DAG). ThL = 1.30; HW/ThL = 0.65; ThL/WL = 0.46; C.I. = 3.40; 4-V = 1.68.



Figs. 198, 199. Distribution of the *neolinea* species-group.

ETYMOLOGY: Latin, “female,” since no males have yet been found.

DISTRIBUTION: Central America (fig. 198).

MATERIAL: (all are paratypes) COSTA RICA: Heredia, 10 km N, X/55, 1♀*; La Suiza de Turrialba, 1/24, 1♀*. EL SALVADOR: Volcan Santa Ana, 5670 ft, 1♀*. MEXICO: Sinaloa, 4.5 mi W El Palmito, VII/20/64, 1♀*. PANAMA: Chiriqui, Boquete, VII/59, 1♀*.

DISCUSSION: Due to a lack of male specimens, this species was not included in the cladogram in figure 160.

DISPAR SPECIES-GROUP, CLADE 1.2.1.2.B (fig. 159)

Three synapomorphies define the group; the first one mentioned below probably evolved convergently or in parallel with several other *Zygothrica* taxa. The traits are no. 74 (large, erect distiphallal scales—they have undoubtedly been lost in several of the species in the group), 88 (in δ , the line extended from the proclinate to the posterior reclinate orbital seta is pointed toward the outer vertical seta or laterad—this is a consequence of expanded frontal-orbital plates), 89 (ocellar triangle with a dorsal width $\frac{4}{5}$ or more the width of the face). With the exception of about five

species having been collected at altitudes intermediate for *Zygothrica*, the majority of *dispar* group species are inhabitants of low-land tropical moist, rain, and inundation forests. Male and female genitalia usually provide the diagnostic characters for distinguishing species in the species-group, but male genitalia show the greatest variation only among the major lineages (e.g., clades B.1, B.2, B.3), rather than among species in any one lineage.

DISPAR SUBGROUP, CLADE 1.2.1.2.B.1

(fig. 161)

Herein are the species possessing some of the most bizarre heads. The group is defined on the basis of two male genitalic synapomorphies: no. 93 (medial surface of the lateral gonopod is evenly smooth and concave) and no. 94 (shape of the distiphallus, in dorsoventral view, is laterally flanged). Genitalic differences among males of different species are not as obvious as the differences among females. In addition, all the species possess the following traits: ventral epandrial lobe small, inconspicuous, adpressed to lateral surface of surstylus; ventral cercal lobe (δ) small, sparsely setulose (three to five setulae); prominent, complete carina present, which is also bulbous near facial margin; surstylus triangular, with broad base and stout, sharp, prensisetae. Relationships among species in the subgroup are based on traits of the genitalia, wing pattern, head shape, and orbital setation.

KEY TO MALES OF THE *DISPAR*
SPECIES-SUBGROUP

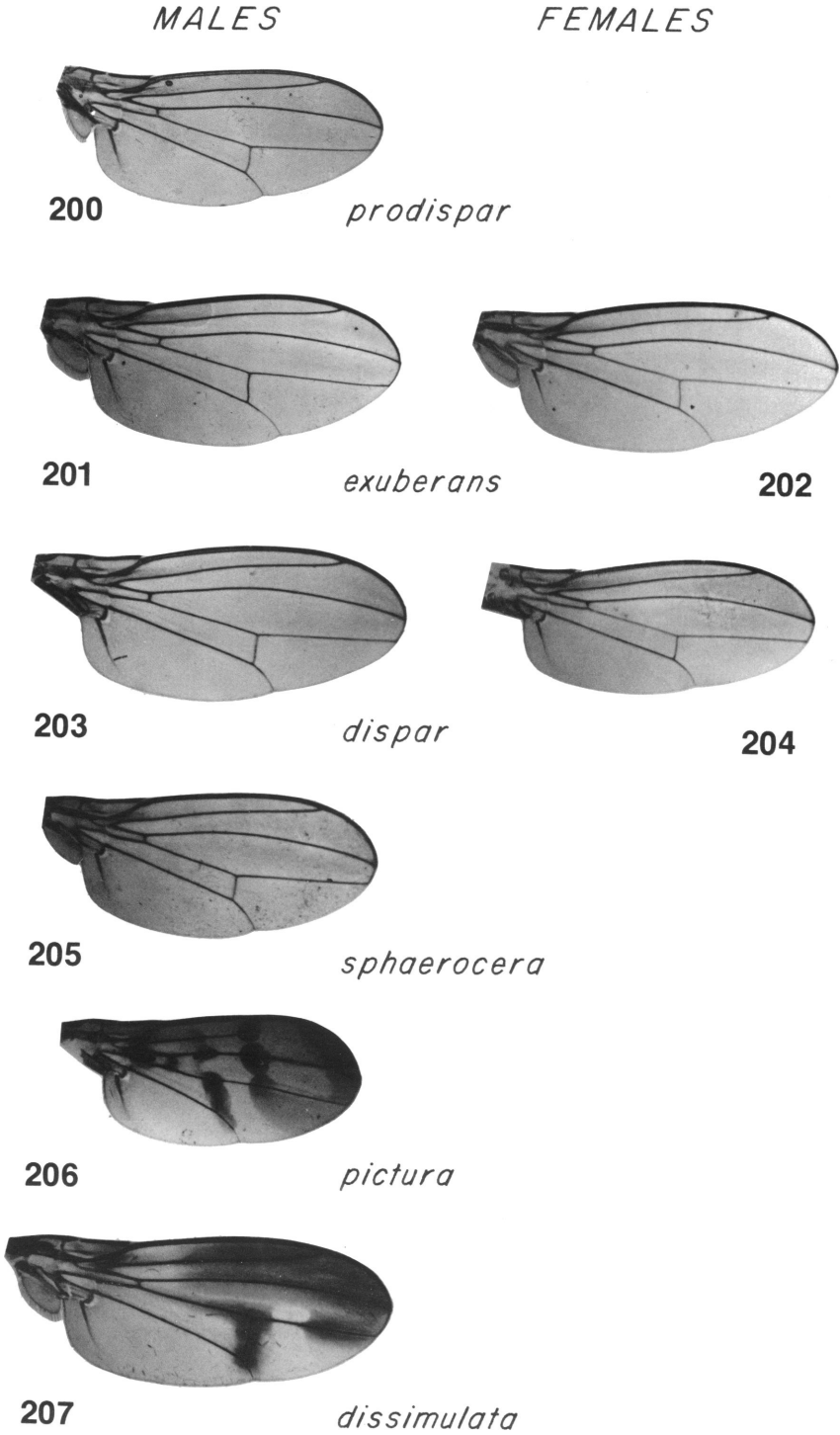
1. Wings elaborately patterned 2
- 1a. Wings hyaline, or with diffuse apical infuscation 4
2. Most of area anterior to M_1 infuscated; dm-cu with heavy spot (fig. 207)
..... *dissimulata*, n. sp.
- 2a. Wings with different pattern (figs. 206, 239), vein dm-cu oblique (rather than perpendicular) to M_1 3
3. Radial-medial band on wing complete to M_1 ; small window present in r-m band over R_{2+3} (fig. 239); anterior margin of hypan-drium acute *fascipennis*
- 3a. Radial-medial wing band interrupted, form-

- ing spots (fig. 206); anterior hypandrial margin truncate *pictura*, n. sp.
4. Hind tibia and tarsi flattened to ca. $2 \times$ normal width, and banded (fig. 228)
..... *sphaerocera*, n. sp.
- 4a. Hind legs without such modifications ... 5
5. Head broadened, either slightly or grossly (HW/ThL = 0.95–2.50); eyes apically distended (figs. 209–213) 7
- 5a. Head not obviously broadened (HW/ThL ca. 0.80), nor eyes apically distended (e.g., fig. 208) 6
6. Dorsum black-brown; distiphallus apex pronged (fig. 216); Bolivia, southern Peru
..... *antedispar*, n. sp.
- 6a. Dorsum fuscous; distiphallus short, wide (fig. 247); Panama *abbrevidispar*, n. sp.
7. Wing apex with diffuse, light brown infuscation (fig. 203); distiphallus truncate (figs. 253, 254) *dispar*
- 7a. Wing completely hyaline 8
8. Head exceptionally broad, apical portion of eye distended into facetless ribbon (fig. 213); distiphallus without scales, with retrorse prong on each side (fig. 259)
..... *exuberans*
- 8a. Eyes without above modification; distiphallus scalate 9
9. Notum dark brown; collar of distiphallus constricted (fig. 224) *dimidiata*
- 9a. Notum dark brown/ochre; aedeagal sides parallel for entire length (fig. 241) ... 10
10. Notum ochre; HW/ThL ca. 0.95–1.60; widespread in Central and South America ...
..... *prodispar*
- 10a. Notum dark brown; HW/ThL ca. 1.00; Peru
..... *kerteszi*

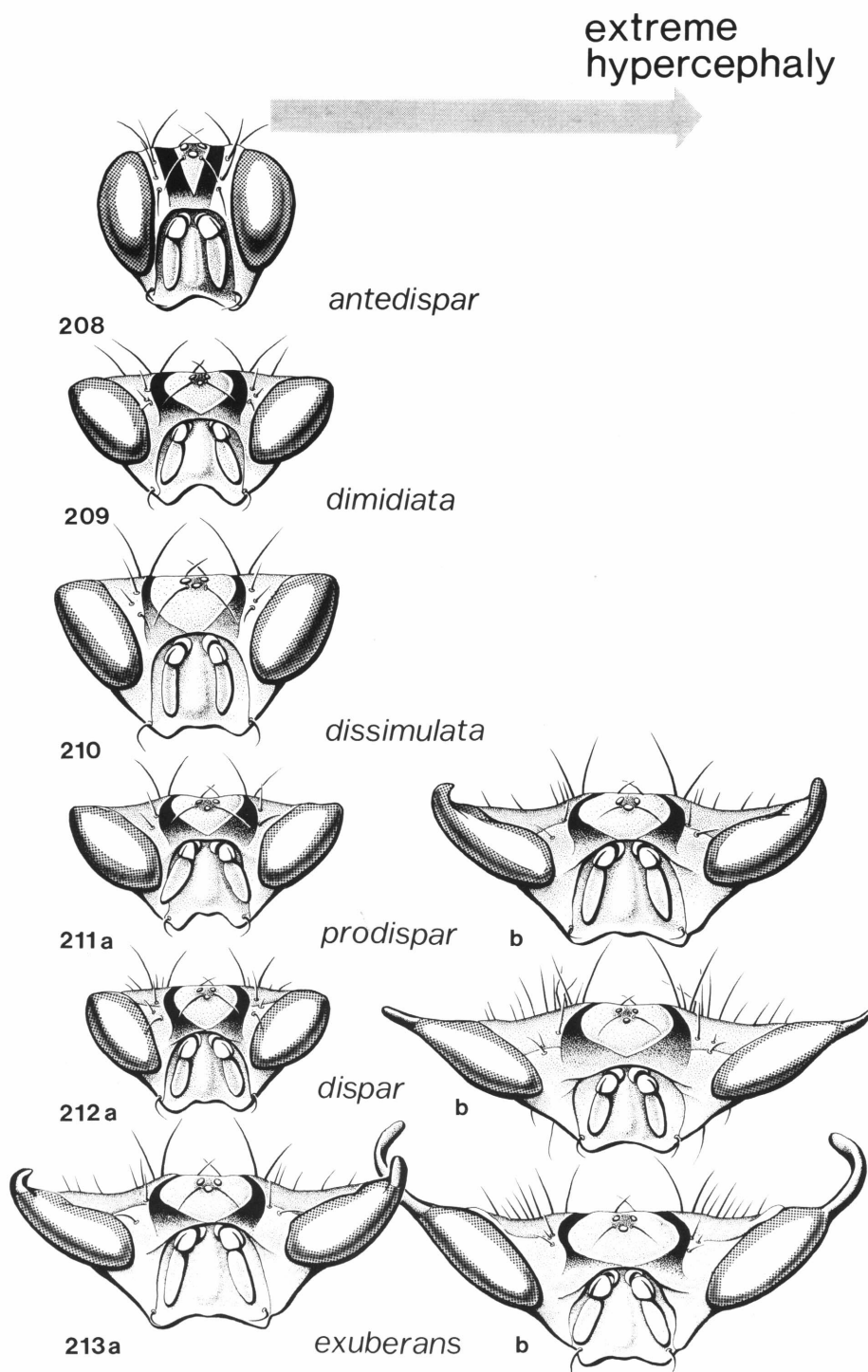
KEY TO KNOWN FEMALES OF
THE *DISPAR* SPECIES-SUBGROUP

Identification requires microscopic examination of the oviscapae and spermathecae.

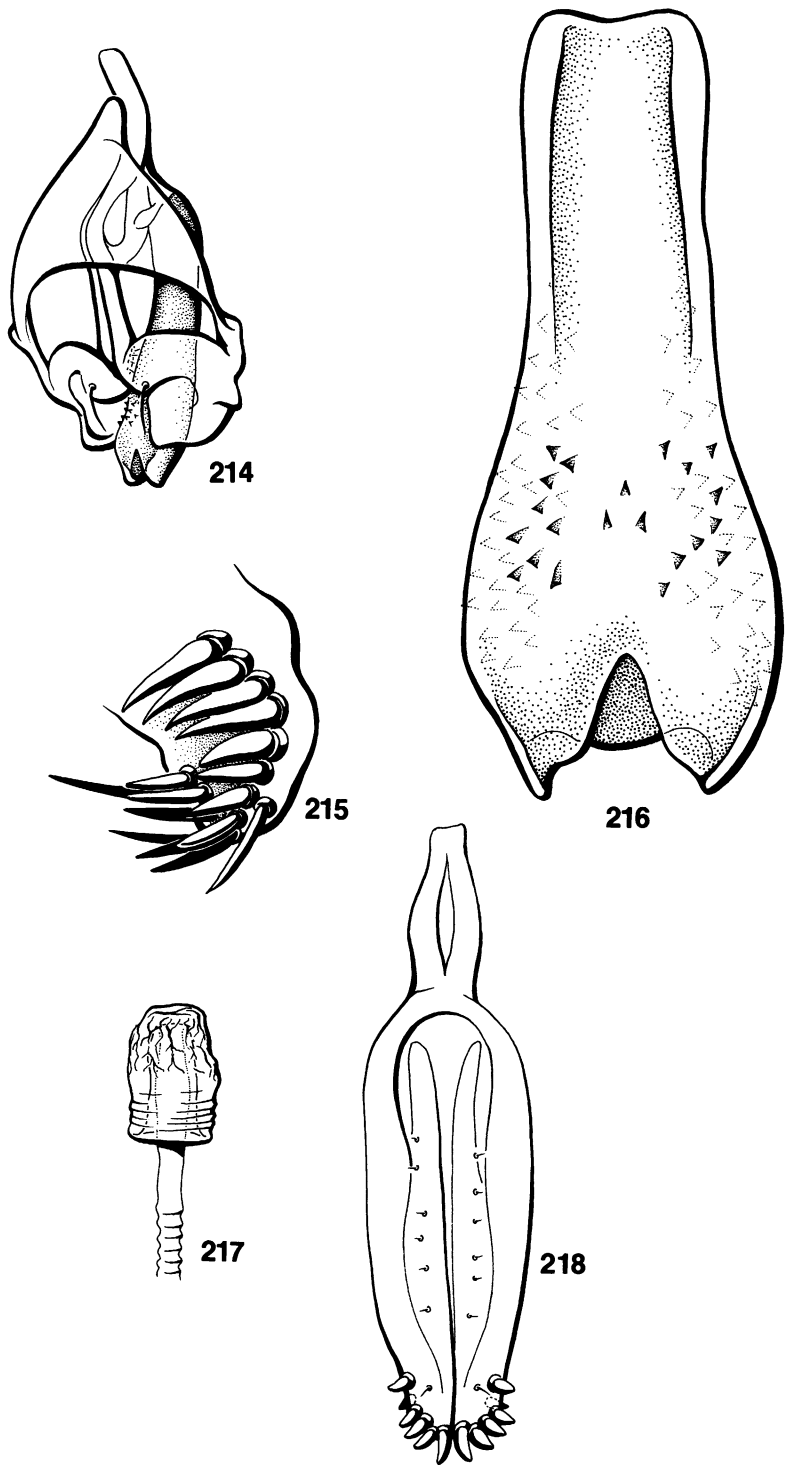
1. Apical margin on each side of oviscapae with 4 large ovisensilla; spermatheca oval, finely wrinkled at apex (figs. 217, 218)
..... *antedispar*, n. sp.
- 1a. Apical margin of oviscapae with 7 or more ovisensilla per side; spermathecae various 2
2. Spermathecal surface bare (wrinkled/smooth), without papillae or scales 3
- 2a. Spermathecal surface papillate/scaled 5
3. Ventrolateral row with 10 ovisensilla; spermathecal surface smooth (figs. 226, 227)
..... *dimidiata*



Figs. 200–207. Wings of some *Zygothrica* in the *dispar* species-subgroup (clade 1.2.1.2.B.1). Figures 205–207 are of the holotypes.



Figs. 208–213. Representative head shapes of males in the *dispar* species-subgroup; frontal views, all to the same scale. *Zygothrica antedispar* is an unmodified relative of the hypercephalic forms; variation in *Z. dimidiata* is negligible and the variation in *Z. dissimulata* is unknown (fig. 210 is of the holotype). Figures 211–213 show the extremes for 3 species from least (a) to the most (b) hypercephalic individuals.



Figs. 214–218. *Zygothrica antedispar*. 214. Aedeagus + hypandrium. 215. Surstylus. 216. Distiphallus (ventral). 217. Spermatheca. 218. Oviscape (ventral).

Zygothrica antedispar, new species

Figures 16, 171, 208, 214–218

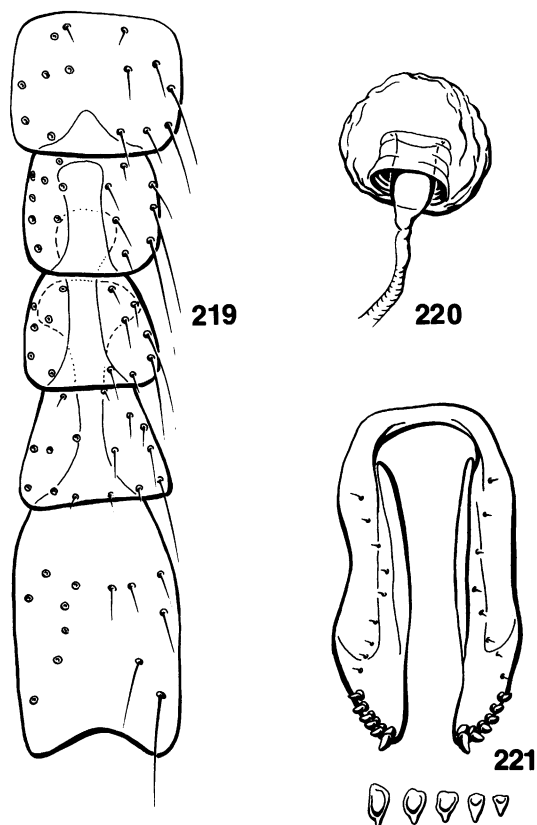
DIAGNOSIS: Distinguished by the presence of hyaline wings, a notum and tergites which are black-brown in males and females, and by genitalic characteristics. For the female, four large marginal ovisensilla and the possession of elongate, apically wrinkled spermathecae are diagnostic. For the male, aedeagal shape and ornamentation, as described below, are diagnostic.

DESCRIPTION: Head and eye shape unmodified. Frontal-orbital plates ochre, $\frac{1}{2}$ width of frontal vittae. Frontal vittae velvety black. Eyes brick-red, bare. Ocellar triangle dark brown, shiny, extended to ptilinal fissure. Anterior reclinate ca. 0.8 length of other orbitals, closest to proclinate. Post. reclinate closest to inner vertical. Ocellar setae extended to slightly past proclinales. Postocellars 0.5–0.6 length of verticals. Face ochre to light brown (darker in ♀); carina prominent, complete. Cheek ca. $\frac{1}{6}$ depth of eye, mostly ochre, with brown spot. Flagellomere I length $3 \times$ pedicel. Arista with 4–5 dorsal and 1 ventral branch. Proboscis light yellow, including labellum and palps.

Notal ground color black-brown; pleura and legs light yellow. Notopleural edge indistinct. Scutellum black-brown, postnotum light brown to tan. 6 rows acrostichal setulae present. Ventral surface of profemur with row of 5 evenly spaced setae, lengths ca. $\frac{3}{4}$ width of femur. Wings hyaline; halteres yellow; legs yellow.

Tergites II–VII black-brown, t VI–VIII shiny. Oviscape apically flattened; apical margin rounded; length $3 \times$ width; with 6–7 large ovisensilla pegs (4 marginals, 2 smaller dorsals), ca. 6 ventral sensilla/side. Oviprovector scales very small to large; narrow-triangular. Spermathecal capsule apically rounded, oblong; surface apically wrinkled, basally finely annulate, without apical indentation. Cerci flat, light brown.

Epandrium black-brown. Surstylus crescentic, with 16 setiform prensisetae: 6 large laterals, 10 shorter and thinner apicals. Hypandrium simple; extended to middle of aedeagal apodeme. Endophallus short, ca. equal in length to aedeagal apodeme, dorsal surface heavily scaled. Distiphallus ca. $2 \times$ wider than basiphallus, dorsally and ventrally scaled,



Figs. 219–221. *Zygothrica kerteszi*, paralectotype. 219. Sternites III–VII. 220. Spermatheca. 221. Oviscape (ventral) + oviprovector scales.

- 3a. Ventrolateral row with 7 ovisensilla; spermathecal capsule wrinkled 4
4. Spermatheca square in lateral view, introvert extended into $\frac{2}{3}$ of capsule (fig. 261); oviscape gradually tapered apicad (fig. 263) *exuberans*
- 4a. Spermatheca round; introvert extended into $\frac{1}{2}$ capsule (fig. 220); apicolateral margins straight, oblique (fig. 221) *kerteszi*
5. Spermathecal height ca. equal to width, with dense covering large scales (fig. 258); 10–11 ovisensilla in apicolateral row on each side (fig. 257) *dispar*
- 5a. Spermathecal height greater than width, with sparse or dense covering of papillae ... 6
6. 8–10 ovisensilla per side in apical row; oviscape length ca. $2 \times$ width; spermatheca sparsely to hardly papillate, usually dome-shaped *prodispar*
- 6a. Oviscape elongate, length ca. $3 \times$ width; 12–13 ovisensilla in apical row (each side) (fig. 251); spermatheca oval, densely and finely papillate *abbrevidispar*, n. sp.

with deep apicomedial notch on ventral surface and 10–12 microsetulae at apex of notch.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.32 ♂ (1.26–1.37); 1.36 ♀ (1.29, 1.44). HW/ThL = 0.80 ♂ (0.76–0.84); 0.81 ♀ (0.78, 0.85). ThL/WL = 0.51 ♂ (0.50–0.53); 0.49 ♀ (0.47–0.52). C.I. = 2.65 (2.02–3.16); 4-V = 1.39 (1.31–1.46).

HOLOTYPE: ♂, PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 19 IX–10 X/84, 290 m, D. A. Grimaldi (AMNH) (genitalia not dissected). ThL = 1.26; HW/ThL = 0.84; ThL/WL = 0.50; C.I. = 2.02; 4-V = 1.37.

ETYMOLOGY: Latin, “before dispar,” in regard to its plesiomorphic position in clade B.1.

DISTRIBUTION: Southern Peru, northern Bolivia (fig. 266).

MATERIAL: (all are paratypes) BOLIVIA: Ichilo, Buenavista, 480 m, V/50, 1♂*. PERU: Madre de Dios, Rio Tambopata Reserve, 19/IX–10/X/84, 1♂*, 2♀*; Cuzco, Quince Mil, 700 m, 15–30/X/62, 1♂*.

DISCUSSION: The holotype and some of the paratypes were captured at a bloom of *Auricularia delicata* fungi (figs. 102–104) by sweeping over the sporophores.

Zygothrica kerteszi

Figures 219–221

Zygothrica kerteszi Duda, 1925: 166.

DIAGNOSIS: ♂ genitalia very similar to *Z. prodispar*; most diagnostic ♂ characters are the black-brown notum and relatively narrower head than is found in *Z. prodispar* (HW/ThL ca. 1.00). Females are more distinctive, as based on the terminalia, especially the spermatheca: oviprovectator scales heavily sclerotized and blunt; oviscape flat, apical margins oblique, with 6 ovisensilla pegs and row of 7–8 ventral sensilla per side, length ca. 1.7× width; spermatheca round, surface wrinkled, with no papillae or scales.

LECTOTYPE: ♀, PERU: [Pasco], [Rio] Pichis, XII/03, Puerto Bermúdez (SMTD) (genitalia dissected, DAG). Not measured.

PARALECTOTYPES: 2♂*, 3♀*, with same label data as lectotype (SMTD). Head missing on 1♂ and 1♀; 3 bear labels with Duda's writing, with “*Z. kerteszi* var. *subopaca*,” or “*Z. aldrichi* var. *subopaca*,” in addition to cotype

labels designating the specimens as *Z. kerteszi*. Not measured. Lectotype and paralectotypes designated by DAG.

DISTRIBUTION: Known only from the types. This species was not included in the cladogram (fig. 161).

Zygothrica dimidiata

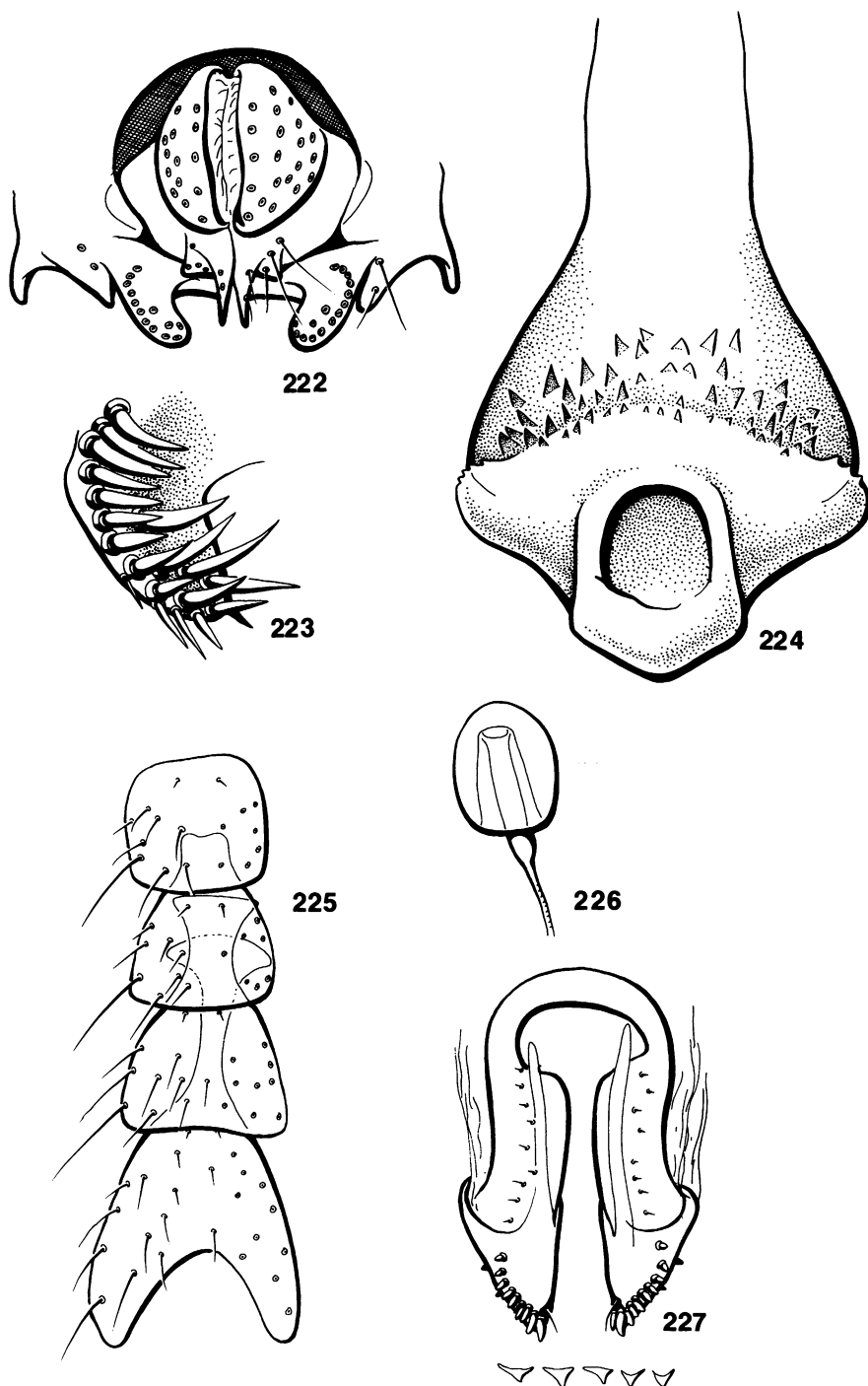
Figures 209, 222–227

Zygothrica dimidiata Duda, 1927: 53.

DIAGNOSIS: Like *Z. kerteszi*, this species is very similar to *Z. prodispar*. Male *Z. dimidiata*, however, have a conspicuously narrow endophallus, and the head is relatively narrower than in *Z. prodispar* (but about the same as *Z. kerteszi*). Other than on the basis of spermathecal shapes, diagnostic external ♀ characters have not yet been found. *Zygothrica dimidiata* has an oval, smooth spermathecal capsule.

DESCRIPTION: Duda has provided a detailed description of external female morphology; only the male and female genitalia and other sexual dimorphisms are described below.

Male head broadened: vertex 2–2.3× wider than face (1.5–1.7× in ♀). Dorsal surface of head nearly flat in frontal view, apex of eye with oblique ventral margin; males with broadest heads have an elongate postvertical seta lateral to the verticals. Ventral surface of profemur with 3–5 setae, length 0.50–0.80× width of femur in ♂, slightly shorter in ♀. Oral margin more protuberant in ♀ than in ♂. Apical margin of oviscape oblique, with 8–9 ovisensilla pegs per side. Dorsal surface of oviscape apex with 3 small ovisensilla pegs, medial margin of apex with 1 trichoid ovisensillum. Row of 9 or 10 sensilla on ventral surface, each side. Oviprovectator scales small, short, placoid. Spermathecal capsule oval in lateral view, surface smooth, no apical indentation present. Sternite VII bifurcate: anterior ramus extended past anterior margin SVI. Surstylus crescentic, broadly attached; with 20–22 setiform prensisetae: row 8–9 large laterals, 5–6 large apicomedials, row of 5–6 fine, short lateroapicals. Hypandrium with lateral margins tapered anteriorly; anterior end slightly expanded; posterior margin even. Distiphallus width ca. 2½× that of basiphallus; abruptly narrowed at collar. Disti-



Figs. 222–227. *Zygotherica dimidiata*. 222. Portion of epandrium. 223. Surstylus. 224. Distiphallus (ventral). 225–227. Holotype (♀). 225. Sternites IV–VII. 226. Spermatheca. 227. Oviscape (ventral) + oviprovector scales.

phallus broadly flanged; heavily scaled on ventral margin.

MEASUREMENTS: N = 5♂, 4♀. ThL = 1.39 ♂ (1.29–1.53); 1.48 ♀ (1.44–1.52). HW/ThL =

0.99 δ (0.84–1.13); 0.88 φ (0.83–0.94). ThL/WL = 0.54 δ (0.51–0.58); 0.53 φ (no range). C.I. = 2.79 (2.42–3.12), 4-V = 1.29 (1.24–1.37).

HOLOTYPE: φ , PERU: [Pasco], [Rio] Pichis, XII/03, Puerto Bermúdez (SMTD) (not measured; genitalia dissected, DAG).

DISTRIBUTION: Southern Peru (fig. 266).

MATERIAL: PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 290 m, 19/IX–10/X/84, 19 δ^* , 22 φ^* .

DISCUSSION: The specimens from Rio Tambopata were swept from over a bloom of *Auricularia delicata* (figs. 102–104).

***Zygothrica sphaerocera*, new species**

Figures 205, 228–230

DIAGNOSIS: Hind tarsi banded black-brown, tarsal segments II + III broadened and flattened; hind tibial spur length 3 $\times$ width of tibia; incomplete, yellow notal vitta pr.2 present; aedeagus short and broad (φ unknown).

DESCRIPTION: Frontal-orbital plates ochre, dorsally 3 $\times$ width of anterior portion. Frontal vittae velvety, black-brown. Eyes brick-red, bare. Ocellar triangle broad, width equal to that of face; shiny, dark brown. Ant. reclinate midway between proclinate and post. reclinate. Post. reclinate ca. midway between inner vertical and proclinate. Face yellow; carina slightly darker. Cheek light yellow, ca. $\frac{1}{6}$ or more height of eye. Arista with 4 dorsal and 1 ventral branch. Proboscis, palpi, clypeus, light yellow.

Notal ground color light brown. Dorsal surface of scutellum brown, apex diffuse yellow. Vitta-1 diffuse, brown; vitta pr.2 yellow, diffuse, equal in width to vitta-1, nearly extended to ant. dorsocentrals. Pleura, postnotum, halter light yellow. 4 rows acrostichal setulae present. Legs yellow, except for hind tarsi. Hind tarsal segments II + III expanded ca. 1.4–1.6 $\times$ normal width. Distal half of tarsal segment I, distal $\frac{3}{4}$ segment II, rest of tarsi dark brown. Ventroapical seta of hind tibia elongate (length ca. 3 $\times$ tibia width). Ventral surface of tarsomeres with elongate, black setae. Wings hyaline.

Abdominal ground color yellow; tergites III–V mostly brown, yellow laterally; t VI with median brown triangle. Surstylus triangular, broadly attached, with 23 prensise-

tae: 7 large laterals, 4 large medials, 8 small apicals, 4 small apicolaterals, all are setiform. Basiphallus short, tapered into distiphallus; length no greater than aedeagal apodeme. Distiphallus broad, width ca. 2 $\times$ basiphallus at narrowest point. Ventral surface distiphallus heavily scaled. Anterior end of aedeagal apodeme near anterior hypandrial margin.

HOLOTYPE: δ , COSTA RICA: La Suiza [de Turrialba], X/25, P. Schild (NMNH) (genitalia dissected, DAG). ThL = 1.37; HW/ThL = 0.81; ThL/WL = 0.54; C.I. = 2.84; 4-V = 1.35.

ETYMOLOGY: After the Sphaeroceridae, a large fly family distinguished in part by swollen hind tarsomeres.

DISTRIBUTION: Known only from the holotype (fig. 265).

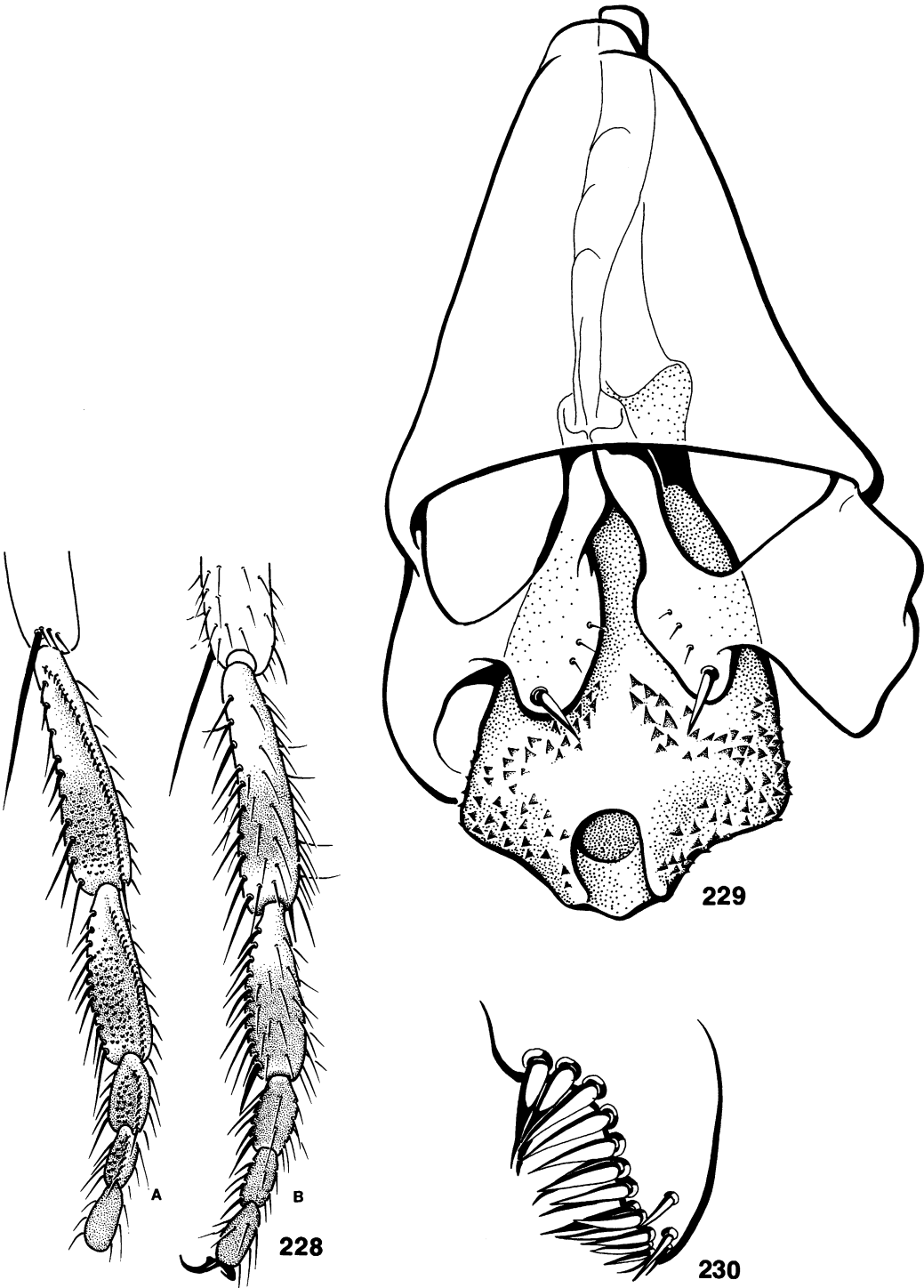
***Zygothrica dissimulata*, new species**

Figures 207, 210, 231–233

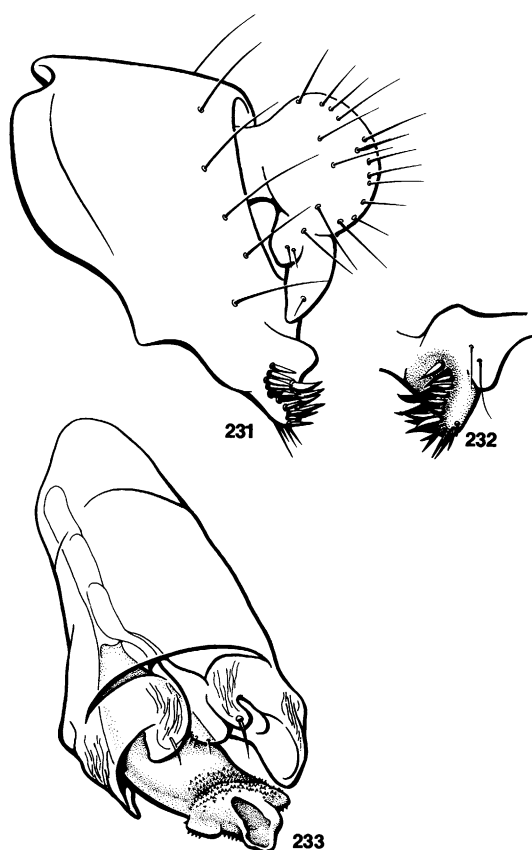
DIAGNOSIS: The wing infuscation pattern is unique for *Zygothrica*, so it is diagnostic in itself. Apart from this, *Z. dissimulata* is distinguished from its two closest relatives, which also possess patterned wings, by the hypermorphic head.

DESCRIPTION: Vertex ground color brown. Head 1.5 $\times$ thorax width. Frontal-orbital plates brown; expanded dorsally, dorsal surface 5 $\times$ width of anterior surfaces. Frontal vittae very narrow, dark brown. Eyes tapered; red; bare. Ocellar triangle equal in width to face; dark brown. Ant. reclinate ca. $\frac{1}{2}$ length of proclinate, midway between other 2 orbitals. Ocellar setae equal to proclimates in length, not nearly extended to proclimates. Outer verticals lie medial to line connecting proclinate and post. reclinate. Face mostly light yellow; carina light brown. Cheek light yellow; high, ca. $\frac{1}{3}$ depth of eye. Flagellomere I 2.5 $\times$ length of pedicel, light brown. Arista with 6 dorsal and 2 ventral branches. Proboscis, clypeus yellow. Labellum light brown.

Notal ground color light brown; lighter, incomplete vitta pr.2 barely evident. Dorsal surface of scutellum light brown. Postnotum, pleura, legs, yellow. 4 rows long acrostichals present. Halter yellow. Wings infuscated gray-brown; present are a diffuse apical Sc spot and very heavy dm-cu spot; most of area anterior to M₁ is infuscated, except for proximal



Figs. 228–230. *Zygothrica sphaerocera*, holotype. 228. Hind tarsi, A (medial), B (lateral). 229. Hypandrium + aedeagus (ventral). 230. Surstylus (lateral).



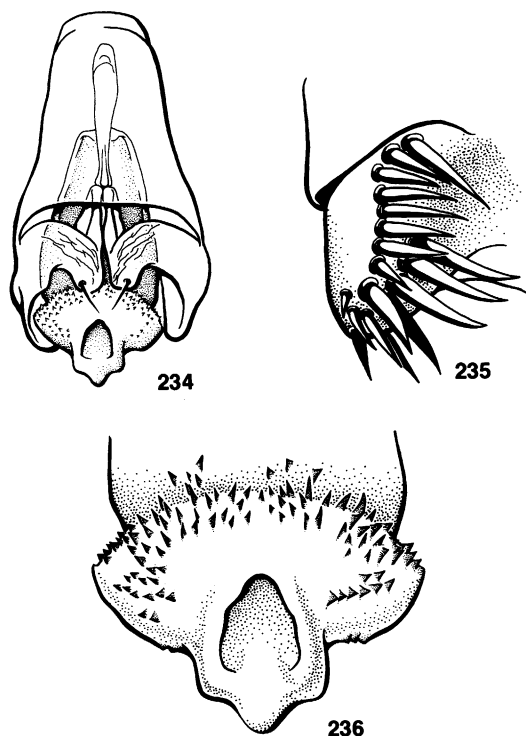
Figs. 231–233. *Zygotherica dissimulata*, holotype. 231. Terminalia (lateral). 232. Surstylus. 233. Hypandrium + aedeagus (ventrolateral).

$\frac{1}{4}$ and small window on M_1 between apex and dm-cu.

Tergite II yellow, t III with yellow anterior portion (brown posteriad), t IV mostly brown with medial yellow spot, t V and posteriad mostly yellow.

Hypoproctal plates broad laterally. Surstylus with 19 setiform prensisetae, smaller ones in lateral row. Gonopod finely wrinkled. Basiphallus slightly narrower than distiphallus; ca. equal to length of aedeagal apodeme, gradually tapered anteriad. Distiphallus with prominent medioapical projection and lateral flanges; heavily scaled dorsally and ventrally.

HOLOTYPE: ♂, ECUADOR: Napo, Coca, Napo River, V/65, 250 m, L. Peña (CNC) (genitalia dissected, DAG). $ThL = 1.58$; $HW/ThL =$



Figs. 234–236. *Zygotherica pictura*, holotype. 234. Aedeagus + hypandrium (ventral). 235. Surstylus. 236. Distiphallus (ventral).

1.57 ; $ThL/WL = 0.55$; $C.I. = 2.43$; $4-V = 1.11$.

ETYMOLOGY: Latin, “disguised,” since the wing infuscation pattern is superficially like that found in another group of flies in clade 1.2.1.2, the *aldrichii* species-subgroup.

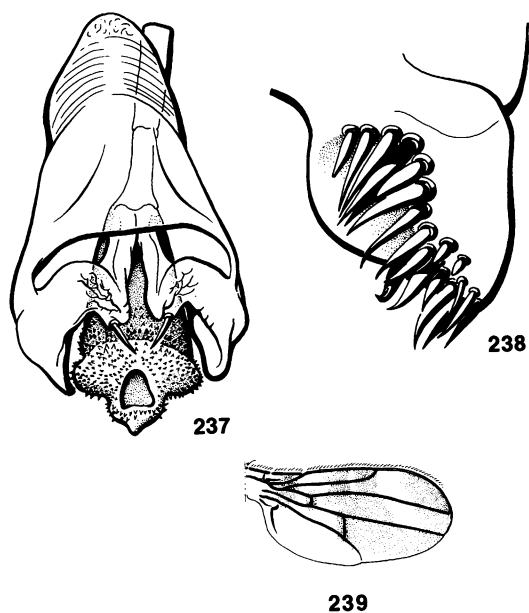
DISTRIBUTION: Known only from the holotype (fig. 266).

Zygotherica pictura, new species

Figures 206, 234–236

DIAGNOSIS: Easily recognized by the pattern of light brown spots on the wing, as figured and described below. Separation of this species from its closest relative is discussed under the Diagnosis of *Z. fascipennis* (♀ unknown).

DESCRIPTION: Ground color of vertex and front light brown. Frontal-orbital plates brown, ca. equal to frontal vittae in width. Frontal vittae flat brown. Eyes brick-red, bare. Ocellar triangle nearly extended to ptilinal



Figs. 237–239. *Zythothrica fascipennis*, holotype. 237. Aedeagus + hypandrium (ventral). 238. Surstylus. 239. Wing.

fissure; brown, shiny. Proclinate slightly thinner and longer than post. reclinate. Ant. reclinate ca. 0.6 length of post. reclinate, midway between ipsilateral orbitals. Post. reclinate midway between proclinate and post. reclinate. Ocellar setae extended to proclينات. Face yellow, carina light brown. Cheek very light yellow, ca. $\frac{1}{5}$ height of eye. Flagellomere I $2\times$ length of pedicel, light brown. Arista with 6 dorsal and 1 ventral branch. Palpi, proboscis, clypeus yellow; labellum very light brown.

Notal ground color light brown, with several diffuse vittae. Vitta-1 very narrow, inconspicuous, incomplete; vitta pr.2 brown; vitta pr.3 light, incomplete; remainder of notum gradually lightened to notopleural suture. Scutellum mostly light brown; subscutellum and postnotum yellow. 4 rows of acrostichal setulae present. Legs, halteres light yellow. Wing patterned with discrete, light brown infuscations. Present are an apical spot (extended to M_1), dm-cu spot, 3 separate spots in r-m band, an r-m spot, and a small proximal r-m band.

Tergites mostly dark brown. Hypoproctal plates laterally broad. Surstylus with 18 stout, setiform prenisetae; apicals are smallest,

medials are largest. Medial gonopod finely wrinkled. Basiphallus ca. $1.5\times$ length of distiphallus; apex ca. $2\times$ width of anterior (basal) portion. Distiphallus with conspicuous apicomedial projection and lateral flanges; dorsally and ventrally heavily scaled.

HOLOTYPE: ♂, COLOMBIA: Amazonas, Leticia, VIII/60, W. B. Heed and H. L. Carson (AMNH) (genitalia dissected, DAG). ThL = 1.26; HW/ThL = 0.80; ThL/WL = 0.56; C.I. = 0.95; 4-V = 3.05.

ETYMOLOGY: Latin, “pictured,” for the elaborate wing pattern.

DISTRIBUTION: Known only from the holotype (fig. 266).

Zythothrica fascipennis

Figures 237–239

Zythothrica fascipennis Duda, 1927: 54.

DIAGNOSIS: Distinguished from *Z. pictura* by the complete radial-medial band on the wing and by the presence of a small window in the r-m band over R_{2+3} (this region is entirely hyaline in *Z. pictura*). Based on genitalia, *Z. fascipennis* has an acute anterior margin on the hypandrium; *Z. pictura* has a flat margin. Also, the endophallus of *Z. fascipennis* is narrower and shorter than the one in *Z. pictura* (♀ unknown).

DESCRIPTION: Duda has provided a description of the unique specimen’s habitus; just an account of the genitalia will be added here.

Surstylus with 19 prenisetae, all setiform except 2 small lateral pegs. Hypandrium with lateral margins tapered apicad, then slightly expanded before final tapering. Posterior margin of hypandrium even. Two pairs of gonopods present; medial pair finely wrinkled. Basiphallus ca. equal in length to aedeagal apodeme; gradually tapered to width of aedeagal apodeme. Dorsal and ventral surfaces of distiphallus densely scaled.

HOLOTYPE: ♂, PERU: [Pasco], [Rio] Pichis, Puerto Bermúdez (SMTD) (genitalia dissected, DAG). Not measured.

DISTRIBUTION: Known only from holotype (fig. 266).

DISCUSSION: There is no doubt about the very close affinity of this species with *Z. pictura* and *Z. dissimulata*. This conclusion is based on the following synapomorphies: ex-

tensive r-m wing band, heavily scaled distiphallus and distiphallal collar, and wrinkled gonopods. Besides the type of wing infuscation pattern, *Z. fascipennis* and *Z. pictura* possess a crossvein dm-cu which is oblique (rather than perpendicular) to M_1 .

Zygothrica prodisar

Figures 23, 25–27, 59, 68–78, 115–116, 200, 211, 240–245, 267i–k; table 1

Zygothrica prodisar Duda, 1927: 63.

Zygothrica prodisar; Burla, 1954: 245.

DIAGNOSIS: Wings hyaline in both sexes; aedeagal apodeme apex close to anterior margin of hypandrium; distiphallus heavily scaled, with prominent median projection; spermatheca at most finely papillate (not coarsely scaled); oviscape apex flattened, with terminal row of ovisensilla; δ head moderately to very strongly broadened. Duda described the δ external features, and Burla (1954) described and illustrated the δ and η genitalia. Figures 240–245 show the genitalia of *Z. prodisar* since these are the most diagnostically important parts of the specimen.

HOLOTYPE: δ , PERU: [Cuzco], [Rio] Piñipiñi [12°58'S, 71°12'W], W. Schnuse, 1911–13 (SMTD) (genitalia dissected, DAG). Not measured.

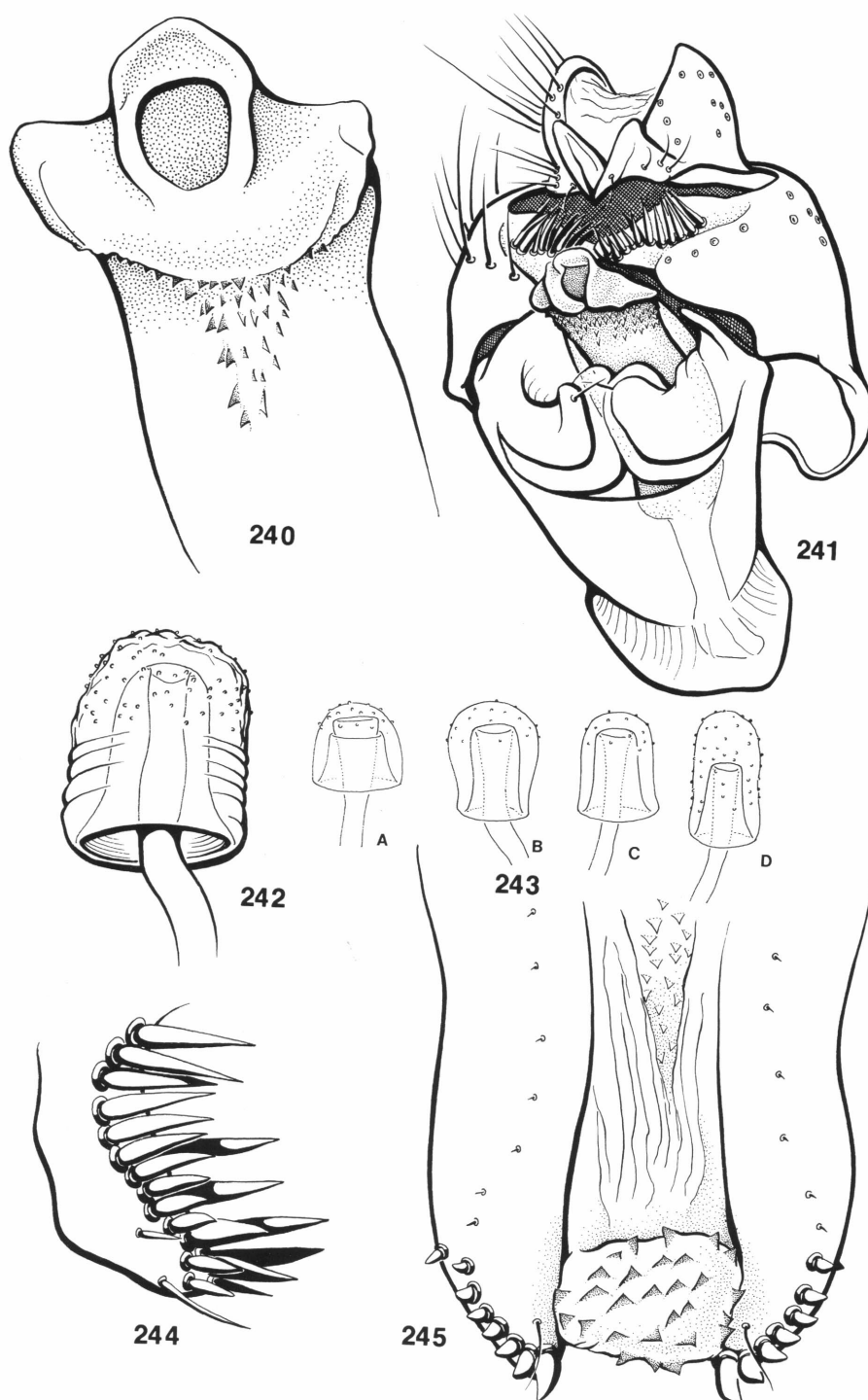
MEASUREMENTS: N = 14 δ , 8 η , from localities spanning the range. ThL = 1.38 δ (1.26–1.54); 1.56 η (1.26–1.72). HW/ThL = 1.26 δ (0.95–1.57); 0.84 η (0.79–0.92). ThL/WL = 0.52 δ (0.48–0.55); 0.54 η (0.49–0.58). C.I. = 2.91 δ (2.26–3.98); 2.63 η (2.18–2.89); 4-V = 1.36 δ (1.21–1.56); 1.38 η (1.21–1.61). 2 δ measured from Guapiles, Costa Rica had the most deviant measurements in the above values, which were C.I. = 3.98 and 3.58 (the remainder of the specimens varied from 2.26–3.16 for this trait in δ).

DISTRIBUTION: Central and Amazonian South America; not present on the Antilles (figs. 265, 266).

MATERIAL: BELIZE: Toledo, 25 m NW Punta Gorda, Salamanca, 28/VIII–4/IX/78, 3 δ^* , 1 η^* . BOLIVIA: Buenavista, Ichilo, 480 m, V/50, 1 δ^* ; S. Inicua, Riv. Alto Beni, 15–18/I/76, 12 δ , 9 η^* ; Tumupasa, XII/21, 1 η^* . BRAZIL: Belém, IV/58, 2 δ^* ; Bahia, Ilheus, VII/30, 2 δ^* , 6 η^* ; Marituba, 19/III/64, 1 δ^* , 1 η ; Mato Grosso, 12°51'S, 51°47'W, 2/III/68, 1 δ^* , 1 η ; Nova

Teutonia, 27°11'S, 52°23'W, XII/6/37, 3 δ^* ; Pará, Barreirinhas, Rio Tapajós, X–XI/70, 43 δ^* , 40 η^* ; Pará, Faz. Taperinha, nr. Santarém, 1–11/II/68, 5 δ^* , 3 η^* ; Petrópolis, 1 η ; Rondonia, Calama, 19–21/XI/75, 5 δ , 2 η^* ; São Paulo, Salesópolis, Est. Biol. Boraceia, IV/69, 3 δ^* ; São Pedro [do Piauí], VII/58–I/59, 10 δ^* . BRITISH GUYANA: Mazaruni (High Forest), 16/VIII/37, 2 δ^* ; Mazaruni-Potaro, Takutu Mtns., 6°15'N, 58°55'W, 3 η ("on white fleshy bracket fungus on fallen tree"). COSTA RICA: Finca Los Cusingsos, San Isidro del General, Quizzara, 3 δ^* , 1 η^* ; Golfito, VI–VII/59, 1 η^* ; Guapiles (Los Diamantes), 31/I/53, 17 δ^* , 7 η^* ("on *Auricularia*"); La Francia, Cairo, 5/II/53, 3 δ^* , 1 η^* ("ex fungus"); San José, 3000 ft, VII–VIII/56, 4 δ^* , 1 η^* ; Siquirres, 6/II/53, 7 δ^* , 4 η^* ("ex fungus"); Turrialba, I–X, various years, 30 δ^* , 10 η^* ; Sarapiquí, Heredia, 4/IV/70, 4 δ^* , 9 η^* . HONDURAS: Monte Vyuca, 10 km NW Zamorano, 5000 ft, 2/III/54, 2 δ^* , 1 η . ECUADOR: Limoncocha, 0°24'S, 76°40'W, 250 m, 9–16/III/76, 3 η^* ; Napo, Coca, Napo R., V/65, 250 m, 1 η^* ; Pichilingue, III/58, 1 δ^* . EL SALVADOR: Lago de Cojutepeque, 27/X/53, 7 δ^* , 7 η^* ; La Palma, 3200 ft, VIII/54, 8 δ^* , 5 η ; Volcan (Boqueron), 4500 ft, 16/V/54, 1 δ^* , 2 η . MEXICO: Chiapas, S. Crist. de las Casas, 7200 ft, 1/VI/69, 2 δ^* ("Malaise trap"); Lake Catemaco, Veracruz, 15/VIII/60, 4 δ^* , 8 η^* ; San Andres, 19 mi E Tuxtla, Veracruz, 27/VI/57, 6 δ^* , 6 η^* ; Tama-zunchale [San Luis Potosi], 23/XI/46, 7 δ^* , 7 η^* ; nr. Xilitla, 26–28/XII/55, 2 η^* . NICARAGUA: El Recreo, VI/55, 10 δ^* , 6 η^* ; Santa Maria de Ostuma, VI/54, 4 δ^* , 3 η^* . PANAMA: Alajuelo, 9/IV/11, 1 δ^* , 4 η^* ; Barro Colorado Island, VII–XI, various years, ca. 40 δ^* , 20 η^* ; "Canal Zone," Las Cruces Trail, 21/VII/67, 32 δ^* , 29 η ; Cerro Campana, 20/IV/60, 4 η^* ; Chiriqui, El Volcan, 8/VIII/61, 1 δ^* , 2 η^* ; El Valle, XI/46, 1 δ^* ; Huile Sta. Clara, X/52, 1 δ ; Trinidad River, 5/V/11, 78 δ^* , 71 η^* (4 δ^* , 5 η^* , "bred from white toad stool"). PERU: Madre de Dios: Avispas, 20–30/IX/62, 400 m, 1 δ^* ; Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 290 m, X/84, 10 δ^* , 10 η^* . SURINAME: Raleigh, Vallen-Voltzberg Reserve, V/8/84, 6 δ^* , 5 η^* ("swept over fungus"). TRINIDAD: Sangre Grande, XII/55, 6 δ^* , 1 η^* ; St. Andrew, Central Range Res., 300 ft, 28/I/76, 1 δ^* , 1 η^* .

DISCUSSION: *Zygothrica prodisar* has probably the most extensive range of any



Figs. 240–245. *Zygothrica prodisar*. **240.** Distiphallus (ventral), Turrialba, COSTA RICA. **241.** Terminalia (♂), holotype (posteroventral). **242.** Spermatheca (400×), most common type. **243.** A–D, spermathecal variants. **244.** Surstylus. **245.** Distal half of oviscap + oviprovector (ventral).

species in the genus. It also appears to be the most common fly in drosophilid aggregations on fungi. Perhaps as a consequence of its broad distribution, both geographically and altitudinally, the variation in morphology among specimens from various localities seems to exceed that found in all other species (except, perhaps, *Z. orbitalis*, which is another widespread species). The most apparent variation is in male head shape and in the genitalia of both sexes, although some wing measurement indices are also quite variable. For females, the spermathecal capsule is occasionally bare, usually papillate, and sometimes possesses fine basal annulations (fig. 243A–D). The oviscapae has six to eight ovisensilla per side, and, in males, the aedeagus more often than not has a basiphallus slightly broader than the distiphallus. Abdomen coloration varies in the intensity of melanization.

Among the *dispar*-subgroup species, *Z. prodyspar* is most closely related to *Z. dispar* and *Z. exuberans*. All three species not only have exceptionally broad heads, but, at least for the most modified individuals among them, the postvertical and postocular setae are hypermorphic (figs. 211–213). Wherever the broad-headedness, or hypercephaly, occurs in *Zygothrica* it is a result of an expanded ocellar triangle, expanded frontal-orbital and occipital plates (it is the latter which has forced most of the eye anteriad), and the apical distension of the eye itself. The face is relatively unmodified in hypercephalic forms.

***Zygothrica abbrevidispar*, new species**

Figures 246–251; table 1

DIAGNOSIS: ♂ and ♀ genitalia are distinct; so this species should not be confused with other members of the *dispar* subgroup: aedeagus short, very broad, length slightly less than $2\times$ width; oviscapae elongate, lateral margins slightly concave, 12–13 ovisensilla per side; spermatheca oval, with extensive fine papillae.

DESCRIPTION: Frontal head ground color dark brown to ptilinal fissure. Frontal-orbital plates brown, wider than frontal vittae. Frontal vittae brown, flat, but not velvety. Eyes red to red-brown. Ocellar triangle dark brown, nearly extended to ptilinal fissure. Ant. rec-

linated ca. $0.5\times$ length of other orbitals, midway between them. Post. reclinate closest to ant. reclinate. Ocellar setae short, not extended to ant. reclinates. Face mostly ochre in ♂ (brown in ♀), oral margin very protuberant; carina brown. Cheek, gena yellow. Flagellomere I brown, length $2\times$ pedicel; pedicel light brown. Arista with 5–6 dorsal and 2 ventral branches. Proboscis yellow in ♂, light brown in ♀. Palpi ca. $3\times$ longer than width; ochre in ♂, apically brown in ♀.

Notal, scutellar, tergal ground color brown in ♂ and ♀. Notopleural edge distinct. Pleura, legs yellow. 6 uneven rows of acrostichals present. Legs ochre. Forecoxa with ventral row of 5–6 evenly spaced, short setae. Wings hyaline, halteres yellow.

Oviscapae flat, lateral margins slightly concave, anterior margin truncate, apical margins oblique. Oviscapae length slightly more than $3.5\times$ width; with ventroapical row 12–13 per ovisensilla per side, plus 3 dorsal pegs, 11–12 tiny ventral sensilla per side. Oviprovector scales large, triangular, with 1 side tapered abruptly. Spermathecal capsule oval, with very narrow basal collar; surface extensively and finely papillate.

Hypoproctal plates narrow in lateral view, extended to dorsal margin surstyli. Surstylus blunt, with broad base; possesses 18–19 prensisetae: 2 tiny apical pegs, remainder are long scaliform. Hypandrium very short; lateral margins abruptly tapered; anterior margin narrow, rounded. Basiphallus ca. equal to length of aedeagal apodeme. Aedeagus length ca. $1.8\times$ width; with sparse scales ventrally, denser scales dorsally. Distiphallus flanged.

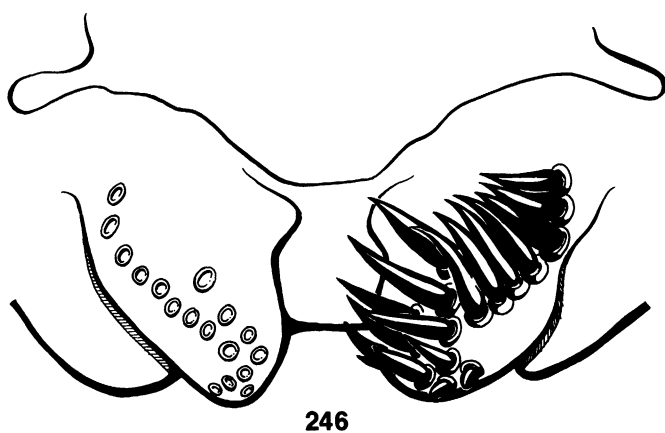
MEASUREMENTS: $N = 3\delta, 2\eta$. ThL = 1.42δ (1.31–1.49); 1.60η (no range). HW/ThL = 0.84δ (0.79–0.87); 0.78η (0.77, 0.80). ThL/WL = 0.54 (0.51–0.57). C.I. = 2.94 (2.48–3.44); 4-V = 1.36 (1.30–1.42).

HOLOTYPE: ♂, PANAMA: Piña, Ft. Sherman Preserve, 20/III/63, S. B. Pipkin, “reared from flower of *Dimerocostus* sp.” (NMNH) (genitalia not dissected). ThL = 1.46 ; HW/ThL = 0.87 ; ThL/WL = 0.51 ; C.I. = 3.38 ; 4-V = 1.44 .

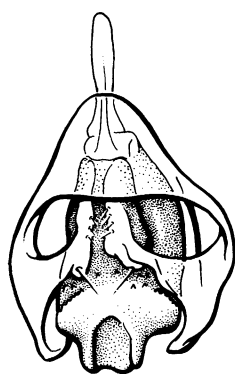
ETYMOLOGY: Latin, “short *dispar*,” for the abbreviated length of the aedeagus compared to most members of the *dispar* subgroup.

DISTRIBUTION: Panama.

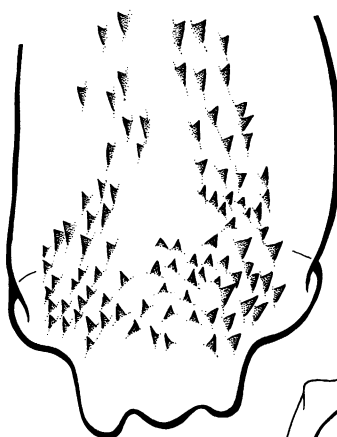
MATERIAL: (all are paratypes) $7\delta^*$, $4\eta^*$, from



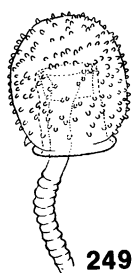
246



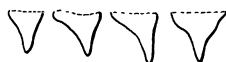
247



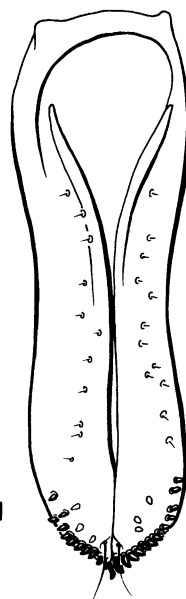
248



249



250



251

Figs. 246–251. *Zygothrica abbrevidispar*. 246. surstyli. 247. Hypandrium + aedeagus (ventral). 248. Distiphallus (dorsal). 249. Spermatheca. 250. Oviprovectator scales. 251. Oviscape (ventral).

same collection site as the holotype. Others: PANAMA: Bocas del Toro, Almirante, 24/VII/64, 1♂*, "bred from flower of *Costus splendens*."

DISCUSSION: The protuberant oral margin, bulbous carina, and flat and apically flanged aedeagus all indicate that this species belongs in the *dispar* species-subgroup. It is not included in the cladogram in figure 161, but seems most closely related to *Z. sphaerocera* because both possess a markedly short aedeagus.

Zygothrica dispar

Figures 46, 54, 203–204, 212,
252–258; 267; table 1

Achias (Zygothrica) dispar Wiedemann, 1830: 16.
Zygothrica dispar; Burla, 1954: 242.

DIAGNOSIS: Males are distinguished best by their very broad heads and by the diffuse, light brown apical infuscation on the wing. (*Z. latipanops*, n. sp., which is Central American, and allopatric to *Z. dispar*, also has these attributes, but it belongs to the *caudata* subgroup.) Also, the aedeagal apodeme is extended well beyond the anterior margin of the hypandrium, and the apical margin of the distiphallus is nearly flat. Females have a darker notum and can be easily confused with females of other species in the *dispar* and *caudata* subgroups. Females are best distinguished on the basis of genitalia: apical margin of the oviscap oblique, with 9–10 ovisensilla/side decreased in size anteriorly; spermatheca densely scaled, scales are large and erect. Abdominal coloration patterns (sensu Burla [1954]) are not reliable for distinguishing between *Z. dispar* and *Z. prodispar*. Malogolowkin (1952) figured and described the male and female genitalia, and these structures were figured as well by Burla (1954) and Wheeler (1968). Burla provided, in addition, a description of the external and several internal features. Male and female genitalia are shown here (figs. 252–258) for diagnostic purposes.

MEASUREMENTS: 8♂, 6♀. ThL = 1.34 ♂ (1.11–1.43); 1.46 ♀ (1.32–1.57). HW/ThL = 1.71 ♂ (1.03–2.14); 0.87 ♀ (0.84–0.90); ThL/WL = 0.52 ♂ + ♀ (0.50–0.53). C.I. = 3.11 (2.68–3.54); 4–V = 1.31 (1.01–1.50). Males from Charuma Forest, Trinidad, had high values

of ThL/WL, which were comparable to those of females (ca. 0.53), but these females were not distinct for any of the wing indices.

HOLOTYPE: "1¼ ♂ ♀ Ex: Brasilia," in original description (Naturhistorisches Museum der Humboldt Universität). The holotype was not examined; based on Wiedemann's description and rather nice but tiny illustrations, there seems to be no urgency for doing so. The only species from Brazil that matches these features in the original description is what is presently regarded as *Z. dispar*.

DISTRIBUTION: Trinidad, south to southern Brazil, west to Bolivia (fig. 266).

MATERIAL: BRAZIL: Campinas, Est. de Goiás, 1♂, 1♀; Espirito Santo, Linhares, 5♂, 5♀; Iguazu, 6/X/27, 1♀; Rio de Janeiro, Jardim Botânico, V/50, 1♀, 1♂ ("bred from *Brunfelsia* flower"; São Pedro [do Piauí], VII/58–I/59, 12♂, 3♀; São Paulo, Salesópolis, Est. Biol. Boracéia, ca. 50♂, 50♀, IV–V, several years; Ipiranga, 17/V/79, 6♂. BOLIVIA: S. Inicua, Riv. Alto Beni, 15–18/I/76, 1100 m, 3♂. TRINIDAD: Port of Spain, Emperor Valley, "on agaric," 8♂, 1♀; Tabaguite, Charuma For., 20/X/54, 25♂, 32♀; St. Andrew Plum, 300 ft, 28/I/76, 2♂.

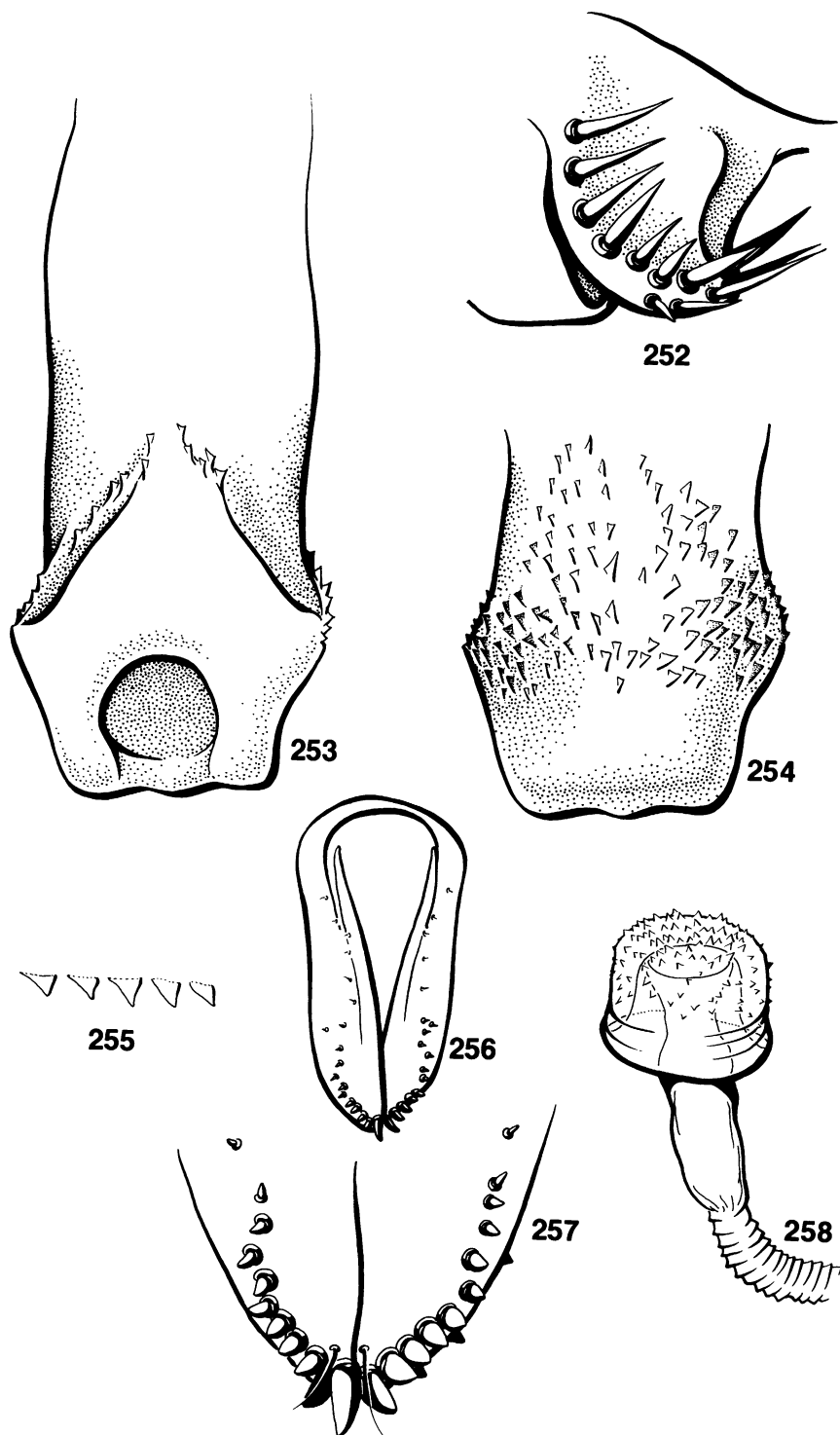
DISCUSSION: Based on the material in the NMNH that was studied by Sturtevant, the specimens that he referred to from Panama (Sturtevant, 1920) are actually *Z. prodispar*. Burla (1954, 1956) described the biphasic allometry of the male head width in this species and in *Z. prodispar* and *Z. laticeps*. Bristowe (1924) was apparently the first one to describe the territorial nature of *Z. dispar* males: "... there were a great number ... on the fungus, and whenever two males came close to each other they put down their heads and a great butting match would follow, ending in the feeble one being driven away" (p. 487). In preparation is a manuscript on the optical and behavioral consequences of the bizarre, allometric modification in male *Zygothrica* (Grimaldi, MS).

Zygothrica exuberans

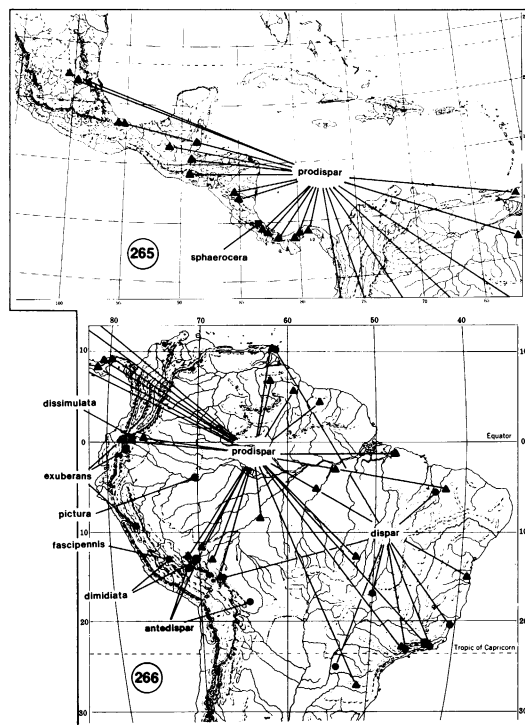
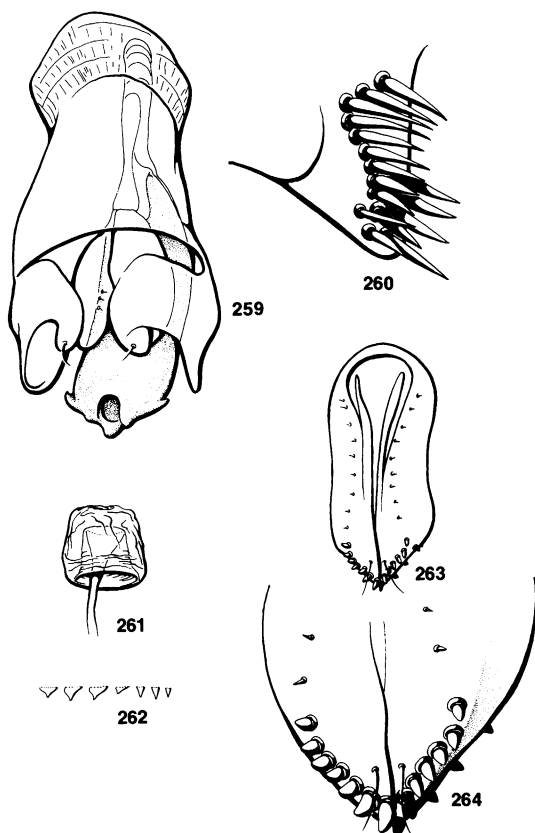
Figures 201–202, 213, 259–264

Zygothrica exuberans Wheeler, 1968: 438.

DIAGNOSIS: Males of this species present no difficulties in separating from *Z. dispar* and *Z. prodispar*, with which *Z. exuberans*



Figs. 252–258. *Zygothrica dispar*. 252. Surstylus. 253. Distiphallus (ventral). 254. Distiphallus (dorsal). 255. Oviprovector scales. 256. Oviscape (ventral). 257. Oviscape, detail of ventral apex. 258. Spermatheca (400×).



Figs. 265, 266. Distribution of the *dispar* species-subgroup.

Figs. 259–264. *Zygothrica exuberans*. 259. Hypandrium + aedeagus (ventral). 260. Surstylus. 261. Spermatheca. 262. Oviprovectores. 263. Oviscape (ventral). 264. Oviscape, detail of ventral apex.

might be sympatric. Externally, *Z. exuberans* has entirely hyaline wings (males and females); in males with the most modified heads, the eyes are so tapered as to have become facetless ribbons at the apices. Some males, but not all, have erect, hypermorphic presutural setae on the notum. Based on genitalia, the presence of a bare distiphallus, which has the lateral flanges hooked anteriorly, and a hypandrium with a distinctly flared anterior margin, are all diagnostic. Only one female is known of this species. The oviscape is symplesiomorphic and very similar in shape and arrangement of ovisensilla to *Z. dispar*, but the spermathecae are unique for the *dispar* subgroup. Spermathecae are nearly square in lateral view, without scales or papillae, and are wrinkled.

MEASUREMENTS: N = 4♂, 1♀. ThL = 1.43 ♂ (1.32–1.48); 1.55 ♀. NW/ThL = 1.87 ♂ (1.50–2.51); 0.87 ♀. ThL/WL = 0.53 (♂ + ♀) (0.51–0.54). C.I. = 2.88 (2.41–3.38); 4-V = 1.73 (1.45–2.36). Head width (HW) measurements were made by drawing the head, extending out the curved apical portions of the eyes, and then by measuring the image.

HOLOTYPE: ♂, ECUADOR: Pichilingue, III/58, M. R. Wheeler (NMNH) (genitalia dissected, MRW). Holotype examined: HW/ThL = 2.39.

DISTRIBUTION: Ecuador, Peru (fig. 266).

MATERIAL: Paratypes (NMNH, UT): 8♂* with same label data as holotype (2 other ♂* in paratype series are *Z. laticeps*). Others: ECUADOR: Pichincha, Santo Domingo, 23/VI/75, 2♂*. PERU: Huanuco, Cochicote, 8–9/IX/65, 1♂*, 1♀*.

DISCUSSION: Males with intermediately broadened and ones with extremely broadened heads occur in this species, as in most of the other hypercephalic *Zygothrica* males.

ALDRICHII SUBGROUP, CLADE 1.2.1.2.B.2

(figs. 163, 164)

This is the largest subgroup of the *dispar* species-group, with 28 species. Members of the group possess velvety black frontal vittae (apomorphy 87—lost in *Z. microeristes*, n. sp.); at least the hind tibia of females has an apical brown band (no. 111); at least the distal portion of the labium in females and often considerably more than this is darkened (no. 112); crossvein dm-cu is infuscated (no. 113—lost in two species, *Z. anota*, n. sp. and *Z. karenae*, n. sp; and appearing in parallel in several species in clade 1.2.2.2); the apex of vein R_{2+3} possesses a spot, or the spot has become coalesced into a midradial spot (no. 114); in males, the anterior hypandrial margin is distinctly lobate (no. 115).

In addition, females often have darker head, notal, tergal, and wing coloration. Unless specified otherwise in the descriptions, most members of the subgroup have the following traits (some of them are primitive at the level of the subgroup): eyes red-brown, bare, or with very short, sparse, setulae; ocellar triangle dark brown (at least in female), shiny, extended to ptilinal fissure; proclinate orbital seta equal in length to posterior reclinate; anterior reclinate midway between the posterior reclinate and proclinate, or slightly closer to the latter; posterior reclinate closest to inner vertical seta, sometimes closer to proclinate; carina prominent, complete, narrow; oral margin protuberant, sides splayed; male cheek yellow, female cheek with brown spot; flagellomere I light to dark brown, pedicel ochre; flagellomere I with short setulae; male legs completely yellow, sometimes with diffuse apical band on hind tibia; ventral cercal lobe (male) flattened, tapered ventrad; ventral epandrial lobes small, adpressed to lateral surfaces of surstyli. The very narrow carina and bauplan of the aedeagus structure (as being clavate and elongate) suggest that the *aldrichii* subgroup is more closely related to the *caudata* subgroup than to the *dispar* subgroup.

One characteristic of at least some members of the group is the habit of keeping the wings slightly raised and parted and swaying them from side-to-side ("swaying semaphoring," see Behavioral section). The distribution of the habit should be comprehensively

investigated, for it might be a synapotypy at the level of the subgroup. Male and female genitalia provide the most diagnostic characters for separating approximately 18 of the 28 species. A study of the intra- and inter-specific behavioral variation, genital morphology, male head shapes, and differences among species in color patterns of the body as well as the wings would provide useful data regarding hypotheses of "specific mate recognition signals" (SMRS) (Paterson, 1978) and the roles in speciation.

KEY TO MALES OF THE
ALDRICHII SPECIES-SUBGROUP

Identification of most species will require examination of terminalia, particularly past the point marked with an asterisk.

1. Wing with extensive radial infuscation, extended to M_{1+2} ; hypercephalic (figs. 426, 427) 2
 - 1a. Wing with radial infuscation either barely apparent or distinct, but at most extended to R_{2+3} ; usually not hypercephalic 3
2. Radial infuscation complete, without hyaline interruption (fig. 420); foretarsi with elongate, erect setae (fig. 428) *radialis*, n. sp.
- 2a. Radial infuscation with hyaline interruption (fig. 422); foretarsal setae not nearly as elongate as above (fig. 430) .. *pilipes*
3. Body color mostly ochre, anterior portion of notum sometimes brown; wing markings light, not extensive: R_{2+3} spot and apical spot separate, not coalesced; proximal r-m band barely to lightly developed 4
 - 3a. Notal and tergal ground color black-brown (except in *Z. microeristes*, which is yellow to ochre); radial wing infuscation dark: apical and R_{2+3} spots coalesced, or at least with narrow bridge; proximal r-m band heavy 9
4. Large (ThL ca. 1.50 mm); aedeagus lanceolate (figs. 282, 287) 5
 - 4a. Smaller flies (ThL ca. 1.20–1.30 mm); aedeagus clavate 6
5. Hind tibia with dark apical band; surstylus with 28–30 prensisetae; Nicaragua to Panama *amplialdrichi*, n. sp.
- 5a. Hind tibia entirely yellow; surstylus with 16–18 prensisetae; northern Bolivia, southern Peru *manni*, n. sp.
6. Surstyli small, pendulous, close together (fig.

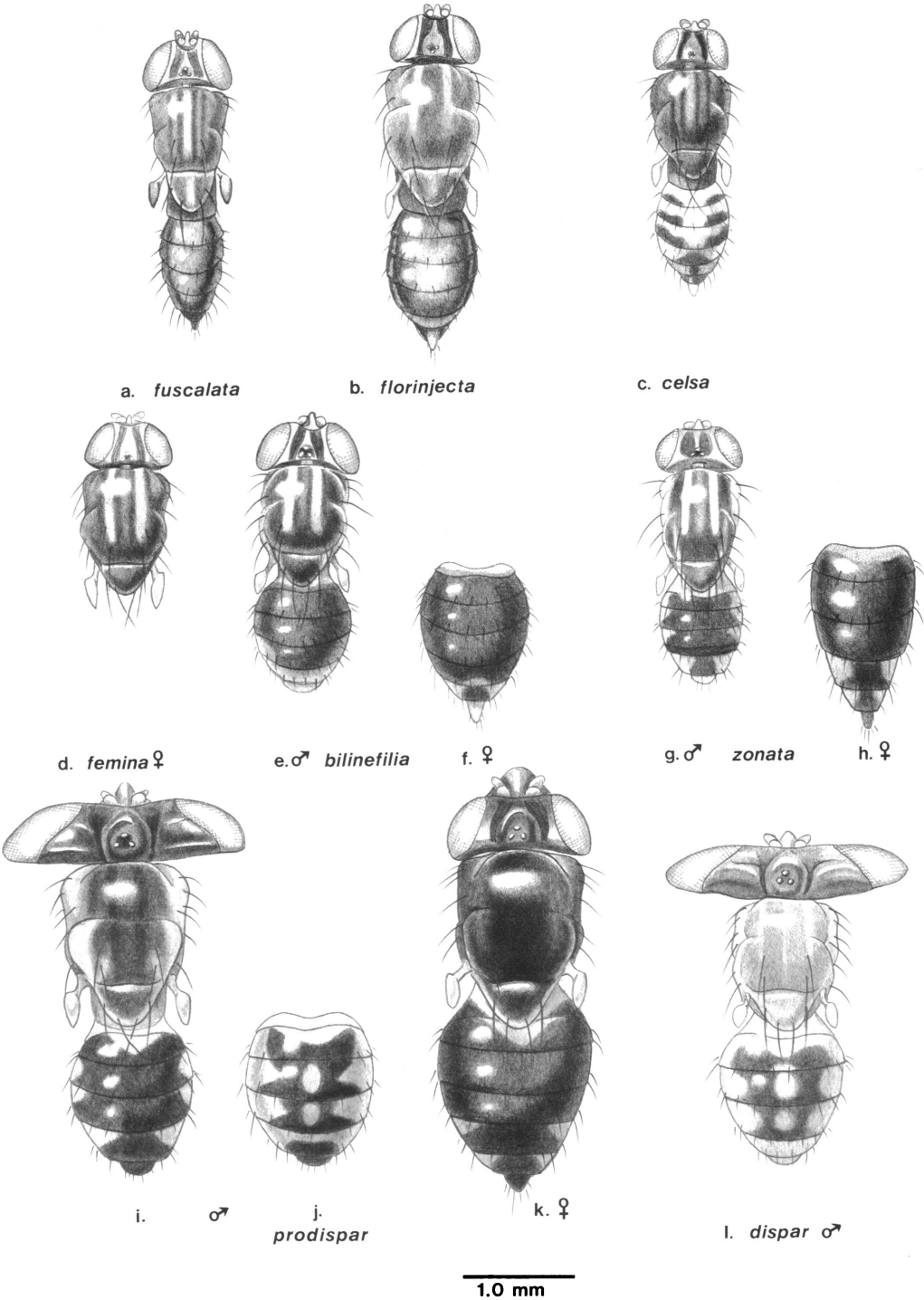


Fig. 267. Dorsal habitus of some *Zygothrica* species, or portions thereof. All are to the same scale. Some of the variation seen in *Z. prodipar* abdominal coloration is shown.

299); distiphallus densely scaled (fig. 301) *spinathigma*, n. sp. 6a. Surstyli with broad bases; distiphallus with much fewer scales 7

7. Distiphallus bulbous, with deep median notch (fig. 308); widespread in Amazon Basin *zygia*, n. sp.
- 7a. Distiphallus $\leq 2 \times$ width of basiphallus, shape not as above 8
8. Surstylus with 14–17 prensisetae; 4-V ca. 1.12; Nicaragua to Panama *pallida*, n. sp.
- 8a. Surstylus with ca. 20 prensisetae; 4-V ca. 1.25; Peru, Bolivia *andea*, n. sp.
- 8b. Similar to above; southeastern Brazil *neoadrichii*
9. Head moderately broadened, eyes slightly tapered (figs. 424, 425) 10
- 9a. Not hypercephalic 11
10. Small (ThL ca. 1.25 mm); body almost entirely ochre; widespread in Amazon Basin *microeristes*, n. sp.
- 10a. Much larger, ThL ca. 1.35 mm; dorsum mostly black-brown; Ecuador to northern Bolivia *tambopata*, n. sp.
11. Crossvein dm-cu not infuscated (figs. 314–317) 12
- 11a. Crossvein dm-cu with extensive, bold infuscation 13
12. Tergites mostly black-brown; with diffuse orange, narrow median stripe; C.I. ca. 2.80 *anota*, n. sp.
- 12a. Tergites completely black-brown; C.I. ca. 2.40; aedeagus stouter, distiphallus broader than in *Z. anota* (fig. 331; cf. fig. 327) *karenae*, n. sp.
13. Pleura black; southeastern Brazil *nigropleura*, n. sp.
- 13a. Pleura yellow, light ochre, or cream .. 14
14. Tergites with broad (ca. 0.5 width of abdomen), median, orange band along abdomen, bordered by black-brown (fig. 457g) *mediogaster*, n. sp.
- 14a. Tergites without such markings 15
15. Anterior half of notum brown, with 2 distinct, yellow, paramedian vittae extended to anterior dorsocentrals; 2 other incomplete vittae laterad, near notal-scutellar suture (fig. 457l) *somatia*, n. sp.
- 15a. Notum either entirely black-brown, or markings not as above 16
16. Notum with distinct, yellow, median vitta, vitta pr.2 narrow and black, pr.3 ochre, pr.4 dark brown (fig. 457k) *mediovitta*, n. sp.
- 16a. Notum entirely black-brown 17
17. Proboscis mostly brown, gradually lightened proximad 18
- 17a. Proboscis either entirely yellow, or with at most the labellum light brown 19
18. Surstylus broadly attached to epandrium (figs. 385, 387); aedeagus short, with distiphallus distinctly broadened (fig. 386); Nicaragua to Panama .. *glossusta*, n. sp.
- 18a. Surstylus truncate (fig. 409); aedeagus elongate, clavate (fig. 410); Trinidad *simulans*, n. sp.
19. Costal edge entirely infuscated (fig. 371); surstylus elongate, narrow; with large, hooked apical prensiseta (fig. 451) (1♂, from Costa Rica) *prensiseta*, n. sp.
- 19a. Costal infuscation with hyaline break; surstylus not as above, broader 20
- *20. Epandrium tapered ventrad; surstyli small, close together, nearly pendulous (figs. 335, 336, 345); hypoproctal plates narrow in lateral view, elongate (fig. 335) 21
- 20a. Epandrium not tapered ventrad; surstyli with broad bases; hypoproctal plates broad in lateral view 22
21. Apical, scaliform prensiseta present (fig. 336); distiphallus scalate (fig. 338), ca. $2 \times$ wider than basiphallus (fig. 337) *cryptica*, n. sp.
- 21a. Apical prensiseta large, but not scaliform (fig. 345); distiphallus glabrous, barely wider than basiphallus (fig. 344) *centralis*, n. sp.
22. Aedeagus short, ca. $2 \times$ length of aedeagal apodeme (fig. 380); gonopods glabrous; distiphallus slightly truncate, with sparse scales dorsally (figs. 380, 381); tergites II–IV black, others ochre with brown *aldrichii*
- 22a. Aedeagus ca. $3 \times$ length of aedeagal apodeme, distinctly clavate; gonopods spiculate; distiphallus scalate; tergites entirely black-brown 23
23. Distiphallus with conspicuous median notch, laterally flared (fig. 397); surstylus crescentic (fig. 396); C.I. ca. 2.30; Panama *panamensis*, n. sp.
- 23a. Not entirely as above; South America 24
24. C.I. ca. 1.90; surstylus with 13–15 prensisetae *paraldrichii*
- 24a. C.I. ca. 2.30; surstylus with 19–20 prensisetae *trinidata*, n. sp.

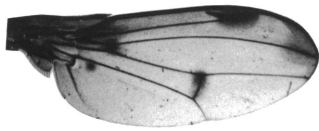
KEY TO FEMALES OF THE ALDRICHII SPECIES-SUBGROUP

1. Wing with R_{2+3} and apical spots separate, not coalesced, light (figs. 269, 271, 273, 276, 280) 2
- 1a. R_{2+3} and apical spots dark, coalesced; extended to midradial region 8
2. Oviscape apex flat (figs. 290, 309), terminal margin oblique; oviprovector scales large (figs. 284, 292, 310) 3

- 2a. Oviscape tapered apicad; terminal margin rounded; ovisensilla are in ventral row 5
3. Terminal row with 5 ovisensilla per side; distolateral margins of oviscape with pre-apical concavity (fig. 309); ThL ca. 1.50 mm *zygia*, n. sp.
- 3a. Terminal row with 10–11 ovisensilla per side; lateral margins not as above (fig. 290); large, ThL ca. 1.80 mm 4
4. Postnotum ochre; C.I. ca. 2.30; Nicaragua to Panama *amplialdrichi*, n. sp.
- 4a. Postnotum dark brown; C.I. ca. 2.45; Bolivia, Peru *manni*, n. sp.
5. Ventroapical row with 5–6 tiny ovisensilla pegs (fig. 305); Peru, Bolivia *andea*, n. sp.
- 5a. 9–10 ovisensilla pegs in ventroapical row, much larger than in *Z. andea* (e.g., fig. 297); Central America/British Guyana 6
6. Spermathecae with minute papillae (fig. 298); Nicaragua to Panama *pallida*, n. sp.
- 6a. Spermatheca with scales (e.g., fig. 291); South America 7
7. Wing with R_{2+3} and apical spots fairly dark, as in figure 271; notum mostly brown; southeastern Brazil *nealdrichi*
- 7a. Wing with faint R_{2+3} and apical spots (fig. 276); notum dark ochre; British Guyana *spinathigma*, n. sp.
8. Crossvein dm-cu not infuscated (figs. 315, 317) 9
- 8a. Crossvein dm-cu heavily infuscated .. 10
9. Tergites mostly black, with diffuse orange, narrow, median stripe; tergites VI–VIII orange; 7–8 ovisensilla in ventroapical row (fig. 328); oviprovectator scales small (fig. 328; cf. fig. 332) *anota*, n. sp.
- 9a. Tergites entirely black; 7 ovisensilla in lateral row; oviscape apex flat, with oblique terminal margins *karenae*, n. sp.
10. Pleura black-brown 11
- 10a. Pleura light ochre or yellow 21
11. Hind, mid + hind, or all femora black-brown 16
- 11a. Femora light yellow 12
12. Oviscape tapered apicad, apex narrow, with ventrolateral row of 5 small ovisensilla pegs (fig. 389) *glossusta*, n. sp.
- 12a. Oviscape with valves much wider; with larger ovisensilla pegs (e.g., figs. 339, 342) 13
13. Most ovisensilla pegs in ventromedial rows (figs. 377, 382) 14
- 13a. Most ovisensilla pegs in apical rows (figs. 339, 342) 15
14. C.I. ca. 2.80, Nicaragua to Panama *aldrichi*
- 14a. C.I. ca. 1.90, Amazon Basin .. *paraldrichi*
15. Lateral margins of oviscape parallel; terminal margins oblique, with row of ca. 9 ovisensilla per side (fig. 339); spermatheca without basal collar . *cryptica*, n. sp.
- 15a. Oviscape tapered apicad; with ventroapical row of ca. 6 large ovisensilla pegs; spermatheca with small basal collar (fig. 343) *centralis*, n. sp.
16. Only mid and/or hind femora are black-brown 17
- 16a. All femora are black-brown 19
17. Only hind femora are black-brown *nigropleura*, n. sp.
- 17a. Mid and hind femora are black-brown .. 18
18. From Trinidad *trinidada*, n. sp.
- 18a. Nicaragua to Panama . *panamensis*, n. sp. (associated males should be examined for material collected at sites between the presently known ranges of these 2 species).
19. Median portion of tergites with broad, orange band along length of abdomen, bordered by black (width of band ca. $\frac{2}{3}$ of abdomen width; fig. 457h); Costa Rica *mediogaster*, n. sp.
- 19a. Tergites entirely black; eastern South America 20
20. Notum mostly orange; pretarsi black, proximal tarsomeres light yellow *joeyesco*, n. sp.
- 20a. Notum black-brown; all tarsomeres light *simulans*, n. sp.
21. Wing with R_{2+3} and apical spot entirely coalesced; infuscation reaches to R_{4+5} and beyond that apically (fig. 421) 22
- 21a. Wing with hyaline constriction between R_{2+3} and apical spot, infuscation not nearly as extensive 23
22. Spermatheca with scales, mostly apically; introvert extended nearly entire length of spermatheca *radialis*, n. sp.
- 22a. Spermatheca with sparse papillae; introvert ca. $0.5 \times$ length of spermatheca . *pilipes*
23. Notum completely black-brown; tergites VI–VIII yellow, others black; Ecuador to northern Bolivia *tambopata*, n. sp.
- 23a. Notal vittae present, variable in length, color, and number 24
24. Notum mostly black-brown, with distinct, yellow vitta pr.2 extended to transverse suture (fig. 457j); widespread in Amazon Basin *microeristes*, n. sp.
- 24a. Notal pattern not as above 25
25. Notum with incomplete, light vitta pr.2 or

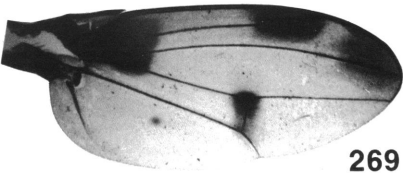
MALES

FEMALES

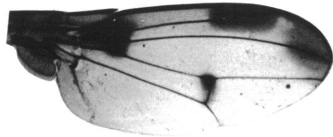


268

manni

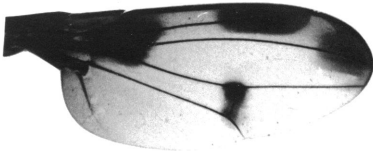


269



270

amplialdrichi

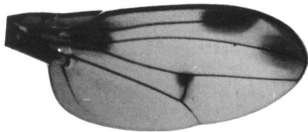


271

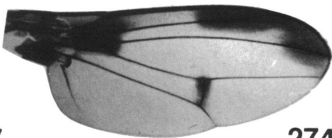


272

pallida

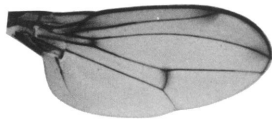


273



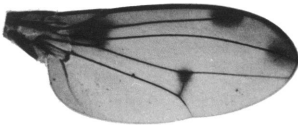
274

paravitta

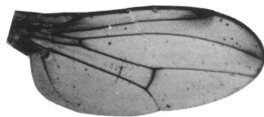


275

spinathigma

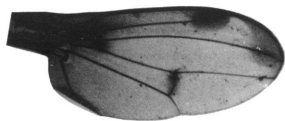


276



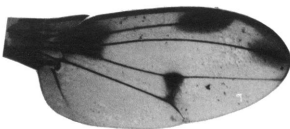
277

andea



279

zygia



280

Figs. 268–280. Wings of some *Zygothrica* in the *aldrichii* species-subgroup (clade 1.2.1.2.B.2).

- others laterad; no median vitta present 26
- 25a. Notum with incomplete, light vitta-1, dark and narrow vitta pr.2, plus ochre and brown vittae pr.3 and pr.4, respectively (fig. 457k); terminal margin of oviscapae with row of 5 widely spaced ovisensilla pegs *mediovitta*, n. sp.
26. Yellow, distinct vitta pr.2 extended to anterior dorsocentral setae; yellow, distinct, incomplete vitta pr.4, near notal scutellar suture (fig. 457l); spermatheca with 3–4 tiny scales on apex; eastern Brazil *somatia*, n. sp.
- 26a. Broad, orange, median band along abdomen; rest of tergite black; spermatheca sparsely and finely papillate; Costa Rica, Panama *paravitta*, n. sp.

***Zygothrica manni*, new species**

Figures 268, 269, 281–286

DIAGNOSIS: Largest species in the *aldrichii* subgroup; also distinguished by the light body color and wing markings in males; spatulate oviscapae, lanceolate aedeagus with sparse and tiny, retrorse scales. This species can be confused only with the allopatric species, *Z. amplialdrichi*; distinguishing features of the 2 are diagnosed under *Z. amplialdrichi*.

DESCRIPTION: Frontal-orbital plates brown, dorsal portion $2 \times$ width of anterior portion. Ant. reclinate ca. $0.8 \times$ length of post. reclinate. Ocellar setae extended to ant. reclinates. Outer verticals in line with orbitals. Face ochre in δ , brown in η ; carina brown. Flagellomere I length $5 \times$ pedicel. Arista with 5–7 dorsal and 2 ventral branches. Proboscis ochre, brown in η . Palpi clavate, base ca. $0.5 \times$ apical width. Palpi, clypeus yellow in δ , brown in η .

Notal ground color ochre in δ , dark brown in η . Anterior half of δ notum dark brown, with indistinct, light, incomplete vitta pr.2, sometimes with obscure median vitta. Pleura ochre; scutellum ochre in δ , black-brown in η (including postnotum). Notopleural edge distinct in η . 6 even rows acrostichals present. Ventral surface of forefemur with 2–4 setae, lengths slightly less than femur width. Wing with small, light, apical spots on R_{2+3} , dm-cu, r-m; η wing spots larger and darker.

Tergal ground color ochre in δ , black-brown in η . Tergites III, IV light brown in δ ; t III with light, inverted triangle. Tergites VI–VII in η ochre to light brown. Oviscapae rectangular, length ca. $2.5 \times$ width, with 11 peg ovisensilla per side (9 on ventroapical margin, 2 dorsally). Laterotergite VIII longer than oviscapae. Oviprovectors scales very large, some placoid, most dentate. Spermathecal capsule dome shaped; scaled.

Hypoproctal plate unmodified, extended to ca. middle of surstylus. Surstylus with broad base, short; with 16–18 prensisetae; 9 sharp lateral pegs; 7–9 longer, broad, setiform medials. Hypandrium narrow. Gonopods broad, lobate; 1 pair present; with sparse, fine wrinkles. Endophallus ca. $2 \times$ length of aedeagal apodeme; gradually widened into distiphallus. Distiphallus apically tapered; ventral margins with several small retrorse scales.

MEASUREMENTS: N = 3 δ , 3 η . ThL = 1.54 δ (1.46–1.67); 1.85 η (1.70, 2.00). HW/ThL = 0.81 δ (0.78–0.83); 0.78 η (0.76, 0.79). ThL/WL = 0.57 (0.55–0.60); C.I. = 2.43 (2.22–2.87); 4-V = 1.16 (1.09–1.20).

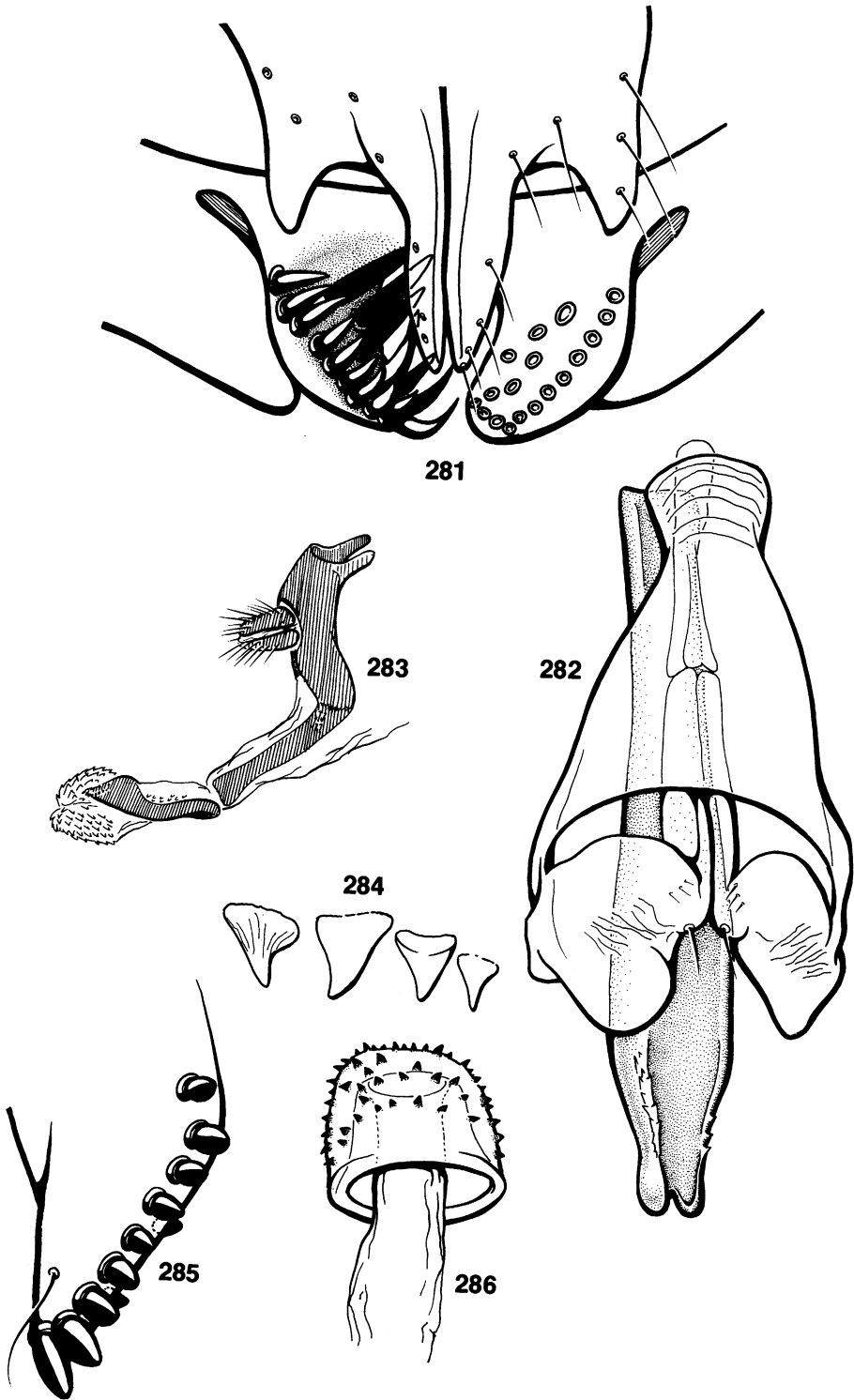
HOLOTYPE: δ , BOLIVIA: Tumupasa, VIII/21, W. M. Mann, Mulford Expedition (NMNH) (genitalia dissected, DAG). ThL = 1.67; HW/ThL = 0.78; ThL/WL = 0.60; C.I. = 2.22; 4-V = 1.09.

ETYMOLOGY: Patronym, in honor of the collector, W. M. Mann. Mann collected this and several other drosophilids, among many other kinds of insects, while on the Mulford Expedition from La Paz, Bolivia, to Manaus, Brazil (1921–22). An entertainingly biased account of the expedition was written by Gordon MacCreagh, who had also dedicated the book to Mann (alias “the Bug-Hunter”) (MacCreagh, 1985).

DISTRIBUTION: Northern Bolivia, southern Peru (fig. 313).

MATERIAL: (all are paratypes) BOLIVIA: S. Inicua Riv., Alto Beni, 15–18/I/76, 1100 m, 3 δ^* , 2 η^* ; Tumupasa, XII/22, 1 δ , 2 η^* . PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 19/IX–10/X/84, 290 m, 5 δ^* , 5 η^* , some “on *Auricularia*.”

DISCUSSION: Placed as the sister-species to *Z. amplialdrichi* because both possess a large,



Figs. 281–286. *Zythricha manni*. 281. Surstyli + hypoproctal plates. 282. Hypandrium + aedeagus. 283. ♀ terminalia. 284. Oviprovectator scales. 285. Oviscape, detail of left apical margin. 286. Spermatheca (400×).

lanceolate distiphallus (apomorphy 116), and the oviscape apex is broadly flattened (no. 35). In addition, not indicated on the cladogram are an oviscape with a truncate (vs. rounded) anterior margin, and an oviprovect bearing very large, heavily sclerotized scales. The females of both species are especially large.

***Zygothrica amplialdrichi*, new species**

Figures 115–116, 270, 271, 287–292, 457b, c

DIAGNOSIS: Allopatric with *Z. manni*; wing pattern slightly darker and more extensive; female of *Z. amplialdrichi* with light postnotum; both sexes with dark apical band on hind tibia. *Z. amplialdrichi* males with many more prensisetae and narrower basiphallus and gonopods than *Z. manni*.

DESCRIPTION: Frontal-orbital plates ochre in ♂, light brown in ♀. Ocellar setae long and fine; extended slightly past proclinate. Inner vertical setae strongly convergent; ends nearly touch. Outer verticals in line with orbitals. Face ochre to light brown in ♂, brown in ♀. Carina light brown. Flagellomere I $5\times$ length of pedicel. Arista with 5–6 dorsal and 2 vental branches. Proboscis light yellow in ♂, distal $\frac{2}{3}$ dark brown in ♀. Palpi slender. Palpi, clypeus yellow in ♂, light brown in ♀.

Notal ground color dark brown to dark-brown in ♂ and ♀. Posterior $\frac{1}{4}$ of ♂ notum ochre; notum completely dark in ♀. Dorsal scutellar surface partly black-brown in ♂, entirely so in ♀. Postnotum, pleura, halteres yellow. 6 even rows acrostichals present. Legs yellow in ♂ and ♀; hind tibia with brown apical band, much darker in ♀. Ventral surface of profemur with row 3–5 evenly spaced setae, lengths less than or equal to femur width. Wings with light spots at apex, R_{2+3} , dm-cu, r-m; spots darker but not much more extensive in ♀.

Tergal ground color ochre in ♂, dark brown in ♀. Tergites II, III dark brown in ♂, with light, inverted triangles; t VII, VIII ochre in ♀, t VI with diffuse, medial, ochre spot. Oviscape rectangular, length $3\times$ width, with 10–11 ovisensilla pegs on apical margin, 3 small pegs on dorsal surface, 7 tiny ventral sensilla per side. Laterotergite VIII ramus longer than oviscape. Oviprovect scales large, heavily sclerotized, dentate. Spermathecal capsule dome shaped, scaled.

Hypoproctal plate unmodified, extended to ca. middle of surstylus. Surstylus elongate, with broad base; with 28–30 prensisetae: 10 laterals, decreased in length apicad; 16–18 longer medials, longest ones proximal. Hypandrium narrow. Gonopods narrow, lobate; surface lightly, finely wrinkled. Paraphysial seta very fine. Basiphallus ca. equal to length of aedeagal apodeme, ca. 0.5 width of distiphallus. Distiphallus tapered gradually into basiphallus. Ventromedial trough broad, with several small, retrorse scales on ventrolateral margins. Apex tapered.

MEASUREMENTS: N = 3♂, 3♀. ThL = 1.51 ♂ (1.44–1.62); 1.76 ♀ (1.72–1.83). HW/ThL = 0.80 ♂ (0.69–0.87); 0.81 ♀ (0.78–0.87). ThL/WL = 0.58 (0.54–0.63); C.I. = 2.29 (1.97–2.58); 4-V = 1.15 (0.97–1.23).

HOLOTYPE: ♂, PANAMA: “Canal Zone,” Barro Colorado Island, VIII/56, W. B. Heed, H. L. Carson, M. W. Wasserman (AMNH) (genitalia not dissected). ThL = 1.62; HW/ThL = 0.85; ThL/WL = 0.63; C.I. = 2.58; 4-V = 1.14.

ETYMOLOGY: Latin, “fuller *aldrichi*,” for the large body size compared to most members of the *aldrichii* subgroup.

DISTRIBUTION: Nicaragua to Panama (fig. 312).

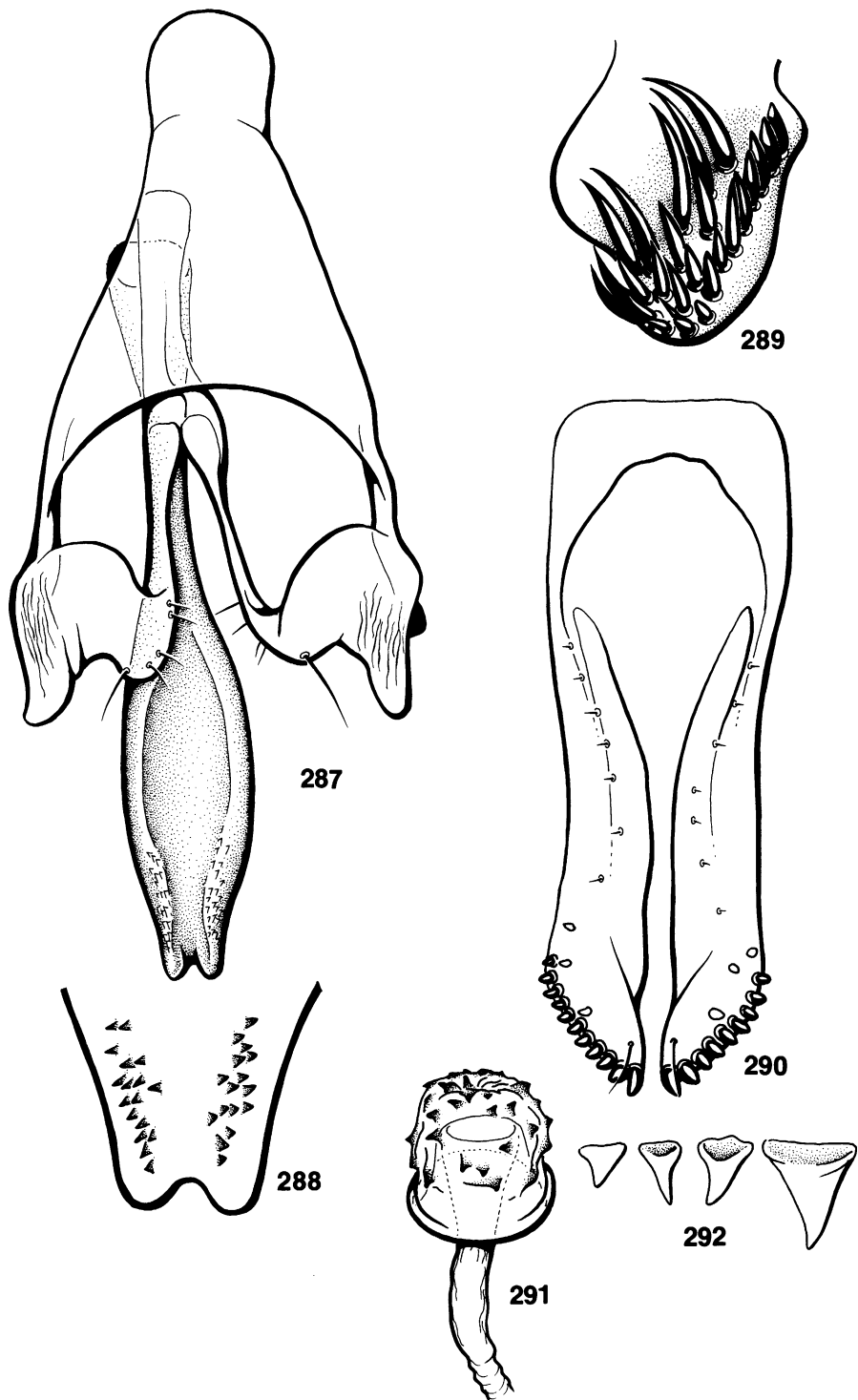
MATERIAL: (Barro Colorado Island specimens are paratypes) COSTA RICA: Sarapiquí, Heredia, 4/IV/70, 2♀. NICARAGUA: El Recreo, VI/54, 5♂*, 3♀*. PANAMA: Barro Colorado Island, III–XI, several years, 6♂*, 6♀*; Cerro Campana, VII/67, 1♂*, 1♀*, 2/III–20/IV/60, 1♂*, 4♀*.

DISCUSSION: Based on the captures from Barro Colorado Island and from Cerro Campana, the species occurs throughout the year in Panama.

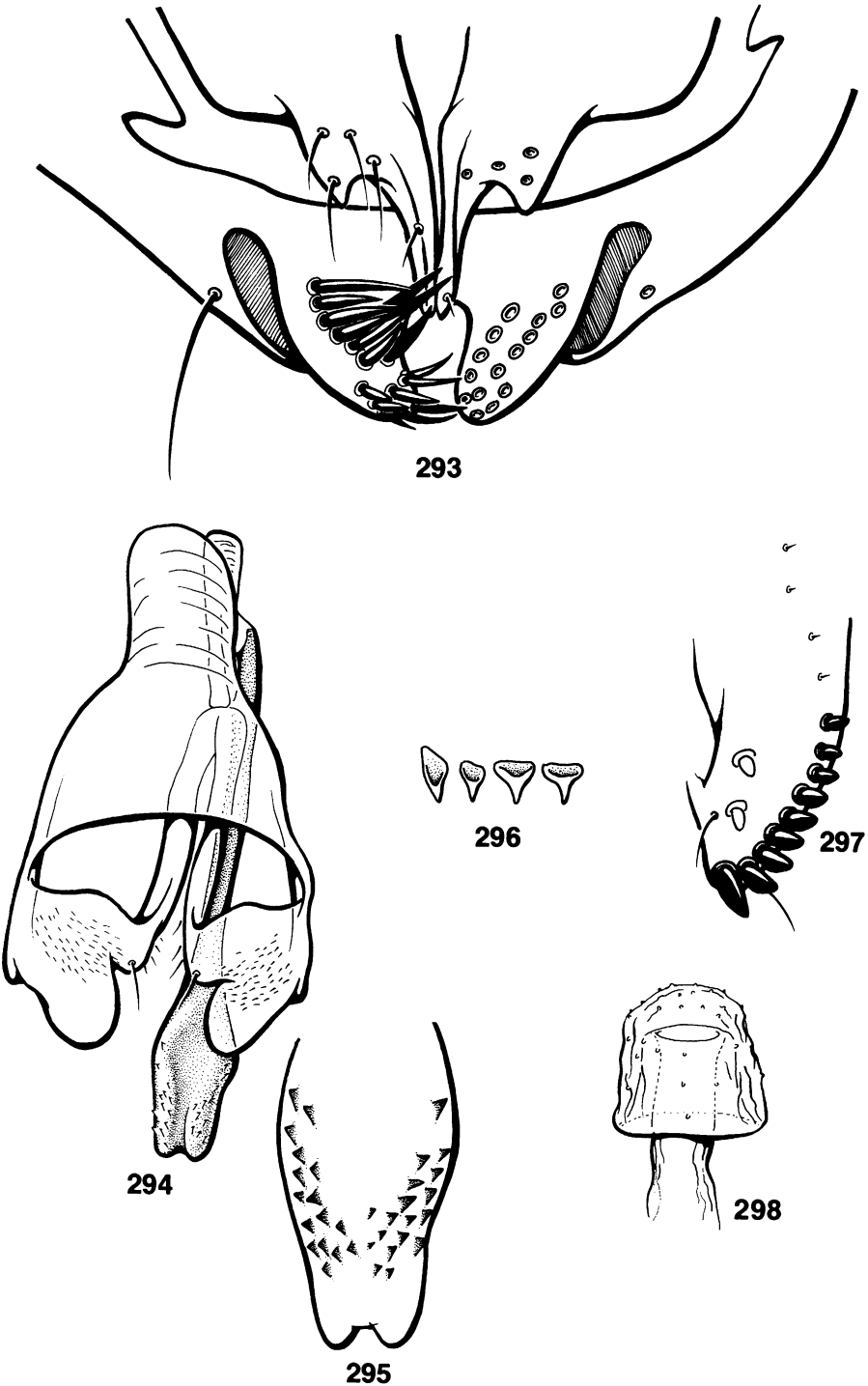
***Zygothrica pallida*, new species**

Figures 3, 4, 61, 272–273, 293–298, 432–433; table 1

DIAGNOSIS: Besides *Z. spinathigma*, this is the palest member of the *aldrichii* subgroup. Males are distinct because of an almost entirely ochre notum. Females are distinguished from most other Central American species on the basis of light wing infuscations. Genitalia provide confirming sources of traits for identification: 14–17 prensisetae present,



Figs. 287–292. *Zygothrica ampliadrichi*. 287. Aedeagus + hypandrium (ventral). 288. Distiphallus, detail of dorsal apex. 289. Surstylus. 290. Oviscape (ventral). 291. Spermatheca (400 ×). 292. Oviprovector scales.



Figs. 293–298. *Zygothrica pallida*. 293. Surstyli + hypoproctal plates. 294. Aedeagus + hypandrium (ventral). 295. Distiphallus (dorsal). 296. Oviprovector scales. 297. Oviscape, detail of left apical margin. 298. Spermatheca.

relatively unmodified in shape and size; spermathecae with tiny papillae.

DESCRIPTION: Frontal-orbital plates ochre to light brown. Ant. reclinate much closer to proclinate than to other orbitals. Post. reclinate ca. midway between proclinate and outer vertical. Ocellar setae extended to proclimates. Outer vertical in line with orbitals (δ). Face light brown to yellow in δ ; darker in η ; carina similar. Flagellomere I length $5\times$ pedicel. Arista with 5–6 dorsal and 1–2 ventral branches. Proboscis yellow in δ , distal $\frac{2}{3}$ brown in η . Apex of palpus, clypeus light brown in δ , darker in η .

Notal ground color ochre in δ , black-brown (including scutellum) in η . Anterior half of δ notum fuscous, with diffuse, yellow, incomplete vitta-1 and pr.2. Scutellum ochre in δ . Pleura, postnotum, halter yellow. 4–6 rows acrostichal setulae present. Legs yellow, with brown apical band on hind tibia, slightly darker in η . Ventral surface of forefemur with 2–3 setae, lengths less than femur width. Wings with variable infuscation: δ usually with very light apical and R_{2+3} spots and barely perceptible dm-cu spot, but may be as dark and extensive as η wing markings.

Tergal ground color ochre in δ , t III, IV sometimes slightly darker. All tergites dark brown to shiny black in η . Oviscape oval, length ca. $2\times$ width, with 11 ovisensilla pegs: 9 on ventral margin, 2 dorsally, per side; with 11–12 tiny ventral sensillae per side. Oviprovectator scales dentate, anterior ones with distinct apical tapering. Spermathecal capsule dome shaped; surface wrinkled, with very tiny papillae.

Epandrium yellow, with slightly elongate dorsal margin. Hypoproctal plates extended to ca. middle of surstylus. Surstylus small, with broad base; possesses 14–17 prenisetae: 6–7 elongate lateral pegs, separated from apicals by slight gap; longest prenisetae mediad. Hypandrium narrow. Gonopods large, lobate; surface finely spiculate. Paraphysial seta fine. Basiphallus ca. $2.5\times$ length of aedeagal apodeme; ca. $3\times$ width of distiphallus. Distiphallus slightly narrowed apicad; with scales dorsally and ventrally.

MEASUREMENTS: N = 4 δ , 3 η . ThL = 1.42 δ (1.36–1.48); 1.52 η (1.47–1.58). HW/ThL = 0.84 δ (0.80–0.88); 0.78 η (0.78, 0.79). ThL/

WL = 0.59 (0.57–0.64); C.I. = 2.54 (2.33–3.03; 4-V = 1.12 (1.00–1.22).

HOLOTYPE: δ , PANAMA: "Canal Zone," Barro Colorado Island, X–XI/55, W. B. Heed (AMNH) (genitalia not dissected). ThL = 1.45; HW/ThL = 0.80; ThL/WL = 0.64; C.I. = 2.33; 4-V = 1.00.

ETYMOLOGY: Latin, "pale," for the light body color.

DISTRIBUTION: Nicaragua to Panama (fig. 312).

MATERIAL: COSTA RICA: Heredia, Sarapiquí, 4/IV/70, 2 η *; Golfito, VI–VII/59, 1 η *; Quizzara, San Isidro de General, Finca Los Cusingos, 23/XII/43, 1 δ *. EL SALVADOR: Lago de Cojutepeque, 29/X/53, 1 δ *. NICARAGUA: El Recreo, VII/54, 32 δ *, 21 η *. PANAMA: Barro Colorado Island, VII–XI, various years, 16 δ *, 17 η *; "Canal Zone," Las Cruces Trail, 21/VII/67, 5 δ *, 1 η * ("bracket fungi"); Trinidad River, 5/V/11, 5 δ , 1 η ; Cerro Campana, 2/III/60, 1 δ ; Bocas del Toro, Almirante, I/63, 1 η (specimens from B.C.I. are paratypes).

DISCUSSION: This is one of the most common Central American species in the *aldrichi* species-subgroup. It appears to be most common during the rainy season, according to label data.

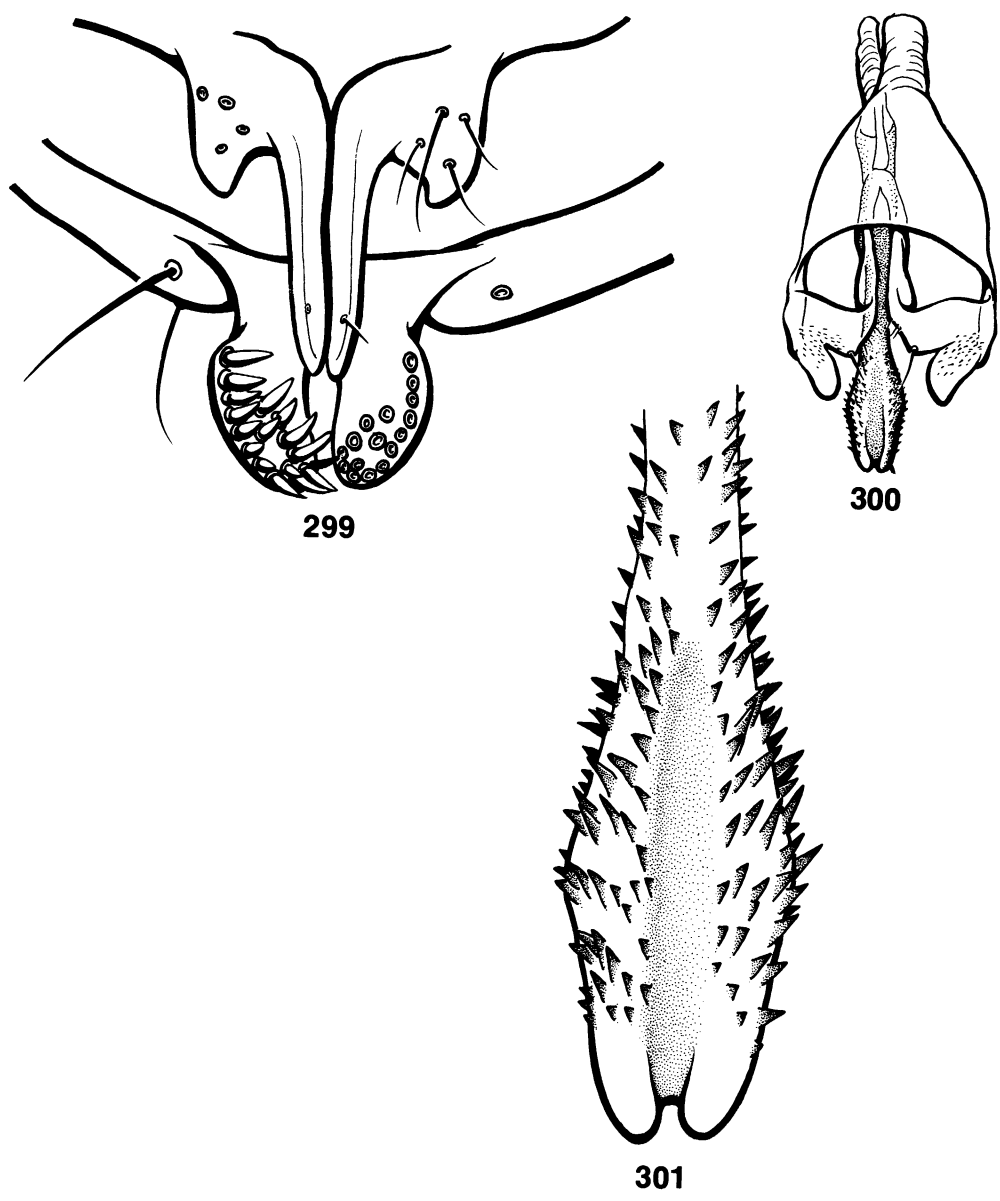
Zygothrica spinathigma, new species

Figures 275–276, 299–301

DIAGNOSIS: Males distinct based just on pallid appearance of body and wings: apex of R_{2+3} and dm-cu spots barely evident in males but much more so in females. Distiphallus densely scaled; hypoproctal plates very narrow in lateral view; surstyli small, pendulous.

DESCRIPTION: Post. reclinate seta closest to inner vertical. Ocellar setae extended to proclimates. Outer verticals in line with orbitals or slightly laterad (δ). Face completely yellow in δ , oral margin fuscous in η . Flagellomere I $5\times$ length of pedicel. Arista with 5 dorsal and 1 ventral branch. Proboscis yellow in δ , fuscous in η . Palpi, clypeus yellow in δ , light brown in η .

Notum, including dorsal surface of scutellum, entirely ochre in δ , dark brown in η . Notopleural edge indistinct in η . Pleura, postnotum, halter light yellow in δ and η . 6 even rows acrostichals present. Ventral surface of

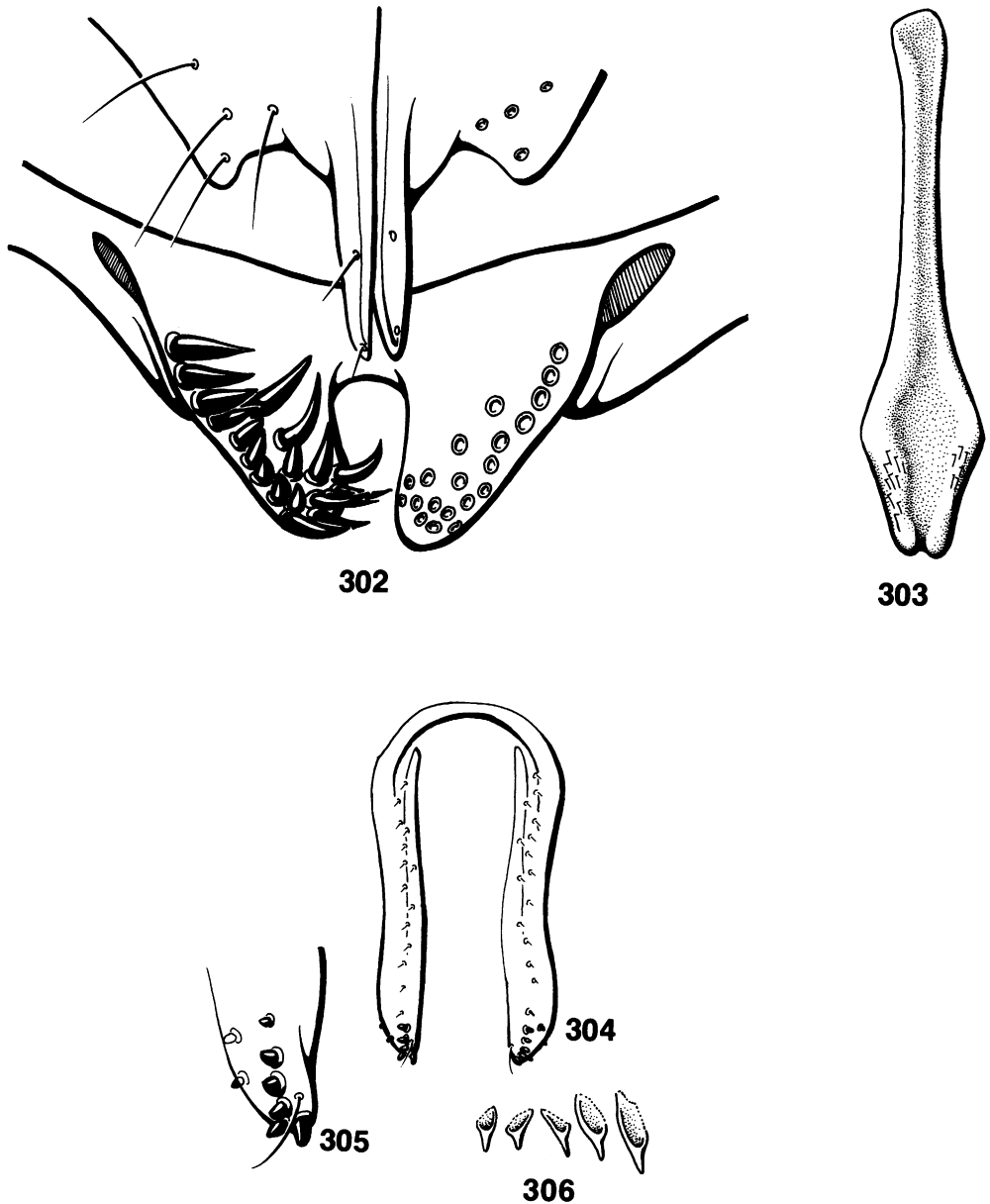


Figs. 299–301. *Zygothrica spinathigma*. 299. Surstyli + hypoproctal plates. 300. Hypandrium + aedeagus (ventral). 301. Distiphallus (ventral).

profemur with 2–3 setae, lengths $\leq \frac{1}{2}$ femur width. Wing with very light infuscation, especially in δ .

Tergites ochre in δ . Tergites III–V black-brown in δ , t VI–VIII ochre (t VI, VII with diffuse, median, brown spot), t III with yellow inverted triangle. Hypoproctal plates very narrow in lateral view, extended to antero-

medial margin of surstyli or to middle of surstyli. Surstylus pendulous, small; with 17–18 prenisetae: 7–8 pegs in evenly spaced lateral row, longest prenisetae apically. Hypandrium with lateral margins slightly convex. Gonopods narrow, lobate, sparsely spiculated. Paraphysial seta fine. Basiphallus ca. $2 \times$ length of aedeagal apodeme, $\frac{1}{2}$ width of



Figs. 302–306. *Zygothrica andea*. 302. Surstyli + hypoproctal plates. 303. Aedeagus (ventral). 304. Oviscape (ventral). 305. Oviscape apex, detail. 306. Oviprovectors scales.

distiphallus. Distiphallus slightly tapered apicad, possesses dense vestiture of elongate, erect, and retrorse scales.

MEASUREMENTS: $N = 3\delta, 3\varphi$. ThL = 1.33 δ (1.31–1.37); 1.38 φ (1.29–1.45). HW/ThL = 0.87 δ (0.84–0.88); 0.82 φ (0.82, 0.83). ThL/WL = 0.57 (0.56–0.61). C.I. = 2.35 (2.21–2.54); 4-V = 1.20 (1.08–1.30).

HOLOTYPE: δ , BRITISH GUYANA: Mazaruni, High Forest, 16/VIII/37, O. W. Richards and J. Smart (“on fungus”) (BMNH) (genitalia not dissected). ThL = 1.37; HW/ThL = 0.88; ThL/WL = 0.61; C.I. = 2.21; 4-V = 1.16.

ETYMOLOGY: Latin, “spiny/thorny,” and Greek, “touch,” for the heavily scaled distiphallus.

DISTRIBUTION: British Guyana.

MATERIAL: All paratypes (of which 2♂, 2♀ were dissected), collected with holotype.

Zygothrica andea, new species

Figures 82–84, 277, 302–306; table 1

DIAGNOSIS: Except for genitalia, males and females of *Z. andea* and *Z. spinathigma* can be confused (they are, however, probably allopatric). A broad distiphallus with sparse scalation, and a surstylus with a broad base and ca. 20 prensisetae will allow easy separation from *Z. spinathigma*. Male genitalia are most similar to the Central American species *Z. mediogaster* (also allopatric), except that *Z. mediogaster* has slightly more robust aedeagus, fewer prensisetae, and narrow hypoproctal plates. Externally, *Z. mediogaster* is quite distinct in coloration. *Z. andea* females are most distinctive on the basis of the tiny ovisensilla pegs.

DESCRIPTION: Frontal-orbital plates yellow in ♂, ochre in ♀. Post. reclinate ca. midway between inner vertical and proclinate. Ocellar setae fine, elongate: extended to bases of proclimates. Outer vertical in line with all ipsilateral orbitals (♂). Face light yellow in ♂, light brown in ♀; carina light yellow in ♂, brown in ♀. Flagellomere I length 3× pedicel. Arista with 4–5 dorsal and 1–2 ventral branches, evenly spaced. Proboscis yellow in ♂, dark brown in ♀. Palpi, clypeus yellow in ♂, brown in ♀.

Notal and dorsal scutellar ground color ochre in ♂; vitta-1 and pr.2 light, diffuse, extended ½ way to ant. dorsocentrals, bordered by brown. Notum, dorsal scutellum black-brown in ♀, with indistinct notopleural edge. Pleura, postnotum, halteres light yellow in ♂ and ♀. 4–5 rows acrostichals present. Wing with very light infuscations, especially in ♂.

Tergal ground color ochre in ♂, dark brown in ♀. ♂ tergites homogeneous in color, ♀ t VI–VIII ochre, t III with yellow inverted triangle. Oviscape narrowly oval, length ca. 2.5× width, with 9 small ovisensilla pegs per side (6 in ventroapical row, 3 dorsally), 15 tiny ventral sensilla per side. Oviprovector scales narrow, dentate. Hypoproctal plates not quite extended to dorsomedial margin of surstyli. Surstylus triangular in posterior view, with broad base, apically tapered; with 20 pre-

sisetae: row of 9 evenly spaced pegs in lateral row, others are longer medials and apicals. Gonopods lobate, surface finely spiculed. Basiphallus ca. 2× length of aedeagal apodeme, 0.3–0.5× width of distiphallus. Distiphallus with lateral broadening at base, tapered to width of basiphallus at apex; ventrally with 10–12 short, retrorse scales on ventral margins.

MEASUREMENTS: N = 3♂, 3♀. ThL = 1.29 ♂ (1.22–1.34); 1.48 ♀ (1.45, 1.52). HW/ThL = 0.78 ♂ + ♀ (0.77–0.82); ThL/WL = 0.57 (0.51–0.67); C.I. = 2.51 (2.21–2.73); 4-V = 1.26 (1.15–1.36).

HOLOTYPE: ♂, PERU: Loreto, Rio Momon (ca. 75 km NW Iquitos), 17/III/84, W. N. Mathis (NMNH) (genitalia dissected, DAG). ThL = 134; HW/ThL = 0.77; ThL/WL = 0.61; C.I. = 2.47; 4-V = 1.26.

ETYMOLOGY: Latin, “of the Andes,” for its distribution, which is the eastern foothills of southern Peruvian and northern Bolivian Andes.

DISTRIBUTION: Peru, Bolivia (fig. 313).

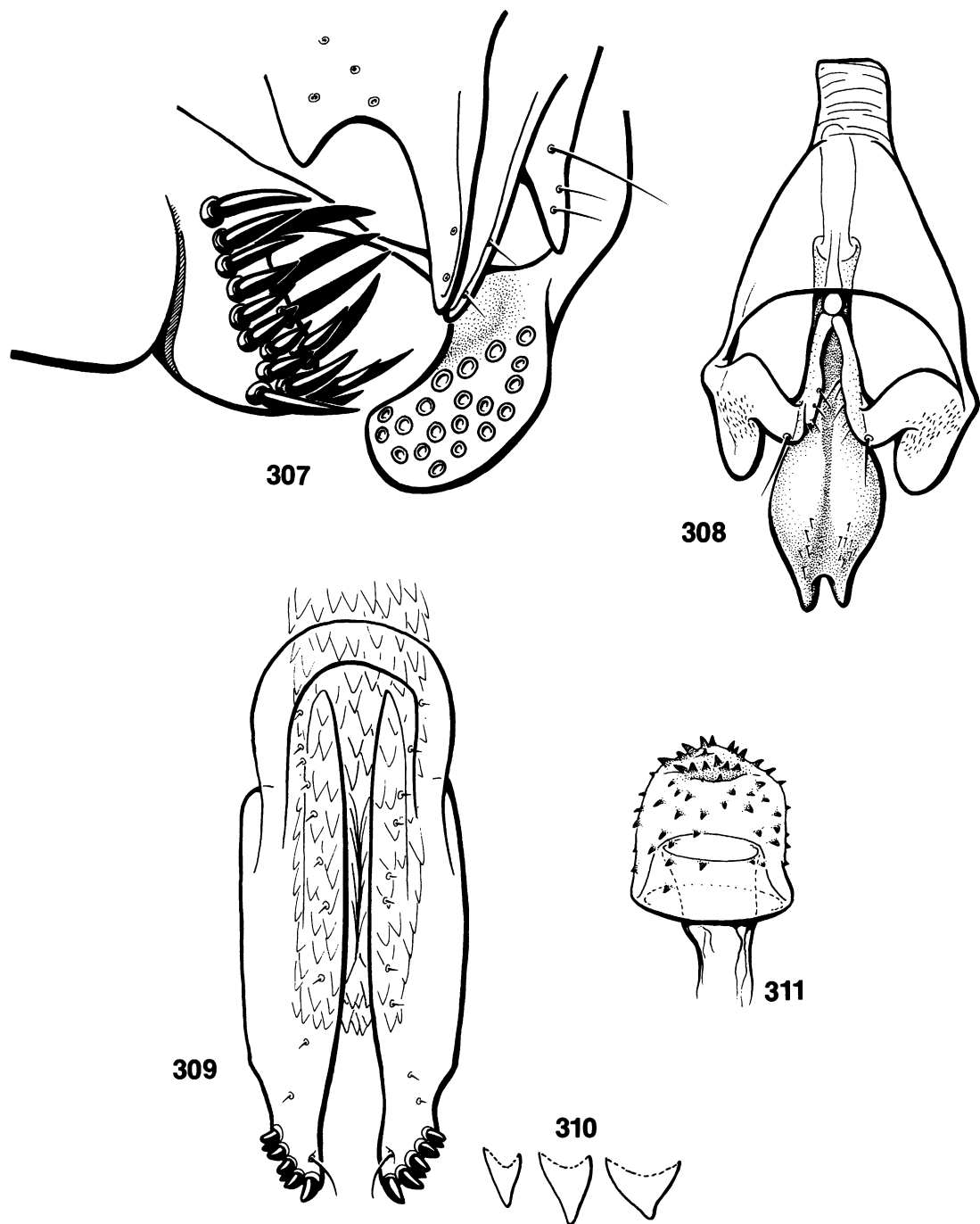
MATERIAL: (all are paratypes) BOLIVIA: S. Inicua Riv., Alto Beni, 15–18/I/76, 1100 m, 7♂*, 1♀*. PERU: Cuzco, Quince Mil, 1–15/XI/62, 700 m, 2♂*, Colonia Perené, Chanchamayo, 16/VII/23, 2♂*, 1♀*; Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 19/IX–10/X/84, 32♂*, 14♀.

Zygothrica zygia, new species

Figures 279–280, 307–311, 423, 457d; table 1

DIAGNOSIS: Sympatric with *Z. andea* in southern Peru, with *Z. spinathigma* in British Guyana; externally separated from other paler species partly by darker and more extensive wing infuscations. Males with narrow hypoproctal plates, distiphallus bulbous and with deep median notch. Oviscape elongate, lateral margins parallel, 5 large ovisensilla on terminal margin of each side; oviprovector scales large, narrow triangular.

DESCRIPTION: Ant. reclinate fine, elongate, length ca. 0.9× other orbitals. Ocellar setae fine, extended to proclimates. Outer verticals in line with orbitals (♂), slightly lateral to line in ♀. Face ochre in ♂, brown in ♀; carina ochre in ♂ and ♀. Flagellomere I length 3× pedicel. Arista with 6 dorsal and 1–2 ventral branch-



Figs. 307–311. *Zygothrica zygia*. 307. Surstyli + hypoproctal plates. 308. Aedeagus + hypandrium (ventral). 309. Oviscape (ventral). 310. Oviprovectur scales. 311. Spermatheca (400×).

es. Proboscis ochre in ♂, brown in ♀. Palpi slender; palpi, clypeus yellow in ♂, slightly darker in ♀.

Notal and scutellar ground color dark brown in ♀, with notopleural edge indistinct; ♂ ground color ochre, anterior $\frac{3}{5}$ brown, with

3 indistinct vittae extended slightly past ant. dorsocentrals. Pleura, postnotum, halteres light yellow. 6 even rows acrostichals present. Fuscous wing spots darker in ♀; apical, R_{2+3} , dm-cu, and r-m spots diffuse. Forefemur with 2 setae on ventral surface.

Tergal ground color entirely ochre in ♂, sometimes brown on t III and lightened posteriorly; t III with yellow inverted triangle. t VII ochre in ♀, anterior tergites black-brown, t VI with large ochre triangle. Oviscape elongate, lateral margins parallel, length ca. $3 \times$ width, with 7 large peg ovisensilla (5 apicals, 2 dorsals, each side) and 10 tiny ventral ovisensilla/side). Oviprovector scales large, triangular. Spermathecal capsule dome shaped; scaled, apical scales largest.

Hypoproctal plates narrow, extended almost to middle of surstyli. Surstylus with broad base; with 18–20 prensisetae: 8–9 elongate lateral pegs, decreased in size apicad. Aedeagal apodeme not extended to anterior margin of hypandrium. Gonopods lobate, sparsely spiculate. Basiphallus ca. $1\frac{1}{2} \times$ length of aedeagal apodeme, gradually widened into distiphallus. Distiphallus with deep apical notch; width ca. $2 \times$ width of basiphallus.

MEASUREMENTS: N = 4♂, 4♀. ThL = 1.21 ♂ (1.14–1.29); 1.52 ♀ (1.44–1.63); HW/ThL = 0.88 ♂ (0.87–0.89); 0.83 ♀ (0.82–0.87). WL/ThL = 0.55 (0.52–0.58); C.I. = 2.47 (2.13–2.93); 4-V = 1.21 (1.11–1.30).

HOLOTYPE: ♂, TRINIDAD: Charuma Forest, Tabaquite, 20/X/54, T. H. G. Aitken (NMNH) (genitalia not dissected). ThL = 1.16; HW/ThL = 0.88; ThL/WL = 0.53; C.I. = 2.53; 4-V = 1.25.

ETYMOLOGY: A feminine derivative of *zygos*, from *Zygothrica*.

DISTRIBUTION: South America, Trinidad to Peru (fig. 313).

MATERIAL: (specimens from Tabaquite, Trinidad are paratypes) BOLIVIA: S. Inicua Riv., Alto Beni, 15–18/I/76, 1100 m, 1♂*, 4♀*; Buenavista, 480 m, V/50, 6♂*, 10♀*. BRAZIL: Amazonas, Curcuça, Rio Madeira, 14–17/XI–3/XII/75, 9♂, 12♀; Puruzinho, Rio Madeira, 14–17/X–3/XII/75, 10♂*, 10♀*; Pará, Pedras, Mun. Obidos, Rio Cuminá-Miri, 20–24/I/68, 10♂*, 10♀*; Faz. Taperinha, nr. Santarém, 1–11/II/68, 10♂*, 10♀*; Rondonia, Calama, 19–21/XI/75, 25♂*, 25♀*; Marituba, 19/III/64, 32♂*, 14♀*. BRITISH

GUYANA: Mazaruni, High Forest, 20/VIII/37 (“on fungus”), 6♂*, 1♀*; Mazaruni-Potaro, Takutu Mtns., 6°15'N, 58°55'W, 10/XII/83, 7♂*. COLOMBIA: Leticia, 20/VI/64, 1♀ (“bred: *Heliconia* sp.”). PERU: Cuzco, Quince Mil, 15/XI/62, 700 m, 1♀*; Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, IX/19–X/10/84, 290 m, 8♂, 6♀ (“on *Auricularia*”). SURINAME: Raleigh, Val-len-Voltzberg Reserve, V/8/84, 2♂* (“on bracket fungus”); Marowijne, Langaman Kondre, VII/65, 5♂*, 3♀*. TRINIDAD: Emperor Valley, Port of Spain, II/15, 25♂*, 1♀*; Charuma For., Tabaquite, 20/X/54, 5♂, 5♀*; Naranja, Tucuche Trail, 30/IX/37, 2000 ft, 1♂* (“on fungus”); Sangre Grande, XII/55, 3♂*.

DISCUSSION: This widespread species is probably one of the most abundant members of the *aldrichii* species-subgroup. Apparently, although its distribution spans the Amazon Basin, it ranges from sea level to about 2000 ft in altitude.

Zygothrica neoaldrichi

Zygothrica neoaldrichi Burla, 1956: 222.

DIAGNOSIS: (♀; ♂ unknown) Wing with very light infuscation: R_{2+3} and apical spots separate, light proximal r-m band and dm-cu spot present; dorsum mostly ochre; oviscape apex flat, with terminal row 9–10 ovisensilla pegs per side and 3 dorsally; oviscape length ca. $1\frac{1}{2} \times$ width; spermatheca apically scaled.

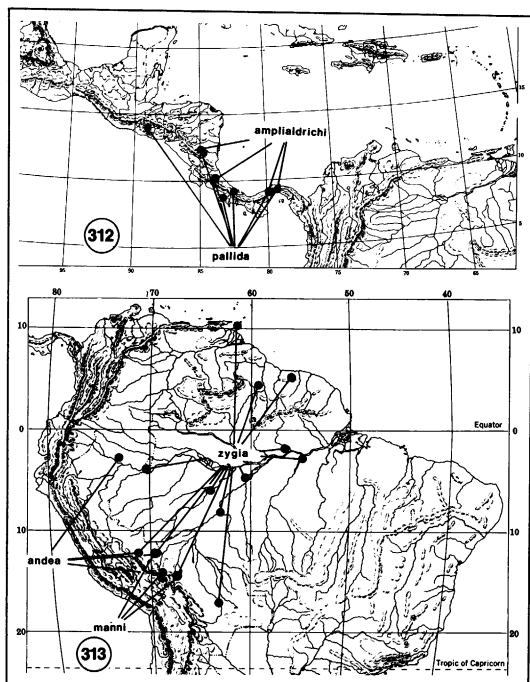
HOLOTYPE: ♀, BRAZIL: Rio de Janeiro, VI/53 (ZMUZ) (genitalia dissected, HB). Type not examined. C.I. = 2.0.

DISCUSSION: I have not seen specimens of this species; so, at present, it is assumed that this is a rare species in southeastern Brazil. The oviscape is distinctive; because of the light body color, but especially because of the large body size and the apically flat oviscape with its evenly spaced rows of terminal ovisensilla, it is likely that this species belongs to the *Z. manni* + *amplialdrichi* clade. The species is not shown on the cladogram in figure 163.

Zygothrica anota, new species

Figures 314–315, 325–329

DIAGNOSIS: Male and female with completely black-brown notum, scutellum, and



Figs. 312, 313. Distribution of some species in the *aldrichii* species-subgroup.

postnotum; ♀ pleura black-brown; dm-cu spot lost; most tergites dark, with diffuse orange, narrow, median stripe, t VI–VIII orange in ♀; oviscap tapered to point, with 9–10 ovisensilla per side. The distinction between this species and *Z. karenae* is given under the diagnosis of the latter.

DESCRIPTION: Post. reclinate midway between proclinate and inner vertical. Ocellar setae extended to proclinate. Outer vertical in line with orbitals (♂). Face light yellow in ♂, light brown in ♀. Carina yellow in ♂, ochre in ♀. Flagellomere I length $2.5 \times$ pedicel; arista with 4–5 dorsal and 1 ventral branch. Proboscis light yellow in ♂; completely black-brown in ♀. Palpi slender; palpi, clypeus light yellow in ♂; ochre to light brown in ♀.

Notum entirely black-brown, including scutellum and postnotum in ♂ and ♀. Noto-pleural edge distinct. Pleura light yellow in ♂; ♀ pleura black-brown, with white proepisternum. 6 even rows of acrostichals present. ♀ forecoxa off-white, other legs ochre; hind femur with light brown apical band. Wing with apical and R_{2+3} spots fused; dm-cu spot lost; distinct interruption between r-m infuscation and R_{2+3} spot.

Tergal ground color black-brown in ♂ and ♀; t III in ♂ and ♀ with large, yellow inverted triangle; t VI–VIII orange in ♀. Most of the dark tergites with diffuse, median, orange spots. Oviscap tapered apicad to a point; length slightly less than $2 \times$ width; with 6–7 peg ovisensilla in ventral row, 3 dorsally, and 15–17 ventral sensilla per side. Oviprovectator scales triangular; most broader than long. Spermathecal capsule narrow, dome shaped; surface with sparse scales on apical half. Hypoproct plates elongate, extended to middle of surstyli. Surstylus small, tapered apicad, with broad base; possesses 14–15 prensisetae: 7–8 pegs in lateral row, longest prensisetae are apical medials. Gonopods large, finely spiculate. Basiphallus ca. $2 \times$ length of aedeagal apodeme, $\frac{1}{2}$ width of distiphallus. Distiphallus gradually and slightly tapered apicad, with sparse (ca. 10–12) scales on dorsal surface.

MEASUREMENTS: $N = 4\delta, 3\eta$. ThL = 1.22 ♂ (1.17–1.30); 1.23 ♀ (1.07–1.32). HW/ThL = 0.88 ♂ (0.86–0.92); 0.81 ♀ (0.80–0.820). ThL/WL = 0.55 (0.53–0.56); C.I. = 2.79 (2.43–2.89); 4-V = 1.34 (1.26–1.41).

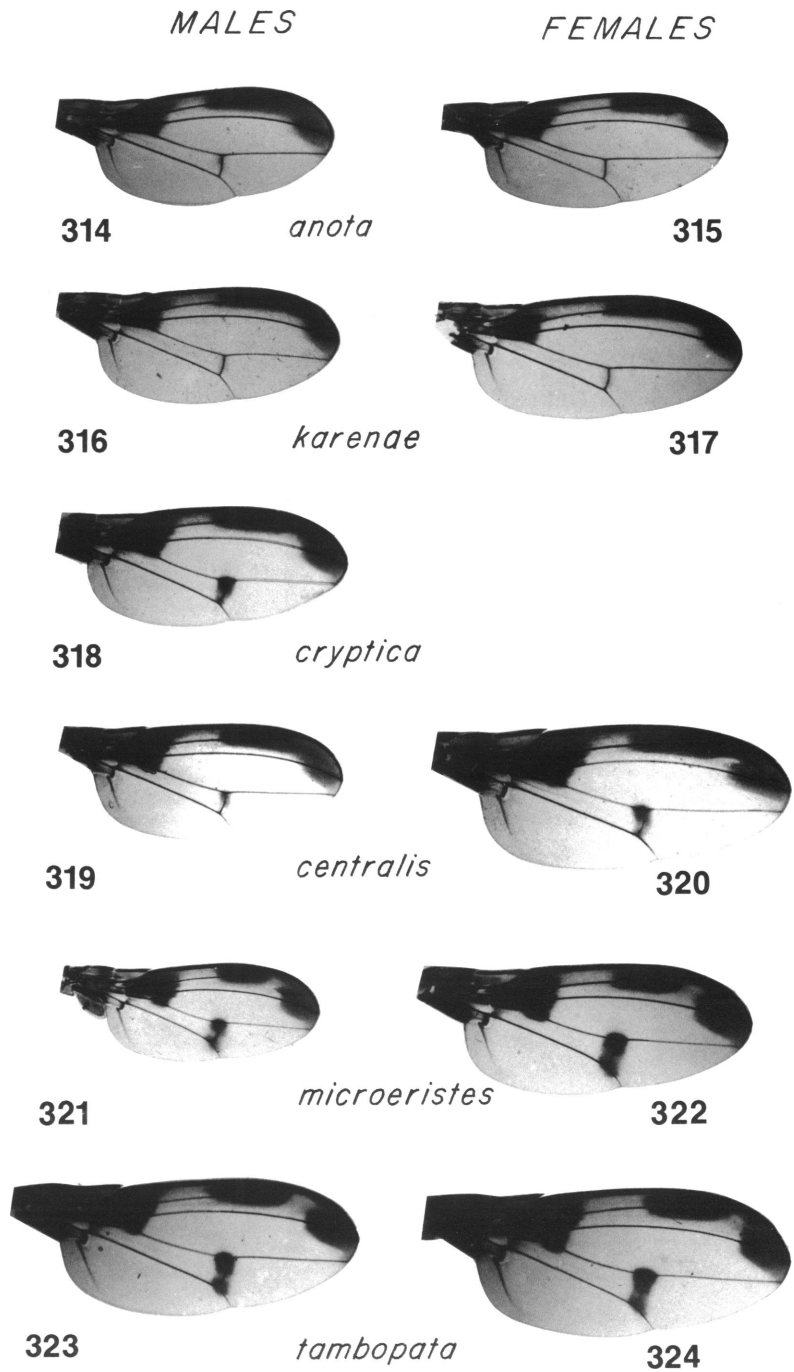
HOLOTYPE: ♂, PANAMA: “Canal Zone,” Las Cruces Trail, 21/VII/67, W. W. Wirth (“on bracket fungi”) (NMNH) (genitalia not dissected). ThL = 1.21; HW/ThL = 0.88; ThL/WL = 0.56; C.I. = 2.89; 4-V = 1.26.

ETYMOLOGY: Latin, “spotless,” for the loss of the wing spot over crossvein dm-cu. This trait occurs as well in *Z. karenae*.

DISTRIBUTION: Southern Mexico to Panama (fig. 355).

MATERIAL: (specimens from Las Cruces Trail, Panama are paratypes) COSTA RICA: Guapiles (Los Diamantes), 31/I/53, 22♂*, 12♀*; Heredia, Sarapiquí, 4/IV/70, 3♂*, 4♀*; Turrialba, X/55 (13♂*, 7♀*), I/24 (1♀), 15–19/VII/53 (1♀); Cairo, La Francia, 5/II/53, 1♂, 1♀; San Mateo, Higuito, 1♀; San Isidro del General, Finca Los Cusingsos, 25/XII/48, 1♂*. MEXICO: Chiapas, 32 km N Ocozacoautla, 762 m, 6/X/74, 1♂*, 1♀*. NICARAGUA: El Recreo, VI/54, 8♂*, 4♀*; Santa Maria de Ostuma, 11 km N Matagalpa, VII/54, 1♀*. PANAMA: Barro Colorado Island, VII–X, several years, 17♂*, 7♀*; Cerro Campana, 20/IV/60 (1♂*), VI/67 (1♂*); El Valle, XI/48, 1♀; Erwin Island, “Canal Zone,” 2♂; Las Cruces Trail, 21/VII/67, 7♂, 9♀*.

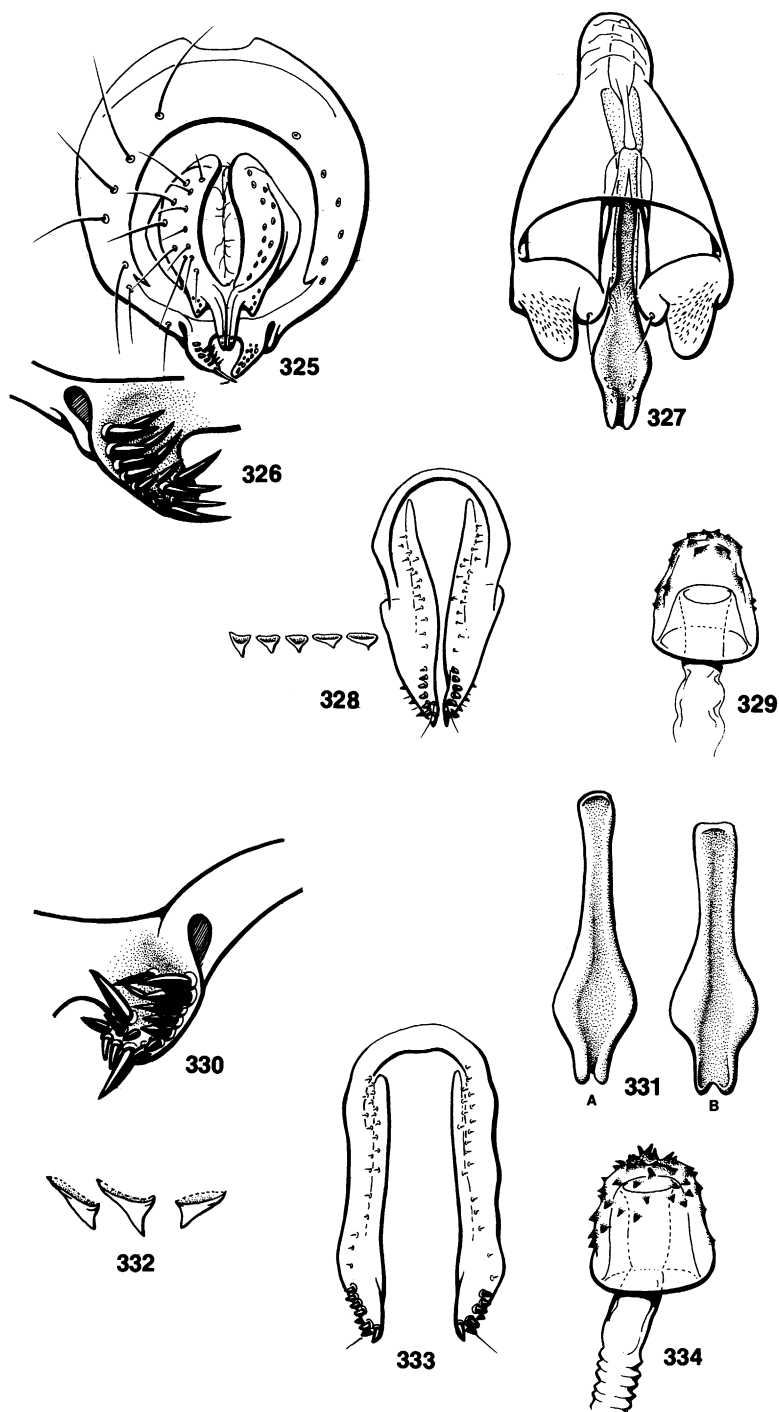
DISCUSSION: An abundant species among



Figs. 314–324. Wings of some *Zygothrica* in the *aldrichii* species-subgroup.

Central American members of the *aldrichii* subgroup. An alternative cladistic hypothesis concerning the relationships of this species and its sister, *Z. karenæ*, is given in figure 164. The alternative hypothesis is more par-

simonious than the one proposed in figure 163 since it is presumed that synapomorphy 121 evolved three instead of four times, and no. 123 evolved once instead of twice; this, however, suggests yet another arisal (instead



Figs. 325–329. *Zygothrica anota*. 325. Epandrium. 326. Surstylus. 327. Aedeagus + hypandrium (ventral). 328. Oviscape (ventral) + oviprovector scales. 329. Spermatheca (400×).

Figs. 330–334. *Zygothrica karenae*. 330. Surstylus. 331. A, B, aedeagus (ventral). 332. Oviprovector scales. 333. Oviscape (ventral). 334. Spermatheca (400×).

of just twice) of synapomorphy 119. The close relationship between *Z. anota* and *Z. karenae* is based on the loss of the spot on crossvein dm-cu. Although a hyaline dm-cu vein is primitive at the level of the *aldrichii* subgroup, it is apparent that for these two species it is a recent derivation because they possess several inclusive synapomorphies for the subgroup.

***Zygothrica karenae*, new species**

Figures 316–317, 330–334

DIAGNOSIS: Crossvein dm-cu hyaline. Distinguished from *Z. anota* by a completely dark abdomen in both sexes; in ♀, by the completely dark mid and hind femora. In addition, the ov scape apex is flattened, slightly expanded laterally, and has flat, oblique, terminal margins. The distiphallus of this species is more bulbous than the one in *Z. anota*.

DESCRIPTION: Ocellar setae not quite extended to proclinate. Outer vertical slightly lateral to line connecting orbitals. Face ochre in ♂, light brown in ♀ but ochre on facial margin. Carina yellow, sides brown. Flagellomere I length 3 × pedicel. Arista with 4–5 dorsal and 0–1 ventral branches. Proboscis yellow in ♂, mentum completely dark brown in ♀. Palpi yellow in ♂, light brown in ♀.

Notum, scutellum, and postnotum evenly dark brown. Pleura light yellow in ♂; dark brown in ♀, with proepisternum light. 4–6 even rows of acrostichals present. Legs entirely light yellow in ♂; ♀ with black-brown hind tibia and proximal ⅓ of hind and mid femora black-brown. Wing lacks dm-cu spot; apical and R_{2+3} spots coalesced, extended half way into 1st radial cell.

Tergites dark brown. Oviscape with lateral margins parallel and apex flattened; length slightly more than 2 × width; with 5–6 peg ovisensilla in terminal row and 3 dorsally, and 17–20 ventral sensilla per side. Ovipositor scales large, dentate, width greater than length. Spermathecal capsule dome shaped, with large apical scales; introvert lightly sclerotized.

Epandrium dark brown. Hypoproct plates elongate, extend past middle of surstyli. Surstylus small, apex tapered, base broad; possesses 13–16 prensisetae: 1 large apical, 6–7

in lateral row. Gonopods spiculed. Basiphallus ca. 1.5 × length of aedeagal apodeme. Distiphallus 2.5–3 × width of basiphallus, with distinct lateral expansion before apical taper. Distiphallus glabrous.

MEASUREMENTS: N = 3♂, 2♀. ThL = 1.14 ♂ (1.09–1.18); 1.25 ♀ (1.09, 1.42). HW/ThL = 0.87 ♂ (0.81–0.92); 0.84 ♀ (0.83, 0.85). ThL/WL = 0.53 (0.47–0.54); C.I. = 2.39 (2.26–2.57); 4-V = 1.28 (1.24–1.38).

HOLOTYPE: ♂, COSTA RICA: Turrialba, X/55, W. B. Heed (AMNH) (genitalia dissected, DAG). ThL = 1.09; HW/ThL = 0.88; ThL/WL = 0.52; C.I. = 2.35; 4-V = 1.24.

ETYMOLOGY: Patronym, in honor of Karen, my wife.

DISTRIBUTION: Costa Rica, Panama (fig. 355).

MATERIAL: (all are paratypes) COSTA RICA: Guapiles Los Diamantes, 31/I/53, 2♂*, 1♀*; Turrialba, X/55, 3♂*, 4♀*. PANAMA: Barro Colorado Island, 24/VII/63, 1♂*; Trinidad River, 5/V/11, 1♂*.

***Zygothrica centralis*, new species**

Figures 319–320, 342–345; table 1

DIAGNOSIS: Notopleural edge distinct; ♀ with dark pleura; distiphallus bare; surstyli short, with large apical prensiseta; ov scape gradually tapered apicad, with 6 large peg ovisensilla in ventroapical row; spermatheca shorter than width, with sparse tiny papillae over most of surface.

DESCRIPTION: Ocellar setae finer than orbitals, extended to proclinate. Outer vertical in line with orbitals (♂). Face light yellow in ♂, light brown in ♀; carina light yellow in ♂, light brown in ♀. Flagellomere I length 3 × pedicel. Arista with 5–6 dorsal and 2 ventral branches. Palpi light yellow in ♂, dark brown in ♀.

Notum, scutellum, and postnotum dark brown in ♂ and ♀, notopleural edge distinct. Pleura light yellow to off-white in ♂; dark brown in ♀ and contrasting with off-white procoxa, proepisternum, and subalar sclerite. 6 even rows acrostichal setulae present. Wing infuscations distinct: apical and R_{2+3} spots coalesced, extended into 1st radial cell ca. to level of dm-cu.

Tergal ground color dark brown in ♂ and ♀, t VII with diffuse, light area medially. Ovi-

scape gradually tapered, length ca. $2 \times$ width, with 11 peg ovisensilla (6 terminal, 4 dorsal) and 10–13 ventral sensilla per side. Oviprovector scales triangular, about as long as wide. Spermathecal capsule length shorter than width; sparse, tiny papillae over most of surface. Epandrium shiny, dark brown with long dorsal surface. Hypoproctral plates elongate, extended to ca. middle of surstyli; narrow in lateral view. Surstyli small, very close, with broad bases; possess 15 prensisetæ: 6 lateral pegs, 1 large setiform apical, the rest are setiform medials. Basiphallus ca. $2 \times$ length of distiphallus. Distiphallus without scales, dorsally or ventrally.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.33 ♂ (1.29–1.36); 1.46 ♀ (1.43, 1.50). HW/ThL = 0.90 ♂ (0.89–0.91); 0.79 ♀. ThL/WL = 0.54 (0.51–0.56); C.I. = 2.80 (2.48–3.17); 4-V = 1.32 (1.16–1.41).

HOLOTYPE: ♂, PANAMA: "Canal Zone," Barro Colorado Island, 21/X/60, S. B. Pipkin (NMNH) (genitalia dissected, DAG). ThL = 1.35; HW/ThL = 0.90; ThL/WL = 0.55; C.I. = 2.54; 4-V = 1.40.

ETYMOLOGY: Latin, "central," for the widespread Central American distribution.

DISTRIBUTION: Costa Rica to northern Colombia.

MATERIAL: (specimens from B.C.I. are paratypes) COLOMBIA: Rio Raposo, V/64, 1♂* ("light trap"). COSTA RICA: Guapiles (Los Diamantes), 31/I/53, 5♂* ("on *Auricularia*"); Sarapiquí, Heredia, 4/IV/70, 2♂*; Turrialba, IX-X/55, 2♂*. PANAMA: Barro Colorado Island, 19/VIII/60 (3♂*), 21/X/60 (7♂*), X-XI/55 (2♂*), XI/41 (4♂*, 6♀*: "ex: *Calathea violacea*").

DISCUSSION: A multivariate discriminant analysis would be a very useful study for being able to easily separate this species (particularly females) from *Z. cryptica* and *Z. aldrichii*.

Zygothrica cryptica, new species

Figures 318, 335–341

DIAGNOSIS: Very similar to *Z. centralis*, distinguished by the following: basiphallus $3 \times$ length of distiphallus (not $2 \times$), with scales; surstylus with apical scaliform prensisetæ; oviscapae with 9 ventroapical and 3 dorsal ovisensilla pegs; oviscapae with oblique apical margins and parallel lateral margins; ♂ wings

with small hyaline constriction just before apical spot on wing.

DESCRIPTION: Ocellar setae not quite extended to proclinate. Inner vertical setae strongly convergent; ends almost touch. Outer vertical lateral to line connecting orbitals (♂). Flagellomere I length $3 \times$ pedicel. Arista with 5 dorsal and 1–2 ventral branches. Proboscis, palpi, light yellow in ♂; palpi ochre, mentum black-brown in ♀. Clypeus light brown in ♂, darker brown in ♀.

Notum and scutellum completely black-brown, postnotum lighter. Pleura light yellow in ♂; mostly dark brown in ♀ (forecoxa, propisternum, subalar sclerite are light yellow). Wings with apical and R_{2+3} spots coalesced, extended into R_{1+2} cell to ca. level of dm-cu. ♂ with small hyaline constriction just before apical spot.

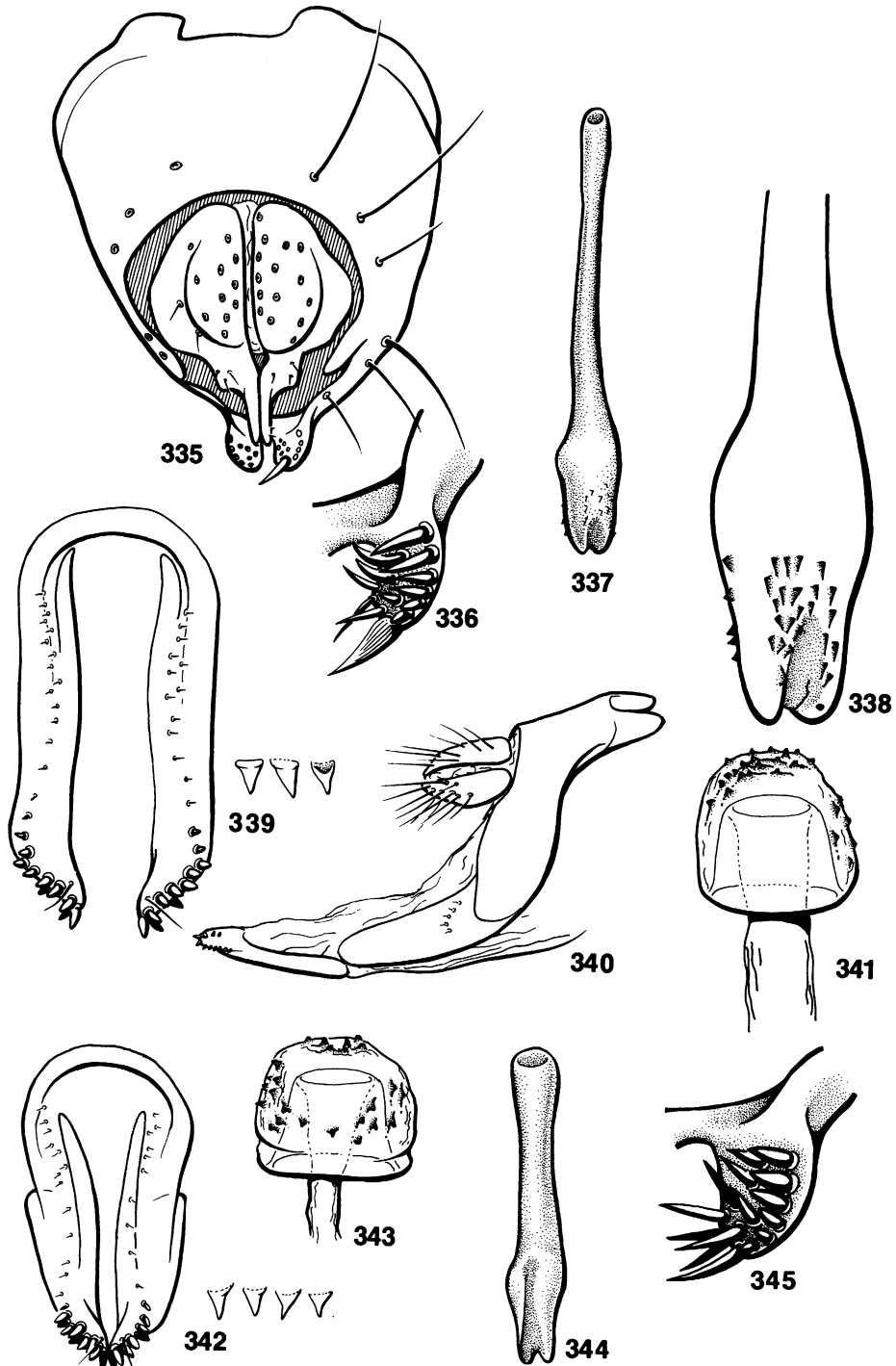
Tergal ground color black-brown; t VI, VII lighter in ♂. Oviscape dorsoventrally flat, lateral margins parallel, apical margins oblique; length ca. $2 \times$ width, with 9 ventroapical ovisensilla pegs and 3 dorsal ones per side (13–15 ventral sensilla). Oviprovector scales triangular, slightly longer than wide. Spermathecal capsule dome shaped, surface with small scales mostly on apex. Laterotergite VIII ramus sclerotized, slightly longer than oviscapae. Epandrium black-brown, with elongate dorsal margin; tapered ventrad. Hypoproctral plates elongate, extended to middle of surstyli, narrow in lateral view. Surstyli small, close together, with broad bases; possess 12 prensisetæ: 6 pegs in lateral row, 1 large and scaliform apical, the rest are setiform medials. Basiphallus ca. $3 \times$ length of distiphallus. Distiphallus with dorsal and ventral scales.

MEASUREMENTS: N = 3♂, 3♀. ThL = 1.33 ♂ (1.28–1.38); 1.55 ♀ (1.49–1.61). HW/ThL = 0.89 ♂ (0.86–0.92); 0.85 ♀ (0.84, 0.85). ThL/WL = 0.56 (0.53–0.58). C.I. = 2.46 ♂ (2.29–2.78); 3.09 ♀ (2.97–3.30). 4-V = 1.24 ♂ (1.19–1.26); 1.42 ♀ (1.36–1.48).

HOLOTYPE: ♂, PANAMA: "Canal Zone," Barro Colorado Island, 19/VIII/60, S. B. Pipkin (NMNH) (genitalia dissected, DAG). ThL = 1.33; HW/ThL = 0.92; ThL/WL = 0.57; C.I. = 2.78; 4-V = 1.27.

ETYMOLOGY: Latin, "cryptic," for the close morphological resemblance between this species and *Z. centralis*.

DISTRIBUTION: Costa Rica, Panama.



Figs. 335–341. *Zygothrica cryptica*. 335. Epandrium. 336. Surstylus. 337. Aedeagus (ventrolateral). 338. Distiphallus (ventrolateral). 339. Oviscape (ventral) + oviprovector scales. 340. ♀ terminalia (lateral). 341. Spermatheca (400×).

Figs. 342–345. *Zygothrica centralis*. 342. Oviscape (ventral) + oviprovector scales. 343. Spermatheca (400×). 344. Aedeagus (ventral). 345. Surstylus.

MATERIAL: (specimens from B.C.I. are paratypes) COSTA RICA: Guapiles (Los Diamantes), 31/I/53, 1♀* ("on *Auricularia*"); La Suiza [de Turrialba], 1♀*. PANAMA: Barro Colorado Island, 24/VII/63 (4♂), 19/VII/78 (4♂*), 21/X/66 (3♂, 1♀, X–XI/55 92♀*).

Zygothrica microeristes, new species

Figures 321–322, 346–350, 425, 457i–j

DIAGNOSIS: ♂ body color mostly ochre, contrasting with dark, distinct wing maculations; ♂ moderately hypercephalic in largest individuals; ♀ separable from *Z. tambopata* by distinct, yellow, incomplete, paramedian notal vittae.

DESCRIPTION: Frontal head ground color entirely ochre in ♂, including frontal vittae. Head width $1.1\text{--}1.6\times$ thorax width. Frontal-orbital plates broad in ♂: anteriorly $2\times$ frontal vitta width, dorsally broader than ocellar triangle. Ocellar triangle shiny, yellow in ♂ (interocellar area dark brown). Proclinate orbital seta on frontal-vitta margin. Ant. reclinate very fine in ♂, at least 0.5 length of other orbitals, lateral to other orbitals by at least length of seta. Post. reclinate far anteriad, closest to proclinate in hypercephalic ♂. Ocellar setae fine, extended to proclimates. Outer vertical in line with proclinate–post. reclinate. Postoculars just lateral to outer vertical are hypermorphic: lengths 0.6–0.7 that of outer vertical. Face very light yellow in ♂, brown in ♀ (dark brown on oral margin); carina broad. Flagellomere I length $2\frac{1}{2}\times$ pedicel. Arista with 6–7 dorsal and 2 ventral branches.

Notal, scutellar, postnotal ground color ochre in ♂; black-brown in ♀. ♂ notum with light yellow, diffuse vitta pr.2 extended to transverse suture, bordered by very light brown; ♀ with distinct yellow vittae of same size. Pleura light yellow. 4 even rows of acrostichals present. Legs light yellow; hind tibia with brown apical band (darkest in ♀). Ventral surface of profemur with 3–4 short setae. Wing maculation distinct, little or no apparent sexual dimorphism, apical spot almost entirely constricted from R_{2+3} spot; dm-cu spot large, dark.

Tergal ground color ochre in ♂, black-brown in ♀. Tergite II, III in ♂ light brown on lateral surface, t VI–VIII yellow in ♀. Oviscape with narrow valves, tapered; length ca. $2\times$ width,

with ventroapical row of 6 and 3 dorsal peg ovisensilla, plus ca. 15 ventral sensilla per side. Scales on oviprovector wider than long, apex abruptly narrowed. Spermathecal capsule dome shaped; surface finely, sparsely papillate; introvert lightly sclerotized.

Epandrium dorsoventrally elongate and tapered, yellow. Hypoproctal plates elongate, narrow in lateral view. Surstyli small, close together, with broad bases; possess 14–15 prensisetæ: 1 large, scaliform apical; others elongate pegs or setiform. Hypandrium short, abruptly tapered. Gonopods broad, extensively spiculed. Paraphysial seta stout. Basiphallus ca. $1.5\times$ length of aedeagal apodeme, ca. $0.6\times$ width of distiphallus. Distiphallus gradually tapered into basiphallus, gonopore large, troughlike, ventral aspect of distiphallus scooplike. Distiphallus devoid of scales.

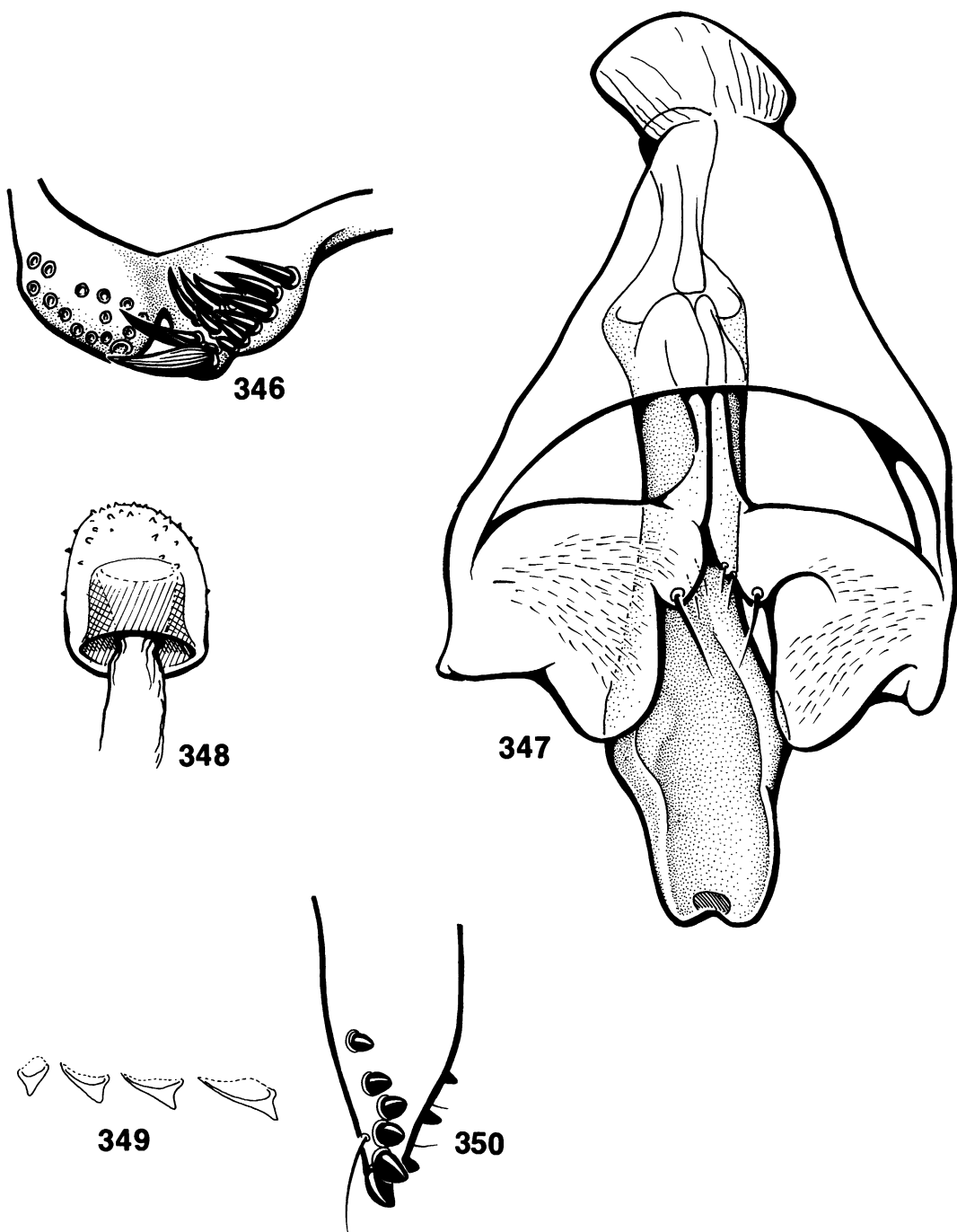
MEASUREMENTS: N = 4♂, 3♀. ThL = 1.25 ♂ (1.12–1.42); 1.40 ♀ (1.33–1.46). HW/Th L = 1.01 ♂ (0.89–1.11); 0.82 ♀ (0.79–0.87). ThL/WL = 0.56 (0.55–0.60); C.I. = 2.40 (2.07–2.90); 4-V = 1.32 (1.17–1.40).

HOLOTYPE: ♂, BRAZIL: Pará, Belem, V/58, M. Wasserman (AMNH) (genitalia not dissected). ThL = 1.28; HW/ThL = 1.11; ThL/WL = 0.60; C.I. = 2.70; 4-V = 1.40.

ETYMOLOGY: Greek, "minute wrangler/fighter," for the broad-headed (and, thus, probably combative) males, and for the small size of the species.

DISTRIBUTION: Amazonian, from Suriname to Peru (fig. 356).

MATERIAL: (specimens from Belém, Brazil are paratypes) BOLIVIA: Alto Beni, S. Inicua Riv., 15–18/I/76, 1100 m, 2♂*; Buenavista, Ichilo, 480 m, V/50, 2♂, 6♀; Tumupasa, VII/21, 1♂*. BRAZIL: Amazonas: Cachoeirinha, Rio Madeira, 13–14/XII/75, 1♂, 2♀; Puruzinho, Rio Madeira, 14–17/XI–3/XII/75, 21♂*, 8♀. Espirito Santo: Linhares, II/70, 5♂, 5♀. Mato Grosso: 12°50'S, 51°47'W, 15/II/68, 2♂, 1♀ ("gallery forest, on white toad stool"). Marituba: 19/III/64, 1♂*, 1♀. Pará: Barreirinhas, Rio Tapajos, X–XI/70, 1♂*, 1♀; Belém, IV/58, 4♂*; Monte Dourado, 20/III/80, 6♂*, 1♀; Pedras, Mun. Obidos, Rio Cuminá–Miri, 20–24/I/68, 3♂*, 6♀*; Rio Trombetas, Lago Jacaré, X/69, 1♂*. Rondonia: Calama, 19–21/XI/75, 12♂*, 3♀. BRITISH GUYANA: Mazaruni, High Forest, 26/VIII/37, 10♂*, 11♀* ("on fungus"); Takutu Mtns., 6°15'N, 58°55'W, 10/XII/83, 2♂*. ECUADOR: Napo, Coca, Rio

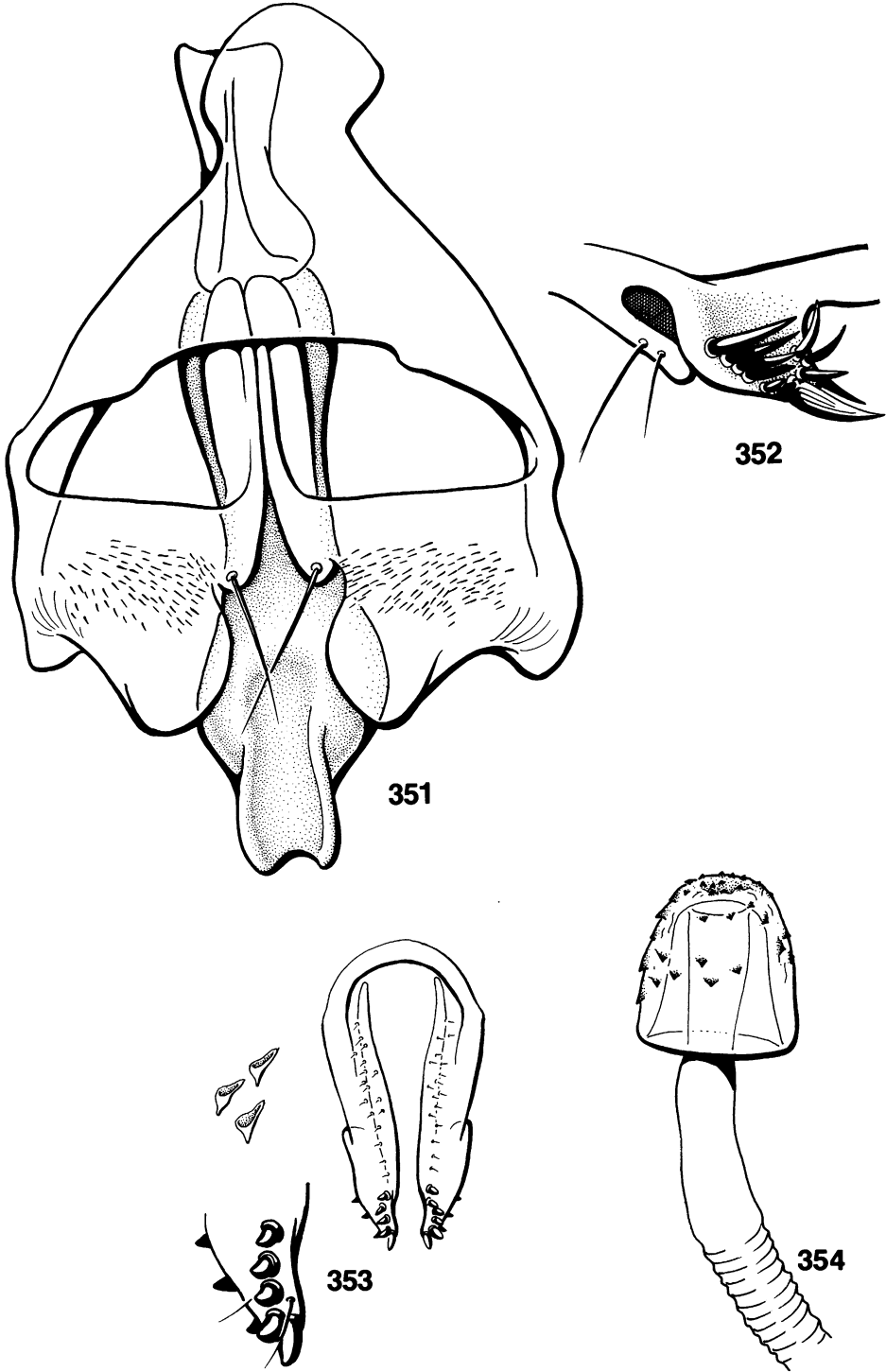


Figs. 346–350. *Zygotherica microeristes*. 346. Surstylus. 347. Aedeagus + hypandrium (ventral). 348. Spermatheca (400 $\times$). 349. Oviprovectator scales. 350. Oviscape (ventral), detail of left apex.

Napo, V/65, 250 m, 1 δ^* . PERU: Loreto, Rio Momon (ca. 25 km NW Iquitos), 17/II/84, 2 δ^* ; Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 290 m,

19/IX–10/X/84, 2 δ^* . SURINAME: Raleigh, Vallen-Voltzberg Reserve, 8/V/84 (“swept over fungus”), 2 f^* .

DISCUSSION: As indicated on the cladogram



Figs. 351–354. *Zygothrica tambopata*. 351. Aedeagus + hypandrium (ventral). 352. Surstylus. 353. Oviscape (ventral), detail of apex, ovipositor scales. 354. Spermatheca (400×).

in figure 163, the closest relative of this species seems to be *Z. tambopata*, due to the male hypercephaly and broad gonopore which gives the distiphallus a scooplike shape. The hypercephaly of these two species does appear distinct from that in the *pilipes-radialis* clade of the *aldrichii* subgroup since the latter two do not possess hypermorphic postoculars. *Zygothrica microeristes* is widespread in the Amazon Basin.

***Zygothrica tambopata*, new species**

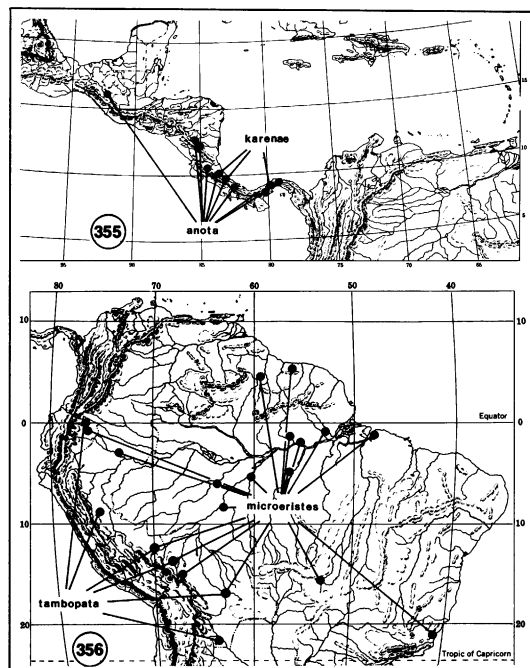
Figures 10, 115, 116, 323–324,
351–354, 424, 431

DIAGNOSIS: Frontal-orbital plates ochre, rest of front of head brown; thorax completely black-brown; tergites II–V completely black-brown in ♂ and ♀, t VI–IX yellow; ♂ head moderately broadened; oviscape tapered, with row of 6 ventroapical ovisensilla; hypandrium with constricted anterior lobe; distiphallus short, scooplike, devoid of scales.

DESCRIPTION: ♂ head width $1.3 \times$ thorax width. Frontal-orbital plates ochre, dorsally brown and $2 \times$ wider than anterior portion. Ocellar triangle brown in ♂ and ♀, shiny. Procline on lateral edge of frontal vitta. Ant. reclinate fine, minute, lateral to other orbitals. Outer vertical medial to line extended from procline to post. reclinate. Postoculars just lateral to outer vertical hypermorphic; lengths ca. $0.5 \times$ outer vertical. Flagellomere I length $3.5 \times$ pedicel. Arista with 5–7 dorsal and 2–3 ventral branches.

Notum, scutellum, and postnotum black-brown. ♂ and ♀ pleura entirely light yellow. 4 even rows acrostichals present. Ventral surface profemur with row 3 setae, lengths less than femur width. Wing with distinct maculation, no sexual dimorphism: apical spot nearly separate from R_{2+3} spot; dm-cu spot large, heavy.

Tergal ground color black-brown in ♂ and ♀; t VI–VIII yellow in ♂; t VII, VIII completely yellow in ♀. Oviscape gradually tapered, length $2 \times$ width, with ventral row of 5–6 peg ovisensilla and 3 dorsal pegs, with 16–17 ventral sensilla. Oviprovector scales ca. $2 \times$ wider than long. Spermathecal capsule dome shaped, small; surface with fine scales, mostly on apical $\frac{2}{3}$. Epandrium yellow with elongate dorsal margin. Hypoproct plates elongate,



Figs. 355, 356. Distribution of some species in the *aldrichii* species-subgroup.

extended to at least middle of surstyli, narrow in lateral view. Surstyli small, very close together, with broad bases; possess 11–12 prenisetae: 1 large, scaliform apical, 6 laterals, 4 setiform medials. Hypandrium short, anterior margin with constricted lobe. Gonopods broad, spiculate. Basiphallus ca. equal to length of aedeagal apodeme, $\frac{1}{2}$ width of distiphallus. Distiphallus without scales; lateral expansion abrupt; gonopore broad, ventral surface scooplike.

MEASUREMENTS: $N = 3\delta, 2\phi$. ThL = 1.36 ♂ (1.22–1.43); 1.54 ♀ HW/ThL = 0.91 ♂ (0.84–0.97); 0.83 ♀ (0.81, 0.84). ThL/WL = 0.54 (0.53–0.56); C.I. = 2.55 (2.24–2.84); 4-V = 1.27 (1.21–1.34).

HOLOTYPE: ♂, PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, 19/IX–10/X/84, $12^{\circ}12'S$, $69^{\circ}16'W$, 290 m (AMNH) (genitalia not dissected). ThL = 1.43; HW/ThL = 0.92; ThL/WL = 0.56; C.I. = 2.57; 4-V = 1.26.

ETYMOLOGY: Derived directly from the type locality, which is the Rio Tambopata Nature Reserve, a small park of tropical inundation forest in southeastern Peru.

DISTRIBUTION: Ecuador to northern Bolivia (fig. 356).

MATERIAL: (Tambopata specimens are paratypes) BOLIVIA: Buenavista [Rio] Ichilo, 480 m, V/50, 8♂, 1♀; Palos Blancos, Alto Beni, 11–15/I/76, 600 m, 1♂; Tumupasa, XII/21, 1♂*. ECUADOR: Limoncocha, 0°24'S, 76°40'W, 9–16/III/76, 250 m, 1♂*. PERU: Huanuco, Tingo Maria, Tingo Maria Natl. Park, 9/II/84, 1♂*; 43 mi E Tingo Maria, 1200 m, 1♀*; Monson Valley, 2/VII/54, 1♀. Madre de Dios, Avispas, 20–30/IX/62, 400 m, 2♀; Rio Tambopata Reserve, 290 m, 37♂*, 18♀*.

DISCUSSION: The Tambopata specimens were captured over a bloom of *Auricularia delicata* (figs. 102–104). Here, 14 other *Zygothrica* and 6 other drosophilids were found to aggregate. Behavioral observations on this species are reported in the section on Behavioral Phylogenetics.

Zygothrica paraldrichi

Figures 29, 39, 357–358, 374–378

Zygothrica paraldrichi Burla, 1956: 223.

DIAGNOSIS: Notum, scutellum, postnotum, terga, black-brown in ♂ and ♀. ♀ pleura black-brown, ♂ pleura entirely light yellow. Legs (♂ and ♀) light yellow. Palpi, proboscis dark brown in ♀; yellow to ochre in ♂. Notopleural edge distinct. Oviscape gradually tapered apicad; with ventroapical row of 6 ovisensilla pegs, 3 dorsals; spermatheca sparsely, finely papillate. Gonopods (♂) narrow, spiculed; aedeagus ca. $2.5 \times$ length of aedeagal apodeme, clavate; distiphallus with ca. 30–40 ventral and 20–30 dorsal scales. Surstyli small, close together, with 13–15 setiform prensisetae.

MEASUREMENTS: N = 4♂, 3♀. ThL = 1.17 ♂ (1.09–1.23); 1.33 ♀ (1.37, 1.29). HW/ThL = 0.88 ♂ (0.88, 0.89); 0.83 ♀ (0.82, 0.84). ThL/WL = 0.56 (0.54–0.59); C.I. = 1.92 (1.43–2.22); 4-V = 1.36 (1.24–1.49).

HOLOTYPE: ♀, BRAZIL: Rio de Janeiro, III/53, H. Burla (ZMUZ) (genitalia dissected, HB). Type not examined.

DISTRIBUTION: South America (Amazon Basin) (fig. 415).

MATERIAL: BOLIVIA: Buenavista, 480 m [nr. Rio] Ichilo, V/50, 1♂*; Palos Blancos, Alto Beni, 11–15/I/76, 600 m, 1♂*; S. Inicua Riv., Alto Beni, 15–18/I/76, 1100 m, 1♂, 4♀*; Tumupasa, XII/21, 1♀*. BRAZIL: Amazonas: Pu-

ruzinho, Rio Madeira, 17/XI–6/XII/75, 1♂. Pará: Belem, IV/58, 2♂*, 1♀*; Rio Jari, Monte Dourado, 20/III/80, 1♂*; Pedras, Mun. Obidos, Rio Cuminá-Miri, 24/I/68, 6♂*; Barreirinhas, Rio Tapajos, X–XI/70, 8♂*; Faz. Tapereinha, nr. Santarém, 11/II/68, 2♂*, 2♀*. Marituba, 19/III/64, 3♂*, 4♀*. Rondonia: Calama, 21/XI/75, 10♂*, 10♀*; São Carlos, Rio Madeira, 29/XI/75, 1♂*. BRITISH GUYANA: Mazaruni, High Forest, 20/VIII/37, 4♂*, 3♀* ("on fungus"). PERU: Loreto, San Antonio, 21/VIII/65, 6♂*, 2♀*; Huanuco, Tingo Maria, 43 mi E, 1200 m, XI/18/54, 1♀*; [Rio] Pichis, Pto. Bermudéz, VII/03, 1♂*; Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado, IX/19–X/10/84, 12♂*, 6♀*. SURINAME: Marowijne, Langaman Kondré, VIII/65, 5♂*; Raleigh, Vallen-Voltzberg Res. 5/8/84, 3♀* ("swept over fungus").

DISCUSSION: Both sexes can be easily mistaken for other species based just on the external features; genitalic dissections must be done. Burla figured the female genitalia.

Zygothrica aldrichii

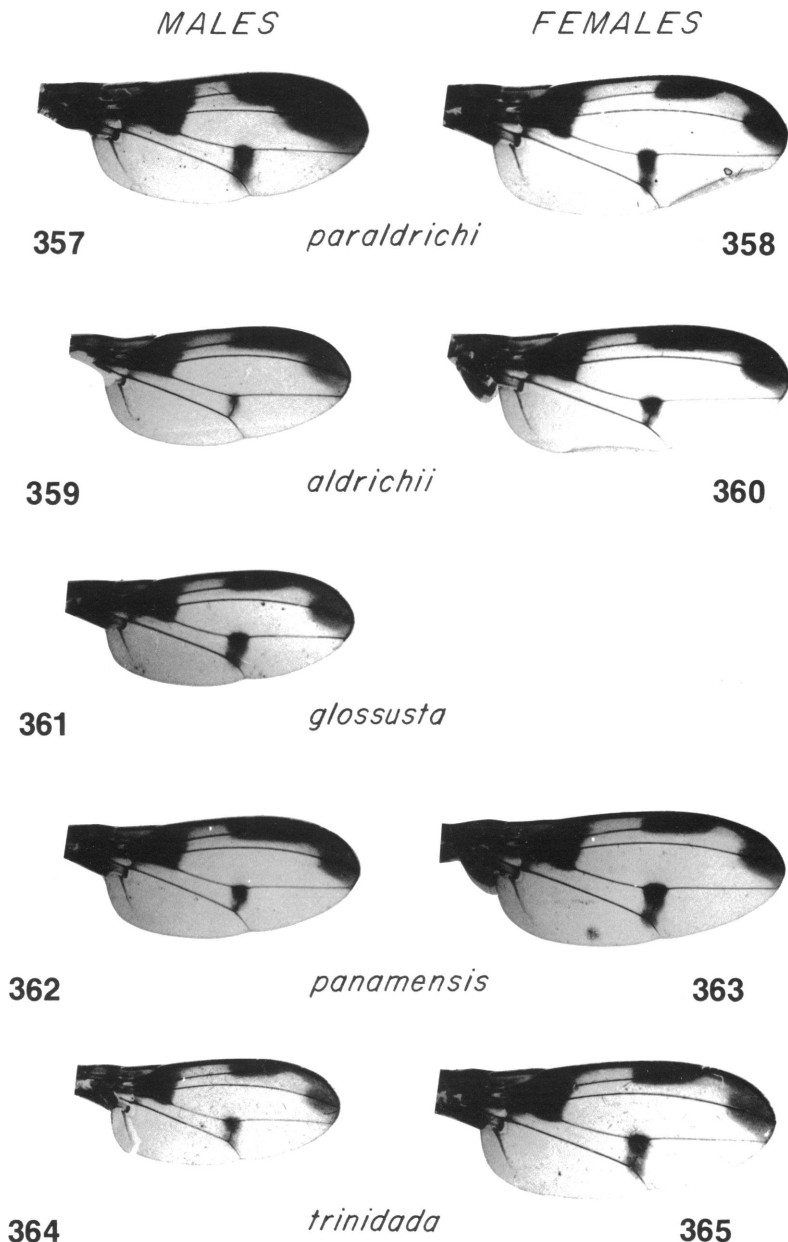
Figures 51, 114, 356–360, 379–384, 457e, f; table 1

Zygothrica aldrichii Sturtevant, 1920: 157.

DIAGNOSIS: ♂ pleura and proboscis light yellow, ♀ pleura and proboscis black-brown; notum of both sexes black-brown, with distinct notopleural edge; tergites II–IV black-brown in ♂, t V–VIII ochre with brown infuscation; t II–V mostly black-brown in ♀, t VI–VIII ochre; legs of both sexes light yellow; ♀ mid- and hind coxae black-brown, hind tibia with apical band. Oviscape tapered apicad to a point, length ca. $2 \times$ width; with 6–7 ovisensilla in ventral row, 3 dorsally; row of 14 ventral sensilla/side; oviprovectors scales dentate; laterotergite VIII ramus ca. $\frac{1}{2}$ length of oviscape; spermatheca dome shaped, slightly tapered, with minute scales. Aedeagus ca. $2 \times$ length of aedeagal apodeme; distiphallus truncate, gradually tapered into basiphallus, with sparse scales dorsally.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.25 ♂ (1.15–1.34); 1.47 ♀ HW/ThL = 0.87 ♂ (0.85–0.90); 0.80 ♀ (0.79, 0.82). ThL/WL = 0.55 (0.54–0.57); C.I. = 2.82 (2.51–3.10); 4-V = 1.32 (1.25–1.34).

HOLOTYPE: ♂, PANAMA: Trinidad River,



Figs. 357–365. Wings of some *Zygothrica* in the *aldrichii* species-subgroup.

5/V/11, A. Busck (NMNH) (type examined; genitalia not dissected). Not measured.

DISTRIBUTION: Nicaragua to Panama (fig. 414).

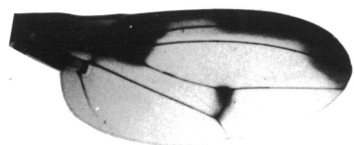
MATERIAL: COSTA RICA: Sarapiquí, Heredia, 4/IV/70, 3♂*, 8♀*; Golfito, VI–VII/59, 1♀*. NICARAGUA: El Recreo, VI/54, 2♂*. PANAMA: Barro Colorado Island, 19/VII–21/X,

various years, 5♂*, 14♀*; “Canal Zone,” Las Cruces Trail, VII/21/67, 13♀* (“bracket fungi”); Trinidad Riv., 5/V/11, 16♀*.

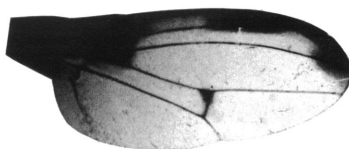
DISCUSSION: It is perplexing that so few males have been taken (10♂, 50♀ examined). This species most closely resembles the allopatric *Z. paraldrichi*, which can be distinguished on the basis of tergal coloration (see

MALES

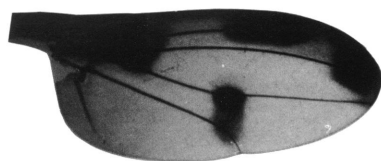
FEMALES



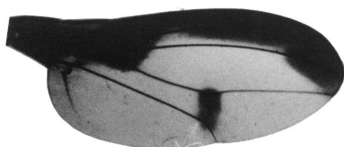
366

simulans

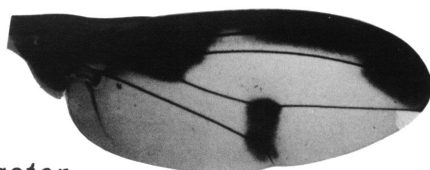
367



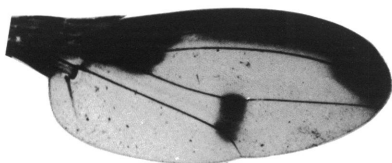
368

joeyesco

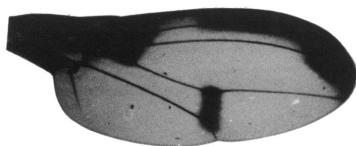
369

mediogaster

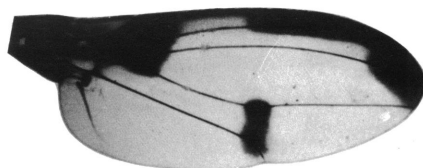
370



371

prensiseta

372

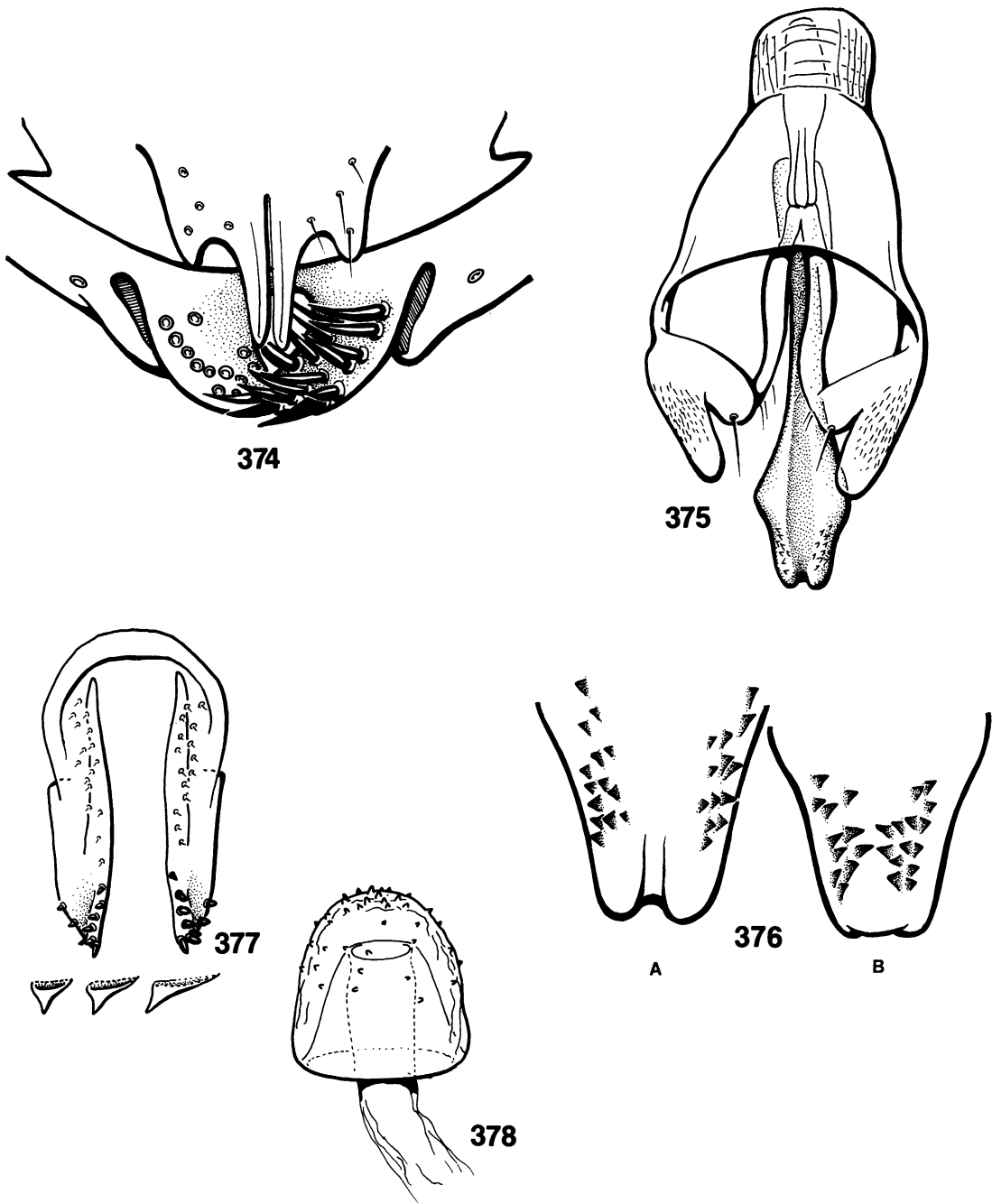
nigropleura

373

Figs. 366–373. Wings of some *Zygothrica* in the *aldrichii* species-subgroup. Figures 368 and 371 are of the holotypes.

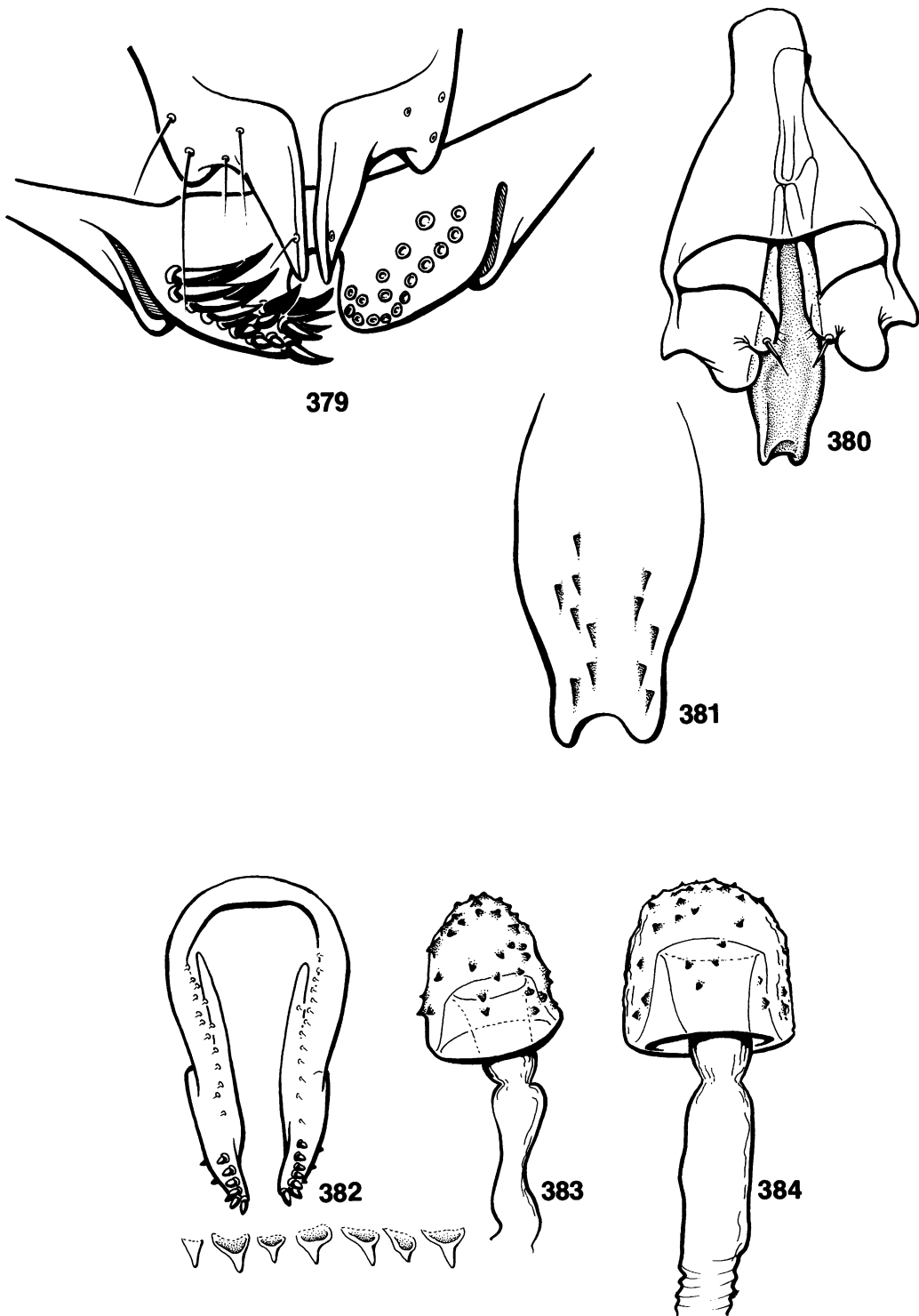
diagnoses). Among specimens in the NMNH, 27 from the type series were found with Stur-

tevant's paratype labels, and these represent six species (16♀ *Z. aldrichii*; 4♂ *Z. panamen-*



Figs. 374–378. *Zygotherica paraldrichi*. 374. Surstyli. 375. Aedeagus + hypandrium (ventral). 376. A, B, distiphallus, apex, ventral (A) and dorsal (B). 377. Oviscape (ventral) + ovipector scales. 378. Spermatheca (400×).

sis; 2♂, 1♀ *Z. pallida*, 2♂ *Z. anota*; 1♂ *Z. kar- enae*; 1♀ *Z. amplaldrichi*). It is quite obvious that study of the genitalia has contributed immensely to our understanding of these flies.



Figs. 379–384. *Zygothrica aldrichii*. 379. Surstlyi. 380. Aedeagus + hypandrium (ventral). 381. Distiphallus (dorsal). 382. Oviscape (ventral) + oviprovector scales. 383, 384. Spermathecae.

Zygothrica glossusta, new species

Figures 361, 385–391

DIAGNOSIS: ♂ most easily identified by the brown proboscis. Notum, scutellum, tergites completely black-brown in ♂ and ♀, notopleural edge distinct; ♂ pleura light yellow, ♀ pleura dark brown; surstyli flat, broad; hypoproctal plates very broad in lateral view; aedeagus short, with expanded, nearly bare distiphallus; ovisensilla small, close to oviscapex apex. This species would rarely be confused with other Central American relatives, particularly if genitalia are examined.

DESCRIPTION: Outer vertical in line with orbitals (♂). Face yellow in ♂, with lateral margins light brown. Cheek with brown spot on anterior half in ♂ and ♀. Flagellomere I length $2\frac{1}{2} \times$ pedicel. Arista with 5–6 dorsal and 2 ventral branches. Distal half of proboscis brown in ♂, completely brown in ♀. Palpi ochre in ♂ and ♀, clypeus light brown.

Notum, scutellum, postnotum completely black-brown. Notopleural edge distinct. Pleura light yellow in ♂; dark brown in ♀, except for light yellow forecoxa, proepisternum, and subalar sclerite (mid + hind coxae dark). 4 even rows of acrostichals present. Wing maculations distinct, with little or no apparent sexual dimorphism. Apical wing spot joined to R_{2+3} spot by narrow bridge; dm-cu spot heavy. Tergites shiny, black-brown in ♂ and ♀.

Oviscape with narrow valves, apex pointed, length $1\frac{1}{2} \times$ width, with ventroapical row of 5 small peg ovisensilla and 1 dorsal ovisensilla, ca. 10 ventral sensilla per side. Oviprovector scales heavily sclerotized; sparse, relatively small, blunt. Spermathecal capsule short, dome shaped; surface scalate, densest at apex. Laterotergite VIII ramus short, lightly sclerotized. Hypoproctal plates very broad in lateral view; width greater than height. Surstyli flat, adpressed, with broad bases, and directed mediad; possess 13–15 setiform prenisetae. Hypandrium short, anterior margin with constricted lobe. Gonopods large, sparsely spiculed. Paraphysal seta short. Basiphallus ca. equal to length of aedeagal apodeme, $\frac{1}{3}$ width of distiphallus. Distiphallus expanded, with large gonopore; possesses 5–6 very small spicules on ventral surface near anterior end of gonopore.

MEASUREMENTS: N = 3♂, 2♀. ThL = 1.28 ♂ (1.23–1.32); 1.46 ♀ (1.44, 1.48). HW/ThL = 0.89 ♂ (0.88, 0.90); 0.82 ♀ (0.79, 0.84). ThL/WL = 0.55 (0.53–0.57); C.I. = 2.47 (2.06–3.48); 4-V = 1.25 (1.22–1.27).

HOLOTYPE: ♂, NICARAGUA: El Recreo, VI/54, W. B. Heed (AMNH) (genitalia not dissected). ThL = 1.29; HW/ThL = 0.90; ThL/WL = 0.56; C.I. = 2.31; 4-V = 1.25.

ETYMOLOGY: Latin, “burnt tongue,” for the brown proboscis present in ♂ as well as ♀.

DISTRIBUTION: Nicaragua to Panama (fig. 414).

MATERIAL: (specimens from El Recreo, Nicaragua are paratypes) COSTA RICA: Guapi-les Los Diamantes, 31/I/53, 5♂* (“on *Auricularia*”); Turrialba, X/55, 4♀*. EL SALVADOR: La Palma, 3200 ft, VIII/54, 1♀*. NICARAGUA: El Recreo, VI/54, 26♂*, 20♀*. PANAMA: “Canal Zone,” Las Cruces Trail, 21/VII/67, 3♂*, 2♀* (“bracket fungi”); Cerro Campana, 2/III/60, 2♀*; Mojinga Swamp, 1♂.

Zygothrica trinidad, new species

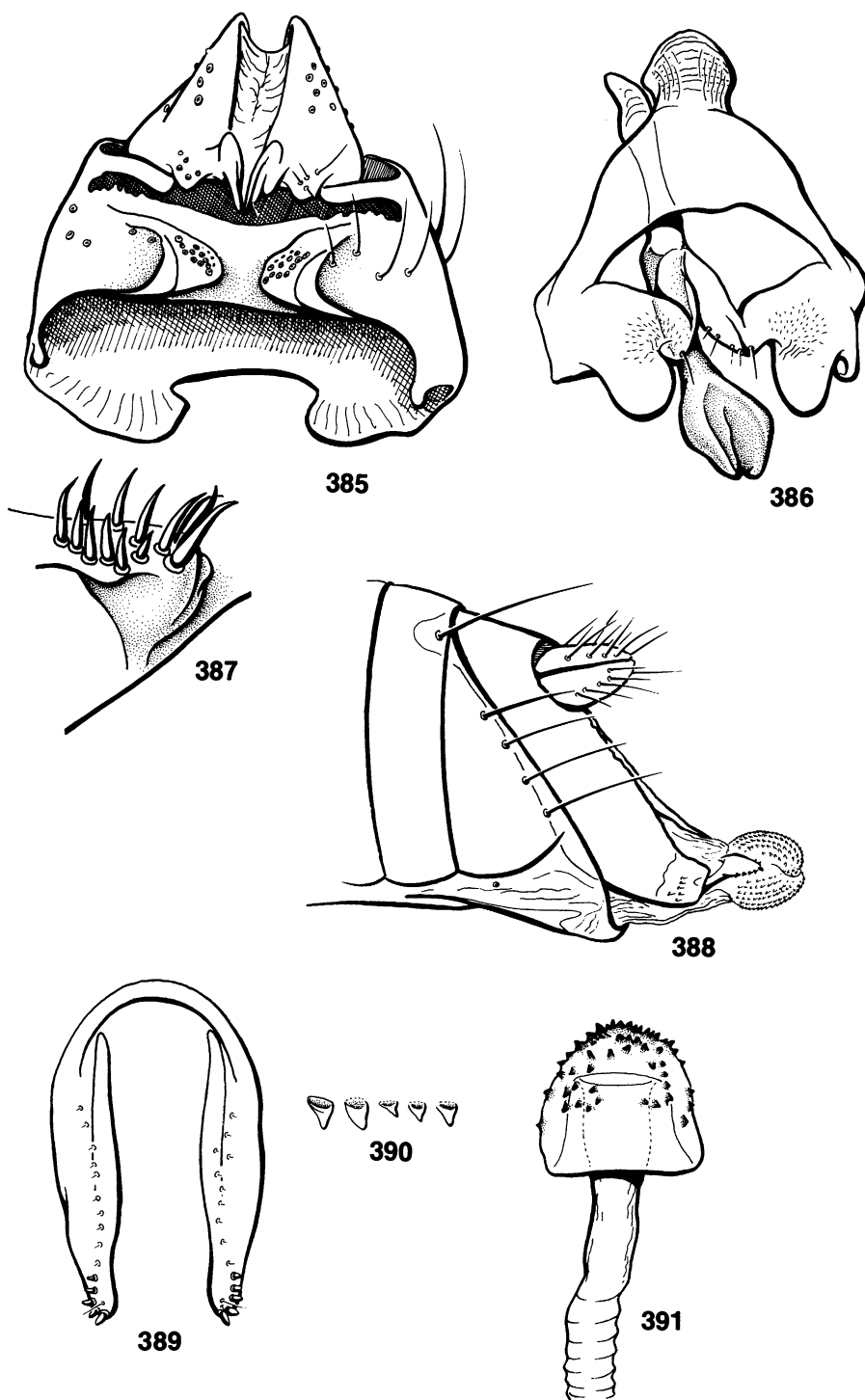
Figures 364–365, 392–395

DIAGNOSIS: ♂ pleura entirely yellow; ♀ pleura, mid + hind coxae and femora mostly black-brown; notum and terga of ♂ and ♀ entirely black-brown; 5 ovisensilla in ventroapical row. Both sexes, especially the ♀, should be available to accurately distinguish *Z. trinidad* from *Z. paraldrichi* (♀ of the latter does not have black-brown femora).

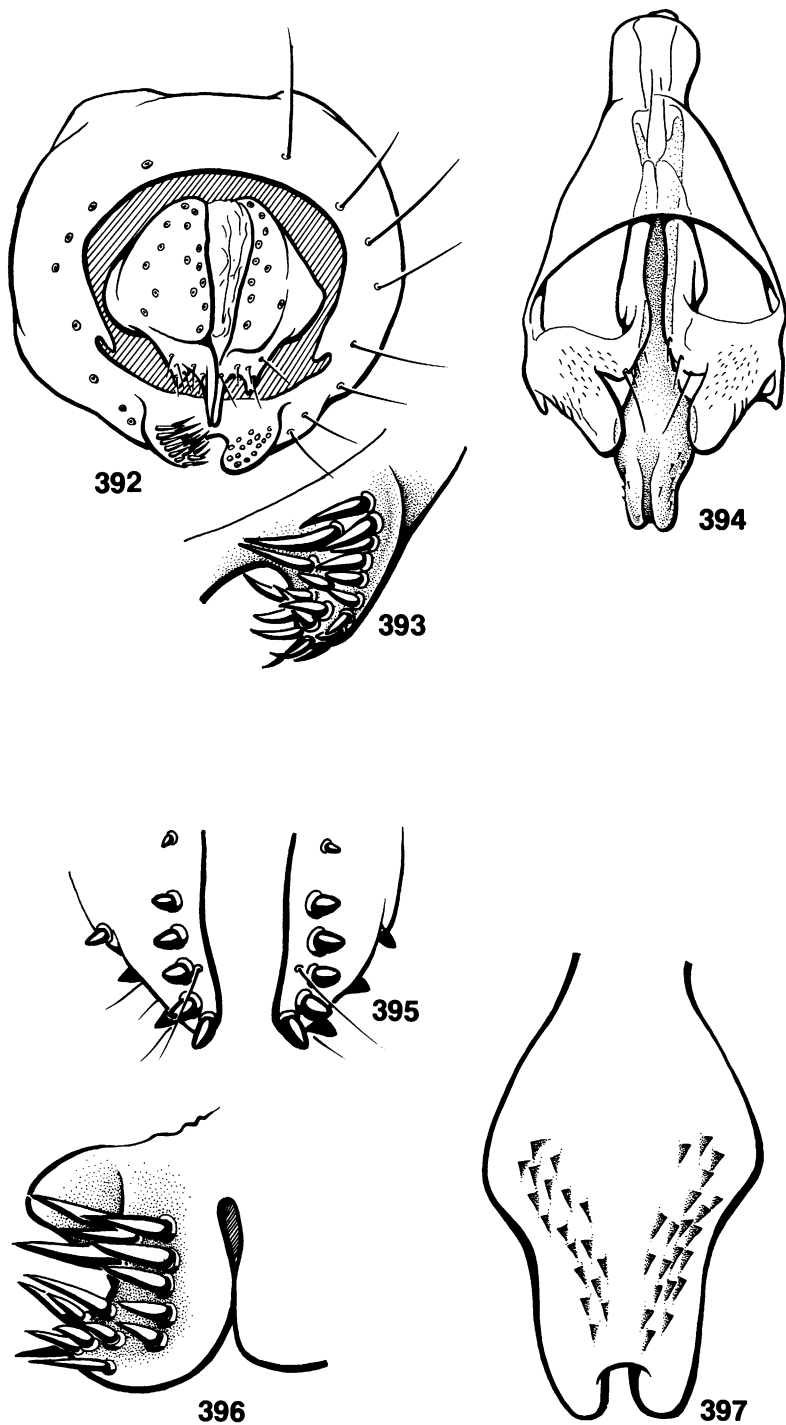
DESCRIPTION: Inner vertical setae strongly convergent, ends almost touch. Outer verticals slightly lateral to line through orbitals (♂). Face ochre to light brown in ♂, darker brown in ♀. Flagellomere I length $2.5 \times$ pedicel. Arista with 5–6 dorsal and 2 ventral branches. Proboscis light yellow in ♂, entirely black-brown in ♀. Palpi ochre in ♂, light brown in ♀.

Notum, scutellum, postnotum, tergites entirely black-brown in ♂ and ♀; notopleural edge distinct. Pleura light in ♂; black-brown in ♀, with proepisternum off-white. Acrostichals in 4 even rows. Mid + hind coxae and most of mid and hind femora black-brown in ♀. Wing maculations distinct; hyaline constriction between apical and R_{2+3} spots.

Oviscape tapered, length $2 \times$ width, with ventroapical row of 5 and dorsal row of 3 peg



Figs. 385–391. *Zygothrica glossusta*. 385. Epandrium (posteroventral). 386. Aedeagus + hypandrium (ventral). 387. Surstylus. 388. ♀ terminalia. 389. Oviscape (ventral). 390. Oviprovectator scales. 391. Spermatheca (400×).



Figs. 392–395. *Zygothrica trinidadensis*. 392. Epandrium. 393. Surstylus. 394. Aedeagus + hypandrium (ventral). 395. Oviscape apex (ventral).

Figs. 396, 397. *Zygothrica panamensis*. 396. Surstylus. 397. Distiphallus (dorsal) (El Recreo, NICARAGUA).

ovisensilla per side, and 13–15 ventral sensilla. Spermathecal capsule dome shaped, surface scaled, denser at apex. Hypoproctal plates extended to dorsomedial margin of surstyli. Surstyli tapered, with bases broad, directed ventromedially; possess 19–20 prenisetae, most are setiform. Hypandrium extended to apex of aedeagal apodeme; anterior margin with distinct lobe. Gonopods narrower than long, spiculate. Paraphysal seta elongate. Basiphallus ca. $2\times$ length of aedeagal apodeme, $\frac{1}{2}$ width of distiphallus. Aedeagus clavate, lightly scaled dorsally and ventrally.

MEASUREMENTS: N = 2♂, 2♀. ThL = 1.28 ♂; 1.40 ♀. HW/ThL = 0.91 ♂; 0.86 ♀. ThL/WL = 0.55; C.I. = 2.29; 4-V = 1.31.

HOLOTYPE: ♂, TRINIDAD: Tabaquite, Charuma Forest, 20/X/54, T. H. G. Aitken (NMNH) (genitalia not dissected). ThL = 1.28; HW/ThL = 0.91; ThL/WL = 0.58; C.I. = 2.28; 4-V = 1.22.

ETYMOLOGY: Latin, "from Trinidad," for the type locality.

MATERIAL: (specimens from Tabaquite are paratypes) TRINIDAD: Port of Spain, II/15, 3♂*, 2♀; Tabaquite, Charuma For., 5♂*, 5♀*.

***Zygothrica panamensis*, new species**

Figures 362–363, 396–397

DIAGNOSIS: Notum, scutellum, tergites entirely black-brown in ♂ and ♀; proboscis light yellow in ♂, dark brown in ♀; ♀ pleura, mid + hind femora dark brown; aedeagus clavate, elongate; surstylus apically truncate. Externally ♂ is confused most with *Z. cryptica*, *Z. centralis*, and *Z. aldrichii*, so examination of the genitalia should confirm identifications.

DESCRIPTION: Ocellar setae extended to proclinate. Outer verticals slightly lateral to line through orbitals. ♂ cheek with anterior portion brown; cheek mostly black-brown in ♀. Flagellomere I length $2\frac{1}{2}\times$ pedicel. Arista with 5–6 and 2 ventral branches. Palpi ochre in ♂, light brown in ♀; clypeus light brown.

Notum, scutellum, postnotum, and tergites completely black-brown in ♂ and ♀. Notopleural edge distinct. Pleura light yellow in ♂; ♀ with mid + hind coxae, pleura (except for off-white proepisternum) black-brown. Acrostichals in 4 even rows. ♀ with dark brown mid and hind femora. Wing patterns distinct. Oviscape tapered. Hypoproctal plates ex-

tended to ca. dorsomedial margin of surstyli. Surstyli with broad bases; apically truncate; possess 16–19 prenisetae: 5 pegs in lateral row; fine setiform apicomedia. Hypandrium elongate. Basiphallus ca. $2\times$ length of aedeagal apodeme, $\frac{1}{2}$ width of distiphallus. Distiphallus with slight preapical expansion (very distinct in some specimens), scaled.

MEASUREMENTS: N = 4♂, 3♀. ThL = 1.27 ♂ (1.19–1.44); 1.51 ♀ (1.41–1.64). HW/ThL = 0.88 ♂ (0.83–0.91); 0.82 ♀ (0.81–0.83). ThL/WL = 0.58 (0.55–0.61); C.I. = 2.30 (2.60–2.69); 4-V = 1.31 (1.23–1.42).

HOLOTYPE: ♂, PANAMA: "Canal Zone," Las Cruces Trail, 21/VII/67, W. W. Wirth ("bracket fungi") (NMNH) (genitalia not dissected). ThL = 1.44; HW/ThL = 0.90; ThL/WL = 0.61; C.I. = 2.44; 4-V = 1.23.

ETYMOLOGY: Latin, "from Panama," for the type locality.

DISTRIBUTION: Nicaragua to Panama.

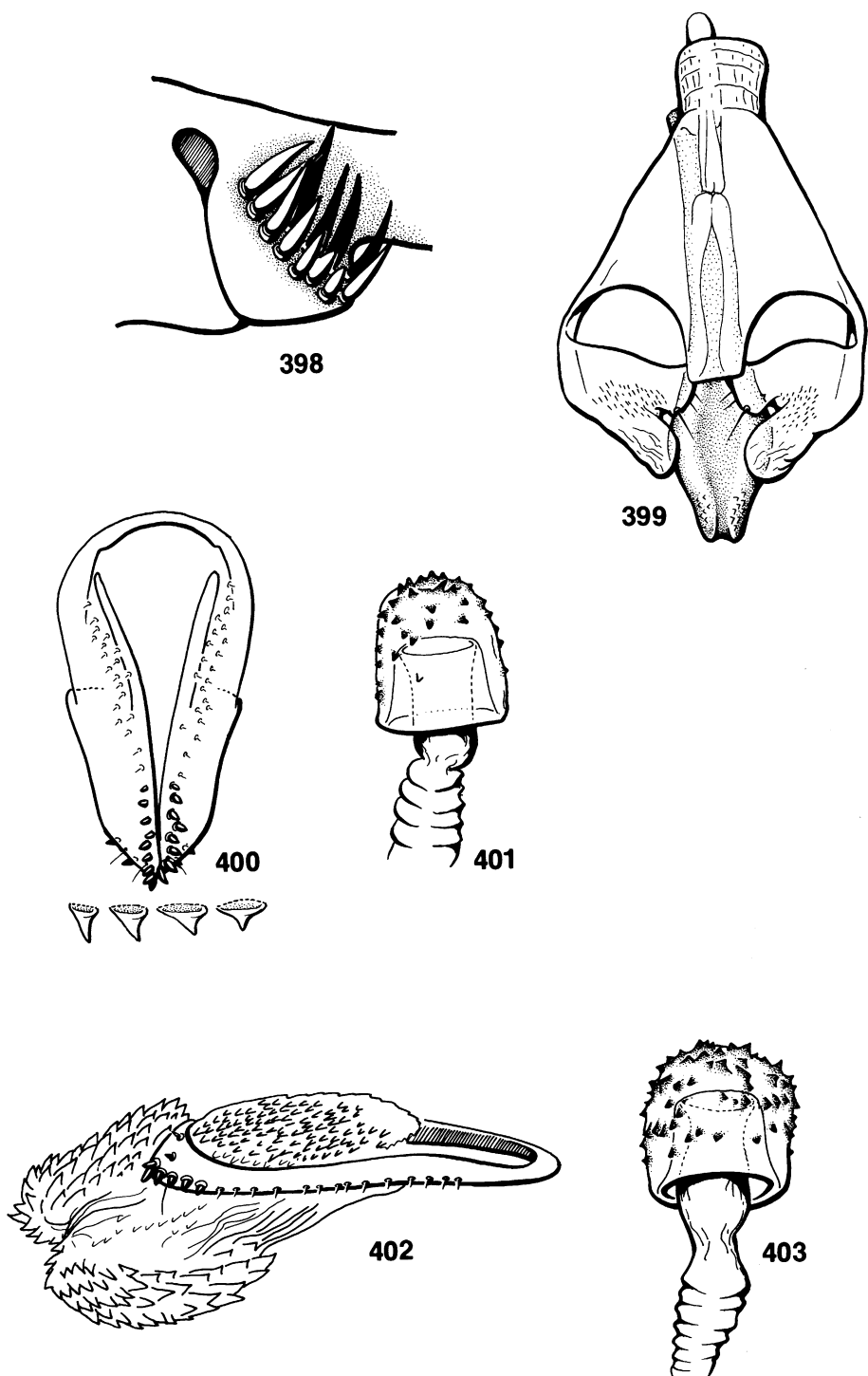
MATERIAL: (specimens from Las Cruces Trail are paratypes) NICARAGUA: El Recreo, VI/54, 1♂*. PANAMA: Barro Colorado Island, 19/VII–XI, various years, 4♂*, 9♀*; Las Cruces Trail, 21/VII/67, 25♂*, 5♀*; Madden Forest, 24/V/61, 1♀*; Trinidad River, V/5/11, 4♂*.

DISCUSSION: The aedeagal length, shape, and vestiture of *Z. panamensis* bears a striking resemblance (although not perfect) to *Z. cryptica*, *Z. mediogaster*, *Z. nigropleura*, *Z. pallida*, *Z. paraldrichi*, and *Z. trinidadensis*. Some of these species overlap in their distributions, but consistent differences in some genitalic and external features (especially body color patterns) leave little doubt about species status of the various forms. *Zygothrica panamensis*, *Z. trinidadensis*, and *Z. nigropleura* are the earliest branching clades of a group of species defined by the possession of dark mid and/or hind femora in the females (apomorphy 123). A further modification upon this state is seen in three species where all of the femora in females are black-brown.

***Zygothrica nigropleura*, new species**

Figures 372–373, 398–401

DIAGNOSIS: This distinctive species should not be confused with any other. Males have dark hind femora; females and males have black-brown pleura, dark brown pretarsi which contrast with other light yellow pre-



Figs. 398–401. *Zygothrica nigropleura*. 398. Surstylus. 399. Aedeagus + hypandrium (ventral). 400. Oviscape (ventral) and ovipositor scales. 401. Spermatheca (400×).

Figs. 402, 403. *Zygothrica joeyesco*. 402. Oviscape + everted ovipositor (lateral). 403. Spermatheca (400×).

tarsi; the notum, scutellum, and tergites of both sexes are entirely black-brown. The hypandrium is lightly melanized and bears a truncate posterior process.

DESCRIPTION: Outer vertical in line with orbitals (δ). Face dark brown in δ and φ ; carina white/light yellow on edge. Cheek dark brown in δ and φ , gena white. Flagellomere I length $2 \times$ pedicel. Arista with 5–6 dorsal and 2 ventral branches. Proboscis completely black-brown in δ and φ . Palpi and clypeus light to dark brown.

Notum, scutellum, postnotum, and tergites are completely black. Notopleural edge distinct. Pleura black-brown in δ and φ , except for proepisternum and dorsal quarter of anepisternum (which are off-white). Acrostichals in 4 even rows. Legs yellow in δ , except for all pretarsi which are dark brown. φ with mid + hind coxae, hind femora, apex of hind tibia, and pretarsi dark brown, remaining leg portions yellow. Ventral surface of forefemur with row of 3–4 setae, lengths ca. $0.8 \times$ femur width. Wing maculations distinct; apical spot not constricted from R_{2+3} spot; no sexual dimorphism apparent. Halteres white.

Oviscape tapered to a point, length $2 \times$ width, with ventroapical row of 8 and dorsal row of 3 ovisensilla pegs, ca. 20 ventral sensilla per side. Oviprovector scales with narrow apex, usually wider than long and abruptly narrowed. Spermatheca dome shaped, scaled mostly at apex; introvert lightly sclerotized. Hypoproctal plates extended to mediadorsal margin of surstyli. Surstylus with broad base, apically truncate; possesses 13–14 prensisetae: 7–8 in lateral row, longer ones medially. Hypandrium melanized; anterior margin with distinct, truncate lobe; posterior margin with lightly melanized process extended to anterior edges of paraphyses. Gonopods large, fleshy, spiculed. Paraphysal seta stout. Basiphallus ca. equal to length of aedeagal apodeme, $\frac{1}{2}$ width of distiphallus. Distiphallus with sparse scales on ventral and dorsal apical surfaces.

MEASUREMENTS: 2 δ , 2 φ . ThL = 1.30 δ ; 1.59 φ . HW/ThL = 0.88 δ ; 0.85 φ . ThL/WL = 0.52; C.I. = 2.81; 4-V = 1.25.

HOLOTYPE: δ , BRAZIL: São Paulo, Salesópolis, Estacion Biologia Boracéia, 30/IV/73, K. Kaneshiro and F. C. Val (MZSP) (genitalia not dissected). ThL = 1.32; HW/ThL = 0.87; ThL/WL = 0.53; C.I. = 2.80; 4-V = 1.27.

ETYMOLOGY: Latin, “black pleura,” for the black-brown pleura found in the δ as well as the φ .

DISTRIBUTION: Southeastern Brazil.

MATERIAL: 7 δ^* , 3 φ^* , all paratypes, from same collection locality as holotype.

Zygothrica mediogaster, new species

Figures 369–370, 404–408, 457g, h

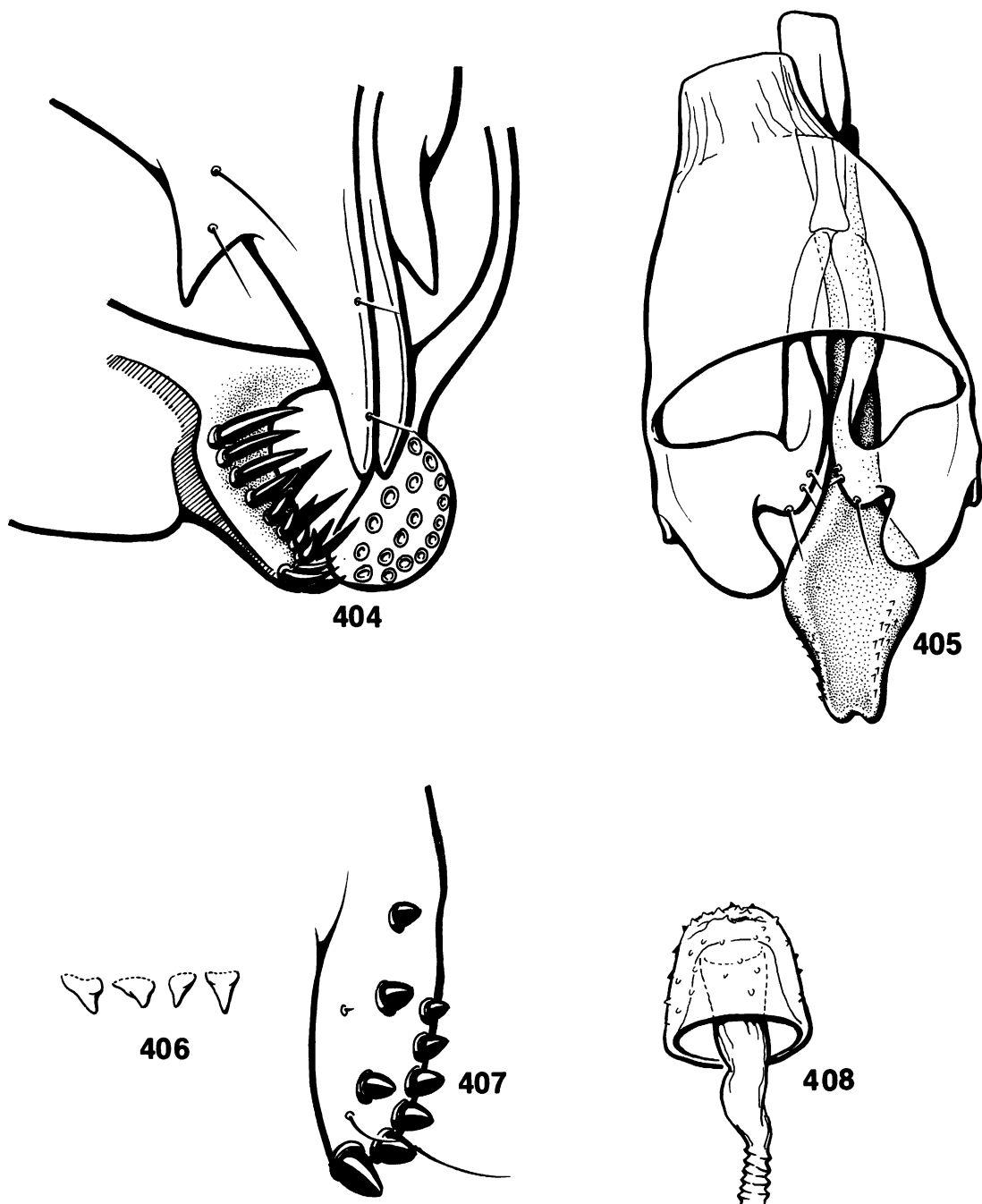
DIAGNOSIS: δ and φ immediately recognizable by broad orange, median band along length of abdomen $\frac{1}{2}$ – $\frac{2}{3}$ abdomen width), flanked by dark brown; φ with all coxae and with basal $\frac{2}{3}$ of femora dark brown; δ with narrow surstylus, anterior lobe on hypandrium truncate.

DESCRIPTION: Outer vertical in line with orbitals. Face, ptilinal fissure light yellow in δ ; face brown in φ ; carina yellow in δ and φ . Flagellomere I length $2\frac{1}{2} \times$ pedicel. Arista with 5 dorsal and 2 ventral branches. Proboscis mostly yellow, with light brown apex in δ ; completely dark brown in φ . Palpi yellow in δ , light brown in φ .

Notum and scutellum shiny, dark brown. Notopleural edge distinct. φ pleura dark brown, proepisternum light yellow. Acrostichals in 4 even rows. φ with coxae and basal $\frac{2}{3}$ of femora dark brown. Wing maculations distinct; apical and R_{2+3} spots coalesced into radial band; spot dm-cu large.

Abdomen with longitudinal, orange band on medial $\frac{1}{2}$ (δ) to $\frac{2}{3}$ (φ) of abdomen, flanked by dark brown. Oviscape tapered, length ca. $2 \times$ width, with ventroapical row of 5 small ovisensilla pegs and 3 dorsal ones, 11–12 ventral sensilla per side. Oviprovector scales small, apices blunt, slightly longer than wide. Spermathecal capsule dome shaped, scales very fine and denser at apex. Hypoproctal plates narrow in lateral view, extended to ca. middle of surstyli. Surstylus narrow, with broad base; possesses 16–18 prensisetae: 8 pegs in lateral row, closely packed, longer ones medially. Hypandrium with anterior margin truncate. Gonopods broad, spiculed. Paraphysal seta fine. Basiphallus ca. $2 \times$ length of aedeagal apodeme, $\frac{1}{3}$ width of distiphallus. Distiphallus with slightly concave lateral margins, broad gonopore. Scales present dorsally and ventrally.

MEASUREMENTS: N = 2 δ , 2 φ . ThL = 1.30



Figs. 404–408. *Zythothrica mediogaster*. **404.** Surstyli + hypoproctal plates. **405.** Aedeagus + hypandrium (ventral). **406.** Oviprovectator scales. **407.** Oviscape (dorsal), apex of right side. **408.** Spermatheca (400×).

♂; 1.66 ♀. HW/ThL = 0.91 ♂; 0.86 ♀. ThL/WL = 0.53; C.I. = 3.02; 4-V = 1.30.

HOLOTYPE: ♂, COSTA RICA: Turrialba, IX-

X/55, W. B. Heed (AMNH) (genitalia not dissected). ThL = 1.37; HW/ThL = 0.92; ThL/WL = 0.53; C.I. = 2.85; 4-V = 1.17.

ETYMOLOGY: Latin, "middle abdomen," in reference to the broad, orange, median abdominal stripe.

DISTRIBUTION: Costa Rica.

MATERIAL: 1♂*, 3♀*, all paratypes, from type locality.

Zygothrica joeyesco, new species

Figures 368, 402–403

DIAGNOSIS: Thorax mostly orange; front light yellow (with brown ocellar triangle), face dark brown; katapisternum, anepisternum, coxae, femora, tibiae, pretarsi (forelegs), entire abdomen, black-brown and shiny. This is one of the most colorful species of *Zygothrica* and is unmistakably recognized (♂ unknown).

DESCRIPTION: Frontal-orbital plates ochre; frontal vittae off-white, dull. Ocellar triangle glassy, light brown, with light median area; intraocellar region dark brown. Anterior margin of front, on ptilinal fissure, is dull light yellow. Cheek light yellow, face dark brown. Carina light yellow, prominent, about 2× width of pedicels. Pedicel ochre, flagellomere I dark brown. Arista with 6 dorsal and 2 ventral branches. Ocellars extended past proclinate. Clypeus, palpi, proboscis dark brown. Apex of palp broad, width ca. ½ length.

Thorax and scutellum yellow-orange; notum with diffuse, light brown vitta pr.2 extended and tapered to anterior dorsocentrals. 4 even rows acrostichals present. Katapisternum and anepisternum black-brown; rest of thorax light yellow. Coxae, basal ⅓ of femora, apical ⅓ of tibiae, forepretarsi are all dark brown. Wing maculations distinct; apical spot nearly constricted from R_{2+3} spot; spot dm-cu large. Halter white.

Postnotum, tergite II light brown, remaining tergites glassy black. Oviscape tapered, length ca. 2× width, with ventroapical row of 5 peg ovisensilla and 1 large + 1 small dorsal peg, ca. 14 ventral sensilla per side. Oviprovectores large, triangular, sharp; widths about equal to lengths. Spermatheca dome shaped, with prominent scales dense at apex.

MEASUREMENTS: N = 3♀. ThL = 1.74 (1.62–1.78); HW/ThL = 0.79 (0.79, 0.80); ThL/WL = 0.60 (0.59–0.61); C.I. = 2.70 (2.35–2.94); 4-V = 1.28 (1.25–1.31).

HOLOTYPE: ♀, SURINAME: Raleigh, Vallen-Voltzberg Reserve, 8/V/84, D. Smith ("swept over fungus") (AMNH) (genitalia not dissected). ThL = 1.77; HW/ThL = 0.79; ThL/WL = 0.60; C.I. = 2.80; 4-V = 1.25.

ETYMOLOGY: From *-esco*, an Italian derivative of the Latin suffix meaning "like," and from "joey," a British theatrical term for clown or pantomime; in reference to the bold, contrasting colors in this species. "Joey" refers originally to Joseph Grimaldi (1779–1837), who was the originator of the clown in English Pantomime and who was also an ardent amateur entomologist and butterfly collector (Boz [Dickens], 1838).

DISTRIBUTION: Hylean South America (fig. 415).

MATERIAL: (both are paratypes) BRAZIL: Rondonia, Calama, 19–21/XI/75, 1♀. VENEZUELA: 0°51'N, 66°10'W, Cerro d.l. Neblina, 140 m, 13–15/III/84, 1♀* ("malaise trap near stream").

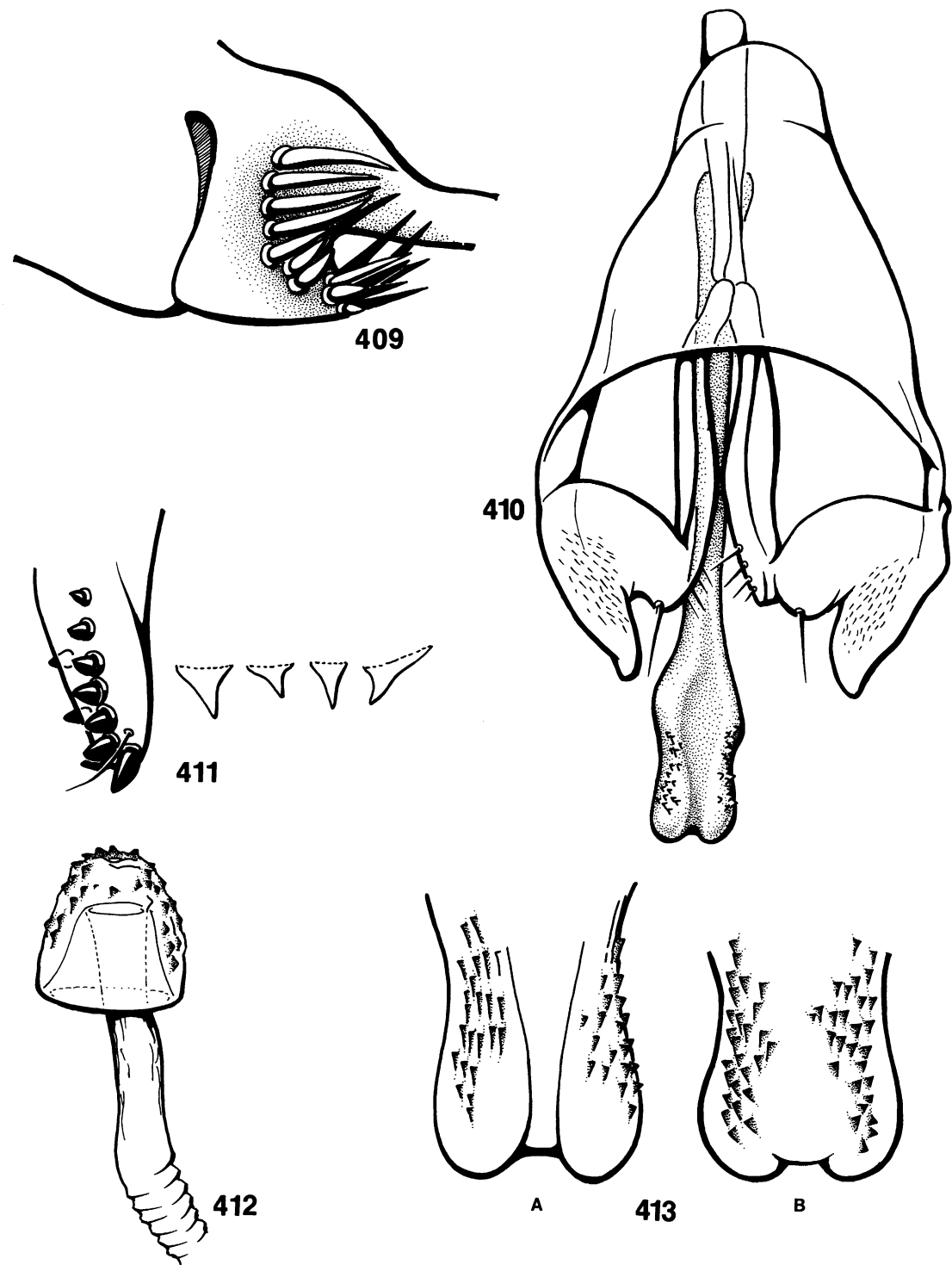
Zygothrica simulans, new species

Figures 366–367, 409–413

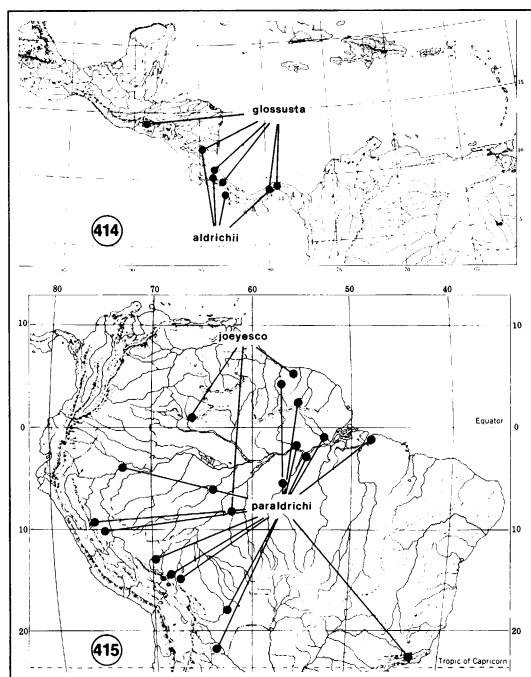
DIAGNOSIS: ♂ proboscis entirely light brown, ♀ proboscis darker; ♂ and ♀ notum, scutellum, tergites entirely dark brown; notopleural edge distinct; ♀ with all femora, coxae, and mid + hind tibiae black-brown; aedeagus elongate, distinctly clavate; distiphallus bulbous with slight medial constriction. The dark proboscis is diagnostic, but genitalic dissection of the ♂ should confirm the identification, particularly in separating from *Z. trinidadensis* and *Z. paraldrichi*.

DESCRIPTION: Ocellar setae extended slightly past proclinate. Inner vertical setae strongly convergent, ends touch. Outer verticals slightly lateral to line through orbitals. Face light brown in ♂, dark brown in ♀. Length of flagellomere I 2½× pedicel. Arista with 5–6 dorsal and 2 ventral branches. Proboscis entirely light brown in ♂, dark brown in ♀. Palpi, clypeus ochre in ♂ and ♀.

Notum, scutellum, postnotum, and tergites entirely dark black-brown in ♂ and ♀. Pleura mostly black-brown in ♀, except at notopleural suture and around ant. spiracle. Notopleural edge distinct. Acrostichals in 4 even rows. ♀ with all coxae and femora, and mid + hind tibiae, dark brown. Forefemur with ventral



Figs. 409–413. *Zygothrica simulans*. 409. Surstylus. 410. Aedeagus + hypandrium (ventral). 411. Oviscape, right apex (ventral) + oviprovector scales. 412. Spermatheca (400×). 413. Distiphallus apex; A, ventral, and B, dorsal.



Figs. 414, 415. Distributions of some species in the *aldrichii* species-subgroup.

row of 3 setae, lengths ca. equal to width of femur. Wing maculations distinct; apical and R_{2+3} spots coalesced into narrow band.

Oviscape black-brown, tapered, length ca. $2 \times$ width, with ventroapical row of 7 small peg ovisensilla and 3 dorsal ovisensilla, ca. 17 tiny ventral sensilla per side. Oviprovector scales large, with sharp points, triangular. Spermathecal capsule dome shaped; scaled, mostly at apex. Hypoproctral plates extended to dorsomedial margin of surstyli. Surstylus apex broadly truncate; with 18–19 prensisetiae, all quite long. Paraphysial seta stout. Basiphallus ca. $3 \times$ length of aedeagal apodeme, ca. $0.25 \times$ width of distiphallus. Distiphallus bulbous, with slight medial constriction; apex truncate; ca. 50–60 scales present on dorsal and ventral surfaces.

MEASUREMENTS: $N = 3\delta, 2\varphi$. ThL = 1.27 δ (1.16–1.35); 1.22 φ (1.13, 1.31). HW/ThL = 0.96 δ (0.93–1.00); 0.88 φ (0.85, 0.92). C.I. = 2.49 (2.28, 2.70); 4-V = 1.30 (1.13, 1.49).

HOLOTYPE: δ , TRINIDAD: Tabaquite, Charuma For., 20/X/54, T. H. G. Aitken (NMNH) (genitalia dissected, DAG). ThL = 1.35; HW/ThL = 0.94.

ETYMOLOGY: Latin, “similar,” for the morphologically cryptic males.

DISTRIBUTION: Trinidad.

MATERIAL: (all are paratypes) TRINIDAD: Morne Blue, 2700 ft, 6/VII/69, 1 δ^* ; Charuma For., Tabaquite, 20/X/54, 1 δ^* , 2 φ^* .

DISCUSSION: The three species that compose the clade to which *Z. simulans* belongs are all quite rare. The clade is defined by females that have all femora dark brown. Females of the three species are distinctive and easily separated from other *Zygothrica*.

Zygothrica somatia, new species

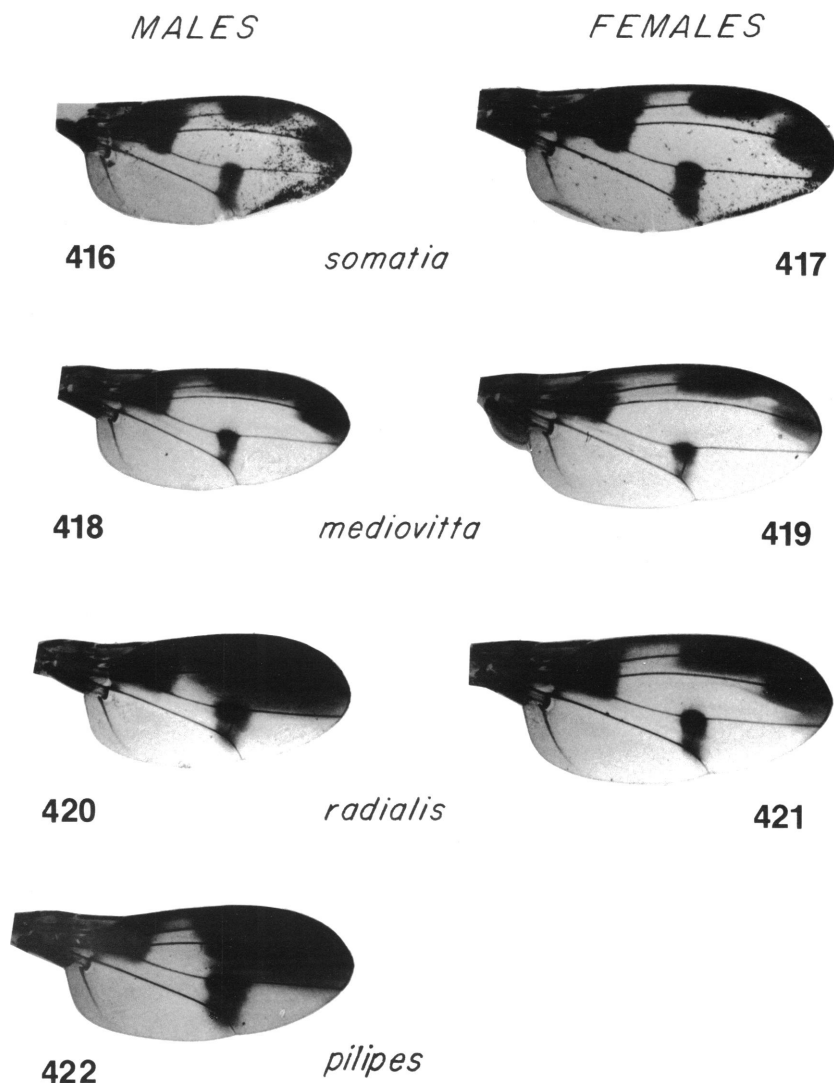
Figures 416–417, 434–437, 4571

DIAGNOSIS: Anterior half of notum brown in δ , all brown in φ , with 2 distinct, yellow, paramedian vittae extended to anterior dorsocentrals; 2 other incomplete vittae laterad, near notal-scutellar suture; δ and φ pleura light yellow; tergites II, III (δ), II–IV (φ) brown, others ochre; aedeagus short with bulbous, almost bare distiphallus; surstylus completely attached to epandrium; spermatheca lightly sclerotized, almost bare. Body coloration alone is sufficient to identify this species; genitalia would provide a set of confirming characters.

DESCRIPTIONS: Frontal-orbital plates yellow. Ocellar triangle dark brown, with light median vitta. Ant. reclinate fine; elongate, length ca. equal to post. reclinate. Outer vertical slightly lateral to line through orbitals. Face yellow in δ , light brown in φ . Flagellomere I length $2.5 \times$ pedicel. Arista with 5 dorsal and 2 ventral branches. Palpi yellow in δ and φ .

Notal ground color brown (posterior half ochre in δ); with distinct, yellow vitta pr.3 extended to ant. dorsocentral; and diffuse vitta pr.5 extended from notal-scutellar suture to almost the transverse suture. Dorsal surface of scutellum dark brown; sides and post-notum yellow. Pleura in δ and φ yellow. Notopleural edge indistinct. Acrostichals in 4 uneven rows. Forefemur with ventral row of 4–5 setae, lengths ca. $0.7 \times$ femur width. Wing maculations distinct.

Tergal ground color ochre to yellow; tergites II, III light brown in δ , II–IV light brown in φ ; brown tergites with diffuse, yellow inverted triangles. Oviscape tapered; length ca.



Figs. 416–422. Wings of some *Zygothrica* in the *aldrichii* species-subgroup.

2× width; with ventroapical row of 7 and dorsoapical row of 3 ovisensilla pegs, ca. 15 sensilla in ventral rows. Oviprovectores triangular, length ca. equal to width. Spermathecal capsule lightly sclerotized; introvert lightly sclerotized; surface almost entirely bare, with 3–4 tiny scales at apex. Hypoproct plates broad in lateral view. Surstylus attached to epandrium for almost entire length; apically truncate; possesses 14–16 mostly setiform prensisetae. Basiphallus ca. equal to length of aedeagal apodeme, ½ width of distiphallus. Distiphallus bulbous,

tapered, with prominent gonopore; ca. 12–15 microspicules at middle of ventral surface.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.20 ♂ (1.08–1.31); 1.44 ♀ (1.47, 1.42). HW/ThL = 0.93 ♂ (0.90–0.96); 0.93 ♀. ThL/WL = 0.54 (0.52–0.57); C.I. = 2.16 (1.86–2.26); 4-V = 1.44 (1.34–1.52).

HOLOTYPE: ♂, BRAZIL: Pará, Monte Douro, Rio Jari, 20/III/80, R. P. Lane (BMNH) (genitalia not dissected). ThL = 1.08; HW/ThL = 0.91; ThL/WL = 0.53; C.I. = 2.23; 4-V = 1.44.

ETYMOLOGY: Derived directly from *So-*

423. *Zygia*424. *tambopata*425. *microeristes*426. *pilipes*427. *radialis*

Figs. 423–427. Representative head shapes of males in the *aldrichii* species-subgroup; frontal views, all to the same scale. *Zygothrica zygia* is shown here as an unmodified form for comparison. Hypercephalic forms which are shown represent the broadest heads seen for each species.

matia, type genus of the Somatiidae (Diptera), since this species and the genus superficially resemble each other based on the wing and body coloration patterns.

DISTRIBUTION: Eastern Brazil (fig. 455).

MATERIAL: (all are paratypes) BRAZIL: Pará: Rio Jari, Monte Dourado, 20/III/80, 4♂*, 2♀*; Pedras, Mun. Obidos, Rio Cuminá-Miri, 24/I/68, 1♀*; Fazenda Taperinha, nr. Santarém, 11/II/68, 1♂*.

DISCUSSION: *Zygothrica somatia* is allied to *Z. radialis*, *Z. pilipes*, and *Z. mediovitta* on the basis of a short aedeagus with a bulbous distiphallus (apomorphy 117). This trait was found as well in the *caudata* species-group (*Z. posthona*, *Z. panopia*, *Z. latipaps*). A distiphallus that is also without scales appears to be another synapomorphy linking the 4 species in this group, although this trait is not included on the cladogram.

Zygothrica mediovitta, new species

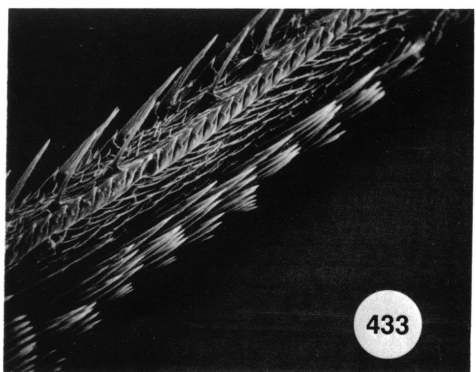
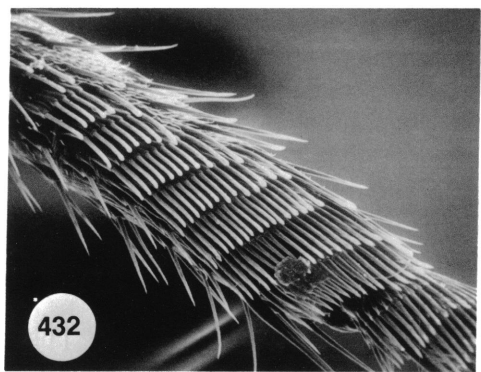
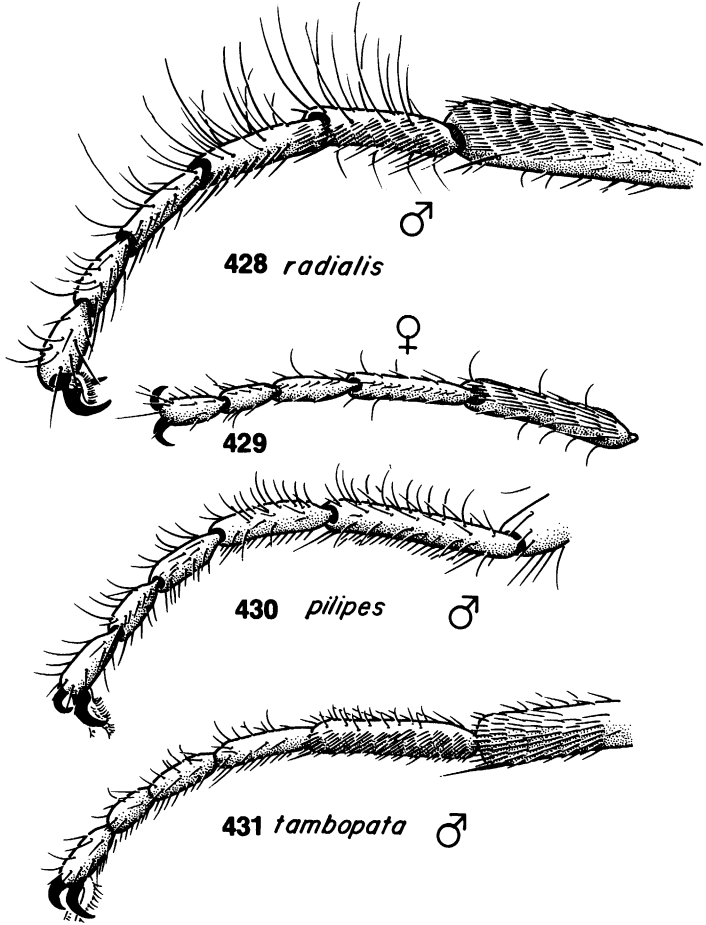
Figures 418–419, 438–441, 457k

DIAGNOSIS: Notum with distinct, yellow, median vitta; vitta pr.2 narrow, dark brown; pr.3 ochre; pr.4 dark brown; vittae except for median one diffuse. Tergite III, IV brown, others ochre. Aedeagus short, distiphallus bulbous and with small apical flanges. Oviscape apically flattened, ovisensilla in terminal row spaced far apart. Like *Z. somatia*, this is a distinct species identifiable solely on the basis of body coloration.

DESCRIPTION: Ocellar setae extended to proclinate. Inner vertical setae convergent, ends almost touch. Outer vertical lateral to line through orbitals. Cheek with anterior portion brown in ♂ and ♀, darker in ♀. Flagellomere I length 3 × pedicel. Arista with 5 dorsal and 1 ventral branch. Proboscis and palpi light yellow.

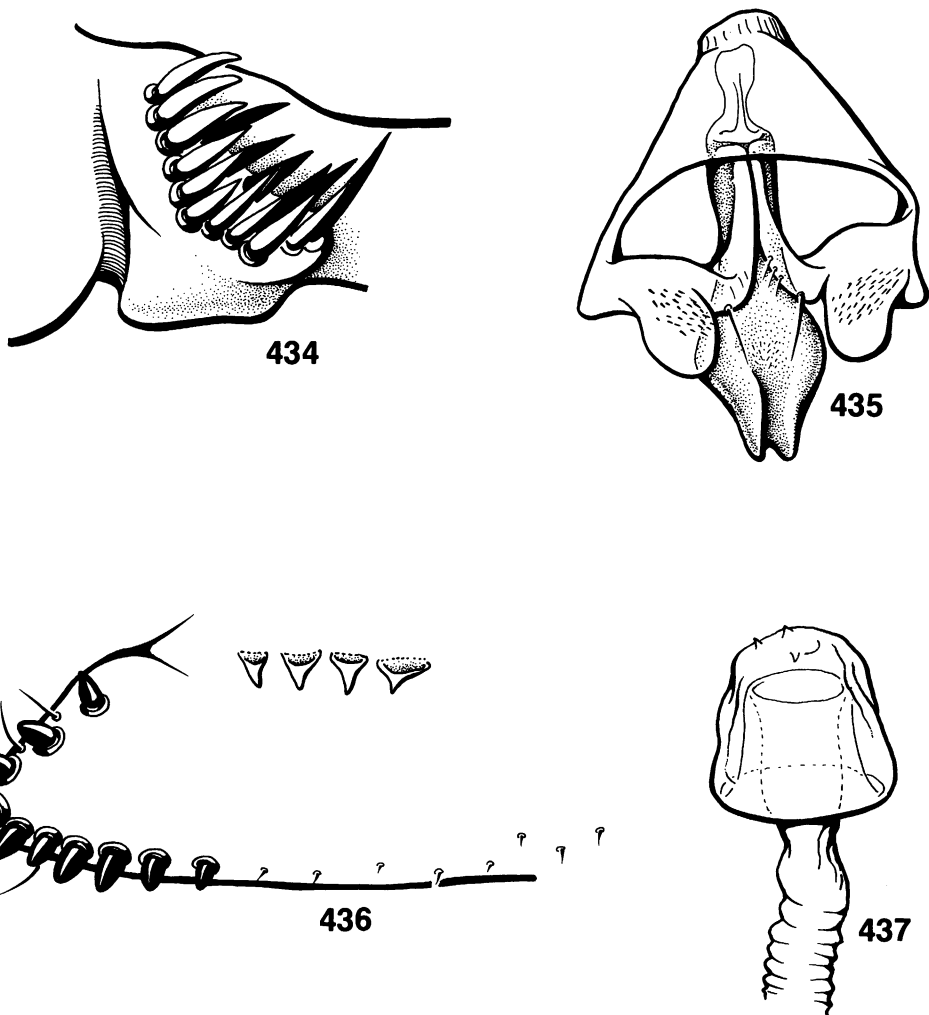
Notal ground color ochre; present are 11 vittae (5 pairs + median one): median vitta distinct, yellow, nearly complete; vitta prs. 2+4 narrow, dark brown, incomplete; vitta pr.3 light brown; vitta pr.5 diffuse yellow. Dorsal surface of scutellum dark brown, flanked by yellow; postnotum yellow. Pleura light yellow; notopleural edge indistinct. ♀ and ♂ with brown apical band on apex of hind tibia. Forefemur with ventral row of 4–5 setae, lengths slightly less than femur width. Wing maculations distinct; apical and R_{2+3} spots coalesced.

Tergal ground color yellow to ochre, tergites III + IV brown; t III with yellow inverted triangle, t IV with median, diffuse brown spot. Oviscape tapered, apical margins oblique, length ca. 2 × width; with apical row of 4 widely spaced and 2 ventromedial ovisensilla pegs, ca. 10 ventral sensilla per side. Oviprovectores triangular, length greater than width. Spermathecal capsule dome shaped, scaled. Hypoproct plates elongate, extended to middle of surstylus. Surstyli small, narrow, almost pendulous: with 19–21 prenisetae. Gonopods short, surface with 4–5 fine annuli, but no spicules. Basiphallus ca. equal to length of aedeagal apodeme or slightly shorter. Distiphallus bulbous, bare; gonopore gaping, with apical flanges.



Figs. 428–431. Foretarsi of some *Zygothrica* species, showing the variation in lengths of setae on the dorsal surface in the males.

Figs. 432, 433. *Zygothrica pallida*, foretarsal segment-1 (ca. 700×). 432. Medial view, showing combs. This setal modification is actually widespread in the *Drosophilidae* and its presence is a primitive condition for *Zygothrica*. 433. Lateral view, showing row of setal scales, which is also a plesiomorph for *Zygothrica*.



Figs. 434–437. *Zygothrica somatia*. 434. Surstylus. 435. Aedeagus + hypandrium (ventral). 436. Oviscape apex (lateral) + oviprovectors. 437. Spermatheca (400 $\times$).

MEASUREMENTS: N = 3 δ , 1 ϕ . ThL = 1.25 δ (1.17–1.33); 1.36 ϕ . HW/ThL = 0.85 δ (0.84, 0.86); 0.84 ϕ . ThL/WL = 0.57 (0.55–0.59); C.I. = 2.58 (2.35–2.72); 4-V = 1.30 (1.24–1.43).

HOLOTYPE: δ , BRITISH GUYANA: Mazaruni-Potaro, Takutu Mountains, 6°15'N, 58°55'W, 10/XI/83, W. E. Steiner (NMNH) (genitalia not dissected). ThL = 1.17; HW/ThL = 0.86; ThL/WL = 0.55; C.I. = 2.68; 4-V = 1.23.

ETYMOLOGY: Latin, “middle stripe,” for the yellow, median notal vitta.

DISTRIBUTION: Eastern Brazil; British Guyana (fig. 455).

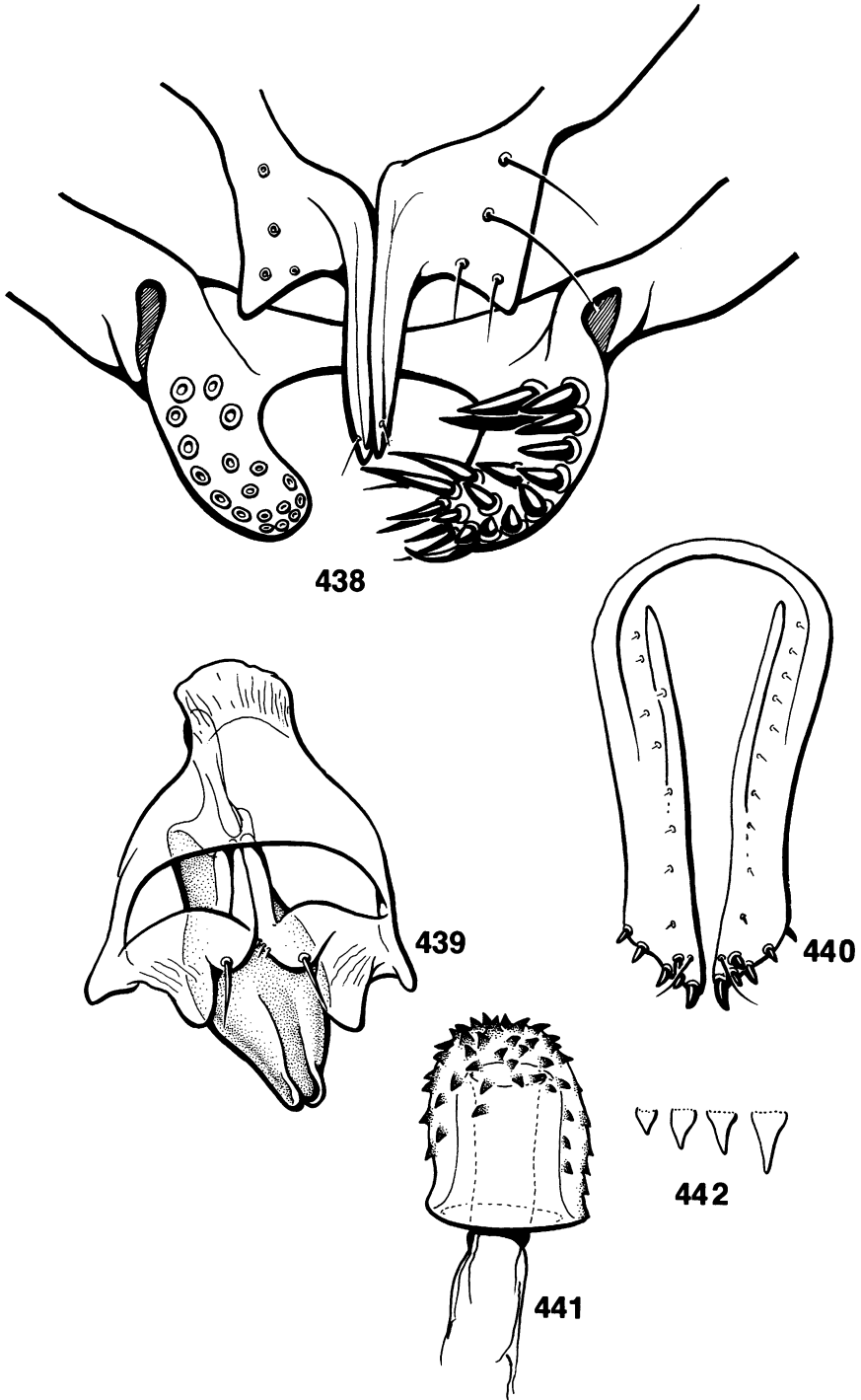
MATERIAL: (all are paratypes) BRAZIL: Pará: Barreirinhas, Rio Tapajós, X–XI/70, 1 δ^* .

BRITISH GUYANA: Mazaruni-Potaro, Takutu Mtns., 10/XII/83, 1 δ^* ; High Forest, 20/VIII/37, 1 ϕ^* (“on fungus”); also, 6 δ^* bearing labels “British Guiana, Parrish,” but with no other information.

Zygothrica radialis, new species

Figures 420–421, 427–429, 443–446

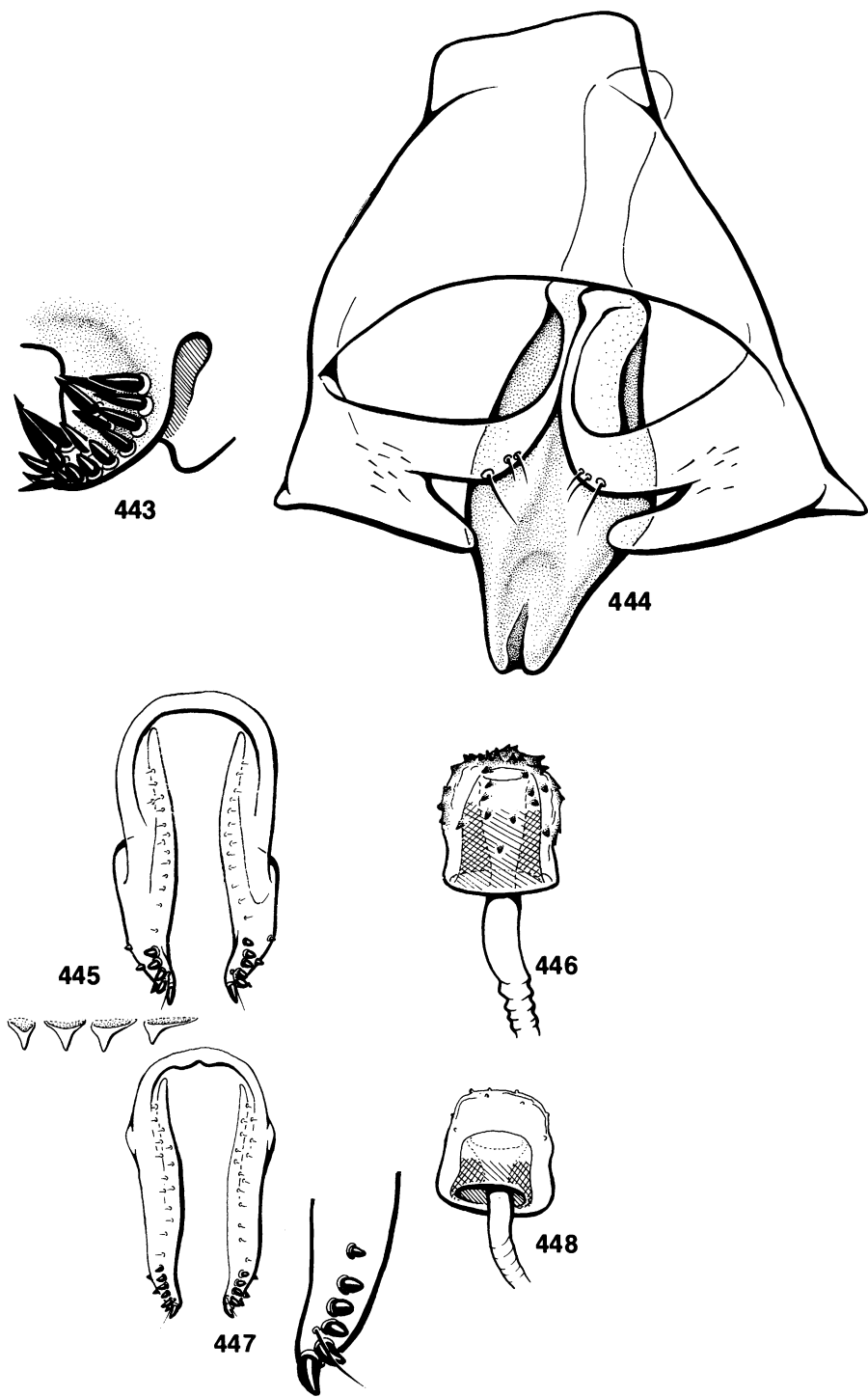
DIAGNOSIS: Males with extensive radial infuscation on wing (extended to M_1), hypercephalic (head width ca. 1.5 $\times$ thorax width), foretarsi with elongate, erect setae; aedeagus short, distiphallus bulbous, surstylus with 18–19 pinnisetae, ϕ radial infuscation extended



Figs. 438–442. *Zygotherica mediovitta*. 438. Surstyli + hypoproctal plates. 439. Aedeagus + hypandrium (ventral). 440. Oviscape (ventral). 441. Spermatheca (440 $\times$). 442. Oviprovectors scales.

to R_{4+5} , spermatheca apically scalate; oviscape with ventroapical row of 6 ovisensilla.

To reliably separate females of this species from *Z. pilipes*, genitalia must be examined.



Figs. 443–446. *Zygothrica radialis*. 443. Surstylus. 444. Aedeagus + hypandrium (ventral). 445. Oviscape (ventral) and ovi-provector scales. 446. Spermatheca (400×).
Figs. 447, 448. *Zygothrica pilipes*. 447. Oviscape (ventral), with detail of left apex. 448. Spermatheca (440×).

DESCRIPTION: Frontal-orbital plates black-brown, dorsally $2-3\times$ anterior width. Procline on lateral margin of frontal vitta. Ant. reclinate near medial margin of eye. Outer vertical lateral to line through procline and post. reclinate. Flagellomere I length $2.5\times$ pedicel. Arista with 5–6 dorsal and 2–3 ventral branches. Proboscis yellow; distal $\frac{2}{3}$ dark brown in ♀. Palpi yellow.

Notum, dorsal surface of scutellum, and most tergites black. Pleura light yellow (♂ and ♀). Notopleural edge indistinct. Acrostichals in 6 even rows. Apex of hind tibia with brown band in ♂ and ♀. Forefemur with ventral row of 4 evenly spaced setae, lengths ca. equal to width of femur. Dorsal surface of foretarsi in ♂ with brush of elongate, erect setae; lengths ca. $3\times$ width of tarsus. Wings with infuscation extended from C to M₁ in ♂; ♀ with infuscation to R₂₊₃ and hyaline gap on R₁.

Oviscape with oblique terminal margins; length $2\times$ width. Tergites VI–VIII in ♂ and t VII, VIII in ♀ are orange. Oviscape with 6 ventroapical, 3 dorsal peg ovisensilla, 13–14 ventral sensilla per side. Oviprovectator scales wider than long, with acute tapering. Spermathecal capsule with introvert lightly sclerotized; scaled, mostly at apex. Hypoproctal plates extended to middle of surstyli. Surstyli with broad bases; possess 18–19 prensisetae, 7–8 pegs in lateral row. Hyandrium short; anterior margin broad, truncate. Gonopods directed mediad, very sparsely spiculed. Paraphysial seta very fine. Basiphallus shorter than aedeagal apodeme. Distiphallus tapered into basiphallus, bulbous, bare.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.32 ♂ (1.25–1.44); 1.39 ♀ (1.34, 1.45). HW/ThL = 0.99 ♂ (0.89–1.12); 0.87 ♀ (0.85, 0.88). ThL/WL = 0.57 (0.54–0.59); C.I. = 2.58 (2.38–2.89); 4-V = 1.19 (1.14–1.24).

HOLOTYPE: ♂, BRITISH GUYANA: Mazaruni-Potaro, Takutu Mountains, 6°15'N, 58°55'W, 10/XII/83, W. E. Steiner ("on white bracket fungus on fallen tree") (NMNH) (genitalia not dissected). ThL = 1.44; HW/ThL = 1.12; ThL/WL = 0.59; C.I. = 2.89; 4-V = 1.14.

ETYMOLOGY: Derived from "radius," due to the extensive infuscation in ♂ wings in the radial area.

DISTRIBUTION: Northeastern South America (fig. 456).

MATERIAL: (specimens from Takutu Mountains, Guyana, are paratypes) BRAZIL: Pará: Barreirinhas, Rio Tapajós, X–XI/70, 1♂*, 6♀; Belem, IV/58, 1♂*, 2♀; Monte Dourado, Rio Jarí, 3♂*, 1♀*. BRITISH GUYANA: Mazaruni-Potaro, Takutu Mtns., 10/XII/83, 13♂*, 13♀; High Forest, 20/VIII/37, 1♂*, 1♀ ("on fungus"). SURINAME: Raleigh, Vallen-Voltzberg Res., 8/V/84, 2♂* ("swept over fungus").

DISCUSSION: Very sparsely spiculed to completely bare gonopods may be a synapomorphy to link *Z. radialis* and *Z. pilipes* with *Z. mediovitta*, since the absence of vestiture among these flies is certainly a loss. *Zygothrica radialis* and *Z. pilipes* are structurally interesting and, like several other species mentioned throughout this paper, a study of their reproductive behavior would be interesting. In particular, such a study should examine the manner in which the extensively infuscated wings are semaphored, and if a male *Z. radialis* engages in elaborate brushing motions with his foretarsi on the posteroventral portion of the female abdomen during courtship.

Zygothrica pilipes

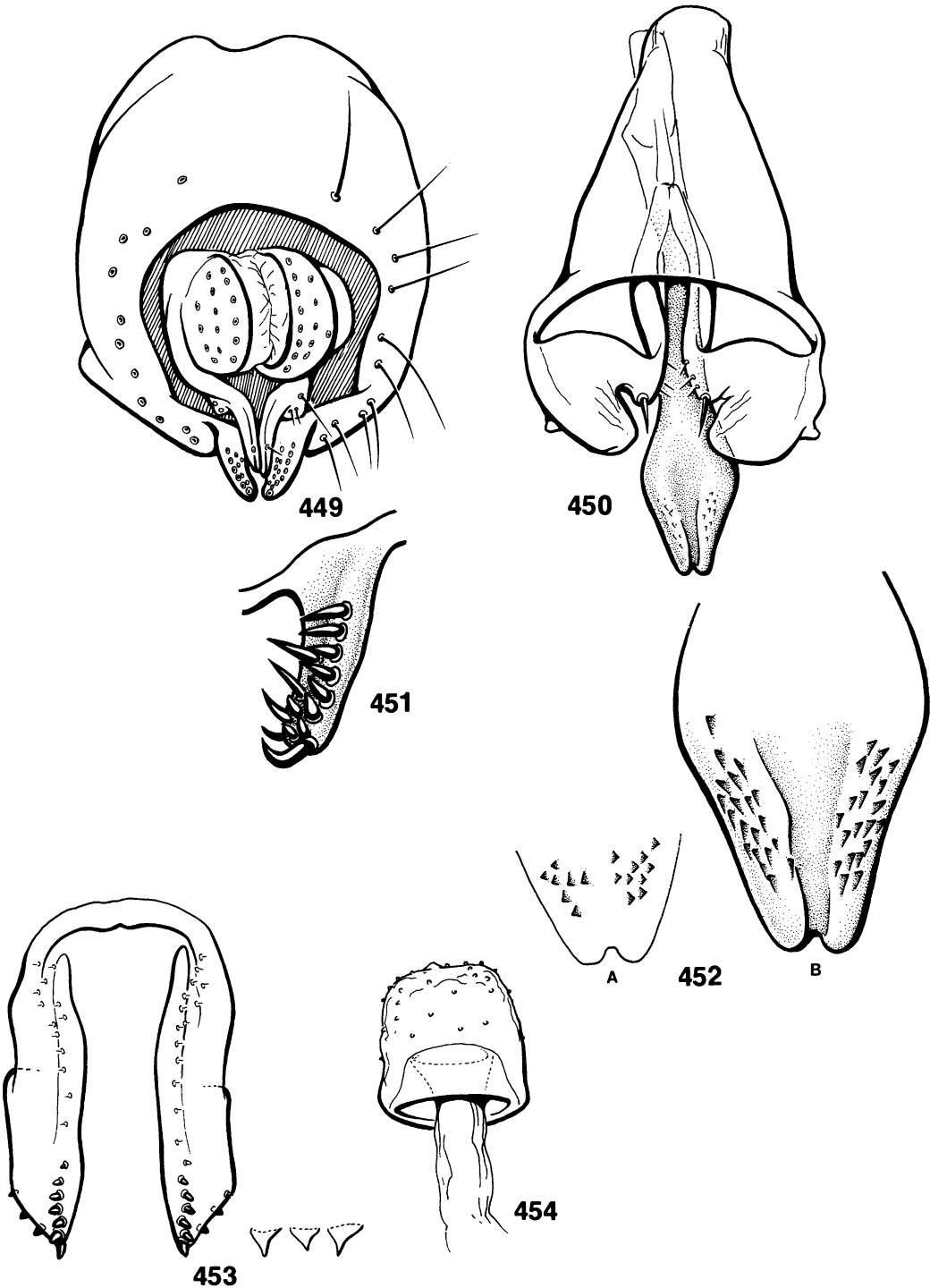
Figures 422, 425, 430, 447–448

Zygothrica pilipes Hendel, 1936: 93.

DIAGNOSIS: This species is very similar to *Z. radialis*, including most features on the genitalia, except for the following: ♂ wing with hyaline band between r-m band and radial infuscation; ♂ foretarsi with slightly elongate and erect setae (lengths ca. equal to tarsus width); surstylus with 13–14 prensisetae; spermatheca lightly sclerotized, nearly bare (ca. 10 small apical papillae present). Like *Z. radialis*, this species possesses extensive radial infuscation on ♂ wings, and the males are moderately hypercephalic.

MEASUREMENTS: N = 4♂, 2♀. ThL = 1.38 ♂ (1.02–1.57); 1.51 ♀ (1.35–1.63). HW/ThL = 1.11 ♂ (0.89–1.49); 0.87 ♀ (0.79–0.92). ThL/WL = 0.57 (0.55–0.62); C.I. = 2.72 (2.37–3.13); 4-V = 1.11 (1.05–1.24).

LECTOTYPE: ♂, BRAZIL: [Pará], "Unt. Amaz. Taperinha, b. Santarem, 1–10/VI/27. Zerny." (NHMW) (type examined, genitalia not dissected). This specimen was sent from among Hendels' "7♂, ♀" cotypes; it was bear-



Figs. 449–452. *Zygothrica prensiseta*, holotype. 449. Epandrium. 450. Distiphallus apex; A, dorsal, and B, ventral.

Figs. 453, 454. *Zygothrica paravitta*. 453. Oviscape (ventral) + oviprovector scales. 454. Spermatheca (440×).

ing the labels "Type" and "syntypus *Zygothrica pilipes* H., G. Bächli det. 1985." ThL = 1.26; HW/ThL = 0.90; WL = 2.20; C.I. = 2.62; 4-V = 1.14.

DISTRIBUTION: Eastern hylea (fig. 456).

MATERIAL: BRAZIL: Amapá, Serra do Navio, 26/V/64, 2♂*, 1♀*; Amazonas, Puruzinho, Rio Madeira, 17/XI-6/XII/75, 1♂*, 1♀; Rondonia, Calama, 21/X/75, 2♂*; Pará, Barreirinhas, Rio Tapajós, X-XI/70, 1♂*, 2♀; Pedras, mun. Obidos, Rio Cuminá-Miri, 20-24?/I/68, 2♂*, 1♀; Faz. Taperinha, nr. Santarém, 1-11/II/68, 1♂*, 1♀. SURINAME: Marowijne, Langaman Kondré, VIII/65, 1♀.

Zygothrica prensisetæ, new species

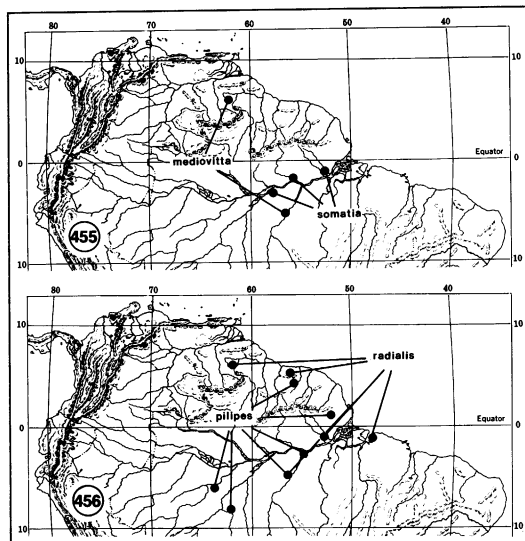
Figures 371, 449-452

DIAGNOSIS: Notum dark brown, with very faint, incomplete, paramedian vittae; clypeus, labellum brown; proboscis yellow; costal edge of wing completely infuscated; surstylus elongate, with hooked apical prensisetæ (♀ unknown).

DESCRIPTION: Outer vertical slightly lateral to line through orbitals. Ocellars extended to proclinales. Cheek, gena, face, carina light yellow. 5 dorsal and 2 ventral branches on arista. Proboscis mostly light yellow; labellar lobes brown, clypeus dark brown, palpi light yellow.

Pleura and legs entirely light yellow. Notum, scutellum, and postnotum dark brown; notum with diffuse, barely discernible vitta pr.2 extended to ant. dorsocentrals. Notopleural edge distinct. Forefemur with ventral row of 3 setae, lengths slightly less than femoral width. Halteres light yellow. Wing maculations distinct: apical, R_{2+3} , and r-m spots coalesced into costal band; dm-cu spot large. Acrostichals in 4 uneven rows.

Tergites dark brown, with very light median abdominal spots. Epandrium black-brown. Hypoproctal plates elongate, narrow; extended to middle of surstyli. Surstyli pendulous, narrow, and long; with 14 prensisetæ each: 1 large, hooked apical, lateral row of 7, medial row of 4 longest ones. Gonopods broad, spiculed. Paraphysial seta stout, short. Basiphallus length $3 \times$ aedeagal apodeme; $\frac{1}{2}$ width of distiphallus. Distiphallus with sparse scales on dorsal surface, ca. $3 \times$ as many on ventral surface.



Figs. 455, 456. Distributions of some species in the *aldrichii* species-subgroup.

HOLOTYPE: ♂, COSTA RICA: La Suiza [de Turrialba], P. Schild (NMNH) (genitalia dissected, DAG). ThL = 1.25; HW/ThL = 0.90; ThL/WL = 0.44; C.I. = 3.45; 4-V = 1.28.

ETYMOLOGY: In regard to unique surstylus and prensisetæ.

DISTRIBUTION: Known only from holotype.

DISCUSSION: This species and *Z. paravitta*, on account of a lack of material of one sex, are not included on the cladogram in figure 163. These 2 species are tentatively incertae sedis in the *aldrichii* subgroup.

Zygothrica paravitta, new species

Figures 274, 453-454, 457a

DIAGNOSIS: ♀ tergites with broad, median, orange band along abdomen; apical and R_{2+3} spots coalesced; pleura light; light brown, incomplete, notal vitta pr.2 present; spermathecal capsule sparsely and finely papillate (♂ unknown).

DESCRIPTION: Ocellar setae elongate, extended slightly past proclinales. Outer vertical lateral to line through orbitals. Face brown. Flagellomere I length $3 \times$ pedicel. Arista with 5-6 dorsal and 1 ventral branch. Distal half of proboscis brown, proximal portion ochre. Palpi narrow, light brown.

Notal ground color light brown, with diffuse, ochraceous vitta pr.2 extended to ant. dorsocentrals. Pleura, postnotum, and hal-

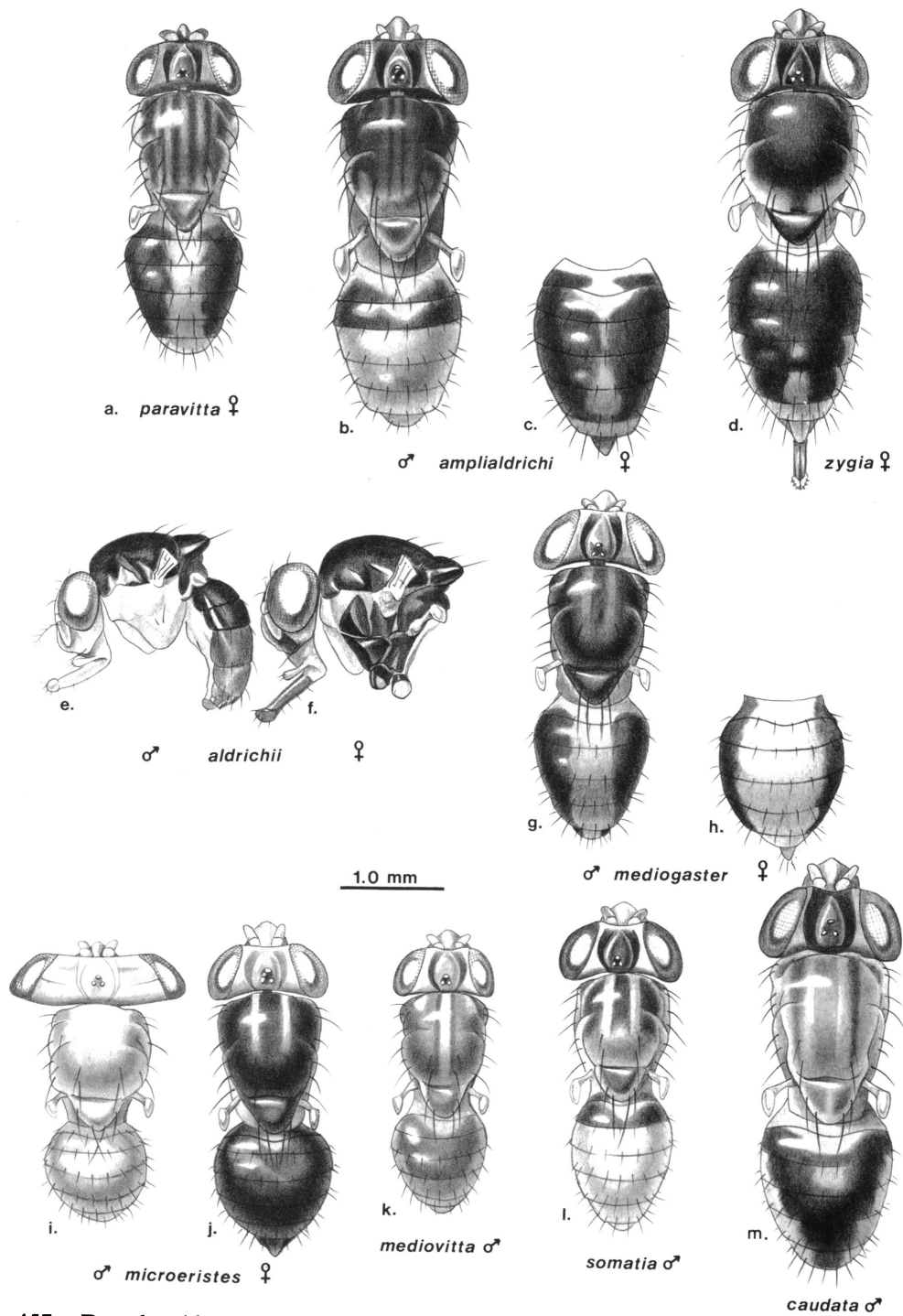


Fig. 457. Dorsal and lateral habitus of some *Zygothrica* species, or portions thereof. All to the same scale.

teres light yellow. Legs light yellow, hind tibia with apical dark brown band. Wing with dark markings; apical and R_{2+3} spots fused. Ventral surface of forefemur with row of 2–3 setae, lengths slightly longer than femur width. Tergites II–VI laterally black-brown, median $\frac{1}{3}$ orange and forming diffuse median band along abdomen; t VII, VIII orange. Oviscape tapered, apical margins oblique; lengths $2\times$ width; with 7 ventral and 3 dorsal peg ovisensilla, 14 ventral sensilla. Oviprovector scales broad, triangular. Spermathecal capsule square in lateral view; surface with tiny, sparse papillae; introvert short. Laterotergite VIII ramus shorter than oviscape.

MEASUREMENTS: N = 3♀. ThL = 1.51 (1.40–1.58); HW/ThL = 0.81 (0.82, 0.80); C.I. = 2.58 (2.52, 2.70); 4-V = 1.22 (1.11–1.30).

HOLOTYPE: ♀, PANAMA: "Canal Zone," Las Cruces Trail, 21/VII/67, W. W. Wirth ("bracket fungi") (genitalia not dissected) (NMNH). ThL = 1.58; HW/ThL = 0.82; ThL/WL = 0.55; C.I. = 2.52; 4-V = 1.30.

ETYMOLOGY: Latin, "almost lined," for the diffuse notal vittae.

DISTRIBUTION: Costa Rica, Panama.

MATERIAL: (all are paratypes) PANAMA: 2♀*, same data as holotype. COSTA RICA: Heredia, Sarapiquí, 4/IV/70, 2♀*.

DISCUSSION: The presence of an orange, wide band on the median portions of the tergites, the wing pattern, and a spermatheca with small papillae, suggest a close relationship of this species with *Z. mediogaster*. However, the pleura and femora of *Z. mediogaster* are black-brown, and for that reason it seems allied to a group of 4 other species possessing this color pattern.

CAUDATA SUBGROUP, CLADE 1.2.1.2.B.3

(fig. 162)

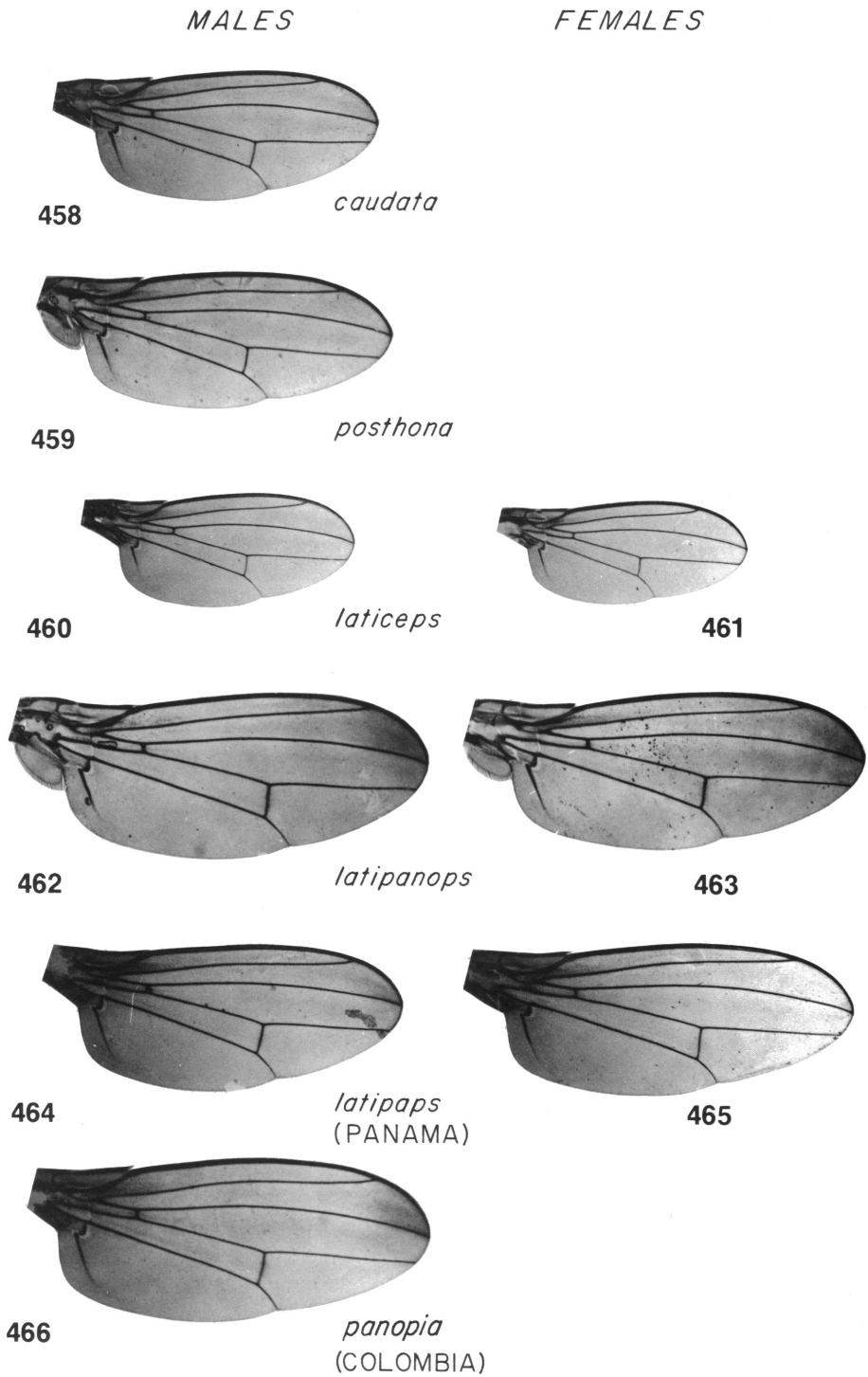
This group of nine species is certainly monophyletic, judging from the five synapomorphies which define it. The synapomorphies are the following: number 98 (ventral surface of the medial gonopod finely wrinkled—seen also in some species of the *dispar* subgroup); 103 (dorsoventral shape of the oviscape flared laterally just prior to the terminal tapering); 104 (surstylus [male] bearing

many short peg prensisetae); 105 (surstylus distinctly crescent shaped); 106 (ventral setae on profemur are stout and sharp). In addition, the largest species in the genus belong to this subgroup, and most of the subgroup members have an ochre body color.

KEY TO SPECIES OF THE CAUDATA SPECIES-SUBGROUP

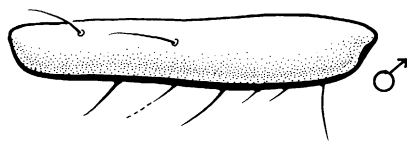
This key is for use with males, and for some females which are associated with males. *Zygothrica nigra*, n. sp., is not included here.

1. Dorsal surface of proboscis (mediolabral surface) bears 5–6 pairs of setae (figs. 33, 34) 2
- 1a. Proboscis without such setae 3
2. Acrostichal setulae in 4 rows; carina narrow (width ca. equal to flagellomere width); oviscape with apical row of 5–6 large ovisensilla/side (fig. 488) (♂ unknown) *ora*, n. sp.
- 2a. Acrostichals in 6 rows; carina ca. $2\times$ broader than flagellomere I; oviscape with 8–9 apical ovisensilla/side (fig. 495) *caudata*
3. Head of ♂ not noticeably broadened, nor eyes tapered 4
- 3a. ♂ head broadened, HW/ThL ≥ 0.95 ; eyes tapered laterad (figs. 477–481) 5
4. Forefemur with ventral row of 4–5 and medial row of 3 stout, sharp setae (fig. 472); aedeagus very short, with an exceptionally bulbous distiphallus (fig. 482); oviscape with apical row of 6 ovisensilla/side (fig. 486) *posthona*, n. sp.
- 4a. Forefemoral setae not so stout; aedeagus with much smaller distiphallus (fig. 497); oviscape with 4–5 large terminal ovisensilla/side (fig. 499) *latipaps*, n. sp.
5. Inner vertical setae exceptionally long, lengths ca. $0.5\times$ head width (fig. 480); distiphallus narrow, glabrous (fig. 513); posterior hypandrial margin with process (fig. 511) (♀ unknown) *caputrichia*, n. sp.
- 5a. Above characteristics are otherwise; distiphallus scaled or glabrous 6
6. ♂ wing with diffuse, light brown, apical infuscation (figs. 462, 463, 466) 7
- 6a. ♂ wing completely hyaline 8
7. ♂ head extremely broad, especially in medium to large-size individuals (fig. 481b), HW/ThL = 1.30–2.20; forefemur with ventral row of long setae (♂ and ♀) (fig. 474); hy-

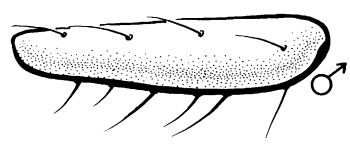


Figs. 458–466. Wings of some *Zygothrica* in the *caudata* species-subgroup (clade 1.2.1.2.B.3).

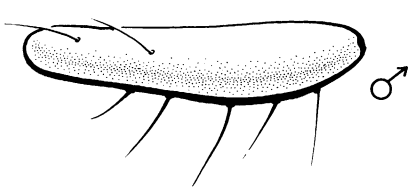
pandrium short, distiphallus glabrous (fig. 516) <i>latipanops</i> , n. sp.	7a. ♂ head moderately broad (fig. 477), HW/ThL = 0.85–0.95; forefemur with shorter setae; hy-
---	---



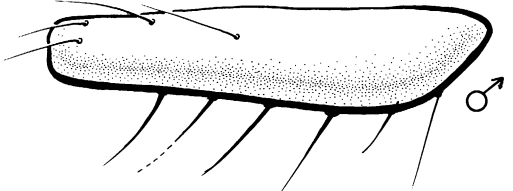
467 *dispar*



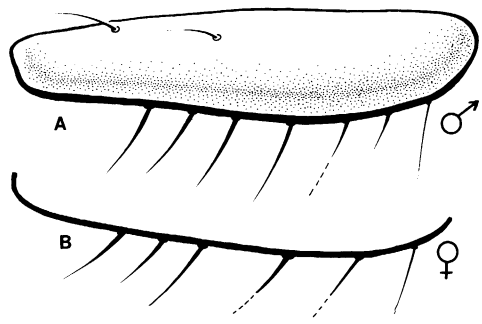
468 *antedispar*



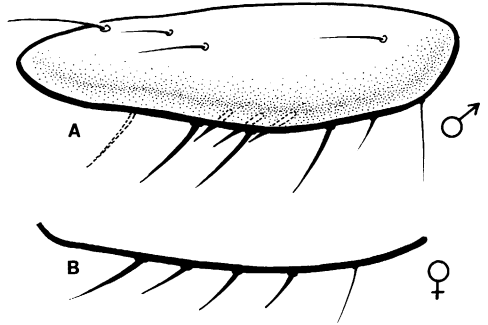
469 *laticeps*



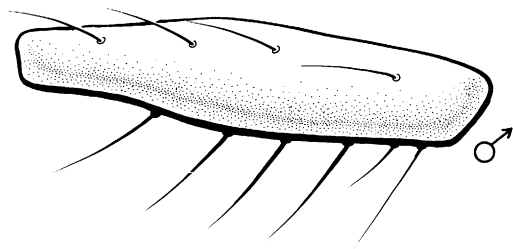
470 *caudata*



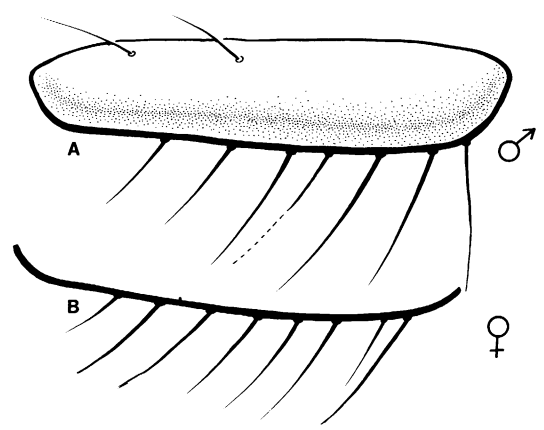
471 *latipaps*



472 *posthona*



473 *aliucapa*

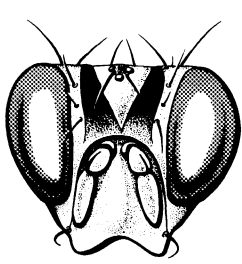


474 *latipanops*

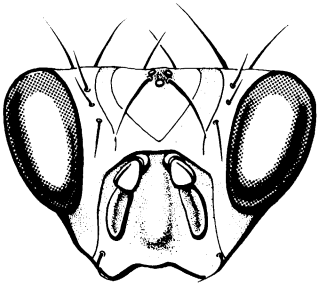
Figs. 467–474. Intra- and interspecific variation of setae on ventral surface of profemur. Lateral views, all to the same scale. Dashed lines indicate variation in lengths and position.

pandrial length unmodified; distiphallus triangular, with sparse scales dorsally (fig. 507)
..... *panopia*, n. sp.

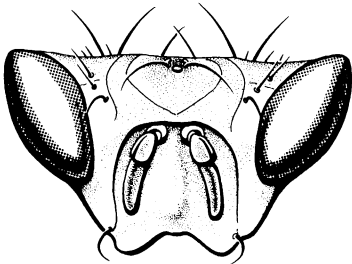
8. Reclinate orbital setae very reduced (♂); surstylus with 2 large, dorsal peg prenisetae (fig. 521); distiphallus barely wider than en-



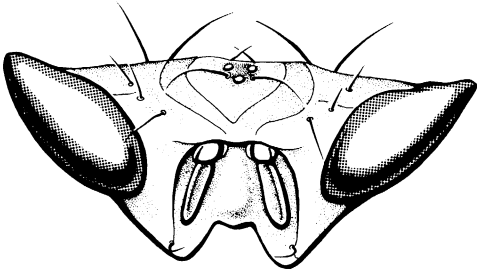
475. *caudata*



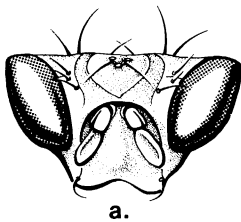
476. *posthona*



477. *panopia*

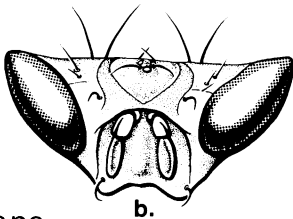


478. *aliucapa*

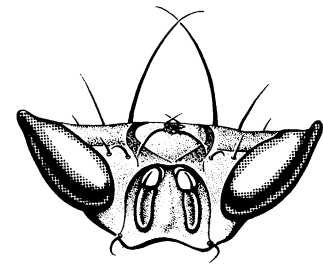


a.

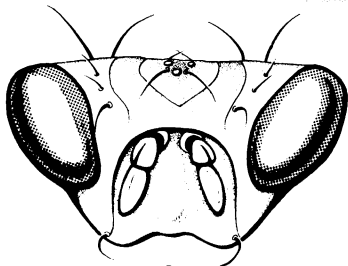
479. *laticeps*



b.

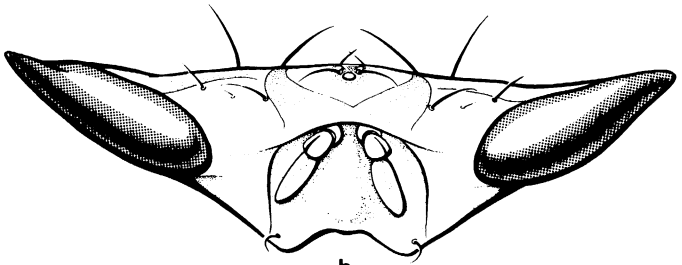


480. *caputrichia*



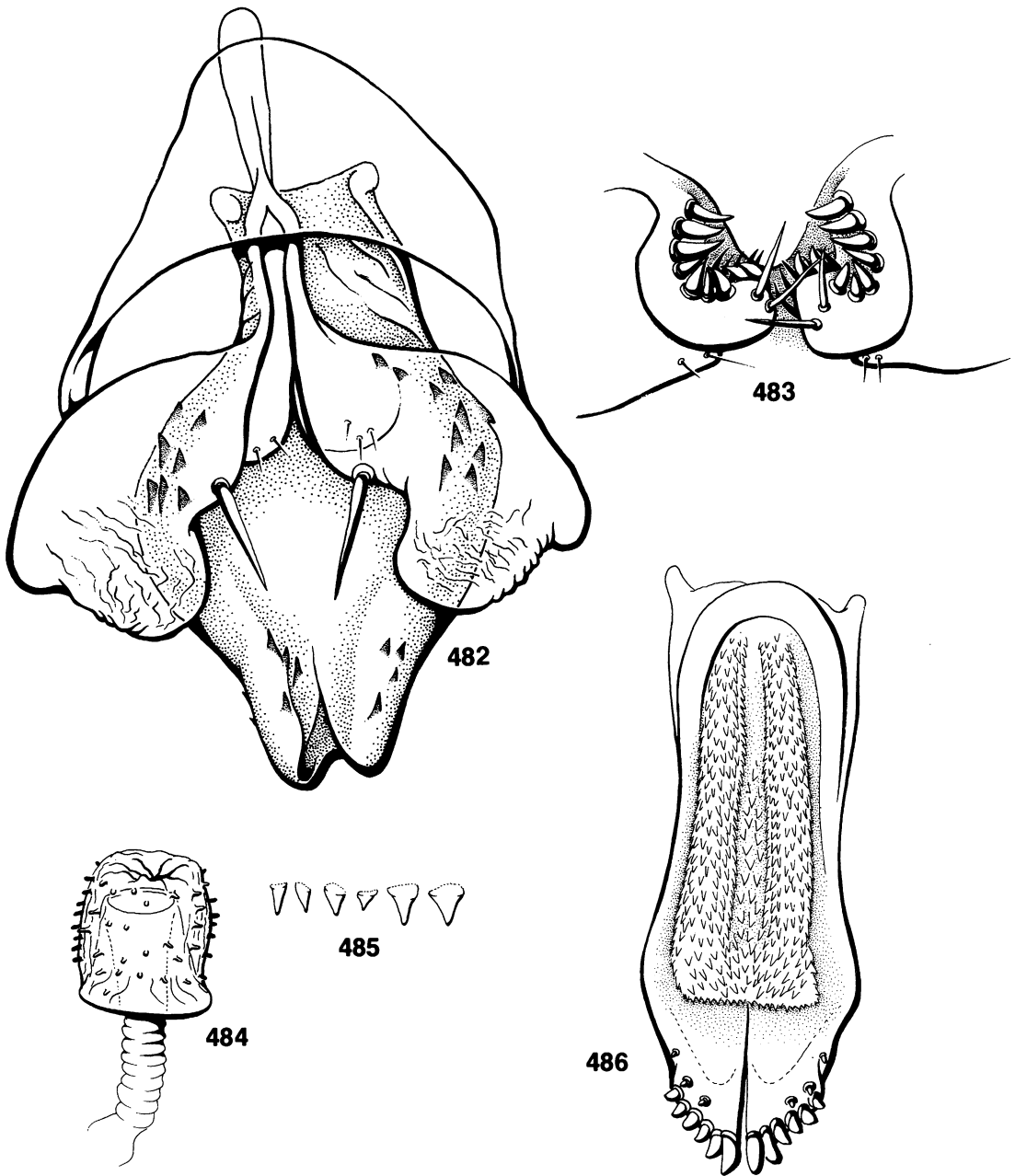
a.

481. *latipanops*



b.

Figs. 475–481. Representative head shapes of males in the *caudata* species-subgroup; frontal views, all to the same scale. *Zygothrica caudata* is unmodified in head breadth and is shown for comparison. Variation in *Z. posthona* and *Z. panopia* was negligible; figures 478 and 480 are of the holotypes. The extremes from least (a) to the most (b) hypercephalic individuals are shown for *Z. laticeps* and *Z. latipanops*.



Figs. 482–486. *Zygothrica posthona*. 482. Aedeagus + hypandrium (ventral). 483. Surstyli. 484. Spermatheca (400×). 485. Oviprovectur scales. 486. Oviscape (dorsal).

- dophallus (fig. 520) (♀ unknown)
..... *aliucapa*, n. sp.
8a. Reclimates of usual size; no distinction between
dorsal and lateral prensisetae (fig. 501); dis-
tiphallus bulbous (fig. 500); spermatheca
wrinkled, without scales *laticeps*

KEY TO KNOWN FEMALES OF THE
CAUDATA SPECIES-SUBGROUP

Use of the key requires that the terminalia
be prepared for examination using com-
pound microscopy. *Zygothrica ora*, n. sp. and

Z. caudata are excluded; see couplets 2 and 2a of the previous key for these females.

1. Face almost entirely black; sides of oviscapae parallel, with apex abruptly narrowed (fig. 490); spermatheca campanulate (fig. 489) *nigra*, n. sp.
- 1a. Face mostly ochre; oviscapae sides with distinct preapical widening, apex tapered; spermatheca dome shaped to rectangular in lateral view 2
2. Apical margin of oviscapae with 4–5 large ovisensilla per side (fig. 499) *latipaps*, n. sp.
- 2a. Apical margin of oviscapae with 6–8 ovisensilla/side 3
3. Spermatheca wrinkled, without scales (figs. 502, 503); oviscapae lanceolate in dorsolateral view (fig. 504) *laticeps*
- 3a. Spermatheca scalate 4
4. Oviscapae elongate, length $3.5 \times$ the width (fig. 510); spermatheca heavily scalate (fig. 508) *panopia*, n. sp.
- 4a. Oviscapae length $2.5 \times$ the width (e.g., fig. 486) 5
5. Forefemur with ventral and ventromedial rows of stout setae (fig. 472); 1–2 ventral arisal branches; spermathecal scales small, erect *posthona*, n. sp.
- 5a. Forefemur with ventral row of long setae (fig. 474); 3–4 ventral arisal branches; spermathecal scales retrorse *latipanops*, n. sp.

Zygothrica caudata

Figures 34, 457m, 458, 470, 475, 491–495

Drosophilura caudata Hendel, 1913: 389.

Zygothrica dispar: Sturtevant, 1920: 157.

Zygothrica aldrichi [sic]: Duda, 1927: 58.

Zygothrica caudata (Hendel), 1936: 92.

Zygothrica caudata: Burla, 1956: 15.

DIAGNOSIS: Male head shape unmodified; inside surface of labial membrane bears row of 5–6 black setae per side, proximal setae pointed mediad, distalmost pair pointed laterad. Notal ground color is diffuse, light brown, with indistinct, yellow, incomplete notal vitta pr.2 (sometimes a very narrow median vitta occurs). Anterior margin of hypandrium square, and the medial and lateral gonopods possess numerous fine, rounded scales. The basiphallus is ca. $3 \times$ the distiphallus length and is arched. Terminal margin of the oviscapae is oblique and bears row of 8–9 evenly spaced and sized ovisensilla per side and 3 per side on the dorsal

margin. Spermatheca heavily scaled; scales rounded and large.

DESCRIPTION: Hendel (1913, 1936) and Burla (1956) gave descriptions. The latter reference provided a description of the male and female genitalia as well. Illustrations of the genitalia are provided here for diagnostic purposes.

MEASUREMENTS: N = 4♂. ThL = 1.79 (1.67–1.96). HW/ThL = 0.81 (0.79–0.84). ThL/WL = 0.56 (0.53–0.59). C.I. = 3.03 (2.68–3.29); 4-V = 1.09 (1.02–1.17).

LECTOTYPE: ♀ [BRAZIL]: [Pará], Unt. Amaz. Taperinha b. Santarém, 1–10/VI/27, Zerny (Vienna Natural History Museum) (genitalia dissected, DAG). ThL = 2.22; HW/ThL = 0.73; ThL/WL = 0.61; C.I. = 3.11; 4-V = 1.17. I examined one of the 2 cotypes, designated as a “holotype” by Dr. Gerhard Bächli in 1985 (and bearing a label as such), to which my lectotype label has also been applied.

DISTRIBUTION: El Salvador to southern Brazil (figs. 524, 525).

MATERIAL: BRAZIL: São Paulo, Salesópolis, Estacion Biol. Boracéia, 3/V/78, 1♂*. EL SALVADOR: 5 km W Santa Tecla, II/54, 1♂*. TRINIDAD: Sangre Grande, XII/55, 1♂*; Ta-baquite, Charuma Forest, 20/X/54, 1♂*.

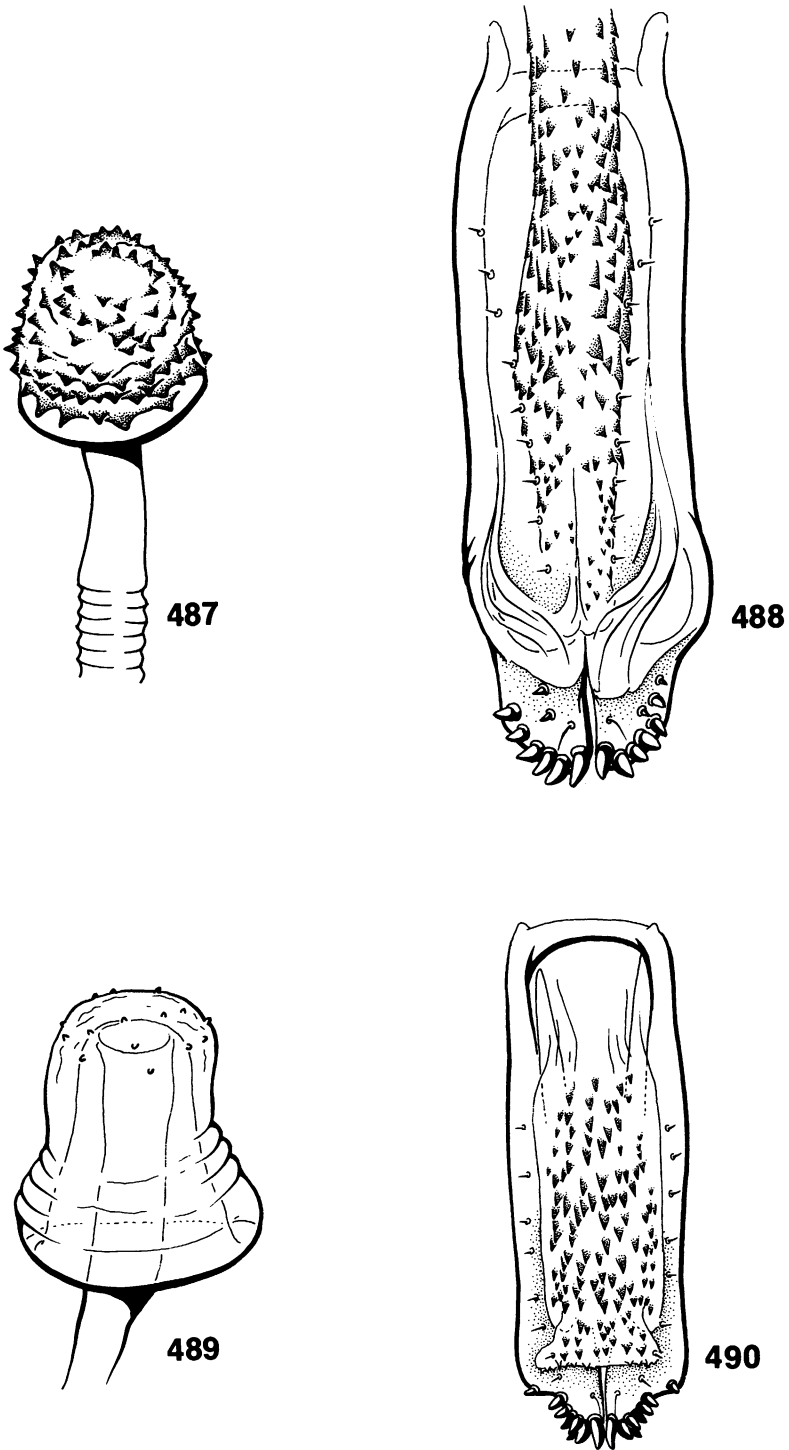
DISCUSSION: This apparently widespread species is rare. Placement of the species in, indeed naming of, the *caudata* species-subgroup rests primarily on terminalia characters. The phylogenetic placement of *Z. ora* close to this species is based on the possession of 10–12 mediolabral setae on the proboscis.

Zygothrica ora, new species

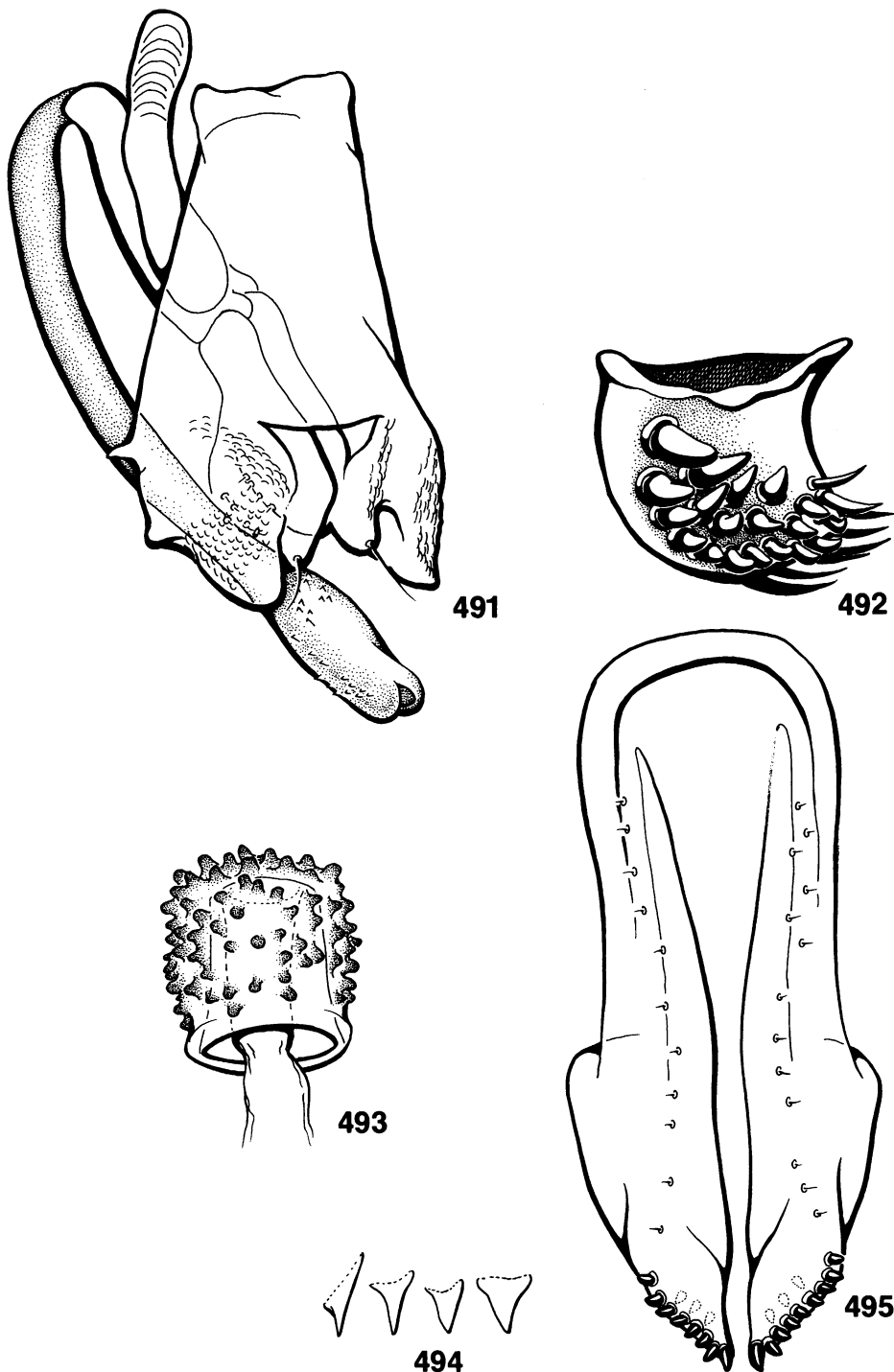
Figures 33, 487–488

DIAGNOSIS: Presence of an exceptionally protuberant face will allow quick separation from *Z. caudata*. The face of *Z. ora* is also considerably darker, and the carina more narrow, than in *Z. caudata*. In addition, *Z. ora* has only 4 instead of 6 rows of acrostichal setulae (♂ unknown).

DESCRIPTION: Frontal-orbital plates ochre, dorsally $2 \times$ width of frontal portion. Frontal vittae velvety black. Eyes light red, bare. Ocellar triangle dark brown, shiny, extended to slightly past proclinate. Proclinate orbital seta equal in length to post. reclinate; ant.



Figs. 487, 488. *Zygothrica ora*. **487.** Spermatheca (400 $\times$). **488.** Oviscape + oviprovector (dorsal).
 Figs. 489, 490. *Zygothrica nigra*. **489.** Spermatheca (400 $\times$). **490.** Oviscape + oviprovector (ventral).



Figs. 491–495. *Zygothrica caudata*. 491. Aedeagus + hypandrium (ventrolateral). 492. Surstylus. 493–495. Lectotype. 493. Spermatheca (400×). 494. Oviprovectator scales. 495. Oviscape (ventral).

recline $0.7 \times$ length of other orbitals, closest to proclinate. Post. reclinate closer to inner vertical than to proclinate. Ocellar seta slightly longer than verticals, extended to procli-

nates. Inner vertical seta equal in length to outer vertical. Outer vertical in line with orbitals. Face brown, including pedicel and flagellomere I. Carina narrow (width ca. equal to that of flagellomere I), complete. Face very protuberant, from anterior margin of eye extended ca. $\frac{1}{2}$ length of eye; anterior (oral) margin deeply cleft. Cheek with dark brown spot, lighter posteriad. Flagellomere I length $3 \times$ pedicel; arista with 6 dorsal and 1 ventral branch. Proboscis off-white to light brown, with 5 mediolabral setae per side. Palp elongate, tan.

Notal ground color brown. Incomplete, diffuse, light brown vitta pair 2 present; surrounded by darkest brown on notum. Pleura, halteres, legs, postnotum, yellow to off-white. Acrostichal setulae in 4 rows. Forefemur with 3 ventral setae, slightly longer than width of femur. Wings hyaline. Dorsal surface of scutellum dark brown.

Abdominal ground color black-brown. Oviscape apex dorsoventrally flattened. Oviscape length $3.5 \times$ the width, distal margin rounded. 8 peg ovisensilla present (5 on terminal margin, 2–3 dorsolaterally). Oviprovectores scales broadly triangular, irregular in size and distribution. Spermathecal capsule campanulate, surface with dense vestiture of large scales. Cerci elongate, black-brown.

HOLOTYPE: ♀, SURINAME: Raleigh, Vallen-Voltzberg Reserve, 8/V/84, D. Smith ("swept over fungus," altitude less than 100 m) (AMNH) (genitalia dissected, DAG). ThL = 1.76; HW/ThL = 0.56; C.I. = 3.35; 4-V = 1.11.

ETYMOLOGY: Latin, "mouth," pertaining to the extremely protuberant oral margin and face.

DISTRIBUTION: Suriname (fig. 525), known only from the holotype.

Zygothrica nigra, new species

Figures 489–490

DIAGNOSIS: A dark-bodied, nondescript species, but the female genitalia are distinct for *Zygothrica*. Viewed from above or below, the apical margin of the oviscape has a prominent lobe that bears the ovisensilla. Sides of the oviscape are parallel for virtually the entire length. The spermathecae are campanu-

late, with a very broad base. Ocellar triangle is nearly entirely black (♂ unknown).

DESCRIPTION: Head ground color ochre. Frontal-orbital plates ochre; frontal vittae velvety black. Eyes light gray-brown, very sparsely setulose. Ocellar triangle black, with tiny ochre spot at apex. Proclinate orbital seta equal in length to post. reclinate. Ant. reclinate midway between proclinate and post. reclinate; length is $\frac{1}{2}$ that of other orbitals. Post. reclinate midway between proclinate and post. reclinate. Inner vertical seta in line with orbitals. Face light ochre, lateral oral margins barely splayed. Carina low, complete, yellow. Median cleft on oral margin extended to apex of flagellomere I. Cheek with dark brown spot, rest is yellow. Flagellomere I brown, length $2 \times$ pedicel. Arista with 3–4 dorsal and 1 ventral branch. Clypeus yellow; proboscis light yellow; palpi black-brown.

Notum entirely black; pleura and legs yellow to ochre, halteres light yellow. Anterior portion of dorsal scutellar surface black, with yellow rim. Ventral scutellar surface yellow, postnotum brown. Yellow spot present immediately dorsal to each postpronotal lobe. Acrostichal setulae in 6 rows. Forefemur with ventrolateral row of 6 black, stout setae; lengths barely longer than femur width. Wings hyaline.

Tergites black, with small lateral portions yellow. Oviscape flat, length ca. $3 \times$ the width; with 7–8 peg ovisensilla per side, all on apical margin. Apical margin with distinct lobe. Oviprovectores scales triangular, very irregular in size and distribution. Spermathecal capsule large, campanulate; surface sparsely papillate at apex, with sparse annulations at collar; base almost $2 \times$ apical width; no apical indentation present. Cerci elongate, black.

HOLOTYPE: ♀, PANAMA: Chiriquí, Guadalupe, Arriba, 1–4/VIII/84, 2100 m, "at light trap," H. Wolda (AMNH) (genitalia dissected, DAG). ThL = 1.23; HW/ThL = 0.74; ThL/WL = 0.44; C.I. = 2.86; 4-V = 1.51.

ETYMOLOGY: Latin, "black," for the nearly all black dorsum of the unique specimen.

DISTRIBUTION: Panama (fig. 524), known only from the holotype.

DISCUSSION: *Zygothrica nigra* is hypothesized to be allied with *Z. caudata* and *Z. ora* based on the possession of frontal vittae which are extensively velvety-black (apomorphy 87 on the cladogram in fig. 162).

Zygothrica posthona, new species

Figures 459, 472, 476, 482–486

DIAGNOSIS: Either sex can be identified on the presence of 4–5 stout, sharp setae on the ventral surface of the profemur. Females possess dark brown palpi, in addition to brown first flagellomeres (males have ochre palpi, like the rest of the head). An elongate ov scape and a very bulbous distiphallus, as described below, are diagnostic genitalic characteristics.

DESCRIPTION: Head ground color ochre to yellow. Head slightly broadened in δ . Frontal-orbital plates narrow anteriorly, width ca. $0.5\times$ that of frontal vitta. Frontal vittae yellow. Eyes dull red, with very sparse, short setulae. Ocellar triangle almost as wide as face, yellow; intraocular area dark brown. Proclinate orbital seta longer than post. reclinate. Ant. reclinate $0.5\times$ length of proclinate, slightly closer to proclinate than to post. reclinate. Post. reclinate midway between inner vertical and proclinate. Outer vertical in line with orbitals. Face yellow; carina prominent, complete, broad. Cheek yellow. Flagellomere I length $2\times$ the pedicel. Flagellomere I brown in δ , darker in φ . Arista with 5–7 dorsal and 1–2 ventral branches. Proboscis yellow; palp yellow in δ , dark brown in φ , with stout black setae.

Notal ground color ochre, without markings. Pleura, halteres, postnotum light yellow. Acrostichal setulae in 6 even rows. Leg color yellow; wings hyaline. Ventrolateral surface of profemur with 4–5 stout, straight, sharp, black setae, lengths slightly less than femur width.

Tergites mostly black. δ t VI, VII with ventral dark brown bands; φ with t II yellow, t III–V with large median yellow spot each, t VI–VII with median brown spot, t VIII black-brown. Oviscape with oblique apical margin, length $3\times$ the width; with 6–7 large, terminal peg ovisensilla and 3 tiny dorsal pegs. Laterotergal ramus elongate: equal to length of oviscape. Dorsolateral ramus of t VIII narrow, elongate. Oviprovector scales heavy, dentate. Spermathecal capsule rectangular, surface with sparse, long papillae. No apical indentation. Cerci dark brown, dorsoventrally flat.

Dorsal margin of epandrium slightly elon-

gate, dorsally dark brown. Ventral epandrial lobes very small, adpressed to surstyli. Cerci rounded, brown; ventral cercal lobes very small. Hypoproctal plates small. Surstylus strongly crescentic, possesses 17–19 prensi-setae: 7 large pegs in lateral row, 2 apicolateral setae, 5–7 apicomедial setiform prensi-setae. Hypandrium very short. Gonopod surface finely wrinkled. Paraphysial seta stout. Basiphallus extremely short, ca. $0.5\times$ length of bulbous distiphallus, with fine folds. Distiphallus extremely large, nearly equal in size to hypandrium, with associated appendages; bulbous, apically narrowed; terminal and lateral scales present.

MEASUREMENTS: N = 5 δ , 7 φ . ThL = 1.74 δ (1.52–1.92); 1.85 φ (1.73–2.03). HW/ThL = 0.85, δ (0.84–0.87); 0.81 φ (0.78–0.88). ThL/WL = 0.51 δ (0.47–0.53); 0.51 φ (0.48–0.53). C.I. = 3.98 (3.65–4.28); 4-V = 1.15 (1.06–1.22).

HOLOTYPE: δ , BOLIVIA: [El Beni] S. Inicua, Riv. Alto Beni, 15–18/I/76, 1100 m, L. Peña (CNC) (genitalia not dissected). ThL = 1.78; HW/ThL = 0.85; ThL/WL = 0.53; C.I. = 3.65; 4-V = 1.11.

ETYMOLOGY: Greek “large penis,” due to the conspicuously large and bulbous distiphallus.

DISTRIBUTION: Colombia to Bolivia (fig. 525).

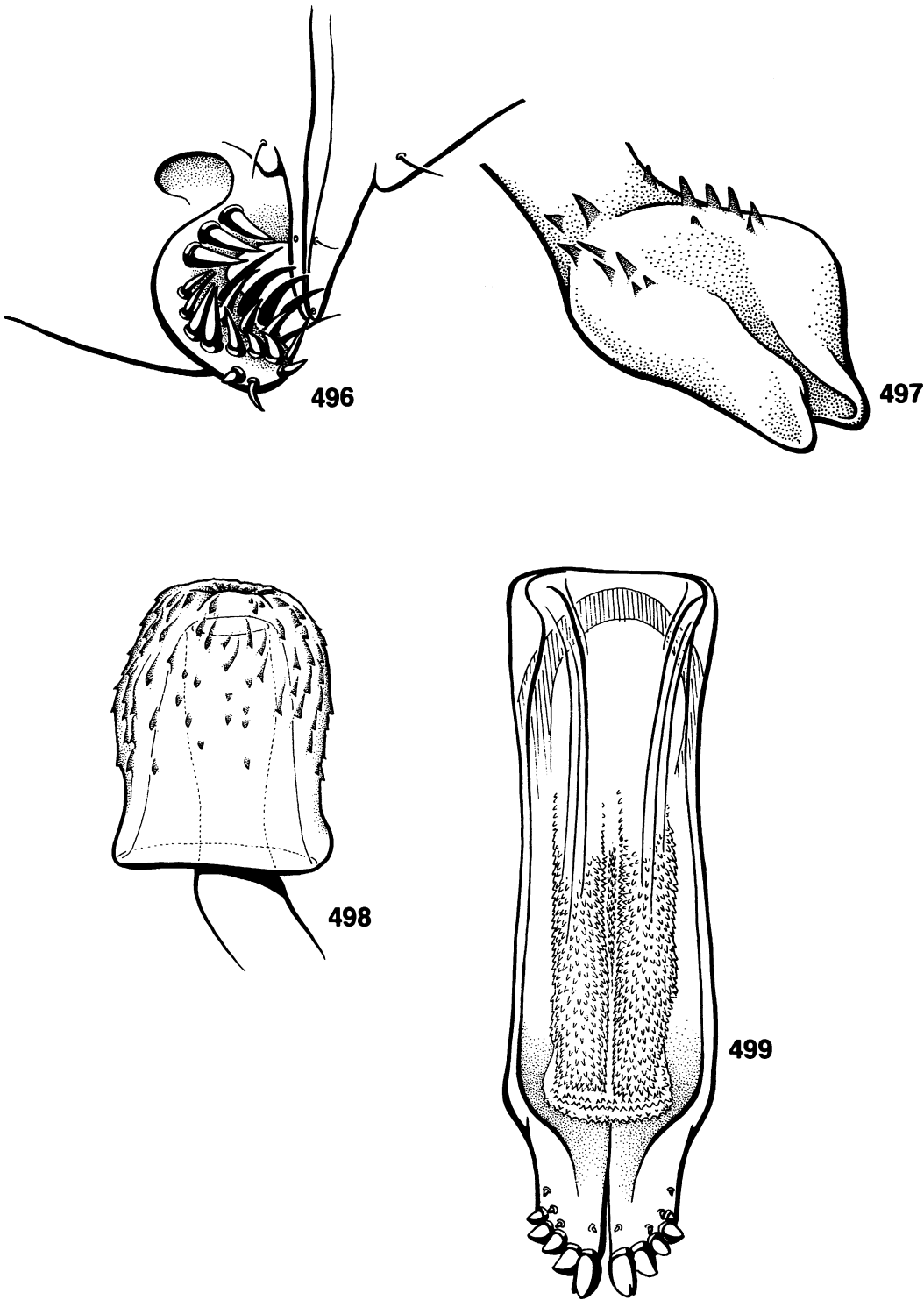
MATERIAL: (all are paratypes) COLOMBIA: [Cauca], 30 km N Popayan, 1 δ^* . BOLIVIA: S. Inicua, Riv. Alto Beni, 15–18/I/76, 1100 m, 1 δ^* , 6 φ^* . PERU: Cuzco, Quince Mil, 13–31/VIII/62, 780 m, 1 δ^* ; Madre de Dios, Avispas, 10–20/IX/62, 400 m, 1 δ^* , 1 φ^* .

Zygothrica latipaps, new species

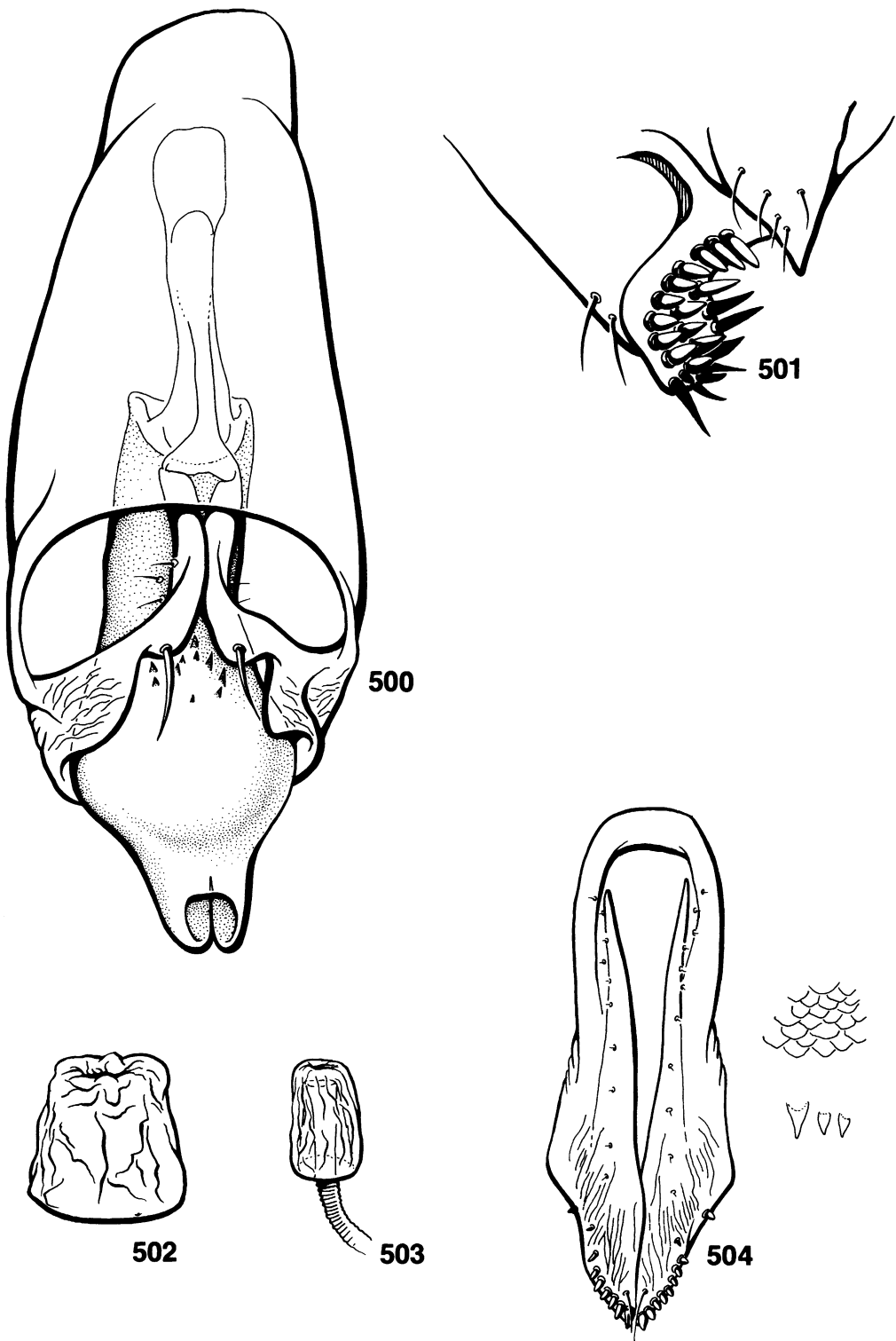
Figures 464–465, 471, 496–499

DIAGNOSIS: A large, tan to ochre species with diffuse, very light brown, apical wing infuscation in the males. The other species with similar coloration are *Z. panopia* and *Z. latipanops*, both of which have broad-headed males. In *Z. latipaps* males, the head is very slightly broadened dorsally, but not enough so that the eyes are tapered apicad.

DESCRIPTION: Head ground color ochre. δ head only very slightly broadened dorsally. Frontal-orbital plates light brown. Frontal vittae dull, gray-brown, median portion yel-



Figs. 496–499. *Zygothrica latipaps*. 496. Surstylus. 497. Distiphallus. 498. Spermatheca (400×). 499. Oviscape and oviprovector (dorsal).



Figs. 500-504. *Zygothrica laticeps*. 500. Hypandrium + aedeagus (ventral). 501. Surstylus. 502. Spermatheca (400×), Turrialba, COSTA RICA. 503. Spermatheca (160×), EL SALVADOR. 504. Oviscape (ventral) and oviprovector scales.

low. Eyes red-brown. Ocellar triangle dorsally dark brown, apex yellow, extended slightly past proclimates. Ant. reclinate divergent, slightly shorter than orbitals, much closer to proclimates than to post. reclinate. Post. reclinate divergent and closest to outer vertical. Ocellar setae extended to ant. reclinate. Outer vertical in line with orbitals. Ptilinal fissure dull yellow. Face light yellow; carina bright yellow to brown, prominent, complete. Cheek yellow, with light brown spot in ♀. Flagellomere I brown, darker in ♀. Flagellomere I $4 \times$ length of pedicel. Arista with 6–7 dorsal and 2 ventral branches. Clypeus, proboscis yellow; palp yellow in ♂, tip black in ♀.

Notum ochre to light brown; no distinct markings. Pleura, legs, halteres yellow to ochre. Apical scutellar setae strongly cruciate for $0.5 \times$ their lengths. Acrostichal setulae in 6 irregular rows. Ventral surface of profemur with 4–5 stout, black setae, lengths less than width of femur. Wings mostly hyaline; in ♂, with very light brown, diffuse, apical infuscation.

Tergites black-brown; t II, anteromedian portion of t III, and median spot on t IV are yellow. Oviscape with sides parallel; apex flat; length ca. $3.5 \times$ the width; with 4–5 large, terminal, peg ovisensilla and 3 tiny pegs on dorsal surface. Oviprovector scales very small, dense. Spermathecal capsule small, rectangular in lateral view, surface very finely scaled; without apical indentation. ♀ cerci dark brown; t VIII dorsally black, laterotergal ramus black and shiny.

Epandrium dorsoventrally elongate, black. Ventral epandrial lobe small, adpressed. Cerci rounded, black; ventral cercal lobes very small, with 1 setula. Surstylus strongly crescentic, possesses 23–25 prensisetae: 11 sharp pegs in lateral row; 3–4 fine, setiform, terminal ones; 10 narrow medials. Gonopod surface finely wrinkled. Basiphallus slightly arched, ca. $\frac{1}{3}$ width of distiphallus. Distiphallus dorsoventrally flattened; tapered apicad, with small notch on apical margin. Ventral surface of distiphallus with ca. 20 erect scales near collar.

MEASUREMENTS: N = 3♂, 5♀. ThL = 1.81 ♂ (1.50–2.03); 2.00 ♀ (1.71–2.37). HW/ThL = 0.83 ♂ (0.81–0.87); 0.81 ♀ (0.79–0.82). ThL/WL = 0.54 ♂ (0.50–0.57); 0.53 ♀ (0.50–0.56). C.I. = 4.23 (3.89–4.82); 4-V = 1.05 (0.97–1.16).

HOLOTYPE: ♂, COSTA RICA: La Suiza [de Turrialba], I/24, Pablo Schild (NMNH) (genitalia dissected, DAG). ThL = 2.03; HW/ThL = 0.87; ThL/WL = 0.57; C.I. = 3.99; 4-V = 1.06.

ETYMOLOGY: Derived from *laticeps*.

DISTRIBUTION: Costa Rica, northern Panama (fig. 524).

MATERIAL: (all are paratypes) COSTA RICA: Turrialba, 15–19/VII/65, 1♂*, I/24, 1♀. EL SALVADOR: Volcan Boqueron, 4500 ft, VII/54, 1♂*, 3♀*. PANAMA: Chiriquí, Boquete, VIII/58, 1♀*.

DISCUSSION: *Zygothrica latipaps* is not shown on the cladogram in figure 162. It probably represents one of four actual basal lineages for clade 1.2.1.2.B.3, or the *caudata* subgroup. It appears very similar to *Z. posthona*, but this is a symplesiomorphic resemblance.

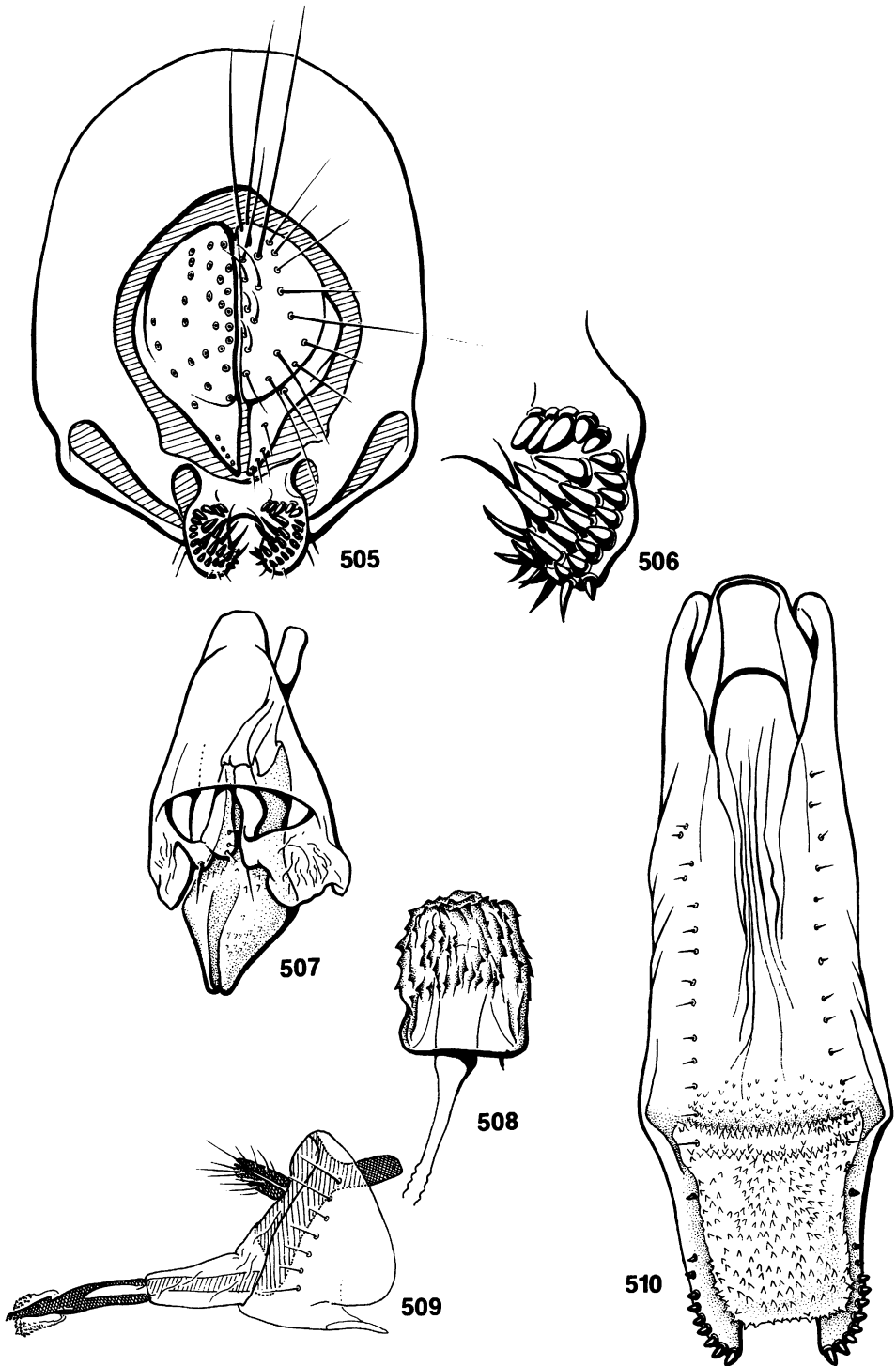
Zygothrica aliucapa, new species

Figures 473, 478, 519–521

DIAGNOSIS: Distinguished from the other 5 hypercephalic species in the *caudata* subgroup by hyaline wings, extremely reduced reclinate orbitals, pendulous surstyli borne on an epandrium which is dorsoventrally very elongate, and the distiphallus, which is slightly wider than the endophallus and is sparsely scalate (♀ unknown).

DESCRIPTION: Head ground color ochre. Head width $2 \times$ the thorax width. Frontal-orbital plates dorsally $0.7 \times$ width of face; frontally $0.3 \times$ width of face, dorsal surface with dark brown band. Frontal vittae dull, light brown. Eyes rosy, apically pointed, bare. Ocellar triangle extended slightly past proclimates; $0.7 \times$ width of face; shiny. Proclinate seta is longest orbital ($2 \times$ the length of post. reclinate). Ant. reclinate midway between proclinate and post. reclinate, slightly shorter and finer than post. reclinate. Post. reclinate much closer to proclinate than to verticals. Outer vertical medial to line extended from orbitals by ca. length of the seta. Face very light tan. Carina complete, prominent, broad, dorsal half ochre. Cheek light tan. Flagellomere I light brown, pedicel ochre. Flagellomere I $2.5 \times$ the length of pedicel. Arista with 6–7 dorsal and 2 ventral branches. Proboscis, clypeus, palpi cream-colored.

Notal and dorsal scutellar ground color ochre; no markings. Pleura, ventral surface



Figs. 505–510. *Zygothrica panopia*. 505. Epandrium. 506. Surstylus. 507. Aedeagus + hypandrium (ventral). 508. Spermatheca (400×). 509. ♀ terminalia (lateral). 510. Oviscape + oviprovector (ventral).

of scutellum, postnotum, and legs cream to light yellow in color. Acrostichal setulae in 6–7 irregular rows. Ventral surface of profemur with row of 4 stout, straight setae, lengths equal to femur width. Wings hyaline, with diffuse and very light brown infuscation at apex.

Epandrium dorsoventrally elongate: dorsal surface short. Ventral epandrial lobes small, adpressed. Ventral cercal lobes fused to lateral surface of hypoproctal plates. Hypoproctal plate broad, gradually tapered. Surstylus lobate, with 19 prenisetae: lateral row with 7 short, stout pegs; 2 stout, dorsal pegs; 6 medial peg and setiform ones; row of 3 lateromedial pegs. Gonopod surface finely wrinkled. Paraphysial seta stout. Basiphallus narrow, ca. $2.5 \times$ the length of distiphallus; slightly arched. Distiphallus narrow, with slight constriction near apex and with apical notch; 20–30 retrorse scales on collar.

HOLOTYPE: ♂, COLOMBIA: [Lima] Anchicaya, 1000 ft, 22–27/VII/70, J. M. Campbell, "Malaise trap" (CNC) (genitalia dissected, DAG). ThL = 1.79; HW/ThL = 1.42; ThL/WL = 0.52; C.I. = 3.54; 4-V = 1.09.

ETYMOLOGY: Latin, "another head," for the morphocryptic nature of this new broad-headed species.

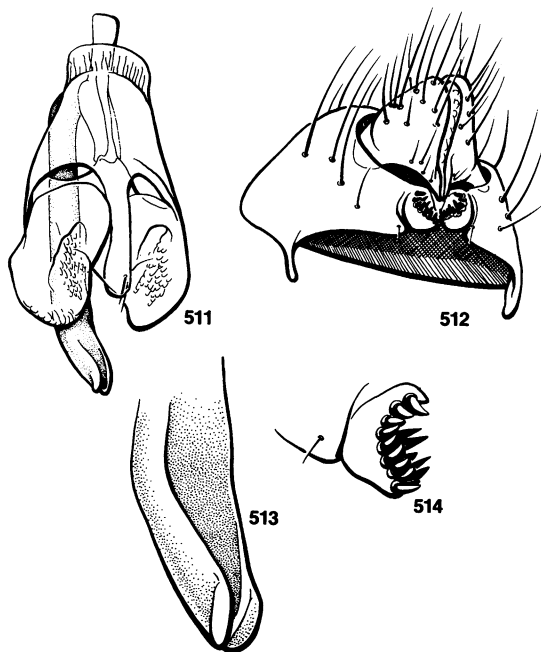
DISTRIBUTION: Colombia (fig. 522), known only from the holotype.

***Zygothrica caputrichia*, new species**

Figures 480, 511–514

DIAGNOSIS: A distinct, broad-headed species, identified by the very elongate inner vertical setae, a dark brown front on the head, loss of the posterior reclinate orbital seta, and by the possession of a very narrow, unadorned distiphallus. In addition, the posterior margin of the hypandrium bears an elongate process (♀ unknown).

DESCRIPTION: Head ground color dark brown. ♂ head broad, width ca. $2.0 \times$ the thorax width. Frontal-orbital plates dorsally $4 \times$ wider than anterior portion; dark brown. Frontal vittae narrow, black-brown. Eyes red-brown, bare, apically pointed. Ocellar triangle dark brown, nearly extended to pitilinal fissure. Proclinate orbital seta $2 \times$ length of ant. reclinate. Ant. reclinate fine, nearly lat-

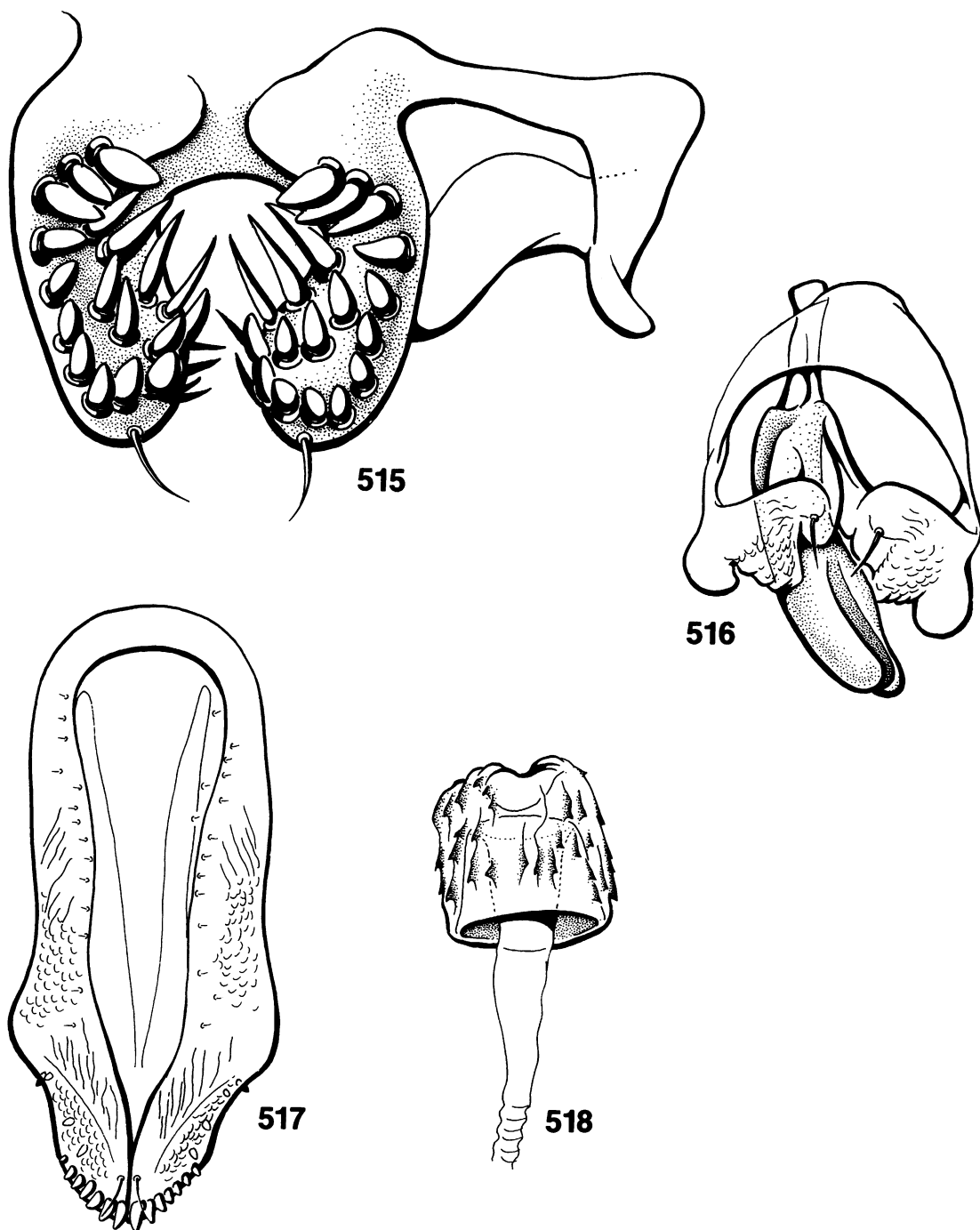


Figs. 511–514. *Zygothrica caputrichia*. Holotype. 511. Hypandrium + aedeagus (ventral). 512. Epandrium. 513. Distiphallus (ventrolateral). 514. Surstylus.

eral to proclinate. Post. reclinate not present. Inner vertical setae extremely long, lengths ca. $0.5 \times$ the head width, cruciate. Outer vertical $0.5 \times$ the length of inner vertical. Face mostly yellow; carina brown, prominent, complete, with narrow edge. Cheek and oral margin yellow. Flagellomere I length $2 \times$ pedicel. Flagellomere I dark brown, pedicel ochre. Arista with 6 dorsal and 1 ventral branch. Proboscis, palpi, and clypeus yellow.

Notum, dorsal surface of scutellum dark brown; no markings. Pleura, legs, halteres yellow; postnotum ochre. Acrostichal setulae in 6 rows. Ventral row of 4 fine, short setae on profemur. Wings hyaline. Tergites mostly dark brown.

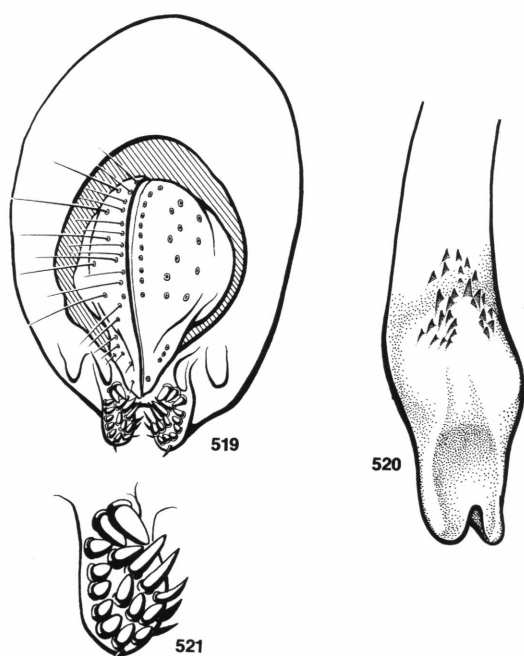
Ventral epandrial lobes very small, adpressed. Cerci conical; ventral cercal lobes lost, but with 3–4 fine setae in this area. Surstylus crescentic; small, adpressed to epandrium, with broad base; possesses 15 prenisetae, which are almost all short, stout pegs. Posterior margin of hypandrium with median projection extended to tips of paraphy-



Figs. 515–518. *Zygotherica latipanops*. **515.** Surstyli. **516.** Aedeagus + hypandrium (ventral). **517.** Oviscape (ventral). **518.** Spermatheca (400×).

sial setae. Gonopod surface finely wrinkled. Paraphysial seta stout. Basiphallus ca. $3.5\times$ the length of the aedeagal apodeme, slightly

arched. Distiphallus tapered into basiphallus, with a ventromedial groove (gonopore) ending with tiny, apical labia. No scales present.



Figs. 519–521. *Zygothrica aliucapa*. Holotype. 519. Epandrium. 520. Distiphallus (ventral). 521. Surstylus.

HOLOTYPE: ♂, PANAMA: Chiriquí, El Volcan, 8/VIII/61 S. B. Pipkin (NMNH) (genitalia dissected, DAG). ThL = 1.34; HW/ThL = 1.24; ThL/WL = 0.49; C.I. = 3.65; 4-V = 1.50.

ETYMOLOGY: Latin, “head thread,” in reference to the very elongate inner vertical setae.

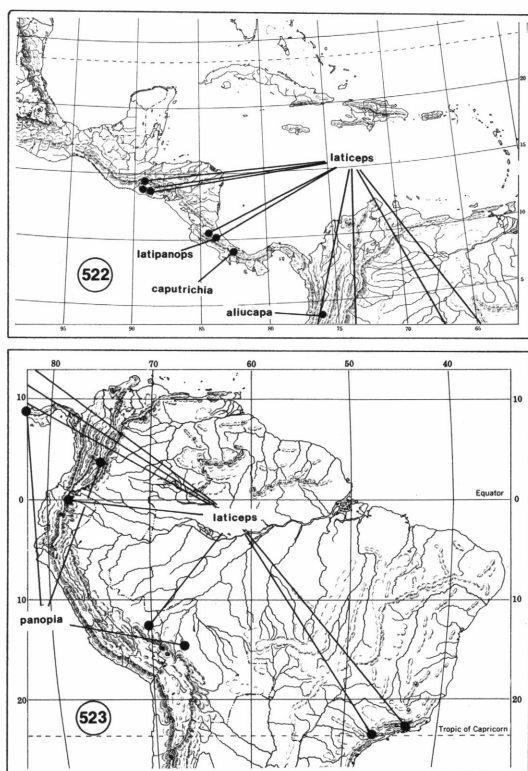
DISTRIBUTION: Northern Panama (fig. 522), known only from the holotype.

Zygothrica laticeps

Figures 460–461, 469, 479, 500–504

Zygothrica laticeps Burla, 1954: 246.

DIAGNOSIS: Besides *Z. caputrichia*, *Z. laticeps* is the smallest hypercephalic species in the *caudata* subgroup. Because of their broad sympatry, *Z. laticeps* males can be confused most easily (on external characters) with small individuals of *Z. prodispar*. These 2 species are separable on the basis of the following external characteristics: the front of *Z. prodispar* is dark brown, but yellow to ochre in *Z. laticeps*; the inner vertical is in line with the proclinate and posterior reclinate orbitals

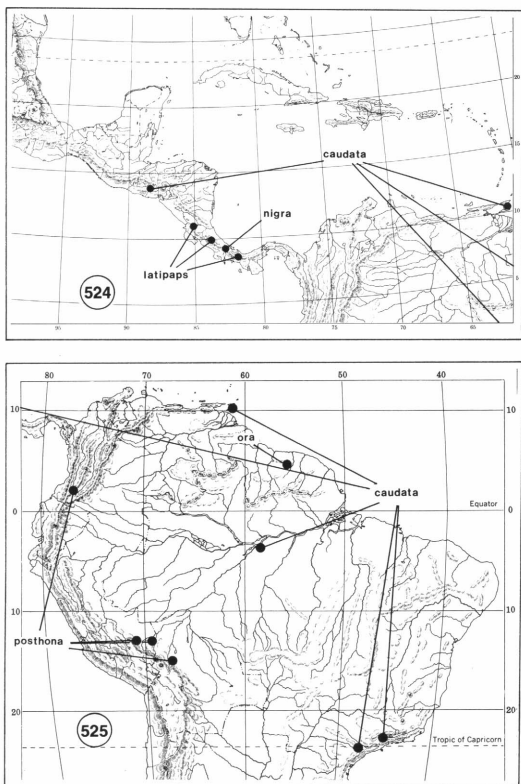


Figs. 522, 523. Distributions of some species in the *caudata* species-subgroup.

in *Z. prodispar*, but in *Z. laticeps* this seta is considerably medial to the line connecting the 2 ipsilateral orbitals. *Zygothrica prodispar* females are nearly black dorsally, whereas *Z. laticeps* females are at most light brown but usually ochre on the notum. Otherwise, genitalic characters are necessary to provide definitive identification: an aedeagus with a short, bulbous, apically tapered distiphallus, an ov scape which is lanceolate, and spermathecae which are finely wrinkled (but not papillate) are diagnostic for *Z. laticeps*.

DESCRIPTION: Burla (1954, 1956) provided descriptions of the male and female, including genitalic figures. The tergal coloration pattern is quite variable among collection sites. Tergites III and IV are entirely dark brown in ♂ and ♀ from El Salvador, but possess a large yellow, median spot each in some Brazilian specimens.

MEASUREMENTS: N = 8♂, 4♀, from various localities. ThL = 1.29 ♂ (1.16–1.31); 1.36 ♀ (1.11–1.54). HW/ThL = 1.07 ♂ (0.93–1.17);



Figs. 524, 525. Distributions of some species in the *caudata* species-subgroup.

0.84 ♀ (0.81–0.87). ThL/WL = 0.51 ♂ (0.50–0.53); 0.52 ♀ (0.47–0.57). C.I. = 2.68 (2.34–3.08); 4-V = 1.31 (1.14–1.49).

COTYPES: 2♂, BRAZIL: São Paulo, near Cantareira, H. Burla (Museu Nacional, Rio de Janeiro) (types not examined) (genitalia dissected, HB).

DISTRIBUTION: El Salvador to southern Peru, southern Brazil (figs. 522–523).

MATERIAL: BRAZIL: São Paulo, São Paulo, Ipiranga, 7/V/79, 1♀*. COSTA RICA: San José, 3000 ft, VIII/54, 1♀; Turrialba, X/55, 3♂*. ECUADOR: Pichilingue, III/58, 2♂*. EL SALVADOR: Lago de Cojutepeque, 27/X/53, 15♂*, 10♀*; La Palma, 3200 ft, VIII/54, 2♀*; San Salvador, IX/55, 1♀*. PERU: Rio Tambopata Reserve, Madre de Dios, 30 km SW Puerto Maldonado, 290 m, 12°12'S, 69°16'W, tropical moist forest, IX/19–X/10/84, 5♂*, "on *Auricularia*."

DISCUSSION: This species is placed phylogenetically close to four other species based

on the possession of a broad head in the males (apomorphy 97) and, also in the males, by the fact that the outer vertical seta lies medial to the line extended from the proclinate to the posterior reclinate orbital setae (apomorphy 109). Characters 97 and 109 may be correlated, but it is difficult to tell at present since both occur in conjunction only in this group of species. Indeed, because of the unique orbital chaetotaxy, the hypercephaly in the five species of the *caudata* subgroup may not be homologous with the hypercephaly seen in other *Zygothrica*. The hypercephalic relatives of *Z. latipaps* are comparatively rare and restricted in their distributions. Based on the altitudinal variation among the collections of *Z. laticeps*, and its broad range, it would not be surprising if several morphologically cryptic species are represented in the series that was studied. However, no morphological variation was reliably sorted among the specimens.

Zygothrica panopia, new species

Figures 466, 477, 505–510

DIAGNOSIS: Because of the apical infuscation on the wings, this species can be confused with females and occasionally with smaller males (which have moderate hypercephaly) of *Z. latipanops*. *Zygothrica panopia* has 1–2 ventral arisal branches and *Z. latipanops* 3–4 branches, and *Z. panopia* has at least some trace of light paramedian notal vittae. Females of the 2 species should be distinguished by the terminalia: the oviscape of *Z. latipanops* is considerably shorter than that of *Z. panopia*. Male genitalia of the 2 species are distinct: *Z. panopia* has a much wider and more scaled distiphallus and the hypantrium is relatively longer.

DESCRIPTION: Head broadened in ♂ ca. 1.2–1.5 × the thorax width. Frontal ground color ochre. Dorsal portion of frontal-orbital plate 3.5–4.5 × the width of the anteroventral portion; frontal-orbital plates ochre. Frontal vittae slightly darker than rest of head, dull. Ocellar triangle shiny, extended to pitilinal fissure. Eyes apically tapered; red-brown; bare. Proclimates 1.3 × the length of other orbitals. Ant. reclinate ≤ length of post. reclinate; closer to post. reclinate than to proclinate. Post-ocellars equal in length to proclimates. In ♂,

outer vertical medial to line extended between ipsilateral orbitals by distance at least equal to length of outer vertical. In ♀, outer vertical in line with orbitals. Face light yellow, including carina. Carina prominent, complete; with broad base. Cheek, genae light yellow; ♀ with light brown spot on cheek. Pedicel yellow; flagellomere I brown (darker in ♀), $2 \times$ length of pedicel. Arista with 6–7 dorsal and 1–2 ventral branches. Clypeus and proboscis yellow. Palp yellow; distal half dark brown in ♀.

Notal ground color ochre; notum with indistinct, incomplete vitta pair 2, which are slightly lighter than the background. Pleura, legs, halteres, and postnotum light yellow. Dorsal surface of scutellum light brown (darkest portion on thorax). Acrostichal setulae in 6 even rows. Row of 5 stout, ventral profemoral setae present; lengths $0.5\text{--}0.7 \times$ width of femur, slightly shorter in ♀. Wing with light brown, diffuse, apical infuscation which is heavier in ♂ (darkest in Colombian series).

In ♂ and ♀, t III–VI black-brown, each with median yellow spot decreased in size posteriad. Tergites II, VII mostly yellow; t VII with median brown spot. In ♀, t VIII dark brown, including posterolateral ramus. In ♂, epandrium black-brown, shiny; median notal spots larger than in ♀. Cerci in both sexes are dark brown. Oviscape elongate, length $3.5 \times$ the width. Apex dorsoventrally flattened; terminal margin rounded, with 7–8 small peg ovisensilla. 3 small peg ovisensilla on dorsal surface. Oviprovector scales small, dense, triangular. Posterolateral ramus of t VIII elongate; length equal to oviscape. 14–15 ventral sensilla per row on oviscape. Spermathecal capsule rectangular in lateral view; no apical indentation; distal half with dense covering of small, retrorse scales. Cerci dorsoventrally flattened.

Epandrium dorsoventrally elongate. Ventral epandrial lobe small, adpressed, but with deep excavation between lobe and posterior portion of epandrium. Ventral cercal lobes lost, fused to broad, elongate, hypoproctal plate. Surstylus pendulous, with deep basolateral excavation. Surstylus with 28–30 prenisetae, mostly stout pegs: 3–4 in dorsal row, and an even row of 8–9 small pegs laterally. 2 pairs of fleshy gonopods present: me-

dian pair large, finely wrinkled. 1 stout paraphysial seta, subtended by 3 fine ones. Aedeagus ca. $2 \times$ length of aedeagal apodeme. Distiphallus ca. equal in length to basiphallus and $3 \times$ the width. Distiphallus tapered, apex with deep notch. Fine, sparse scales on dorsal surface of distiphallus; larger, retrorse ones near collar on ventral surface.

MEASUREMENTS: N = 8♂, 5♀. ThL = 1.81 ♂ (1.66–1.94); 1.80 ♀ (1.60–2.04). HW/ThL = 0.90 ♂ (0.84–0.96); 0.85 ♀ (0.76–1.01). ThL/WL = 0.51 ♂ (0.46–0.53); 0.46 ♀ (0.40–0.53). C.I. = 4.13 (3.33–4.90); 4-V = 1.13 (1.04–1.19).

HOLOTYPE: ♂, PANAMA: Chiriquí, El Volcan, 8/VIII/61, S. B. Pipkin (NMNH) (genitalia not dissected).

ETYMOLOGY: Greek, *panops*, meaning “all seeing,” in reference to the broad heads in the male. The hypercephalic trait in male *Zygothrica* modifies vision by primarily improving the optical resolution of the frontal field.

DISTRIBUTION: Bolivia to Costa Rica; not known in the Amazon Basin (fig. 523).

MATERIAL: (all are paratypes) BOLIVIA: S. Inicua Riv., Alto Beni, 15–18/I/76, 3♂*. COLOMBIA: 30 km SW Bogotá, Tequendama Falls, 27/II–6/III/72, “dung trap,” 11♂*, 4♀*. COSTA RICA: Turrialba, III/54, 1♀*, 15–19/VII/65, 1♀*. PANAMA: Chiriquí, El Volcan, 8/VIII/62, 8♂, 1♀*.

DISCUSSION: Specimens from Colombia are considerably darker than the others, which includes a darker front (especially the ocellar triangle and frontal vittae), darker notum, the median tergal spots, and apical wing spots. Otherwise, all features indicate that these specimens are the same species as the other specimens.

Zygothrica latipanops, new species

Figures 462–463, 474, 481, 515–518

DIAGNOSIS: Because of an exceptionally broad head, males of this species would be confused with *Z. dispar* or *Z. exuberans* based only on gross external appearance. However, all 3 species are allopatric. Like *Z. dispar*, *Z. latipanops* possesses diffuse apical infuscations on the wings of the male. Male and female genitalia are distinct: the aedeagus and hypandrium are very short, and the disti-

phallus is bare and rather narrow. The ov scape is short compared to those of close relatives, and it has a rounded apical margin and prominent distolateral flanges.

DESCRIPTION: ♂ head exceptionally broad, $1.7\text{--}2.6\times$ the thorax width. Ground color of head light ochre, darker in ♀. Frontal-orbital plates ochre, dorsally expanded to $3\times$ the width of the anteroventral portion. Frontal vittae dull, same yellowish color as rest of head. Eyes apically very pointed in ♂; dull red-brown; bare. Ocellar triangle yellow, width slightly less than that of face, extended past proclimates and nearly to ptilinal fissure. Reclinate orbitals tiny (proportionally larger in less hypercephalic ♂), lengths ca. $0.3\times$ that of proclinate. Ant. reclinate lateral to proclinate by distance at least equal to ant. reclinate length. Post. reclinate posterolateral to ant. reclinate by distance ca. equal to length of ant. reclinate. Ptilinal suture dull yellow. Face entirely yellow-ochre. Carina complete, wide, prominent. Pedicel and flagellomere I yellow, light brown in ♀. Flagellomere I $2\times$ length of pedicel. Cheek, gena, back of head light yellow; occiput with brown stripe across width. Arista with 7–8 dorsal and 3–4 ventral branches. Proboscis, palp, and clypeus yellow.

Notal ground color ochre in ♂, light brown in ♀, with no distinct markings. Pleura, scutellum, postnotum, legs, and halteres yellow to ochre. Ant. dorsocentrals may be duplicated on one or both sides in ♂. Acrostichals in 6–7 irregular rows. Row of 5–6 elongate, evenly spaced, ventral profemoral setae; lengths ca. equal to width of femur, slightly shorter in ♀. Wing hyaline except for diffuse, light brown, apical infuscation which is darker in ♂.

In ♀, t II is mostly yellow, t III–VI are dark brown, each with a median yellow spot decreased in size posteriad; t VII mostly yellow with a dark median spot; t VIII dorsoventrally elongate, dark brown, glassy, with dark brown laterotergal rami. Rami short, ca. $\frac{1}{2}$ length of ov scape. Median yellow spots larger in ♂. Ov scape with prominent lateroapical flanges; length ca. $2.5\times$ the width. Apex flat, with rounded margin bearing 7 ovisensilla pegs per side. Dorsolateral surface of ov scape apex with 3 small ovisensilla pegs per side; ventrally, with 14–15 fine ventral sen-

silla per row. Oviprovectator scales dense, small, triangular. Ventrolateral surface of ov scape apex with very fine scales.

Epandrium dorsoventrally very elongate, yellow. Ventral epandrial lobes small, adpressed; with 2–3 setulae. Cerci with rounded apical margin, yellow. Ventral cercal lobes lost; hypoproctal plate small. Surstylus pendulous, bears 5–6 setiform prensisetae (medial), 15–16 stout peg prensisetae (3 dorsals, 2–3 medials, 6 laterals, 4–5 apicals). Hypandrium and aedeagus short. 2 pairs of lobate gonopods present; medial pair finely striate and scaled. Aedeagus ca. $2\times$ the length of the aedeagal apodeme. Basiphallus short, gradually joined to the slightly wider distiphallus. Distiphallus glabrous; with a deep dorsal-apical notch; ca. $1.5\times$ the width of the basiphallus.

MEASUREMENTS: N = 3♂, 4♀. ThL = 1.91 ♂ (1.88–1.95); 1.98 ♀ (1.94–2.16). HW/ThL = 1.71 ♂ (1.30–2.21); 0.92 ♀ (0.90–0.97). ThL/WL = 0.51 (♂ + ♀) (0.50–0.53). C.I. = 3.52 (2.99–4.02); 4-V = 1.14 (0.91–1.22).

HOLOTYPE: ♂, COSTA RICA: La Suiza [de Turrialba], [I/24], Pablo Schild (NMNH) (genitalia dissected, DAG). ThL = 1.90; HW/ThL = 2.09; ThL/WL = 0.52; C.I. = 3.34; 4-V = 1.22.

ETYMOLOGY: Greek, derived from *panops* ("all seeing") and *laticeps*, for *Z. laticeps*, which is a widespread hypercephalic relative.

DISTRIBUTION: Costa Rica (fig. 522).

MATERIAL: (all are paratypes) COSTA RICA: Turrialba, I/24, 14♂*, 4♀*; VII/56, 1♂*; 15–19/VII/65, 1♂*.

DISCUSSION: This large *Zygothrica* would be a superb subject for a behavioral study. The males have the broadest heads of any *Zygothrica* and are, therefore, probably very aggressive and highly territorial. In addition, the ventral row of profemoral setae are very long in males. The light infuscation on the wing apex is darker in males, which suggests that the wings are vibrated extensively during encounters with other flies.

REFERENCES CITED

- Ashburner, M.
1981. Entomophagous and other bizarre Drosophilidae, pp. 395–429. In M. Ashburner et al. (eds.), The genetics and bi-

- ology of *Drosophila*, vol. 3a. London: Academic Press.
- Bastock, M., and A. Manning
1955. The courtship of *Drosophila melanogaster*. Behaviour, 8: 85–111.
- Bock, I. R.
1982. Drosophilidae of Australia. V. Remaining genera and synopsis (Insecta: Diptera). Australian J. Zool., suppl. ser., 89: 1–164.
- Boz [Charles Dickens]
1938. The life of Joseph Grimaldi. London.
- Bristowe, W. S.
1924. Notes on the habits of insects and spiders in Brazil. Trans. Entomol. Soc. London, 1924: 475–504.
- Burla, H.
1954. Study on the polymorphism in *Zygothrica dispar* and *Z. prodipar*, and description of *Z. laticeps* sp.n. (Drosophilidae, Diptera). Arq. Museu Para., 10: 232–252.
1956. Die Drosophiliden-Gattung *Zygothrica* und ihre Beziehung zur *Drosophila*-Untergattung *Hirtodrosophila*. Mitt. Zool. Mus. Berlin, 32: 189–321.
- Carson, H. L.
1971. The ecology of *Drosophila* breeding sites. H. L. Lyon Arbor. Lect., 2: 1–27.
- Cordeiro, A. R.
1952. *Drosophila (Hirtodrosophila) caxiensis*, a new species of fungus-feeding fly from Brasil. Dusenja, 3: 303–308.
- Dennis, R. W. G.
1970. Fungus flora of Venezuela and adjacent countries. Kew Bull. Add. Ser. III.
- Duda, O.
1925. Die costaricanischen Drosophiliden des ungarischen National-Museums zu Budapest. Ann. Musei Nat. Hung., 12: 149–221.
1927. Die südamerikanischen Drosophiliden (Dipteren) unter Berücksichtigung auch der anderen neotropischen sowie der nearktischen Arten. Arch. Naturg., 91(A 11–12): 1–228.
- Ewing, A.
1983. Functional aspects of *Drosophila* courtship. Biol. Rev., 58: 275–292.
- Farris, J.
1982. The logical basis of phylogenetic analysis. In N. I. Platnick and V. A. Funk (eds.), Advances in cladistics, vol. 2. Proceedings of the Willi Hennig Society, pp. 7–36. New York: Columbia Univ. Press.
- Gordh, G., and J. C. Hall
1979. A critical point drier used as a method of mounting insects from alcohol. Entomol. News, 90: 57–59.
- Grimaldi, D.
1988. Relicts in the Drosophilidae (Diptera). In J. K. Liebherr (ed.), Zoogeography of the Caribbean insect fauna. Cornell Univ. Press.
- Grodowitz, M. J., J. Krchma, and A. B. Broce
1982. A method for preparing soft bodied larval Diptera for scanning electron microscopy. Kansas Entomol. Soc., 55: 751–753.
- Heed, W. B., H. L. Carson, and M. S. Carson
1960. A list of flowers utilized by drosophilids in the Bogotá region of Colombia. Dros. Inf. Serv., 34: 84–85.
- Hendel, F.
1913. Neue Drosophiliden aus Südamerika und Neuguinea. Entomol. Mitt., 2: 386–390.
1936. Ergebnisse einer zoologischen Sammelreise nach Brasilien, insbesondere in das Amazonasgebiet, ausgeführt von Dr. H. Zerny. X. Diptera: Muscidae acalyptratae (excl. Chloropidae). Ann. Naturh. Mus. Wien, 47: 61–106.
- Hennig, W.
1950. Grundzüge einer Theorie der Phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.
1965. Phylogenetic systematics. Ann. Rev. Entomol., 10: 97–116.
- International Commission on Zoological Nomenclature
1985. International Code of Zoological Nomenclature, 3rd ed. Berkeley: Univ. of California Press.
- Loew, H.
1873. Monographs of the Diptera of North America. III. Smithsonian. Misc. Coll., 11: 1–351.
- MacCreagh, G.
1985. White waters and black, 3rd ed. Univ. of Chicago Press.
- Maddison, W., M. J. Donoghue, and D. R. Maddison
1984. Outgroup analysis and parsimony. Syst. Zool., 33: 83–103.
- Malloch, J. R.
1934. Drosophilidae. In Insects of Samoa, 6(8): 267–312.
- Malogolowkin, C.
1952. Notas sobre *Zygothrica dispar* (Diptera, Drosophilidae). Rev. Bras. Biol., 12: 455–457.
- McAlpine, J. F.
1981. Morphology and terminology—adults. In J. F. McAlpine et al., Manual of

- Nearctic Diptera, vol. 1, chap. 2. Agriculture Canada Monograph No. 27. Ottawa: Minister of Supply and Services.
- Meigen, J. W.
1803. Versuch einer neuen Gattungseintheilung der europäischen zweiflügeligen Insekten. Mag. Insek., 2: 259–281.
- Okada, T.
1968. Systematic study of the early stages of Drosophilidae. Tokyo: Bunka Zugsisha Co., Ltd. 188 pp.
1984. The genus *Collessia* of Japan (Diptera: Drosophilidae). Proc. Jap. Soc. Syst. Zool., 29: 57–58.
- Parsons, P.
1977. Lek behavior in *Drosophila* (*Hirtodrosophila*) *polypori* Malloch—an Australian rainforest species. Evolution, 31: 223–225.
- Paterson, H. E. H.
1978. More evidence against speciation by reinforcement. S. Afr. J. Sci., 74: 369–371.
- Pipkin, S. B., R. L. Rodríguez, and J. León
1966. Plant host specificity among flower-feeding neotropical *Drosophila* (Diptera: Drosophilidae). Am. Nat., 100: 135–156.
- Ryvarden, L., and I. Johansen
1980. A preliminary polypore flora of East Africa. Oslo, Norway: Fungiflora. 636 pp.
- Spieth, H. T.
1968. Evolutionary implications of sexual behavior in *Drosophila*. Evol. Biol., 2: 157–193.
1985. Courtship behavior of the Hawaiian picture-winged *Drosophila*. Univ. Cal. Publ. Entomol., 103: 1–92.
- Steyskal, G.
1979. Biological, anatomical, and distributional notes on the genus *Callopietomyia* Hendel (Diptera: Otitidae). Proc. Entomol. Soc. Wash., 81: 450–455.
- Sturtevant, A. H.
1916. Notes on North American Drosophilidae with descriptions of twenty-three new species. Ann. Entomol. Soc. Am., 9: 323–343.
1920. The dipterous genus *Zygothrica* of Wiedemann. Proc. U.S. Natl. Mus., 58: 155–158.
1921. The North American species of *Drosophila*. Carnegie Institution of Washington, publ. no. 301.
- Takada, H.
1976. Distribution and population constitution of *Drosophila* in southeast Asia and Oceania. III. The genus *Zygothrica* with description of three new species. Kontyû, 44: 65–72.
- Throckmorton, L. H.
1962. X. The problem of phylogeny in the genus *Drosophila*. Univ. Tex. Publ., 6205: 207–373.
1965. Similarity versus relationship in *Drosophila*. Syst. Zool., 14: 221–236.
1975. The phylogeny, ecology, and geography of *Drosophila*. In R. C. King (ed.), Handbook of genetics, vol. 3, pp. 421–469. New York: Plenum.
- Vilela, C. R.
1984. Occurrence of the *Drosophila flavopilosa* species group (Diptera, Drosophilidae) in the state of São Paulo (Brazil) with description of one new species. Rev. Bras. Zool., 2: 63–69.
- Villa, J.
1980. “Frogflies” from Central and South America with notes on the other organisms of the amphibian egg microhabitat. Brenesia, 17: 49–68.
1985. Biology of a neotropical glass frog, *Centrolenella fleischmanni* (Boettger), with special reference to its frogfly associates. Milwaukee Publ. Mus. Contrib., 55: 1–60.
- Watrous, L., and Q. D. Wheeler
1981. The out-group comparison method of character analysis. Syst. Zool., 30: 1–11.
- Wheeler, M. R.
1952. XI. The Drosophilidae of the Nearctic Region, exclusive of the genus *Drosophila*. Univ. Tex. Publ., 5204: 162–218.
1968. XXI. Some remarkable new species of neotropical Drosophilidae. Univ. Tex. Publ., 6818: 429–442.
- Wiedemann, C. R. W.
1830. *Achias* Diptorum Genus. Kilias Hol-satorum.
- Williston, S. W.
1896. XI. On the Diptera of St. Vincent (West Indies). Trans. Entomol. Soc. London, 1896: 253–446.

