

No. 6885

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T. OKADA

*To Toyohi Okada,
with best wishes, and many
thanks for all of your help.*

- David

A PHYLOGENETIC,
REVISED CLASSIFICATION
OF GENERA IN THE
DROSOPHILIDAE (DIPTERA)

DAVID A. GRIMALDI

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
NUMBER 197
NEW YORK : 1990

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A PHYLOGENETIC,
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OF GENERA IN THE
DROSOPHILIDAE (DIPTERA)

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 197, 139 pages, 79 illustrations, 11 tables, 3 appendices

Issued October 30, 1990

Price: \$12.55 a copy

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ABSTRACT

A phylogenetic system and classification of most genera and subgenera of the Drosophilidae are proposed that incorporate tribes, subtribes, infratribes, and genus groups. The new classification is based on a cladistic analysis using the computer parsimony program HENNIG86 and 217 adult morphological characters for a representative set of 120 species. A more complete matrix is provided, with 160 species in most genera and subgenera of the family.

The history of drosophilid classification is reviewed, and the relevance of morphological (vs. molecular) data in phylogenetic reconstruction is briefly discussed. Position of the family in the superfamily Ephydroidea is examined and based on previously published data and new characters. The family Drosophilidae is the sister group to the Curtonotidae; this pair is the sister group to the rest of the Ephydroidea (Diastatidae, Campichoetidae, Camillidae, and Ephydriidae). The Drosophilidae are monophyletic and diagnosed as possessing two basal costal wing vein breaks, a lateral seam in the pedicel, three pairs of frontal orbital setae (1 being proclinate, others reclinate), abdominal spiracle pairs VI + VII lying at base of tergite VI in males, sternite VI and tergite VII lost in males, small basal-medial wing cell lost (rederived in some taxa), and minute spines on the mesal surface of the fore femur lost. Each of the 217 characters is described and most are illustrated in detail; many are newly discovered, including features from the proboscis to the male and female terminalia.

The traditional subfamily classification of the Steganinae and Drosophilinae is preserved, based on new, apomorphic evidence. An alternative classification to that of Okada (1989) is proposed, with 4 tribes, 6 subtribes, 2 infratribes, and 13 genus complexes/groups (informal categories), and all but 5 genera and subgenera are classified within these taxa. In addition, the *Drosophila* subgenera *Hirtodrosophila*, *Lordiphosa*, and *Scaptodrosophila* are each removed from that genus and elevated to generic rank. The Hawaiian drosophilids formerly placed in the subgenus *Drosophila* were found not to belong to this genus. Genus *Idiomya*, new status, is used to include this large, obviously monophyletic group of Hawaiian endemic species, as well as the genera *Ateledrosophila* and *Nudidrosophila*. The closest relative of *Idiomya* sensu lato appears to be the *Zygothrica* genus group (including *Hirtodrosophila*, *Mycodrosophila*, *Paramycodrosophila*, *Paraliodrosophila*, and *Zygothrica*). *Scaptomyza*, including the Hawaiian species in this genus, is monophyletic; *Drosophila* (*Engiscaptomyza*) is most closely related to *Scaptomyza*.

The cladogram based on morphological data is compared to trees of Throckmorton, Okada, and several based on molecular data for a smaller set of drosophilid taxa. Inconsistencies between hypotheses are discussed. All higher-level generic group taxa and new genera are diagnosed.

INTRODUCTION

HISTORY OF DROSOPHILID CLASSIFICATION

When W. E. Castle (1906) first reported the potential use of *Drosophila melanogaster* Meigen in understanding genetics, he was certainly underestimating the situation. In the eight decades since then *Drosophila* has become the premier experimental organism for eukaryotic biology, particularly in genetics and development. It might well be said that it was the development of *Drosophila* genetics which fueled Dobzhansky, Mayr, and others into developing their "modern synthesis" view of evolution, particularly as regards modes and mechanisms of speciation. Unfortunately, it is precisely the devout attention lavished on genetics and evolutionary

mechanisms that distracted from synthetic work being done on the major phylogenetic patterns in the family. Until very recently (Okada, 1989), no subfamily or other formal generic groups have been proposed in the family since Duda (1924) proposed the subfamily Steganinae. Although Duda's work was probably the most comprehensive ever on the Drosophilidae, it is Alfred H. Sturtevant who apparently has had the most impact on drosophilid classification.

Sturtevant, more than anyone else, deserves the recognition of being the "founder of drosophilology." His first major paper described the linear arrangement of genes along the chromosome (Sturtevant, 1913), which was his undergraduate thesis. The great majority of his some 150 publications deal with

Mendelian genetics in *Drosophila*, but in 1921 he published the first comprehensive taxonomic treatment of New World drosophilids. His interest in ants (e.g., 1925a) and especially in other acalyptrate flies, resulted in about 20 taxonomic publications, including such important works as the classic study on comparative morphology of reproductive organs in acalyptrates (Sturtevant, 1925b, 1926), the subgeneric classification (still used) of the genus *Drosophila* (Sturtevant, 1939, 1942), and a revision of North American Ephydriidae (Sturtevant and Wheeler, 1954) and Periscelididae (Sturtevant, 1954). In the 1942 paper, his matrix and analysis of derived features in *Drosophila* predates the analytic technique of Hennig (especially Hennig, 1953, which is probably the original formulation of cladistics). Despite Sturtevant's very broad background with Diptera, he still placed in the Drosophilidae, among other genera, *Aulacigaster* (now in the Aulacigastridae), *Apsinota* and *Curtonotum* (now in the Curtonotidae), and *Camilla* (now in the Camillidae) (Sturtevant, 1921). The convention at the time was to include in the family small acalyptrates that possessed a proclinate orbital seta and a plumose or dense and long-pubescent arista, such as *Asteia*, *Sigaloessa*, and *Stenomicro* (Aldrich, 1905; Williston, 1896), as well as *Planinasus* and *Diastata* (Curran, 1934).

The dominant feature of drosophilid taxonomy today is the preponderance of regional revisions and faunal treatments. Among the most important of these are the following: Duda (1925, 1926, 1935), on the Costa Rican, New World [especially Neotropical], and Palearctic species, respectively; Patterson (1943), on southwestern U.S. species; Wheeler (1952), on the non-*Drosophila* species of drosophilids in the Nearctic Region; Burla (1954), on the species of Ivory Coast, Africa; Okada (1956, 1966, many papers thereafter and cited later), on the species of Japan, Nepal, and his many revisions of genera dealing with Pacific Ocean species; Wheeler and Takada (1964), on the species of Micronesia; Bock (1976 and thereafter) in his series "The Drosophilidae of Australia"; Brncic (1957), on the Chilean species; and the papers by Hardy on the large fauna of endemic Hawaiian species (Hardy, 1965, and thereafter). Each of these faunal treatments is important

for the new species and genera described in it, but they serve little in understanding the relationships among the genera of the world and other major groups of species. Indeed, all of these studies incorporate genera into the two traditional subfamilies, the Steganiinae and Drosophilinae. As Bock (1981: 4) wrote: "It is less than satisfying to a taxonomist to be able to do no better than diagnose any taxon by a series of 'usuallies,' but if the subfamilies [of Drosophilidae] are not to be ignored altogether there is no present alternative. The classification of the Drosophilidae clearly merits revision, a major undertaking which could hardly be attempted on the basis of one regional fauna." Wheeler's catalog (1981, 1986) has assembled all valid names and original citations of the world species of Drosophilidae into the current classification (see below). It is probably the most important work on the family, and should facilitate worldwide revisions of monophyletic taxa.

The papers of Throckmorton (1962, 1966, and especially 1975) are undoubtedly the most cited ones with regard to phylogenetic relationships among genera of the Drosophilidae. The 1975 paper deals mostly with subgenera and species groups of *Drosophila*. Unfortunately, it is very difficult to evaluate, as none of the characters presented in 1962 and 1966, on which the branching diagrams are based, were included; also, some of the branching sequences in the trees presented in these three papers differ. In this paper I will reconstruct Throckmorton's (1975) trees from the morphological features presented in 1962 and 1966, and then compare my results with his. The import of Throckmorton's findings is that paraphyly is widespread among drosophilid groups. For example, he views the genera *Chymomyza*, *Hypselothyrea*, *Liodrosophila*, and *Neotanygastrella* as most closely related to several species groups in the subgenus *Sophophora* of *Drosophila* (there are eight other genera which he stated as being most closely related to groups within various other subgenera of *Drosophila*). The nominal genus in families of many organisms is often paraphyletic because, traditionally, genera subsequently designated to a family had species with very peculiar features, and phenetically would appear completely unrelated

to described taxa. The result is a nominal genus devoid of a diagnosis, or a nominal diagnosis devoid of derived features.

The paraphyly that Throckmorton hypothesized is substantiated by further evidence. However, if the classification of the Drosophilidae is to reflect phylogenetic relationships, then the genus *Drosophila* would apparently need dismembering to bring some subgenera to generic and higher levels, or many genera would need to be sunk within this already huge genus of 1600 species. It is my view that a name should allow predictability, falsifiability, and inference; this is achieved only if the names reflect phylogenetic relationships. True, cladistic classifications can be exceedingly cumbersome to use, for the large number of hierarchical taxa that can be proposed (cf. Boudreaux, 1979; Griffiths, 1972), but convenience is no substitute for accuracy. Unfortunately, Throckmorton appears to believe in a reality of "paraphyletic groups," which is doubtless one reason why Throckmorton never proposed a new classification that reflected his hypotheses on relationships. For example: "Those [species groups] that have diverged in their external and traditionally diagnostic features are classified as other genera. Where these same features have remained unchanged, and in spite of other changes, the forms are classified as *Drosophila*" (Throckmorton, 1965: 233).

My work was conceived and undertaken for several reasons. First, to test Throckmorton's hypotheses about higher relationships in the family (e.g., among genera) by producing a cladogram based on an independent set of adult morphological characters. Adult morphology, which can be diagnostically informative and convenient (see below), was hardly treated by Throckmorton. Secondly, to devise a classification emphasizing phylogenetic relationships among higher monophyletic groups. Thirdly, to divide the family into a hierarchy of monophyletic groups, as a means of taxonomically handling various aspects of the world fauna of the Drosophilidae. Below is the present classification of the genera of the world. The genera *Drosophilella* Duda and *Thyrecephala* Okada are omitted, since these were recently synonymized by Okada.

TRADITIONAL CLASSIFICATION OF GENERA [mostly from Wheeler (1981, 1986)]

Subfamily STEGANINAE

Genus *Acletoxenus* Frauenfeld, 1868
Amiota Loew, 1862

Subgenus *Amiota*

Asiphortica Okada, 1971
Erima Kertész, 1899
Paraphortica Duda, 1934
Phortica Schiner, 1862
Sinophthalmus Coquillett, 1904
Apenthecia Tsacas, 1983
Cacoxenus Loew, 1858
Cacoxenus
Gitonides Knab, 1914
Paracacoxenus Hardy, 1960
Crincosia Bock, 1982
†*Electrophortica* Hennig, 1965
Eostegana Hendel, 1913
Gitona Meigen, 1830
Leucophenga Mik, 1886
Leucophenga
Neoleucophenga Oldenberg, 1915
Luzonimyia Malloch, 1926
Mayagueza Wheeler, 1960
Paraleucophenga Duda, 1924
Pararhinoleucophenga Duda, 1924
Pseudiasata Coquillett, 1908
Hyalistata Wheeler, 1960
Pseudiasata
Pyrgometopa Kertész, 1901
Rhinoleucophenga Hendel, 1917
Soederbomia Hendel, 1938
Stegana Meigen, 1830
Ceratostylus Enderlein, 1922
Orthostegana Hendel, 1913
Oxyphortica Duda, 1923
Parastegana Okada, 1971
Pseudostegana Okada, 1978
Stegana
Steganina Wheeler, 1960
Trachyleucophenga Hendel, 1917

Subfamily DROSOPHILINAE

Ateledrosophila Hardy, 1965
Baedrosophila Wheeler & Takada, 1964
Balara Bock, 1982
Bialba Bock, 1989
Calodrosophila Wheeler & Takada, 1964
Celidosoma Hardy, 1965
Chymomyza Czerny, 1903
Cladochaeta Coquillett, 1900
Collessia Bock, 1982
Dettopsomyia Lamb, 1914
Diathoneura Duda, 1924
Calatila Strand, 1927
Diathoneura

Dicladochaeta Malloch, 1932
Drosophila Fallén, 1823
Antopocerus Hardy, 1965
Chusqueophila Brncic, 1957
Dichaetophora Duda, 1940
Dorsilopha Sturtevant, 1942
Drosophila
Dudaica Strand, 1943
Engiscaptomyza Kaneshiro, 1969
Hirtodrosophila Duda, 1923
Lordiphosa Basden, 1961
Phloridosa Sturtevant, 1942
Psilodorha Okada, 1968
Scaptodrosophila Duda, 1923
Siphlodora Patterson & Mainland, 1944
Sophophora Sturtevant, 1939
Spinodrosophila Duda, 1924
Grimshawomyia Hardy, 1965
Hypselothyrea Meijere, 1906
Deplanothyrea Okada, 1980
Hypselothyrea
Jeannelopsis Séguy, 1938
Liodrosophila Duda, 1922
Lissocephala Malloch, 1929
Marquesia Malloch, 1932
Microdrosophila Malloch, 1921
Microdrosophila
Oxystyloptera Duda, 1924
†*Miomyia* Grimaldi, 1987
Mulgravea Bock, 1982
Mycodrosophila Oldenberg, 1914
Neorhinoleucophenga Duda, 1924
Neotanygastrella Duda, 1925
Nesiodrosophila Wheeler & Takada, 1964
Nudidrosophila Hardy, 1965
Paraliodrosophila Duda, 1925
Paramycodrosophila Duda, 1924
Phorticella Duda, 1923
Phorticella
Xenophorticella Okada & Carson, 1983
Poliocephala Bock, 1989
†*Protochymomyza* Grimaldi, 1987
Samoia Malloch, 1934
Scaptomyza Hardy, 1849
Alloscaptomyza Hackman, 1962
Boninoscaptomyza Okada, 1973
Bunostoma Malloch, 1932
Dentiscaptomyza Takada, 1965
Elmomyza Hackman, 1982
Euscaptomyza Séguy, 1938
Exalloscaptomyza Hardy, 1965
Hemiscaptomyza Hackman, 1959
Lauxanomyza Tsacas & Cogan, 1976
Macrosaptomyza Frey, 1954
Mesoscaptomyza Hackman, 1959
Metascaptomyza Hackman, 1959
Parascaptomyza Duda, 1924
Rosenwaldia Malloch, 1934

Scaptomyza
Tantalia Malloch, 1938
Trogloscaptomyza Frey, 1954
Sphaerogastrella Duda, 1922
Sphyrnoceps Meijere, 1915
Styloptera Duda, 1924
Tambourella Wheeler, 1957
Titanochaeta Knab, 1914
Zaprionus Coquillett, 1901
Aprionus Okada & Carson, 1983
Zaprionus
Zygothrica Wiedemann, 1830
 Genera of Uncertain Affinity
Apacrochaeta Duda, 1927
Colocasiomyia Meijere, 1914
Laccodrosophila Duda, 1927
Pseudocacoxenus Duda, 1925
Zapriothrica Wheeler, 1956

†indicates amber fossil taxa.

METHODS

The original effort in assembling a synoptic collection of the family was to obtain the type species of each genus and subgenus, as was done in the recent comprehensive study by Kitching (1987) on the plusiine noctuids. This later proved somewhat difficult, because not all type species are diagnostic of the taxa which they represent, and some type species are too rare to use as synoptic material.

Nonetheless, the type species was used where it was logistically possible and taxonomically useful; otherwise, a species was chosen as being a typical representative of the genus/subgenus (e.g., being obviously within the original diagnosis of the taxon and/or not too highly modified). Where a large series of paratypes existed, those specimens were used in the synoptic collection in order to insure proper identifications. In other cases, material was compared to the respective holotype, particularly where the species was of uncertain identity or even possibly undescribed. In the latter case I used the designation "sp." The species that were studied appear on the cladograms.

The phylogenetic computer algorithm package, HENNIG86, version 1.5 (Farris, 1988) was used to analyze the large data matrix of drosophilid genera. The program was chosen because of its efficiency, calculation time, options of analyses, character weighting, multiple character states, tree interaction

capabilities, and storage space (e.g., number of characters and taxa that could be analyzed, number of trees that could be stored in memory). Briefly, the program occupies only 49K of memory, and apparently can analyze (depending on analysis options and fit of the data) 180 taxa and 999 characters. Ten states per character are allowed, and weights 0–100 can be assigned to each character. HENNIG86 was run on an IBM PS/2-80 (80386, 16 MHz system). Comparison of HENNIG86 to other available cladistic programs was made by Platnick (1987, 1989) and also reviewed by Fitzhugh (1989), to which readers are referred for specific information on running and performance ability of the program. The much smaller matrix of ephydroid families was originally analyzed (prior to the release of HENNIG86, 1.5) using the PAUP program, version 2.4.1. Similar results were later obtained using HENNIG86.

All data in this paper derives from adult morphology. This does not imply that larval morphology (e.g., Grimaldi, 1988), chromosomal, molecular, and behavioral information cannot be applied to such a study. The choice was made because adult morphology is easily preserved and can be surveyed more comprehensively (by someone with a penchant for microscopy and minute dissection) than any of the other phenotypic levels of characters mentioned above. Also, adult morphology can be very complex and exceedingly diverse, as attested to by the use of 217 characters in this study. Explicit rules for homology decisions in morphological studies are usually more feasible than for many molecular studies; in this case, relative size, shape, position, and ornamentation were used in initially assessing whether or not a structure in two species was homologous. For molecular biologists, it is important to remember that, in a study such as this one, the expressions of undoubtedly thousands of genes have been surveyed. For example, shape of the epandrium ("genital arch") in close relatives of the *Drosophila melanogaster* species subgroup is controlled by at least four to five loci (Coyne, 1983). Val (1977) had studied the genetics of head shapes in two closely related Hawaiian species, *Drosophila heteroneura* and *D. silvestris*. In a reanalysis of her data, Templeton (1977) found that be-

tween 9 and 10 loci (depending on the method of estimation) were involved in head shape. Since Templeton assumed free recombination among all the loci in his estimate (some are actually very likely to be linked), this is therefore a minimum estimate [Lande (1981) also reanalyzed Val's data and concluded that between six and eight "genetic factors" contributed to head shape]. The number and arrangement of rows of male foretibial setae in these same two species is controlled by at least three loci (Carson and Lande, 1984). Biologists should not conclude that the use of morphology is an antiquated approach simply because it has been the traditional approach in insect systematics. Contrary to what may have been implied in popular circuits, morphologically based cladograms are as much a test of biochemically based ones as is the reverse situation (e.g., Novacek, 1985; McKenna, 1987; Wyss et al., 1987). Toward the end of this paper I evaluate some biochemically based trees with morphological evidence.

ACKNOWLEDGMENTS

Besides the material in the AMNH collection that was used in this study, material was borrowed from the following institutions, and the help of the respective curators is gratefully appreciated: Smithsonian Institution (Wayne Mathis), British Museum (Natural History) (John Chainey, Brian Pitkin), Bishop Museum (Neal Evenhuis), Tokyo Metropolitan University (Toyohi Okada), Univ. of Texas collection (now at the AMNH) (Marshall Wheeler). In addition, Mr. Andrew Simon and Ms. Peling Fong are thanked for their help in preparing the scanning electron micrographs. My colleagues at the AMNH, Jim Miller and Lee Herman, read the manuscript and provided useful comments on it, as did Gerhard Bächli (University of Zurich), Ian Bock (La Trobe University, Australia), Rob DeSalle (Yale University), Wayne Mathis (Smithsonian Institution), Shane McEvey (CNRS, Paris), Toyohi Okada (Tokyo), and Hampton Carson and Ken Kaneshiro (University of Hawaii). Greg Spicer (Linus Pauling Institute) examined the portions dealing with molecular data. Norman Platnick ran several data sets on PAUP for me, oriented

me to the program HENNIG86, and was very helpful in his general support. Julian Stark, AMNH Scientific Assistant, deserves special thanks for diligently spending many hours

with HENNIG86 analyses, and Allma Edwards helped with word processing and figure labels.

RESULTS

POSITION OF THE DROSOPHILIDAE IN THE SUPERFAMILY EPHYDROIDEA

Several studies have addressed the question: What is the sister group of the Drosophilidae? Two that I will deal with here are the Cyclorrhaphan phylogeny study by Griffiths (1972) and the study by Chandler (1987); they discuss and build upon the work of Hennig (1958, 1973), so I will not summarize Hennig's work here. Griffiths and Chandler presented only matrices of character states, not a cladogram. In attempting to derive a cladogram of the ephydroid families, I examined the characters on the matrices in both papers, revised and/or added characters, and ran a PAUP analysis (Phylogenetic Analysis Using Parsimony, version 2.4.1, courtesy of David L. Swofford) on that data. A tree was then selected based on several preferred character transformations. First I will present a discussion of the characters used in the phylogenetic analysis, then the cladograms and final conclusions. I then compare the results of these analyses to the most recent hypothesis on ephydroid relationships, that of McAlpine (1989). Character numbers preceded by a C are those referred to by Chandler; the ones preceded by G are Griffiths' numbers; the taxa for which there is agreement between the two studies are boldfaced. Risidae, a small family proposed originally by Papp in 1977, was obviously not included in Griffiths' 1972 study; since the family may be synonymous with Ephydridae (Chandler, 1987), reference to it is not crucial in understanding ephydroid phylogeny, but it is included here for completeness. Note that McAlpine (1989) did not place the Risidae even in the Ephydroidea.

C-1 (no G). Proclinate orbital seta is anterior and lateral to the reclinate orbitals (plesiomorphically, it is at the same level or posterior to the [anterior] reclinate and medial

to or in line with the reclinate[s]). Found in the Curtonotidae, Camillidae, and Drosophilidae according to Chandler.

G-1 (no C). The "second antennal article" (pedicel) has a cleft on the lateral surface. Found in all five ephydroid families examined by Griffiths, and so it would be a synapomorphy for the Ephydroidea.

C-2 (G-7). Presence of an angulate anal cross vein (a straight cross vein being plesiomorphic). According to Chandler, found in the Diastatidae and **Campichoetidae**; according to Griffiths, found in the Curtonotidae, **Campichoetidae**, and Ephydridae.

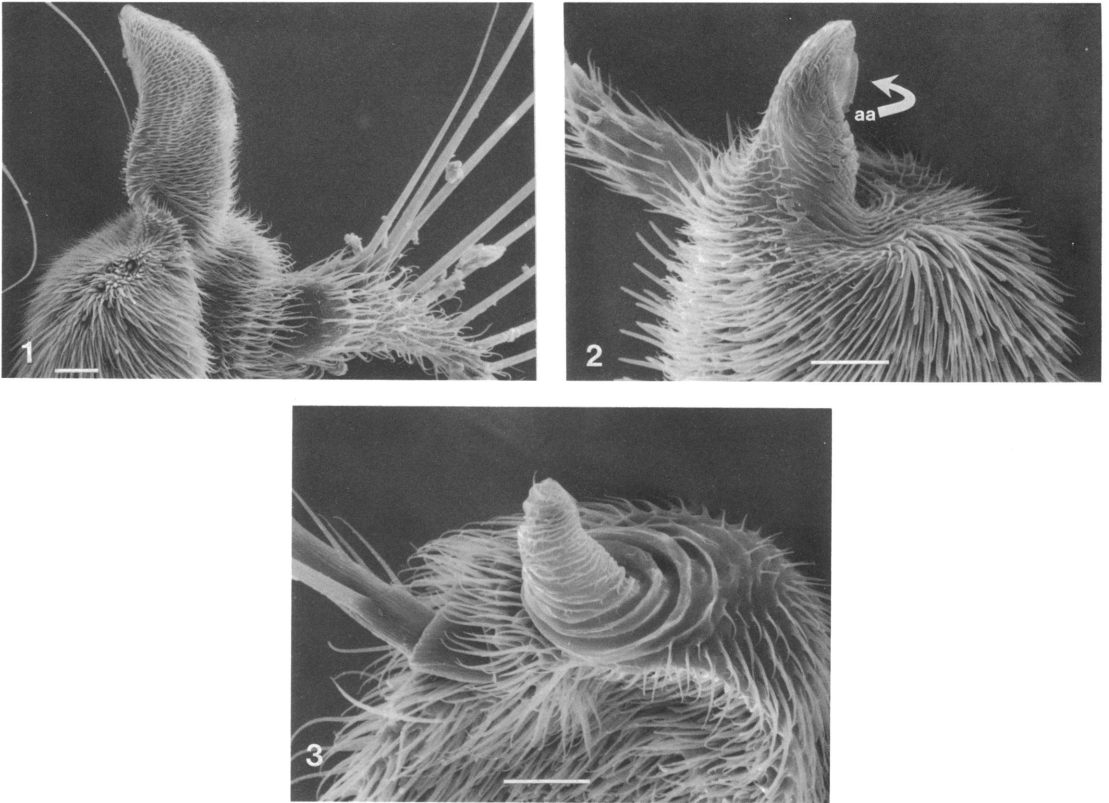
C-2a (G-8). The anal cell and anal cross vein are lost. According to Chandler, found in the Ephydridae, Risidae, and **Camillidae**; found only in the **Camillidae** according to Griffiths. This loss occurs in many drosophilids, as discussed later.

C-3 (G-5). Break in the costal vein near the humeral cross vein ("humeral break") is absent. According to Chandler, this feature is found only in the **Campichoetidae**; according to Griffiths it is in the **Campichoetidae** and Ephydridae. I believe that this feature may be plesiomorphic at the superfamily level, for most outgroup taxa, among acalyprates, do not possess a costal break.

G-3 (no C). Presence of a pair of proclinate orbital setae (plesiomorphically, the orbitals would all be reclinate, or at most some of them would be inclinate [convergent]). Found in all five families examined by Griffiths and is synapomorphic for the Ephydroidea.

C-4 (no G). Anepisternal setae absent. Found in the **Campichoetidae** and the **Drosophilidae** according to Chandler. There are several exceptions in the **Drosophilidae**, but these are probably reversals.

G-4 (no C). Postocellar setae convergent (parallel and extended posteriad, plesiomorphically). Found in all five families examined by Griffiths, so would be synapomorphic for the Ephydroidea.



Figs. 1–3. Conus on flagellomere 1 of various ephydroids. 1. *Curtonotum helvum* (Curtonotidae). 2. *Camilla glabra* (Camillidae). 3. *Cladochaeta nebulosa* (Drosophilidae). aa = apical aperture. Scale = 209 μm .

C-5 (no G). Postocellar setae rudimentary or absent (plesiomorphically, present and convergent). Found in the Ephydridae and the Risidae according to Chandler.

G-5a (no C). Break is present in the costal vein at the end of the subcostal and first radial vein. Present in the Camillidae, Curtonotidae, and Drosophilidae, according to Griffiths. I have found it to actually be present in all the ephydroids, including *Campichoeta* and Diastatidae.

C-6 (G-2). The feature was discussed extensively first by Hennig (1973), and is the presence on flagellomere I of a dorsal, conical process, which extends up into the pedicel, sometimes termed the “conus” (figs. 1–3). Disney (1988) presented a recent comprehensive and historical account of this feature. Plesiomorphically, there is no process, or only a lateral flange. Found in the Drosophilinae,

Curtonotidae, and Camillidae, according to Chandler; but only in the Drosophilidae according to Griffiths. Disney (1988) mentioned it in *Notiphila* (Ephydridae). After my inspection of the feature it is quite apparent that the processes seen in the above three taxa are structurally different and, therefore, most likely independently derived (see below, apomorphy 54). The process in *Curtonotum* is slightly twisted with a distinctly narrowed tip, and entirely covered with a dense vestiture of microtrichiae. The processes in *Camilla* and the Drosophilidae are virtually bare, and these two differ by the Drosophilidae having concentric annuli at the base of the process (figs. 1–3). The *Notiphila* conus, I have found, lies very close to a flange that rests against the surface of the face, just beneath the pedicel, and in many species it is very narrow and quite small. These fine distinctions be-

tween the *Notiphila* and drosophiline conus, plus the many obviously distinctive ephydrid characters of *Notiphila*, show that the familial placement of this ephydrid is, contrary to what Disney (1988) indicated, not in doubt.

G-6 (no C). The subcostal vein is closely approximate to vein R_1 . Found in only the Curtonotidae according to Griffiths, but inclusive of the taxa in apomorphy G-6a.

G-6a (no C). This is a further modification of the state in G-6, being a subcostal vein that is faded or distally fused with vein R_1 . Found in four of the five families examined by Griffiths, the exception being the Curtonotidae.

C-7 (no G). Crossvein bm-cu is lost in the Curtonotidae and the [Camillidae + (Risidae + Ephydridae)] according to Chandler. It has also been lost in most drosophilids, but secondarily gained in some Steganinae (see apomorphy 114, below). Vein bm-cu is slightly reduced in *Campichoeta* but present (plesiomorphically?) in *Diastata*.

C-8 (G-10). Crossvein dm-cu is lost (plesiomorphically present). Only in Risidae according to Chandler; in the Camillidae and Curtonotidae according to Griffiths. I must agree with Chandler in this regard, as I have found vein dm-cu to be present in *Camilla glabra* and the Curtonotidae.

C-9 (no G). Abdominal spiracles are in the tergites (plesiomorphically they are in the pleural membrane). Found in the Ephydridae and the Risidae according to Chandler. This feature is independently derived in some Drosophilidae, as discussed under apomorphy 124.

G-9 (no C). The anal vein does not reach to the wing margin as a distinct vein, but perhaps as a fold. Found in all five families examined by Griffiths.

C-10 (G-13). Sternite VII in males is lost ("reduced" according to Griffiths). Found in all the families except the Curtonotidae according to Chandler and Griffiths. Wheeler's (1960) fine study showed that most drosophilids possessed this feature and some retained seven pairs of spiracles.

C-11 (G-12). Sternite VI in males is divided (or "reduced" according to Griffiths). Found in the Diastatidae according to Chandler; in the Camillidae and Ephydridae according to Griffiths.

C-11a (no G). Sternite VI in males is en-

tirely lost. Sternite VI is reduced in the Diastatidae, but entirely lost in the Ephydridae, Risidae, and Camillidae according to Chandler.

C-12 (G-14a, part). Tergite VII is lost in males (Chandler); according to Griffiths, tergite VI is reduced and VII is lost. Found in the Ephydridae, Risidae, and Camillidae according to Chandler; in only the Camillidae according to Griffiths. Wirth et al. (1987) stated that tergites VI + VII are lost in the Ephydridae (see fig. 381).

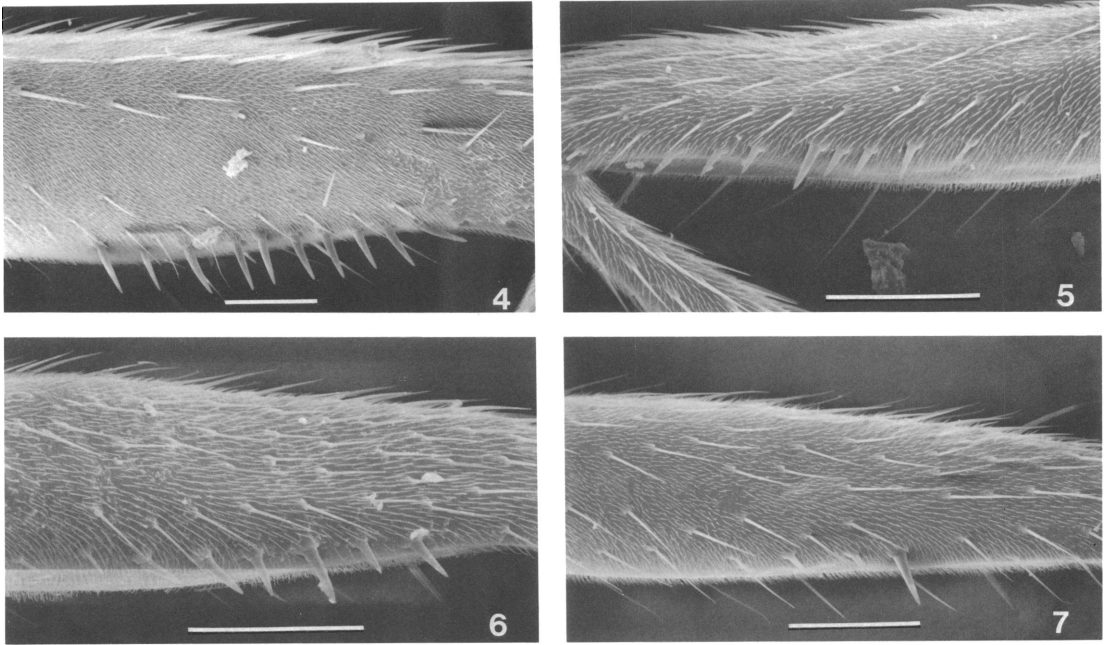
C-12a (no G). Male tergite VII is fused with t VI. According to Chandler it is autapomorphic to the Drosophilidae. However, in at least *Curtonotum helvum* spiracles VI + VII lie very close together, near the ventral edge of a small tergal strip (the remnant of tergites VI + VII), so this may be considered as well to be a result of fusion. Also, in *Chymomyza*, most *Scaptomyza*, and some other drosophilids, t VII remains as a narrow strip, with spiracles VI + VII lying close together (figs. 384, 385). It is most likely that a syntergite VI + VII in the Drosophilidae + Curtonotidae is a result of the loss of t VII as well as fusion, and a synapomorphy for the two families.

C-13 [G-14, 14a (part)]. Tergite VI is reduced in males, according to Chandler and Griffiths. Found in the Diastatidae according to Chandler; in the Curtonotidae, Ephydridae, and Camillidae according to Griffiths. I agree with Chandler in that it is reduced in the Diastatidae, and with Griffiths in that the Camillidae have a reduced tergite VI (but not the Curtonotidae) (figs. 378–382). Apparently, then, C-13a would be the end result (loss of tVI) in the transformation series toward reduction of tVI.

C-13a (no G). Tergite VI lost in the males (reduced in the Diastatidae). Complete loss of the tergite occurs in the Ephydridae and Risidae according to Chandler, and no doubt is synapomorphic.

C-14 (G-11). Abdominal spiracle VII lost in both sexes. In the Ephydridae and Camillidae according to Chandler and Griffiths, as well as the Risidae according to Chandler. I have found that some female drosophilids possess sVII, which is interpreted here as a secondary gain. See apomorphy 206 for the distribution of this feature.

C-15 (no G). In addition to the pair of sur-



Figs. 4–7. Row of small spines on the anteromesal surface of the forefemur in various ephydroids. 4. *Curtonotum helvum* (Curtonotidae). 5. *Campichoeta griseola* (Campichoetidae). 6. *Diastata* sp. (Diastatidae). 7. *Diastata repleta*. Scale = 100 μ m.

styli, which often function as claspers (or are at least adorned for apparently the function of clasping the female), there are two pairs of other “claspers” (plesiomorphically there would just be the surstyli). Autapomorphic to the Diastatidae according to Chandler.

C-16 (no G). In the females there is a loss of sternites VI and VII. Found only in the Camillidae according to Chandler.

C-17 (no G). Sternite and tergite VI are fused into a ring in females (separate, but may articulate, plesiomorphically). Found only in the Diastatidae, according to Chandler.

C-18 (G-16a). Spermathecae (female) are reduced (small and unsclerotized), the ventral receptacles are large and heavily sclerotized. In the Ephydridae and Risidae according to Chandler; also in the Ephydridae according to Griffiths.

In addition to the above characters, ones not used in the matrices by Griffiths and Chandler but which I incorporated into the analysis follow.

Gr-1. Row of minute spines on the mesal surface of the forefemur (the ctenidium) is present (figs. 4–7). This would be synapomorphic at the level of the superfamily

Ephydroidea since it is possessed by the Curtonotidae, Campichoetidae, Diastatidae, and Camillidae. It appears to be secondarily lost in the Drosophilidae and the Ephydridae + Risidae. Those in *Drosophila immigrans* plus close relatives and in *Chymomyza* (Drosophilidae) are certainly not homologous with the stouter, blunt spines in the other families. In *Chymomyza* there are two rows of the spines along the length of the femur, in males only, and the spines are longer and thinner than in the other, abovementioned groups. In the *Drosophila immigrans* group and *D. monochaeta* the spines are approximately equal in size, number, and placement to those in the four other families, but they are much sharper. The femoral spines of *Scaptomyza* (*Euscaptomyza*) *chylizosoma* differ with all the above species by having stout, heavy, peglike spines.

Gr-2. Presence of a plumose arista (flagellomere 3), which bears dorsal and ventral branches that are at least three or four times the length of tiny medial branches, is synapomorphic for the Curtonotidae + Drosophilidae. This type of arista has been secondarily reduced to a pubescent or even

completely bare one in some drosophilids (see apomorphy 44). The plumose type of arista seen in the Ephydriidae is certainly independently derived, for it lacks most of the tiny medial branches and the long branches are exclusively on the dorsal edge.

PAUP was run using branch-and-bound and Farris optimization, ancestor rooting, and outgroup comparison. It generated three trees of equal length (25.0, C.I. = 0.68) (figs. 8–10). Figure 10 shows the preferred tree with the apomorphies added to it. The sister group to the Drosophilidae is the Curtonotidae, supported by the following synapomorphies: proclinate anterior to the two ipsilateral reclinate (C-1) (convergent with the situation in the Camillidae), tergite VII fused with VI in males (C-12a), and the presence of a plumose arista with dorsal and ventral rays (Gr-2). It is quite doubtful that apomorphy C-6 (G-2), the dorsal process on flagellomere 1, should be considered synapomorphic for the Curtonotidae + Drosophilidae, since it appears to be independently derived. If synapomorphic, it would require hypothesizing a loss for the Steganinae; if convergent, it would require hypothesizing two origins. I favor the latter interpretation since the curtonotid and drosophilid dorsal processes differ slightly in structure (as discussed above), and because this structure has obviously evolved independently in the Camillidae as well. The monophyly of the Drosophilidae is supported by the absence of anepisternal setae (C-4) (convergent with the situation in the Campichoetidae), and by the presence of a pair of proclinate setae with two pairs of reclinate setae.

McAlpine (1989) alluded to the cibarium (also called “fulcrum”) and arrangement of sensillae fields (“filter apparatus,” after Frey, 1921) as potential synapomorphies in the Ephydroidea. I deal with these features in characters 26, 27, 29, and 30 below for the Drosophilidae. I concur with McAlpine that *Camilla* and *Diastata* have the “filter apparatus,” but I have found that *Campichoeta* and at least *Notiphila* are plesiomorphic for the feature (many more ephydriids need to be surveyed). McAlpine (1989) stated (p. 1489) “certainly [the filter apparatus] is present in some genera [of the Drosophilidae] (Frey,

1921), but its occurrence and comparative structure in the more primitive genera and generally throughout the family needs further investigation.” Variation in the drosophilid “filter apparatus” is described below: it is a significant character system for several synapomorphies within the family, but not at the family level.

The most recent hypothesis on ephydroid relationships is by McAlpine (1989), which differs considerably from the one I present here. He proposed the following relationships: Curtonotidae [(Camillidae + Drosophilidae) (Diastatidae + Ephydriidae)]. McAlpine did not recognize a separate family for *Campichoeta*, as did Griffiths (1972), and he kept *Campichoeta* and *Diastata* in one family (Griffiths put *Diastata* in the Ephydriidae). Also, McAlpine (1989) indicated that *Risa* (Risidae) was allied to the Milichiidae, on the basis of several features including a distinctive geniculate proboscis (which does also occur in some ephydriids, such as *Pseudohecamele*). Neither I nor McAlpine examined *Risa*, so definitive family placement should await a detailed morphological study of it.

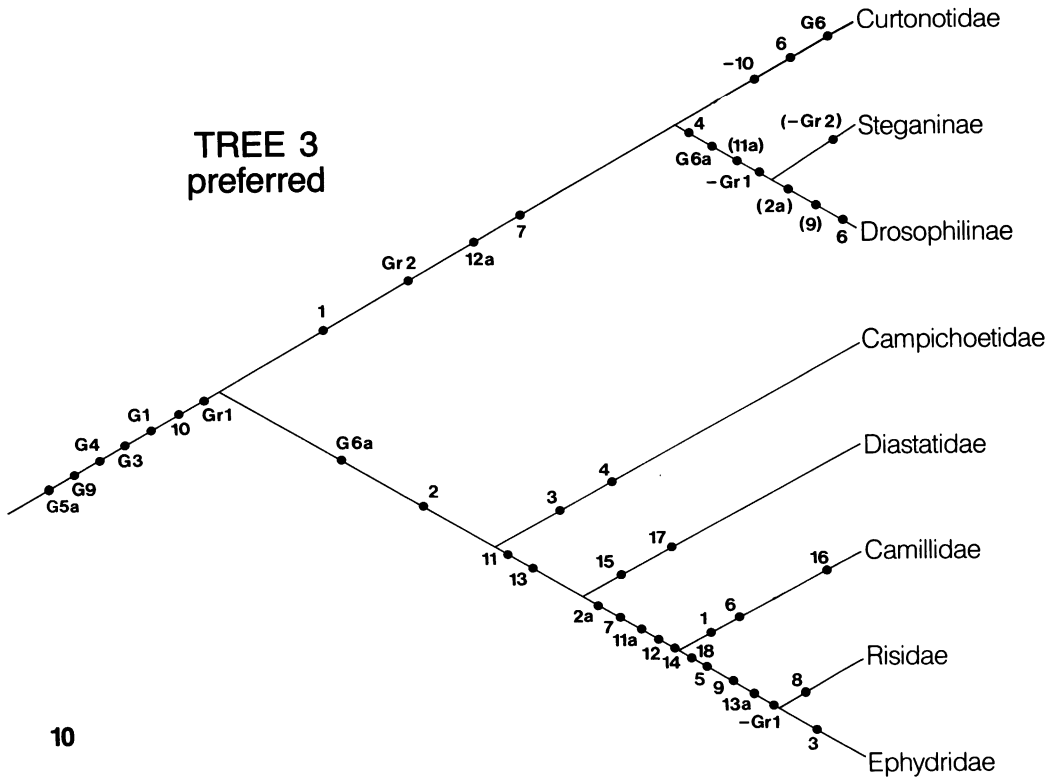
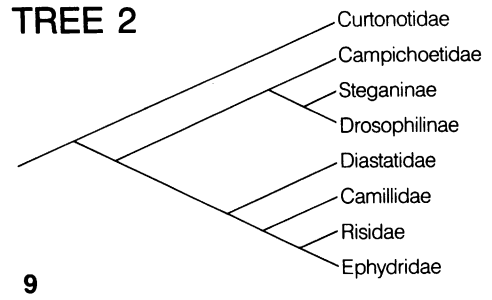
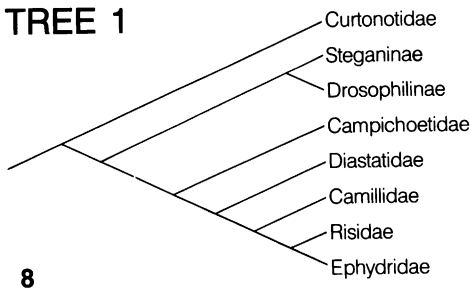
Of more pressing importance is how McAlpine diagnosed and defined the monophyly of the Drosophilidae. He indicated “7 autapomorphic characters (AA) [that] firmly attest the monophyly of Drosophilidae.” I agree with five of these, but two of them are certainly not in the ground plan of the family. Both “haired compound eyes” and presence of a facial carina occur sporadically throughout more derived portions of the family, and these have been independent developments of each “character,” as I describe below for all characters.

DESCRIPTIONS OF CHARACTERS IN THE CLADISTIC ANALYSIS

HEAD

POSTOCCIPUT

1. The number of supracervical setae (on the back of the head, just above the occipital foramen) falls within an extensive range of 3 to about 50. By plotting a frequency distribution of the trait it is apparent that few discrete gaps in the supracervical number exist,

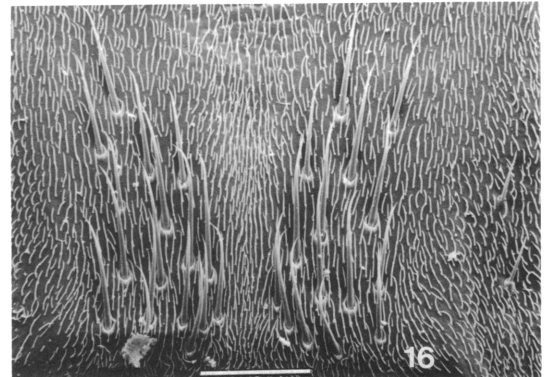
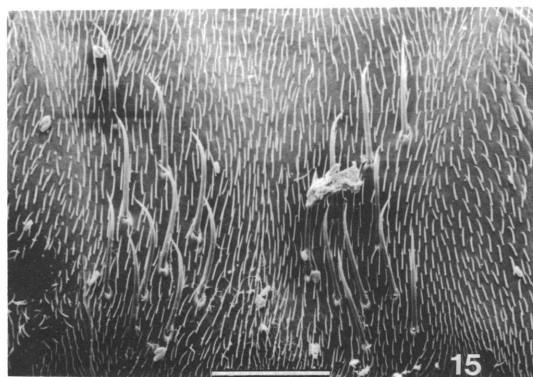
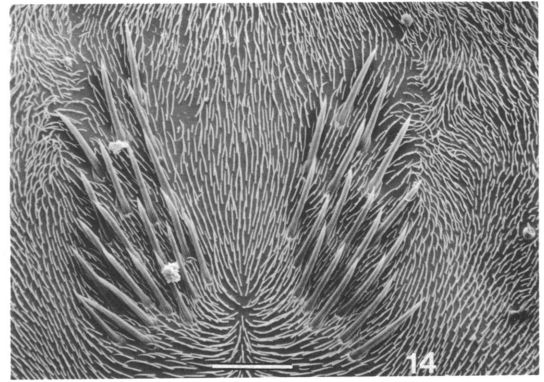
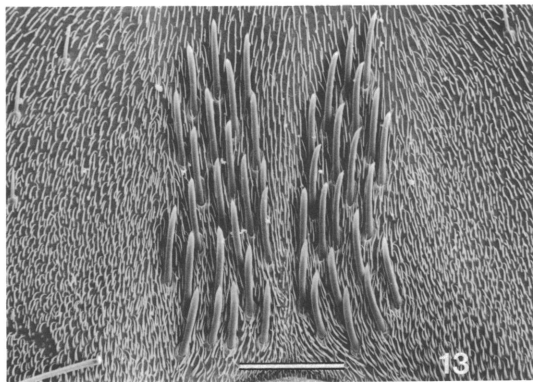
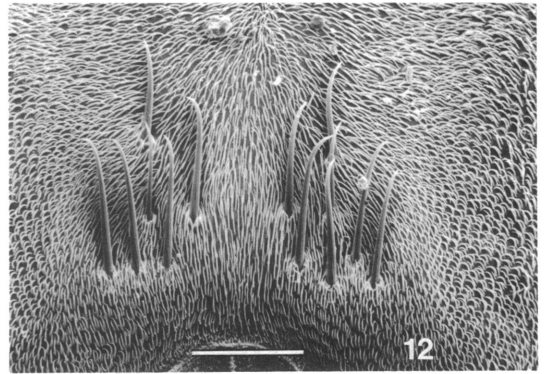
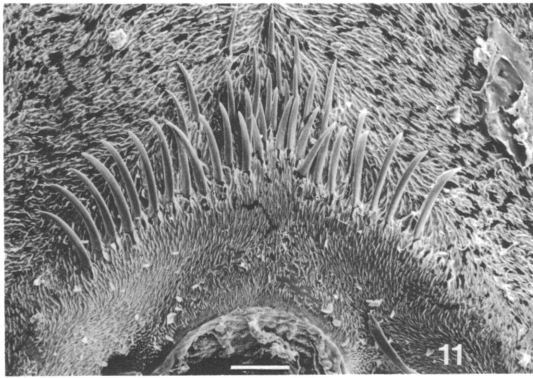


Figs. 8–10. Three equally parsimonious hypotheses on relationships of families in the Ephydroidea. 8, 9. Alternative hypotheses. 10. Preferred hypothesis, showing apomorphies supporting each node. Refer to text for apomorphies.

the apparent one being at the high end of the distribution (> 33 setae). Due to the large number of setae, it is very difficult to homologize each one based on position. Such a large number of supracervicals is undoubtedly apomorphic since *Diastata* and *Campichoeta* (the outgroup taxa used for this trait) possess 6–10 setae. *Curtonotum* possesses about 50 supracervicals, so this high number presum-

ably is independently derived from the state in the drosophilids.

2. Shape of the supracervical setae can be blunt—as in *Leucophenga*, *Stegana*, and *Gitona*—or sharp. The blunt state appears in *Curtonotum*, *Notiphila*, and various other Muscomorpha, so is plesiomorphic. The apomorphic state is a seta that is distinctively tapered, thin, and with an apex that is curved

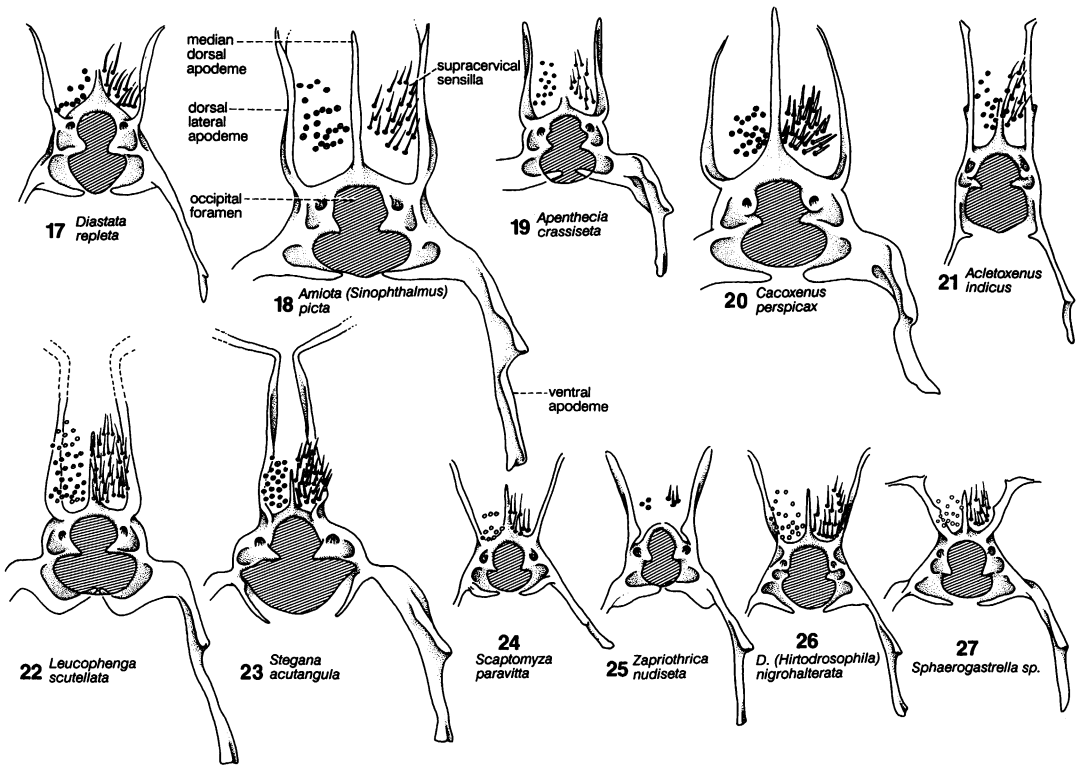


Figs. 11–16. Supracervical setae in various ephydroids. 11. *Notiphila teres* (Ephydriidae). 12. *Diastata* sp. (Diastatidae). 13–16. Drosophilidae. 13. *Leucophenga varia*. 14. *Gitona bivisualis*. 15. *Zygothrica orbitalis*. 16. *Drosophila affinis*. Scale = 50 μ m.

and sharp (figs. 15 and 16). The trait appears to have been derived twice in the Drosophilidae, in the Drosophilinae, and again in some Steganinae.

3. Postocular setae that are evenly spaced in a row (and, sometimes, at least for segments of the postocular margin, in two rows)

and that point laterad were found to vary in number from 12 to 40 per side. Since setal number can vary between the two sides of the head, the number taken was a mean of the two values. There is little doubt that the plesiomorphic state falls within the range of 12–34, the interspecific variation of which



Figs. 17-27. Portion of postocciptus of Diastidae (17) and various Drosophilidae (18-27), showing tentorial apodemes, supracervical setae, and occipital foramen.

falls within a normal distribution. Clearly outside the normal distribution are taxa with 40 or more postoculars, which is the derived condition. Again, as in apomorphy 1, the numerous number of setae precluded homologizing each one based on position.

4. The dorsolateral tentorial apodeme, to which some of the intrinsic muscles of the head are attached, varies in shape in several ways. At this level the presence of apodemes that are parallel is apomorphic, particularly the basal two-thirds of each arm [the distal third can diverge strongly, as in *Amiota (Sinophthalmus) picta*] (figs. 18-20). Apodemes diverging along their entire length is plesiomorphic, as seen in the outgroup taxa and some drosophilids (fig. 17). The apodeme is mostly internal (visible in cleared specimens), and external traces of it are the fine sutures where the cuticle is invaginated.

5. Within apomorphy 4 are parallel dorsolateral tentorial apodemes that lie very close

together [i.e., separated by a distance one-half or less than the apodeme length (fig. 21); in the plesiomorphic state the distance is three-quarters or more than the length of the parallel portion of the apodeme]. Thus, apomorphies 4 and 5 are additively binary. Possessing the synapomorphy are *Acletoxenus* and *Mayagueza*, which provides additional evidence that these two genera are sister groups (Grimaldi, 1988). Although apparently similar, this feature is not synapomorphic with the condition in *Stegana* and *Leucophenga* (apomorphy 6): these two taxa have convergent apodemes which, albeit very close together, are strongly divergent dorsally and have the primitive condition of the ventral arms having a broad attachment to the foramen that projects laterad. In *Mayagueza* and *Acletoxenus*, the dorsal and ventral apodemes are nearly in line and quite narrow, and they have greatly reduced ventromedial tentorial apodeme arms.

6. Dorsolateral tentorial apodeme arms that slightly converge and then markedly diverge dorsally (figs. 22, 23) were seen only in *Leucophenga* (using *L. scutellata* and *L. varia*), *Eostegana*, and *Stegana* [using *S. (Orthostegana) acutangula*, *S. (O.)* sp., and *S. (Stegantina) coleoprata*]. *Stegana (Stegana) vittata* has apodemes close together, and dorsally divergent, but the ventral portion of the dorsolateral arm is parallel instead of slightly convergent. This might represent a reversal to the plesiomorphic state.

7. The dorsal third of the dorsolateral tentorial apodeme arm is flared out (strongly projected laterad, or divergent), with the basal two-thirds parallel (figs. 18, 19), which is a condition apomorphic with respect to a simply parallel pair of apodemes and is nested within apomorphy 4. The trait occurs in *Amiota (A.) humeralis*, *A. leucostoma*, and *A. (Sinophthalmus) picta*. *Apenethecia crassiseta* has the parallel portion of the apodeme pair strongly sclerotized, but the dorsal, divergent portion is very weakly sclerotized and not immediately noticeable (fig. 19).

8. The dorsomedial tentorial apodeme arm is completely lost in *Zapriothrica* (fig. 25), which is apparently autapomorphic for this genus. A small dorsomedial arm (less than one-half the length of the dorsolateral arms) is widespread in the Drosophilidae and the trait is plesiomorphic at the family level.

9. In the following taxa the dorsomedial arm of the tentorium is highly developed, such that its length equals or exceeds three-quarters the length of the dorsolateral arms (figs. 18, 20): *Amiota (A.) leucostoma*, *A. humeralis*, *A. (Sinophthalmus) picta*, *Gitona distigma*, *G. bivisualis*, and *Cacoxenus (Gitonides) perspicax*. This is convergent with the trait in *Drosophila lurida*.

10. Bases of the ventrolateral arms of the tentorial apodeme are broad (at least twice the width of the apical portion) (figs. 18–20, 22) in the following taxa: *Amiota*, *Apenethecia*, *Cacoxenus*, *Gitona*, *Drosophila lurida*, *Dithoneura opaca* (or near), *Drosophila superba*, and *Leucophenga*. The mesal surface of the broadened section is concave.

11. In lateral view of the head, at about the median level of the eye and where its posterior margin is extended most posteriad, the postgena is thick in relation to the cheek or

gena. In this area the postgena is from three-quarters to nearly equal the width of the gena (figs. 243–245, 247–250, 252–256). This trait is predominant among the endemic Hawaiian species and *Scaptomyza*, and is apparently derived independently between the two groups.

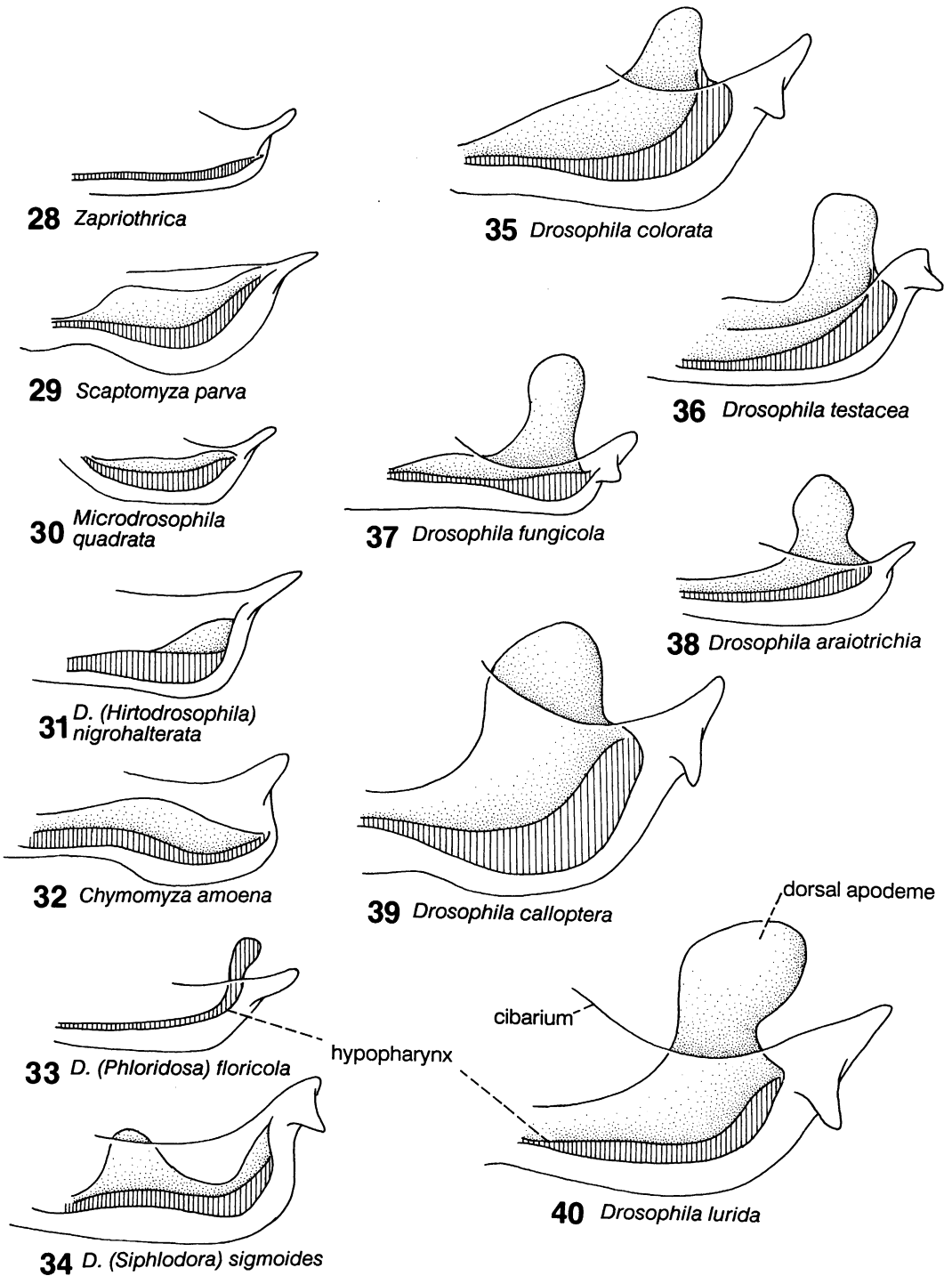
12. In lateral view of the head, the ventralmost portion of the posterior margin of the head (on the gena) makes an acute angle with the oral margin. The space between the angle and the eye margin closest to it is deep. The posteroventral margin of the eye, which opposes the genal angle, is flat [in *Dicladochaeta*, *Celidosoma*, *Scaptomyza graminum*, *S. (Tantalia)*, *S. (Trogloscaptomyza)*, *Ateledrosophila*, *Zapriothrica*, to a minor extent in *Titanochaeta*]. This feature is obviously independently derived numerous times.

13. In *Dettopsomyia*, *Hypselothyrea*, *Liodrosophila*, *Sphaerogastrella*, and *Tambourella*, there are very few, tiny postocular setulae. Plesiomorphically there is a row of setulae along the entire posteromedian margin of the eye, but in the above taxa there are just five to six small setulae in the dorsal part of the postociput near the eye.

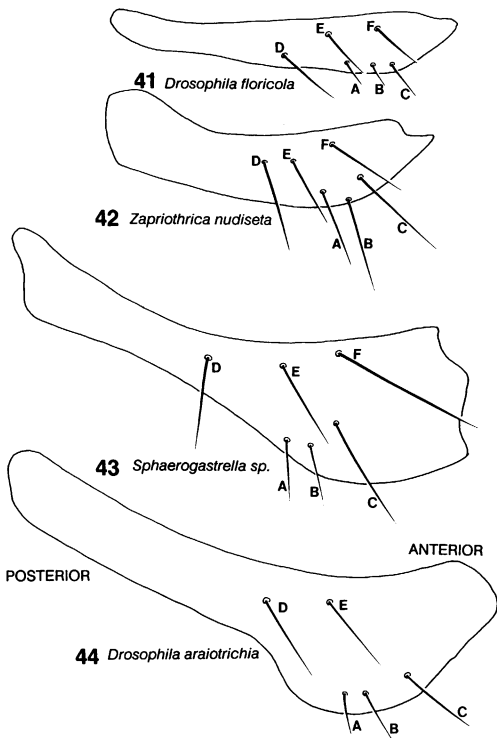
PROBOSCIS

14. The ventral margin of the cibarium [termed the "fulcrum" by many authors, including Frey (1921) and McAlpine (1989)] in lateral view apomorphically has a sharp angle at the posterior end (figs. 31–40). Plesiomorphically, it is slightly and evenly concave, with no heavy sclerotization at the proximal end (figs. 28–30). In the cibaria with an acutely angled margin there is usually a heavily sclerotized bulb near the angle, which is part of the hypopharynx. Apomorphy 14 links many drosophiline genera.

15. Also in lateral view of the cibarium, above the point where a sharp angle and heavily sclerotized bulb occur (see apomorphy 14), there is a laterally flattened, broad apodeme that is projected dorsad (figs. 34–40). This apomorphy is undoubtedly a further modification within apomorphy 14, and some variation in shape was found. Comparison of the apodeme shape required detailed and destructive dissection, so only 24 representative species were examined. A large,



Figs. 28-40. Lateral view of proximal end of cibarium of various *Drosophilidae*. Hatched structure is hypopharynx; stippled structure is apodeme.



Figs. 41-44. Labia of several drosophilids, showing development of apical (anterior) bulge.

keellike cibarial apodeme probably functions as an attachment for large muscles that originate from the clypeus and, when contracted, the muscles would create suction by dilating the heavily sclerotized bulb of the hypopharynx. This was shown by Graham-Smith (1930) for *Calliphora*. Plesiomorphically, there is no apodeme, or only a slight swelling on the floor (ventral surface) of the cibarium (figs. 28-33). The feature is apparently independently derived in Hawaiian *Drosophila* and at least two groups of drosophilines, but a more comprehensive survey is needed.

16. In lateral view of the cibarium, the hypopharyngeal apodeme described in apomorphy 15 is narrow, not broad (fig. 33). It stands upright (projected anterodorsad) as in the broad type of keel. The feature appears to be autapomorphic to the subgenus *Phloridosa* of *Drosophila* (for which *D. floricola* and *D. lutzii* were examined).

17. In lateral view the prementum has a swelling at the distal end of the ventral mar-

gin. The swelling is gradual in some taxa (*Sphaerogastrella*, fig. 43) and in others it is a discrete bump, as in *Liodrosophila* and particularly the Hawaiian "*Drosophila*" (i.e., *D. araiotricha*, state 2, fig. 44). Thus, the feature may not be synapomorphic for all these taxa (it apparently is for *Sphaerogastrella* and *Liodrosophila*, and coded as state 1), but is perhaps independently derived. Plesiomorphically the prementum has a flat ventral margin (figs. 41, 42). States 1 and 2 were unordered.

18. The lacinia in lateral view possesses a spatulate ventral arm: the arm is longer than the dorsal arm and is about three times as wide. The mesal surface of the ventral arm is concave (probably the area of muscle attachment), and the profile of the arm is either rounded or slightly flattened at the apex (figs. 53-55). Many of the Hawaiian species possess this trait (state 2), and it may be a very inclusive synapomorphy for the endemic species. The non-Hawaiian species with a lacinial arm most similar to this are *Drosophila floricola* and *D. lutzii* (fig. 92), but in these species, the arm is much less concave (not really spatulate, coded as state 1). The broad ventral lacinial arm in *Pseudiastata vorax* (fig. 75) is not considered a homologous modification because of a lack of concavity and a dissimilarity in contour. Plesiomorphic to apomorphy 18 is a ventral arm of width and length approximately equal to that of the dorsal arm (e.g., fig. 48). States 1 and 2 were unordered.

19. Apomorphically, the lacinia in lateral view has the dorsal and ventral (proximal) arms long, thin, and opposing each other at an angle of nearly 180°. In addition, the anterior arm is fusiform in shape: the anterior half is about twice the width of the posterior half, with a concave mesal surface (figs. 69-72). The mesal concavity is probably an attachment site for muscles that manipulate the lacinia. The apomorphy was found in *Diathoneura*, *Cladochaeta*, and *Drosophila superba*, and is considered synapomorphic for these taxa. Plesiomorphically, the lacinial shape has an anterior arm that differs in width along its length by not more than 1½ times the narrowest width.

20. A lateral outline of the lacinia apomorphically has long, thin dorsal and ventral

arms. Lengths of the arms equal or exceed half that of the anterior arm and the widths are equal to or less than that of the anterior arm (figs. 63–65, 68). Lacinial shapes varied considerably among the 65 or so species examined, but the variation could be categorized into only three obvious states (apomorphies 18, 19, 20). This apomorphic state of the lacinia (20) is the most widespread. Apomorphy 20 was divided into two derived, ordered states.

21. Little doubt exists as to the plesiomorphic status in the Drosophilidae of a long, cylindrical palpus (figs. 95, 96), which is found in *Curtonotum*, *Campichoeta*, *Camilla*, and some *Diastata*. McAlpine (1981) mentioned that most Muscomorpha have one palpal segment, but I have found that a very small, basal segment occurs in some drosophilids (presence or absence of the feature among the few taxa examined was not scored, since it is difficult to survey for this feature). One apomorphy of the palp described above is a short, cylindrical type, found in many Hawaiian species; these palpi have as well a very elongate terminal or apical seta (seta A), the length of which is about equal to the palpus length (figs. 128, 129).

22. Another apomorphy (cf. 16, 18) of the subgenus *Phloridosa* of *Drosophila* is a palpus with short, stout and sharp setae (fig. 125), which is also found in *Baeodrosophila*.

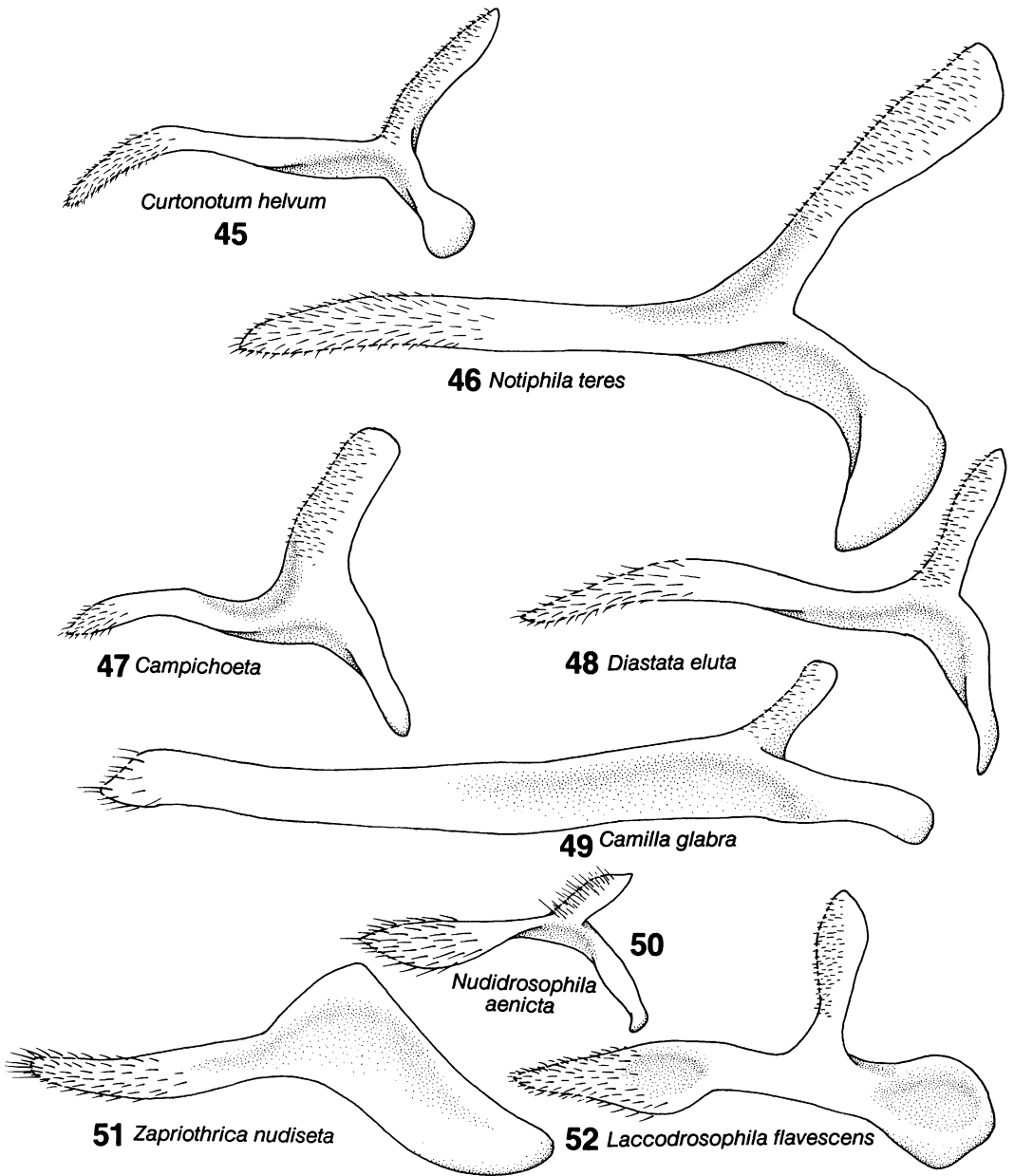
23. In cleared preparations of the palpi there was noticed in some species an internal, round structure that has a dense covering of setulae (probably sensilla chaetica) (figs. 109–111). The structure is no doubt a gustatory or olfactory organ, and was found in *Amiota humeralis*, *A. (Sinophthalmus) picta*, and *Apenethecia crassisetata*. The structure was largest in *A. picta* and much smaller in the other two species. The sense organ is near the transverse, anteroventral margin in *A. picta* and *Apenethecia crassisetata*, but in *A. humeralis* it was near the base of the palp. The feature supports the hypothesis that *Apenethecia* and *A. (Sinophthalmus)* are sister groups (Grimaldi, 1988). *Apenethecia* and *A. (Sinophthalmus)*, however, have considerably different male genitalia: many of the apomorphies diagnostic for the genus *Amiota* are recognizable in *A. (Sinophthalmus)*, but *Apenethecia* lacks several features.

24. Apomorphically, in lateral view the ventral margin of the palpus meets, at an acute angle, the dorsal margin. The dorsal margin is nearly straight and the apex of the palpus is narrow, giving the entire palpus an almost triangular shape (figs. 108–114). Plesiomorphically, the shape of the palpus may be as described in apomorphy no. 21, or paddle-shaped (having a rounded distal end). This feature is synapomorphic for some Steganiinae.

25. On the ventral and apical margins of the palpus is generally a row of setae that are larger than those on the flat surfaces (figs. 95–137). Apomorphically, the ventral and apical setae have been lost and only an apical seta (seta A) remains (fig. 116).

26. The cibarium possesses three major fields or groups of setae: a posterior one (generally in two even rows, one on each side), a medial one (also usually in two rows), and an anterior group of four. Plesiomorphically, the posterior sensilla chaetica (or “trichoid” sensilla) are rather short: they are not extended much past the ubiquitous pair of sensilla campaniformia flanking the hypopharynx and which separate the medial and posterior sensilla fields. The posterior sensilla chaetica are also few in number: two to three per side were found in all the outgroup taxa (figs. 145, 146). Thus, that part of the frequency distribution that peaks at about 18 sensilla, and with a range of 10–23 per side, represents apomorphic state 1. The condition where 25 to 26 posterior sensilla are present is apomorphic state 2, since this number is separated by a discrete gap from the normal distribution. The species possessing state 2 are *Drosophila scaptomyzoidea*, *Neotanygastrella tricoloripes*, and *Scaptomyza paravitta*. States 1 and 2 were unordered. With 43 and 35 posterior sensilla, *Lissocephala sabroskyi* and *Chymomyza amoena*, respectively, were autapomorphically high among the 65 drosophilids examined. This feature may be synapomorphic for *Lissocephala*, *Chymomyza*, *Neotanygastrella*, and perhaps *Scaptodrosophila*. As in some other cases regarding sensilla and seta numbers, it was not feasible to homologize each seta because of the number involved.

Frey (1921) termed these sensilla chaetica a “filter apparatus,” which name McAlpine

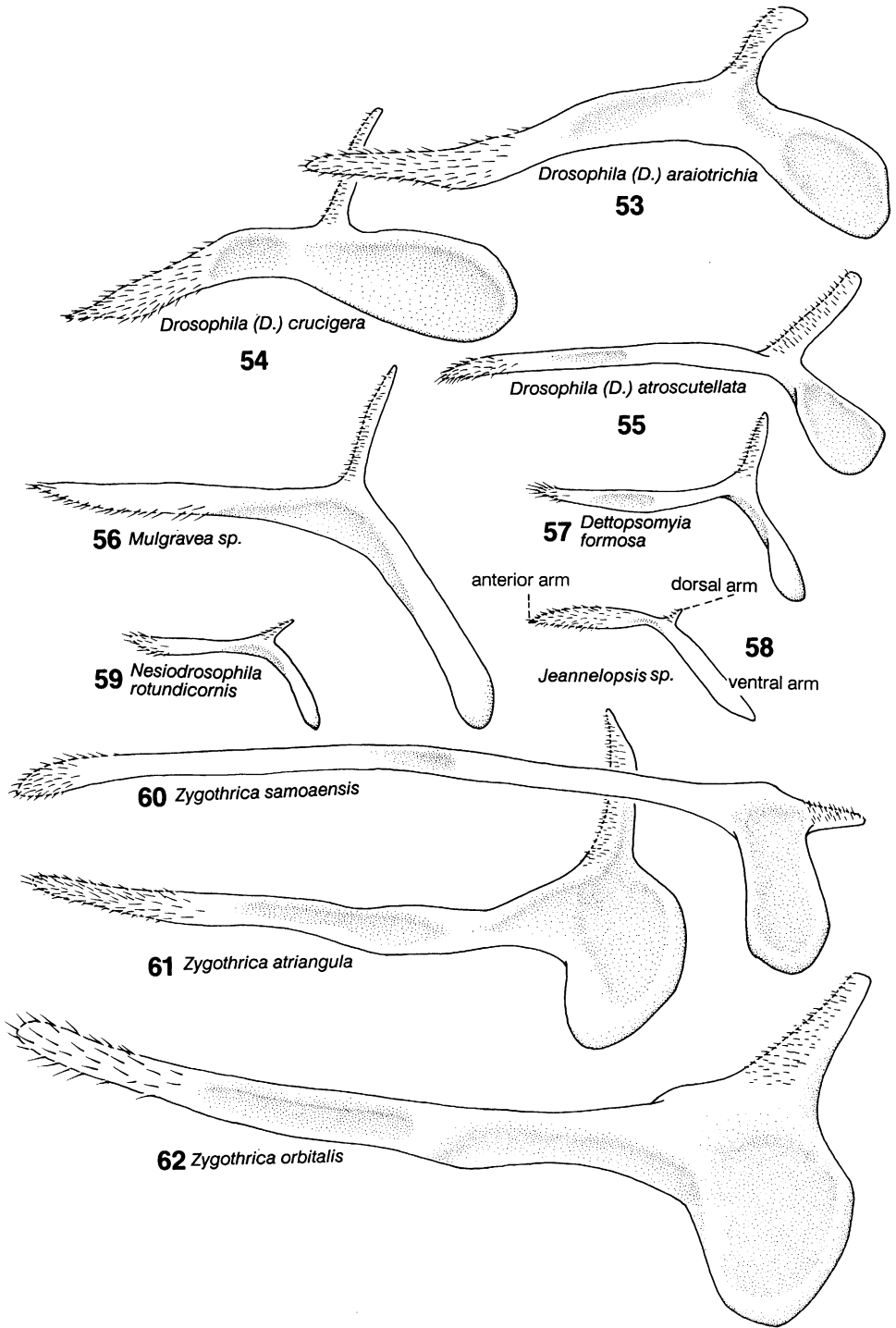


Figs. 45-52. Laciniae of various ephydroids. 45. Curtonotidae. 46. Ephydriidae. 47. Campichoetidae. 48. Diastatidae. 49. Camillidae. 50-52. Drosophilidae. Not to the same scale.

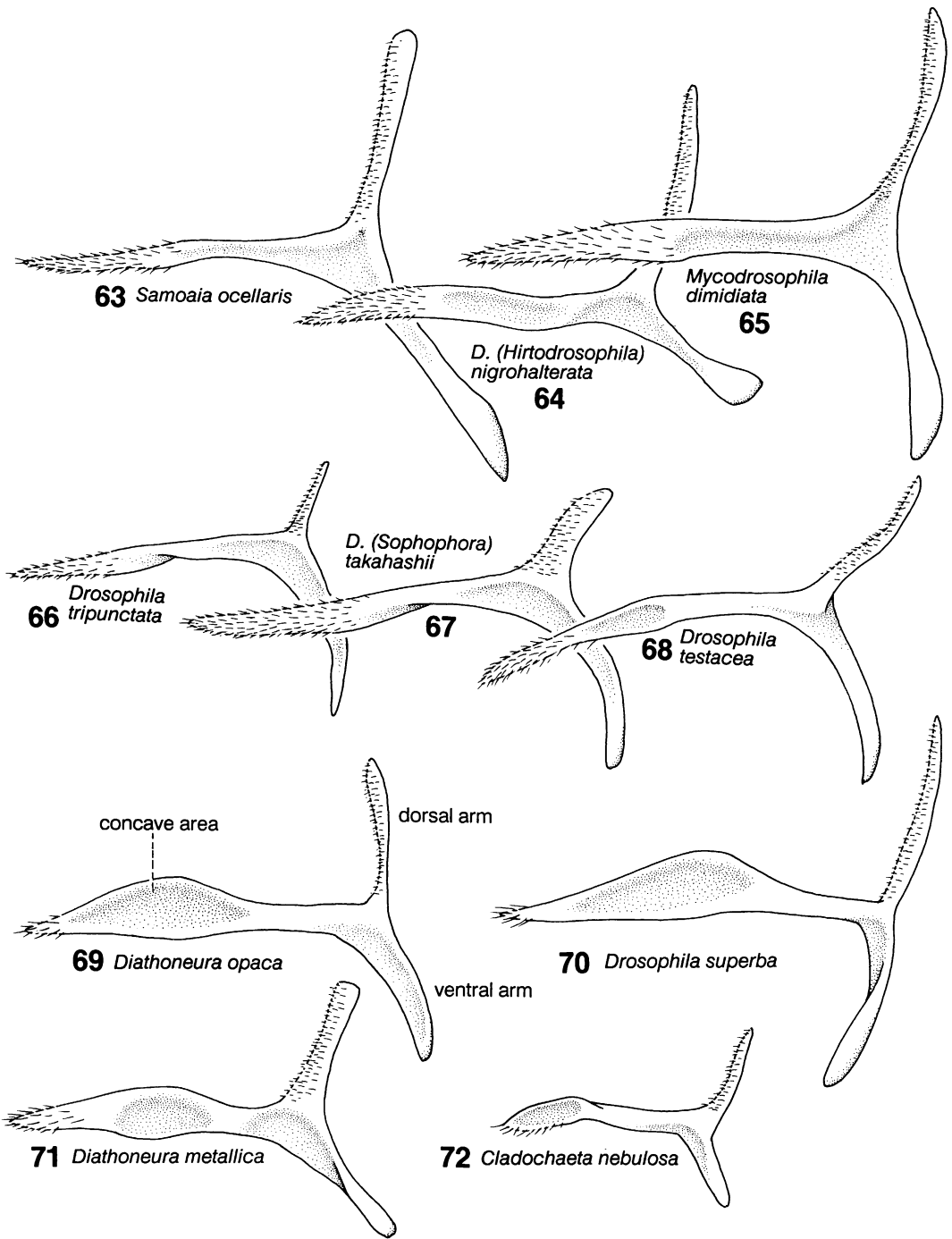
(1989) also used. This term should not be used, for these structures are sensory in nature, and not a mechanism for filtering [Graham-Smith (1930) simply called them setae]. They are in fact *cibarial stretch receptors* (Rice, 1970; Dethier, 1976), which detect distur-

tions in the cibarial wall due to muscle contractions. This is what Hertweck (1931) had also concluded.

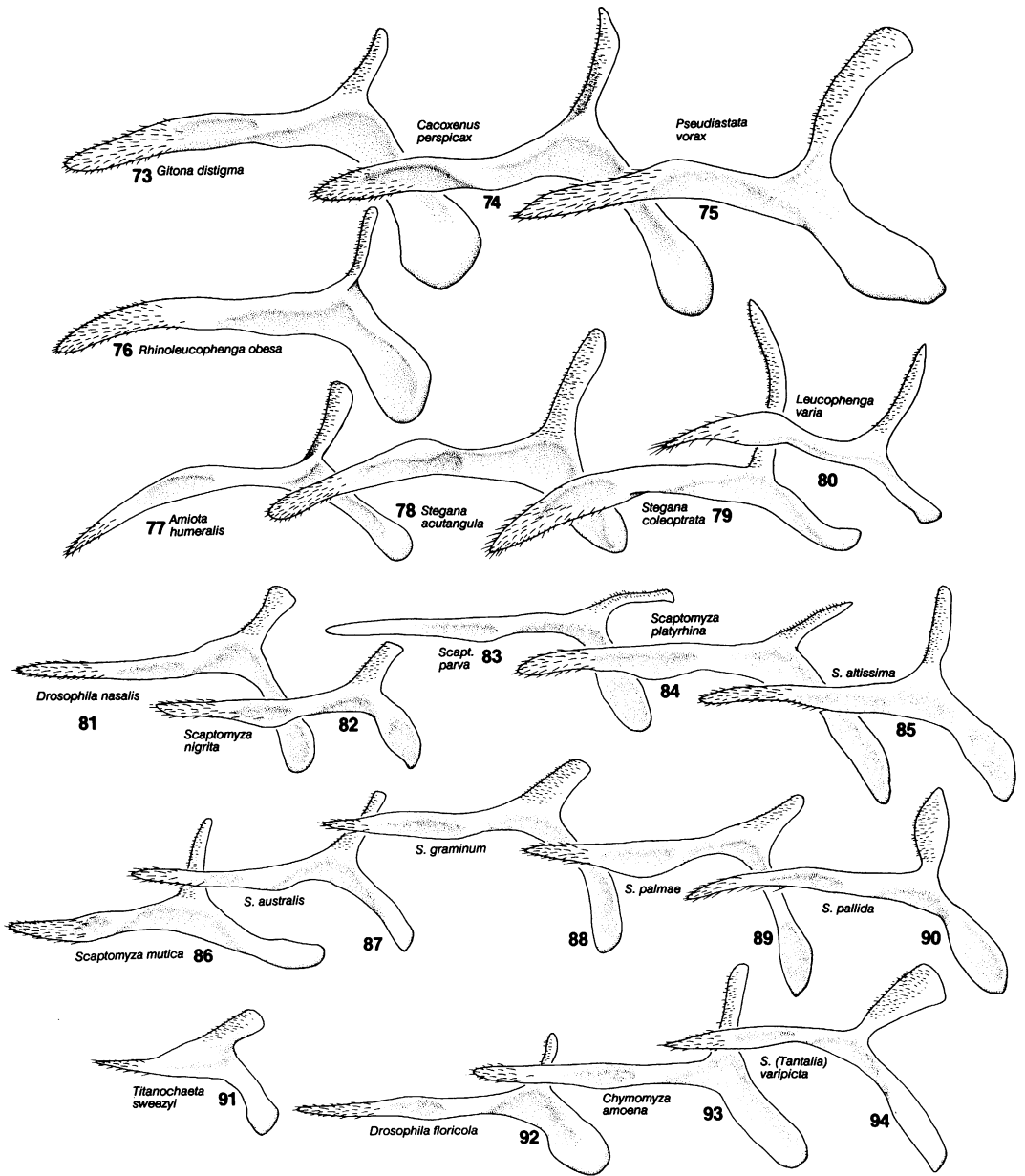
27. The frequency distribution in the number of medial cibarial sensilla was much more skewed than was that for the posterior sen-



Figs. 53-62. Laciniae of various Drosophilidae.



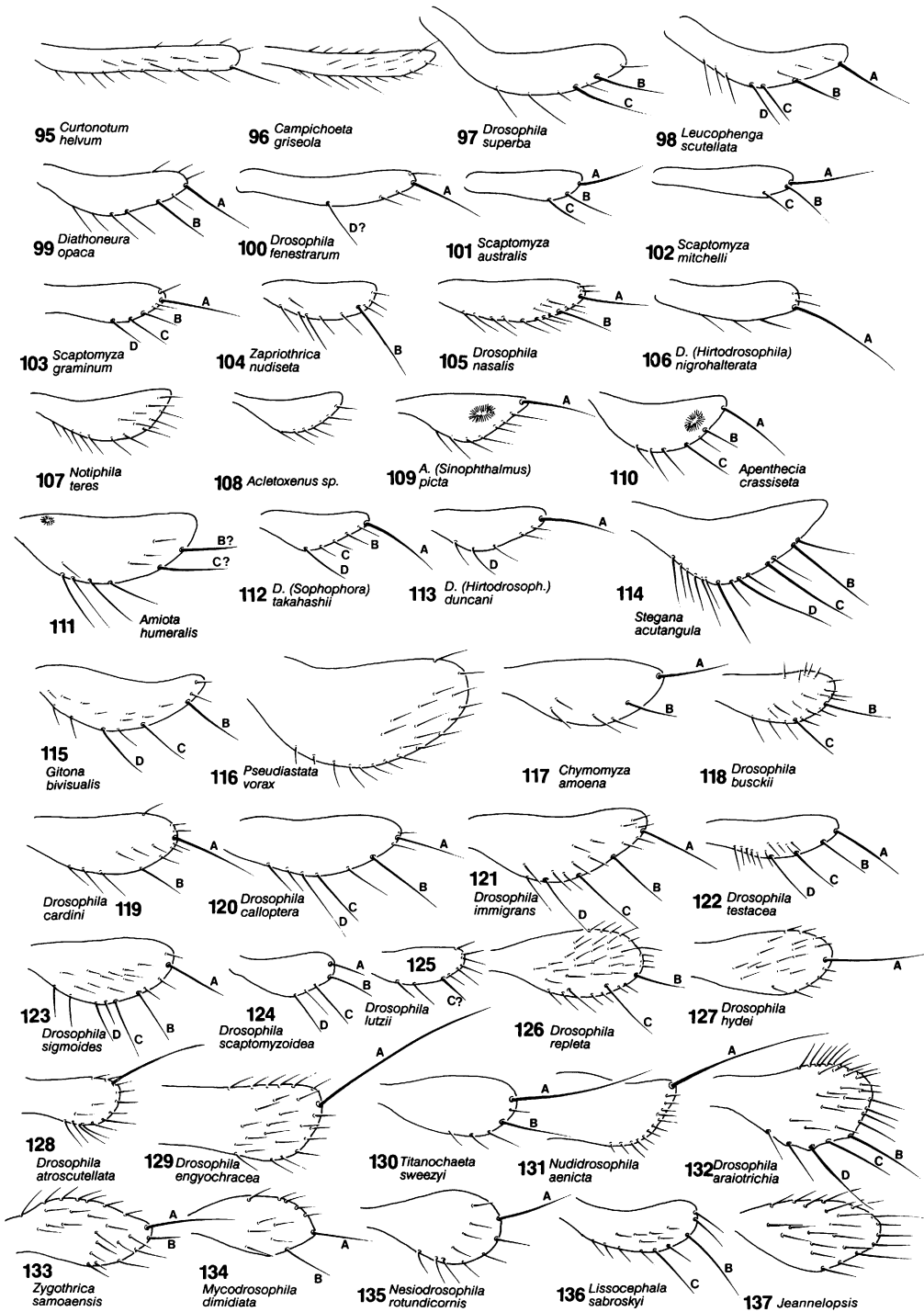
Figs. 63-72. Laciniae of various Drosophilidae.



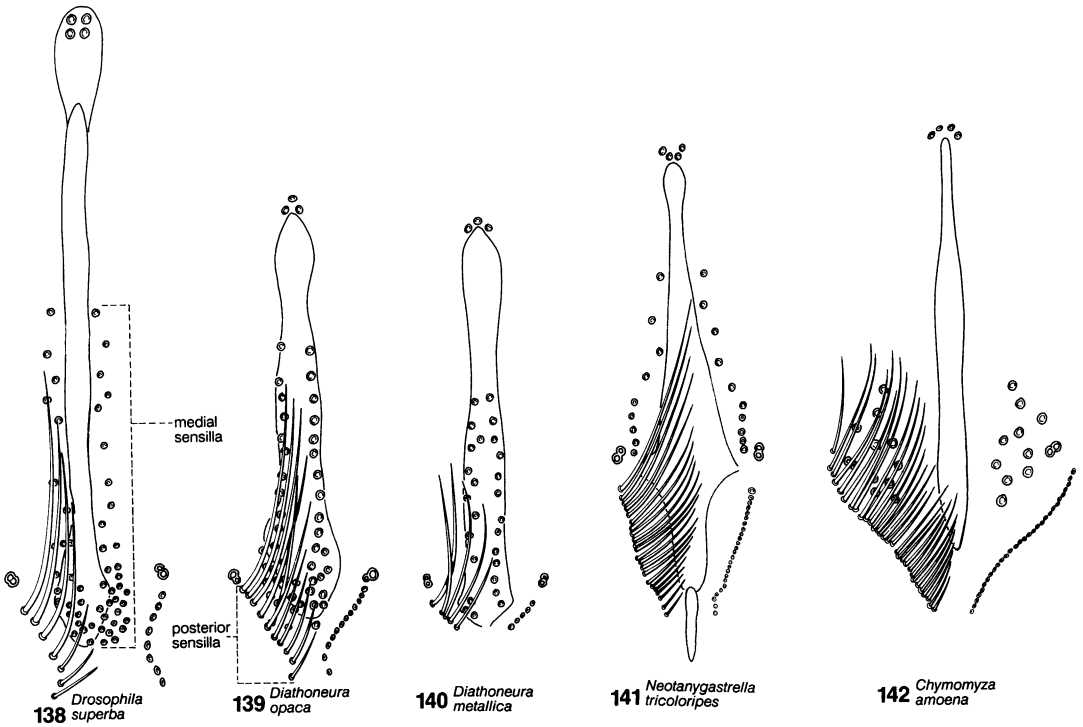
Figs. 73–94. Laciniae of various Drosophilidae. 73–80. Steganinae. 81–94. *Scaptomyza* and relatives.

silla. The skew was toward a peak of five to six sensilla per side (including the outgroup taxa; thus, the numbers falling within the normal curve represent the plesiomorphic state). Medial sensilla 18–21 in number (per side) apparently lie outside the tail of the leptokurtic curve and partially define apomorphy

27, which is found in the following taxa: *Scaptomyza* (*Rosenwaldia*) *mittchelli*, *Pseudiasata vorax*, and *Diathoneura opaca* (or nr.) (fig. 139). With 28 and 29 medials are *Scaptomyza* (*Tantalia*) *varipicta* and *Drosophila superba*. I hesitate to designate a state 2 for this condition because evidence from other



Figs. 95-137. Palpi of various ephyroids. 95. Curtonotidae. 96. Campichoetidae. 97-137. Drosophilidae.



Figs. 138-142. Hypopharynx and associated fields of sensilla in representative Drosophilidae, principally showing irregular arrangement of medial sensilla.

apomorphies clearly indicates a close relationship of *Diathoneura* and *Drosophila superba*. Thus, a conservative grouping in number of medial cibarial sensilla, where *Diathoneura* and *D. superba* are not separated, seems best for now. *Drosophila fenestrarum* had the autapomorphically highest number of medials at 35.

28. At the anterior end of the sclerotized, median tube on the cibarium, the hypopharynx [the "ductus salivarium" to Frey (1921), which it is not] is a group of four sensilla campaniformia (rarely three, or even reduced to one). Plesiomorphically, these sensilla make a square, with one each at a corner (figs. 138, 143). The apomorphy is an arrangement into a row of four sensilla, continued in the line of the hypopharynx, which apparently is a synapomorphy for some of the steganines (fig. 147). The linear arrangement also occurs in *Camilla glabra*, but is assumed here to be an independently derived feature. Very rare is the situation where two sensilla are in line

with the hypopharynx and two are perpendicular to these at about the midline, as in *Gitona bivisualis* and *Campichoeta* (fig. 146). In *Scaptomyza* (*Alloscaphomyza*) *mutica* and two *Diathoneura* species, there were three sensilla forming a triangle (figs. 139, 140). This last arrangement can be scored as plesiomorphic, but an alternative, multistate coding sequence (used in the analysis) is the following: squared arrangement (plesiomorphic)—[2 sensilla in line with hypopharynx + triangular arrangement (intermediate: apomorphic state 1)]—linear arrangement (most derived: apomorphic state 2). These campaniform sensilla probably detect direction and/or rate of saliva flow. After analysis with HENNIG86, it becomes apparent that the polarity of the feature indicated above may be incorrect. The linear arrangement is probably derived and thus would be synapomorphic for the Steganinae. This is in agreement with polarization based on outgroup comparison as well.

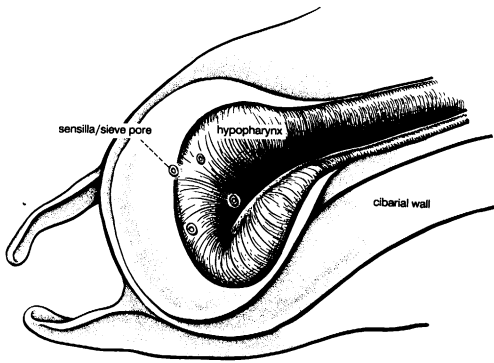


Fig. 143. Proximal end of derived type of drosophilid cibarium and hypopharynx.

29. Loss (apomorphic) of the trichia portion of the medial sensilla chaetica on the cibarium (figs. 138–142) is found in the following taxa: *Chymomyza*, *Diathoneura*, *Neotanygastrella*, *Drosophila superba*, *Lissocephala*, and *Nesiodrosophila*. It is likely that the trichia were reduced to a size too minute to observe under $700\times$ using light microscopy. Presence of a well-defined sensilla chaetica in the medial field is plesiomorphic.

30. Nested within apomorphy 29 is a state where the medial cibarial sensilla do not lie close to each other in a regular and evenly spaced row, particularly so at the posterior end of the hypopharynx where they can be very scattered (figs. 138–140, 142). In *Neotanygastrella tricoloripes* these sensilla form a sinuous, irregular row (state 1) (fig. 141). In addition, the medial sensilla are extended posteriad, past the level of the bases of the posterior cibarial sensilla (in *Neotanygastrella* they just reach to the two pairs of sensilla campaniformia flanking the hypopharynx). Possessing apomorphy 30 state 2 are *Chymomyza*, *Diathoneura*, and *Drosophila superba*. States 1 and 2 were unordered.

31. Apomorphically, the ventral wall of the cibarium is formed into a pear-shaped sclerite, with the posterior and medial cibarial sensilla in the broad end and the anterior end of the hypopharynx being narrow (fig. 152). Plesiomorphically, the ventral wall of the cibarium shows no such constriction and is oval or oblong (figs. 144–147).

32. In four taxa examined there was a scler-

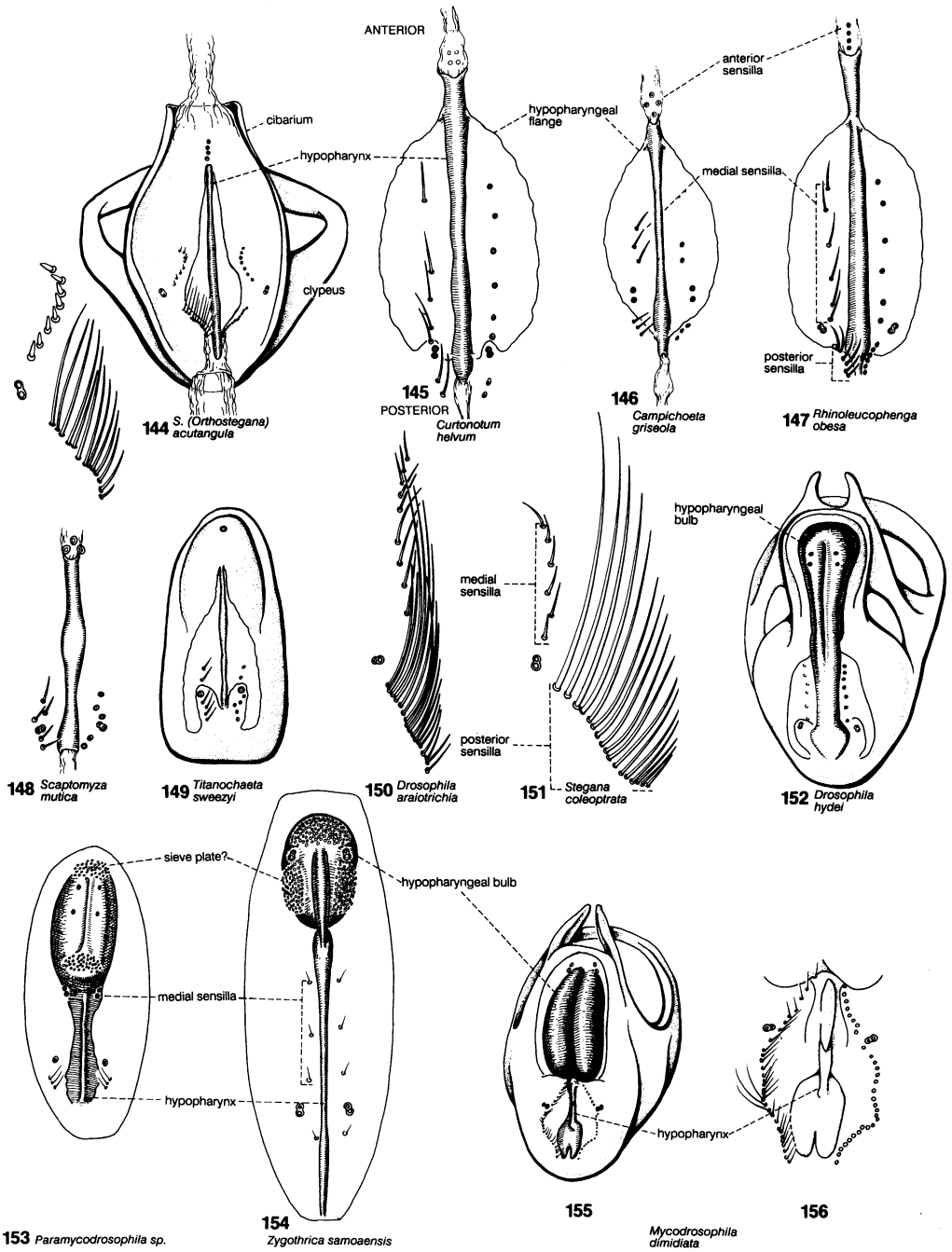
rotized, hypopharyngeal bulb [at the anterior end], which is very large and, thus, has reduced the length of the remaining, tubular portion of the hypopharynx (figs. 153–155). These taxa were *Zygothrica*, *Paramycodrosophila*, *Mycodrosophila*, and *Drosophila* (*Hirtodrosophila*) *nigrohalterata*. The length of the bulb exceeds or equals that of the tubular portion of the hypopharynx. Only in *Mycodrosophila dimidiata* were the posterior cibarial sensilla (autapomorphically) in a sinuous row (fig. 156). In *Paramycodrosophila* and *Paraliodrosophila bipartita* the medial sensilla were reduced to only one to two per side (state 2, other taxa above as state 1; series ordered).

33. Plesiomorphically, when the labella are separated they expose the fleshy lobes of the mesal surface. The pseudotracheal surface of the lobes generally faces forward and is lowered while the fly feeds. In *Drosophila* (*Phloridosia*), and even more pronounced in *Zaprionothrica*, are labella that are folded posteroventrad from the main part of the proboscis, somewhat like the proboscis in some milichiids. The feature is independently derived in the two taxa.

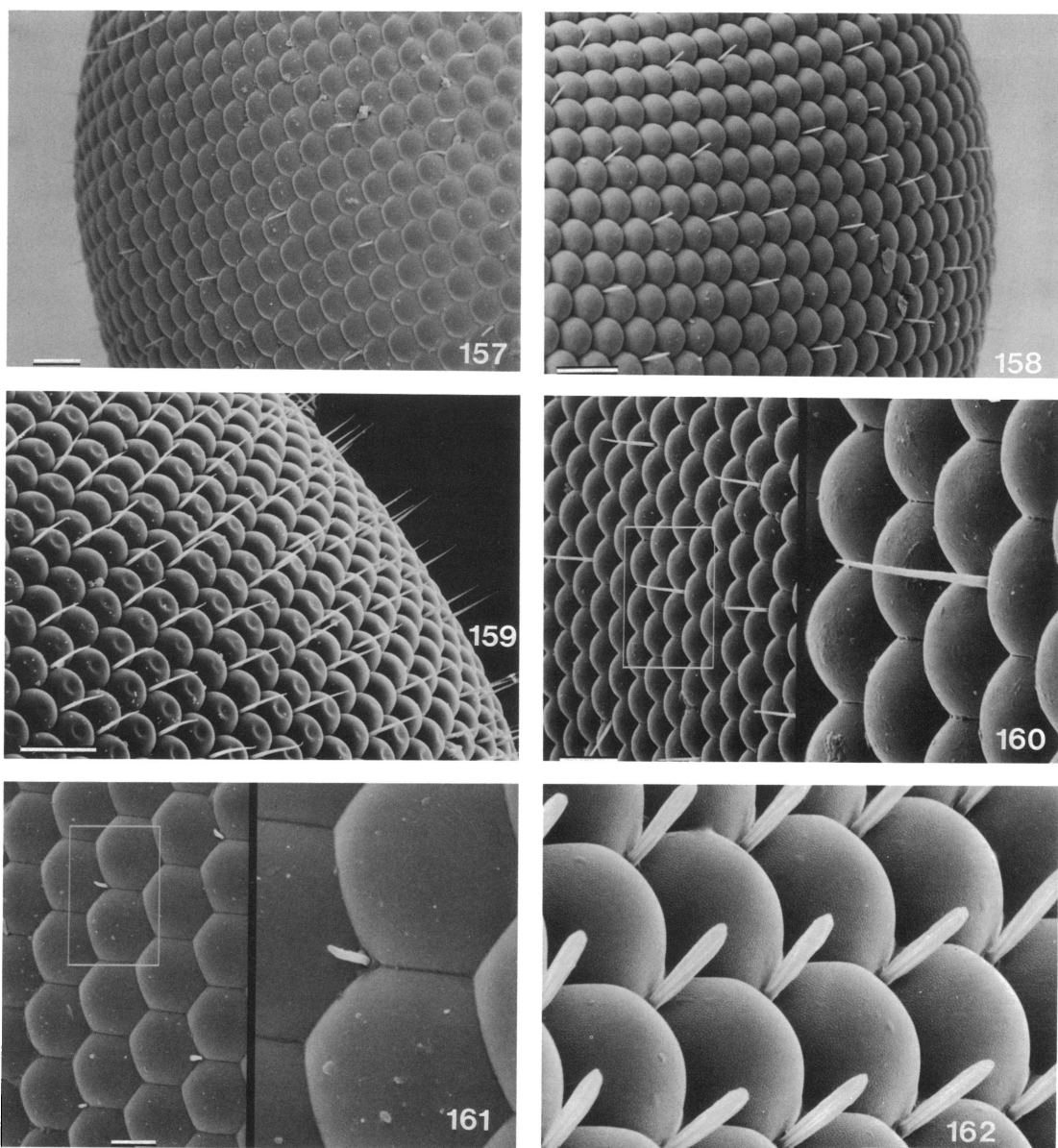
34. Four Hawaiian species studied have one of the most remarkable features known in drosophilids: the setae along the mesal edge of the labellar lobes in males are stout, sharp, and hooked, and they are several times longer than normal. Such setae are employed by males during that part of the courtship when they are closely tailing a female. The species surveyed having the trait were *Drosophila* (*D.*) *adiastola*, *D. araiotrichia*, *D. mimica*, and *D. scolostoma*.

35. Apomorphic to the condition where only one long, thin seta occurs at the apex of the palp, is the presence of two (sometimes three) stout setae (figs. 101–103). This feature is considered here to be synapomorphic for a large group in *Scaptomyza*.

36. In *Diathoneura*, *Cladochaeta*, and *Drosophila superba*, there is a broad, sclerotized, troughlike labium. The labellum folds up into the labium, between it and the clypeus (as seen in pinned specimens). This feature is derived from the state where the labium is not nearly so large and does not accommodate the labellum.



Figs. 144-156. Cibarium, hypopharynx, and associated sensilla in Curtonotidae (145), Campichoetidae (146), and Drosophilidae (144, 147-156).

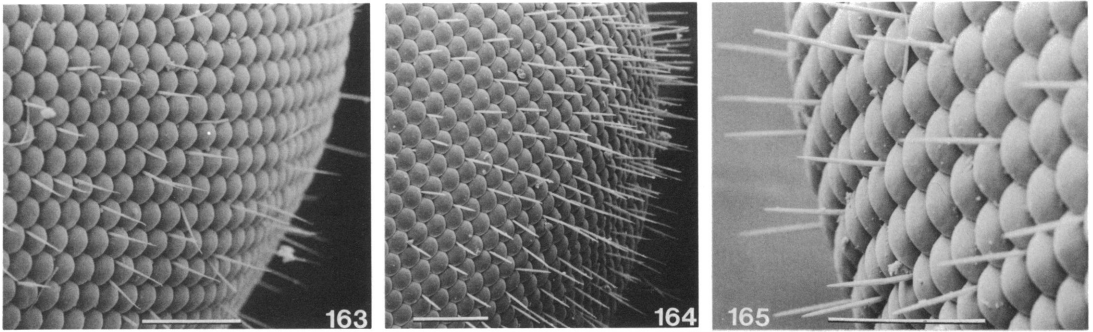


Figs. 157–162. Interfacetal setulae on eyes of Ephydroidea. 157. *Camilla glabra* (Camillidae). 158–162. Drosophilidae. 158. *Chymomyza amoena*. 159. *Cladochaeta inversa*. 160. *Stegana coleoptera*, with detail. 161. *Sphaerogastrella* sp., with detail. 162. *Drosophila duncani*, detail. Scale = 20 μ m.

EYES

37. Scanning electron microscopy has aided immensely toward understanding characteristics of the fine structure of drosophilid eyes. Eye (interfacetal) setulae can vary in density, length, and shape. Plesiomorphically, the eye has very sparse setae that are thin

and straight, the lengths of which are generally not much more than the diameter of a facet (figs. 157–160). This is true even at the middle portion of the eye, where eye setulae in drosophilids are longer and more dense. Derived directly from this condition are eye setulae that are thin and straight, but much longer (length up to twice the diameter of an



Figs. 163–165. Elongate, thin, dense, interfacetal setulae characteristic of some Hawaiian *Drosophilidae*. 163. *Ateledrosophila preapicula*. 164. *Titanochaeta ichneumon*. 165. *Drosophila atroscutellata*. Scale = 40 μm .

eye facet) (figs. 163–165). Such setae are usually most dense in the center of the eye (e.g., *Titanochaeta*), but here it lacks the even arrangement of setulae seen in apomorphy 38. Apomorphy 37 is found in some species endemic to the Hawaiian islands.

38. Another apomorphy of the plesiomorphic state described in character 37 is one where the eye setula is stout (length only three to eight times the diameter), lanceolate, and ribbed (figs. 168–177). In cross section the setulae appear as seven-pointed stars, as a result of the prominent ribs and deep furrows. Setulae of this form generally occur at high density: three setulae, each separated by an empty corner, surround a facet. The fact that this type of setula is independently derived from that in some Ephydriidae is seen by two fine structural details observed for *Hydrellia*: four, not three, setulae surround each facet, and the stout setulae have five, not seven, ribs (figs. 166, 167). This apomorphy is widespread among the *Drosophilidae*, particularly the more recently derived groups, and has been lost in one small group of southeast Asian genera (see ap. 41).

39. A modification of apomorphy 38 are eye setulae that are very stout (length is only three times the diameter; plesiomorphically the length is about eight times the diameter). These stout setulae have a tip tapered to a sharp point, except in *Drosophila (Dorsilopha) busckii*, which has a blunt tip (fig. 169). Apomorphy 39 was found in a variety of different drosophilid taxa, so may very well be independently derived, particularly since, as

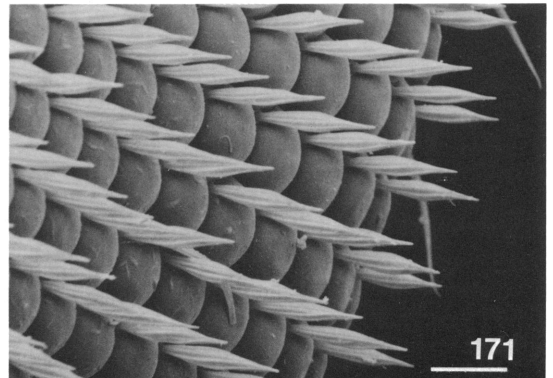
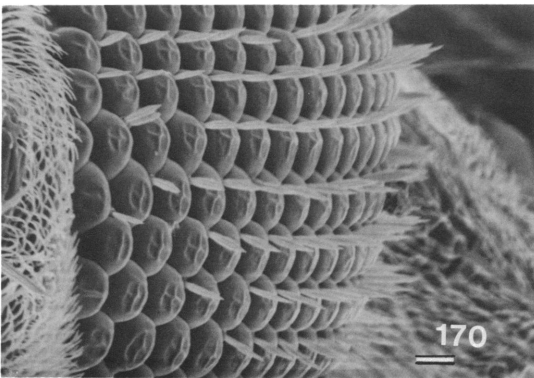
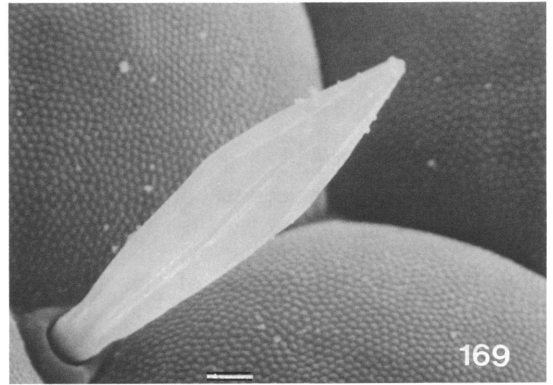
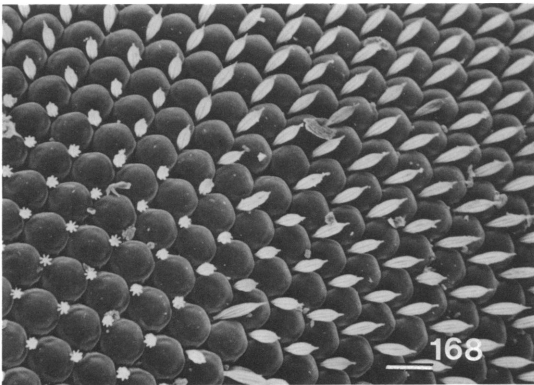
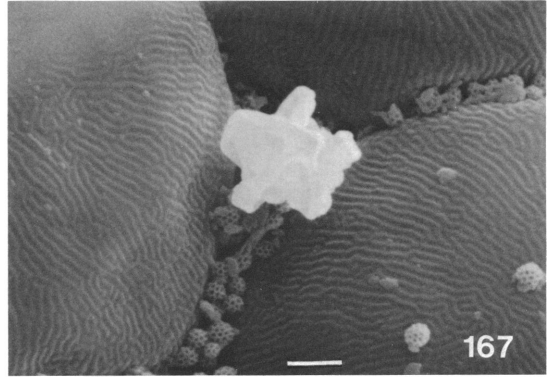
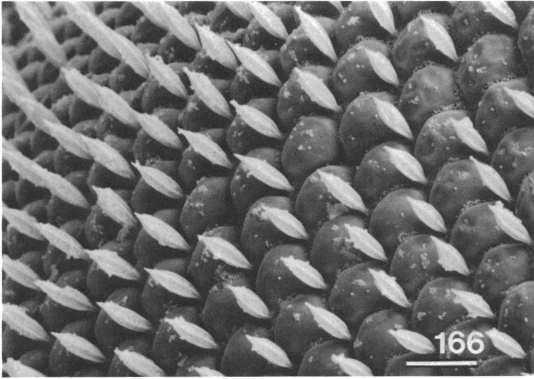
mentioned for *D. busckii*, slight structural differences exist.

40. Apparently another modification of apomorphy 38 is stout eye setulae that are not tapered to a narrow point, but blunt (fig. 162). This hypothesis is based on the arrangement of three setulae per facet, and the thickness and ribbing of the setulae. The feature was found only in *Drosophila (Hirtodrosophila) duncani*.

41. Apomorphic to the plesiomorphic condition described in character 37 are eye setulae that are very sparse (primitive), but also rudimentary in size and structure: the diameter of the facet is four to five times the length of the setula, and the setula tip is blunt (fig. 161). No ribbing is apparent on the setula. This feature was found in several of the Old World tropical genera: *Sphaerogastrella*, *Hypselothyrea*, *Lissocephala*, *Liodrosophila*, and *Tambourella*.

ANTENNAE

42. In three species examined there are two distinctive features of the pedicel and flagellomere 1. Apomorphy 42 is a pedicel that has an oblique ventral margin in lateral view, such that the anterior pedicel surface is much longer than the posterior surface (at least twice the length) (figs. 242, 243). This trait was found in three genera, all endemic to Hawaii (*Ateledrosophila preapicula*, *Celidosoma nigrocincta*, and *Grimshawomyia pallata*). It is considered here a synapomorphy for only the last two genera, defining these genera as a

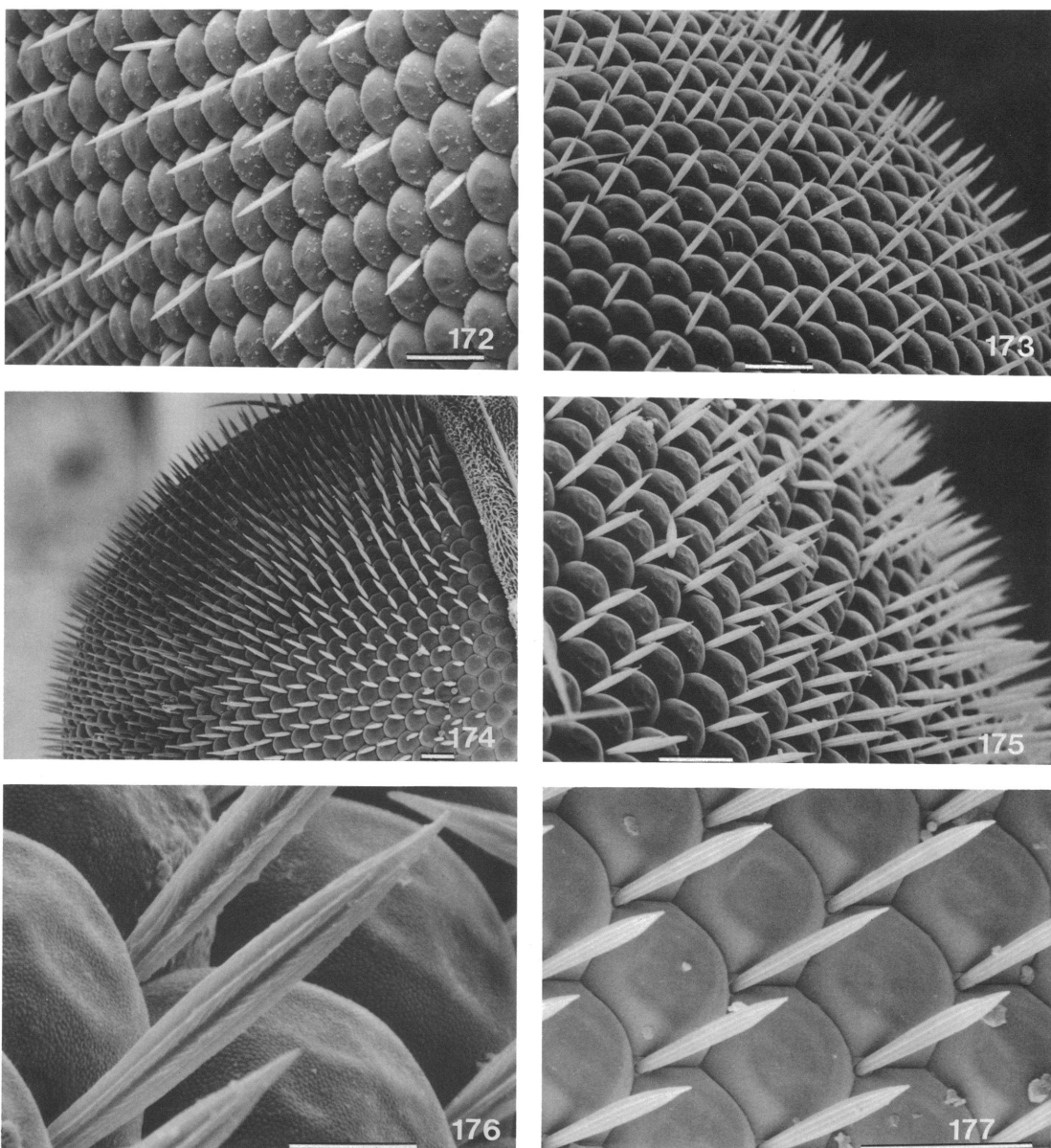


Figs. 166–171. Interfacetal setulae of an ephyrid (166, 167) and Drosophilidae (168–171). 166, 167. *Hydrellia griseola*, arrangement and detail. 168. *Dicladochaeta biseriata*. 169. *Drosophila busckii*, detail. 170. *Dettopsomyia formosa*. 171. *Scaptomyza* (*Rosenwaldia*) *abrupta*. Scale = 1 (figs. 167, 169) and 10 μm .

natural group. Plesiomorphically, the length of the anterior pedicel surface is about equal to that of the posterior surface. The pedicel is also situated very high on the face (figs. 242, 243, 253, 254), and this unusual placement may be synapomorphic with that seen

in the other Hawaiian group, *D.* (*Antopoce-*
rus).

43. Also found in the three taxa discussed in apomorphy 42 is a placement of the tiny flagellomere 2 on flagellomere 1 that is considerably below the ventral margin of the

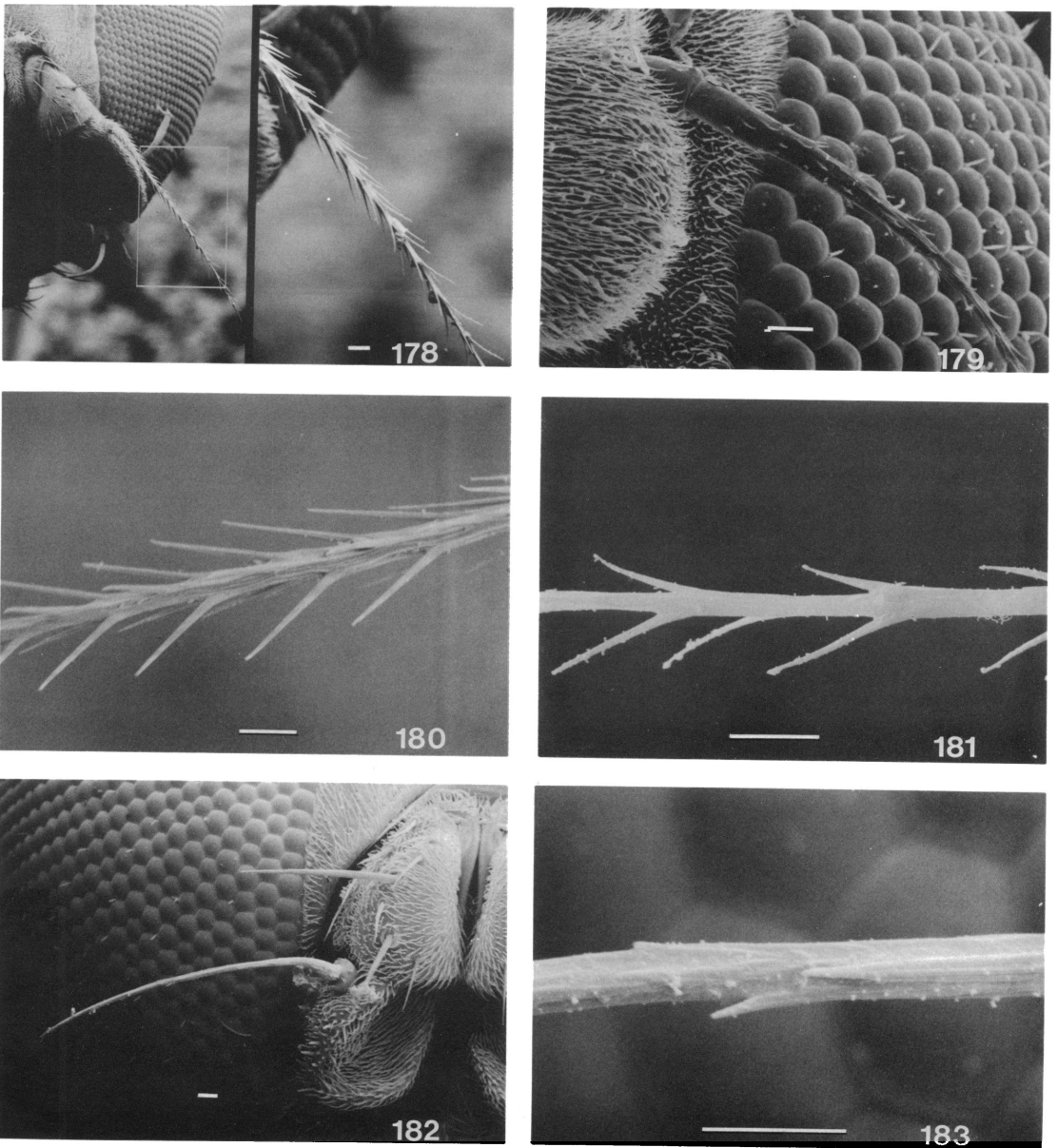


Figs. 172–177. Interfacetal setulae of Drosophilidae, showing stout, ribbed, dense type. 172. *Scaptomyza* (*Euscaptomyza*) *chylizosoma*. 173. *Drosophila* *quinaria*. 174. *Drosophila* *melanica*. 175, 176. *Drosophila* *repleta*, and detail. 177. *Zaprionus* *multistriatus*. Scales = 20 μm , 5 μm (177).

pedicel (fig. 186). The distance from flagellomere 2 to the ventral margin of the pedicel is equal to at least the length of flagellomere 2. Plesiomorphically the placement is near the ventral margin of the pedicel.

44. This apomorphy is the possession of a micropubescent arista (figs. 178, 179, 181–

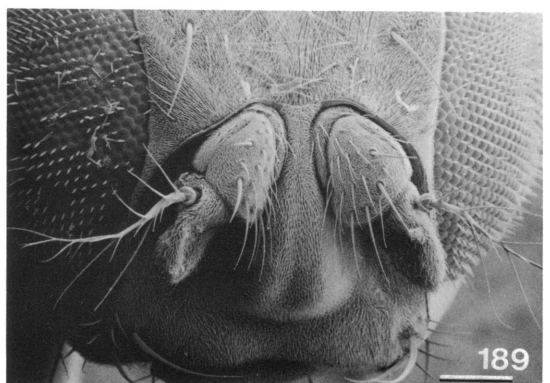
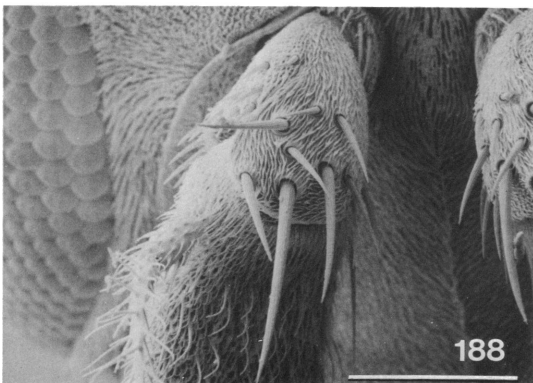
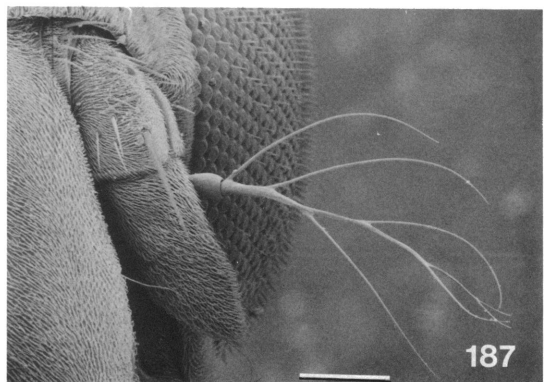
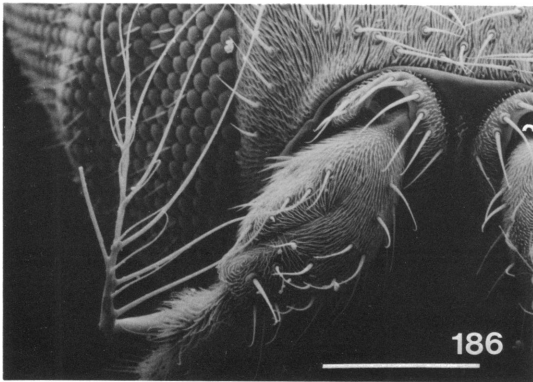
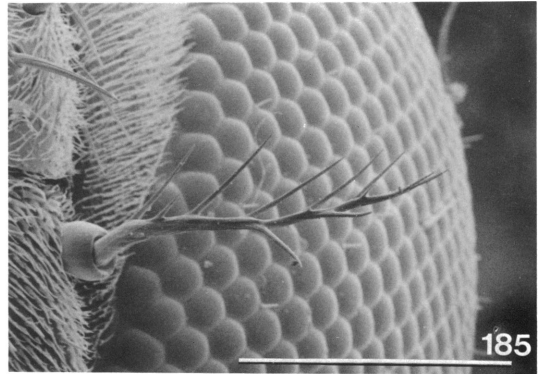
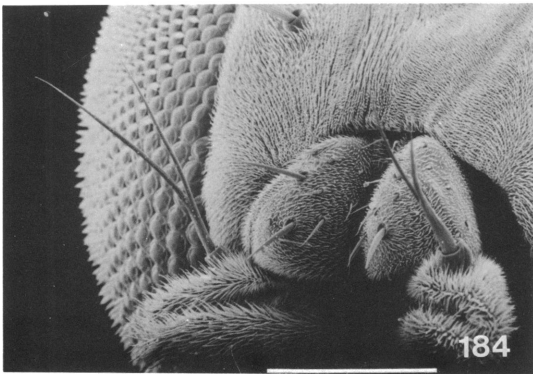
183). A plumose arista, where the dorsal and ventral branches are long (usually at least one-half the length of the arista trunk) and evenly spaced, has traditionally been a diagnostic character for the Drosophilidae. In some Ephydriidae (e.g., Hydrelliinae) and the Curtonotidae, a plumose arista occurs: at least



Figs. 178–183. Aristae with reductions/losses or primitive absence (180) of long dorsal-ventral branches. 178. *Cacoxenus guttatus*, with detail. 179. *Colocasiomyia stamenicola*. 180. *Campichoeta griseola* (Campichoetidae, all others Drosophilidae). 181. *Acletoxenus* sp. 182, 183. *Zapriothraca nudiseta*, with detail. Scale = 10 μ m.

for the Ephydridae it is quite distinctive, possessing only dorsal branches spaced increasingly farther apart apicad, and with very few, if any, minute medial branches. So the ephydrid and drosophilid plumose aristae are no doubt independently derived. Less ob-

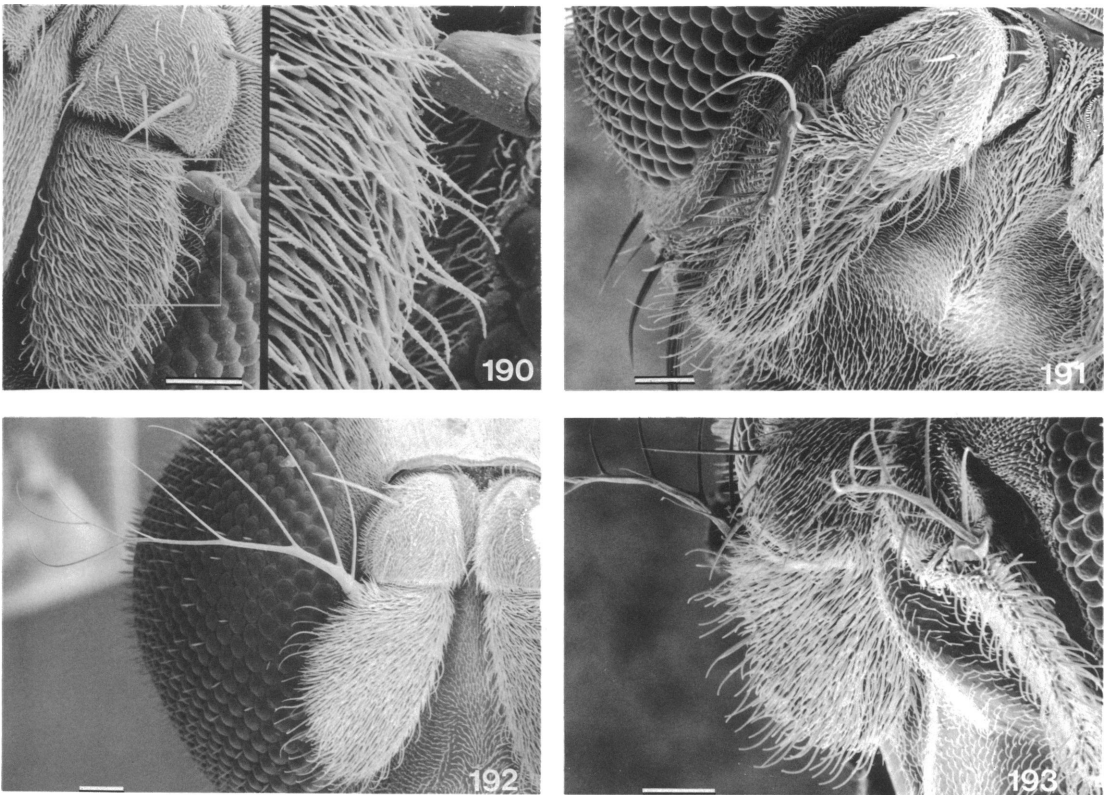
vious is the situation in *Camilla* (Camillidae), some *Diastata* (Diastatidae), and particularly the Curtonotidae. In the first two taxa the arista bears numerous short, medial branches and the dorsal + ventral branches can be two to four times the length of the



Figs. 184–189. Antennae or portions thereof of representative drosophilids (184–187, 189) and a diastatid (188). **184.** *Dicladochaeta biseriata*. **185.** *Zapriothrica dispar*. **186.** *Ateledrosophila preapicula*. **187.** *Zaprionus multistriatus*. **188.** *Diastata eluta*, pedicel. **189.** *Drosophila virilis*, face, showing numerous long setulae on mesal surface of pedicel. Scale = 100 μm .

medials; this is still shorter than the plumose arista type seen in most drosophilids. *Curtonotum* has an arista with a distinctive, derived-drosophilid structure: long dorsal and ventral aristal branches and the possession of short medial branches. The *Camilla* and

Diastata type of arista is viewed here as pleiomorphic for the Drosophilidae at the family level, and apomorphic to the situation seen in *Campichoeta* (Campichoetidae) (where the dorsal and ventral branches are about equal in length to the medials) (fig. 180). *Gitona*



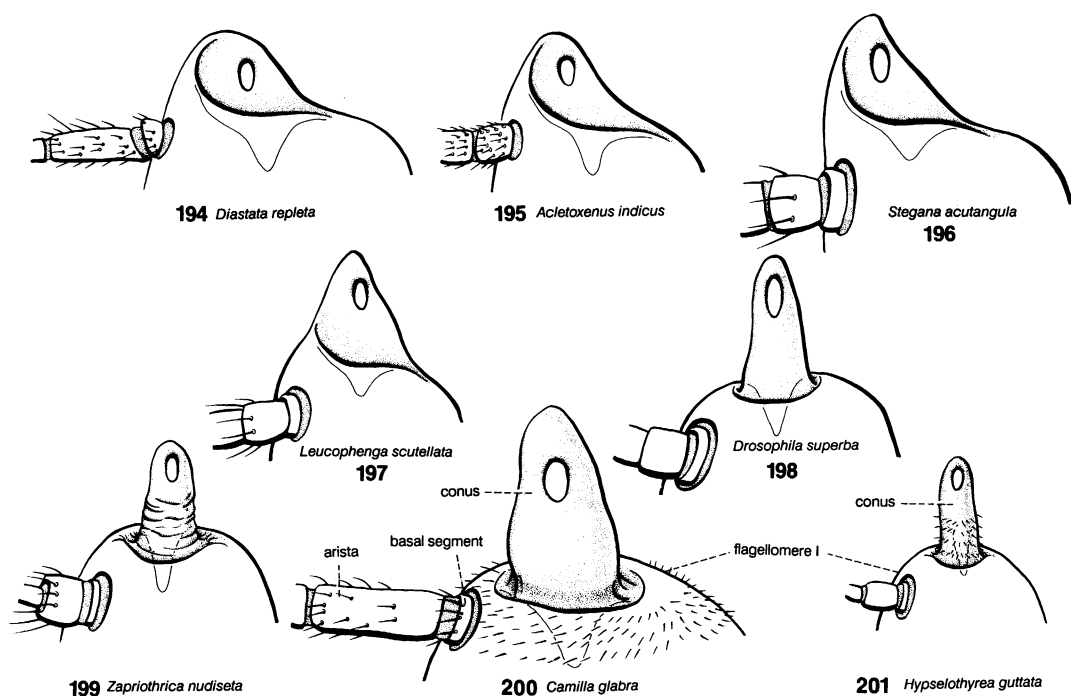
Figs. 190–193. Sensilla on flagellomere 1 of representative drosophilids, showing development of elongate sensilla in *Hirtodrosophila* (191–193). 190. *Drosophila testacea*, and detail. 191. *D. (Hirtodrosophila) duncani*. 192, 193. *D. (Hirtodrosophila)* spp. Scale = 40 μm .

bivisualis (Drosophilidae) has an arista superficially similar to that of *Campichoeta*, with the dorsal and ventral branch lengths only about twice that of the medials.

Thus, there are two opposing trends in the dorsal + ventral branch lengths: elongation of the branches, and reduction to one that is micropubescent (dorsal + ventral branch lengths less than five times diameter of the trunk) (figs. 178, 181) or even virtually bare (e.g., as in *Zapriothrica nudisetia*) (fig. 183). Apomorphy 44 is found in *Acletoxenus*, *Amiota (Sinophthalmus)*, *Apenethecia*, *Baeodrosophila pubescens*, *Cacoxenus (Gitonides)*, *C. (Paracacoxenus)*, *Colocasiomyia*, *Gitona brasiliensis*, *G. distigma*, *Mayagueza*, *Pseudistata*, *Rhinoleucophenga*, and *Zapriothrica*. In *Amiota picta* and *Apenethecia* the vestigial branches are small, fine hairs; in *Mayagueza* and *Acletoxenus* those hairs are much more dense and scaliform [see SEMs in Grimaldi

(1988)]. The arista condition in *A. picta* and *Apenethecia* is probably a further modification of the reduction in arista branch number and lengths, from that seen in, say, *Amiota (Phortica) variegata*.

45. The medial surface of the arista bears several rows of evenly and densely spaced setae, which resemble micropile, along either the entire or most of its length. Lengths of the branches are one to three times the width of the arista trunk; the trunk is very thick at the base of the arista. This unusual trait occurs only in some endemic Hawaiian species, as seen in *Drosophila (Antopocerus) adunca*, *D. (A.) longiseta*, and *D. (D.) hanaulae*. *Drosophila hanaulae* is plesiomorphic for the feature with respect to the other two species, for it retains in the male and female [not just in the female, as in *Drosophila (Antopocerus)*] the relatively longer dorsal and ventral branches. In all three species, as well, is the



Figs. 194–201. Proximal end of flagellomere 1 and basal aristemeres (flagellomeres 2–3/4) in Drosophilidae (195–199, 201), Diastatidae (194), and Camillidae (200).

additional condition, perhaps correlated, of short, evenly spaced dorsal and ventral branches. These are the largest drosophilids known.

46. Shared between the two *Drosophila* (*Phloridosa*) species and one of the two *Zaprionothrica* species studied is a derived type of arista with the medials reduced or lost, at least at the base; the trunk and branches are stout and short (fig. 185). *Phloridosa* and *Zaprionothrica dispar* have very similar antennae, but in *Z. nudiseta* and *Colocasiomyia stamenicola* vestiges of the branches remain only as a few scattered, tiny scales (further modification of apomorphy 46). Plesiomorphically, the arista bears dorsal and ventral branches about twice the length of the ones described above. The feature appears to be derived independently in the above two taxa.

47. Flagellomere 1 is plesiomorphically covered with a dense vestiture of setulae (actually, most are sensilla basiconica, etc.) that are even in length. At this node in the cladogram are those species with flagellomere 1 possessing setulae of two distinctive lengths:

the shorter, denser, “ground” ones and the sparser, long ones three to four times the length of the ground setulae (figs. 191–193). The trait occurs in most *Drosophila* (*Hirtodrosophila*) species, including *D. (H.) duncani*, *Microdrosophila quadrata*, and in some plesiomorphic *Zygothrica*, such as *Z. atriangula* (Grimaldi, 1987b). The trait apparently does not occur in *Mycodrosophila*, despite the close relationship of this genus to the above taxa. Some species in the subgenus *Drosophila* (e.g., *testacea* group; fig. 190) and in *Chymomyza* have long setulae on flagellomere 1, but these are only two to three times the length of the ground setulae.

48. Shared between *Drosophila* (*D.*) *virilis* and *D. (Dorsilopha)* *busckii* is a pedicel with 10–12 long setulae on the medial surface (fig. 189). Plesiomorphically, this surface has about five stout, short setulae. Distributions of other apomorphies, based on the HENNIG86 analysis, reveals these features to be independently derived.

49. Loss of all or all but one ventral, distal branch on the arista is apomorphic to the

condition where there are two, and usually more, long ventral branches. Dorsal and ventral branches are counted excluding the small terminal fork. This trait occurs in *D. (Hirtodrosophila)*, *Mycodrosophila*, *Paramycodrosophila*, and *Zygothrica*, and a few *Drosophila* (e.g., *cameraria*). In some large species of *Zygothrica* there is an unusually high number of ventral branches, perhaps allometrically related to a large increase in size and/or male hypercephaly.

50. The apomorphic state is an arista with the number of branches reduced to two or three (including the terminal portion of the trunk) (fig. 184). However, the trait can be intraspecifically quite variable [as in *Cladochaeta* “*nebulosa*” (there are several morphocryptic species), see Wheeler and Takada (1971)], and can differ considerably in fine details among species. In *Dicladochaeta* and *Laccodrosophila*, the first bifurcation is quite distal along the trunk; *Laccodrosophila*, however, has one and sometimes two ventral branches. The most common state in *Cladochaeta* “*nebulosa*” is a single bifurcation, at the base of the trunk; this one dorsal branch is about half the length of the trunk. In *Titanochaeta* and for eight *Scaptomyza* [(*Rosenwaldia*) and (*Tantalia*)] examined there is a large terminal bifurcation, and proximal to this is but one bifurcation in *Titanochaeta* and two in the *Scaptomyza* and in *Drosophila nigrosparsa* (obviously independently derived in the last two groups). The minute medial branches are virtually lost in all of the above species; the largest remnants of the branches are in the Hawaiian *Scaptomyza*. Apomorphy 50 is no doubt a feature appearing convergently, and will need to be redefined at various levels. The situation seen in *Scaptomyza*, and perhaps *Titanochaeta*, is probably synapomorphic.

51. There is a derived state of the arista at this node where five to seven long dorsal and about three long ventral branches are noticeably curved apicad (much more so than in some *Drosophila*), especially at the tips of the dorsal branches. This feature is seen in a group of genera endemic to the Indo-Pacific (*Hypselothyrea*, *Liodrosophila*, *Mulgravea*, *Sphaerogastrella*, and *Tambourella*). Plesiomorphically, long aristal branches are straight, with very little curvature.

52. There are four taxa that have the dorsal margin of the pedicel (best seen in lateral view) at the same level as or slightly higher than the dorsal margin of the eye (figs. 258–260): *Dettopsomyia*, *Mulgravea*, *Sphaerogastrella*, and *Tambourella*. The feature is most pronounced in *Dettopsomyia*, which has the dorsal part of the head nearly flat, and the pedicel is projected the most (among the other taxa) from the front of the head. Plesiomorphically, the vertical placement of the pedicel lies well within the height of the eye. Apomorphy 52 is very similar to the situation in several Hawaiian taxa, but it is not synapomorphic. In *Celidosoma* and *Antopocerus* the dorsal margins of the pedicel and eye are in line (nearly so in *Ateledrosophila*). Among the Hawaiian taxa, though, the trait is more developed in males, and the pedicels are of different structure (see apomorphy 42).

53. On the posterior (the proximal, or inner) surface of the pedicel are numerous stout, black setae, found in some picture-winged Hawaiian *Drosophila* species, such as *crucigera* and *engyochracea*. This may be homologous to those structures seen in some outgroup taxa, but it is lacking (plesiomorphically) in most *Drosophila*.

54. This feature was discussed under the section of “Position of the Drosophilidae in the Superfamily Ephydroidea,” as apomorphy C-6 and G-2, originally discovered by Hennig. The feature, termed the conus, is a tubular process, with an apical opening (fenestrum), that is on the dorsal surface of flagellomere 1 (figs. 198–201). It inserts into a deep concavity in the pedicel. I discussed this feature previously with respect to its structural variation and independent origin in three families that possess it; within the Drosophilidae, however, it does appear as a synapomorphy linking many genera. The feature is easily observed by disarticulating the pedicel from the rest of the antenna; they need not be KOH cleared. Minor variation was seen among drosophilids in the extent of basal annulation and the microtrichiation of portions of the dorsal process, but no consistent types were identified, nor were there any distinguishable differences seen in shapes.

Plesiomorphically the central portion of the dorsal surface of flagellomere 1 is concave, but there is a mediolateral flange which also

bears an apical fenestrum (figs. 194–197). The mediolateral flange and the dorsocentral process are obviously homologous, given the presence and position of the fenestrum on each. There are actually very few drosophilids, which are apparently rather primitive, that do not possess the dorsal process. *Leucophenga* and *Stegana* have a flange that is slightly longer and thinner than in other drosophilids, yet certainly not tubular; it possibly can be interpreted as transitional between the two states, but was not scored that way here. This feature is another one supporting the monophyly of the Drosophilinae.

55. Found in *Cacoxenus*, *Apenethecia*, and *Amiota* (*Sinophthalmus*) is a flagellomere 1 that is round or nearly so in the profile of its broadest side. Plesiomorphically it is ovoid or almost rectangular in shape.

56. Autapomorphic to *Drosophila* (*Antopocerus*) is a loss of aristomere 1 (flagellomere 2).

FRONT

57. Plesiomorphically, the front of the head is very finely striated on the frontal vittae and each ridge between furrows possesses a row of curved microtrichia. The density, length, and shape of the microtrichia vary: curved microtrichia that are separated from each other in the same row by two to three times their thickness are considered plesiomorphic (figs. 214, 215). Shared among *Hypselothyreia*, *Liodrosophila*, *Mulgravea*, and *Sphaerogastrella*, is a very large, shiny, ocellar triangle, often with a metallic sheen. [The large shiny area on the front seen in *D. (Hirtodros.) glabrifrons* is obviously convergent, for it is actually the frontal vittae devoid of microtrichia but still finely striate and thus shiny.] The triangle is devoid of striae (completely smooth in *Sphaerogastrella* and slightly rugose in *Mulgravea*). It has displaced the frontal vittae into narrow, densely micropubescent strips lying between the triangle and a similarly glabrous frontal-orbital plate (figs. 206, 222). *Tambourella* has a finely pruinose front and would thus be plesiomorphic to the above taxa for this trait.

58. Seen in several genera, including one drosophilid outgroup, *Camilla glabra*, is a frontal vitta that is devoid of microtrichia.

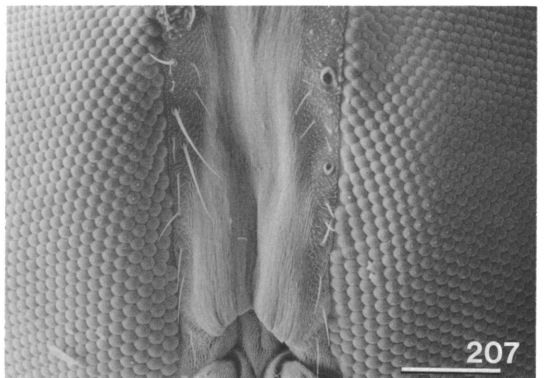
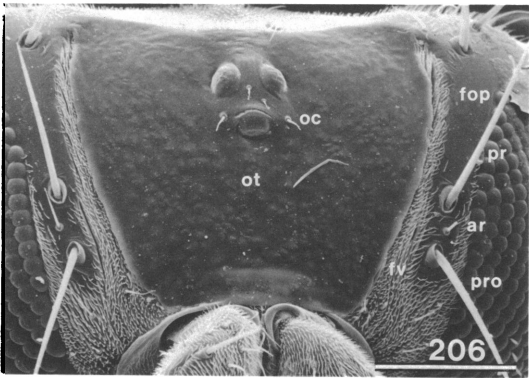
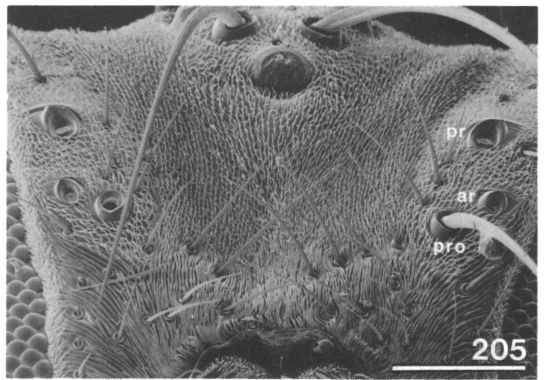
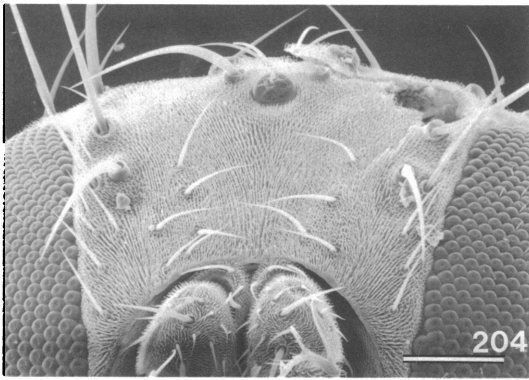
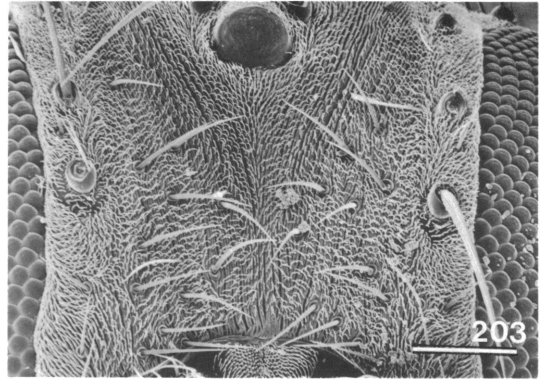
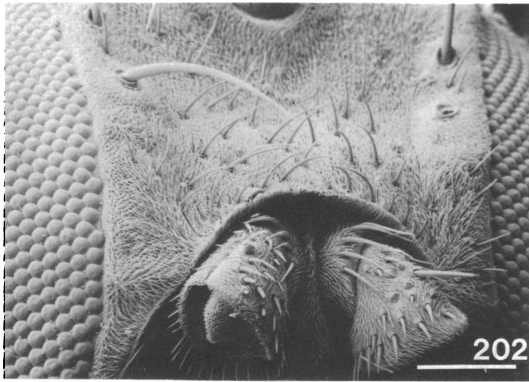
Instead, the striae are the conspicuous features on the surface (figs. 216–219). Heads of this sort, as observed for *Lissocephala unipuncta*, *L. sabroskyi*, and *Camilla glabra* are entirely shiny in frontal view. However, a fine striation is apparent on the frontal vitta using incident light, which gives it as well a slightly dull shine compared to the ocellar triangle and the frontal-orbital plates. The plesiomorphic state is discussed under apomorphy 57 (see also apomorphy 62 for another derived state similar to apomorphy 58).

59. *Drosophila xiphophora* and *Laccodrosophila flavescens* both possess an extensive pair of frontal vittae, being coalesced along most of the front of the head. They are black-brown and finely striate (but shiny) under incident light. Under SEM magnifications of *L. flavescens*, the vittae are rugose and devoid of microtrichia (fig. 218). In *D. xiphophora* the vittae are also rugose, but possess fine, erect microtrichia (fig. 223), which are shorter and less dense than those discussed under apomorphy 60.

60. Autapomorphic to *Zapriothrica* is a deeply striate, but narrow, frontal vitta that possesses microtrichia that are long and fine, erect, and quite dense. The microtrichia extend to the ocellar triangle and the frontal-orbital plates, but here they are much less dense (figs. 224, 225).

61. The plesiomorphic state for the number and distribution of interfrontal setulae is the presence of about 20 short setulae scattered on the anterior half of the front of the head (figs. 203, 208, 209). Several opposing trends are apparent, in the reduction and multiplication of the plesiomorphic number. Apomorphy 61, the presence of 50 or more interfrontal setulae, is found in *Pseudiasata* and *Rhinoleucophenga* (the latter has about twice the number of interfrontals as the former) (fig. 213). This trait was discussed in relation to the phylogenetics of several genera of lower Drosophilidae [apomorphy 18A in Grimaldi (1988)]. In that study, numerous interfrontals were hypothesized to be independently derived between the above two genera. See apomorphies 65 and 66 for modifications of the interfrontals similar to that of apomorphy 61.

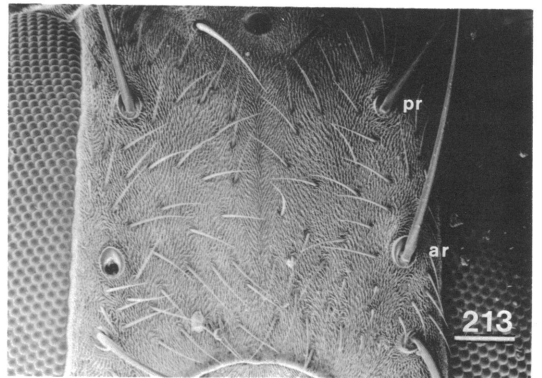
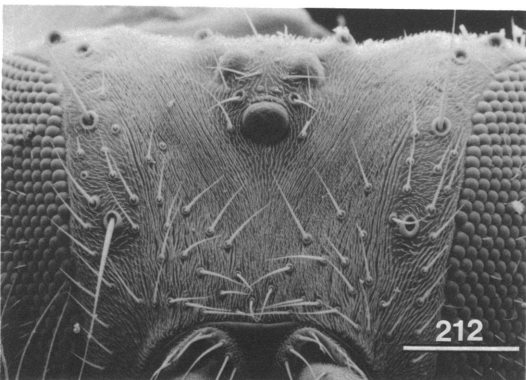
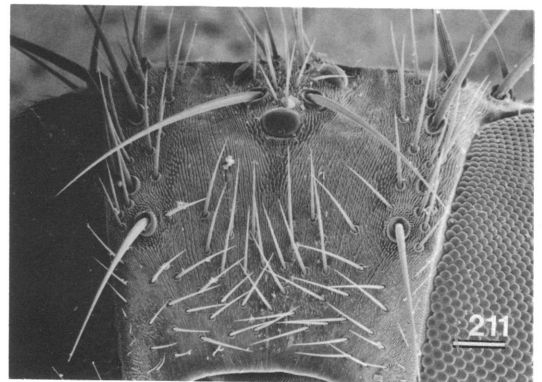
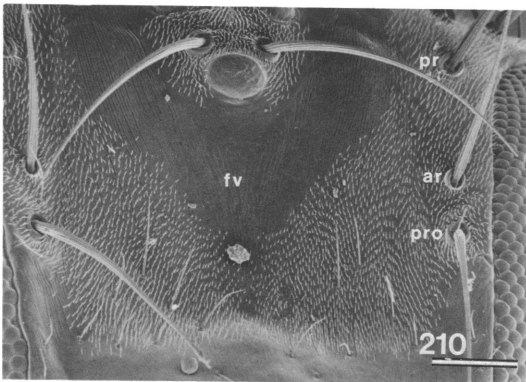
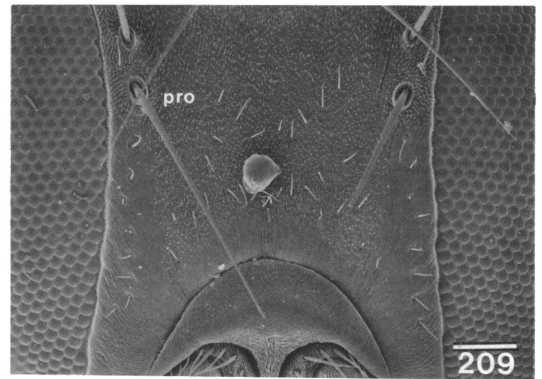
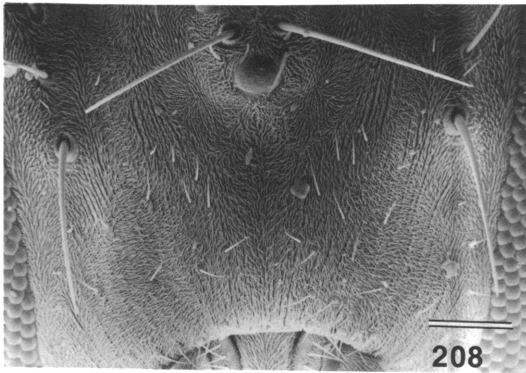
62. Also discussed in Grimaldi (1988) are the apomorphies that illustrate an *Acletoxe-*



Figs. 202–207. Frontal portions of drosophilid heads. 202. *Cacoxenus perspicax*. 203. *Gitona bivisualis*. 204. *Cladochaeta inversa*. 205. *Titanochaeta sweezyi*. 206. *Mulgravea* sp. 207. *Acletoxenus* sp. ar, anterior reclinate orbital seta; fv, frontal vitta; fop, frontal orbital plate; oc, ocellar seta; ot, ocellar triangle; pr, posterior reclinate orbital seta; pro, proclinate orbital. Scale = 100 μ m.

nus-Mayagueza sister-group relationship. Apomorphy 16 of that study, but 62 of this one, is a narrow facial and frontal region, the width of which is equal to only about the distance between the outer ocelli (fig. 207). Plesiomorphically, this width is three times

or more the width between the outer ocelli. Also seen in these two genera, and not discussed in my earlier paper, is a front devoid of microtrichia: only the rugosities, which run parallel to the long front, still remain (fig. 219). The frontal vittae are joined and occupy

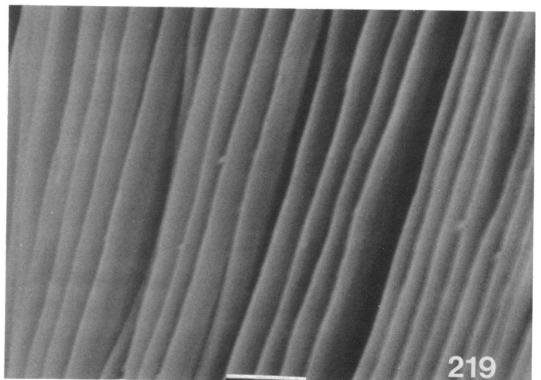
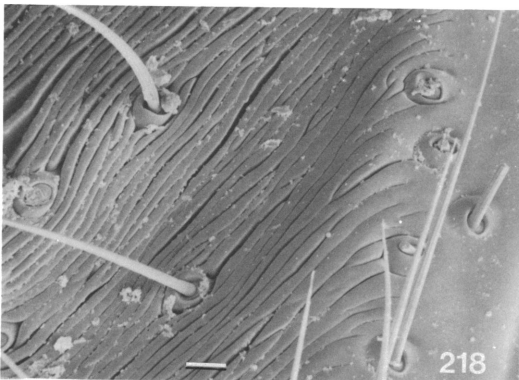
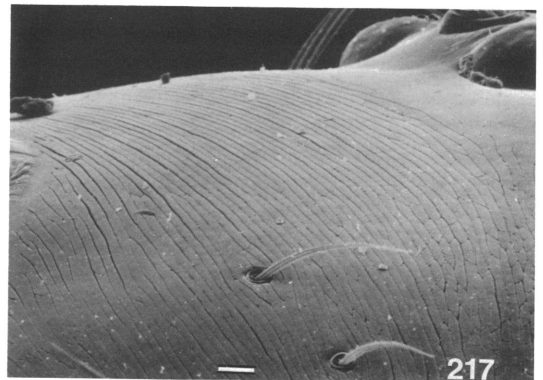
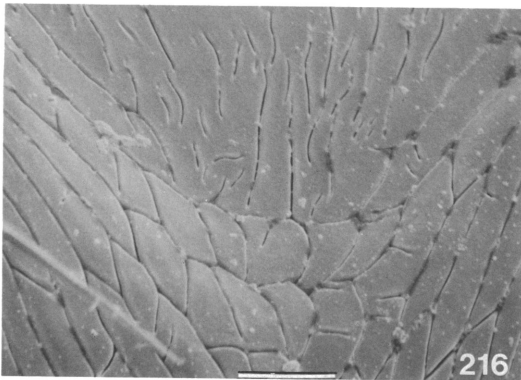
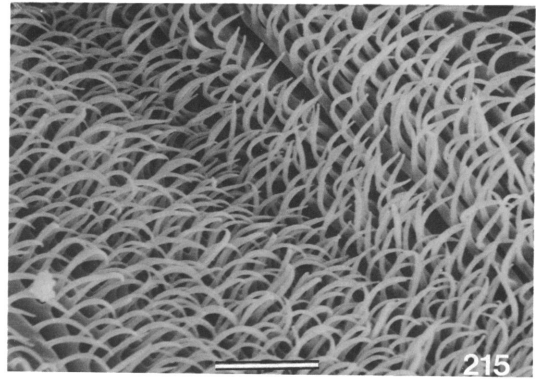
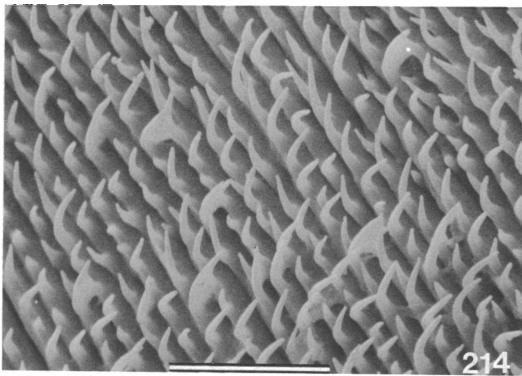


Figs. 208–213. Frontal portions of drosophilid heads. 208. *Amiota* (*Sinophthalmus*) *picta*. 209. *Stegana* (*Stegana*) *vittata*. 210. *Stegana* *coleoptrata*. 211. *S.* (*Orthostegana*) *sp.* 212. *Ateledrosophila* *preapicula*. 213. *Pseudiasata* *vorax*. Abbreviations as in fig. 206. Scale = 100 μm .

the entire middle portion of the front of the head.

63. Short, stout interfrontal setulae are seen in *Cacoxenus* and in three of the *Gitona* species that were studied (fig. 202). Most of the interfrontals point mediad. The plesiomorphic condition is discussed under apomorphy 61.

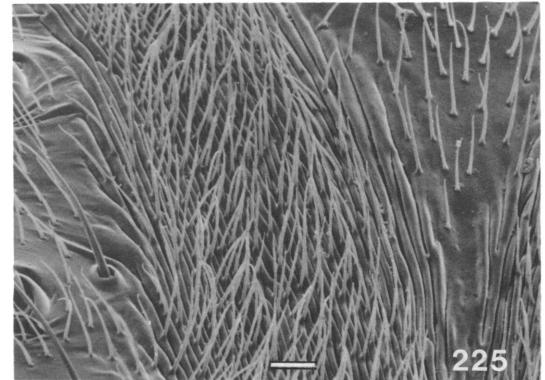
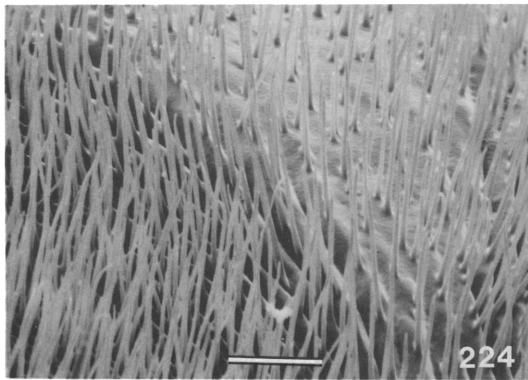
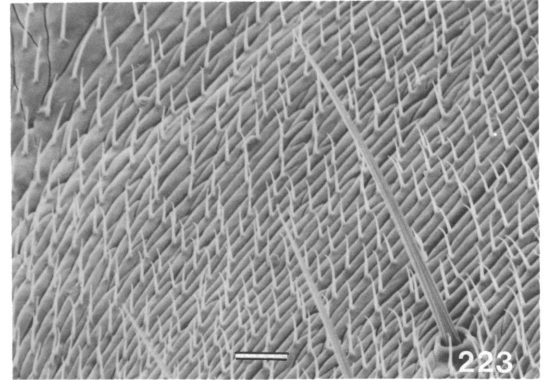
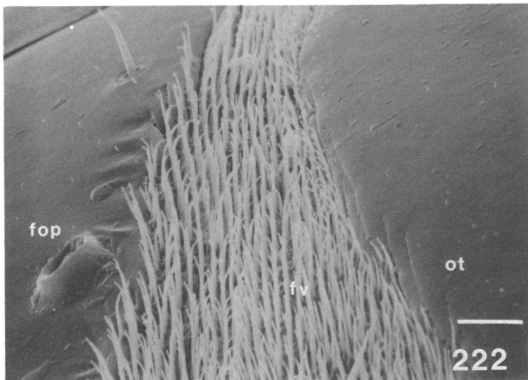
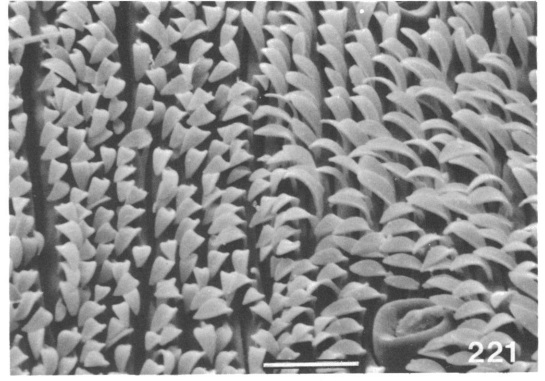
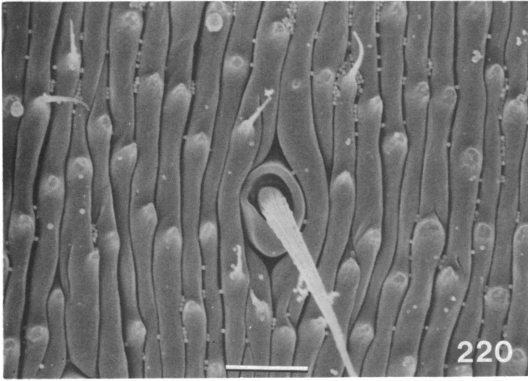
64. Frontal microtrichia that are tiny and scalelike were found in *Stegana* (*Stegana*) *vittata*, *S.* (*Steganina*) *coleoptrata*, and were most developed in *Eostegana* *ortalidoides* (of these three species that were examined using the SEM, and grouped under state 2) (figs. 220, 221). In *Stegana* (*Orthostegana*) these minute scaliform microtrichia are sparse and



Figs. 214–219. Detail of frontal vittae of some ephydroids. 214. *Diastata eluta* (Diastatidae). 215. *S. (Alloscaptomyza) stramineifrons* (Drosophilidae). 216. *Camilla glabra* (Camillidae) apex of ocellar triangle and junction of vittae. 217–219: Drosophilidae. 217. *Lissocephala unipuncta*. 218. *Laccodrosophila flavescens*. 219. *Acletoxenus* sp. Scale = 10 μm , 2 μm (219).

only occur on the anterior portion of the front (state 1); the rest of the front is densely microtrichose. Under incident light the frontal vitta appears bare. The plesiomorphic state of the frontal vitta is discussed under apomorphy 57. States 1 and 2 were unordered.

65. In the two species examined here in the subgenus *Orthostegana* (*acutangula* and a species from Luzon, Philippines) there are numerous, spikelike interfrontal setulae (fig. 211). The dorsomedial ones point dorsad, and the others point mediad. In *Eostegana or-*

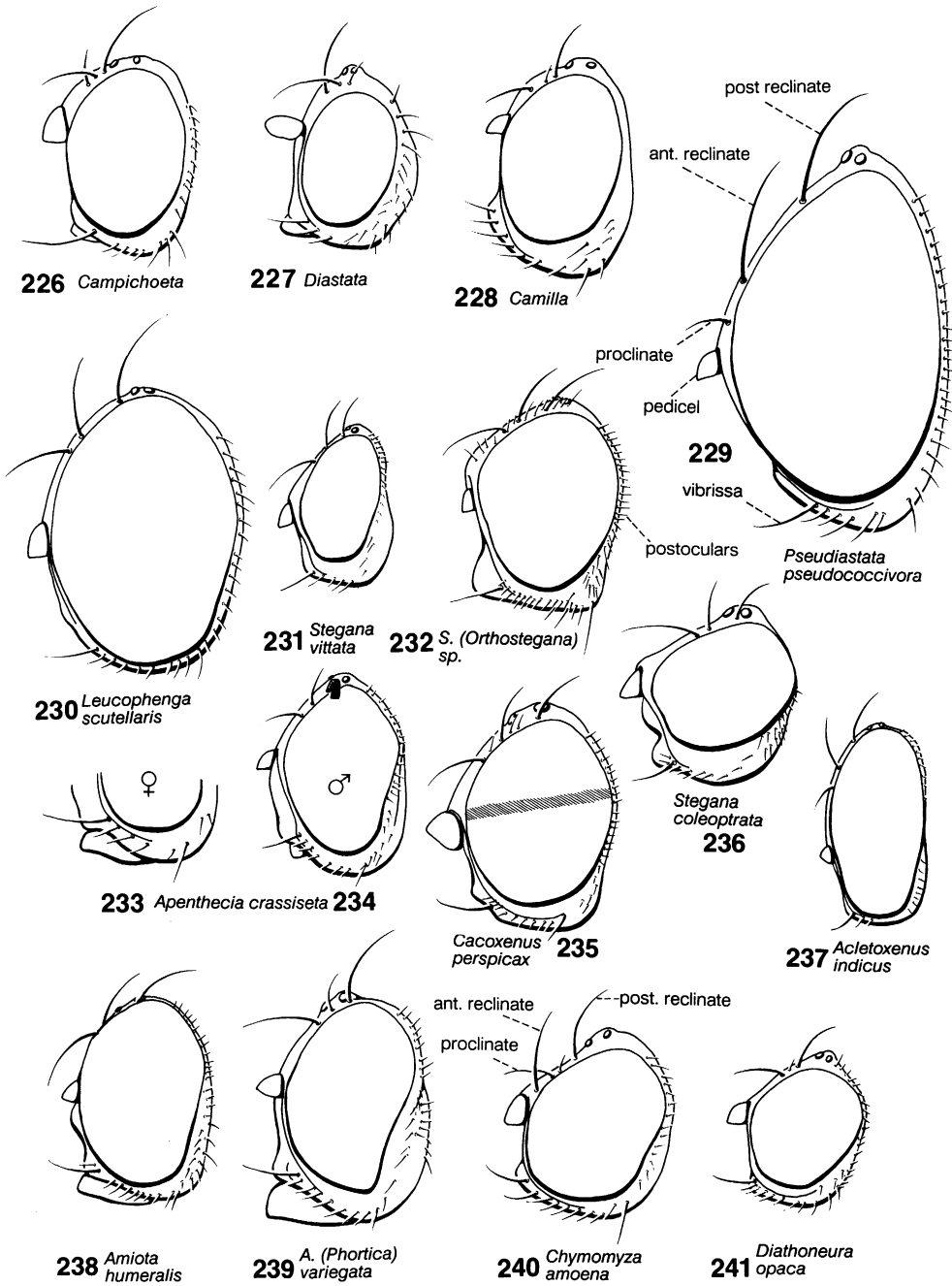


Figs. 220–225. Detail of frontal vittae of drosophilids. 220. *Stegana vittata*. 221. *Eostegana ortalioides*. 222. *Sphaerogastrella* sp. (showing frontal orbital plate, frontal vittae, and ocellar triangle). 223. *Drosophila xiphophora*. 224. *Zaprothrica dispar*. 225. *Zapriothrica nudiseta*. Scale = 10 μm .

talidoides the interfrontals are also numerous, with the dorsomedial ones pointed dorsad, but all of the interfrontals are considerably shorter than those in *Orthostegana*. The state in *Eostegana* is plesiomorphic to that in *Orthostegana*.

66. Shared between *Titanochaeta* and *At-*

eledrosophila are long interfrontal setulae (fig. 212), which are exceptionally long in *Titanochaeta* (like all setae on the head), and so species in this genus are grouped under state 2. Ocellar setae in *Titanochaeta* are also very long; those in *Ateledrosophila* are rudimentary (being shorter than the interfrontals).

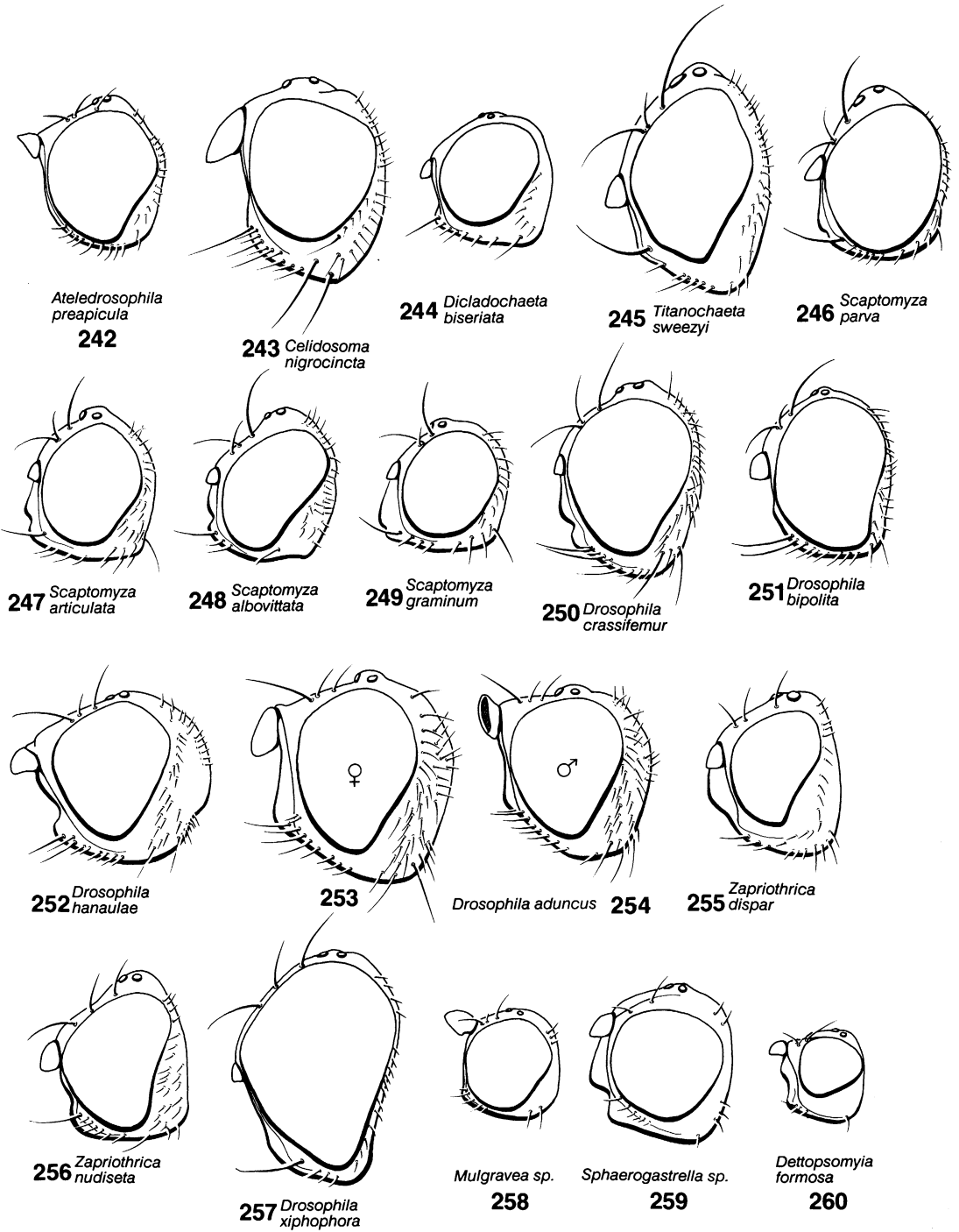


Figs. 226-241. Lateral view of heads of ephyroids. 229-241. Drosophilidae. All to same scale.

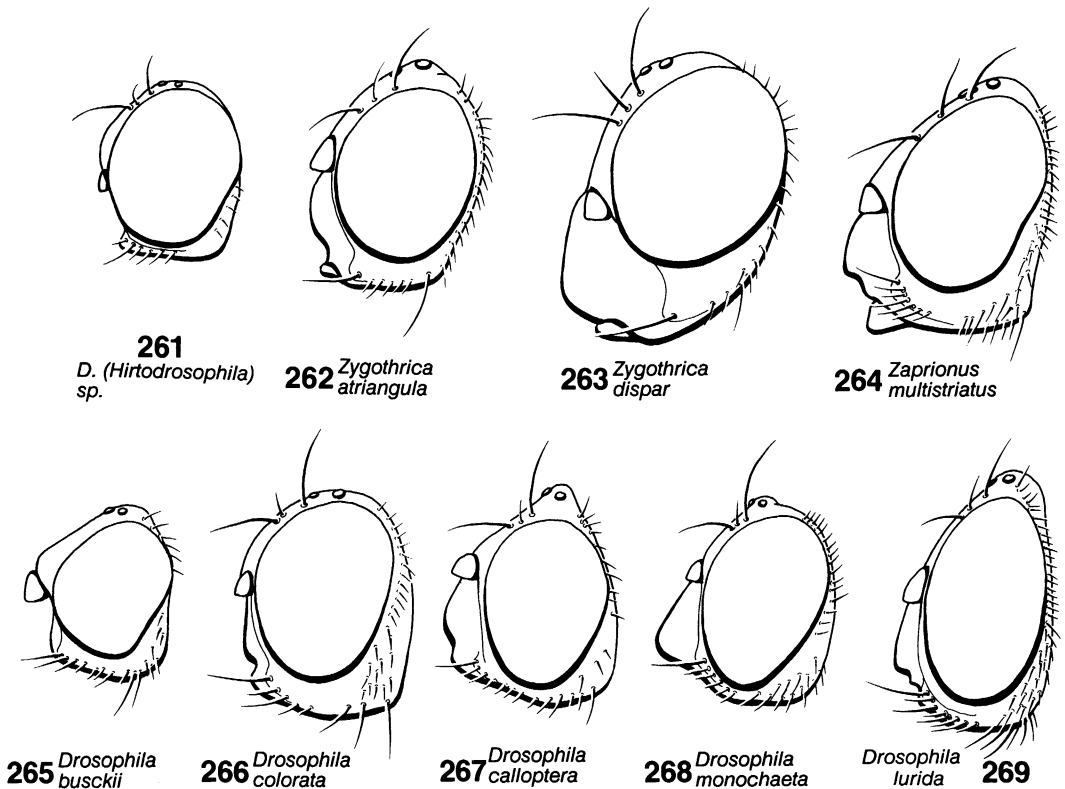
States 1 and 2 were unordered. This feature is apparently independently derived between the two groups.

67. In a large number of *Scaptomyza* species

there is reduction in the plesiomorphic number of interfrontal setulae of about 20 to between two and six. These setulae are of standard size.



Figs. 242-260. Lateral view of heads of Drosophilidae. Not all to the same scale.



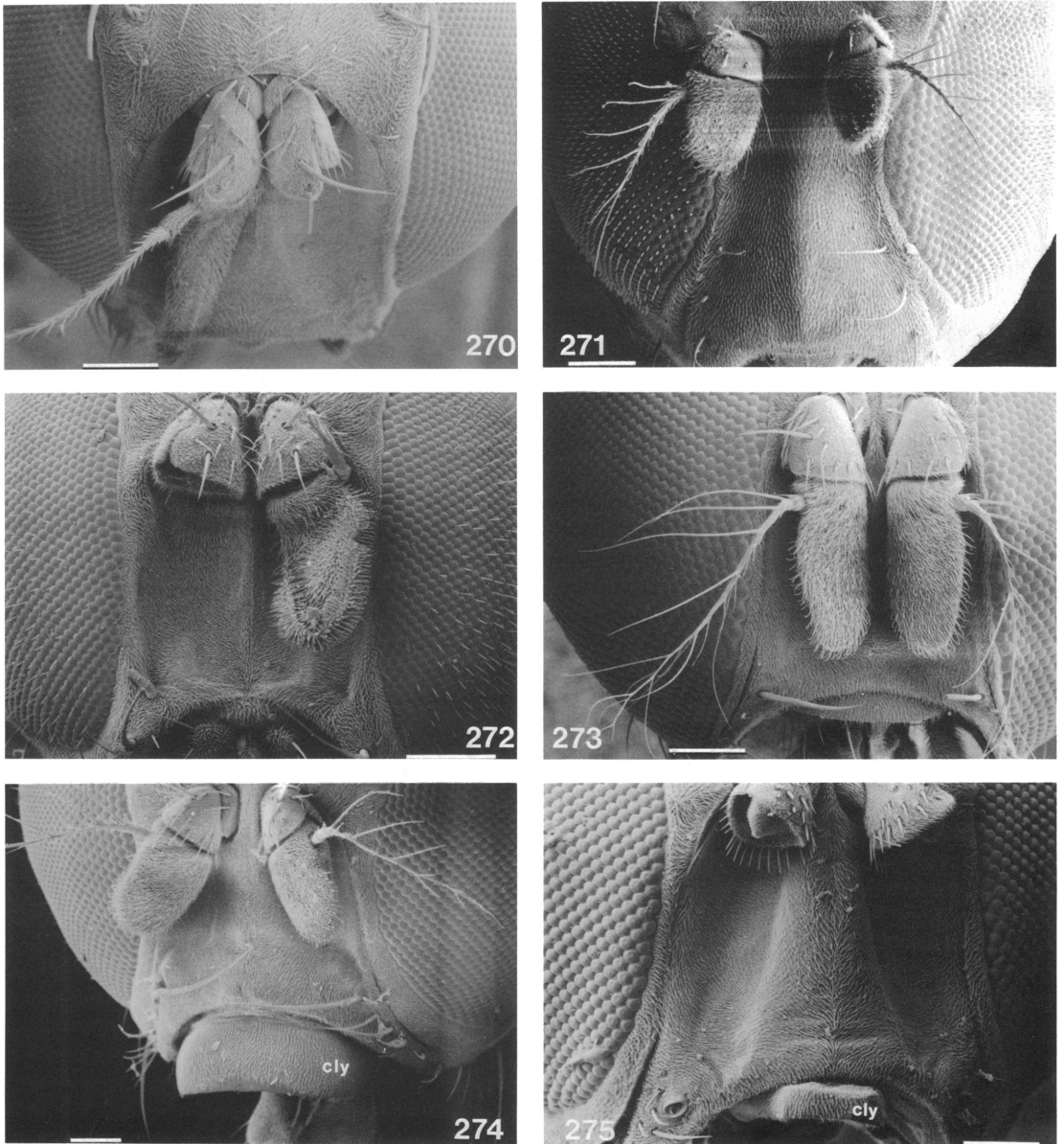
Figs. 261-269. Lateral view of heads of Drosophilidae. All to the same scale.

68. In order from anterior to posterior is the following plesiomorphic arrangement of the orbital setae: proclinate, anterior reclinate, posterior reclinate, with the anterior reclinate lying about one-half of the distance between the other two ipsilateral orbitals (e.g., figs. 228-239). In lateral view of the head the anterior reclinate apomorphically lies just lateral or slightly anterolateral to the proclinate (apomorphy state 1) (figs. 246-251). This situation is found in *Cladochaeta*, *D. (Scaptodrosophila)*, *Dettopsomyia*, and related genera, several Hawaiian *Drosophila*, *Scaptomyza*, and in *Neotanygastrella*. The trait can be slightly variable within a species. For example, in *S. (Tantalia) albovittata* the anterior reclinate was found to lie anterior as well as lateral to the proclinate to various degrees. In apomorphy state 2, the arrangement of orbitals in *Chymomyza* (fig. 240) is an even further modification in the anterior displacement of the anterior reclinate orbital

seta. In *Chymomyza* this seta may be either slightly lateral to or directly in front of the proclinate. States 1 and 2 were unordered; the trait is most likely convergent among several genera.

69. In lateral view of the head the proclinate and anterior reclinate orbital setae are very close together, the anterior reclinate thus being separated from the posterior reclinate by a distance two or more times that between the anterior reclinate and the proclinate (fig. 230). In addition, the posterior reclinate is approximately at the level of the median sulcus or even higher. This trait is autapomorphic to *Leucophenga*; plesiomorphically, the arrangement of the orbitals is as described in apomorphy 68.

70. Plesiomorphically (at this level), the anterior reclinate is about one-third to one-quarter the length of the other orbitals, but in *Dettopsomyia* and *Diathoneura* the anterior reclinate is minute (about one-eighth the

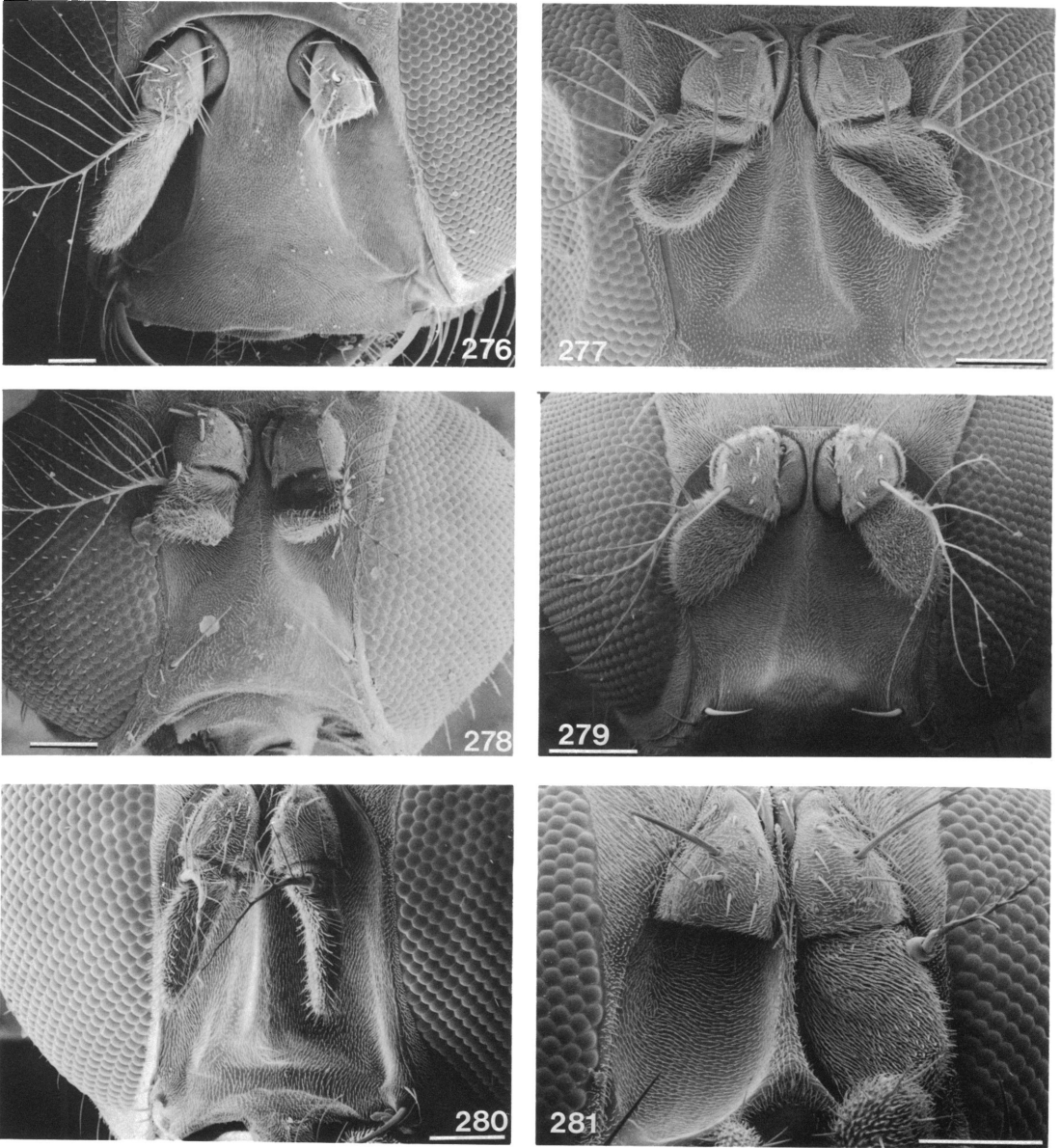


Figs. 270–275. Faces of representative ephydroids. 270. *Campichoeta griseola* (Campichoetidae). 271. *Hydrellia griseola* (Ephydriidae). 272–275. Drosophilidae. 272. *Titanochaeta ichneumon*. 273. *Leucophenga varia*. 274. *Amiota (Phortica) variegata*. 275. *Cadoxenus perspicax*. cly, clypeus. Scale = 100 μm .

other orbitals) (state 1) (figs. 241, 260). In *Hypselothyrea*, *Liodrosophila*, *Lissocephala unipuncta* (but not *sabroskyi*), *Microdrosophila*, *Mulgravea*, *Sphaerogastrella*, and *Tambourella*, the anterior reclinate is either extremely minute or completely lost (even under

SEM magnifications) (e.g., fig. 206). These seven taxa should represent another apomorphy, nested within state 1, which would be apomorphy state 2. States 1 and 2 were unordered.

71. *Laccodrosophila flavescens* was found



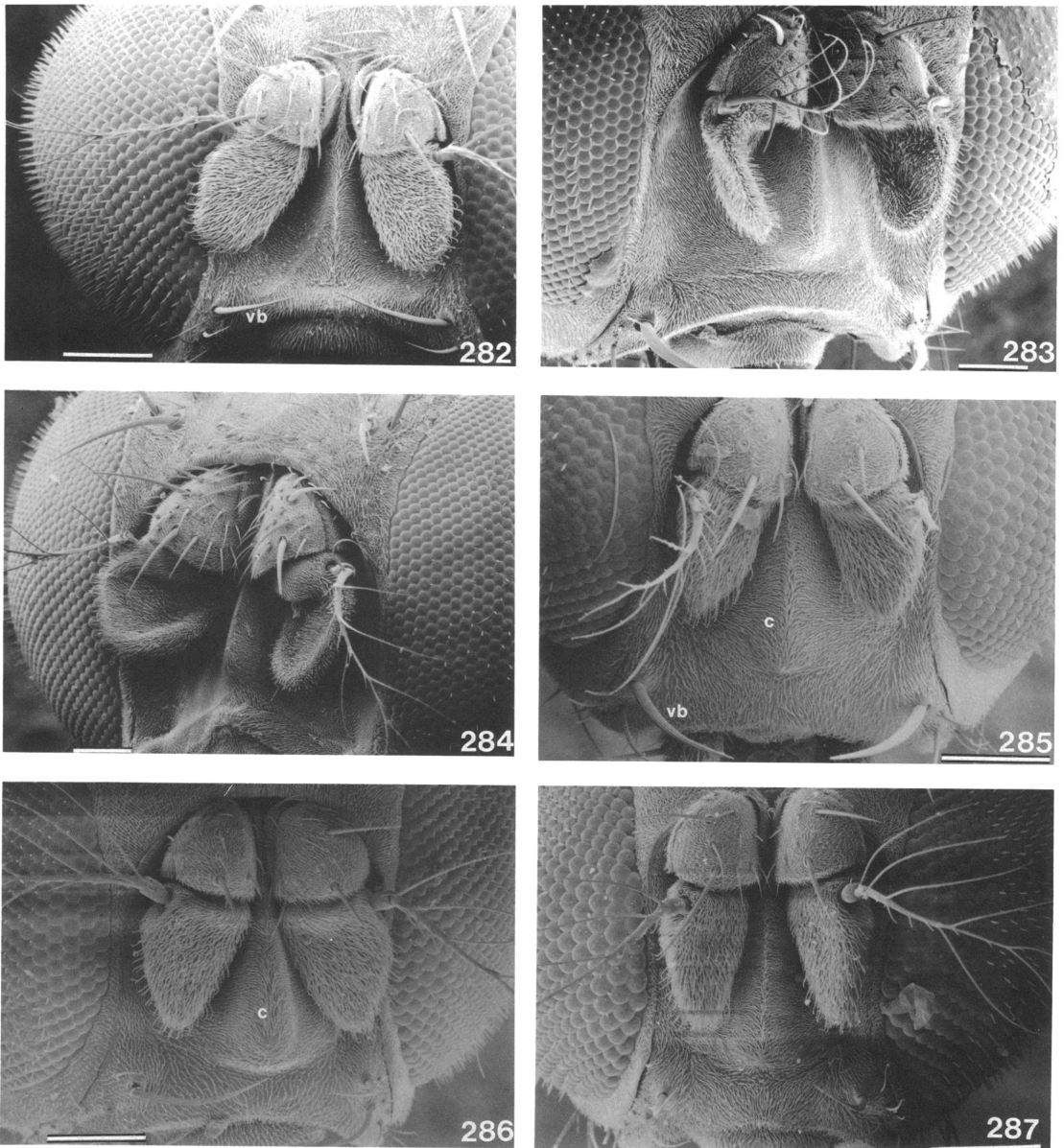
Figs. 276–281. Faces of representative Drosophilidae, showing various facial carinae. 276. *S. (Orthostegana)* sp. 277. *Drosophila hirtitarsus*. 278. *Scaptomyza (Bunostoma)* sp. 279. *Neotanygastrella tricoloripes*. 280. *Drosophila xiphophora*. 281. *Zapriothrica dispar*. Scale = 100 μ m.

to autapomorphically have strongly divergent posterior reclinate orbitals. Plesiomorphically, they are projected backward and are parallel to slightly divergent. In *Zapriothrica* the reclinate orbitals are directed slightly posterolaterad.

72. *Nudidrosophila aenicta* has autapo-

morphically lost the orbital setae in males. These appear to have been replaced by numerous interfrontal setulae in two forms: a setose type and a scalate type, the latter of which gives the head a pollinose shimmer when viewed at an oblique angle.

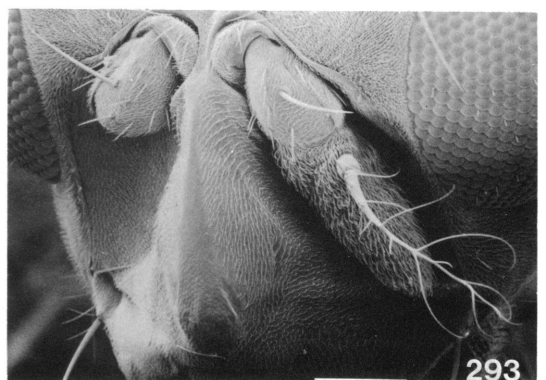
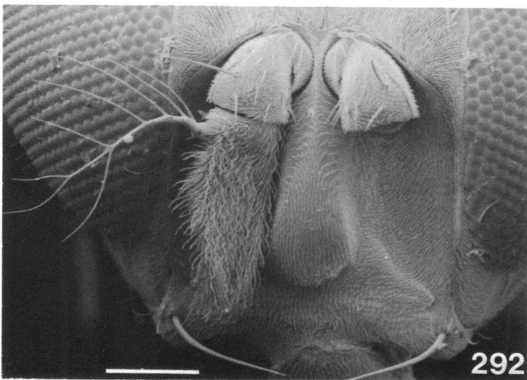
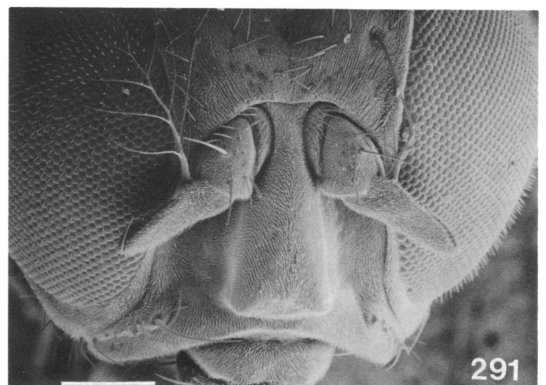
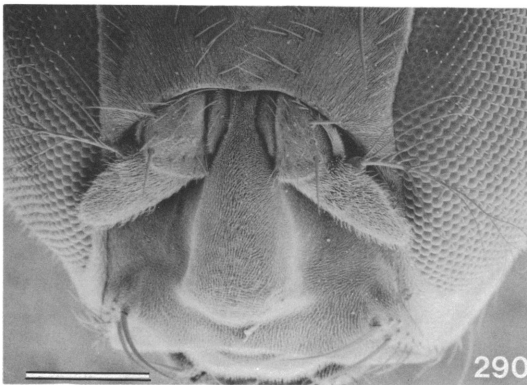
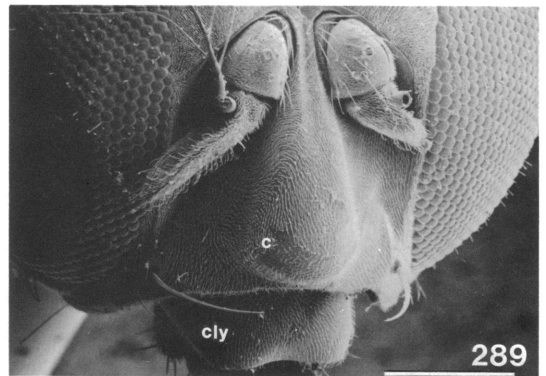
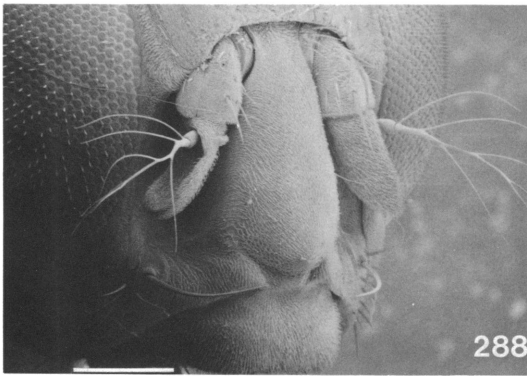
73. Apparently autapomorphic to *Rhino-*



Figs. 282–287. Faces of Drosophilidae, showing intermediate development of facial carinae. **282.** *Drosophila affinis*. **283.** *Drosophila nasalis*. **284.** *Drosophila crassifemur*. **285.** *S. (Hemiscaptomyza) apicata*. **286.** *Scaptomyza australis*. **287.** *Scaptomyza graminum*. c, carina; vb, vibrissa. Scale = 100 μ m.

leucophenga is the placement of the orbital setae far back on the front of the head, all of them being well within the dorsal half of the front. In most other drosophilids, at least the proclinate lies in the ventral half of the front, and in some taxa the orbitals occupy the entire length of the front (e.g., figs. 229–269).

74. Extended to, or nearly to, the ptilinal fissure is the apex of a large, shiny ocellar triangle in the following *Scaptomyza*: *S. (Bunostoma) anomala*, *S. (B.) palmae*, *S. (Trogloscaptomyza) intricata*, and *S. (T.) platyrhina*. Because the trait occurs in distantly related taxa, such as *Zygothrica*, it is

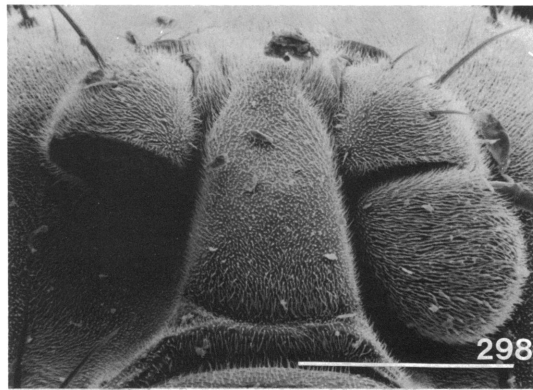
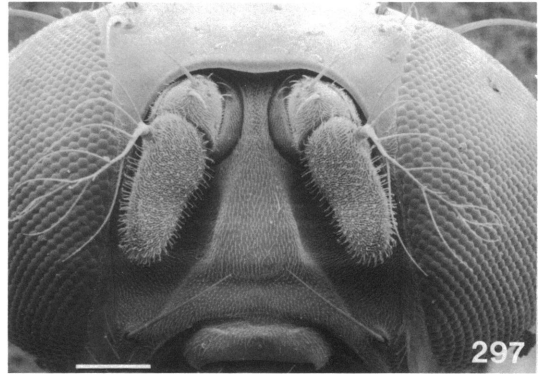
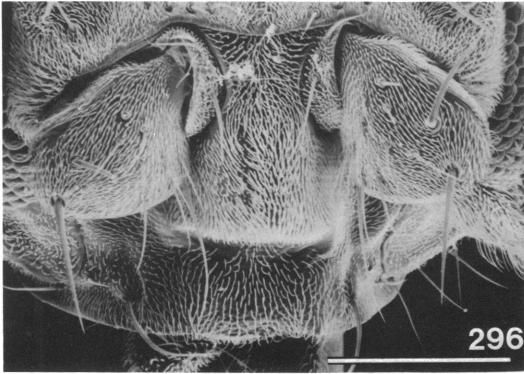
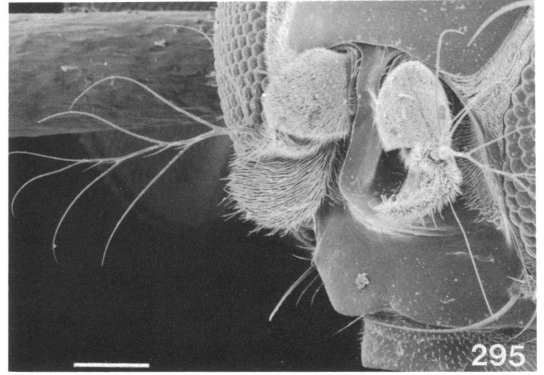
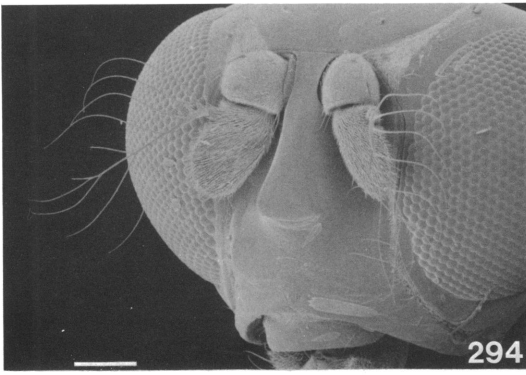


Figs. 288–293. Faces of Drosophilidae, showing types of bulbous, prominent carinae. 288. *Zaprionus multistriatus*. 289. *Drosophila monochaeta*. 290. *Drosophila immigrans*. 291. *Drosophila lurida*. 292. *Zygotherica atriangula*. 293. *Zygotherica dispar* ♀. Scale = 200 μ m.

certainly not synapomorphic for all of the taxa that possess it. Plesiomorphically, the triangle is extended to about the middle of the front of the head.

75. Common to *Pseudiastata* and *Mayagueza* are very small, cruciate ocellar setae (state 1) (fig. 213). Plesiomorphically, the ocellars are extended to about the level of the

proclinate orbital setae and are divergent. In *Acletoxenus* this trait has been even further modified, so that the tiny ocellars are indistinguishable from the intraocellar setulae, or else they are completely lost (state 2). This feature is apomorphy 13 in Grimaldi (1988), where it was used previously to illustrate the close relationship among *Mayagueza*, *Pseud-*



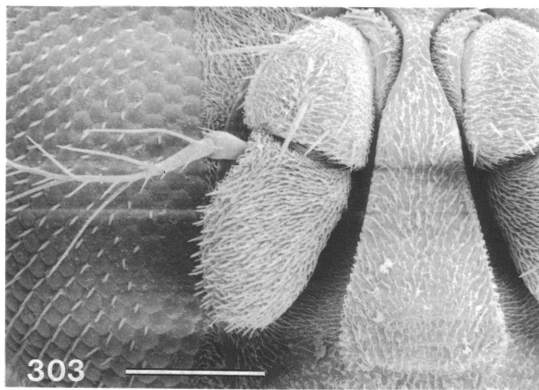
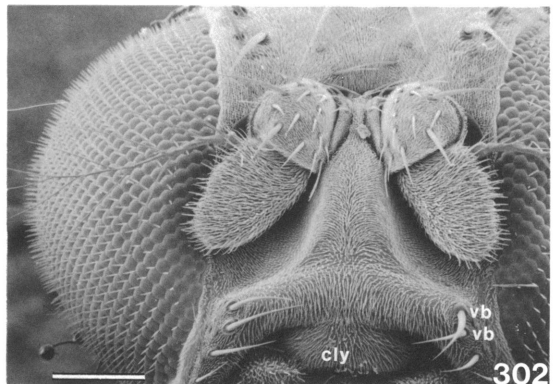
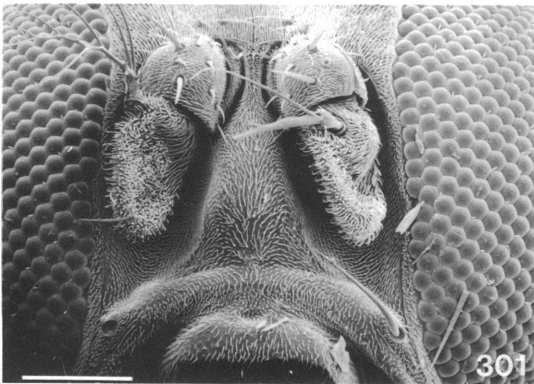
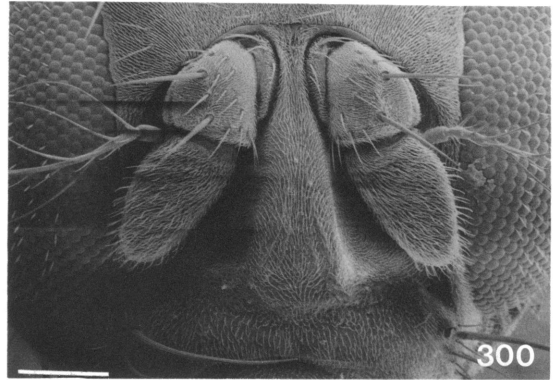
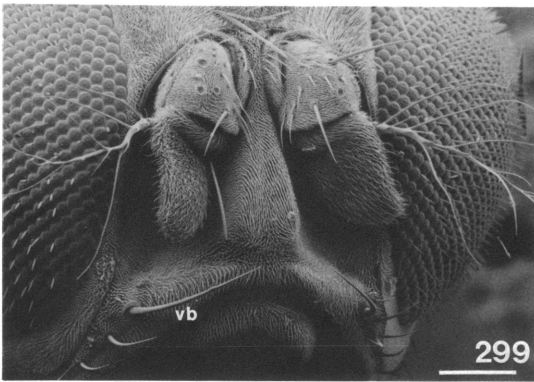
Figs. 294–298. Faces of Drosophilidae, showing truncate (figs. 294–296) and broad (297, 298) carinae. 294. *Sphaerogastrella* sp. 295. *Hypselothyrea guttata*. 296. *Dettopsomyia formosa*. 297. *Lissocephala unipuncta*. 298. *Colocasiomyia stamenicola*. Scale = 100 μm .

iastata, and *Acletoxenus*. *Ateledrosophila* preapicula has also lost the ocellars, but here it is considered convergent with that in the above taxa and was not scored in the matrix.

76. *Phorticella* and *Zaprionus* both have short, stout vertical setae (e.g., they are about the same size as the postocellar setae). The

vertical setae are plesiomorphically two or three times longer than the postocellars.

77. *Phorticella* and *Zaprionus* also possess several colored frontal vittae: a narrow medial one, and a pair of frontal-orbital ones, each of them being bordered by dark brown and orange. These vittae are normally absent.



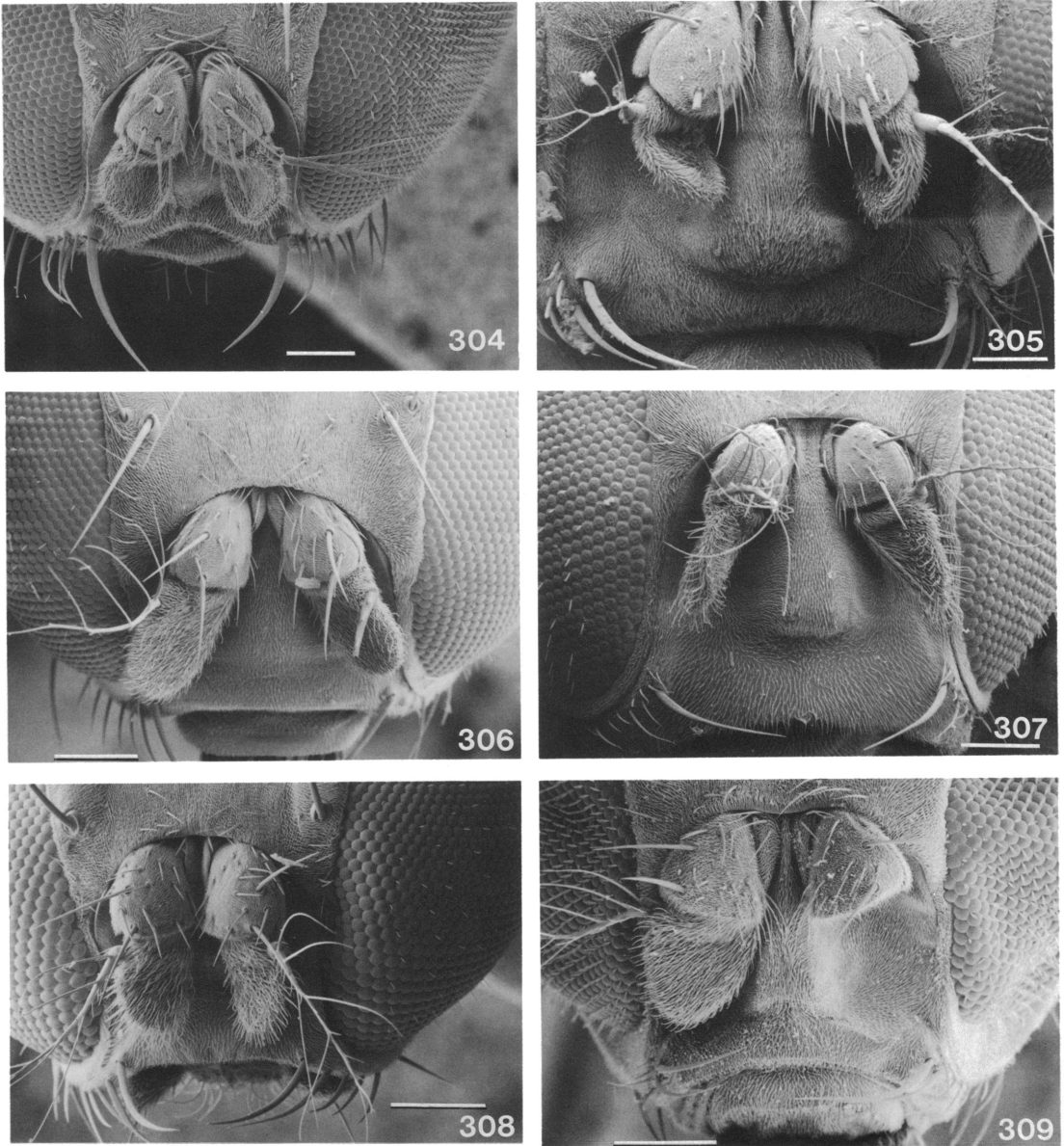
Figs. 299–303. Faces of Drosophilidae, showing broad carina typical of most *Drosophila*. **299.** *Drosophila repleta*. **300.** *D. quinaria*. **301.** *D. scaptomyzoidea* (not developed as broad). **302.** *D. melanogaster*. **303.** *D. floricola*. Scale = 100 μm .

78. Autapomorphic to the genus *Pseudias-tata* are proclينات that are convergent, with the ends nearly touching. Plesiomorphically the proclينات are parallel.

79. Autapomorphic to *Laccodrosophila* (as seen in *flavescens*) is a tiny patch of light gold-

en, fine setulae just behind the ocellar triangle (plesiomorphically, this is absent). In addition, the supracervicals are equally light and fine.

80. Autapomorphic to *Dettopsomyia* (as seen in *D. formosa*) is an outer vertical seta



Figs. 304–309. Faces of Drosophilidae, showing various carinae, or lack thereof (figs. 304, 306, 308). **304.** *Scaptomyza platyrhina*. **305.** *S. (Macrosaptomyza) altissima*. **306.** *Drosophila achiza*. **307.** *S. (Euscaptomyza) chylizosoma*. **308.** *Chymomyza amoena*. **309.** *Drosophila busckii*. Scale = 100 μm .

that lies behind the inner vertical, and an arrangement of the orbital setae where they all lie nearly on the ptilinal fissure.

FACE

Facial carinae are found in many sizes and shapes in the Drosophilidae. Such develop-

ment and variation in carinae are atypical of Muscomorpha, so it is likely that carina apomorphies will remain diagnostic for many groups in the family. The carina houses the cibarium, which folds up into the recessed, concave surface when the prementum is retracted into the oral cavity. No concordance was observed between carina and cibarium

shape. At the family level the plesiomorphic state of carina development is where there is a flat face, or only a slight swelling (figs. 270, 304, 306, 308). Because of the various carina types, mere presence of a carina is certainly not a synapomorphy for all the various groups that possess one, but is synapomorphic at various levels. The SEM has aided immensely in the description and illustration of the carina.

81. In *Stegana* [with the exception of *S. (O.) acutangula*] the face is broad and has a very broad carina (fig. 276). The carina is quite low, and may end near the apex of the pedicel (e.g., *S. vittata*), or may gradually taper most of the facial height.

82. Also apomorphic to a face without a carina is one with a narrow, low, short ("incomplete," or not reaching the oral margin) carina (figs. 282–285). This type of carina is quite widespread among a variety of taxa and is a synapomorphy at numerous nodes on the cladogram. It is apparently derived three times, according to the final HENNIG86 analyses.

83. This apomorphic state of carinal modification is where the carina is low and narrow (almost sharp), and abruptly ended before the lip (figs. 286, 287). It is found in *Marquesia femoralis*, *Microdrosophila quadrata*, and various *Scaptomyza* (state 1), except the following: *S. (Alloscaphomyza) mutica*, *S. (Scaptomyza) adusta*, and *S. (S.) nigrita*, which lack carinae (either plesiomorphically or secondarily); *S. parva*, *S. pallida*, *S. graminum*, and *S. denticauda*, which have a nearly complete carina (extended to the oral margin) (state 2) (fig. 287); and *Scaptomyza (Bunostoma)* species + *S. (Macrosaptomyza) altissima* which have the ventral end of the carina spread to almost the full width of face (fig. 278). The long carina and the type with a bulbous ventral end are considered derived states (state 2 and 3, respectively) of apomorphy **83**. This is because other evidence shows the genus *Scaptomyza* to be a monophyletic group and because the ventral modification of the *Scaptomyza* carina is likely just to have been added to a preexisting short carina. States 1–3 were unordered.

84. In *Apenethecia crassiseta* and *Amiota (S.) picta* there is a short, square carina with

a flat surface. The carina ends at about the level of the apex of flagellomere 1. Also, the distance between the inner margins of the scape in *Apenethecia* and *A. (Sinophthalmus)* is almost as wide as the flat portion of the carina (plesiomorphically the scapes nearly touch). The lip (upper oral margin) of these two species is quite thick. Plesiomorphic to this carina is that found in *Amiota (Phortica) variegata*, which lacks a carina.

85. The carina in *Gitona bivisualis* (state 1) is intermediate between the type described above and the more complete carina found in *Cacoxenus*. *Gitona distigma* shares with *Cacoxenus* a complete carina that is gradually flared toward the oral margin (state 2) (fig. 275). States 1 and 2 were unordered.

86. A carina that is broad, extended into the lip and sometimes to the edge of the oral margin, and prominently raised (figs. 288–291) occurs in *Drosophila (D.) immigrans*, *D. (D.) monochaeta*, *Phorticella*, and *Zaprionus*, and *Samoaia* (the trait is synapomorphic for the first two and the last three taxa). *Drosophila lurida* is similar, but distinct by having the ventral margin of the carina squared and the anterior surface flattened (fig. 291). The carina in the other taxa is rounded, making the face appear to have a bulbous nose. This feature may be synapomorphic with the situation in *Zygothrica*. Most *Zygothrica*, however, possess a carina that is narrower (although still quite prominent and bulbous) (figs. 292, 293). The plesiomorphic state of apomorphy **86** is a carina that is narrow and either incomplete or fully extended to the oral margin.

87. The following taxa that were examined have a very distinctive carina: *Dettopsomyia*, *Hypselothyrea*, *Liodrosophila*, *Lissocephala*, *Samoaia*, *Sphaerogastrella*, and *Tambourella*. The carina is square in all but *Tambourella*: the sides and the ventral margin have sharp, straight edges. In all of the above species the ventral margin is abruptly ended before the lip (figs. 294–296), except in *Lissocephala* where a raised area connects the lip to the carina (state 1; other taxa are state 2; states were ordered) (fig. 297). The scapes and pedicels are well separated, by a distance equal at least to one-half the width of the pedicel. This interantennal distance is (plesiomorphi-

cally) most narrow in *Lissocephala*. The plesiomorphic state to apomorphy 87 is a face without a carina, or a narrow carina that is gradually sloped.

88. A very distinctive, narrow carina was observed in *Drosophila xiphophora*, *Laccodrosophila flavescens*, and *Zapriothrica* (state 1) (figs. 280, 281). Width of the carinal edge is at most one-quarter that of the pedicel. In the *Laccodrosophila* and *Zapriothrica* faces there are smooth, evenly rounded concavities flanking the carina, into each of which flagellomere one fits (state 2). Lack of a carina is probably plesiomorphic at this level on the cladogram.

89. *Neotanygastrella* and *Mulgravea* have a carina with a width not exceeding that of the pedicel, but which is widest and most prominent—indeed, bulbous—on the oral margin (fig. 279). A flat face, as seen in *Chymomyza* (fig. 308), is plesiomorphic to the shape of the carina seen in *Neotanygastrella*. *Scaptomyza* (*Bunostoma*) has a carina that is basally bulbous, but this is probably independently derived, for the bulbous portion of the carina in *Bunostoma* is much more extensive, with a less conspicuous swelling (fig. 278).

90. Apomorphic to the type of facial carina that is narrow and incomplete is one that is broad (width about three-quarters to equal that of the pedicel), extended to the lip, and has a flat anterior surface. The medial surfaces of the pedicels are barely separated (plesiomorphic), and a prominent swelling along the upper oral margin (the “lip”) is present. This feature is widespread among the species in the subgenus *Drosophila* (figs. 299, 300). *Colocasiomyia* (fig. 298) and *Drosophila* (*Phloridosa*) (fig. 303) have very broad, flat carinae (spanning the distance between the antennae—a state that was not scored). In *D. (Drosophila) colorata*, *lurida*, *hydei*, *melanica*, *repleta*, *virilis*, and *D. (Siphodora)* (among the species examined in the synoptic collection) there is a shallow median furrow down the center of the carina (state 2). This feature occurs in many other species belonging to the same species groups as the species listed above. States 1 and 2 were unordered.

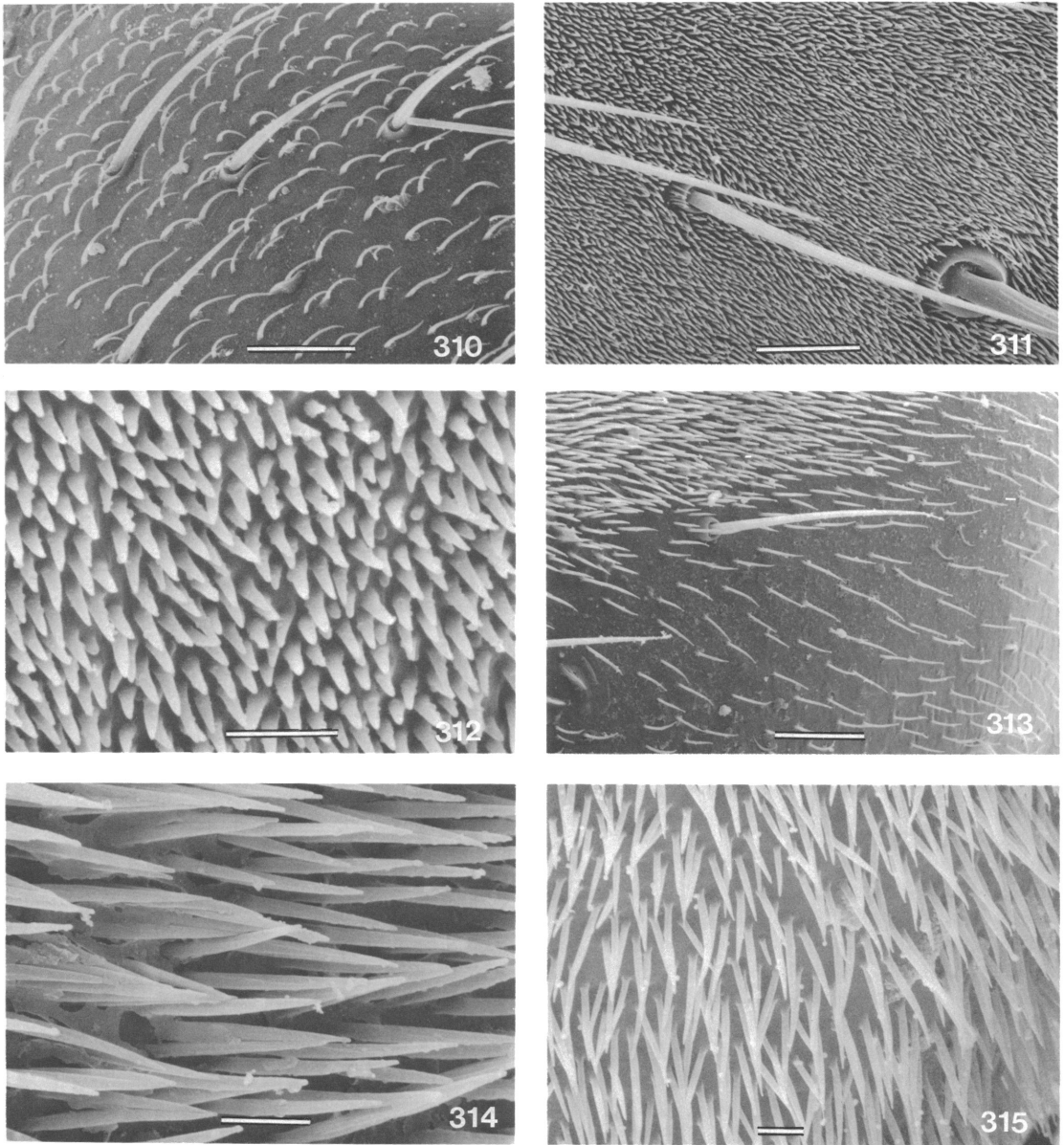
91. From an anterior and/or lateral view of the proboscis in resting position, the ven-

tral margin of the clypeus never reaches the level of the ventral margin of the cheek (plesiomorphic), but it is slightly extended beyond that margin in *Apenthecia crassiseta* (in the female), *Amiota* (*Sinophthalmus*), and *Amiota* (*Phortica*) *variegata*. In addition, the clypeus in these three taxa is high (about one-third the face height), bulbous in front, and about equal in its width to the distance between the frontogenal sutures (these run just medial to the eye) (fig. 274). These characteristics corroborate the hypothesis that *Apenthecia* and *Sinophthalmus* are sister groups (Grimaldi, 1988). An even more prominent clypeus, that is structurally slightly different, is found in several other taxa (see apomorphy 92).

92. A very similar apomorphy to no. 91 is found in *Phorticella*, *Zapriionus*, and *Drosophila monochaeta* (but not in *Drosophila immigrans*, which is apparently plesiomorphic for the trait). The clypeus is very prominent and bulbous (figs. 288, 289), but not as wide as in apomorphy 91.

93. Although autapomorphic in this scheme, the presence of a bulbous clypeus in *Mycodrosophila* is recorded here to help decipher relationships between *Mycodrosophila* and certain members of the *D. (Hirtodrosophila) thoracis* species group that have a similar clypeus, such as *Drosophila clypeata* Wheeler and *D. clypitata* Grimaldi.

94. Little doubt exists about the apomorphic status of two pairs of vibrissae (vs. the plesiomorphic status of just one pair). In all of the outgroup taxa examined, only *Camilla glabra* possessed two pairs of vibrissae. The subvibrissal setae are distinguished from the vibrissae by size and the fact that they are very close together (separated by a distance not much greater than the vibrissa diameter). The setae are about one-half or less the length and thickness of the vibrissae. Two pairs of vibrissae are found in *Chymomyza*, some *Scaptomyza*, and some continental species of the subgenera *Drosophila*, *Sophophora*, and in *Dorsilopha* (figs. 290, 302, 305, 308, 309). It occurs, independently from any of these taxa, in several Hawaiian species such as *Drosophila fungiperda*. Its absence in species of the subgenus *Drosophila* is considered to be a loss.



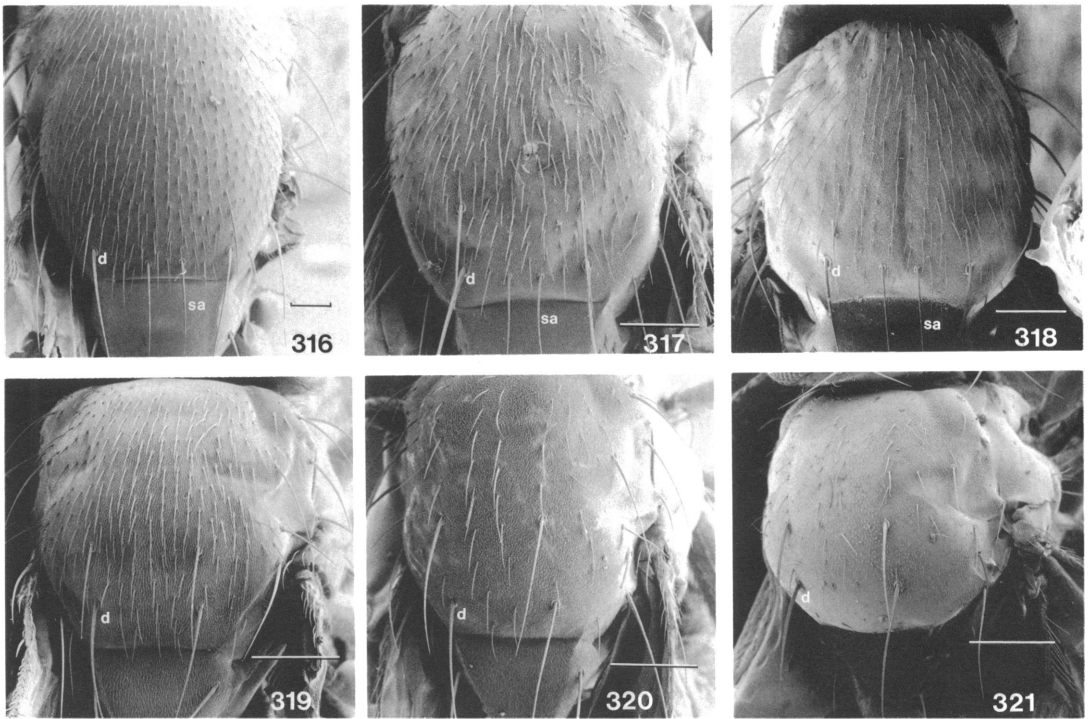
Figs. 310–315. Fine structure of cuticular covering in various drosophilids, particularly glossy-metallic (figs. 310, 313) and velvety (figs. 311, 312, 314, 315) surfaces. **310.** *Diathoneura metallica* notum. **311.** *Diathoneura opaca* notum. **312.** *Diathoneura metallica* scutellum. **313.** *Mulgravea* sp., notal spot detail. **315.** *Hypselothyrea guttata* scutellum. Scales = 20 μm (figs. 310, 311, 313), others 4 μm .

THORAX

NOTUM AND PLEURA

95. The plesiomorphic state is a pair or two of prescutellar setae; the absence of these setae is certainly a loss. In some instances the

prescutellars are reduced, being about twice the length of the acrostichal setulae (but still smaller than the dorsocentrals), so a ranking was made in the state of the prescutellars: 0 = prescutellars present, only slightly shorter and thinner than the dorsocentrals; 1 = re-



Figs. 316–321. Thoraces of representative drosophilids, showing arrangement of acrostichal setulae, dorsocentral (d), presutural, and prescutellar setae (sa). 316. *Rhinoleucophenga obesa*. 317. *Scaptodrosophila* sp. 318. *Leucophenga varia*. 319. *Drosophila melanogaster*. 320. *Scaptomyza pallida*. 321. *Liodrosophila* sp.

duced, as described above; 2 = completely lost. The presence/absence of this feature is one that was originally used to define the Steganinae and the Drosophilinae. Using the presence of prescutellars as a sole diagnostic feature of the Steganinae would make this grouping paraphyletic. States 1 and 2 were unordered. Presence of prescutellars in *Scaptodrosophila* is considered to be a secondary gain.

96. The tergum and scutellum (of the mesonotum, in flies) plesiomorphically has a dull shine. The dullness is due to minute microtrichiae which scatter the reflection from the otherwise smooth cuticular surface. In some taxa, however, the notum is apomorphically glabrous to the point of being glassy, reflective, and even sometimes with a metallic sheen. This is due to a reduction in the density of the microtrichiae (figs. 310, 313), which appear never to be completely lost, except in *Sphaerogastrella*.

97. Occurring in some of the taxa with apo-

morphy **96** (except *Calodrosophila*, which does not have a shiny notum) is a scutellum with a velvety surface, usually black. This is due to microtrichia that are so dense as to virtually obscure, under high magnifications, the cuticle underneath (figs. 311, 312, 315). Plesiomorphically, the cuticle of the scutellum has a dull shine like the notum.

98. Plesiomorphically, the acrostichals are irregularly arranged (they are not in rows, longitudinal to the length of the thorax), and are very numerous. Among the drosophilids that have the acrostichals arranged in rows, which is the great majority of them, those with the higher number of rows (e.g., 12, 10, 8) have the plesiomorphic state; the presence of four or only two rows is a reduction and thus is apomorphic (*Sphaerogastrella* has even lost the acrostichals). Since there is no discrete gap in the number of acrostichals, this was coded as a multistate, nonadditive (unordered) character, having seven states as follows: state 0 (12 rows) > state 1 (10 rows)

> state 2 (8 rows) > state 3 (6 rows) > state 4 (4 rows) > state 5 (2 rows) > state 6 (no rows). After the final analysis, states 0 and 6 became derived at two extremes of a continuum.

99. Another traditional taxonomic feature used for subfamily diagnoses is the presence of two equally long katepisternal setae (the plesiomorphic state, also diagnostic for the Steganinae). The reduction of (usually) the anterior one to ca. $\frac{1}{3}$ the length of the posterior one is derived. *Hypselothyrea* has entirely lost the anterior katepisternal, and in *Sphaerogastrella* both have been lost. Using the presence of two long katepisternals to diagnose the Steganinae is, again, constructing a paraphyletic group by the use of a plesiomorphic feature.

100. Plesiomorphically, there is just one humeral (postpronotal lobe) seta; apomorphically there are two. In a few taxa (e.g., *Zaprionus multistriatus*, *Drosophila lurida*, *Dros. repleta*) there are three well-developed humerals, which I consider to be an ordered state 2 (nested within state 1). To be developed a humeral seta must have a thickness equal to that of a dorsocentral and with the length several times that of an acrostichal setula. A few taxa have lost the humerals, such as *Hypselothyrea*, some *Scaptomyza*, and *Sphaerogastrella*, which coincides with the loss/reduction of acrostichals and dorsocentrals in these genera.

101. Plesiomorphically, the acrostichals that are in line with and anterior to an anterior dorsocentral seta are the same size as the acrostichals in the row flanking this one. Apomorphically, the acrostichals in front of the dorsocentrals are obviously thicker than other acrostichals, and are up to twice the length. This feature is most common in *Scaptomyza*. It can be so developed, as in *Celidosoma* and *Scaptomyza altissima*, that it appears as if there are four pairs of dorsocentrals (the enlarged acrostichals are simply grossly out of proportion). Some larger acrostichals can also be found in the middle two rows, but they are usually not as large as the ones anterior to the dorsocentrals.

102. The katepisternum has ventral to the two prominent setae a group/row of fine setulae, which usually run from the ventral surface of the katepisternum to between the two

setae. The dorsalmost setula is plesiomorphically the same size as the others; apomorphically it is at least twice the length.

103. Obviously independently derived in each case, based on the distribution of other apomorphies, is a loss of the anterior pair of dorsocentral setae in *Pseudostegana*, *Drosophila (Dichaetophora) abberans*, *Mycodrosophila dimidiata*, and *Baeodrosophila pubescens*. Plesiomorphically, there are two pairs of dorsocentrals, the anterior and posterior.

104. A spotted notum (and usually the abdomen) occurs several times in various drosophilids. Each time, though, the feature is represented by a small dark spot at the base of each seta and setula, such as the dorsocentrals and the acrostichals. In the following taxa the ground color of the integument surrounding each spot is dull (no reflectiveness), pruinose, with a slight greenish-silvery sheen: the *Amiota* subgenera *Phortica* and *Sinophthalmus*, and in the genera *Apenethecia*, *Cacoxenus*, and *Gitona*. Because this type of spotting is obviously different from that in *Drosophila lurida* and the *Drosophila repleta* species group, this apomorphy pertains only to the taxa listed above. In *D. lurida* and the *repleta* group, the ground color is a dull brown, with dark brown spots at the bases of the setae/setulae. Plesiomorphically no spots occur.

105. In the following taxa the pair of anterior dorsocentral setae is very far anterior: *Colocasiomyia*, *Dettopsomyia*, *Hypselothyrea*, *Microdrosophila*, *Mulgravea*, *Scaptomyza*, *Sphaerogastrella*, *Styloptera*, and *Tambourella*. Plesiomorphically the distance from the anterior to the posterior dorsocentrals is about one-half the distance that the anterior dorsocentrals are to the transverse suture. In the above taxa, the anterior dorsocentral-transverse suture distance is less than that between the anterior dorsocentral and the posterior dorsocentral, and the anterior dorsocentrals are even *between* the incomplete portions of the transverse suture in *Tambourella*. *Microdrosophila*, *Colocasiomyia*, and *Scaptomyza* have apparently each derived the feature independently from the group of other genera.

106. The genera *Acletoxenus* and *Mayagueza* both have, synapomorphically, a small pair of anterior dorsocentral setae (barely

longer than the acrostichals) which are situated very close to the posterior dorsocentrals (the distance being about one-half the length of the anterior dorsocentral). This feature was not previously described by Grimaldi (1988) in a discussion of steganine relationships, but it corroborates the sister-group relationship of the above two genera.

107. Common to the genera *Zaprionus* and *Phorticella* is a flat (not shining), velvety notum with one or more pairs of longitudinal vittae running the length of the notum. *Drosophila lurida* shares with these two groups a flat, velvety notum, but lacks the vittae. Also, the notum is usually a light orange in *Zaprionus* and *Phorticella*, but is dark brown in *Drosophila lurida*.

WINGS

108. In the various species of *Stegana* studied thus far, a useful diagnostic feature, autapomorphic to the genus, are veins R_{4+5} and M_1 that are convergent toward the wing tip (figs. 323–325). This feature is also apparently related to the development of a pointed wing tip; together, the two structural modifications probably serve to strengthen the distal portion of the wing in flight, and this might be related as well to the peculiarly folded wings in the genus. One of the original diagnostic features of the genus *Stegana* is that the wings fold along the sides of the body. This is due to a weak spot cutting across several longitudinal veins in the humeral area.

109. Found in the genera *Leucophenga* and *Stegana*, and certainly a reliable diagnostic feature linking these two genera, is the presence of a row of stout, but sharp, thornlike spines (“warts” sensu Okada) along the section of the costal vein between the apex of R_{2+3} and R_{4+5} , on the ventral surface of the wing (figs. 326–328). There are usually about six such spines; they are heavily sclerotized, and distinctively hooked. Plesiomorphically, these spines are not present. Okada (1956) mentioned these structures as present in the subgenus *Amiota*, but not in other subgenera of the genus. I have never found them to occur in *Amiota*.

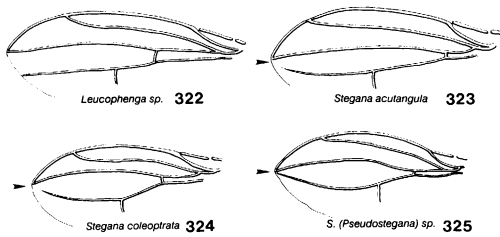
110. Distinctive to various drosophilids is a vein R_{2+3} that is turned abruptly costad (figs. 329–334). It is not a homologous mod-

ification in all of the species that possess them, but it is apparently synapomorphic for the following species: *Drosophila (D.) reticulata* (not on the matrix) and species near it, *Jeannelopsis*, *Scaptomyza chylizosoma*, *Hypselothyrea tenuis*, and *Tambourella endiandrae* (figs. 329–332). This is because, for these species the apex of R_{2+3} is turned costad rather abruptly [and is less so in *Tambourella ornata*, *Zygothrica fuscalata* and *microstoma*, and *S. (Tantalia) albovittata*]. The distortion of vein R_{2+3} in *Dettopsomyia* (fig. 334) is not homologous because it is so extremely turned and ends only near the middle of the wing, so this would be an autapomorphy for *Dettopsomyia*.

Jeannelopsis and *S. (Tantalia) albovittata* possess crossveins between the costal and R_{2+3} veins (figs. 332, 333). These are undoubtedly independently derived: R_{2+3} in *Jeannelopsis* is scalloped, that in *S. albovittata* is not; *Jeannelopsis* has usually five crossveins; three are in *S. albovittata* (in one specimen of *Jeannelopsis* out of five, there were no crossveins; so presence/absence of them can be intraspecifically variable); the crossveins in *Jeannelopsis* are all perpendicular to the costal vein, but the proximal one in *S. albovittata* is oblique to this vein.

Jeannelopsis and *Drosophila reticulata* both have a distinctive indentation or series of indentations in the wing membrane. In *D. reticulata* and a close relative, the indentation is in the sinuous portion of R_{2+3} , between this vein and R_{4+5} (fig. 331); in *Jeannelopsis*, there are three indentations between R_{4+5} and M_1 (fig. 332). The indentations are apparently functionally related to some aspect for which numerous costal crossveins might serve, but they are not homologous because of their different positions. Analysis with HENNIG86 shows this feature to be independently derived in all of the above taxa, which also reflects the variation in fine structure of the trait.

111. Costal lappets, where the portion of the costal vein proximal to the subcostal break is thickened and dark, occur in *Styloptera*, *Dettopsomyia*, *Mycodrosophila*, and *Paramycodrosophila* (figs. 335–338). Those in the first pair of genera are most similar to each other (apomorphy 111) and likewise for those in the latter pair of genera (apomorphy 112).



Figs. 322-325. Portions of wings of *Leucophenga* and *Stegana*, showing convergence of veins R_{4+5} and M_1 .

The lappet bears on the (distal) apex in the former two genera two very long setae and the overall shape of the lappet is triangular. The lappet in the latter pair of genera is broader, more flattened, and the edge bears dense, flattened, short spinules, but no long setae.

113. It is difficult to decide on the plesiomorphic and apomorphic status of the anal portion of the wing, wherein vein $A_1 + CuA_2$ is very short or absent, and, subsequently, the area of wing membrane posterior to it is quite small. In many of the outgroup ephydroid taxa, except the Curtonotidae, vein $A_1 + CuA_2$ is small and obscure (even absent in *Camilla* and the Ephydridae). Yet, where $A_1 + CuA_2$ is well developed in drosophilids, it appears in many primitive taxa such as *Amiota* (as well as more recently derived forms). Since cell cup is absent (a loss for drosophilids) in those taxa with an extremely small $A_1 + CuA_2$ vein (or without one), then it is probably best to regard the $A_1 + CuA$ vein condition as a loss/reduction. *Cladochaeta* lacks a vein $A_1 + CuA_2$, and apparently a cup cell (fig. 344), but the anal lobe of the wing is intact (there is slightly less area in the anal lobe of *Diathoneura*). I have grouped *Cladochaeta* and *Diathoneura* under state 1. An extremely small $A_1 + CuA_2$ vein, loss of cell cup, and a small anal lobe is found in that group of small genera endemic to the Indo-Pacific (state 2: see matrix; states unordered) (figs. 345-347). In contrast, the anal lobe in *Zygothrica microstoma* and *fuscalata* is virtually lost, but an entire cup cell exists and there is a small $A_1 + CuA_2$ vein (fig. 343), so this reduction in the anal portion of the

wing is not homologous with all of the above taxa.

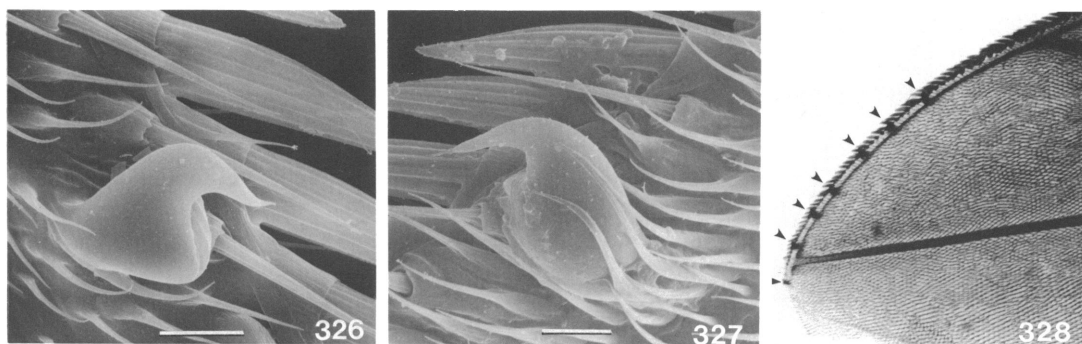
114. Apparently what would seem to be a derived feature for the Drosophilidae is a loss of the small basal-medial wing cell (or, loss of crossvein $bm-cu$). However, loss of $bm-cu$ is a ground plan of the ephydroids. So, presence of crossvein $bm-cu$ in *Cacoxenus*, *Apenethecia*, the subgenera of *Amiota*, and in *Stegana* is a reversal, or regain (independent among them) (figs. 340, 342). It is not present in *Leucophenga* (the sister group of *Stegana*) as well as in most other drosophilids, including other steganines such as *Mayagueza* + *Acletoxenus*, *Pseudistata*, *Rhinoleucophenga*, and *Gitona*.

115. A synapomorphy for the genus *Amiota*, with the exception of *A. (Sinophthalmus)*, are wing veins R_{4+5} and M_1 that are convergent toward the wing tip (plesiomorphically they are parallel). The convergence is not nearly as abrupt as in *Stegana*. *Apenethecia crassiseta* has these veins slightly convergent, which is another indication of the probable close relationship with *Amiota*.

116. Synapomorphic for *Collessia* (this genus not in the matrix) and *Tambourella ornata* Okada (but not *T. endiandrae* Wheeler) is a crossvein $dm-cu$ that is oblique with respect to veins R_{4+5} and M_1 . Plesiomorphically, the crossvein is perpendicular. It slants proximally (on vein R_{4+5}) to distally (on M_1). This evidence indicates that *Tambourella ornata* should probably be in the genus *Collessia*.

LEGS

The legs are among some of the most morphologically interesting and variable parts of drosophilids, particularly for sexual dimorphisms. Along the length of the lateroventral and dorsoventral portions of the forefemur is a row each of long, heavy setae. They are variable in number and size, with some of the Hawaiian *Drosophila* species possessing among the largest and most numerous of these setae. Considerable effort would be needed to quantify the variations in order to code for various states; therefore, this feature is not included below. Also badly needed is a comparative study of the small, stout, peglike setae that occur in pairs on the ventral (plan-



Figs. 326–328. Minute curved costal pegs in *Stegana* and *Leucophenga*. 326. *Leucophenga regina*, detail. 327. *S. (Orthostegana)* sp., detail. 328. Arrangement of pegs in row on distal segment of costal vein in *Stegana acutangula*. Scale = 10 μ m in 326, 327.

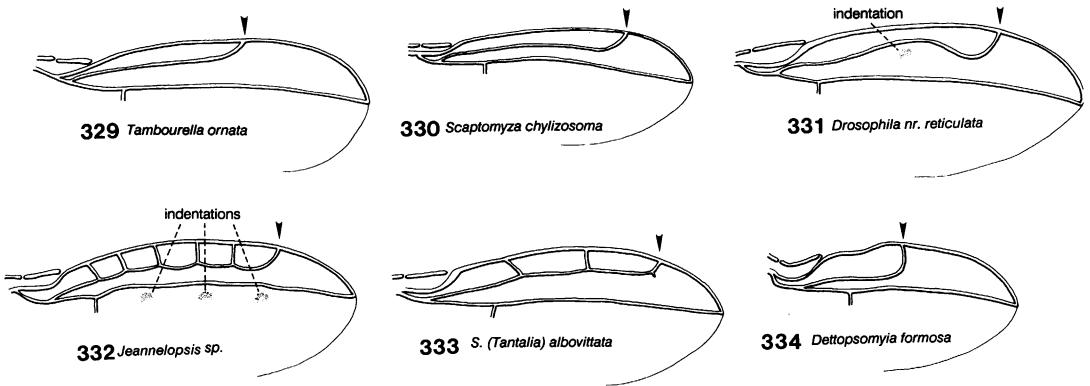
tar) surface of the tarsomeres, particularly the midtarsomeres (e.g., figs. 362, 363). The presence of these minute pegs might be the plesiomorphic state, in which event the various arrangements and numbers seen in drosophilids would represent stages of reductions, and complete loss in some groups. I also did not include below several autapomorphies (at the generic level and elsewhere) that have been described in detail and are quite well known (e.g., the two rows of spines on the ventral surface of the forefemur in male *Chymomyza*, the spinelike setae on tubercles on the forefemur of *Zaprionus*, and the truly bizarre modifications seen in some male Hawaiian drosophilids).

117. A pretarsus with spatulate setalike outgrowths (but without basal sockets) on the pulvillus of the pretarsus, which are the retineriae (figs. 348–354), appears in several taxa that are anthophagous (breeding as larvae in flowers): *Drosophila (Phloridosa)*, *Drosophila* (subgenus uncertain) *xiphophora*, *Laccodrosophila*, and *Zaprionothrica*. As in most flies, each retineria is presumably hollow and secretory, and serves for adhesion to smooth surfaces. In the drosophilids above, each retineria has the apex flared to three or four times the width of the stalk, and with the apical edge truncate (figs. 351–354). *Zaprionothrica* has the most modified retineriae. This trait has not been as comprehensively surveyed as would be desirable, but it does appear to represent a possible synapomorphy. Plesiomorphically the pulvilli can be quite large and densely clothed with setae, but the setae have a tip that is only slightly

expanded, at most to about twice the width of the setal stalk. Among the drosophilid pretarsi examined with an SEM, some had an empodium composed of two rows of flattened, tapered, scaliform retineriae, with the trait being most developed in *Drosophila xiphophora*. In *D. xiphophora* the empodial retineriae are very broad and with dissected edges similar to true scales. All the other taxa with scaliform empodial retineriae have not been completely determined.

118. In the section on the relationships of families in the Ephydroidea, apomorphy Gr-1 is described as the presence of a row of small spines, the ctinidium, on the ventromesal surface of the forefemur. Its loss is considered to be a synapomorphy for the Drosophilidae, but, as previously mentioned, there are some drosophilids that possess femoral spines (figs. 355–360). Also as described previously, the fine structure of these spines indicates that they are not homologous with those in the other ephydroids. The drosophilid taxa with apomorphy **118** are *Drosophila monochaeta* and the species in the *Drosophila immigrans* species group (only *D. immigrans* is included in the analyses here). Analysis with HENNIG86 indicates the feature to be independently derived in these two taxa. A reinspection of the spines corroborates this fact: there are about 15 stouter spines in *Drosophila monochaeta*, but fewer (ca. 10) narrower ones in *Drosophila immigrans*.

119. Along the length of the tarsal segments on the mid and hind legs in some drosophilids is a lateral and/or medial row of distinctive setae, termed “cuneiform setae” by Oka-



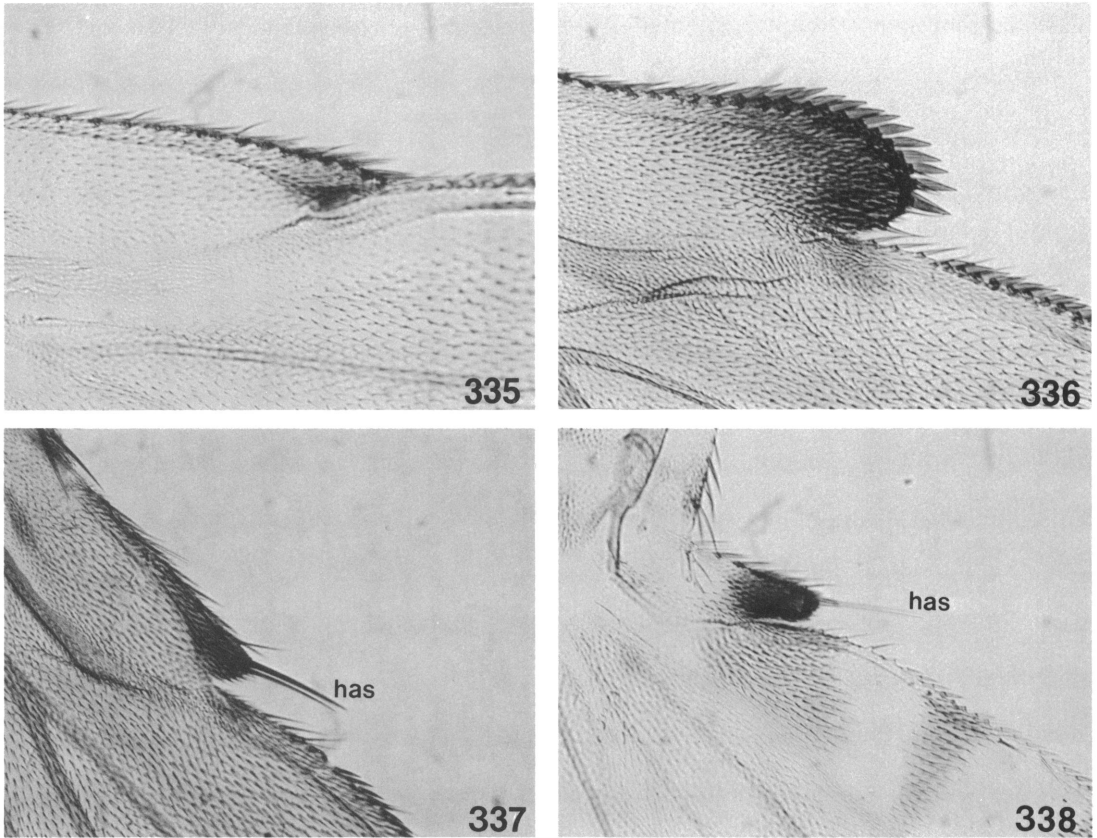
Figs. 329–334. Convergent development in drosophilids of vein R_{2+3} turned abruptly costad (arrows), multiple radial-costal crossveins (figs. 332, 333) and of membrane indentations (figs. 331, 332).

da. This feature has been treated in most detail by de Castro (1953, see below). They are elongate, triangular setae, somewhat flattened, striated, socketed, and with a length about half that of the narrower, unmodified setae on the same tarsal segments. There are two rows each on the mid and hind tarsi in *Stegana* and *Leucophenga* (figs. 363, 370, 371).

120. There is just one row each of cuneiform setae on the two pairs of tarsi in the subgenera *Amiota*, *Sinophthalmus*, and *Phortica*; in the genus *Apenothecia*; and a variety of drosophiline genera including *Ateledrosophila*, *Mycodrosophila*, *Nudidrosophila*, *Paramycodrosophila*, *Samoaia*, *Zaprionus*, and *Zygothrica*. Some *Drosophila* (e.g., *Siphlodora*), *Hirtodrosophila*, and the Hawaiian species placed in *Drosophila* also have a row on the mid and hind tarsi (figs. 364–369). All the outgroup taxa in the Ephydroidea lack these tarsal setae, except *Curtonotum* (Curtonotidae) (fig. 362). In *Curtonotum* there are two rows on the mid tarsus and one on the hind tarsus, thus being somewhat intermediate between *Stegana* + *Leucophenga* and the other taxa. In *Stegana* and *Leucophenga* the lateralmost row in particular has setae with tips that are narrowed into a fine strand (fig. 371). Thus, number of rows and fine structure of the setae indicates that either (A) the trait is independently evolved (between *Stegana* + *Leucophenga*, and the other taxa mentioned above), or (B) the trait in *Leucophenga* + *Stegana* is a further modification

of the basic plan of the apomorphy seen in the other taxa. Since many other apomorphies are shared between *Leucophenga* + *Stegana*, apomorphy 119 corroborates the close relationship of the two genera. The two genera lack, however, a suite of derived features found in the other taxa. Thus, I am most inclined to believe that the presence of cuneiform setae on the tarsi is independently derived in *Curtonotum*, another time in *Stegana* + *Leucophenga* (apomorphy 119), and at least once more in the other drosophilids mentioned above (apomorphy 120). Results of de Castro (1953) confirmed the independent development of cuneiform setae in steganines and several times in drosophilines, as based on his four types of fine structure.

121. Several genera of drosophilids have large, dark, heavily sclerotized setae (spines) on the foretarsi, including *Laccodrosophila* (figs. 372, 373) and *Colocasiomyia* (formerly *Drosophilella*) (figs. 374, 375), the species in the *Drosophila* *obscura* and *melanogaster* species groups of the subgenus *Sophophora* (for which apomorphy 121 is actually designated) (fig. 376, 377), and *Drosophila* (*Lordiphosa*) *miki*. In *Laccodrosophila*, *Colocasiomyia*, and *D. miki* the trait is found in both sexes, but it is a male feature in the *Sophophora* and structurally considerably different. In *Laccodrosophila* there is a pair of spines on the apex of the basitarsus and a pair on the apex of tarsal segment 2. (This combination is found in *Zaprionthrica*, but for the hind legs only, so is presumably not a syn-



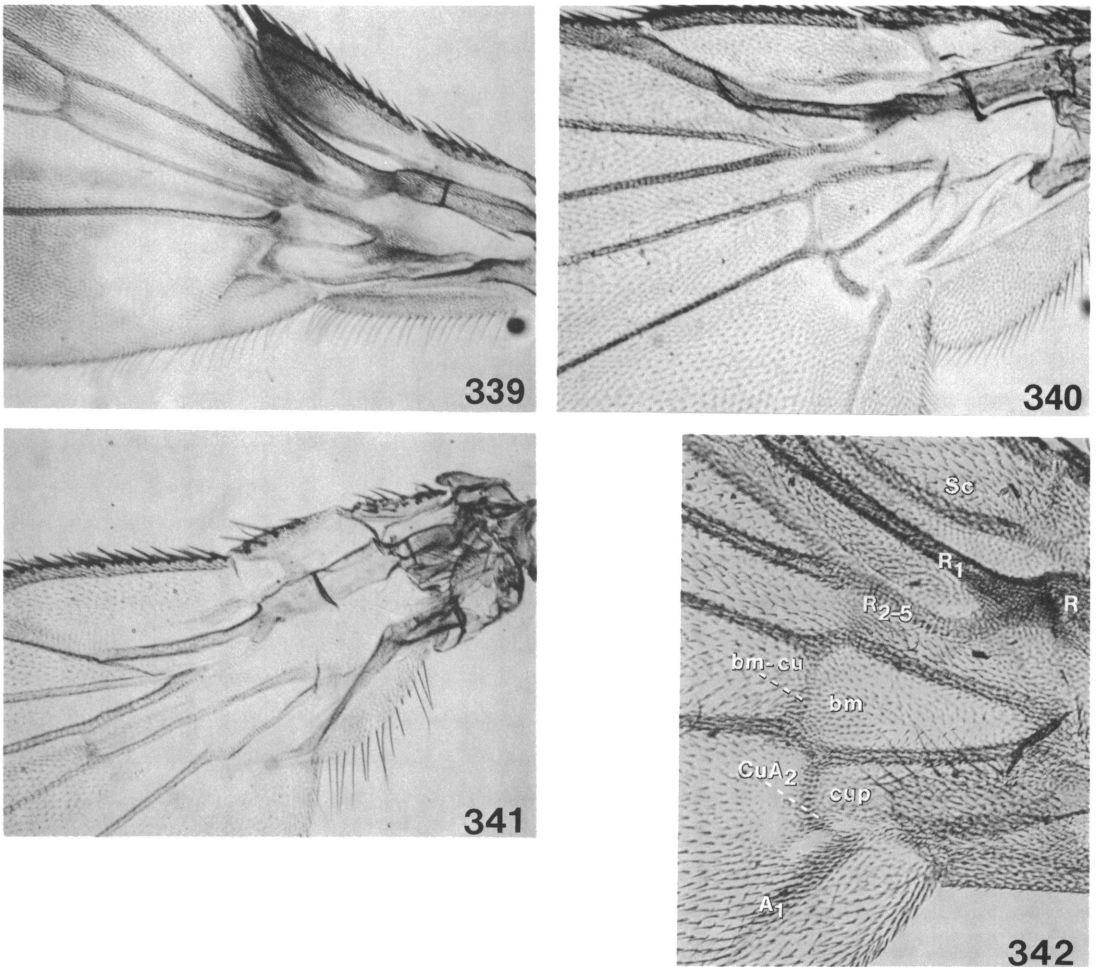
Figs. 335–338. Convergent development of costal lappet in Drosophilidae. 335. *Mycodrosophila dimidata*. 336. *Paramycodrosophila* sp. 337. *Styloptera alocasiae*. 338. *Dettopsomyia formosa*. has, humeral apical seta. To the same scale (dorsal views).

apomorphy for the two genera.) In *Colocasiomyia* there are two to four pairs of spines on the apex of tarsal segment 2 only, and they are borne (unlike in *Laccodrosophila*) at the apex of a distended portion of tarsal segment 2. In *Sophophora* the tarsal spines are evenly arranged into rows, not paired, forming a “sex comb.” In the *melanogaster* species group the sex combs can be on the apex of the basitarsus or on the basitarsus + tarsal segment 2. (If on the basitarsus there can be one or two rows of combs—there is just one in the *obscura* species group, which is presumably the most plesiomorphic condition.) Thus, tarsal spines are autapomorphic at the genus level for *Laccodrosophila* and *Colocasiomyia* each, and synapomorphic for the *obscura* and *melanogaster* species groups of *Drosophila*.

122. On the midtibia in *Pseudiasata*,

Rhinoleucophenga, *Mayagueza*, and *Acletoxenus* are two dorsopreapical setae, opposing the ventroapical seta. Plesiomorphically, there is just one dorsopreapical. The pair of dorsopreapicals in *Pseudiasata* and *Rhinoleucophenga* are heavily sclerotized and black, so are easy to see under a stereoscope; the other two genera have lightly sclerotized, fine, yellow setae, not easily observed without high magnification under compound microscopy.

123. Autapomorphic to the genus *Stegana* is the presence of a row of three to five heavy, pointed, long setae on the dorsoproximal surface of the midtibia. Plesiomorphically, setae in this area are not much differentiated from the other setae that cover the tibia. There has been no doubt about the monophyly of *Stegana* because of some very distinctive apomorphies (e.g., for wings, apomorphy 108;



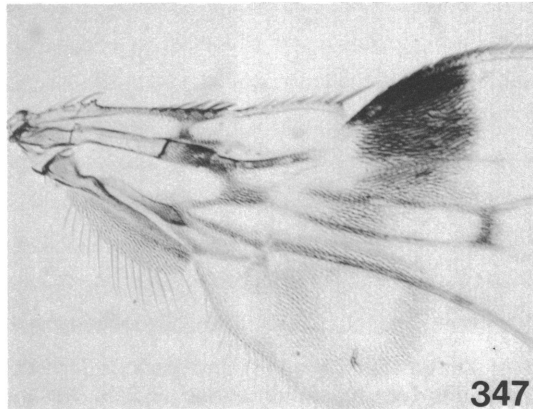
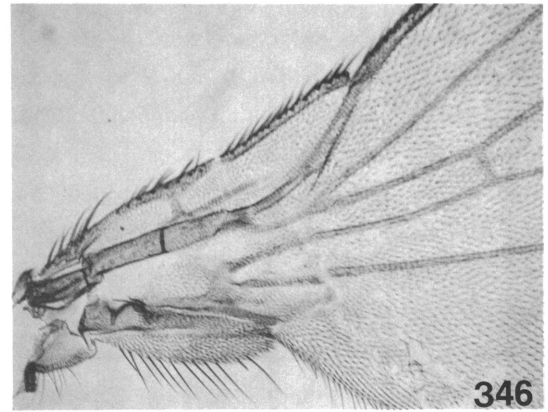
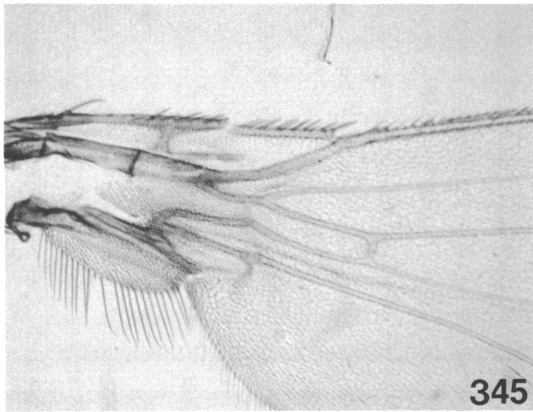
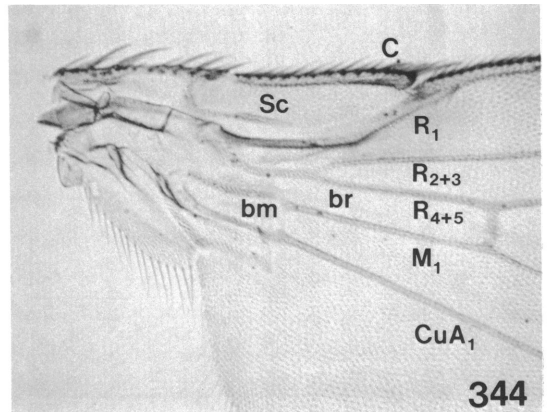
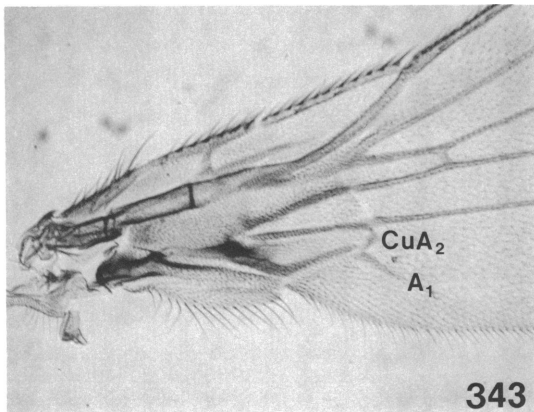
Figs. 339–342. Presence (figs. 339, 340, 341) and absence (341) of closed bm and cup cells in ephydroid wings. 339. *Diastata repleta*. 340. *Amiota humeralis*. 341. *Camilla glabra*. 342. *Apenthecia crassiseta*. 339–341 to same scale; 342 is enlarged. Vein and cell abbreviations using standard letters (dorsal views).

for male genitalia, apomorphy 127; for spermathecae, apomorphy 216). Apomorphy 123 is described here because it has not been discussed in the literature, to my knowledge, and corroborates the monophyly of the genus.

ABDOMEN

124. As a result of reduction toward the complete loss of tergite VII in the male abdomen, spiracles VI + VII reside at the ventral or posteroventral margin of tergite VI, either in the membrane (most commonly) (figs. 384–386), or in the tergite (e.g., *Sa-*

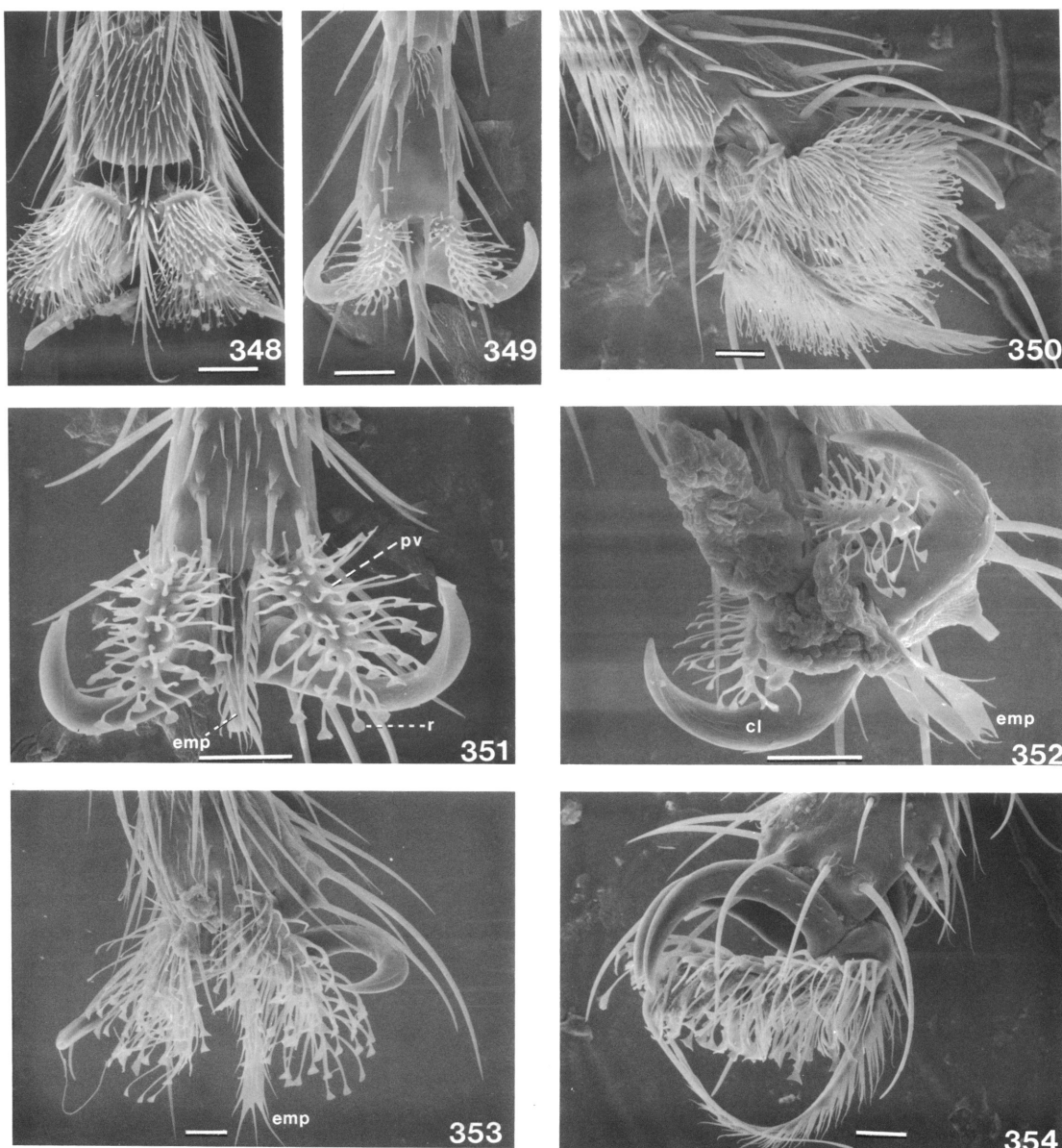
moia, *Tambourella*). Tergite VIII has been lost in the Camillidae, Curtonotidae, Drosophilidae, and Ephyridae. Tergite VI may be considered to be fused (syntergite) tergites VI + VII, but because small, unattached remnants of tVII appear in some groups (e.g., *Scaptomyza*, *Chymomyza*) (fig. 384, 385), and because such a tergite is not larger than the others, this suggests that the largest segment penultimate to the epandrium (tergite IX) in drosophilids is only tVI. Thus, the tergite but not spiracle VII has been lost in many drosophilids (apomorphy 125). A spiracle lying near a vestigial tergite VII is certainly plesio-



Figs. 343–347. Basal portion of wings in Drosophilidae, showing convergent loss of anal vein (figs. 344–347). 343. *Zygothrica microstoma*. 344. *Cladochaeta inversa*. 345. *Sphaerogastrella* sp. 346. *Liodrosophila onchopyga*. 347. *Hypselothyrea guttata*. All to the same scale (dorsal views).

morphic, since the full complement of eight tergites is plesiomorphic at the family level (as seen in the outgroup taxa *Campichoeta*, *Diastata*, and *Curtonotum*) (figs. 378, 379, 382). *Hydrellia* has an autapomorphic male

abdomen segmentation in that tV is very large, and tergite VI + VII has been lost (this is seen in the retention of the spiracles of these segments) (fig. 381). *Camilla*, however, has lost tergite VII (fig. 380), as have some dro-

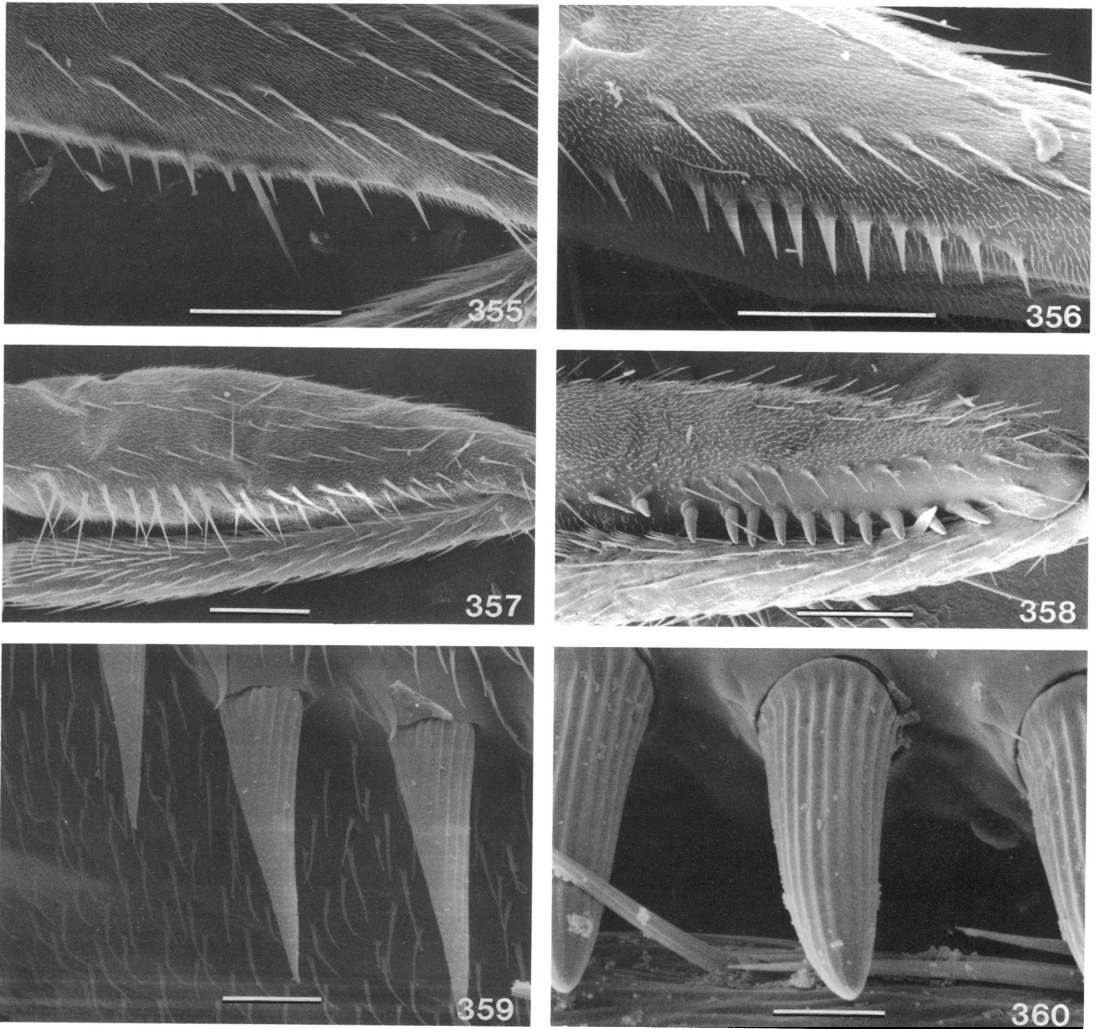


Figs. 348–354. Pretarsi in Diastatidae (fig. 348) and various Drosophilidae (349–354), showing variation in pulvillus (pv), empodium (emp), and retinerae (r). 348. *Diastata* sp. (hind). 349. *Drosophila disticha* (fore). 350. *Scaptomyza intricata* (fore). 351. *Drosophila floricola* (fore). 352. *Drosophila xiphophora*. 353. *Laccodrosophila flavescens* (fore). 354. *Zapriothrica nudiseta* (fore). Scale = 20 μ m. cl, claw.

sophilids (apomorphy 125). Reduction of the drosophilid tergite VII can be seen as a narrow, lightly sclerotized strip or patch lying beneath tergite VI (as in *Scaptomyza denticauda*). In *Chymomyza*, the remnant of tergite VII is folded, and may be related to tuck-

ing the genitalia beneath the abdomen, as in dolichopodids.

125. Nested within apomorphy 124 is a state of tergite VII reduction in males to one of complete loss (fig. 380). This situation occurs in *Camilla glabra* (Camillidae), but is



Figs. 355–360. Convergent development of row of spines on distal-mesal surface of forefemur in the Drosophilidae. 355. *Drosophila immigrans*. 356. *Drosophila monochaeta*. 357. *Chymomyza amoena* (males only). 358, 360. *S. (Euscaptomyza) chylizosoma*, and detail. 359. *D. monochaeta*, detail. Scales = 100 μm (355–358), 10 μm (359, 360).

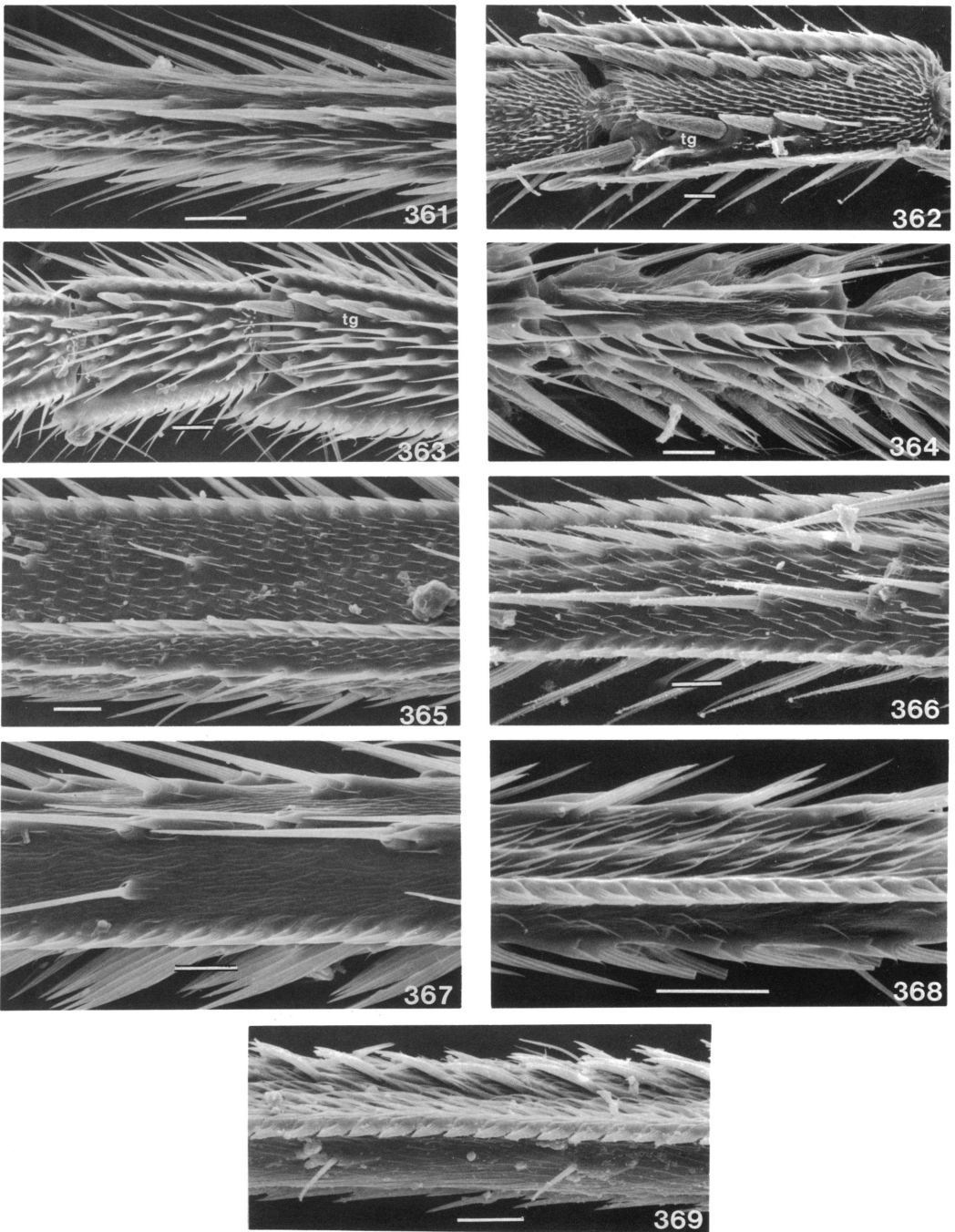
probably not synapomorphic with drosophilids since spiracle VI, but not the other spiracles, resides in tergite and not in membrane (figs. 381–387) [note, however, that McAlpine (1987) indicates this spiracle as being in membrane]. This, plus the fact that tergites V + VI are quite small (tIV is at least twice the length of any other tergite) suggests a loss of tVII in *Camilla* independent from that in the Drosophilidae.

126. Nested within apomorphy 125 and no doubt a natural consequence of it is a sub-

sequent loss of spiracle pair VII in the male abdomen (fig. 387).

MALE GENITALIA

It is important to note here that Wheeler (1987) termed the aedeagal guide what I have been terming (Grimaldi, 1986, 1987) and continue to term here the paraphyses. He termed the paramere what I take to be posterolateral arms of the hypandrium. Arms or (articulating) lobes posterolateral to the hy-



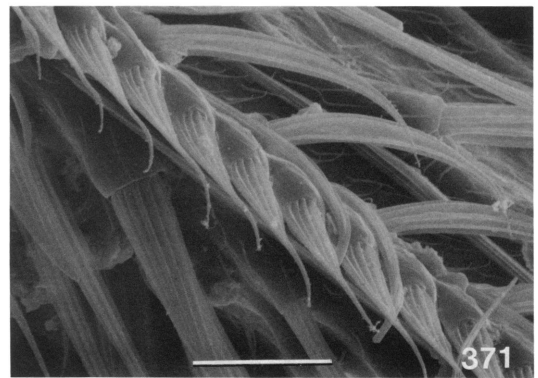
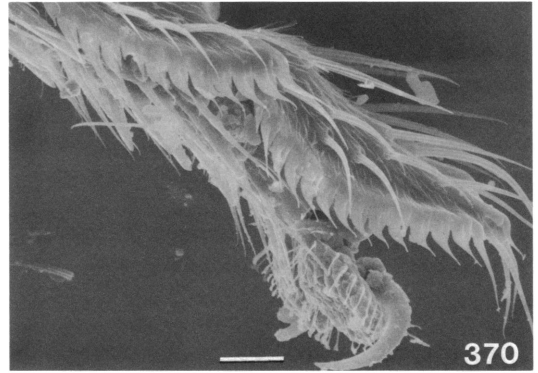
Figs. 361–369. Rows of cuneiform tibial-tarsal setulae (figs. 362–369) and primitive absence (fig. 361). **361.** *Scaptomyza apicata* (mid). **362.** *Curtonotum helvum* (midtarsomere 3). **363.** *Stegana coleoptrata* (midtarsomere 3, apex of 2). **364.** *Amiota humeralis* (midtarsomere 1). **365.** *Drosophila lurida* (hind tibia). **366.** *A. (Phortica) variegata* (midtibia). **367.** *Drosophila scolostoma* (hind tibia). **368.** *Zygothrica samoensis* (hind tarsomere 1). **369.** *Samoia ocellaris* (hind tibia). Scale = 20 μ m. tg, tarsal peg.

pandrium have been consistently identified as the gonopods in various acalyptates by McAlpine (1988), which is how I apply that term here. To clarify the situation: paraphyses are the lobes (usually small and bearing a few setulae or a setula at the apex) which flank the base of the aedeagus. The "aedeagal guide" of McAlpine (1988) is a paired structure connecting the hypandrium to the base of the aedeagus.

127. In *Stegana* is a surstylus [termed the "clasper" by Lastovka and Máca (1982) and most other drosophilid workers] that is obviously separated from and articulating with the ventral margin of the epandrium. The surstylus is simple: it bears several to numerous small, fine setae; the tip is pointed and usually sclerotized into an apical tooth (fig. 399), or it may be only very slightly sclerotized. Sometimes the tooth is a discrete, socketed peg. Apomorphy 127 is unique to *Stegana*. Plesiomorphically the surstylus is without such a tooth. In *Acletoxenus*, *Gitona*, and *Mayagueza*, such an apical tooth occurs on the ventral lobe of the epandrium. *Eostegana* has a ventral epandrial lobe that is sclerotized, hooked, and pointed, and probably has a function similar to the surstylus of *Stegana*.

128. Linking the subgenera *Stegana* and *Steganina* (but not *Eostegana*, *Orthostegana*, or *Pseudostegana*, which are plesiomorphic for the trait) is a distiphallus that terminates in or is ringed with fine, long projections, evenly spaced around the apex in a row or two. They are not sharp, like setae, but more blunt at the apices. A glabrous distiphallus, or one with microtrichia, is plesiomorphic to this state.

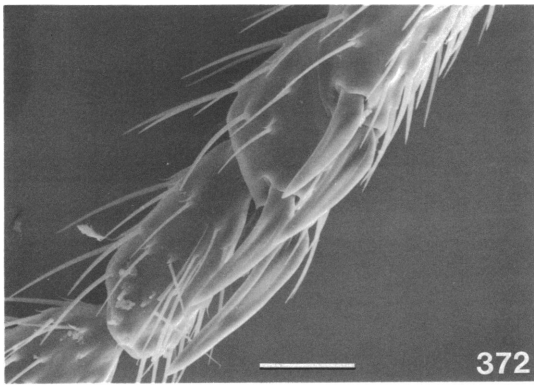
129. A sclerite that lies beneath the cercus and spans the gap between the surstyli is well developed; given its relative placement, it is probably the tenth sternite (decasternum). Various shapes occur, but in the following taxa there is always a thick central portion and small lateral arms (fig. 399). The arms articulate with the two posterior corners of the hypandrium and with the surstyli. This feature links the subgenera *Orthostegana*, *Steganina*, and *Stegana*, and the genus *Eostegana*, but *Pseudostegana* has a plesiomorphically rudimentary decasternum. Ple-



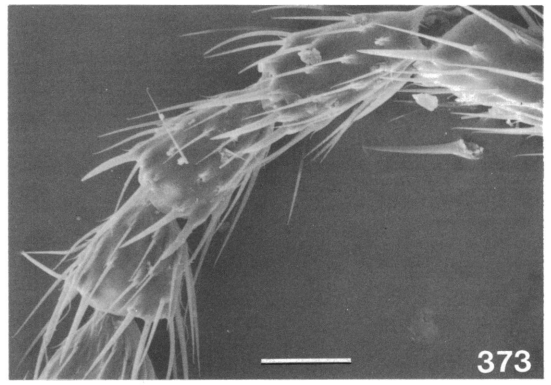
Figs. 370, 371. Tarsal cuneiform setulae in *Stegana* and *Leucophenga*. 370. *Leucophenga scutellata* (midtarsus). 371. *S. (Orthostegana) acutangula* (detail of midtarsal comb). Scale = 20 μ m.

siomorphically these arms are not present, although the decasternum may be large.

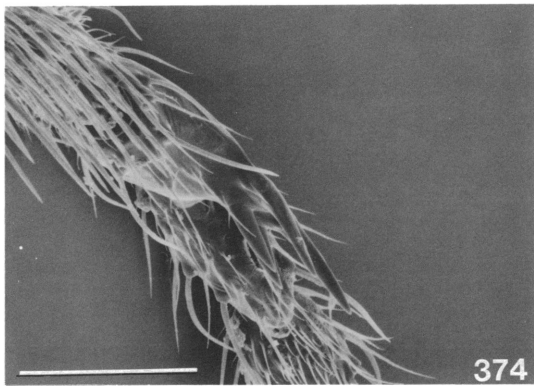
130. A number of autapomorphies distinguish *Leucophenga*, so there is little doubt about the monophyly of this genus. Among these are several genitalic features. One is a dorsal process lying over the aedeagus and slightly longer than it, which folds anteriorly just above the tip of the distiphallus (figs. 391, 392). The end of the folded portion articulates with the middle portion of the decasternum. What is the homologous counterpart of this structure in other drosophilids is very much uncertain, but it is certainly not homologous to the elongate tines connected to the decasternum in *Cacoxenus*. They are structurally quite different. Although *Trachyleucophenga* sp. [from Louisiana—cf. fig. 5 in Wheeler and Takada (1971)] is plesiomorphic for most *Leucophenga* traits [ab-



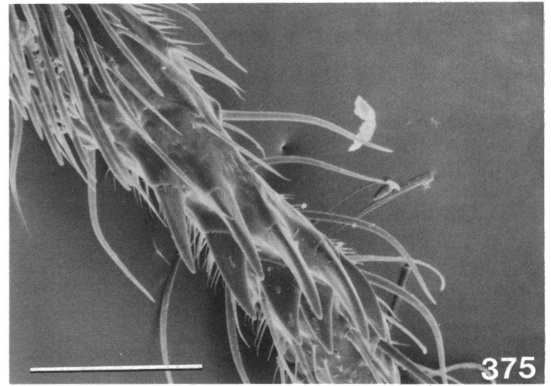
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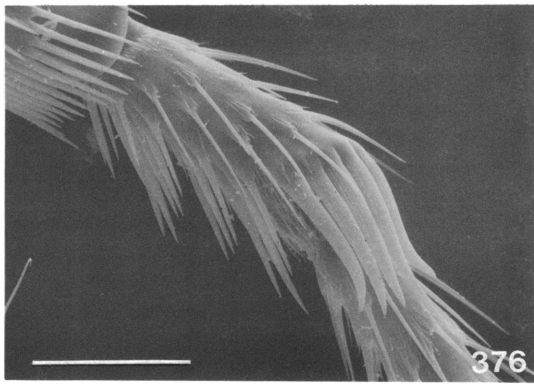
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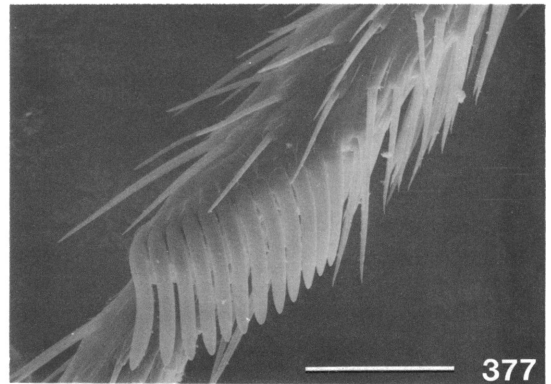
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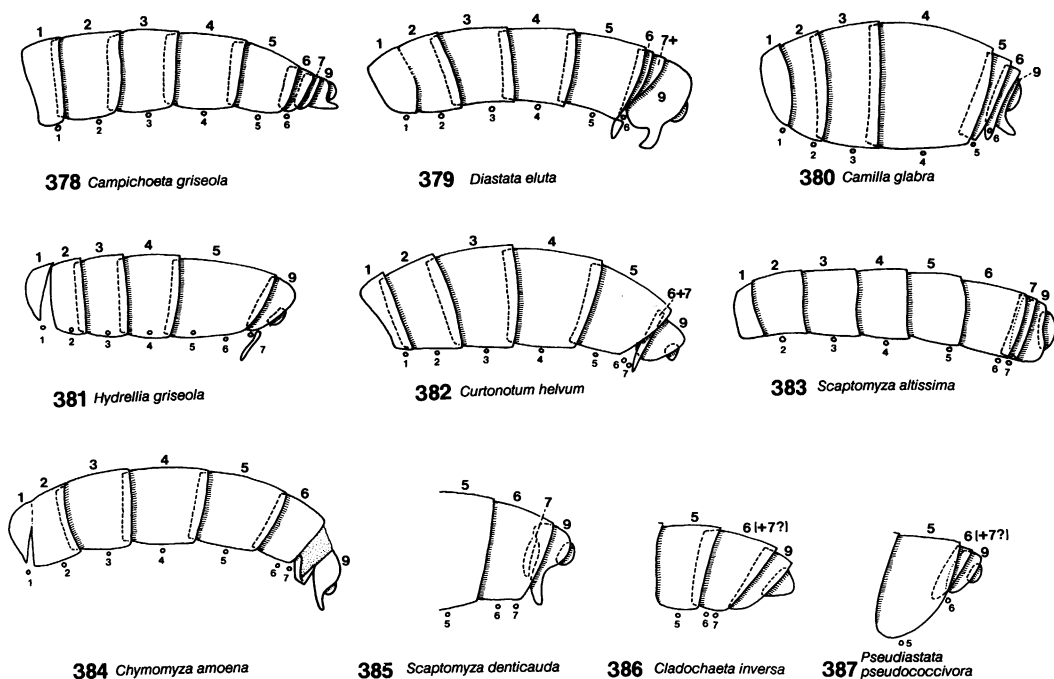


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Figs. 372–377. Convergent development of tibial-tarsal spines and spine combs in drosophilids. 372, 373. *Laccodrosophila flavescens*, fore- and midtarsus respectively. 374. *Colocasiomyia stamenicola*, fore-tarsus. 375. *Colocasiomyia* sp., foretarsus. 376. *D. (Sophophora) affinis* ♂, foretarsus. 377. *D. (Sophophora) melanogaster* ♂, foretarsus.

dominal coloration (apomorphy 133), distiphallal vestiture (apomorphy 132)], it does possess the folded, dorsal process. A spiculed surface on the membranous portion of the folded, dorsal process was found in *L. maculata* and in a species from the Dominican

Republic, but I have not surveyed enough species to determine if this trait too is always found with the dorsal process. According to Gerhard Bächli (personal commun.), a spiculed surface is not found in all dorsal processes.



Figs. 378–387. Segmentation of the male ephydroid abdomen, showing tergites and spiracles.

131. Apomorphic for *Leucophenga* and *Trachyleucophenga* is a very reduced hypandrium: in *Leucophenga* it is reduced to a narrow U-shaped strip, with two narrow arms in the middle which are the bases of the paraphyses (or these arms can be fused, in some species, into a single median rod) (figs. 391, 392). The long, lateral arms of the hypandrium always flare out to three or four times the basal width. A decasternum is present in *Leucophenga*, but it is not nearly as large and developed as in *Stegana*.

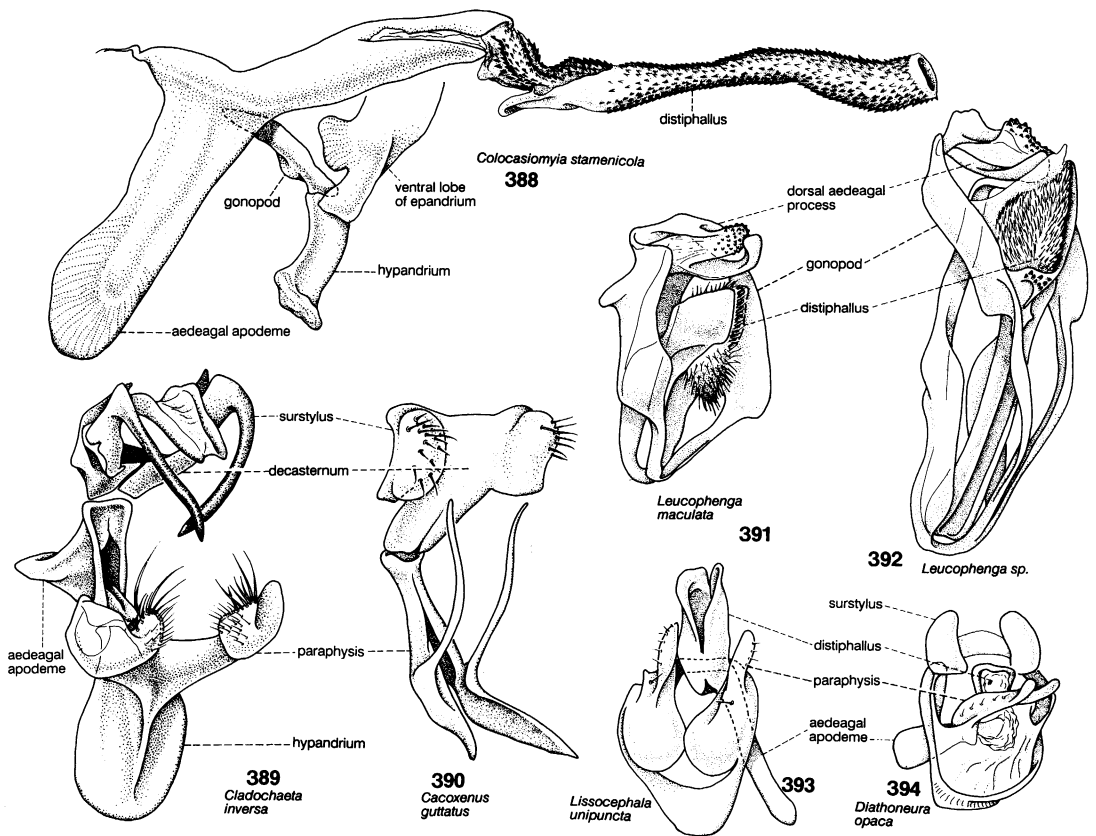
132. Another apomorphy of some *Leucophenga* is a distiphallus with dense, fine, numerous spicules or microtrichia such that the aedeagus resembles an artist's brush (figs. 391, 392). Not all *Leucophenga* possess it; those plesiomorphically lacking it are several species in the *proxima* and *subpollinosa* groups (Okada, 1987). Distribution of the features needs yet to be carefully surveyed. *Trachyleucophenga* also plesiomorphically lacks microtrichia on the distiphallus.

133. Apomorphic to *Leucophenga* is an abdomen with a distinctive pattern of tergal spots. There is always one and usually three

or more median spots (one per tergite, aligned in a median row). Bordering these on some tergites are long spots, or short bands, extended down the lateral portion of the tergite. In some *Leucophenga* the male has a black abdomen (e.g., *L. nigriventris*), but the females have the normal, spotted abdomen. In other species, the male has one or more highly reflective, silvery areas on the tergites (when viewed at an angle), such as in *L. scutellata*. Plesiomorphically, the abdomen is unicolorously dark or infuscate; if patterned, the pattern is diffuse.

134. Yet another apomorphy of *Leucophenga* is the broad surstylus (males). In this genus it is usually squared in view of the broadest surface, and quite flat; short, heavy setae are scattered over the distal half (this vestiture is plesiomorphic) (fig. 494). These setae are never developed into the heavily sclerotized pegs (prensisetae) seen in some other drosophilids. The plesiomorphic surstylar shape is a rounded or crescentic, but not truncate, form.

135. Apomorphic to the state where the ventral epandrial lobe is only setose is one



Figs. 388–394. Male genitalia (hypandrium, aedeagus, and associated structures) of representative drosophilids, lateral (fig. 388) and oblique ventral (389–394) views.

that possesses a row of evenly spaced long teeth on the medial margin. This is found in *Rhinoleucophenga*, *Gitona* (*distigma* and *bivisualis*, but not in *americana*), and *Trachyleucophenga* (figs. 404, 406). *Gitona americana* is superficially similar to *Cacoxenus guttatus* in that there is a sharp, sclerotized, apical tooth that is pointed mediad on the terminal tergites (see apomorphy 150) (fig. 405). (The pointed lobe in *Cacoxenus* is on the posterolateral margin of syntergum VI + VII; that in *Gitona americana* is on the epandrium.) The row of long, evenly spaced teeth on the male genitalia of some *Amiota* (*Amiota*) is on the surstylus; thus, these are the true prenisetae and are not homologous with the teeth in the above taxa. The toothed lobe in *Trachyleucophenga* appears like a surstylus, but is a constricted lobe of the ventral portion of the epandrium. Recognizing these

criteria, and as discussed for apomorphy 136, I don't necessarily agree with Wheeler (1987) that the North American species of *Gitona* do not belong in the same genus as *Gitona distigma*. Apomorphy 135 is independently derived in the three taxa.

136. The surstyli are apomorphically absent (lost) in *Rhinoleucophenga*, *Gitona*, *Pseudiasata*, *Trachyleucophenga*, and the pair of sister genera, *Mayagueza* and *Acletoxenus*. Some workers have suggested fusion of the surstyli to the epandrium, but I have found no evidence for this. The surstyli are a pair of lobes lying between the ventral epandrial lobes and the aedeagus, and each surstylus is usually connected by a bridge (deca sternum) articulating with the base of the surstylus (e.g., figs. 492–507). With very few exceptions the surstylus has prenisetae, which vary tremendously among various taxa

of drosophilids. In their basic form prensisetae are heavily sclerotized, peglike, socketed setae on the mesal surface (figs. 492, 495–507). Their number, arrangement, size, and shape vary. It is probably no coincidence that, without a surstylus, taxa in the above three genera have subsequently developed prensisetae-like setae on other clasping, lobate structures. For example, there are the structures discussed for apomorphy 135, and in *Pseudiastata pseudococcivora* there are about 25 small, short pegs on the ventral surfaces of the cerci (fig. 407). Presumably, these toothed lobate structures function similarly to the surstyli in clasping females during copulation.

137. Also seen in *Rhinoleucophenga*, *Gitona*, *Pseudiastata*, and *Trachyleucophenga* are greatly reduced male genitalia (figs. 420–423). The paraphysis is either absent (*Gitona bivisualis*, *G. brasiliensis*) or highly reduced (i.e., *Gitona americana*, *Rhinoleucophenga pallida*, *Trachyleucophenga* sp., and *Acletoxenus* + *Mayagueza*). A short, simple, squared hypandrial plate is present. Most importantly, the aedeagus is nothing but a bulbous, lightly sclerotized, saclike distiphallus, devoid of vestiture, which articulates directly with the aedeagal apodeme (there is basically no endophallus). The aedeagus is shorter than the aedeagal apodeme. These various features were not split into separate apomorphies because they all occur uniquely in the above taxa, so they may belong to one complex of characters that are interrelated (functionally, developmentally, or otherwise).

138. Common to some *Diathoneura* species (e.g., *opaca* and *laticeps*) and to *Drosophila superba* is a pair of long, fleshy, lobelike paraphyses that have a row of 5 or 6 minute sensilla trichodea on the lateral surface (fig. 394). Plesiomorphically the paraphyses may be lobes, but are much smaller, and have a prominent apical seta and smaller (usually two or three) lateral setae. The feature is convergent with that of *Lissocephala* (fig. 393).

139. Also common to *Diathoneura* and to *Drosophila superba* is a crescentic surstylus bearing a row of prensisetae pegs on the medial edge. In some species the prensisetae are stout and peglike (*opaca*, *nana*, *laticeps*—state 1), in *Drosophila superba* they are about twice the length with a sharp apex (state 3—fig.

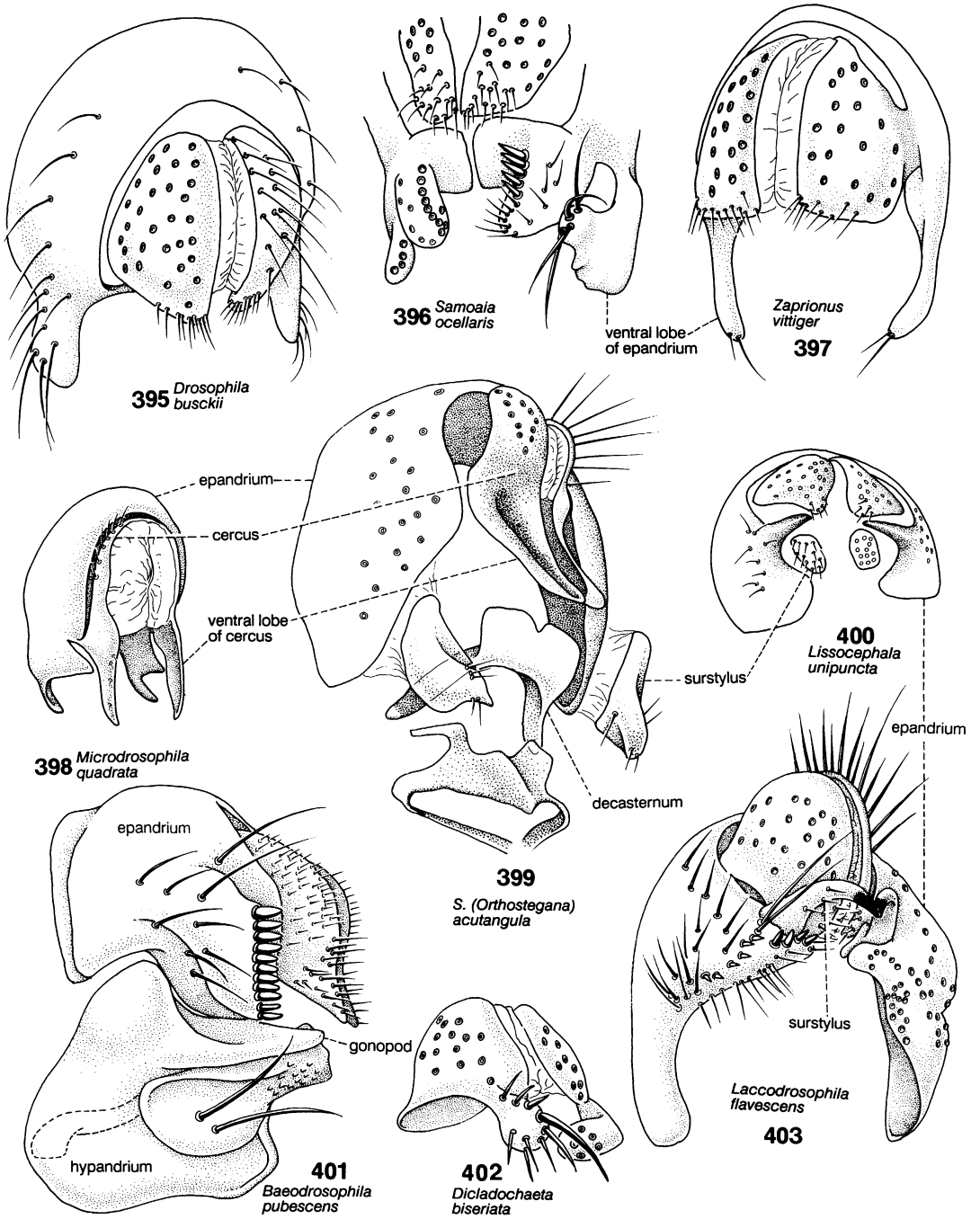
498). The prensisetae in *Diathoneura metallica* are intermediate between the two (state 2). As found in *Cladochaeta*, which has an elongate pair of surstyli, the presence of numerous fine setae on the surstyli is plesiomorphic. States 1 and 2 were unordered.

140. As mentioned in apomorphy 139, *Cladochaeta* [which includes the junior synonym *Clastopteromyia* (Wheeler, 1981)] autapomorphically has a surstylus that is long and projected posteriad (fig. 389). It plesiomorphically bears fine, minute setae. *Cladochaeta sturtevantii* has the apex of the surstylus developed into a small hook that is directed upward. Plesiomorphically, the surstylus is small and crescentic.

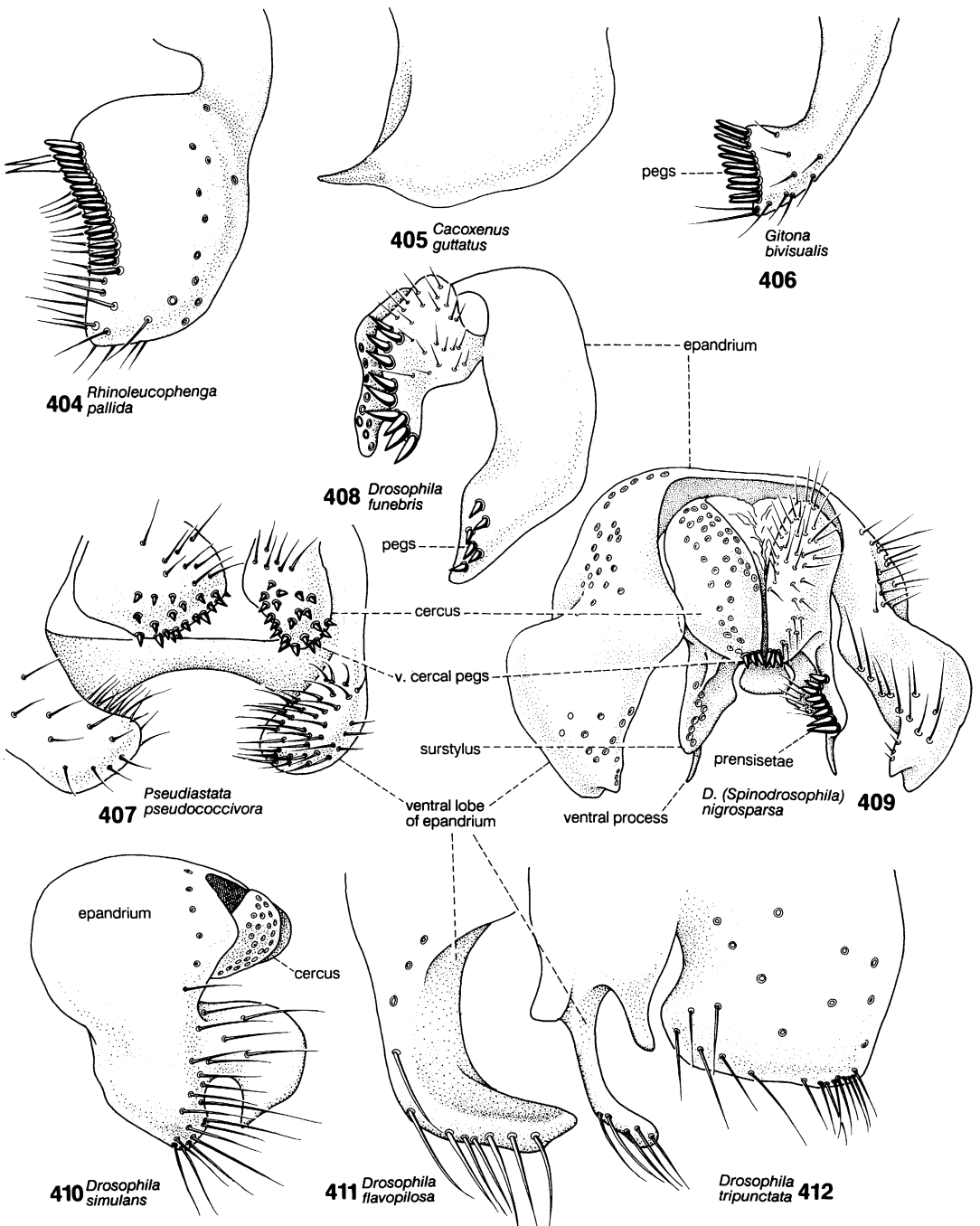
141. Synapomorphic for *Drosophila superba*, *Cladochaeta*, and at least one *Diathoneura* (*laticeps*, but not *opaca* or *metallica*) is a ventral margin on the male cercus that is extended ventrad into a narrow lobelike strip. The apex of the ventral strip can be narrowed and twisted, producing a hook, such as in *Drosophila superba*. This is structurally different from that seen in some *Scaptomyza*. Plesiomorphically, the ventral margin of the cercus matches the contour of the rest of the cercus.

142. In *Diathoneura*, *Cladochaeta*, and *Drosophila superba*, the aedeagus is reduced and the aedeagal apodeme is well developed (figs. 389, 394). (*Cladochaeta* has a distinctive aedeagal apodeme; fig. 389.) Interpretation of the aedeagus, surstylus, and aedeagal apodeme in *Cladochaeta* has been difficult, because of the extreme modification in shapes of many of the structures. Identification of the aedeagus was only possible because of its relative position, between the paraphyses and posterior to the aedeagal apodeme, and by the ubiquitous (for this group) membranous sac forming part of the distiphallus. The aedeagus is reduced to a narrow arched sclerite with a distal membranous sac, as seen best in *Cladochaeta* and some *Diathoneura* (especially *opaca*). The aedeagus is less reduced in *Drosophila superba*, which has a dorsal projection on the sclerotized arch. Despite the numerous fine illustrations in Wheeler and Takada (1971) of male genitalia for various species in this group, they did not discuss nor label the structures and their homologies.

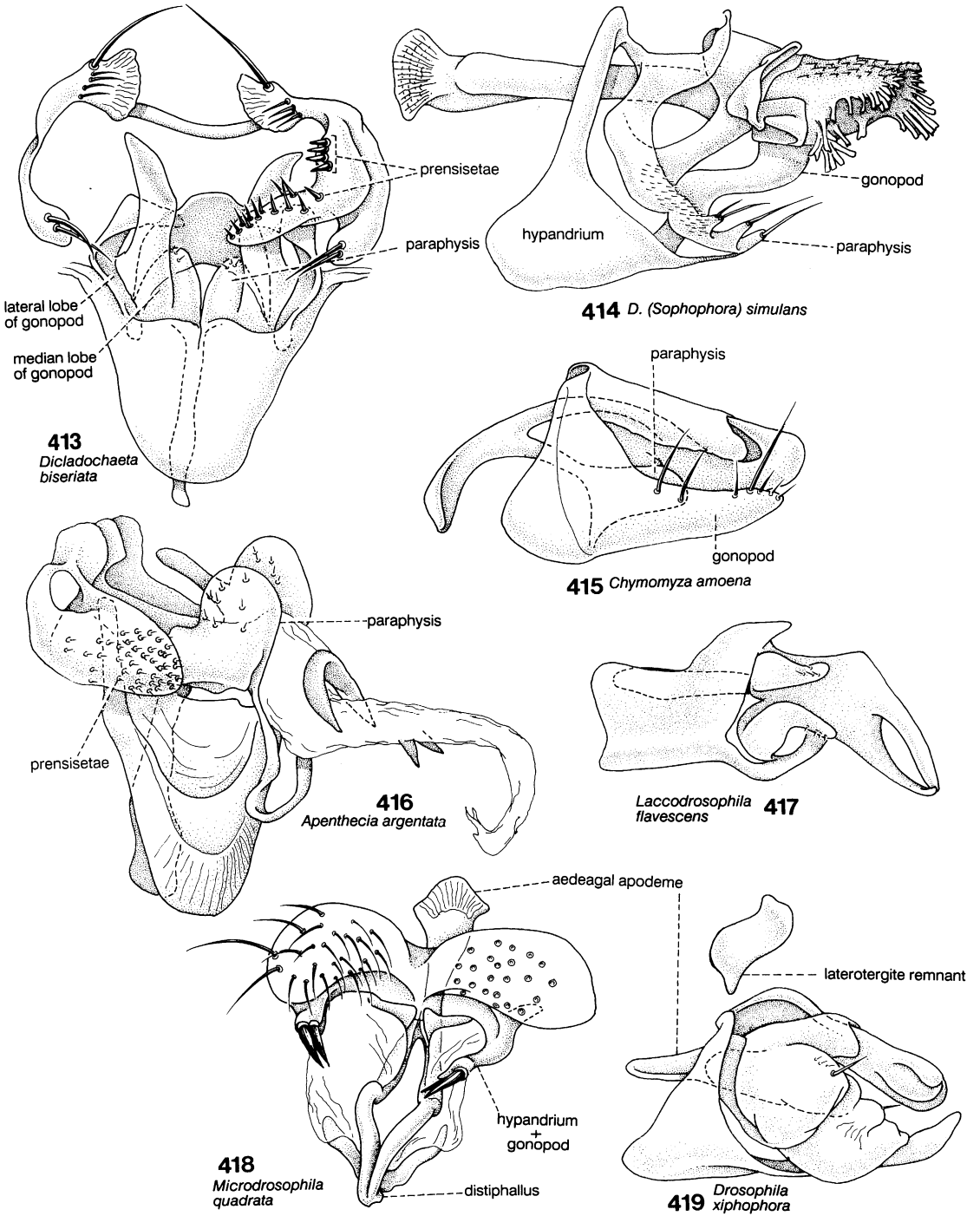
143. Autapomorphic to *Cladochaeta* is a



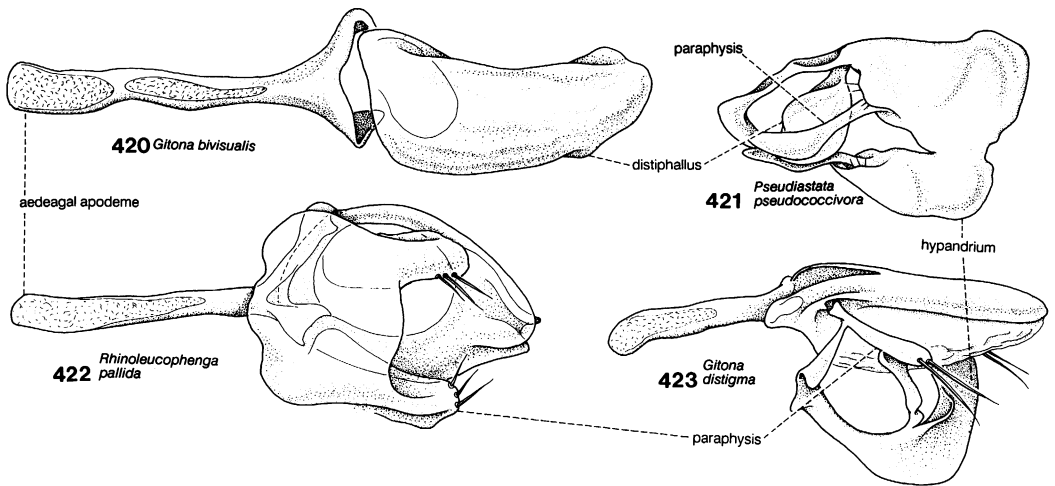
Figs. 395-403. Male genitalia (epandrium, associated structures) of representative drosophilids, in lateral (fig. 401) and oblique posterior views.



Figs. 404–412. Epandrium, cerci, and associated structures in male drosophilids. 404, 406. Ventral lobe of epandrium, showing convergent development in “prensisetae” (lateral views). 405. Posterolateral margin of sytergite VI + VII in *Cacoxenus guttatus*. 407–409. Convergent development of ventral cercal pegs.



Figs. 413-419. Male genitalia (hyandrium, aedeagus, associated structures) in drosophilids. 414-417, 419: oblique lateral view. 413, 418: ventral view.



Figs. 420–423. Male genitalic reduction in some steganine drosophilids, oblique ventral views.

pair of paraphyses that are quite distinctive: they are long and narrow, heavily setose lobes (fig. 389). This feature is not found in *Diathoneura*, which is plesiomorphic for the trait.

144. Also autapomorphic for *Cladochaeta* is an hypandrium distinguished by its unique shape (*Diathoneura* is plesiomorphic for this feature). The hypandrium in broadest view is paddle-shaped and with a central keel that splits off at the base of each surstylus (fig. 389). *Colocasiomyia* has a similar, but not identical, keeled hypandrium. Plesiomorphically the hypandrium is a simple, flat sclerite.

145. Apomorphic to the situation where the paraphysis bears from one to three small setae (the apical one being largest) is where, in *Neotanygastrella* and *Chymomyza*, there are two, sometimes more, long straight setae (fig. 415). The setae are often the length of the paraphysis; in *Neotanygastrella* they are exceptionally prominent and always with one pair on each paraphysis.

146. Also apomorphic for *Neotanygastrella* and *Chymomyza* is a prominent ventral lobe of the epandrium, which bears numerous long setae, particularly toward the apex. Length of the setae is usually equal to that of the lobe or even longer. The lobe is quite narrow and apically tapered in *Neotanygastrella* and some *Chymomyza*. In some *Chymomyza* it is further modified into a broad, paddle-shaped lobe (e.g., in *amoena*, *vaidyai*, *obscuroides*).

At this cladistic level the plesiomorphic state is a small, barely distinguishable lobe on the posteroventral margin of the epandrium.

147. Another apomorphy uniting the genera *Neotanygastrella* and *Chymomyza* is the presence of a small surstylus (partially hidden, usually, behind the lateral wall of the epandrium), which bears a row of prenisetae on the medial edge (figs. 495, 496). The prenisetae are closely and evenly spaced and usually quite long (the length being three times or more the width).

148. Autapomorphic to *Chymomyza* is a pair of long gonopods, flanking (lateral to) the paraphyses (fig. 415). They are always longer than the paraphyses, either slightly or considerably more so; they bear on the dorsal margin a row of long, straight, but not evenly spaced, setae that are pointed toward the epandrium. This structure is plesiomorphically absent.

149. Two subgenera in *Cacoxenus* (*Paracacoxenus* and *Gitonides*) appear to be linked by a derived trait of the gonopods [“anterior gonopods” in McAlpine (1968)]. In both taxa the gonopod is long (nearly extended to the apex of the aedeagus), narrow, and with the small base as the only articulating point for the entire lobe. Homologizing these two lobes lateral to the aedeagus also appears certain because of the five to ten fine, short setulae at the apex of the gonopod.

150. *Cacoxenus (Gitonides)* and *C. (Paracacoxenus)* also appear linked by having the posteroventral corner of syntergum VI + VII narrowed and sclerotized. In *C. guttatus* it is further modified into a sharp tooth at the apex of the lobe, which is pointed mediad (fig. 405). Plesiomorphically, this margin of syntergum VI + VII is simple.

If variation in number, sizes, and shapes of lobes, apodemes, processes, and the various components of the male genitalia is a measure of the complexity of the genitalia, then *Amiota* and *Scaptomyza* must be considered to have the most complex genitalia in the Drosophilidae. For *Amiota* the complexity is a progression in the development of accessory lobes and spines to the paraphysis, a dorsal process (perhaps just a monstrously overdeveloped floor of the decasternum), and, ultimately, loss of the aedeagus in the subgenus *Amiota*. Except for Okada's (1971, 1977) work, there has unfortunately been very little attention paid to the homologies of various male genitalic structures in *Amiota*. *Amiota (Sinophthalmus) picta* was one of the three species used in Griffiths' (1972) study, yet there is no discussion of the special genitalic features. Indeed, this is an unusual, highly modified drosophilid to choose (among the three that were studied) for a synoptic collection of such major taxonomic level that was studied by Griffiths; he erroneously labeled the paraphyses as the hypandrium in the sketch of *A. picta* genitalia. Wheeler and Takada (1971) figured the genitalia of several *Amiota* species, but identified only the epandrium ("genital arch"), hypandrium, and surstyli ("claspers"); the remaining structures were referred to as the "inner genital complex."

The holotype of *A. (Apsiphortica) lini* was sent to me by Toyohi Okada; the subgenus is apparently known only as this species from Taiwan. In most of the genitalic features that are diagnostic it is plesiomorphic: (anterior) paraphysis is small and lobate (not as in 151); hypandrium is large and platelike (not a narrow strip, as in 152); aedeagal apodeme is rodlike (not distinctively platelike, as in 153); there is a lack of the "dorsal mantle of aedeagus" (sensu Okada, 1971) (not as in 154, where it is present); the surstylus is without

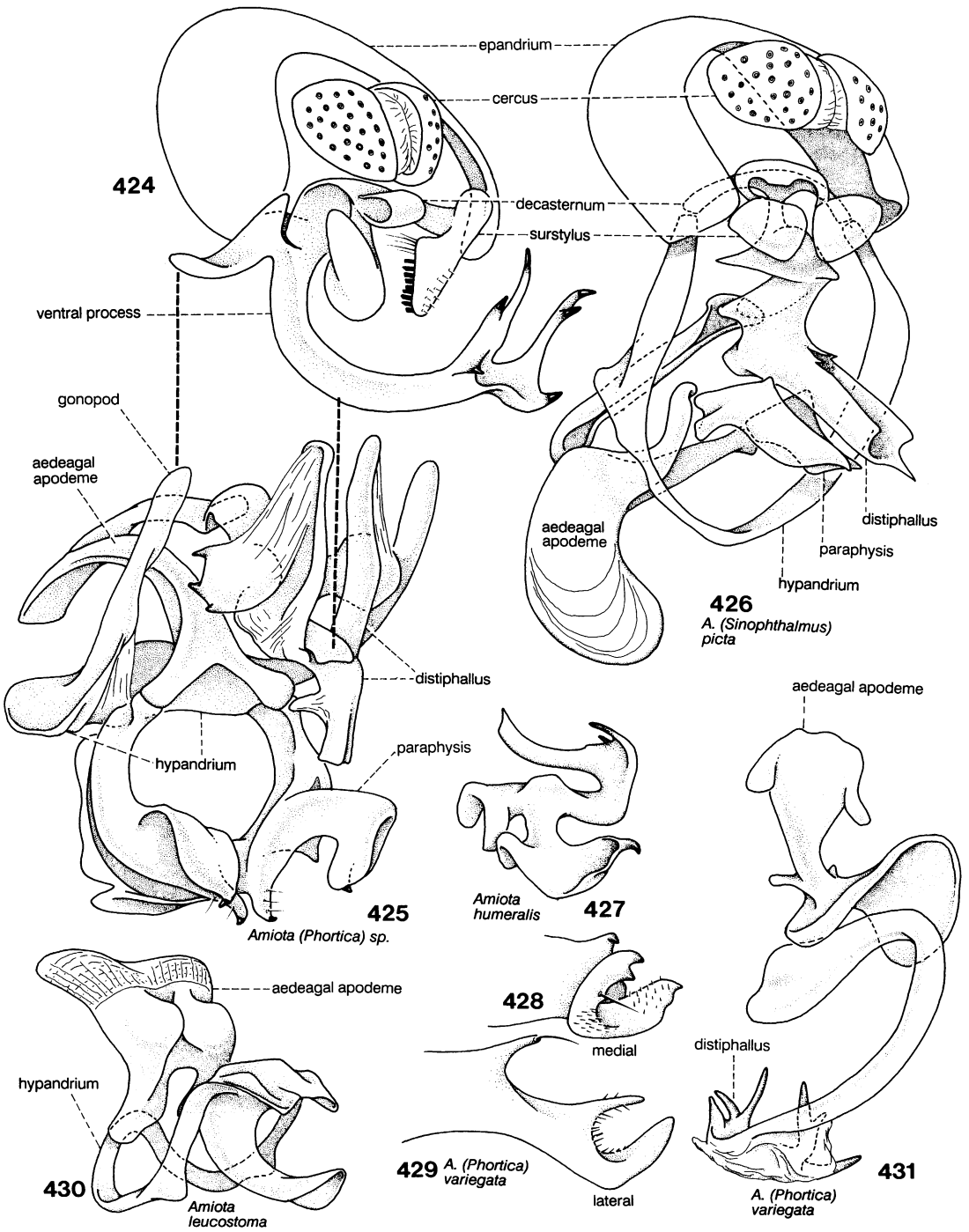
peglike prenisetae (not as in 155); and the aedeagus is present (not lost, as in 156). Only because some nongenitalic features are diagnostic of *Amiota* do we in fact have any idea that *A. lini* belongs in this genus. These are the shape of the head [as described in Okada (1971)], presence of "warts" on the apex of the costal vein on the wing (109) (as mentioned by Okada, but I have not found this to be an *Amiota* character), and the slightly convergent wing veins R_{4+5} and M_1 (like apomorphy 108, but not as developed).

151. Perhaps the most distinctive feature of *Amiota* genitalia is an anterior pair of large, heavily sclerotized paraphyses, that are often modified into various shapes but all with some sort of hooks and spines on them (figs. 425–430). The structure of the various types seems to indicate that these lobes might move laterally, and thus perhaps they grip the ovipositor of the female (with the teeth and spines) during copulation. The development of this pair of lobes no doubt functionally replaces the intromittent organ, the aedeagus, and allows the gonopores of the mating pair to come into close contact.

152. Also an apomorphy for the various subgenera of *Amiota* is a very reduced hypandrium (figs. 426, 430). Instead of the plesiomorphic structure wherein a simple sclerotized plate is present, there is instead a thin, U-shaped strip.

153. There appears to be a transformation series in *Amiota* for the development of the aedeagal apodeme, from its plesiomorphic shape in *Sinophthalmus* and most *Phortica*, to the most modified type, seen in *A. (Amiota)*. In the subgenus *Amiota* the aedeagal apodeme is a very broad plate, usually with an arm on each posterior corner that articulates with a paraphysis (apomorphy 153). This aedeagal apodeme actually rests above the hypandrium and is not (plesiomorphically) arched over and anterior to it (figs. 425, 426, 428, 431). Plesiomorphically, the aedeagal apodeme is also laterally flat.

154. Ventral to the pair of surstyli and their connecting bridge (the decasternum) is an elongate, heavily sclerotized process having an apex adorned with spines (fig. 424). This feature is found in *Amiota (Phortica)*; it is (plesiomorphically) absent in all other drosophilids, except for *Cacoxenus* (which has



Figs. 424-431. Male genitalia in the genus *Amiota*.

developed one independently—see below). Okada's (1971) term, "dorsal mantle of aedeagus," is the only one ever proposed for this structure, and apparently would seem as appropriate as any. It is bewildering to try homologizing this structure with any other in the drosophilids, but I don't believe it to be part of the aedeagus. Instead, it seems to be a grotesque, huge extension of the floor of the decasternum, and articulates with or is attached to the anteroventral margin of the decasternum.

Cacoxenus (Paracacoxenus) guttatus has a similar structure, labeled as the "posterior gonopod" by McAlpine (1968). It clearly articulates with the decasternum in *C. guttatus*, it is a paired structure, and it is formed from four arms (two posteriorly directed ones, two dorsally directed ones) (fig. 390). The posteriorly directed arms are two to three times the width of the others and they have a concave mesal surface. Because of the unique shape, and the fact that it is paired, it is most likely that this structure is not apomorphy 154. As such, this structure would be autapomorphic to *Cacoxenus (Paracacoxenus)*.

155. Apomorphic in the subgenus *Amiota* is a surstylus possessing a row of evenly spaced, peglike prenisetae (fig. 492). The apex of the surstylus normally has a narrow lobe pointed in the same direction as the prenisetae and about the same size. The plesiomorphic state of surstylar adornment is seen in *Apenthecia* and the subgenera *Apsiphortica*, *Erima*, *Phortica* (e.g., fig. 493), and *Sinophthalmus*, which have numerous, small, short, peglike prenisetae scattered over the mesal surface of the surstylus.

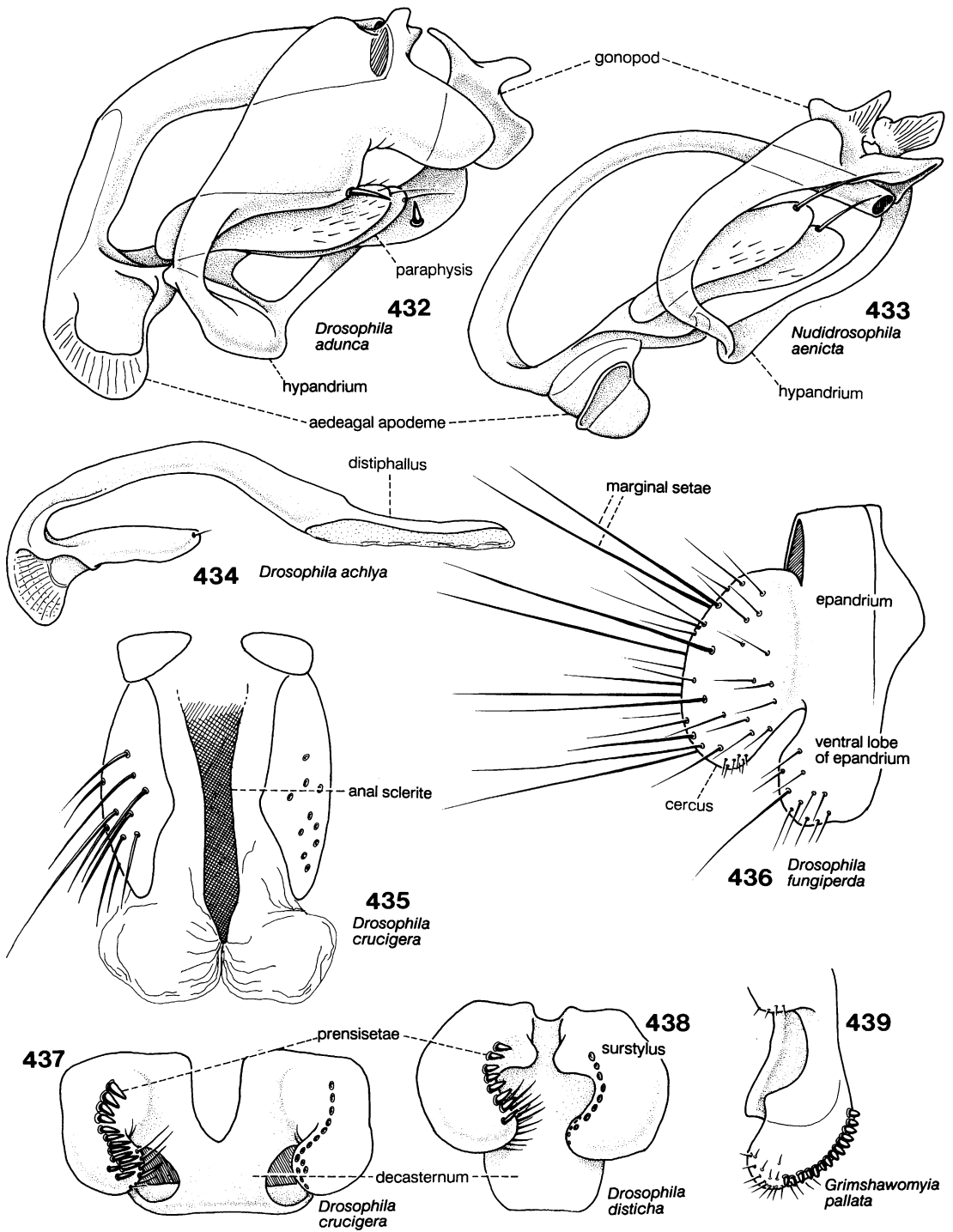
156. Autapomorphic for most species in the subgenus *Amiota* is a loss of the aedeagus. Incredibly, not even a membranous remnant of the aedeagus remains (the ejaculatory apodeme, however, is present) (fig. 430). Development of the large aedeagal apodeme, as described for apomorphy 153, must have something to do with insemination. Structurally the paraphyses of *Amiota* appear to be able to distend the female gonopore, like a hooked speculum. It is possible that, after such possible distension, the aedeagal apodeme is contracted ventrally (by attached muscles), thus jettisoning the sperm out of the male gonopore. Obviously the plesio-

morphic state is the possession of an aedeagus, which the other subgenera in *Amiota* have. Certainly the highly modified paraphyses in the genus *Amiota* are not related only to loss of the aedeagus, for *Phortica* has a very elaborate distiphallus and among the most highly developed paraphyses in *Amiota*.

A great deal has been studied with respect to the Hawaiian drosophilids. For the purposes of this work, the paper by Takada (1966) and the ones by Hardy (1965) and Kaneshiro (1969) were most useful. Takada (1966) provided a scheme of genitalic evolution and simple phylogeny for Hawaiian drosophilids. My purpose is not to construct new hierarchies within this group, nor to test those that have been proposed (e.g., Kaneshiro, 1969; 1976). It is necessary to examine Hawaiian drosophilids simply to see at what taxonomic level among drosophilid genera the group(s) is (are) monophyletic. Based on features of the male genitalia, distinct groups within the endemic assemblage of Hawaiian species can be discerned, but few of these features appear of use regarding relationships to mainland taxa.

157. In lateral view of the aedeagus it is apomorphically as follows: long (distiphallus projected well beyond the hypandrial margin), narrow, with a slight arch, and a short keel-shaped aedeagal apodeme (figs. 432–434). Also, the distiphallus is usually (in lateral view) tapered to a narrow dorsal strip (the ventral portion below the strip is only membrane). The distiphallus can be truncate [e.g., *Ateledrosophila preapicula*, *Drosophila (Antopocerus) adunca* (although other *Antopocerus* have the tapered type of distiphallus)]. In most species as well, the dorsal surface of the distiphallus bears a process which can be developed anywhere from a prominent tooth to a modest swelling (plesiomorphically absent, as in *Ateledrosophila*). This basic type of aedeagus is found in the endemic species assigned to *Drosophila*, in the subgenera *Antopocerus* and *Drosophila*, and in *Nudidrosophila* (examined in *aenicta*) and *Ateledrosophila* (examined for *preapicula*). Plesiomorphically the aedeagus is not extended beyond the hypandrial margin nor so narrowed and arching.

158. Also shared among *Ateledrosophila*,



Figs. 432–439. Male genitalia in Hawaiian *Drosophila*. 432, 433. Aedeagus, hypandrium, associated structures. 434. Aedeagus and paraphysis (lateral). 435. Cerci (dorsal view). 436. Epandrium and cercus (lateral). 437–439. Surstylus (439), with decasternum (437, 438).

Nudidrosophila, *Antopocerus*, and the endemic Hawaiian *D. (Drosophila)* species is an hypandrium with the following apomorphic features: anterior margin of the hypandrium is curled ventrad; the ventromedial surface bears a pair of stout setae (short and spinelike in some species); a pair of gonopods (lobate extensions of the posterolateral corners of the hypandrium) are present, and well developed in some species (figs. 432, 433). In *Nudidrosophila aenicta*, for example, the gonopods are fused medially at the posterior end of the hypandrium, forming a triangular guide over the distiphallus, and two flanges (fig. 433). In *Antopocerus*, the gonopods are projected posteriorly, are slightly concave, and appear to envelop (channel?) the distiphallus. Plesiomorphically, the hypandrium has a straight, not curled, margin, no setae/spines on the ventromesal surface, and no gonopods (or at least no prominent ones).

159. Also apomorphic to *Ateledrosophila*, *D. (Antopocerus)*, *Nudidrosophila*, and endemic Hawaiian *D. (Drosophila)* is a pair of long paraphyses (normally extended to slightly beyond the pair of setae on the ventral margin of the hypandrium), each bearing an apical seta (figs. 432–434). Some species have, in addition, a sparse vestiture of fine setulae on usually the apical half of the paraphysis (found in *Ateledrosophila*, *Nudidrosophila*, and *Antopocerus*) (figs. 432, 433).

160. Another apomorphy of the clade discussed above is a ventral epandrial lobe that is apically truncate (and usually turned posteriorly). Always it is with at least one very long and prominent seta (sometimes two or three) near the base of the lobe and approximately 10 or more smaller ones around it (fig. 436). Plesiomorphically there is no one, large prominent seta; the ventral epandrial lobe is not truncate or turned posteriorly, and bears only a few setae (sometimes none).

161. Apomorphic, and found in the taxa discussed in apomorphy **159**, is a cercus bearing an indistinct row of very long, straight setae on the apical margin (fig. 436). The apical setae are about twice the length of the other cercal setae. Plesiomorphically the apical setae are only slightly longer than the other cercal setae.

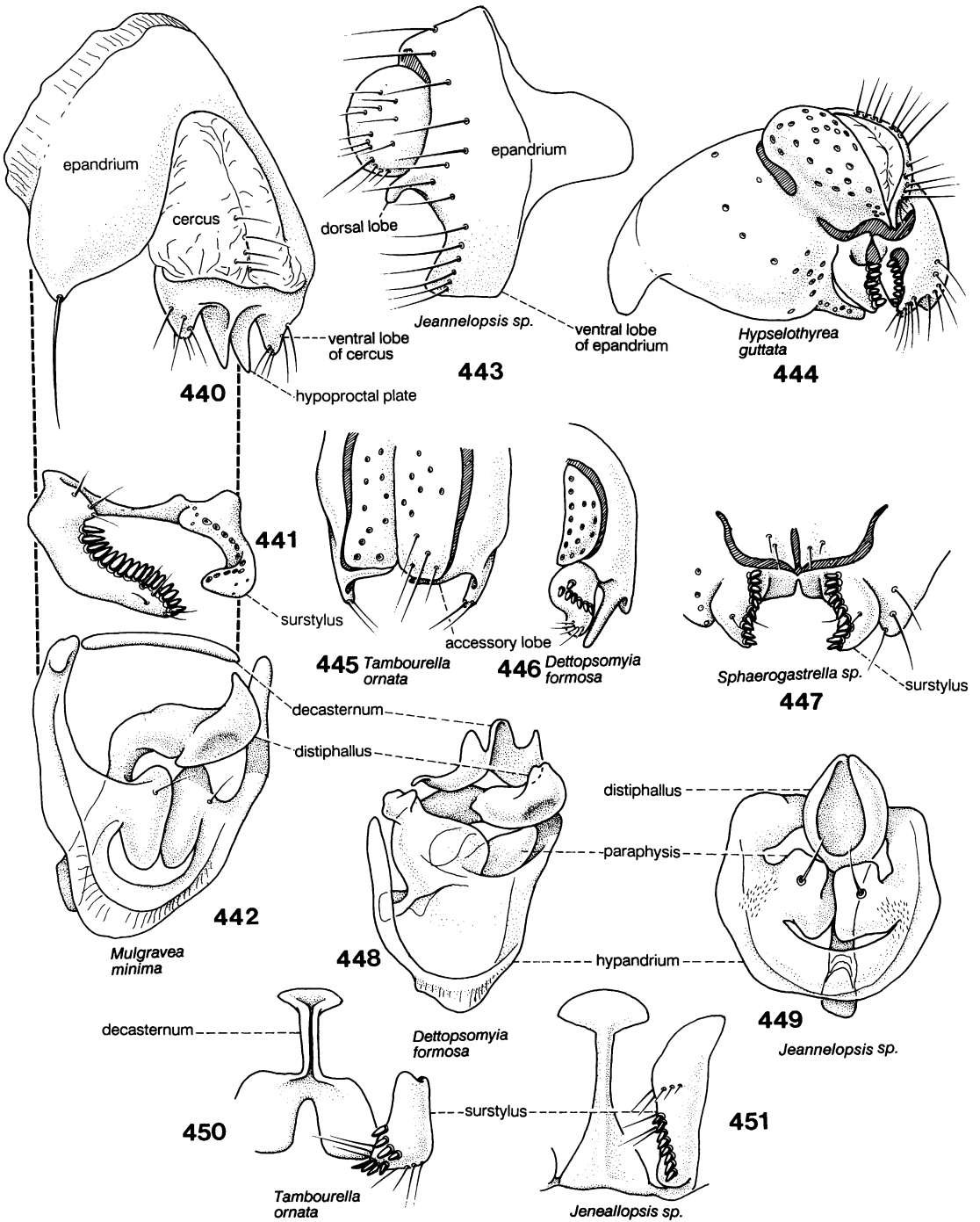
162. Apomorphically present in some Hawaiian *Drosophila* species, but not in the

other groups discussed for apomorphies **157–160**, is a narrow, light sclerite that lies in the membrane between the dorsal surfaces of the cerci in males (fig. 435). It is always apically pointed. This sclerite would define a group within the Hawaiian *Drosophila*. It is plesiomorphically absent.

163. Also apomorphic to the taxa discussed above is a small, usually crescentic surstylus that is broadly attached to a wide decasternum (figs. 437, 438). There is always a row of short, peglike prenisetae along most of the length of the surstylus near the lateral surface (sometimes they are quite long, as in *Drosophila bipolita*). The plesiomorphic state is a pendulous surstylus without this arrangement of prenisetae, as in the Hawaiian *Scaptomyza*, and perhaps with no peglike prenisetae at all.

164. Common to most species of *Mulgravea* (see Okada, 1987, for a recent synonymization of *Thyrecephala* Okada with *Mulgravea* Bock) are the following features, all lumped under apomorphy **164** (but no doubt functionally separate). Surstylus is elongate and bears prenisetae along most of its length; the decasternum (surstyliar bridge) is narrow; and medial to the surstylus is a ventral lobe of the cercus bearing several fine setulae (fig. 441). Plesiomorphically, the surstylus is crescentic, broadly attached to the decasternum, and a ventral lobe of the cercus is absent. *Mulgravea* autapomorphically has the ventral half of the cercus sclerotized and the remainder unsclerotized (fig. 440); also, there is a pair of sclerotized, pointed, flanges (hypoproctal plates), similar to those in *Zygothrica* (see apomorphy **189**) (fig. 440).

165. Linking the two genera *Tambourella* (fig. 445) and *Jeannelopsis* (fig. 443) are very similar genitalia, in particular possessing apomorphies **165–167**. Just beneath the ventral surfaces of the cerci is a pair of sclerotized lobes that point medially; they are dorsomedial to the ventral epandrial lobe and just above (dorsal to) the surstyli. This is also seen in *Lissocephala unipuncta* (but not *sabroskyi*) (fig. 400). These are not homologous with the sclerotized lobes, also pointed medially, seen in *Hypselothyrea*, since in this genus the lobes are ventral, not dorsal, to the surstyli. Plesiomorphically, these lobes are absent. I examined *Tambourella ornata*, but *T. endian-*



Figs. 440–451. Male genitalia in a group of Indo-Pacific genera. 440, 441, 443–447. Epandrium, cercus, surstylus. 442, 448, 449. Aedeagus, hypandrium, associated structures. 450, 451. Surstyli and decasternum.

drae, the type species, appears to be plesiomorphic for these three apomorphies (as discussed and figured by Bock, 1982). According to the cladistic analysis, the feature is independently derived in *Tambourella* and *Jeannelopsis*.

166. The derived structure of the decasternum in *Tambourella ornata* and *Jeannelopsis* is considered synapomorphic. In both, there is a broad base (between the surstyli) that then is narrowed into a neck, and finally apically expanded into a flange (figs. 450, 451). Plesiomorphically, the decasternum is a simple, nonlobed plate. *Tambourella ornata* has the additional feature of a notch on the basal portion of the decasternum, and the sides of the neck are folded mediad, producing a groove. This trait, like **165**, is considered to be independently derived.

167. Also shared between *T. ornata* and *Jeannelopsis* is a similar vestiture on the paraphyses. In both there is a small patch of dense, fine microtrichia on the ventral surface of the lobate paraphysis (fig. 449), which is more dense and with longer microtrichia in *T. ornata*. Plesiomorphically the paraphysis is bare.

168. Shared between *Lissocephala* and *Liodrosophila* is a paraphysis which has a fleshy apical extension and (state 2) bears a row of five to six minute setulae (see apomorphy **138**) (fig. 393). *Lissocephala* has, in addition, an aedeagus with a long aedeagal apodeme and a short distiphallus. The distiphallus is normally bulbous and with "lips" at the apical opening. *Sphaerogastrella* has the extension, but not the setulae, so would be plesiomorphic to the situation in the other two genera (state 1).

169. The genus *Microdrosophila* possesses a very distinctive array of genitalic features. Most species have paraphyses with an additional pair of ventral lobes, which are flat, setose, and attached to each other medially (fig. 418). In some species (e.g., *M. quadrata* and *M. jarrae*) the apex of each paraphysis bears two to four heavily sclerotized spines that are pointed posteriad. Various shapes of the distiphallus exist. In *M. quadrata* and *M. jarrae*, there is a pair of prominent spines, making the distiphallus pronged, and the gap between the spines is membranous. Other species have a simple, membranous, bulbous

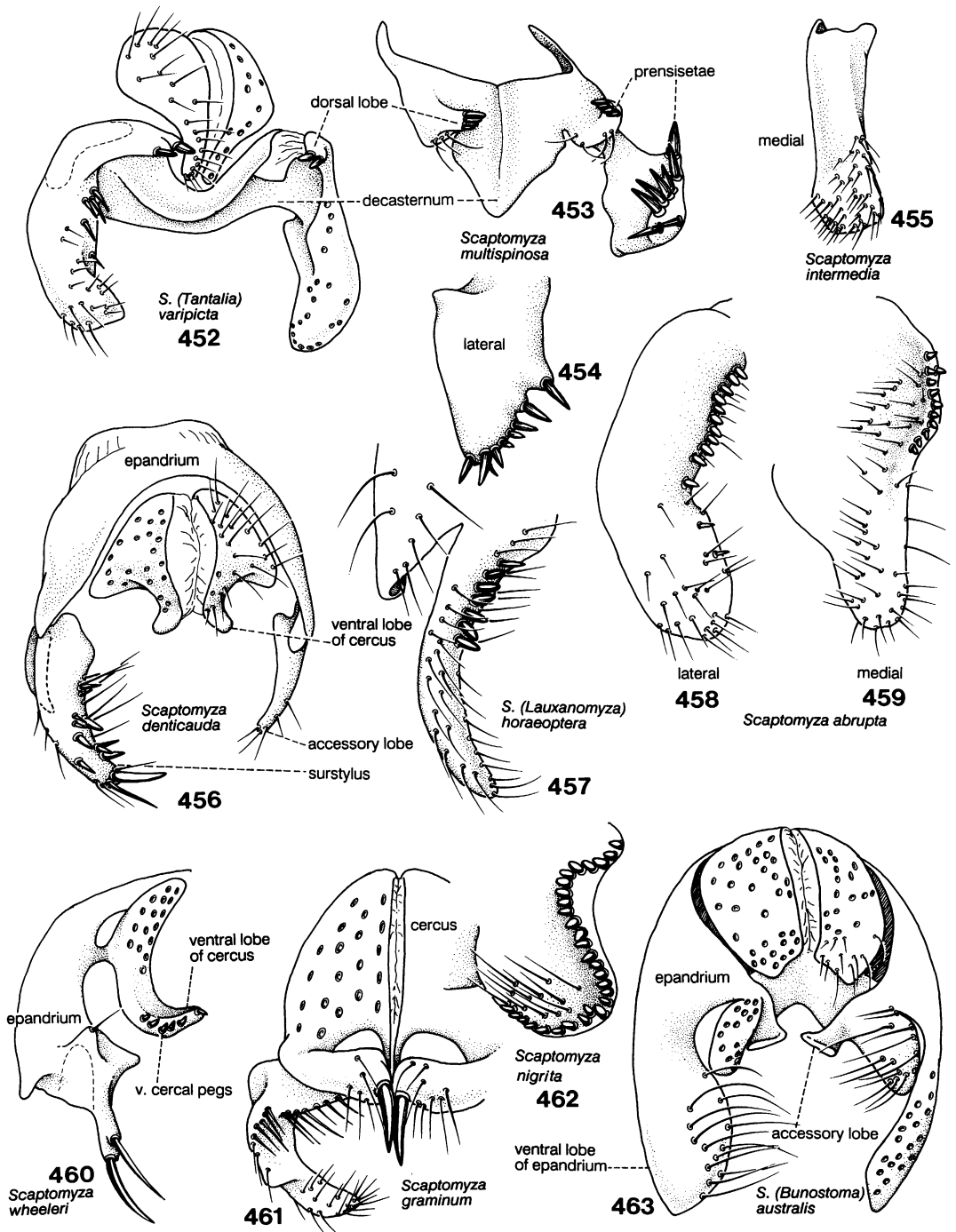
distiphallus. The cerci are usually attached to the epandrium, occasionally broadly, and sometimes possess a pair of elongate ventral lobes. The lack of a pair of setose paraphysal plates is plesiomorphic.

170. The following genera have a distiphallus that is bulbous, apically narrowed, and with a small dorsal knob (figs. 448, 449): *Dettopsomyia*, *Drosophila* (*Dichaetophora*), *Hypselothyrea*, *Jeannelopsis*, *Liodrosophila*, *Mulgravea*, *Sphaerogastrella*, *Styloptera*, and *Tambourella*. Plesiomorphically the distiphallus is probably just bulbous, and without the characteristic apical narrowing and upturned tip.

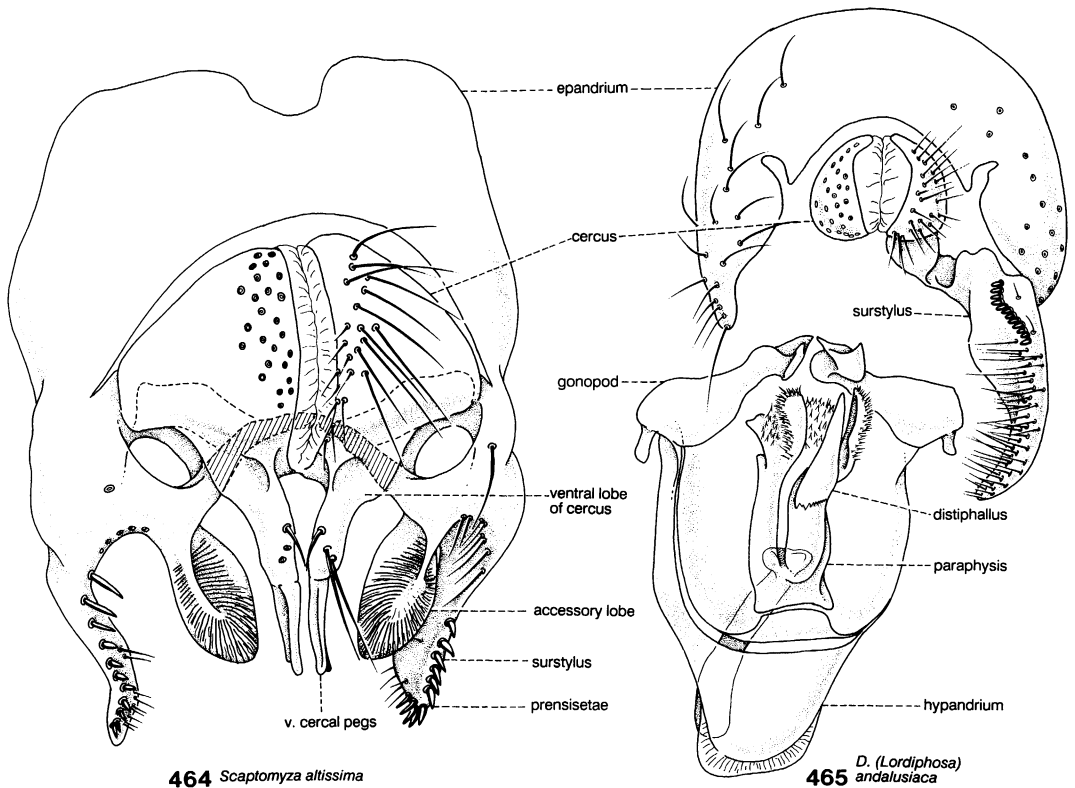
171. Most species of the genera listed above possess a short hypandrium (figs. 442, 448, 449) and almost always have a single row of short, peglike prenisetae on the surstylus (figs. 444, 446, 447). Plesiomorphically, the hypandrium is not like a band or strip, but is like a broad plate, and the prenisetae are irregularly arranged.

The genus *Scaptomyza* has numerous genitalic apomorphies, 17 of which are listed below. As I mentioned previously, this genus has, with *Amiota*, some of the most complex male genitalia in the Drosophilidae.

172. Apomorphically there are heavily sclerotized spines on the ventral surface of the cercus (figs. 460, 461). These can vary considerably in number, placement, and shape, but they are always rather stout, sharp, and easily distinguished from the cercal setae. In *Scaptomyza wheeleri*, for example, about five to six small spines, actually pegs, occur on an upturned surface of the cercus, and in *S. graminum*, there is one large spine at the apex of each ventral cercal lobe (the lobes in both species are pointed mediad). Plesiomorphically there is a small patch of fine setulae on this area of the cercus, and an elongate lobe on the ventral surface is not present. Wheeler and Takada (1966) termed this feature the *vittata* and *pallida* type of external male genitalia in *Scaptomyza* (among eight types that were described). These cercal spines are definitely distinguishable from those in *S. (Macroscaptomyza) altissima*, for in this species the ventral surface of the cercus itself is distended ventrally for a length about equal to the apical spines. The spines in this species



Figs. 452-463. Male genitalia in *Scaptomyza*, showing variation in the cercus, surstyli, and decasternum (figs. 453-459, 462) and ventral lobe of epandrium.



Figs. 464, 465. Male genitalia of *Scaptomyza* and relative (*Lordiphosa*). 464. Epandrium and cercus, posterior view. 465. Epandrium, cercus, surstyli, aedeagus, hypandrium, and associated structures.

also differ in shape: they are narrow, not very sharp, and occur in two pairs. Several other drosophilid taxa have ventral spines on the cercus, but are not to be considered homologous with those in *Scaptomyza*. For example, as discussed for apomorphy 136, *Pseudiastata* has numerous cercal spines, as does *Drosophila funebris* (fig. 408). In these taxa the spines are much shorter than in *Scaptomyza*, but equally stout, and more numerous.

173. A short and bulbous distiphallus is actually widespread among various groups of *Scaptomyza*, and is considered to be apomorphic here. Such a distiphallus is almost always apically narrowed, and shorter in length than the aedeagal apodeme (figs. 466–474). Plesiomorphically, the distiphallus is not apically narrowed, although it may be bulbous, and it is longer than the aedeagal apodeme.

174. Another widespread feature of *Scaptomyza*, indeed a diagnostic feature for a large part of the genus, is the presence of a pair of sclerotized, narrow gonopods that are conspicuously projected posterodorsad (figs. 466–474). It seems quite certain that these lobes are not the paraphyses, for they lack the standard array of tiny apical sensilla seen on paraphyses, and they are lateral to the paraphyses in *Scaptomyza*. In fact, the gonopods are obviously extensions of the posterolateral corners of the hypandrium, modified into various shapes. In some species the gonopods have become detached from the hypandrium (e.g., *S. intermedia*), and in others they are virtually fused dorsally, to produce a sheath on one side of the aedeagus (e.g., *S. horaeoptera*, *trochanterata*) (figs. 470, 471). A well-developed, projecting gonopod is also present in *Drosophila (Lordiphosa)* (fig. 465), but here it is plesiomorphically situated at the poste-

rior end of the genitalia (the lobes are not immediately lateral to the paraphyses). Plesiomorphically, the gonopods are not developed at the genus level for *Scaptomyza*.

175. Also very widespread in *Scaptomyza* are small, bulbous paraphyses. They lie near the base of the gonopods and bear either several fine sensilla or one large seta on the apex (figs. 466–474). Plesiomorphically the paraphyses are longer than wide, and perhaps one-half the length of the aedeagus.

176. The ventral lobe of the epandrium is apomorphically long (two to three times longer than wide) and bears long setae at or near its apex (state 1). At least the longest of these setae are usually equal to the length of the epandrial lobe. This feature is no doubt not homologous among all the *Scaptomyza* possessing elongate epandrial lobes; for example, *S. wheeleri* has a very narrow lobe with two stout, spinelike apical setae, and *S. australis* has a laterally broad lobe with numerous fine setae along most of the lobe's length (fig. 463). This feature corresponds with the epandrial lobes found in the *wheeleri* and *denticauda* type of *Scaptomyza* genitalia, sensu Wheeler and Takada (1966). Plesiomorphically the ventral margin of the epandrium has only a small lobe, if one at all, and may bear several long setae (but never as stout or long as in apomorphy 157). The development of long, or at least prominent, ventral lobes on the epandrium has obviously occurred repeatedly among the drosophilids, but here it is considered a synapomorphy for the *Scaptomyza* which possess it (state 2 or apomorphy 176). States 1 and 2 were ordered.

177. Synapomorphic for *Scaptomyza*, and perhaps for some other genera, is an epandrium that is devoid of setae except on the ventral lobes. Other genera in which this occurs are *Drosophila* (*Dichaetophora*), *Phorticella* + *Zaprionus*, and *Drosophila* (*Lordiphosa*) but I am unsure if this condition in these taxa is homologous with that in *Scaptomyza*. At least *D. (Dichaetophora) abberans* has a well-developed ventral lobe of the epandrium and a distiphallal shape which would indicate its affinities with *Scaptomyza*. The plesiomorphic state is for the epandrium to have setae, with at least a row being on the posterior margin.

178. In most *Scaptomyza* there is a single

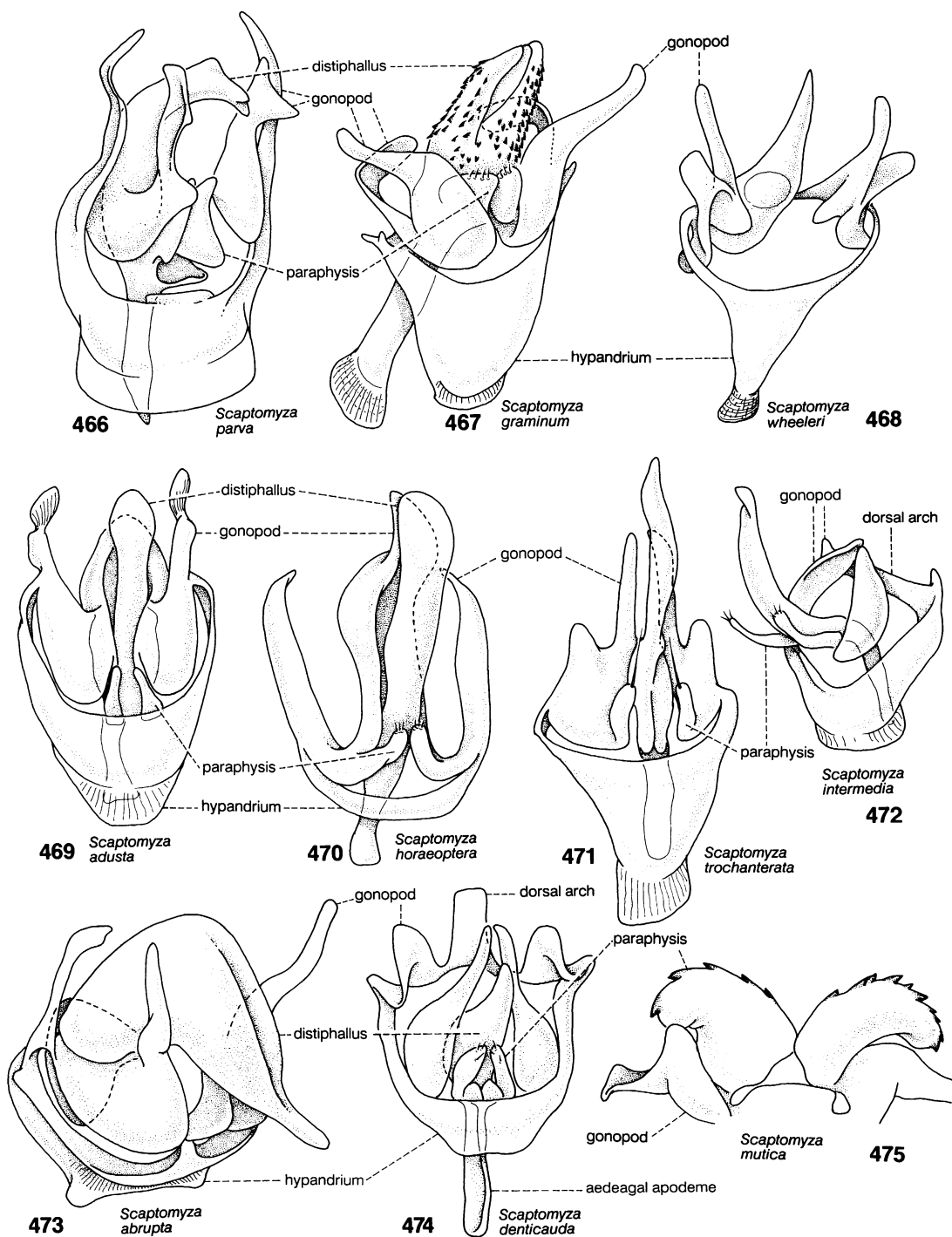
row of stout, peglike prenisetae on the surstylus, arranged in the direction of the length of the surstylus (figs. 458, 459). The surstylus also has several long setae (two to three times the length of the prenisetae) along the mesal surface and at the apex, and is slightly to strongly crescentic in shape (state 1). Apomorphically there is a short row of the peg prenisetae on the proximal half of the surstylus, with setal prenisetae distal to this row (state 2). States 1 and 2 were ordered. The situation seen in apomorphy 186 is a further modification on apomorphy 178 (the proximal row of prenisetae has become separated on a separate median lobe). Plesiomorphically the prenisetae are either in a row extended the length of the surstylus (e.g., *S. nigrita*, fig. 462), irregularly arranged along most of the surstylus (e.g., *S. denticauda*, e.g., fig. 456), or perhaps just setose (not in the shape of pegs) over most of the surstylus (e.g., *S. australis*). It is important to note that *Drosophila* (*Lordiphosa*) possesses a surstylus with apomorphy 178.

179. Apomorphically the hypandrium of *Scaptomyza* has a broad, flat posterior margin, and the length of the hypandrium is quite short (in some cases, just a strip connecting the bases of the gonites) (fig. 473). Plesiomorphically, the hypandrium is a broad, simple plate.

180. Found in some *Rosenwaldia* (and obviously synapomorphic), and in some other *Scaptomyza* [e.g., *S. (Bunostoma) australis* and *S. (Trogloscaptomyza) platyrhina*], is a pair of gonopods that are directed strongly dorsad (fig. 473). This feature is a modification of apomorphy 174, and is apparently not homologous between *Rosenwaldia* and the other *Scaptomyza*. Plesiomorphically, at this level, the gonopods are projected posterodorsad, not strongly dorsad.

181. Several species of Hawaiian *Scaptomyza* in three subgenera were found to have a hypandrium with a median process on the anterior margin. The process is extended to between the paraphyses, and can be rather short and squared (fig. 473). Plesiomorphically, no median process exists.

182. A distinctive genitalic feature, also linking several subgenera the of Hawaiian *Scaptomyza*, is an aedeagus which is virtually entirely distiphallus; it is bulbous, short, and



Figs. 466-475. Male genitalia (aedeagus, hypandrium, paraphyses, gonopods) in *Scaptomyza*. 475, detail of paraphyses in *S. mutica*.

forms a cup over the rest of the genitalia (fig. 473). Plesiomorphically, the distiphallus is a distinct portion of the entire aedeagus; it is bulbous but not nearly so as in apomorphy 182, and does not cover other portions of the genitalia.

183. The ventral portion of each cercal lobe apomorphically has a narrow, ventral extension that is projected slightly anteriorly (figs. 452, 456, 476). This feature, too, links several groups of Hawaiian *Scaptomyza*. The ventral strip of the cercus is usually setose. Plesiomorphically the ventral margin of the cercus is simple and flat.

184. Found in three species of *Trogloscapto-myza* is an unusual feature of the epandrium, which is autapomorphic within the Drosophilidae. It is an accessory, ventral lobe of the epandrium that is conical and separated from, but articulated with, the rest of the epandrium (fig. 456). Plesiomorphically, if a well-developed ventral lobe of the epandrium is present, it is fully attached and not articulating.

185. Linking two species of *Alloscapto-myza* that were examined is another equally distinctive feature, also autapomorphic within the Drosophilidae. The surstyli have been lost, but apparently the paraphyses replace them functionally. The paraphyses have become toothed, and thus might function in clasping females during copulation like the surstyli (fig. 475). The loss of the surstyli and development of a paired structure modified for clasping is another parallel instance of the phenomenon described in apomorphy 136. The plesiomorphic state is for the surstyli to be present and the paraphyses to lack teeth.

186. Linking several species of Hawaiian *Scaptomyza* in three subgenera, and synapomorphic for *Tantalia* and *Trogloscapto-myza*, is a surstylus that has a distinct dorsal lobe. The lobe bears two to four stout prenisetae (apparently a portion of the prenisetae in the row normally found on the proximal half of the surstylus—see apomorphy 178); it is also pointed strongly medially (figs. 452, 453). Plesiomorphically, there is no separation of prenisetae within the row, nor the development of a medial lobe to the surstylus.

187. Surstyli in *Scaptomyza* which do not bear peglike prenisetae, but instead only setal prenisetae, are considered a reversal to a

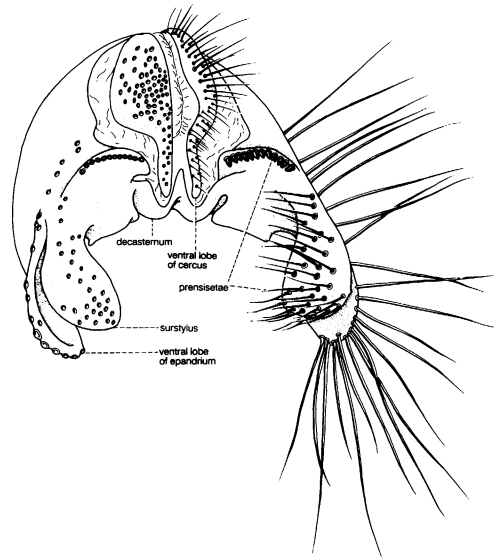
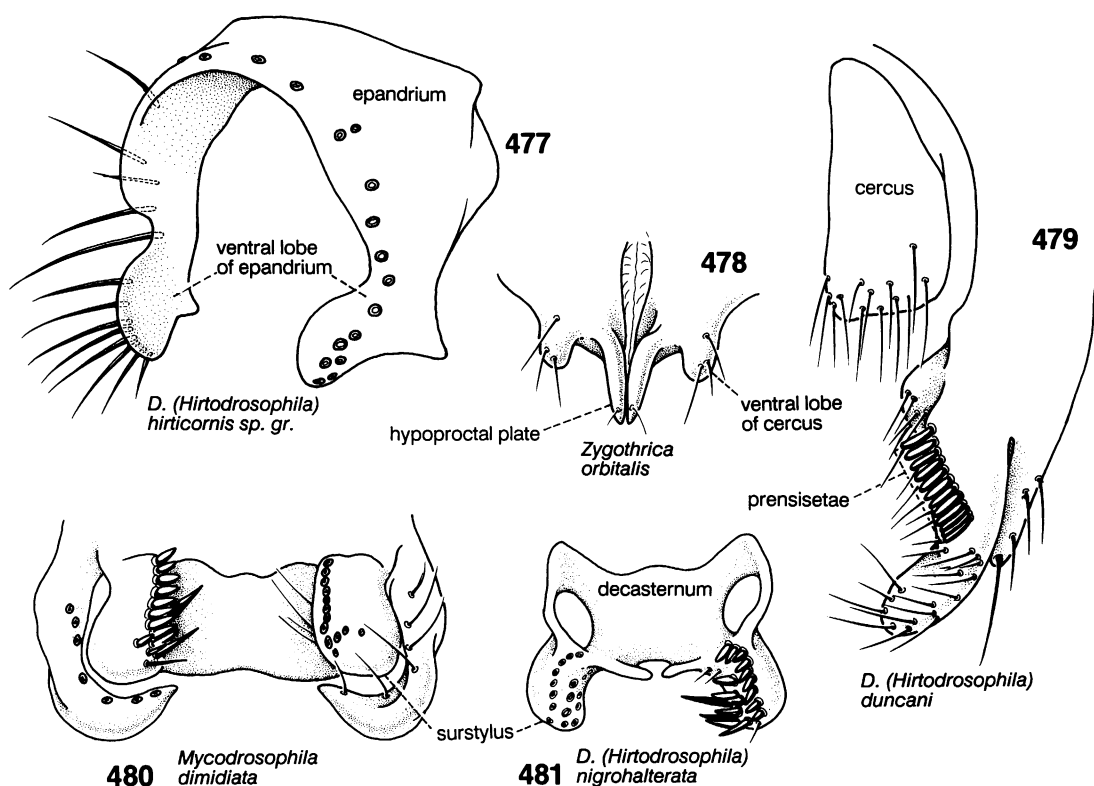


Fig. 476. Epandrium, cercus, and surstyli of *Scaptomyza* (*Engiscapto-myza*) *nasalis*.

plesiomorphic state. Thus, they are apomorphic for *Scaptomyza*, and for two species of *Bunostoma* and a species of *Dentiscapto-myza*, in particular.

188. Found in three subgenera of *Scapto-myza* is an aedeagus that is narrow and long (fig. 471, 472), in contrast to the usual short, bulbous aedeagus. Like most *Scaptomyza* aedeagi, here it is unadorned with spines or spicules and appears like a simple lobe.

189. Found in most species of *Zygothrica* (Grimaldi, 1987b), and in species of *Hirtodrosophila* and *Paramycodrosophila* that I examined, is a pair of sclerotized plates on the medial portion of the ventral surface of the cercus (fig. 478). They are normally triangular, or at least pointed at the apex. Plesiomorphically this structure is absent. As mentioned in apomorphy 164, *Mulgravea* also has a pair of sclerotized plates attached to this area of the cercus, which may be homologous to those in *Hirtodrosophila*. I have called these plates the hypoproct plates (e.g., Grimaldi, 1987b), even though the hypoproct and epiproct in more recently derived male drosophilids have apparently been lost. This paired structure, however, may be a reversal to a plesiomorphic state, and a modification on the basic plan of a simple, lobe-like, unpaired hypoproct.



Figs. 477-481. Epandrial, cercal, and surstylar structures in male *Hirtodrosophila* and relatives.

190. Found only in *Hirtodrosophila* and *Paramycodrosophila* is a ventral epandrial lobe that apomorphically has a comblike row of long setae along the length of the ventral epandrial lobe (fig. 477). I have found these setae, too, in a few primitive species of *Zygotherica* (not in the matrix), which possess them either as a primitive state or as independently acquired from *Hirtodrosophila*. Plesiomorphically, the setae on the ventral lobe of the epandrium are not as long, nor are they arranged into a row.

191. In *Zygotherica atriangula* (and a few close relatives not in the matrix) and *Mycodrosophila dimidiata* there is an accessory ventral lobe of the epandrium. It is more sclerotized than the main ventral lobe of the epandrium, and lies between the ventral epandrial lobe and the surstylus (fig. 480). It is hook-shaped (bent mediad) and possesses a few setae. Plesiomorphically there is no lobe medial to the ventral epandrial lobe.

192. Found thus far only in several species of *Zygotherica* (among them only *atriangula* and *orbitalis* are on the matrix) is a narrow process on the posterior margin of the hypandrium, which projects toward the distiphallus. It is an extension of the hypandrium and might be considered to be an aedeagal guide of some sort. *Zygotherica samoensis* (the third species in the genus on the matrix) is plesiomorphic for the feature, by having a simple hypandrial margin. This feature was discussed in Grimaldi (1987b) as apomorphy number 51 of that study.

193. Coinciding with apomorphy 190 (except that *Z. samoensis* is included here with *Hirtodrosophila*) is a pair of small tufts of setulae on the ventral margin of each cercal lobe (fig. 479). This feature appears to also be present in *Drosophila duncani*. Plesiomorphically the ventral margin of the cercus bears perhaps a few more fine setae than on other parts of the cercus, but there is not a

distinctive patch. Various species of *Scaptomyza* also have patches of setae on the cercus, which are not homologous because they are much finer and not nearly as long as those in *Hirtodrosophila*.

194. Found in several *Zygothrica* and a (Neotropical) species of *Hirtodrosophila* that was examined is a pair of small lobes just lateral to the hypoproctal plates (this is one of the few species of the subgenus that was found to have the plates) (fig. 478). The lobes project only about half the length of the plates and bear about three to five setae. Plesiomorphically the lobes are absent.

195. On the ventromesal margin of the cercal lobes in males of *Drosophila funebris* and *D. (Spinodrosophila) nigrosparsa* there is apomorphically a row of large, stout, heavily sclerotized pegs or spines (figs. 408, 409). These are apparently not homologous with the cercal spines found in some *Sophophora*, and in *Pseudiasata pseudococcivora* (apomorphy 136). In *Sophophora*, there is usually just one to three spines on each cercal lobe, located on a small ventral lobe; the spines are much longer than in *D. funebris* and *D. nigrosparsa*, and slightly curved (these spines are probably synapomorphic for those *Sophophora* that possess them). In *Pseudiasata*, the spines are actually pegs, being quite short, and are not arranged in a row.

196. In *Drosophila (Lordiphosa)* there is apomorphically a pair of long, sclerotized lobes flanking the aedeagus, which are the paraphyses ("anterior parameres" sensu Lastovka and Máca, 1978) (state 1). The lobes articulate with the base of the aedeagus and the distal end of the aedeagal apodeme; they are usually extended the length of the aedeagus, and the widened apex of each bears a vestiture of fine scales or microtrichia (fig. 465). In most species of the subgenus there is as well a row of fine trichoid sensilla along the length of the lobe, as in *Cladochaeta*, *Dithoneura*, and some *Sophophora* (state 2). States 1 and 2 were unordered. Long paraphyses are also apomorphically found in *Chymomyza*, *Neotanygastrella*, *Scaptomyza*, and *Sophophora*, which appear as if they might be homologous with those in *Lordiphosa*. Plesiomorphically the paraphyses are short, small lobes.

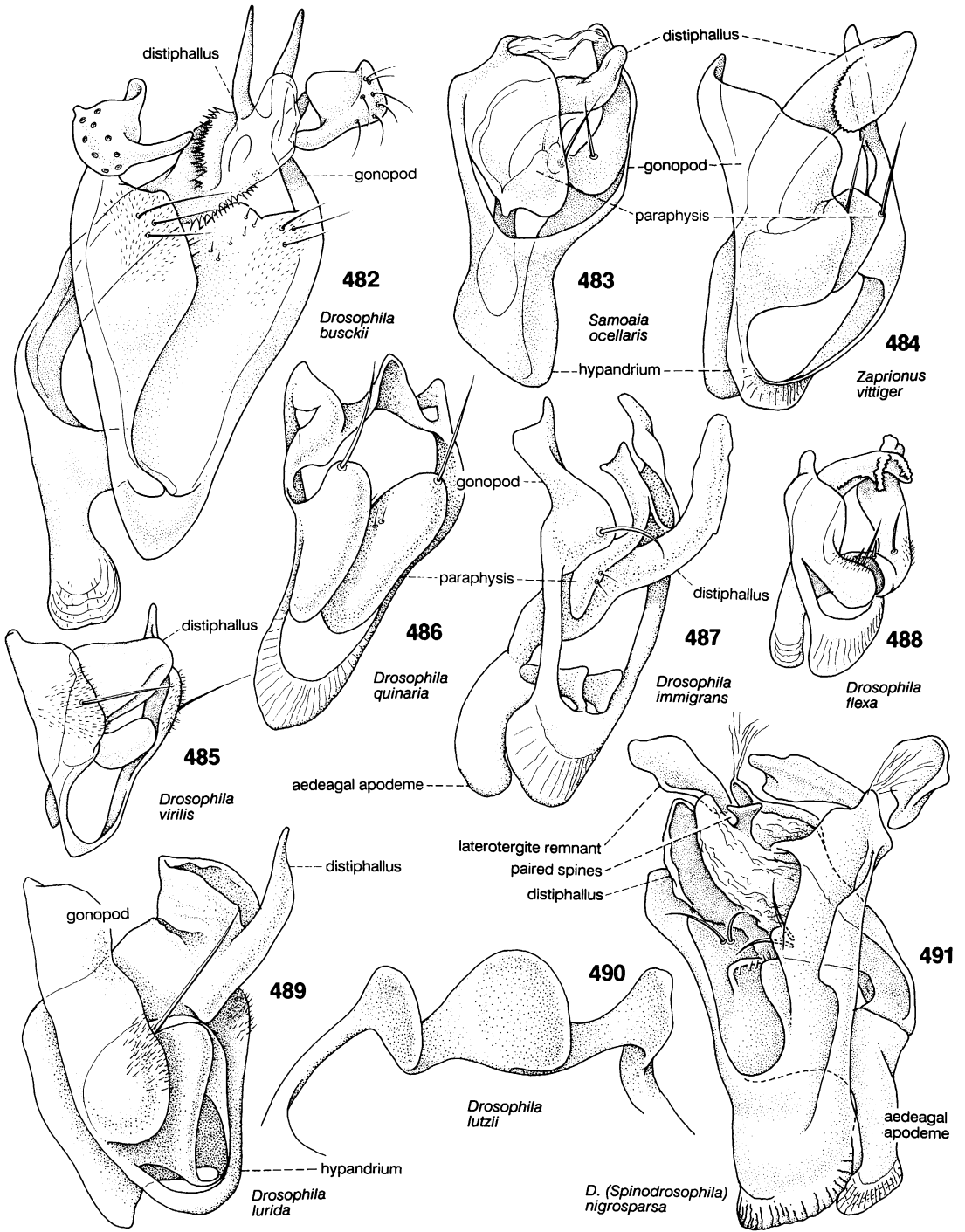
197. Common to virtually all species of

Drosophila (Sophophora) (fig. 414) and in *Baedrosophila* there is a pair of setalike, paramedian spines on the posterior margin of the hypandrium [called the "paramedian spines" by Wheeler and Magalhães (1962)] (fig. 401). These spines apparently represent a fusion of the median lobes of the hypandrium (the paraphyses); smaller lobes lie dorsolateral to the pair of paramedian spines, which have three or four minute trichoid sensilla. Plesiomorphically, these spines are each separated on a lobe.

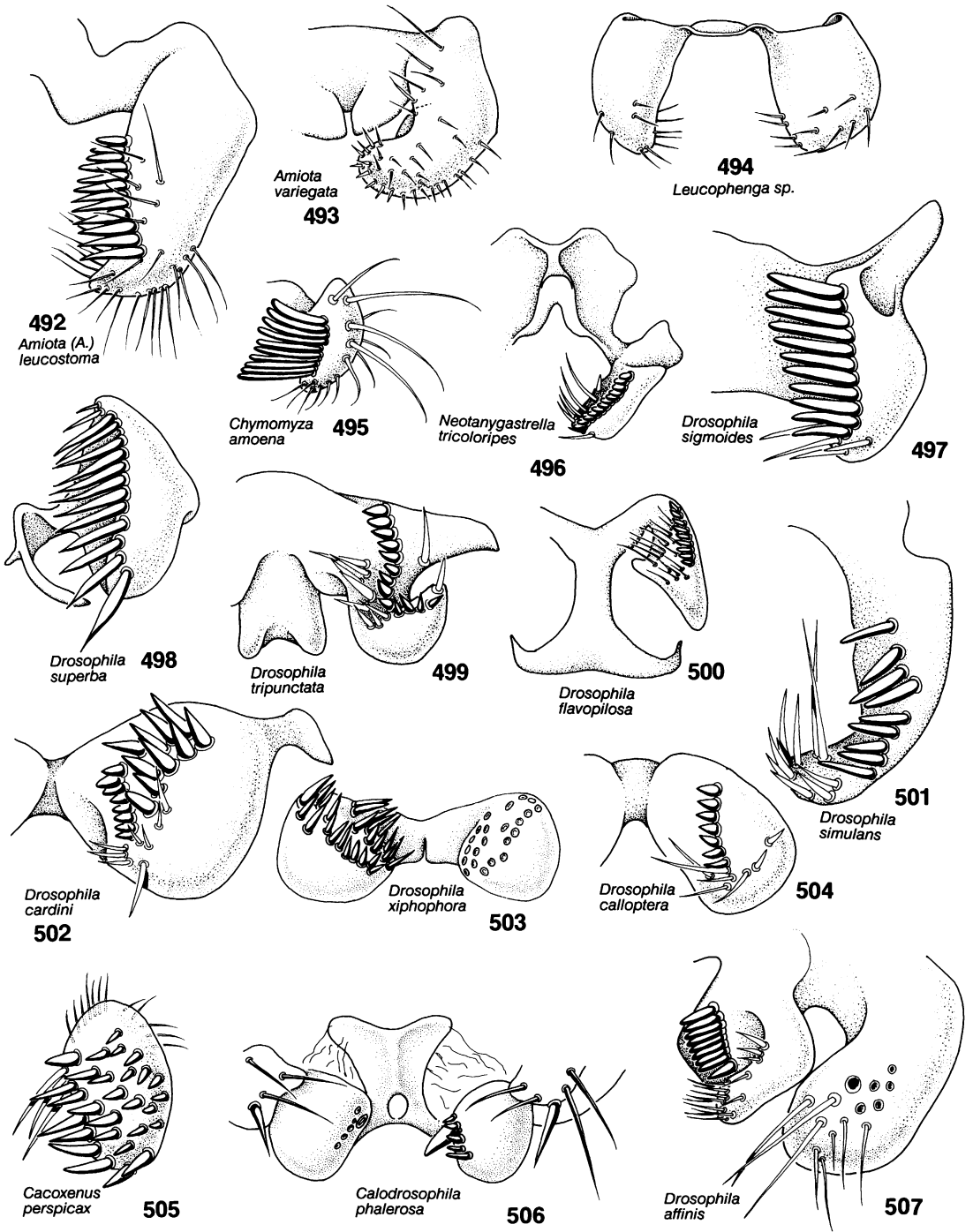
198. There is apomorphically a very long, straight seta at the apex of each of the two paraphyses in *Drosophila (Drosophila) calloptera*, *cardini*, *lurida*, *quinaria*, and *virilis*, *D. (Phloridosa)*, and in *Zaprionus* (figs. 484–486, 489). The seta is projected posteriad. Plesiomorphically, the seta is about one-half the length of the paraphysis, not equal to the length of the paraphysis as in the above taxa.

199. The gonites are apomorphically connected dorsal to the aedeagus, thus forming a bridge. The bridge has a median flange or cup, which probably serves as a guide for the aedeagus (figs. 486, 487). The dorsal bridge occurs in *Drosophila (Drosophila) calloptera*, *caradini* (but not *monochaeta*), *quinaria*, *testacea*, and *tripunctata*, among the species of the subgenus that were examined. It was also found in *Drosophila (Phloridosa)* (fig. 490), with which the feature is considered homologous, and with some Hawaiian *Drosophila*, with which it is not. In *Drosophila immigrans* (but not *monochaeta*) a dorsal bridge is formed by the fusion of the paraphyses.

200. Present in all the species in the subgenus *Drosophila* that were examined, as well as in the species of *Dorsilopa*, *Phloridosa*, *Siphodora*, *Sophophora*, *Spinodrosophila*, and virtually all drosophilines is a row of stout, sclerotized prenisetae pegs on the mesal surface of the surstylus (figs. 499–502, 504, 507). Plesiomorphically, the prenisetae are not arranged in a row on the surstylus, but are scattered, and as well the prenisetae may not be peglike in shape but longer and sharp (stout, setalike). For example, the prenisetae in *A. (Amiota)* are three to four times longer than wide, and are arranged into a closely packed comb on the mesal surface (apomorphy 155). Many *Scaptomyza* have a short row of peglike prenisetae on the prox-



Figs. 482-491. Male genitalia (hypandrium, aedeagus, associated structures) of *Drosophila* and relatives. 490, detail of dorsal arch portion of joined gonopods. Not to same scale, oblique posterior views.



Figs. 492-507. Surstyli of various drosophilids, with decasternum (figs. 493, 496, 498, 499, 500, 503, 506), showing variation in size, shape, and prensisetae.

imal portion of the surstylus (apomorphy 178), so this will fall out as a subset of that feature described in the above taxa.

201. Covering the lateral, broad surface of each paraphysis is a field/patch of fine, dense microtrichia, which is plesiomorphically absent. The feature occurs in *D. (Drosophila) calloptera*, *colorata*, *lurida*, *melanica*, and *virilis*, and in *Dorsilopha*, *Phloridosa*, *Siphlodora*, *Sophophora*, and *Spinodrosophila* (figs. 482, 485, 488, 489).

202. Quite widespread is the type of vestiture on the ventromedial margin of each cercal lobe where there is a patch of fine, dense setae. The setae can be straight and sharp, but are always differentiated in shape and size from the other setae on the cercus. Plesiomorphically these differentiated setae are absent. The patch of setae occurs in *D. (Drosophila) colorata*, *flavopilosa*, *hydei*, *immigrans*, *lurida*, *monochaeta*, *quinaria*, *repleta*, *testacea*, *tripunctata*, and *virilis*, of the species examined for the trait (fig. 412). *Drosophila cardini* has these setae modified into a pair (on each cercus) of long, sclerotized, spinelike setae. The feature also occurs in *Sophophora* and most *Scaptomyza* (again, with many modifications to the Bauplan).

203. Species in four groups of *D. (Drosophila)* have a short, bulbous aedeagus, as well as in *Spinodrosophila*. These are the *melanica*, *repleta*, *robusta*, and *virilis* groups (figs. 485, 491). In each, the aedeagus is virtually entirely distiphallus, which is usually shorter than the aedeagal apodeme. In some groups, such as some species of the *fasciola* subgroup of the *repleta* group, there is the development of a pair of unsocketed spines on the distiphallus. Otherwise, the distiphallus has no vestiture and appears baglike.

204. At the apex of the ventral lobe of the epandrium there is apomorphically a small patch of short, stout, straight setae (figs. 411, 412). It was found in various species in the subgenus *Drosophila* (i.e., *colorata*, *flavopilosa*, *lurida*, *monochaeta*, *testacea*, and *tripunctata*) and in *Siphlodora*. The short, peg-like spines in *D. funebris* are considered to be a possible modification on the basic plan of apomorphy 204. In some taxa, such as *D. monochaeta* and *D. tripunctata*, the ventral lobe is a very narrow strip, about four to five times longer than wide (fig. 412).

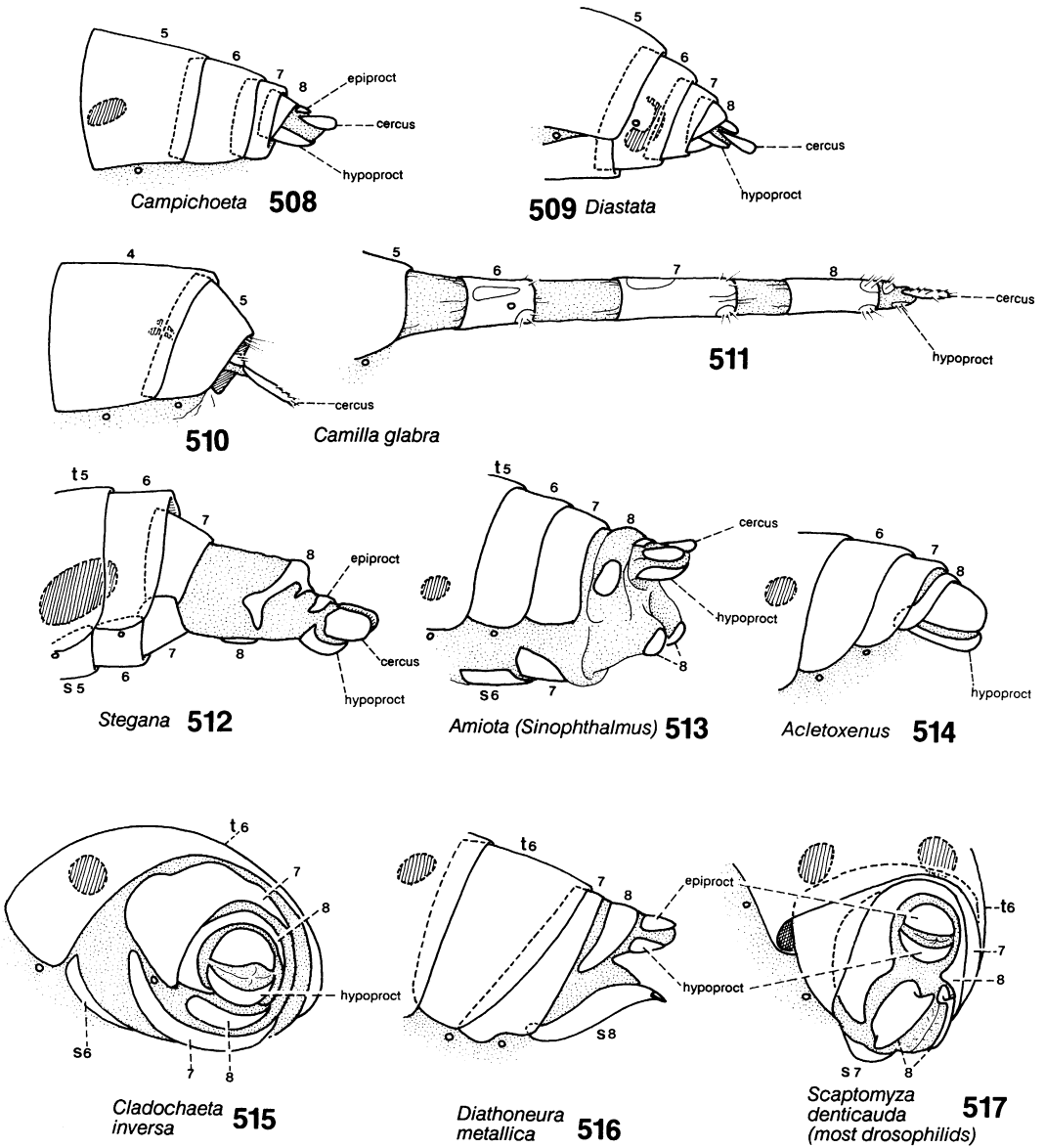
205. Discussed in Grimaldi (1988) (apomorphy 16 of that study) is an epandrium with a pair of glabrous, pincerlike ventral lobes. Each lobe is not at all articulated with the rest of the epandrium; it is tapered apicad to a narrow point, where it is sclerotized into a tooth. This feature is found in *Acletoxenus*, *Mayagueza*, and a few species of *Gitona* (e.g., *americana*, *sonoita*). However, I consider the feature to be synapomorphic only between the first two genera, since in *Gitona*, the lobes are setose and sometimes bear two or three socketed teeth.

FEMALE GENITALIA

Sternite VIII in female drosophilids has been modified in many species into a lobate, paired structure, protruding from the apex of the abdomen, just under the epiproct and hypoproct. Elsewhere I have called this structure the oviscape (Grimaldi, 19887b), even though the common usage is oviscapt (this term is used, in Diptera, to distinguish between this and an ovipositor, the latter of which is appendicular in origin). Although oviscape is etymologically correct (from the Greek noun, *scaphe*, or scoop, trough; versus the verb, *scaptos*, to dig), I will adopt hereafter the common usage.

206. The absence of spiracle pair VII in the female abdomen is not a loss in the Drosophilidae, since all outgroup taxa do not have them (figs. 508–511). Spiracle pair VI in *Camilla glabra* is in tergite (and tergites VI–VIII telescope within the abdomen), as is the case in *Diastata eluta* (Diastatidae) and *Hydrellia* and *Notiphila* (Ephydridae; as mentioned in apomorphy C-9 all spiracles for both sexes of ephydrids have spiracles in the laterotergites). *Campichoeta* has even lost spiracle pair VI (fig. 508). Apomorphy 206 is the presence of spiracle pair VII. This apomorphy is found in all drosophilids except the various subgenera of *Leucophenga* and *Stegana* (e.g., fig. 512), thus illustrating the plesiomorphic nature of this sister pair of genera.

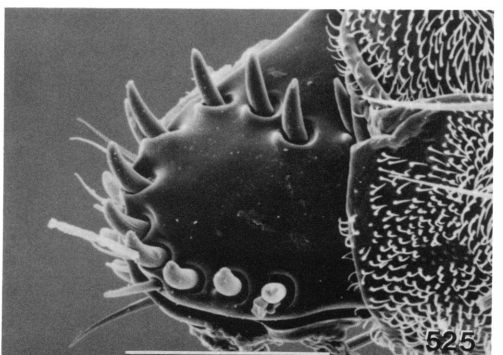
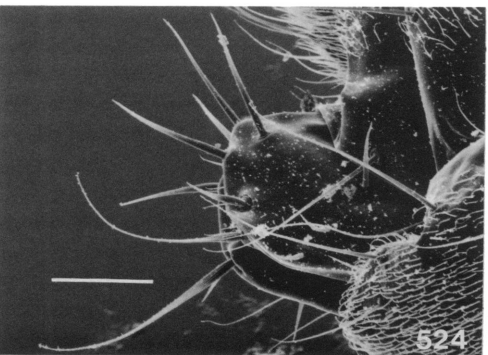
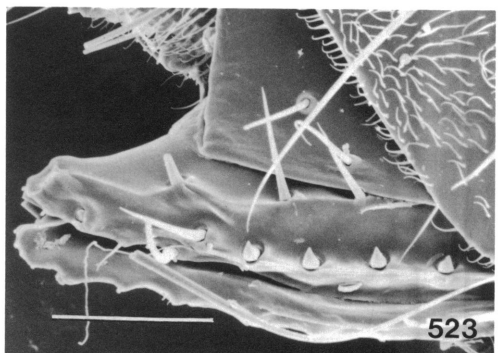
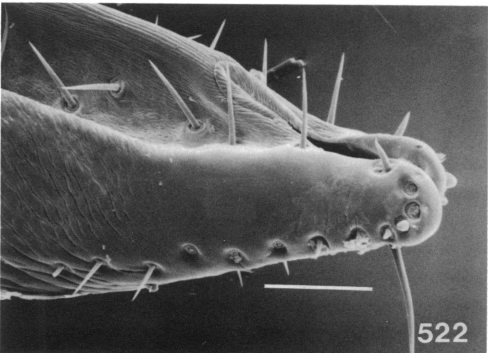
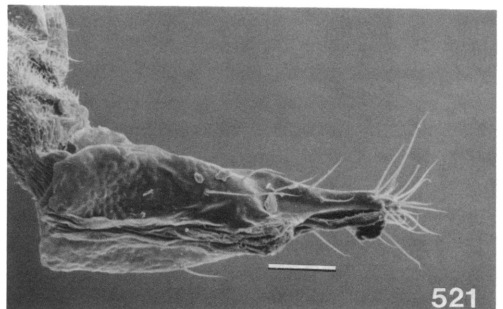
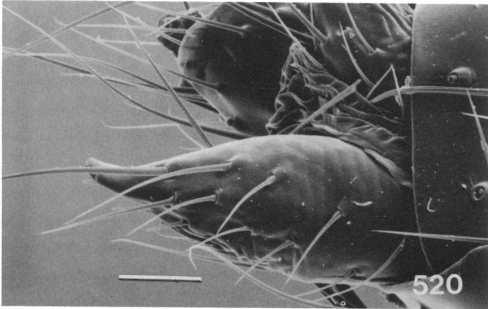
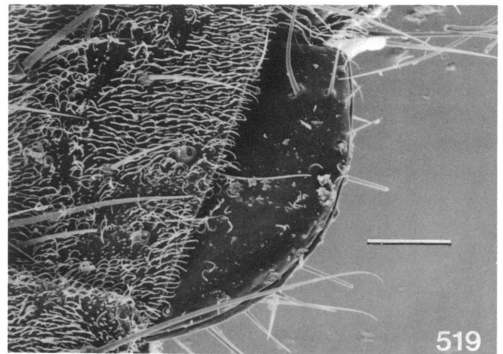
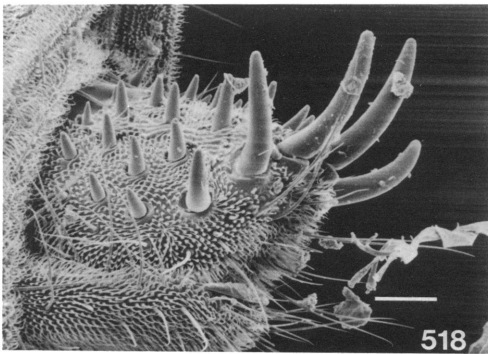
207. Plesiomorphically the pair of cerci are present with the epiproct and hypoproct in female drosophilids (figs. 508–513). Apomorphically, only the epiproct and hypoproct are present: the cerci have been lost (figs. 514–



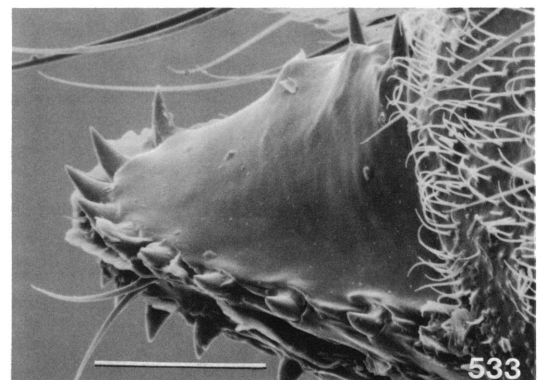
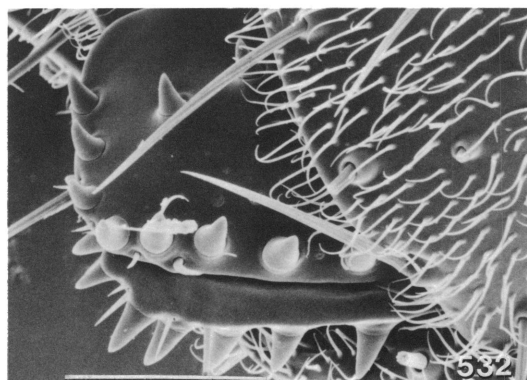
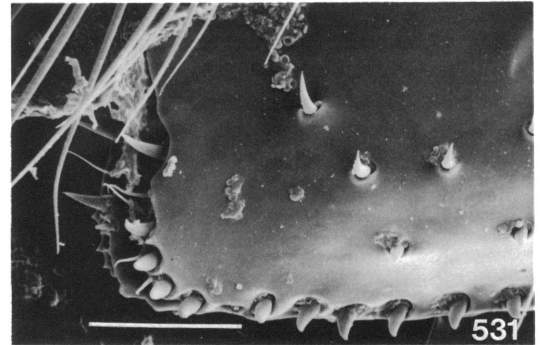
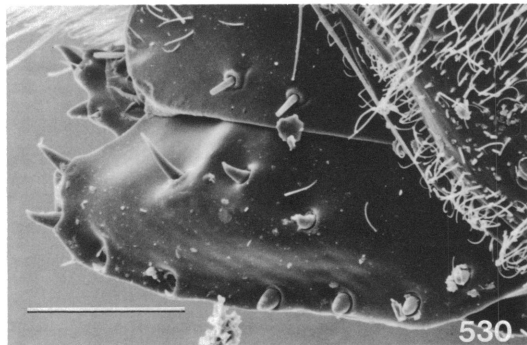
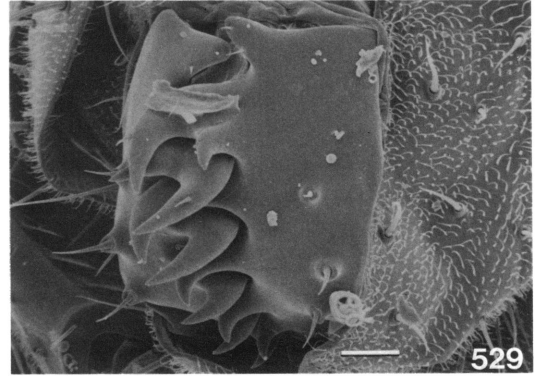
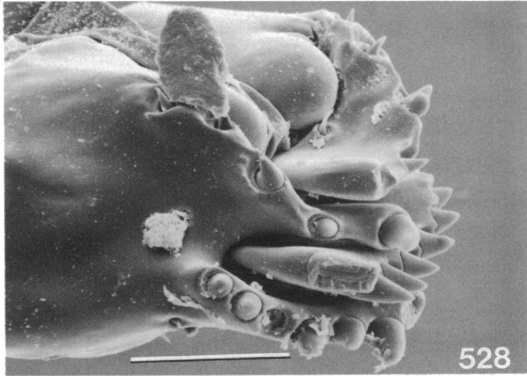
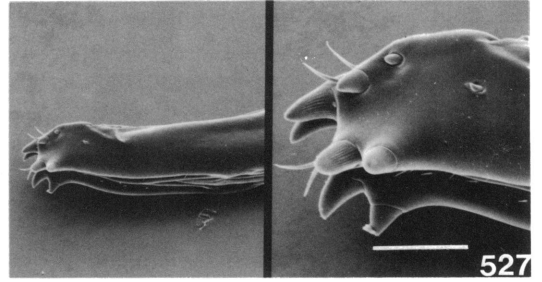
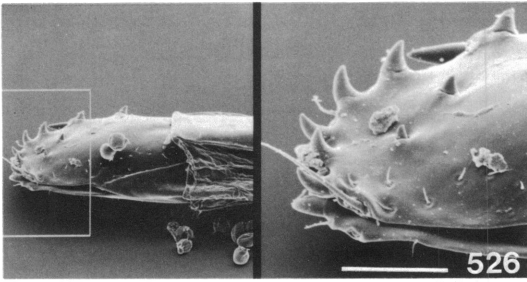
Figs. 508-517. Female terminalia in ephydroids, showing development of the oviscapt (sternite 8) in some drosophilines.

517). There is some debate as to the homologies of the anal segments in the Muscomorpha, particularly the ones posterior to and including segment 8. According to McAlpine (1981), the true epiproct and hypoproct are the tergite and sternite, respectively, of segment 11 in insects (also called the proctiger), but this segment supposedly is lacking in fe-

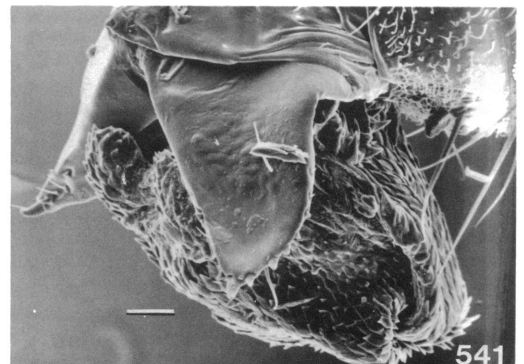
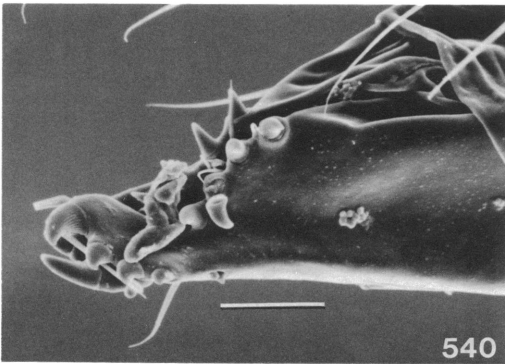
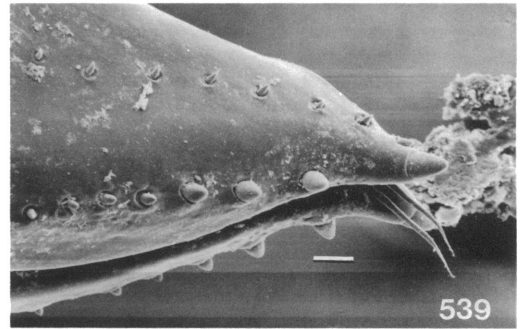
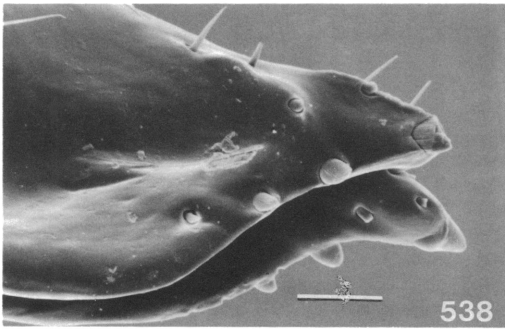
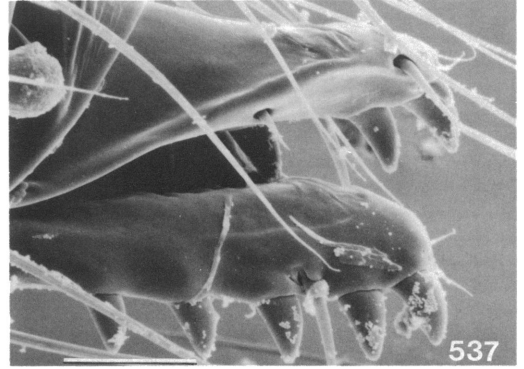
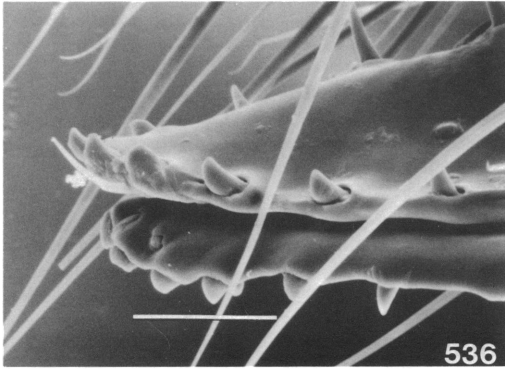
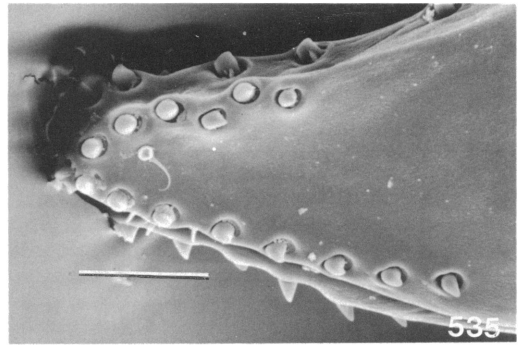
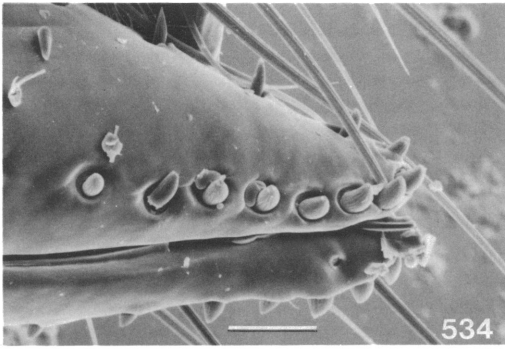
male Diptera. What I will term here as the hypoproct and epiproct are the sternite and tergite, respectively, of segment 9 in the Ephydroidea: they are serially homologous in shape and position to the other, anterior, abdominal sclerites. The cerci, which is what most workers call the terminal pair of lobate structures (also "anal papillae," particularly



Figs. 518–525. Terminal abdominal structures in female ephydroids. 518. Epiproctal spines in *Curtonotum helvum*. 519–525. Oviscapt (sternite 8) in drosophilids, showing variation in peg and trichoid sensilla. 519. *Drosophila flexa*. 520. *Drosophila crassifemur*. 521. *Colocasiomyia stamenicola*. 522. *Drosophila crucigera*. 523. *Drosophila (Scaptodrosophila) scaptomyzoidea*. 524. *Chymomyza amoena*. 525. *Neotanygastrella tricoloripes*. Scale = 40 μ m.



Figs. 526–533. Ovisensilla pegs on oviscapt (sternite 8) of various female drosophilids. 526. *Zaprionothrica nudisetata*. 527. *Drosophila xiphophora*. 528. *Laccodrosophila flavescens*. 529. *Drosophila flavopilosa*. 530. *Scaptomyza apicata*. 531. *Drosophila funebris*. 532. *Drosophila floricola*. 533. *Drosophila quinaria*. Taxa in figs. 526–529, 532 breed in flowers. Scale = 40 μm .



Figs. 534–541. Ovisensilla pegs on oviscapt (sternite 8) in female drosophilids. 534. *Drosophila achlya*. 535. *Lissocephala sabroskyi*. 536. *Diathoneura opaca*. 537. *Dettopsomyia formosa*. 538. *Mulgravea* sp. 539. *Antopocerus aduncus*. 540. *D. (Hirtodrosophila) hirticornis* group sp. 541. *Zygothrica atriangula*, showing everted oviprovectrix (scaled intersegmental membrane of sternites 7 and 8).

among drosophilid workers), are actually lost in most drosophilids; when present they are a paired structure lying partially between and lateral to the epiproct and hypoproct.

208. Several genera of drosophilids that have mycophagous species also possess a distinctive oviscapt. I am coding the variation in the feature as an ordered transformation series, consisting of the following. State 1, as a ventral row of ovisensilla pegs on the oviscapt that are splayed out, such that they are pointed laterad or posterolaterad (not pointed ventrally, which is plesiomorphic) (found in *Mycodrosophila*). State 2 is a large gap between the two ventral rows of ovisensilla pegs and one (as in *Dros.* sp. 4) or more (taxa in state 3) dorsal pegs; also, the surface with the dorsal peg(s) is nearly vertical to the horizontal surface bearing the ventral pegs. State 3 is found in those taxa where there are two or three pegs aligned in a dorsal row [found in the *D. (Hirtodrosophila) hirticornis* group, *D. nigrohalterata*, and in *Paramycodrosophila*] (fig. 540).

209. The anthophagous species, those whose larvae breed in various flowers, have among the most modified oviscapt. In three taxa (*Drosophila xiphophora*, *Laccodrosophila*, and *Zapriothrica*) there is an oviscapt that is apomorphically extrusible and with stout, black, heavily sclerotized ovisensilla pegs at the apex of the oviscapt (figs. 526–528). It would not be at all surprising if the trait was independently derived in all three groups. For one, the distribution, sizes, and number of ovisensilla pegs in these taxa are quite different: *Zapriothrica nudiseta* (fig. 526) has six to seven curved, retrorse ovisensilla pegs on the apical and dorsal margins of each oviscapt half or valve; *Drosophila xiphophora* (fig. 527) has only four large ovisensilla pegs (two dorsal, two ventral, at the apex); *Laccodrosophila flavescens* (fig. 528) has the most specialized oviscapt, for it has two rows of sharp ovisensilla pegs on each valve, with a groove between the rows and into which the ventral row from the opposite valve fits. No doubt *L. flavescens* females saw their way into an oviposition spot.

Secondly, the modified oviscapt of the three taxa discussed above may not be synapomorphic because of similar modifications in other anthophagous, albeit obviously dis-

tantly related, drosophilids. Species in the *Drosophila flavopilosa* species group have among the most bizarre oviscapt, with the ventral rows of ovisensilla pegs as large, strongly hooked, interlocking teeth (fig. 529). In *Zygothrica florinjecta*, which breeds in *Salvia* flowers in the Colombian paramos, the large ovisensilla pegs are crowded on a short apical row; the oviscapt is distinctly spatulate (Grimaldi, 1987b).

210. The oviprovector is a term originally used by Steyskal (1979) to describe the intersegmental membrane between sternites VII and VIII in some Otitidae that is heavily scaled, which bears the gonopore and through which the egg passes. It must function in some specialized way for oviposition. I have applied it to drosophilids (Grimaldi, 1987b) that have a similarly heavily scaled, but obviously independently derived, intersegmental membrane (fig. 541). In an everted oviprovector there is apomorphically a pointed, lightly sclerotized process or tooth at the apex, just dorsal to the gonopore (plesiomorphically it is absent). This is found in *Samoaia* and *Drosophila monochaeta*, but was not observed in my preparation of *D. immigrans*, nor in *Phorticella* and *Zaprionus* (on the basis of the structure of the facial carina these taxa would be closely related). This structure is not the same one that occurs in some *Zygothrica* and in *Zapriothrica nudiseta*. In an Amazonian and Caribbean group of *Zygothrica*, the oviprovector bears one or three heavily sclerotized, sharp, rhamphate scales (Grimaldi, 1988). In *Zapriothrica nudiseta*, there are two apical teeth on the apex of the oviprovector, which are pointed posteriad.

211. The oviscapt is a term applied to sternite VIII in drosophilids that apomorphically protrudes beyond the hypo/epiproct as a lobe. There appears to be a natural progression from a simple sternite VIII (resembling the other sternites) to one that is lobate (apomorphy **211**), then divided along the midline by a lack of sclerotization, then with completely separated right and left halves (connected by a narrow anterior bridge) with a row of trichoid ovisensilla along the apical and ventral margin, and finally to one with the ovisensilla being peglike. While I believe the possession of an oviscapt to be synapomorphic in drosophilids, the synapomorphic status of the

other features mentioned above is very much uncertain (see below).

212. The oviscapt apomorphically possesses peglike ovisensilla (figs. 522, 523, 525–541); plesiomorphically, sensilla on the oviscapt are all trichoid or like setae, as can be found on any sternite. This is a perfect example of the utility of computerized phylogenetic algorithms. Given the differences in number, position, size, and shapes of ovisensilla pegs, it would not be at all surprising if the peglike state were derived numerous times (see apomorphy **213**).

Parsimony analysis can divide the distribution of this feature into one that most closely matches the distributions of other features. Unfortunately, it appears that some drosophilids may have *secondarily lost* the pegs, and possess only the setalike ovisensilla [e.g., *Chymomyza* (fig. 524), *Celidosoma*, *Cladochaeta*, *Siphlodora*, some of the Hawaiian *Drosophila*, and perhaps *Colocasiomyia* (fig. 521), *Microdrosophila*, and many *Scaptomyza*]. But, again, parsimony analysis will allow a reinterpretation of the polarities of the trichoid ovisensilla at various levels. Analysis using HENNIG86 revealed *Chymomyza*, *Celidosoma*, *Siphlodora*, *Microdrosophila*, and the few *Scaptomyza* and Hawaiian *Drosophila* to have secondarily lost the feature. *Colocasiomyia*, *Cladochaeta*, and relatives primitively lack the pegs. Some species of *Diathoneura* have derived ovisensilla pegs independent of other drosophilids.

213. This is the possession of an oviscapt that is tapered and narrowed to an apical point that bears a large peg (figs. 538, 539). The apices of the valves are usually slightly curved laterally, away from each other. It is most likely, based on structural evidence, that the Hawaiian species possessing this feature have developed it independently from *Jeannelopsis*, *D. (Dichaetophora)*, *Sphaerogastrella*,

Mulgravea, and *Liodrosophila*. This latter group of genera apparently possess it synapomorphically. In the Hawaiian species the ventral margins of each oviscapt valve are less acutely angled toward the apex than in the other taxa, and the apices of the valves are not curved laterad as much.

214. This is not an exclusively female feature. Four genera possess abdominal spiracles in the female and male that synapomorphically lie in their respective tergites: *Hypselothyrea*, *Liodrosophila*, *Samoaia*, and *Sphaerogastrella*. Plesiomorphically all of the spiracles lie in the pleural membrane. It was mentioned in apomorphy **124** that the males of *Samoaia* and *Tambourella* have the abdominal spiracles in the tergites; I did not have a female *Tambourella* to dissect, but it is reasonable to assume that, since the trait is shared by both sexes in these other genera, the trait can be found in this genus as well.

215. Shared among all of the *Leucophenga* species that I have dissected is a spermathecal capsule that is in the shape of a long cylinder with irregular annulations. Plesiomorphically, the spermathecal capsule is ovoid or spherical and without annulations.

216. Shared among all *Stegana* species that have been dissected and illustrated is an apomorphic shape of the spermathecal capsule. The capsule is spherical with a thin, curled apical filament. The plesiomorphic state is described in apomorphy **215**.

217. Synapomorphic for most species of Hawaiian drosophilids is a spermathecal capsule that is very simple: it is spherical or subspherical, and almost always possesses a very short introvert, one that is barely perceptible. Plesiomorphically there is a long introvert, resembling a sleeve that is invaginated at least halfway into the capsule from the basal opening.

CLADISTIC ANALYSIS

The original data matrix is shown in Appendix 1. It has 158 taxa and 217 apomorphies (apomorphy "0" is found in all of the drosophilids; it is present just to satisfy the condition of apomorphy 0 actually being

number 1 in the HENNIG program). Initial runs on HENNIG86 using the complete matrix were never finished, so the matrix was gradually pared down until it was found that 127 taxa was the maximum number that the

program could analyze (at least using the *m*h;bb* commands). Those taxa ($N = 120$) in the matrix with an asterisk (*) were run on HENNIG86; the other taxa were not included in the analysis but were kept in the matrix for the sake of a complete record.

Initially, the *m*h;bb* algorithms were run on the reduced matrix, from which 100 equal-length trees were stored in memory and a Nelson (strict) consensus tree was derived. This tree was 993 steps in length, approximately 30% (295) of the steps of which were due to 13 characters (4% of the total number of characters). These 13 characters, or apomorphies, were arbitrarily defined as being 16 or more steps in length (median = 35, mean = 23); all others were 14 or fewer steps in length (total range in no. steps/character was 1 to 54). It was subsequently found that 6 of the 13 (55%) "most homoplasious" characters were multistate, even though 23 of the 217 characters (total) (ca. 10%) were originally coded as multistate [2 or more derived states, all of which were ordered (e.g., state 1 > state 2 > 3 . . .)]. These apomorphies were 12, 20, 26, 67, 68, 82, 83, 98, 100, 101, 125, 196, 212. By unordering the multiple

states of characters 26, 68, 83, 90, 98, 100, and 196, the length of the tree was then 888 steps. All the other multiple-state characters were left ordered for reasons pertaining to my original hypotheses on homology and character evolution (discussed for each apomorphy).

The matrix, now with 23 ordered and unordered multistate characters, was run again using the *m*h;bb* algorithm, with the "w" option, which is the command for successive weighting. Characters were weighted according to, in the initial cladograms, a product of the consistency index (CI) and character retention index (RI), on a scale of 0–10. A printout of the weights is available from the author. One hundred trees were stored in memory, from which a strict consensus tree was derived. Figures 542–545 show the resultant cladogram, which has a length of 816 steps, CI = 0.31, RI = 69. The position of each character was checked by hand on the cladogram; in several instances it was found that two or more taxa could have been linked by shared apomorphies but were not. These hand revisions were incorporated into figures 542–545.

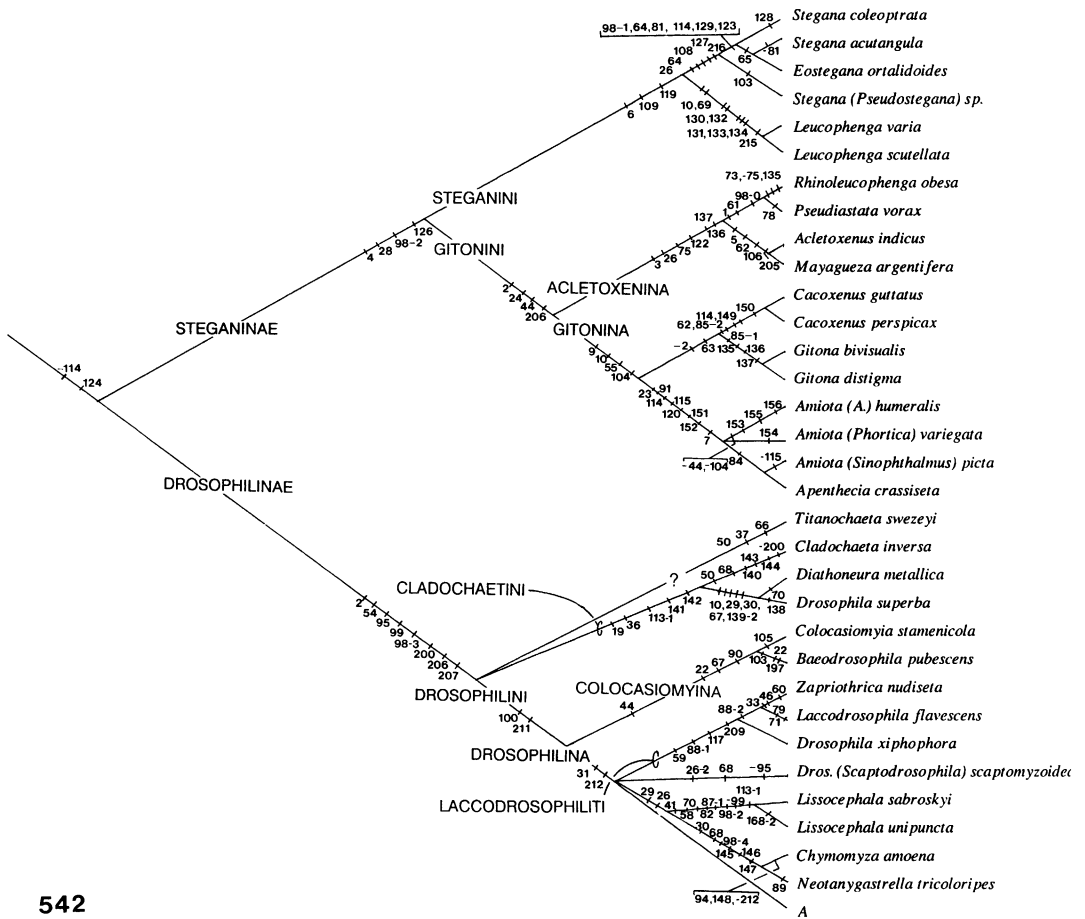
COMPARISONS TO OTHER STUDIES

THROCKMORTON'S PHYLOGENIES

Wherever comparative studies on *Drosophila* require statements of relationships, Throckmorton's 1975 paper is most often cited. This paper contains no data and is just extensive discourse on the geological periods in which certain groups arose and detailed reconstruction of colonization patterns. His 1962 and 1966 papers contain the data; each character system is described in detail, well illustrated, the evolution of each structure is discussed, and extensive comparisons for each are made. In evaluating Throckmorton's hypotheses on drosophilid relationships, one problem is not only his presentation of data, but which hypothesis to adopt. I have redrawn Throckmorton's trees to represent *relative* relationships; in several instances he made ancestor-descendant hypotheses. In such cases I made the presumed ancestor and

descendant sister groups. The topologies of these trees were then compared among each other and with newly generated trees. As figure 547 shows, there are some inconsistencies in relative relationships given in the 1962 and 1975 papers.

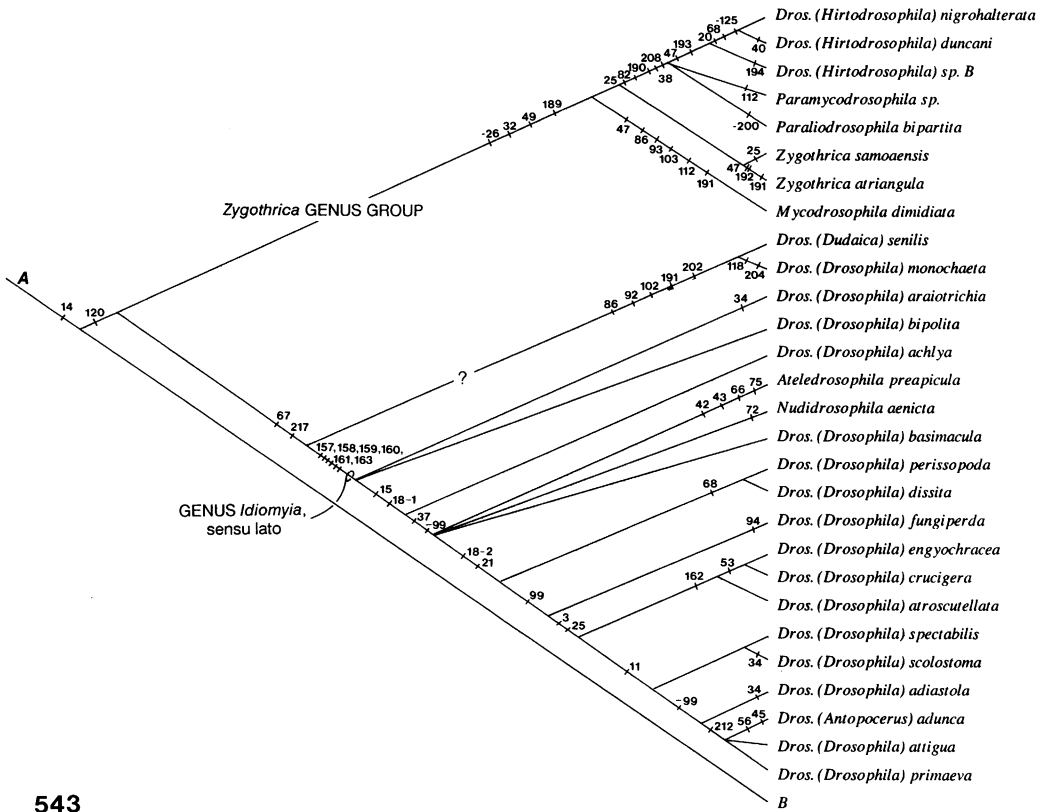
For example, in 1962 Throckmorton hypothesized the sister-group relationship of *Sophophora*, *Chymomyza*, and the remaining drosophilines, with the exception of *Pholadoris* (a synonym of *Scaptodrosophila*). Also, in 1962 he proposed *Zaprionus* as the sister group to *Mycodrosophila*, *Phloridosa*, and what is essentially the subgenus *Drosophila*. In 1965, however, *Sophophora* and *Chymomyza* became sister groups, as did *Zaprionus* and his "quinaria section" of the subgenus *Drosophila*. Yet, again, in 1966, his original 1962 hypothesis on the plesiomorphic positions of *Zaprionus*, *Sophophora*, and *Chymomyza* with respect to the other dro-



Figs. 542, 543. Hennig86-derived strict consensus cladogram of representative drosophilids. Numbers refer to apomorphies discussed in text. Continued to figs. 544, 545.

sophilines was adopted. In 1965, he hypothesized *Scaptomyza* and the Hawaiian “*Drosophila*” to be sister groups to *Zaprionus* and the remainder of the drosophilines. In 1966, *Scaptomyza* and the Hawaiian “*Drosophila*” became sister groups. In fact, Throckmorton concluded after his large morphological study in 1966 that the features distinguishing Hawaiian endemic *Scaptomyza* and “*Drosophila*” blended there, and that perhaps one genus was simply a grade of the other (in Throckmorton’s discussion, *Scaptomyza* being ancestral to *Drosophila*, perhaps even originating in Hawaii). Figure 547 shows a more detailed summary of his views on the relationships of the Hawaiian “*Drosophila*” and *Scaptomyza*.

In order to completely evaluate Throckmorton’s 1975 tree, I found it necessary to first compare it with the topology of his 1962 data supported tree. There are some differences in topologies between the two trees, but there is more consensus than difference (fig. 547), thus making a reanalysis of the 1962 data directly applicable to his 1975 hypotheses. A character state data matrix was made for the taxa discussed in Throckmorton (1962, 1966) and for the morphological features described there. For some taxa with characters not described or insufficiently described, I referred to Okada (1956) and Patterson (1943). Throckmorton used outgroup comparison to polarize character state change, and sometimes used a common-equals-primitive cri-



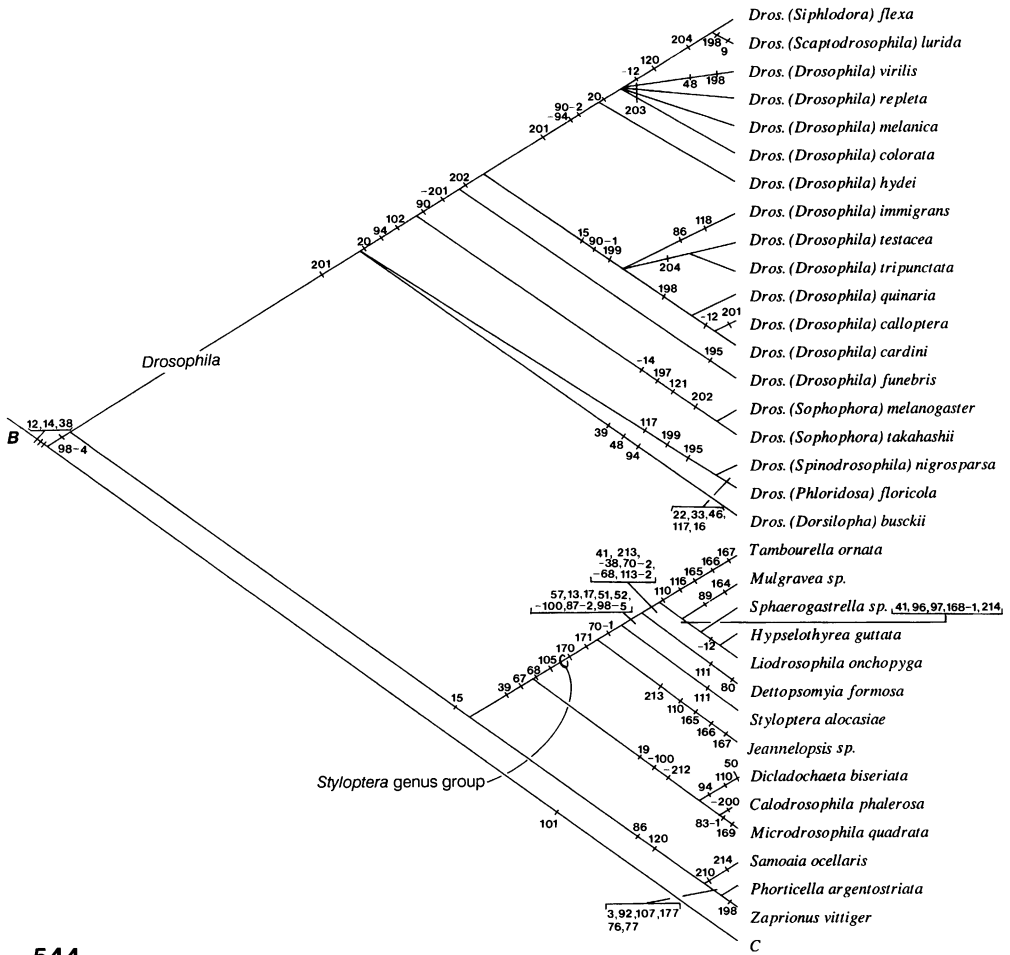
543

terion (e.g., for the ejaculatory apodeme shape) for the more morphologically heterogeneous groups. After coding and/or recoding 17 characters used by Throckmorton (with the exception of the pupal spiracles), they were incorporated into a matrix, presented in Appendix II. Two of the 18 characters have two or more derived states; all others have just one. Throckmorton's bias toward internal reproductive characters was undoubtedly heavily influenced by Patterson, Stone, and others at the University of Texas *Drosophila* genetics group (where he was a graduate student); this view is graphically apparent in the monographs by Patterson (1943) and Patterson and Stone (1952). Reliance on internal characters was probably the dogma of the time, propagated by Mayr (1942), who reasoned that such features, being less exposed to external environmental fluctuations, are less subject to selection and, therefore, less

likely to show convergence. Of course, it was not taken into consideration that convergence is identified by doing a phylogenetic analysis, not a priori. Below is a brief description of 18 characters used by Throckmorton (numbers are mine) and employed in a reanalysis of his data. For complete descriptions, consult Throckmorton (1962, 1966).

A. Ejaculatory apodeme has a base that is nearly equal in length and width to the shaft, or slightly longer, and at nearly a right angle (state 1). State 2 is where the apodeme base is flat, at a right angle to the shaft, and with the base of the shaft lying in the center of the base. Plesiomorphically, the shaft is distinctly slanted and about one-third the length of the base.

B. Posterior caecae of the ejaculatory bulb (male) are long (plesiomorphically, they are absent).



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Figs. 544, 545. HENNIG86-derived consensus cladogram of drosophilids, continued from fig. 543.

C. The ends of the pair of posterior caecae of the ejaculatory bulb are fused (plesiomorphically, they are unfused).

D. Posterior caecae of the ejaculatory bulb are long and curled or folded (plesiomorphically, they are neither curled nor folded).

E. Posterior caecae of the ejaculatory bulb are curled, long, and with the ends abruptly tapered (absence of the tapering is plesiomorphic).

F. Posterior caecae of the ejaculatory bulb are very long and with one or more (sometimes up to 10) bifurcating branches (plesiomorphically, the caecae are unbranched).

G. The presence of a pair each of anterior and posterior caecae on the ejaculatory bulb

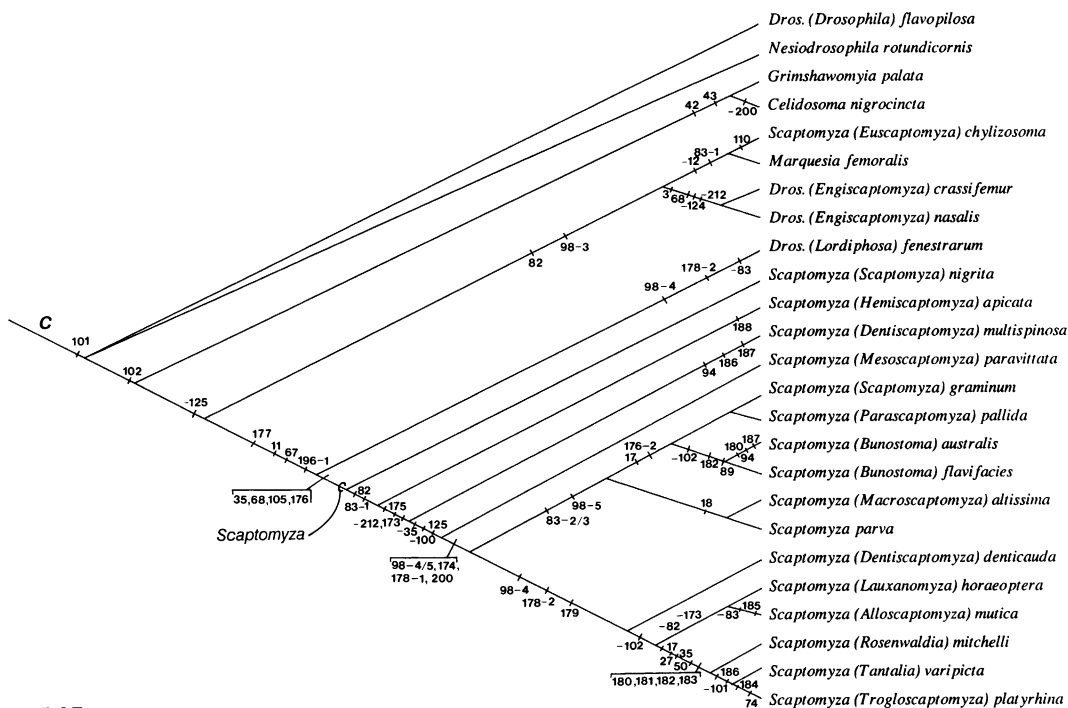
(plesiomorphically, there is just the posterior pair, in any shape).

H. Vas deferens are fused basally, with a common stalk leading to the aedeagus (plesiomorphically, they are not fused).

I. Paragonium is plesiomorphically folded twice; apomorphically it is folded just once.

J. The testes are apomorphically long and coiled, generally with five or more tight coils [plesiomorphically, they are oval, or with only a few (e.g., three) loose coils].

K. The ventral receptacle is apomorphically either folded three or more times (up to about 20) (state 1) or tightly and repeatedly coiled (state 2). Absence of the folding or coiling is plesiomorphic.



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L. The spermathecal capsule is cylindrical (plesiomorphically, it is small and spherical).

M. The spermathecal capsule has a deep introvert (plesiomorphically, it is without this structure).

N. The spermathecal capsule is pear-shaped (plesiomorphically, it is small, spherical, or oval).

O. The spermathecal capsule is membranous, wrinkled, and minute (vestigial) (plesiomorphically, it is sclerotized and with a smooth or distinctly sculptured surface).

P. The spermathecal capsule is small, saucer-shaped, and capping a very thick apical portion of the spermathecal duct (plesiomorphically, it is neither small, nor of this shape, and it is without the distinct thickening in this portion of the duct).

Q. There are five derived states to the filament morphology of the eggs: (1) with two short filaments, one on each side of the central groove, at one end; (2) with four short filaments; (3) with two fine, long, ventral filaments; (4) with four fine, long, ventral fila-

ments; (5) with six filaments, which are always short.

R. The malpighian tubules are apomorphically with apposed posterior tips (state 1) or apposed and fused (state 2). Plesiomorphically, the tips are neither apposed nor fused.

The matrix was analyzed using the HENNIG86 program, version 1.5, employing the m*, bb* algorithm (branch swapping on initial cladograms, best results for each being passed to bb). Characters A and Q were unordered. This generated at least 100 equal-

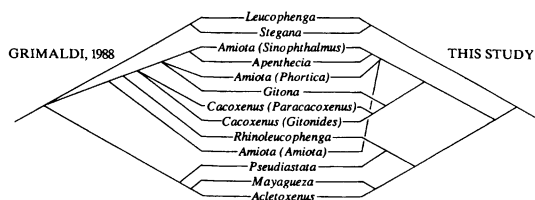


Fig. 546. Comparison of cladograms of steganinae relationships, based on Grimaldi (1988) and the hypothesis in the present work.

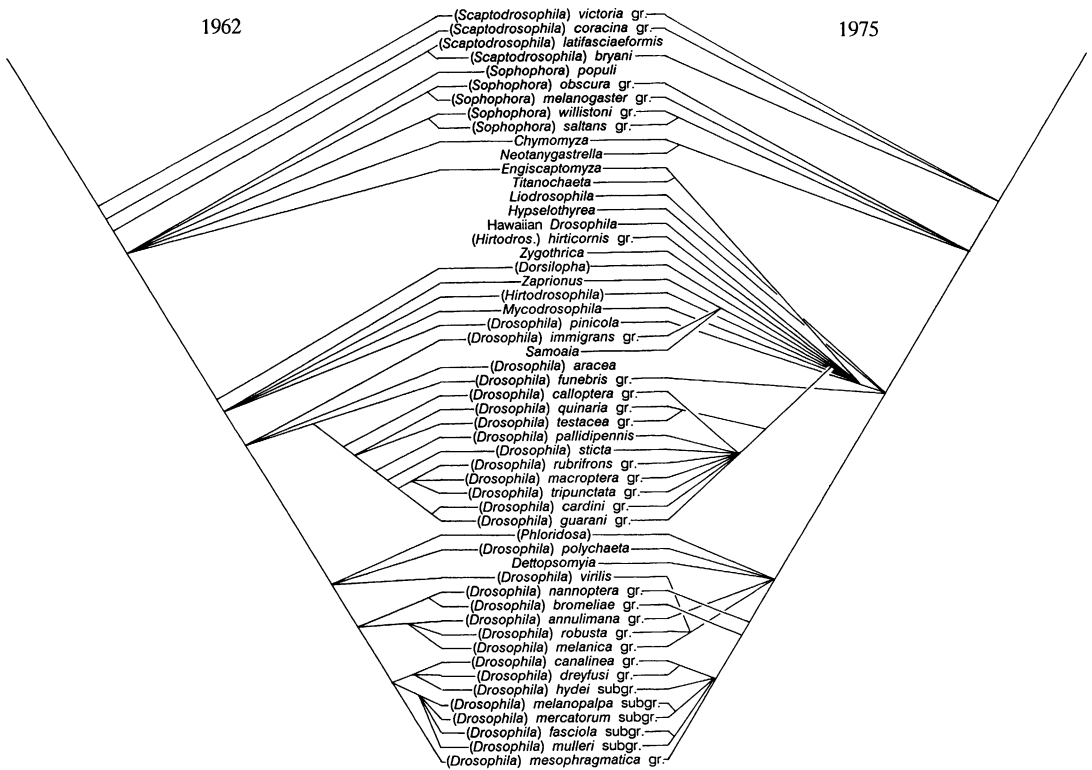


Fig. 547. Comparison of hypotheses on phylogenetic relationships in some Drosophilinae according to Throckmorton (1962, 1975). Throckmorton's original trees are represented here showing only relative relationships, not ancestry and descendency.

length trees, and a Nelson consensus tree was produced from this array, the topology of which is shown in figure 548 and is compared with the combined trees of Throckmorton's 1966 and 1975 papers. The tree has a length of 121 steps, consistency index of 0.20, and retention index of 63. Only those taxa are shown for the Throckmorton 1966 + 1975 tree which have data presented for them in the 1962 and 1966 papers. (The 1975 paper, for example, discussed many taxa additional to those in fig. 548 but for which Throckmorton never provided any data.) The topology of Throckmorton's tree was not imposed on an analysis of the data matrix, but the two trees can be seen to be obviously very different anyway. For instance, the *Drosophila mesophragmatica* group + *hydei* subgroup + *melanopalpa* subgroup are grouped, with members of the *repleta* group, at a terminal node. The HENNIG86 tree split the *hydei* +

melanopalpa subgroups, incorrectly in my view, from the rest of the *repleta* group. The internal morphology of the *repleta* group is extremely variable among species, so Throckmorton no doubt used other, probably external, adult and genitalic characters to keep the *repleta* group monophyletic. The HENNIG86 tree grouped Hawaiian *Drosophila* with *Sophophora* and *Scaptomyza*. The Throckmorton 1966 + 1975 tree put Hawaiian *Drosophila* at a basal node from which other genera, including *Scaptomyza*, originate. Nine species groups of the subgenus *Drosophila* are placed close to the subgenus *Dorsilopha* at one of the basal polytomies in the 1966 + 1975 tree, but represent a monophyletic group among 22 polytomous lineages in the HENNIG86 tree.

There are also a number of similarities between the two trees, such as the close relationships of species groups in the subgenus

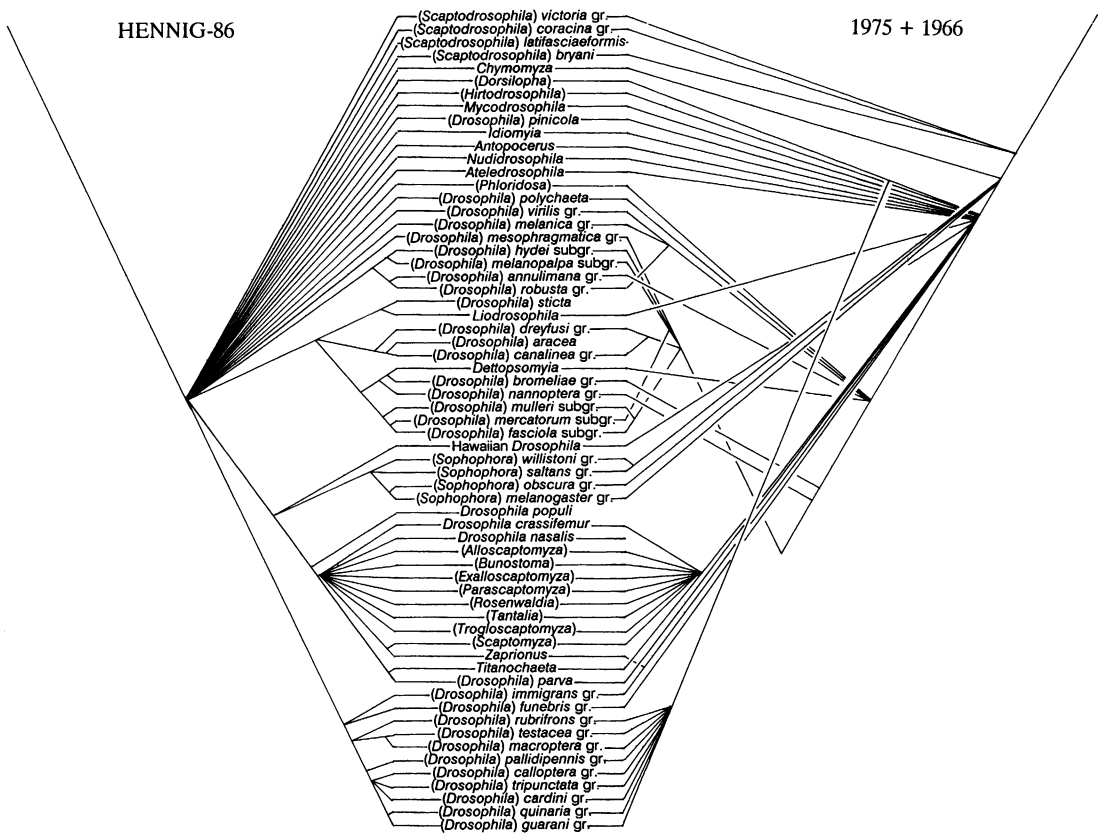


Fig. 548. Comparison of hypotheses on phylogenetic relationships in some Drosophilinae. 1975 + 1966 is a consensus of the trees from Throckmorton (1966, 1975); HENNIG86 is the consensus cladogram derived from a reanalysis of Throckmorton's data (1962, 1966), appearing in the matrix in Appendix 2. See text for discussion.

Drosophila, the subgenera of *Scaptomyza* (indeed, their monophyly), and the basal, unresolved relationships of *Scaptodrosophila*, *Chymomyza*, *Hirtodrosophila*, *Mycodrosophila*, and several genera endemic to Hawaii. *Titanochaeta* is placed close to *Scaptomyza* in both trees. The point of this exercise is to determine how reproducible Throckmorton's results are, using his own data. Granted, opinion between Throckmorton and I may differ as to some particular character states in the matrix of Throckmorton's data (Appendix II), but I don't believe that this difference is significant or even substantial. The major difference between the two trees probably lies in the methods of analyses. Since the HENNIG86 tree is the simplest, most parsimonious scheme of character state

change for Throckmorton's data, the Throckmorton 1966 + 1975 tree must be based on supplementary and/or alternative criteria. A perusal of an often overlooked paper (Throckmorton, 1968) would reveal that character weighting was probably not used in constructing his trees. However, that paper also mentions the use of 60 characters of *Drosophila*, used in an analytical data set. Despite what is cited by Beverley and Wilson (1982), in all of Throckmorton's papers no more than 30 total characters were described and discussed. (Throckmorton's 1968 paper was essentially an effort to quantify the degree to which characters agreed with each other in a tree. He apparently did not base his drosophilid phylogenies on the trees therein, and he gave no data as to the nature of each character

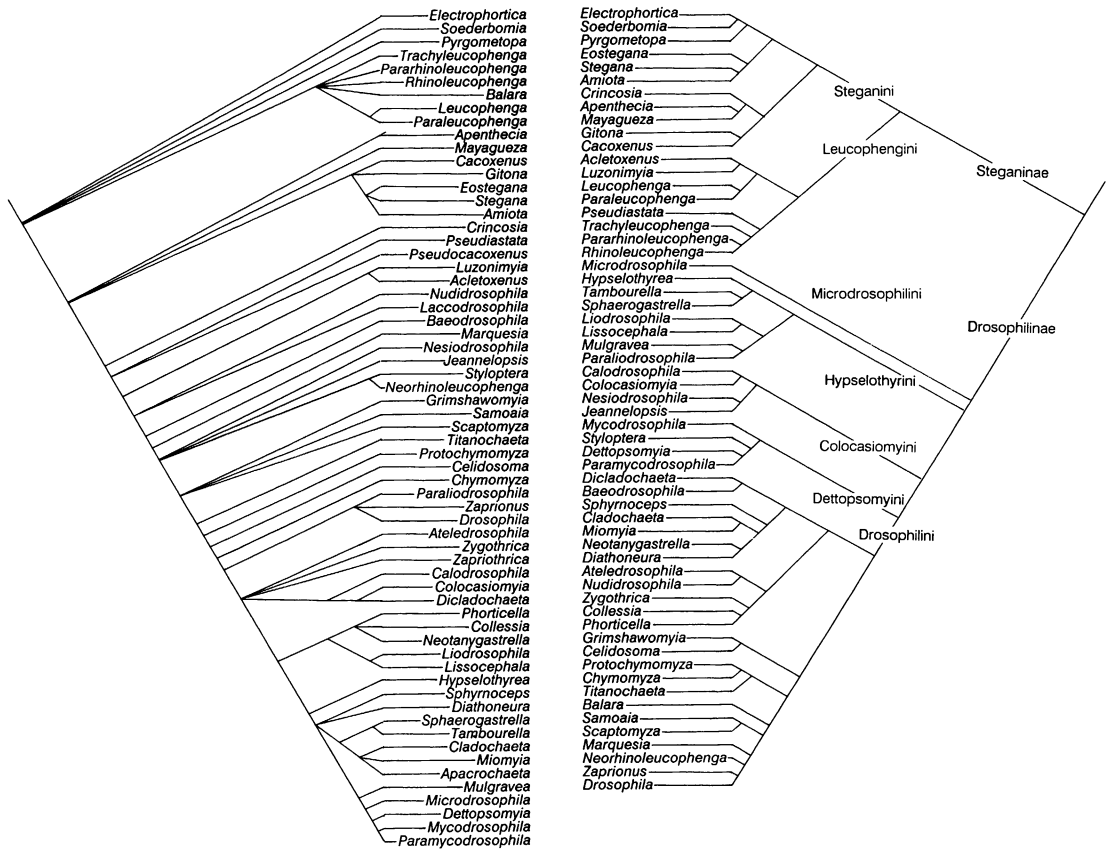


Fig. 549. Comparison of hypotheses on phylogenetic relationships among genera of the Drosophilidae, according to the data of Okada (1989) (Appendix 3). Right: tree and groupings presented in Okada (1989), analyzed using his phenetic method. Left: consensus cladogram produced using HENNIG86 analysis of original data matrix (Appendix 3). See text for discussion.

numbered 1–60. As such, it is impossible to evaluate the data matrix in that paper.) It is possible that Throckmorton occasionally resorted to unpublished data to support or maintain the monophyly of traditional groups. For instance, he often relied on Wasserman’s chromosome inversion sequences for relationships in the *repleta* group, in lieu of and even despite his own internal morphological characters.

OKADA’S TREES

Okada (1989) very recently proposed tribes and subtribes in the Drosophilidae, for the first time in drosophilid taxonomy. Obviously, given the purpose of my work, an analysis of his results is a logical step.

Okada examined specimens or consulted the descriptions for 63 genera and used 14 adult morphological characters to arrive at his reclassification. His original data matrix is presented in Appendix III. Applied to the matrix was his “even dichotomous diagram method,” to which one of his papers (Okada, 1985) is referenced as the source for the derivation of this method. The method apparently is used for constructing keys and branching diagrams, and, according to Okada (1985), is an MCD proximity and UPGMA cluster analysis. The dual utility and phenetic basis of this analysis is no doubt why Okada obtained such unusual results. Figure 549 shows Okada’s branching diagram, with his proposed taxonomic groups, compared to the cladogram based on his data matrix and ana-

lyzed with the HENNIG86 program. The cladogram in figure 549 (left side) was produced from an initial application of the m*;bb** algorithm, from which at least 100 equal-length trees were generated. A Nelson consensus tree was derived from this set of 100 trees.

Simple visual inspection alone of the two trees in figure 549 shows disparate results between the two methods of analysis. Okada's tree is fully resolved; there are 12 nodes on the HENNIG86 tree with three or more branches. Just the fact that Okada used 14 characters to arrive at a fully resolved tree indicates the phenetic method of his analysis: many of the nodes on his tree lack any of the derived characters that he proposed. Also, some of the most substantial differences between the two trees are the taxa that are encompassed at basal nodes, which grossly affect his results on suprageneric groupings. Okada omitted from his analysis (but included in his matrix) the four genera *Apachrochaeta* [sic], *Laccodrosophila*, *Pseudocacoxenus*, and *Zapriothrica* [which, coincidentally, are four of the five genera that Wheeler (1981) placed as incertae sedis to subfamily]. Length of the HENNIG86 tree is 56, consistency index (CI) = 0.24, and retention index (RI) = 78. When the topology of Okada's tree (the parttre* procedure) was imposed on a m*;bb analysis of the Okada data matrix, the result showed his tree to have a length of 86, CI = 0.16, and RI = 63. Thus, even with four more taxa, the HENNIG86 tree is about three-fourths the length of Okada's tree and with fewer reversals and convergences. I would reject Okada's classification on analytical grounds alone, but there are morphological and biological criteria for doing so as well.

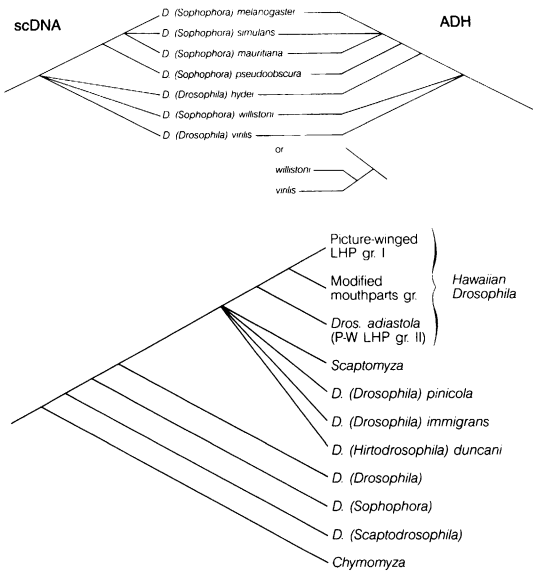
First, Okada hypothesized no losses of a character on his tree where that character is present at a more basal node. Obviously this is no a priori criterion to apply in constructing a cladogram, but secondary losses seem almost always to occur in trees emphasizing parsimony, and that possibility should not be excluded. Secondly, Okada's choice of morphological characters was similar to my own, except that in several cases he lumped as synapomorphic several different apomorphies that superficially look similar. In particular, the "piled" eye (his character A), as I have

shown here previously based on scanning electron microscopy (apomorphies 37-41; figs. 157-177), differs in the fine structure of the interfacetal setula itself. For example, in some Hawaiian drosophilids the interfacetal setulae are very long and thin, and the subgenus *Drosophila* has these setulae stout and ribbed. Also, the presence of a "developed facial carina" (his character E) is certainly not a single apomorphy, as this structure differs dramatically in many genera (see my apomorphies 81-90; figs. 272-309). Likewise, Okada links the genera *Mycodrosophila*, *Paramycodrosophila*, *Styloptera*, and *Dettopsomyia* on the presence of a costal lappet on the wing. As I have shown (figs. 335-338; apomorphies 111, 112), the costal lappet is apomorphically most similar only for the first pair and for the last pair of genera, but is certainly convergent between the two pairs, again based on fine morphological details of this structure. Lastly, Okada assumed that certain groups were monophyletic, in particular, the genus *Drosophila*. Given that *Drosophila* is certainly not monophyletic (a group of only some of the subgenera is monophyletic—see figs. 543, 544, and diagnoses below), this calls into question how one can code a paraphyletic assemblage.

MOLECULAR TREES

Despite popular belief, there are very few phylogenetic hypotheses for drosophilid genera based on molecular data. The great majority of molecular trees are concerned with relationships among closely related species, such as in the *Drosophila melanogaster* species subgroup (reviewed in Lachaise et al., 1988). Here, I review and briefly discuss the results of three molecular studies that deal with relationships of drosophilid genera or with subgenera and species groups of *Drosophila*.

The study by Zweibel et al. (1982) examined scDNA hybridization among seven *Drosophila* species, three being in the *melanogaster* species group, another in the *obscura* group, and the other in the *willistoni* group (all subgenus *Sophophora*), as well as two species in the subgenus *Drosophila* (*hydei* and *virilis*). The left-hand tree in figure 550 was drawn based on a table of ΔT_m values in Zweibel et al. (1982). Zweibel et al. also used



Figs. 550, 551. Phylogenetic hypotheses of some drosophilids derived from molecular data. 550. Zweibel et al. (1982). 551. Beverley and Wilson (1982, 1984), using microcomplement fixation distances of larval hemolymph protein.

probed Southern transfers of total genomic DNA, labeled with ADH (alcohol dehydrogenase) DNA; the right-hand tree in figure 550 is derived from their figure 4 on hydroxyapatite thermal elution curves of the duplexes formed between a 610 nucleotide fragment of pSAC and genomic DNA. The basal relationship of *willistoni* and *virilis* to the remaining species is equivocal based solely on the elution curve values. Both methods are phenetic and measure degree of divergence; homologous features linking groups of species were not identified. The trees from both methods match reasonably well, the only difference being that the ADH-based tree resolves a basal polytomy of four branches in the scDNA tree. However, both trees do not recognize the monophyly of the subgenus *Sophophora*, and, in fact, the ADH tree placed *D. (Drosophila) hydei* more closely to *Sophophora* than it does *D. (Sophophora) willistoni*, which is contrary to all other hypotheses of these species groups, including the following two other molecular trees.

Probably the most taxonomically comprehensive molecular comparisons are in the

study by Beverley and Wilson (1982, 1984, 1985), which is also a phenetic analysis. They used the larval hemolymph protein (LHP) of 29 species of Drosophilidae, which they compared by immunological distance using microcomplement fixation. A summary tree of the major groups treated by Beverley and Wilson is given in figure 551. Comparison of my results with those of Beverley and Wilson indicates some substantial differences. The major similarities between the two hypotheses are that *Chymomyza* and *Scaptomyza* represent sister groups to other taxa involved (B & W resolved what my hypothesis showed to be a basal tritomy). However, according to my hypothesis, *Sophophora* is the sister group to the subgenus *Drosophila* (not to all the remaining taxa being considered), and *D. immigrans* indeed does belong in the subgenus *Drosophila* (not among a polytomy with *Hirtodrosophila*, *Scaptomyza*, and Hawaiian "*Drosophila*"). Also, *Scaptomyza* represents the sister group to the genus *Drosophila*, and should not be placed in the above polytomy. Lastly, *Hirtodrosophila* and Hawaiian "*Drosophila*" represent sister groups in my analysis but are one pair of sister taxa among five proposed by B & W. With such substantial differences, clearly the data and/or methods of analysis of one of the hypotheses are in error.

A few corrections and qualifications of statements by Beverley and Wilson are appropriate here. First, they (B & W, 1982: 257) stated that the "LHP relationships shown among the 5 species of Drosophilidae agree exactly with the branching order obtained by quantitative phylogenetic analysis of 60 morphological traits (Throckmorton, 1968; 1975)." The reader is referred to my previous discussion on how Throckmorton's trees *may* have been derived. Also, as I have just shown using a computer cladistic algorithm employing parsimony criteria, Throckmorton's results are not reproducible. Also, B & W's results do not agree well with those of Throckmorton (1975). *Chymomyza*, for example, is placed basal to all the other drosophilines by B & W, but Throckmorton consistently placed *Chymomyza* near *Sophophora*. My analysis of data from Throckmorton's work (fig. 548) shows *Chymomyza* to lie among a basal polytomy of 22 branches.

Nonetheless, in addressing what they view as perfect correspondence, B & W (1982) concluded that "a protein such as LHP may contain about as much cladistic information as 60 anatomical traits" (p. 260). B & W extrapolated the date of origin of certain clades using a calibration of estimated 1 percent amino acid divergence per unit time (B & W, 1984; 1985) and the very limited fossil evidence known at that time, but which has subsequently been extensively revised (Grimaldi, 1987a).

Lastly, Spicer (1988) examined two-dimensional electrophoresis patterns using a synoptic set of eight *Drosophila* species in seven species groups [all in the subgenus *Drosophila*, except *D. (Sophophora) melanogaster*].

Each gel spot was scored as present or absent, its presence in the outgroup indicating a plesiomorphic state. Thus, position on the gel would be a criterion for assigning spots on different gels as being homologous. From a matrix of 135 characters (spots), a cladogram was produced using Swofford's (1982) CONTREE program and a strict and Adams-2 consensus tree. Spicer's results agree well with the tree topology of Beverley and Wilson; at the level of the present paper, the most important aspect is that the subgenus *Sophophora* was found to be the sister group to the subgenus *Drosophila* (although *Scaptomyza*, Hawaiian *Drosophila*, *Chymomyza*, and *Scaptodrosophila* were not examined).

REVISED, CLADISTIC CLASSIFICATION

Family Drosophilidae

- clade 1
 - Subfamily Steganinae
 - Tribe Steganini, Revised Status
 - Subtribe Steganina, Revised Status
 - Genus *Stegana*
 - Genus *Eostegana*
 - Subtribe Leucophengina, New Subtribe
 - Genus *Leucophenga*
 - Tribe Gitonini, New Tribe
 - Genus *Pararhinoleucophenga*
 - Genus *Electrophortica*
 - Subtribe Acletoxenina, New Subtribe
 - Genus *Trachyleucophenga*
 - Pseudiasata* Genus Group
 - Genus *Rhinoleucophenga*
 - Genus *Pseudiasata*
 - Acletoxenus* Genus Group
 - Genus *Mayagueza*
 - Genus *Acletoxenus*
 - Subtribe Gitonina, New Subtribe
 - Genus *Paraleucophenga*
 - Genus *Crincosia*
 - Genus *Cacoxenus*
 - Genus *Gitona*
 - Amiota* Genus Group
 - Genus *Amiota*
 - Genus *Apenthecia*
- clade 2
 - Subfamily Drosophilinae
 - Tribe Cladochaetini, New Tribe
 - Genus *Cladochaeta*
 - Genus *Diathoneura*
 - Tribe Drosophilini, Revised Status

- 2.2.1 Subtribe Colocasiomyina, New Subtribe
 Genus *Colocasiomyia*
 Genus *Baeodrosophila*
- 2.2.2 Subtribe Drosophilina, Revised Status
- 2.2.2.1 Infratribe Laccodrosophiliti, New Infratribe
 Genus *Zapriothrica*
 Genus *Laccodrosophila*
- 2.2.2.2 Infratribe Drosophiliti, New Infratribe
- 2.2.2.2.1 Genus *Dichaetophora*
- 2.2.2.2.2 Genus *Scaptodrosophila*, Revised Status
- 2.2.2.2.3 Genus *Lissocephala*
- 2.2.2.2.4 *Chymomyza* Genus Group
 Genus *Protochymomyza*
 Genus *Chymomyza*
 Genus *Neotanygastrella*
- 2.2.2.2.5.1 *Hirtodrosophila* Genus Complex
- 2.2.2.2.5.1.1 *Zygothrica* Genus Group
 Genus *Zygothrica*
 Genus *Hirtodrosophila*, Revised Status
 Genus *Bialba*
 Genus *Poliocephala*
 Genus *Mycodrosophila*
 Genus *Paramycodrosophila*
 Genus *Paraliodrosophila*
- 2.2.2.2.5.1.2 Genus *Idiomyia*, Revised Status
- 2.2.2.2.5.2 *Drosophila* Genus Complex
- 2.2.2.2.5.2.1 Genus *Drosophila*
- 2.2.2.2.5.2.2.1 *Styloptera* Genus Group
 Genus *Jeannelopsis*
 Genus *Styloptera*
 Genus *Dettopsomyia*
 Genus *Liodrosophila*
 Genus *Hypselothyrea*
 Genus *Sphaerogastrella*
 Genus *Mulgravea*
 Genus *Tambourella*
- 2.2.2.2.5.2.2.2 *Dicladochaeta* Genus Group
 Genus *Dicladochaeta*
 Genus *Calodrosophila*
 Genus *Microdrosophila*
- 2.2.2.2.5.2.2.3 *Zaprionus* Genus Group
 Genus *Zaprionus*
 Genus *Phorticella*
 Genus *Samoia*
- 2.2.2.2.5.2.2.4 *Scaptomyza* Genus Group
 Genus *Marquesia*
 Genus *Nesiodrosophila*
- 2.2.2.2.5.2.2.4.1 Genus *Celidosoma* Genus Subgroup
 Genus *Grimshawomyia*
 Genus *Celidosoma*
- 2.2.2.2.5.2.2.4.2 *Scaptomyza* Genus Subgroup
 Genus *Lordiphosa*, Revised Status
 Genus *Scaptomyza*

DIAGNOSES OF NEW AND REVISED HIGHER TAXA

FAMILY DROSOPHILIDAE

DIAGNOSIS: Small to large-size Muscomorphans with three pairs of orbital setae, including anteriormost pair of proclimates (occasionally posterior to anterior reclinate orbital), others reclinate (figs. 229–257) [anterior reclinate occasionally highly reduced or lost, such as in *Sphaerogastrella* (figs. 258–260)]; basal-medial wing cell lost [secondarily gained in *Amiota*, *Apenethecia* (figs. 340, 342), *Cacoxenus*, and *Stegana*]; subcostal vein incomplete; spiracles VI + VII near ventral margin of tergite VI in ♂ (figs. 383–386); tVII in males lost (figs. 338–386); anepisternal setae almost always absent [an exception is *Zaprionus obscuricornis* (Meijere)]; sternite VI lost in males; minute spines on mesal surface of forefemur (ctenidium) (figs. 4–7) lost [secondarily gained in several taxa (figs. 355–360)].

SUBFAMILY STEGANINAE

DIAGNOSIS: Dorsolateral tentorial apodeme arms (on postocciput) parallel, at least the basal two-thirds of arms (ap. 4; figs. 18–23); group of anterior cibarial sensilla in a row, not a squared or triangular arrangement (figs. 144, 147) (ap. 28); spiracle pair VII (abdomen) lost in males (fig. 387) (ap. 126). A character that I did not survey, but which was treated in a study by Wheeler (1960), is loss of one of the abdominal sternites in male Steganinae. This is another apomorphy that supports the monophyly of the subfamily, but which has not traditionally been used as a diagnostic feature. Wheeler was able to detect sternite loss based on the conservative presence of paired sensilla trichodea at each segment on the ventral surface of the abdomen.

TYPE GENUS: *Stegana* Meigen, 1830.

Bock (1982) gave a brief survey of drosophilid classification and a traditional diagnosis of the Steganinae: prescutellars present and generally large, anterior reclinate large, discal and second basal wing cells “in many genera” are separate, and the katapisternum (“sternopleuron”) has two large subequal bristles. All of these features are plesiomorphic at the family level, or else are too

sporadically distributed to be of diagnostic use at this level. Okada (1954: 14) likewise gave a diagnosis for the subfamily.

Figure 546 shows a comparison of two of my hypotheses on steganine relationships, from this study and from Grimaldi (1988). The 1988 study was based on fewer adult characters, but utilized characters from immatures as well. Correspondence, particularly among pairs or triplets of taxa, is quite good, but there are some notable differences among larger sets of genera. First, *Amiota* is monophyletic in this study, and it probably should not be split up as suggested in the 1988 study. The male genitalic characters supporting this appear to be faithful homologies, and their complexity was at first misleading. Also, *Rhinoleucophenga* + *Pseudiasata* is the sister-group pair to *Acletoxenus* + *Mayagueza*, not just *Pseudiasata*. This does not change the hypothesis in Grimaldi (1988) on the relict distribution of *Mayagueza*. In this study, *Gitona* and *Cacoxenus* are sister groups. Furthermore, this study resolves the basal tritomy in the 1988 hypothesis. In all, more confidence should be placed in this more recent hypothesis, simply because of the many more characters that support it.

TRIBE STEGANINI, REVISED STATUS

Steganini Okada, 1989: 396 (as tribe).

DIAGNOSIS: Dorsolateral tentorial apodeme arms converge slightly or are parallel, then acutely diverge dorsally (figs. 22, 23) (ap. 6); ventral surface of the costal vein between R_{2+3} and R_{4+5} with approximately six heavily sclerotized, hooked, peglike spines (figs. 326–328) (ap. 109); mid and hind tarsomeres each with two rows of cuneiform setae (figs. 363, 370, 371) (ap. 119). Okada (1989) proposed this tribe for those genera with confluent basal wing cells, composed of the genera *Acletoxenus*, *Luzonimyia*, *Leucophenga*, *Paraleucophenga*, *Pseudiasata*, *Trachyleucophenga*, *Pararhinoleucophenga*, and *Rhinoleucophenga*. As shown in this work, this feature is not restricted to those taxa, and in fact may be a synapomorphy for the family (with some secondary arisals of separated cells).

TYPE GENUS: *Stegana*.

SUBTRIBE STEGANINA,
REVISED STATUS

Steganina Hendel, 1917: 43 (as genus group);
Wheeler, 1960: 110 (as subgenus).

DIAGNOSIS: Cibarial posterior sensilla chaetica in group of ca. 18 per side (figs. 144, 151) (ap. 26-1); interfrontal microtrichia short, scaliform (figs. 220, 221) (ap. 64); wings with veins R_{4+5} and M_1 converged apicad, tip pointed (figs. 323-325); line of weakness through basal section of costal and subcostal veins, with wings folded along sides of body (ap. 108); surstylus (male) articulated with ventral margin of epandrium, simple, tip pointed and sclerotized (fig. 399) (ap. 127); spermathecal capsule spherical, sclerotized, with a thin, curled, apical filament (ap. 126).

TYPE GENUS: *Stegana*.

INCLUDED TAXA: Genera *Stegana*, *Eostegana*. I examined representatives of only three subgenera (*Stegana*, *Steganina*, *Pseudostegana*), plus an *Eostegana* species. The results of this study are in agreement with those of Okada (1981), in that *Pseudostegana* is the sister group to all other *Stegana*. (In the present study, *Eostegana* is more closely related to the subgenera *Stegana* and *Steganina* than is *Pseudostegana*.) This suggests that either *Pseudostegana* be separated as a genus, or *Eostegana* be included as a subgenus of *Stegana*. In Okada's 1978 study, *Parastegana* + *Pseudostegana* was the sister-group pair to the rest of *Stegana*. Nomenclatural changes should await a full revision of the genus.

SUBTRIBE LEUCOPHENGINA,
NEW SUBTRIBE

DIAGNOSIS: Width of bases of dorsolateral arms of tentorium (postocciput) at least twice that of apical portion (fig. 22) (ap. 10); proclinate and anterior reclinate very close together, separated by distance less than one-half that between anterior reclinate and posterior reclinate (fig. 230) (ap. 69); male with folded, dorsal process over distiphallus (figs. 391, 392) (ap. 130); distiphallus with brush of fine spicules (not in all species of *Leucophenga*) (figs. 391, 392) (ap. 132); males sometimes, females often with a tergal color pattern of a row of medial spots, bordered by lateral rows (ap. 133); surstylus (male) squared, flat, broad

(fig. 494) (ap. 134); spermathecal capsule elongate, irregularly cylindrical, annulate (ap. 215).

TYPE GENUS: *Leucophenga*.

INCLUDED TAXA: Genus *Leucophenga*.

TRIBE GITONINI, NEW TRIBE

DIAGNOSIS: Palp almost triangular, with flat ventral margin at acute angle to dorsal margin (figs. 109-111) (ap. 24); arista micropubescent (fig. 178) (ap. 44), but secondarily plumose in *Amiota*; spiracle pair VII present in females (ap. 206).

TYPE GENUS: *Gitona* Meigen, 1830.

INCLUDED TAXA: Genus *Pararhinoleucophenga* (unplaced to subtribe), genus *Electrophortica* (Eocene?: Baltic amber), subtribes *Acletoxenina* and *Gitonina*. Okada (1988) figured the male genitalia (but not the female) of *Pararhinoleucophenga nuda* and *P. maura*. The bilobed, brushy distiphallus, plus the presence of pegs on the distal part of the costal vein, indicate placement of this genus in tribe Steganini, perhaps in subtribe Leucophengina.

SUBTRIBE ACLETOXENINA,
NEW SUBTRIBE

DIAGNOSIS: Supracervical setae thin and sharp (e.g., figs. 12, 15, 16) (ap. 2); cibarial posterior sensilla chaetica in group of ca. 18 (fig. 144) (ap. 26-1); ocellar setae very small, cruciate (ap. 75-1), or absent/extremely minute (in *Acletoxenus*, ap. 75-2); midtibia with two dorsopreapical setae, opposing ventroapical setae (ap. 122); pair of surstyli (males) lost (ap. 136); male genitalia reduced, with membranous saclike distiphallus; hypandrium short, simple; paraphysis either very small or absent (figs. 420-422) (ap. 137).

TYPE GENUS: *Acletoxenus* Frauenfeld, 1868.

INCLUDED TAXA: Genus *Trachyleucophenga*, *Pseudiasata* genus group, *Acletoxenus* genus group. Wheeler and Takada (1971) described and illustrated the male genitalia of a species of *Trachyleucophenga* from Louisiana. This specimen has not been retrieved from the University of Texas drosophilid collection, but based on the genitalic features alone, which Duda did not describe in sufficient detail, this genus is certainly in sub-

tribe *Acletoxenina*, and perhaps even in the *Pseudiasata* genus group. These features are the following: prensisetae comb on the ventral lobe of the epandrium, with surstylus lost (ap. 136); aedeagus very simple, bulbous (with an apical point), short, and with a longer aedeagal apodeme (ap. 137); paraphyses reduced, very small, near a remnant of the hypandrium. Hopefully, newly collected material will confirm placement of the genus by allowing use of external characters.

PSEUDIASATA GENUS GROUP

DIAGNOSIS: Supracervical setae greater than about 35 in number (ap. 1); 50 or more interfrontal setulae present (fig. 213) (ap. 61); acrostichal setulae in 12 rows (ap. 98-0).

INCLUDED TAXA: Genus *Pseudiasata*, *Rhinoleucophenga*.

ACLETOXENUS GENUS GROUP

DIAGNOSIS: Dorsolateral tentorial apodeme arms parallel and very close together (fig. 211) (ap. 5); facial and frontal region very narrow and parallel (fig. 207) (ap. 62); anterior dorsocentral setae (on notum) barely longer than acrostichals, separated from posterior dorsocentrals by about one-half the length of anterior dorsocentral (ap. 106); ventral lobes of epandrium (male) tapered, with pointed and sclerotized apices, pincerlike (ap. 205).

INCLUDED TAXA: Genera *Acletoxenus*, *Mayagueza*.

SUBTRIBE GITONINA, NEW SUBTRIBE

DIAGNOSIS: Length of dorsomedial tentorial arm at least three-quarters the length of dorsolateral arm (figs. 18, 20) (ap. 9); base of dorsolateral tentorial arm broad, at least twice the width of apical portion (ap. 10); flagellomere 1 round or nearly so in view of broadest surface (ap. 55)—not present in subgenera *Amiota* and *Phortica*; interfrontal setulae short, stout (fig. 202) (ap. 63) (not present in genus *Amiota*); notum (sometimes abdomen) with small dark spot at base of each seta/setulae (ap. 104)—not present in subgenus *Amiota*.

TYPE GENUS: *Gitona* Meigen, 1830.

INCLUDED TAXA: Genera *Paraleucophen-*

ga, *Crincosia*, *Cacoxenus*, *Gitona*, and the *Amiota* genus group. Okada (1988) figured the male genitalia of three species of *Paraleucophenga*. They have a sclerotized, hooked, and lobed paraphysis and a U-shaped, ribbon hypandrium, thus indicating a relationship within the subtribe *Gitonina*. Bächli (1971) provided a very nice illustration of *P. semiplumata* male and female genitalia. The spermatheca of this species is *Leucophenga*-like, in being slightly longer than wide, and with fine annuli (not the characteristic series of ringlike annuli). There is a large dorsal process to the decasternum, and the paraphyses are large and hooked. However, the hypandrium is quadrate and long, not thin and U-shaped. This species may lie at the base of subtribe *Gitonina*, which a revision of the group should really determine.

Genus *Cacoxenus*

Domomyza Rondani, 1856: 121. Type species: *cincta* Rondani (as *Agromyzidae*. *Cacoxenus* Loew, 1858: 217. Type species *indagator* Loew (junior synonym of *D. cincta*—see Deeming, 1988).

DIAGNOSIS: Interfrontal setulae short, stout (fig. 202) (ap. 63); facial carina prominent, complete, flared at oral margin (fig. 275) (ap. 85-2); wing with basal-medial cell (figs. 340, 342) (ap. 114) (a secondary gain); paraphysis long, narrow, with small basal articulation (ap. 149); ventrolateral lobe of syntergite VI + VII with sclerotized point (fig. 405) (ap. 150).

DISCUSSION: The genus *Cacoxenus* has had a confusing taxonomic history. *Paracacoxenus* was described in 1960 by Hardy (Hardy and Wheeler, 1960), and McAlpine (1968) applied this name to subsequently designated taxa. Wheeler (1981) then synonymized the genus with *Cacoxenus*, making *Paracacoxenus* a subgenus. Recently, Wheeler (1987) and Macá (1980a) used *Paracacoxenus* as a generic name. To add to the confusion, *Gitonides* was also originally described as a genus (Knab, 1914), to which McAlpine adhered (1968), but which Wheeler (1981) designated as a subgenus of *Cacoxenus*. Wheeler (1987) apparently kept *Gitonides* as a subgenus of *Cacoxenus*. Questions on the relationship(s) of the subgenera of *Cacoxenus* must await a

revision of the genus. Of the greatest nomenclatural impact thus far is the paper by Deeming (1988), which indicated *Cacoxenus indagator* to be a junior synonym of *Domomyza cincta* Rondani. This is apparently correct, but I have not used *Domomyza* here for stability purposes and hope to address a possible suppression of *Domomyza* in favor of *Cacoxenus*.

Genus *Gitona*

Gitona Meigen, 1830: 129. Type species: *distigma* Meigen.

DIAGNOSIS: Interfrontal setulae short, stout (fig. 202) (ap. 63); facial carina prominent, complete (ap. 85-1) but flared at oral margin in *G. distigma*; ventral lobe of epandrium with evenly spaced row of teeth on medial margin (except *G. americana*; convergent with *Rhinoleucophenga* and *Trachyleucophenga*) (fig. 406) (ap. 135); surstyli absent (ap. 136); male genitalia greatly reduced (fig. 423) (ap. 137).

AMIOTA GENUS GROUP

DIAGNOSIS: Supracervical setae thin, sharp (e.g., figs. 15, 16) (ap. 2); palp with internal, round gustatory/olfactory organ (figs. 109–111) (ap. 23); clypeus bulbous, prominent, with ventral margin protruding beyond oral margin (figs. 233, 274) (ap. 91); wing with basal-medial cell present (secondary gain) (figs. 340, 342) (ap. 114); wing veins R_{4+5} and M_1 slightly converged apicad, except in *A. (Sinophthalmus)* (ap. 115); in *Amiota*, large, heavily sclerotized, often elaborate paraphyses (figs. 425–429) (ap. 151).

INCLUDED TAXA: Genera *Amiota*, *Apenethecia*. Results of this study and that of Grimaldi (1988) indicate *Apenethecia* and *Sinophthalmus* as being sister groups; *Apenethecia* may indeed need to be ranked as a genus. As Tsacas (1983) has illustrated, the male genitalia are considerably simpler (and plesiomorphic) than in *Amiota*: the hypandrium is large, paraphyses simple and lobate, and an aedeagus is present (which is curled, membranous, and tubular, much as in *Sinophthalmus*). If *Apenethecia* is indeed closest to *Sinophthalmus*, then some of the genitalic modifications are due to reduction.

SUBFAMILY DROSOPHILINAE

DIAGNOSIS: Supracervical setae thin and sharp (figs. 15, 16) (ap. 2); flagellomere 1 with conus, a tubular dorsal process inserted into the pedicel (figs. 3, 199–201) (ap. 54); prescutellar setae lost (ap. 95); anterior katepisternal seta shorter than posterior one, or lost (ap. 99); surstylus (male) with stout, heavily sclerotized pegs (prensisetae) (figs. 495–504) (ap. 200)—secondarily lost in several taxa; spiracle pair VII present in female (figs. 515–517) (ap. 206); cerci lost in female, only epi-proct and hypoproct present (figs. 515–517) (ap. 207).

Okada (1989) described the monophyly of the subfamily on the basis of the posterior reclinate orbital seta being nearer to the proclinate than to the inner vertical seta (his character g). I believe this to be a reliable subfamily character, along with the loss of the prescutellar setae (his character h, my ap. 95). Okada divided the subfamily into five tribes; it is divided here into the Cladochaetini and Drosophilini.

TYPE GENUS: *Drosophila* Fallén, 1823.

TRIBE CLADOCHAETINI, NEW TRIBE

DIAGNOSIS: Lacinia with dorsal and ventral arms long and thin, opposite at nearly 180°, anterior arm fusiform (figs. 69–72) (ap. 19); anterior cibarial sensilla (campaniformia) in triangular arrangement (figs. 139, 140) (ap. 28-1); labium broad, sclerotized, forming trough into which labellum folds (ap. 36); loss of vein $A_1 + CuA_2$ and cell cup (ap. 113-1); ventral margin of cercus (male) extended into a thin lobe (ap. 141)—not in *Diathoneura opaca* or *metallica*; aedeagus reduced and membranous, aedeagal apodeme large (figs. 389, 394) (ap. 142).

TYPE GENUS: *Cladochaeta* Coquillett, 1900.

INCLUDED TAXA: Genus *Cladochaeta*, *Diathoneura*.

DISCUSSION: Little taxonomic attention has been paid to this incredibly speciose, poorly described group. There is apparently only one (described) Old World *Diathoneura* species (*ripa* Okada, from Nepal: I have not examined it); all other *Diathoneura* and *Cladochaeta* are Neotropical. Wheeler and Takada (1971) concluded that the species limits of both genera are vague and seem to intergrade.

This short study also presented the most comprehensive treatment yet made of the very distinctive male genitalia. Frota-Pessoa (1947) synonymized *Diathoneura* and *Claspteroomyia*, the latter synonym with which Wheeler (1981) concurred (but as a synonym of *Cladochaeta*). *Drosophila superba* Sturtevant is a *Diathoneura*, as concluded by Frota-Pessoa (1947) as well. The work by Duda (1925) still remains as the only major treatment of *Diathoneura* and the study by Frota-Pessoa (1947) for *Cladochaeta*.

TRIBE DROSOPHILINI, REVISED STATUS

Drosophilini Okada, 1989: 398.

DIAGNOSIS: Postpronotal (humeral) lobe with two setae (ap. 100); oviscapt (sternite VIII lobate, with narrow anteroventral bridge) is present. Okada (1989) diagnosed his tribe *Drosophilini* on the basis of a shallow "second" (subcostal) break on the costal wing vein (his character L), and by a small costal lappet (his M). Both of these are primitive features at the family level. My diagnosis would make this group monophyletic, but changes the taxa that are included in the tribe.

SUBTRIBE COLOCASIOMYINA, REVISED STATUS

Colocasiomyini [sic] Okada, 1989: 393 (as tribe). (Proper spelling should be *Colocasiomyiini*.)

DIAGNOSIS: Palpus with short, stout, sharp setae (ap. 22); number of interfrontal setulae reduced to 4–6 (ap. 67); carina with very broad, flat anterior surface (fig. 298) (ap. 90).

TYPE GENUS: *Colocasiomyia* Meijere, 1914.

INCLUDED TAXA: *Colocasiomyia*, *Baeodrosophila*.

DISCUSSION: Okada erected the tribe *Colocasiomyini* on the basis of "second costal break shallow" (his character L—a sympleiomorphy at the family level, used by Okada also as a synapomorphy for the tribe *Drosophilini*). Okada (1989) also diagnosed the group on the basis of ocellar setae lying outside the ocellar triangle (his character c). His tribe would include *Colocasiomyia*, *Calodrosophila*, *Nesiodrosophila*, and *Jeannelopsis*. In these genera, as well as in *Baeodrosophila* and several other groups, the ocellar setae were found to lie just lateral to the anterior

ocellus. My analyses show that the genera included in Okada's tribe *Colocasiomyini* have relationships with disparate other groups.

SUBTRIBE DROSOPHILINA, REVISED STATUS

Drosophilini Rondani, 1856.

DIAGNOSIS: Distinguished by the possession of heavily sclerotized, thick, peg ovisensilla on the oviscapt (figs. 525–541) (ap. 212). This feature has been subsequently lost numerous times: in *Chymomyza* (fig. 524), *Celidosoma*, *Siphlodora* (fig. 519), some Hawaiian *drosophilids* (fig. 520), *Microdrosophila*, and some *Scaptomyza*.

TYPE GENUS: *Drosophila* Fallén, 1823.

INFRA TRIBE LACCODROSOPHILITI, NEW INFRA TRIBE

DIAGNOSIS: Frontal vittae extensive, black-brown, and either finely striate and glabrous (fig. 218) (ap. 59) or with long, fine, erect setulae (figs. 224, 225) (ap. 60) (*Zapriothrica*); facial carina very narrow, flanked by smooth, even concavities for the antennae in *Laccodrosophila* and *Zapriothrica* (figs. 280, 281) (ap. 88-1, 88-2, respectively); pretarsus with spatulate retinerae (on pulvillus) (figs. 352–354) (ap. 117); oviscapt telescoping, elongate, with few, stout, black ovisensilla pegs at apex (figs. 526–528) (ap. 209).

TYPE GENUS: *Laccodrosophila* Duda, 1927.

INCLUDED TAXA: *Zapriothrica*, *Laccodrosophila*, and *Drosophila xiphophora* Pipkin, the latter of which was placed *incerta sedis* to subgenus by Wheeler (1981).

INFRA TRIBE DROSOPHILITI, NEW INFRA TRIBE

DIAGNOSIS: Each row of posterior sensilla chaetica on cibarium with approximately 20 or more sensilla (fig. 150) (ap. 26); ventral wall of cibarium with medial constriction, pear-shaped (anterior end narrow) (figs. 152) (ap. 31).

TYPE GENUS: *Drosophila*.

INCLUDED TAXA: Genera *Dichaetophora*, *Lissocephala*, *Scaptodrosophila* (new rank), *Chymomyza* genus group, *Hirtodrosophila* genus complex, *Drosophila* genus complex.

DISCUSSION: There are unfortunately no obvious external characters to use in diagnosing this group, which would greatly aid in rapid identification. It may be sufficient for identification, though, that the *Drosophilini* can be identified as those species in the subtribe *Drosophilina* without the obvious and distinctive features of the *Zaprithriciti*. The mouthpart characters described above were apparently discovered (but not diagnostically used) by Duda. He described and illustrated the cibarium for various acalyptrate families in the series *Die Fliegen der Palaearktischen Region*. He made no mention of the variation in shape and structure of the drosophilid cibarium.

Genus *Scaptodrosophila*, Revised Status

Scaptodrosophila Duda, 1923: 37 (as genus).
Wheeler, 1970, 1981 (synonyms). Bock, 1976
(all as subgenera of *Drosophila*).

DIAGNOSIS: Large pair of prescutellar setae (secondary gain); three katepisternal setae, subequal; eggs with 6–10 filaments; hypandrium large, often with pair of large, straight setae on the posterior margin (similar to *Baeodrosophila*, *Neotanygastrella*); paraphysis with row of 3–10 sensilla, sometimes longer than distiphallus; distiphallus almost always shorter than aedeagal apodeme, usually triangular (with an apical point). Some species have lost the surstylus, with prensisetae-like structures instead on the ventral lobe of the epandrium.

DISCUSSION: Bock (1978) gave the most detailed account of the history of *Scaptodrosophila* taxonomy and distribution of the genus, and he extensively described a large endemic Australian fauna. Apparently, Duda was unsure of the limits of *Scaptodrosophila* and possible relationships within *Drosophila*. Bock (1978) also concluded that "several of the genera originally established by Duda (1923) are now regarded as not sufficiently different from *Drosophila* to warrant more than subgeneric rank . . ." (p. 91). *Scaptodrosophila* is here excluded from genus *Drosophila* because of the possession of one, instead of (apomorphically) two, vibrissae, and most species (plesiomorphically) have bare eyes (ap. 38). Some species have a well-de-

veloped carina, but this is structurally quite different from that in most *Drosophila*: this, plus the fact that *Scaptodrosophila* plesiomorphically lacks a carina, would also exclude this group from *Drosophila*.

CHYMOMYZA GENUS GROUP

DIAGNOSIS: Trichia portion of medial cibarial sensilla group lost (convergent with *Diathoneurini*) (ap. 29); medial cibarial sensilla in an irregular row, or even scattered (fig. 141) (ap. 30); anterior reclinate orbital seta lateral to or anterolateral/anterior to proclinate (fig. 240) (ap. 68) (convergent with several other genera); acrostichals in four rows (ap. 98-4); paraphysis (male) with two or more long, straight setae (fig. 415) (ap. 145); ventral lobe of epandrium large, with many long setae (ap. 146); surstylus (male) small, with single row of prensisetae on medial edge (figs. 495, 496) (ap. 147).

INCLUDED TAXA: *Chymomyza*, *Neotanygastrella*, and *Protochymomyza*. *Protochymomyza* is represented by an extinct species from Dominican amber (Grimaldi, 1987a) and was not included in the cladistic analysis because of the many missing character states, but it is included in the data matrix. Its relationships are undoubtedly close to those of *Chymomyza*, as I have discussed previously (Grimaldi, 1987a), but retain several plesiomorphic features not seen in *Chymomyza*.

HIRTODROSOPHILA GENUS COMPLEX

DIAGNOSIS: Mid and hind tarsi each with one row of cuneiform setae along the medial surface (fig. 368) (ap. 120) (convergent with *Zaprionus* genus group and *Amiota*); ventral margin of cibarium in lateral view with an acute angle at the posterior end in some species (fig. 31) (ap. 14), and also usually with a sclerotized swelling surrounding the hypopharynx in this area (figs. 153–155).

INCLUDED TAXA: *Zygothrica* genus group and genus *Idiomyia*.

ZYGOTHRICA GENUS GROUP

DIAGNOSIS: Posterior end of cibarial portion of hypopharynx with large, heavily sclerotized bulb (ap. 32); arista with one ventral

branch (ap. 49) (secondarily increased in some taxa); medial portion of ventral surface of cercus (male) with flat, tapered (in lateral view) plate (fig. 478) (ap. 189), which is lost in some species in this group.

INCLUDED TAXA: *Paramycodrosophila*, *Mycodrosophila*, *Zygothrica*, *Paraliiodrosophila*, genus *Hirtodrosophila*, and possibly *Bialba* and *Poliocephala*.

DISCUSSION: Grimaldi (1987a, 1987b) discussed relationships among *Mycodrosophila*, *Paramycodrosophila*, *Hirtodrosophila*, and *Zygothrica* (but not *Paraliiodrosophila*). These studies indicate *Zygothrica* + *Hirtodrosophila* and *Mycodrosophila* + *Paramycodrosophila* to be two pairs of sister groups. There is no doubt that these four genera, with *Paraliiodrosophila*, are a monophyletic group, as based on the characters in the diagnosis. However, relationships hypothesized in Grimaldi (1987a, 1987b) are not in agreement with those in figure 543. There are slight structural differences in the costal lappet of *Mycodrosophila* and *Paramycodrosophila* (figs. 335, 336), suggesting them to be independently derived, and the distribution of other apomorphies forces this conclusion as well. *Mycodrosophila* is presently fairly well studied; I am in the midst of revising *Zygothrica*, and the genera *Paraliiodrosophila* and *Paramycodrosophila* could easily be revised in their entirety. *Hirtodrosophila*, however, is a very speciose, variable group, in dire need of worldwide revision—a task no doubt requiring many years. Until that is done, the definitive answer to the question of the relationships among these genera must remain unsettled.

Apomorphies were not shown on the cladogram in figure 543 for *Zygothrica*, although there are many, as discussed in Grimaldi (1987b). One which I have subsequently found to be extremely reliable is the shape of the lacinia: it has a very short ventral arm, indeed almost round, no dorsal arm, and a very long anterior arm (figs. 60–62). This feature was discovered by Burla (1956).

Okada (1986) described and discussed "atypical" *Mycodrosophila*, or those without costal lappets, for which he described the subgenus *Promycodrosophila*. It is not possible at present to decide whether the absence of a costal lappet in Okada's atypical *Mycodro-*

sophila is (syn?)apomorphic (a loss of the lappet) or plesiomorphic. If plesiomorphic, *Promycodrosophila* is obviously a paraphyletic group. If the lappet has indeed been lost in *Promycodrosophila*, then the question remains, at what taxonomic level with respect to the remainder of the genus is *Promycodrosophila* derived? Based on the aedeagus structure (a short hypandrium and a pair of distiphallal flanges), the group appears monophyletic and most closely related to certain species in the subgenus *Mycodrosophila* (e.g., *missima*, *aqua*).

Bock (1989) recently described two genera, *Bialba* and *Poliocephala*, each based on one species from Iron Range, Queensland, Australia. They are known from very few specimens, so examination for the purposes of this work was not possible. According to Bock (1989), both genera may be "specialized offshoot[s] of *Mycodrosophila*." The number of ventral branches of the arista (three or four in *Poliocephala*, two in *Bialba*) does not agree with *Mycodrosophila*, which almost always has just one branch. Also, the lack of a costal lappet, dense interfacetal setulae, and two pairs of dorsocentrals do not generally agree with *Mycodrosophila*. The oviscapt of *Bialba* is very unusual for all *Mycodrosophila* and related genera, for the lack of ovisensilla pegs. My placement of these two genera in the *Zygothrica* genus group is based on Bock's (1989) suggestion, and needs to be substantiated with dissections of additional material.

Genus *Hirtodrosophila*, Revised Status

Hirtodrosophila Duda, 1923: 41 (as genus). Wheeler, 1981: 52 (synonyms).

DIAGNOSIS: Carina either lost or present and very narrow, knifelike (e.g., fig. 283); flagellomere 1 with long to very long setulae (ap. 47) (figs. 191–193); ventral margin of cercus with tuft of fine, short setulae in most species (ap. 193) (fig. 479); most species with comb of long setae in row along ventral lobe of epandrium (ap. 190) (fig. 477); oviscapt usually with several (two or more) ovisensilla pegs on dorsal margin, separated by a gap from one or two large, apical ovisensilla pegs.

TYPE SPECIES: *carinata* Duda.

DISCUSSION: *Hirtodrosophila* is plesio-

morphically excluded from *Drosophila* for the same reason that *Scaptodrosophila* was (see previous discussion). The type species, *carinata* Duda, was designated by Wheeler (1981) because of position precedence (in this case, it was the first of several new species of *Hirtodrosophila* that were described by Duda, and Duda did not designate any type species). Then, when Sturtevant transferred it as a subgenus to genus *Drosophila*, *carinata* Duda (1923) was preoccupied by *Drosophila* (*Drosophila*) *carinata* Grimshaw, 1901. [This name has been suppressed in favor of *Drosophila mercatorum* Patterson and Wheeler, 1942 (Carson et al., 1973).] Thus, when Frota-Pessoa described *D. (Hirtodrosophila) latifrontata* in 1945, which was actually the same species as *carinata* Duda, *latifrontata* became the senior synonym. Now that *Hirtodrosophila* resumes generic status, *carinata* Duda is no longer a synonym of *carinata* Grimshaw, and *latifrontata* is a junior synonym. To add to the confusion, Sturtevant (1942), who originally designated *Hirtodrosophila* as a subgenus of *Drosophila*, mentioned *longecrinita* Duda as the type species. That is incorrect, for, as indicated in Wheeler (1981), the 1923 (p. 42) mention of *longecrinita* has no diagnosis and is, therefore, a nomen nudum (requirement 13a of the Zoological Code). *Hirtodrosophila longecrinita* Duda did not become an available name until 1924, after *Hirtodrosophila* had been used for the first time.

Drosophila duncani had originally been placed in the subgenus *Hirtodrosophila* [by Sturtevant (1942)] because of apomorphy 47 (the presence of long sensilla trichodea on the first flagellomere). However, apart from this feature, *D. duncani* has no other *Hirtodrosophila* features. In fact, this species possesses several *Scaptomyza* genitalia features, such as the row of prensisetae pegs on the proximal half of an elongate surstylus (apomorphy 178, state 2) (the distal half has setal prensisetae).

Genus *Idiomyia*, Revised Status

Idiomyia Grimshaw, 1901: 50 (as genus). Hardy, 1965: 539 (as genus).

Drosophila (pro part): Carson et al., 1967: 1284. Hardy, 1969. Kaneshiro, 1976. Wheeler, 1981: 36.

Antopocerus Hardy, 1965: 42 (as genus). Hardy, 1977 (as subgenus of *Drosophila*). Wheeler, 1981: 36 (as subgenus of *Drosophila*).

Ateledrosophila Hardy, 1965: 62 (as genus). Wheeler, 1981: 72 (as subgenus of *Drosophila*).

DIAGNOSIS: With largest drosophilids in the world, some with wing span of about 2 cm; lacinia with short, spatulate ventral arm, and thin, short dorsal arm (ap. 18-1) (figs. 53-55); spermatheca simple (spherical, with reduced introvert) (ap. 217); most species with interfacetal setula long and thin, with three surrounding each eye facet (ap. 37) (figs. 163-165); oviscapt elongate, rarely without ovisensilla pegs, pegs are small (figs. 522, 534); there are numerous male genitalic features: aedeagus long, narrow, slightly arched, with a short keel-shaped aedeagal apodeme (ap. 157); hypandrium with anterior margin curled ventrad, ventromedial surface with pair of stout setae (ap. 158); paraphyses long, each with prominent apical seta (figs. 432-434) (ap. 159); ventral lobe of epandrium apically truncate, with at least one very long seta near base (fig. 436) (ap. 160); cercus with indistinct row of very long, straight setae along apical margin (fig. 436) (ap. 161); surstylus small, crescentic, and broadly attached to a wide decasternum (ap. 163) (figs. 437, 438).

TYPE SPECIES: *Idiomyia perkinsi* Grimshaw.

INCLUDED TAXA: *Ateledrosophila* (subgenus), *Nudidrosophila* (as subgenus), species formerly as Hawaiian "*Drosophila*," and subgenus *Antopocerus* [formerly as subgenus of *Drosophila* (Wheeler, 1981)].

DISCUSSION: Erection of this genus to include the species heretofore referred to as Hawaiian "*Drosophila*" may meet with opposition by some evolutionary biologists. Firstly, some may suggest that a new name will be a confusing reference for a group already discussed extensively as *Drosophila* in the literature (I have used the name with date precedence). Secondly, evolutionary biologists may find the present theories and hypotheses on the origin and evolution of genus *Idiomyia* sensu lato to be affected by the cladistic results here. I discussed in the introduction why it is biologically and scientifically preferable to have a classification reflecting phylogenetic relationships. To call *Idiomyia* s.l. "*Drosophila*," despite the mor-

phological evidence, would be diluting the diagnosis of the genus *Drosophila*, as a monophyletic group, of biological meaning.

The purpose of this work was not to address relationships among the Hawaiian species, but rather to test their monophyly and to decipher relationships of the group to other, continental drosophilids (it has been the latter goal which has defied taxonomic efforts). The monophyly of major groups of Hawaiian drosophilids has never been in much question, although even here new morphological features have been found which further support this fact. The results of this study agree with those of Kaneshiro (1974, 1976) and Throckmorton (1966, 1975) to the extent that there are two major clades of endemic Hawaiian drosophilids: one being *Scaptomyza*, the other not. Throckmorton and Kaneshiro sometimes applied the names "scaptoid" and "drosophiloid" in referring to these two lineages; these terms should be strictly avoided [-oids, -oidea (pl.), suffices used in superfamily names]. Kaneshiro (1966, 1974, 1976) and I are also in agreement that *Antopocerus*, *Nudidrosophila*, and *Ateledrosophila* should not be given generic rank, but are subjective synonyms of *Idiomyia* s.l. (Kaneshiro's Hawaiian *Drosophila*). This conclusion, however, is for different reasons, stemming in part from Kaneshiro's concept of *Drosophila*.

As stated by Kaneshiro (1976): "It must be shown that one must determine what structures are secondary sexual characters of males, . . . , before selecting various taxonomic characters for the evaluation of major groupings" (p. 256). Does this imply that sexual dimorphisms are worthless taxonomically? This is actually a reaction against placing inflated, phenetic weight on bizarre features, which would artificially elevate the rank of a group. Obviously, even characters considered to be highly adaptive and therefore subject to extreme convergence are also synapomorphic at some level (e.g., wings in birds, bats, and insects; or the modifications of the male foretarsi, used to define the spoon-tarsi and bristle-tarsi groups of *Idiomyia* as monophyletic). Kaneshiro (1969, 1974, 1976) actually synonymized the above four genera with *Drosophila* because "females cannot be distinguished from females of typical *Dro-*

sophila species." Firstly, many features of the females of *Idiomyia* s.l. and *Drosophila* are very distinguishable and exclusive of each other. Secondly, for the meaning of "typical *Drosophila*," one must probably refer to the diagnosis of *Drosophila* in Hardy (1965), the monograph in which the great bulk of Hawaiian "*Drosophila*" were described. That diagnosis included the following: six or more rows of acrostichals; one or more ventral branches of the arista; two pairs of humeral bristles (ap. 100); antennal segment 1 small; antennae not porrect (to exclude *Grimshawomyia*, *Celidosoma*, *Antopocerus*, and *Ateledrosophila*); female ovipositor sclerotized, conspicuous (ap. 211), and "dentate along margins" (ap. 212); male claspers (surstyli) hidden behind ventral lobes of the epandrium and bearing a row of teeth (ap. 163). Some of these features, such as the state of the acrostichals, arista, and antenna, are plesiomorphic at the family level; other features, such as the "ovipositor" (my ap. 211, 212) and humeral (postpronotal lobe) bristles (my ap. 100) are diagnostic for the tribe Drosophilini. With such an inclusive diagnosis of *Drosophila*, it is no surprise that Hawaiian species were described in and continually referred to this genus; by this definition, however, virtually all of the drosophiline genera would also need to be included in *Drosophila*.

In the final, consensus cladogram (fig. 543), *Idiomyia* s.l. is placed close to *Drosophila* (*Dudaica*) and *Drosophila monochaeta*. I am not confident of the homologies for the two features suggesting this relationship [reduction in number of interfrontal setulae (ap. 67) and a reduced, simple spermatheca (ap. 217)]. I would not propose *Dudaica* to be removed from *Drosophila* on these grounds alone, although the bare eyes in these two taxa can be reasonably interpreted to be a plesiomorphic absence instead of a loss. Exact placement of *Drosophila monochaeta* and *D. (Dudaica) senilis* must await more, thoroughly studied specimens. *Idiomyia* s.l. is apparently closely related, however, to the *Hirtodrosophila* genus complex, because of synapomorphy 120. This synapomorphy is a row of cuneiform setae on the mid and hind tarsi, which occurs convergently with that in *Drosophila* (*Siphlodora*) and in the group composed of *Samoaia* + *Phorticella* + *Zapriopus*.

Genus *Drosophila*

Drosophila Fallén, 1823: 4. Wheeler, 1981: 36 (synonymies, nomenclature, world catalog).

TYPE SPECIES: *Musca funebris* Fabricius, 1787 (a common, cosmopolitan species, presumably originally restricted to western Europe).

DIAGNOSIS: Interfacetal setulae (of eye) stout, lanceolate, ribbed, and generally with three setulae in the six corners surrounding each facet (figs. 174–177) (ap. 38). Lacinia with dorsal and ventral arms long, thin (figs. 66–68) (ap. 20); vibrissae in two pairs of equal or very similar size (fig. 302, 309) (ap. 94), but lost in some species of subgenus *Drosophila*; ventral to the two katepisternal setae and between them is a group/row of fine setulae (ap. 102); carina always present, and usually broad (ap. 90) (figs. 299, 300, 302, 303, 309).

DISCUSSION: Being removed from the genus *Drosophila* are the subgenera *Scaptodrosophila*, *Hirtodrosophila*, *Antopocerus*, other Hawaiian species previously referred to *Drosophila* (see discussions above), and *Engiscaptomyza* and *Lordiphosa* (see below). Although the cladogram in figure 545 indicates the *Drosophila flavopilosa* species group as being more closely related to *Scaptomyza*, it is still probably more judicious not to remove this group from *Drosophila*. Removing the taxa listed above would make the remaining species in *Drosophila*, which possess the features in the diagnosis, a monophyletic group. Traditionally, the genus has been a taxonomic “catchall”: groups or species without distinctive features, among others, were placed by default in *Drosophila*. Witness, in virtually any regional key to drosophilid genera, how the genus *Drosophila* is split up among several couplets (bearing in mind, too, that keys are not constructed to reflect relationships). A traditional diagnosis of *Drosophila* was given by Wheeler and Takada (1964), and adopted by Bock (1976). Unfortunately, most of those diagnostic features are plesiomorphic at the generic or higher level (see discussion under *Idiomyia* s.l.).

Sturtevant’s (1939) classification of *Drosophila* subgenera was greatly expanded upon later (Sturtevant, 1942) and is the classification most generally used. He recognized six

subgenera: *Hirtodrosophila*, *Pholadoris* (= *Scaptodrosophila*), *Dorsilopha*, *Phloridosa*, *Sophophora*, and *Drosophila*. Okada (1989) placed *Drosophila* most closely to *Zaprionus*, on the basis of dense eye “pile” (which, as shown previously, is plesiomorphic at the generic level for these taxa, or apomorphic at the tribal level). Both of these genera were placed close to *Neorhinoleucophenga*, for which no characters were proposed (Okada, 1989). The relationships of subgenus *Chusqueophila* Brncic and *Psilodorha* Okada, which I have not examined, remain to be determined. A definitive, comprehensive study on relationships of subgenera and species groups in *Drosophila* remains to be done, and compared to Throckmorton’s (1962, 1975) results, discussed earlier.

STYLOPTERA GENUS GROUP

DIAGNOSIS: Anterior reclinate seta lies just lateral to or slightly anterolateral to proclinate (fig. 260) (ap. 68-1), or is very reduced (fig. 206); pair of anterior dorsocentral setae very far anterior (ap. 105); distiphallus bulbous, apically narrowed, with small dorsal knob (figs. 442, 448, 449) (ap. 170); hypandrium short; surstylus generally with single row of short, peglike prenisetae (figs. 441, 444, 446, 447, 450, 451) (ap. 171).

INCLUDED TAXA: *Jeannelopsis*, *Styloptera*, *Dettopsomyia*, *Tambourella*, *Mulgravea*, *Sphaerogastrella*, *Hypselothyrea*, and *Liodrosophila*.

DISCUSSION: This is a very distinctive assemblage and obviously monophyletic group, the great majority of the taxonomic work having been done by Toyohi Okada. As seen in the final cladogram (fig. 544), the following are relationships proposed within the genus group: ({{({{(Hypselothyrea + Liodrosophila) + Sphaerogastrella) + Mulgravea} + Tambourella) + Dettopsomyia] + Styloptera} + Jeannelopsis). According to Okada’s (1989) hypothesis, he also included most of these genera into one group (but not *Styloptera*, *Dettopsomyia*, and *Jeannelopsis*; including instead *Paraliodrosophila* and *Lissocephala*—see my previous discussions on the placement of these genera). However, Okada’s diagnostic features (his characters C and L) are plesiomorphic at the family level: ocellar se-

tae inside the ocellar triangle (C) and second costal (subcostal) break shallow (L). Evidently, there are other characters of which Okada is aware for this group that were not described or mentioned. Figure 552 is a summary of Okada's 1989 hypothesis compared with three other hypotheses (Okada, 1974, 1980, 1985).

My hypothesis here is in agreement with that of Okada (1974) in that *Sphaerogastrella* and *Liodrosophila* are very closely related (to which I would add *Hypselothyrea*). The hypotheses of Okada (1980, 1985), that the genus pairs *Hypselothyrea* + *Tambourella* and *Lissocephala* + *Mulgravea*, respectively, are very closely related, are not at all in agreement with the present work (cladogram, fig. 544). It is apparent that the group of small Indo-Pacific genera, including at least *Tambourella*, *Mulgravea*, *Sphaerogastrella*, *Hypselothyrea*, and *Liodrosophila*, is inflated in rank. Pending a revision of the entire group, it may be useful to eventually synonymize all the genera under one, in order to make the one genus cladistically more equivalent (e.g., at a similar phylogenetic level) to other genera.

DICLADOCHAETA GENUS GROUP

DIAGNOSIS: Distinguished by two features: the loss of the two humeral setae (ap. 100), and loss of ovisensilla pegs on the oviscapt (the oviscapt has only trichoid ovisensilla) (ap. 212).

INCLUDED TAXA: *Dicladochaeta*, *Calodrosophila*, *Microdrosophila*.

ZAPRIONUS GENUS GROUP

DIAGNOSIS: Facial carina broad, extended to oral margin, prominent, and rounded on edge (fig. 288) (ap. 86); mid and hind tarsi each with row of cuneiform setae along medial surface (fig. 369) (ap. 120) (convergent with *Hirtodrosophila* genus complex); *Zaprionus* + *Phorticella* share, as well, a prominent and bulbous clypeus (figs. 288, 289) (ap. 92), a velvety notum with one or more pairs of longitudinal vittae (ap. 107), and an epanthrium devoid of setae except for on the ventral lobes (fig. 397) (ap. 177).

INCLUDED TAXA: *Samoaia*, *Phorticella*, *Zaprionus*.

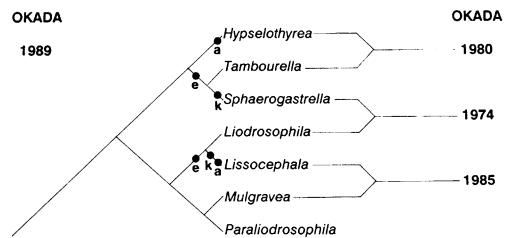


Fig. 552. Comparison of hypotheses of relationships among a group of Old World tropical genera, according to Okada.

SCAPTOMYZA GENUS GROUP

DIAGNOSIS: Acrostichal setulae anterior to and in line with dorsocentral setae are thicker and up to twice the length of other acrostichals (ap. 101).

INCLUDED TAXA: *Nesiodrosophila*, *Grimshawomyia*, *Celidosoma*, *Marquesia*, *Scaptomyza*, genus *Lordiphosa* (new rank).

CELIDOSOMA GENUS SUBGROUP

DIAGNOSIS: Pedicel with ventral margin oblique, the anterior surface being longer than the posterior (attached) surface (fig. 243) (ap. 42); base of arista (flagellomere 2) well below ventral margin of pedicel.

INCLUDED TAXA: *Celidosoma*, *Grimshawomyia*.

SCAPTOMYZA GENUS SUBGROUP

DIAGNOSIS: Postgena in lateral view is thicker than cheek or gena (figs. 247–250) (ap. 11); interfrontal setulae reduced to two to six (ap. 67); paraphyses developed into pair of long, sclerotized lobes (figs. 464, 474) (ap. 196-1).

TYPE GENUS: *Scaptomyza*.

INCLUDED TAXA: Genus *Lordiphosa* (new rank), *Scaptomyza*.

Genus *Lordiphosa*, New Rank

Lordiphosa Basden, 1961: 186 (as subgenus of *Drosophila*).

TYPE SPECIES: *fenestrarum* Fallén.

DIAGNOSIS: Basden gave the following as some of the features diagnostic of *Lordiphosa*: carina small, on upper part of face; three katepisternal setae; acrostichals in four

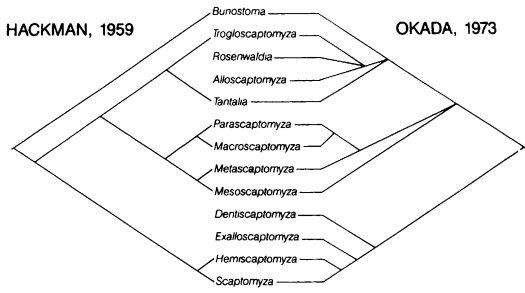


Fig. 553. Comparison of hypotheses of phylogenetic relationships among subgenera of *Scaptomyza*.

rows (sometimes six irregular rows); one to two enlarged presutural dorsocentral setae. In addition are the following genitalic features: gonites (male) large, bent mediad, jointed or nearly jointed at their ends; paraphyses long, clublike, immediately flanking aedeagus, and with densely microsetulose apex; aedeagus pointed, much shorter than aedeagal apodeme, with densely scaled dorsal flap (fig. 465).

DISCUSSION: *Lordiphosa* presently includes 13 species; all except for *basdeni* Wheeler (Michigan, Ohio) are Old World, principally Palearctic. Basden split the subgenus into two species groups based on male genitalia, but gave no male genitalic characters as diagnostic for the subgenus. Lastovka and Macá (1978) revised the taxonomy of *Lordiphosa*. With their survey of genitalia done, it has been possible to provide the genitalic diagnoses given above. Those authors hypothesized *Lordiphosa* as being most closely related to subgenus *Sophophora* of *Drosophila*, based on "characters of the [male] terminalia, antennae, carina, and pigmentation of the abdomen." Hackman (1982) stated that *Lordiphosa* is most closely related to *Scaptomyza*, in particular to the subgenus *Bunostoma* (this was one reason why he felt *Scaptomyza* to be paraphyletic), and he presented about 12 characters in support of his hypothesis. The hypothesis in the present paper agrees most with Hackman's, that *Lordiphosa* is indeed closely related to the genus *Scaptomyza*, but not necessarily specifically with the subgenus *Bunostoma*.

Features in support of the *Lordiphosa* + *Scaptomyza* relationship are the following: postocular part of gena thick (ap. 11) (figs.

247–249); interfrontal setulae reduced to two to six (ap. 67); acrostichals generally reduced to four rows (ap. 98) (the ground plan state—two rows and six rows exists in some species); acrostichals in front of dorsocentrals enlarged (ap. 101); tergite VII in males present (ap. -125) (figs. 383, 385); epandrium bare (ap. 177); prenisetae in short row on surstylus, especially when only on proximal half of surstylus (ap. 178-2); paraphyses elongate, sclerotized (ap. 196-1) (fig. 465).

Genus *Scaptomyza*

Scaptomyza Hardy, 1849: 361. Wheeler, 1981 (synonyms, world catalog, subgeneric classification). Hackman, 1982 (subgeneric relationships).

TYPE SPECIES: *graminum* Fallén.

DIAGNOSIS: Among the drosophilids (e.g., *Lordiphosa*) with a bare epandrium (ap. 177), thick postgena (ap. 11), interfrontal setulae reduced to two to six (ap. 67), and long, sclerotized paraphyses, the following features are restricted solely to the genus *Scaptomyza*: apex of palp with two to three stout setae (ap. 35); anterior reclinate lateral to or slightly anterolateral to proclinate (ap. 68); anterior dorsocentral setae very far anterior (ap. 105) (distance between transverse suture and anterior dorsocentral less than the distance between the anterior and posterior dorsocentral); ventral lobe of epandrium long (ap. 176) (fig. 476), with long setae at or near the apex; surstylus with single row of peglike prenisetae, usually on dorsal (proximal) half (figs. 452–464) (ap. 200).

DISCUSSION: It was not intended in this study to address the relationships among subgenera of *Scaptomyza*. Rather, it was to test Hackman's (1982) claim that the genus is paraphyletic, and to place it into a context with other monophyletic genera. As can be seen from the diagnosis and the cladogram (fig. 545), the present composition of species in the genus (e.g., Wheeler, 1981, 1986) appears to be a monophyletic group. However, hypotheses of relationships within this large genus and between it and other genera differ, and deserve comment.

Hackman (1959, 1982) has given the most extensive treatment of *Scaptomyza* relationships, which is compared to that of Okada

(1973) (fig. 553). First, concerning Hackman's results: we differ mostly in the position of subgenus *Bunostoma* (it is the sister group to the rest of *Scaptomyza* according to Hackman, and perhaps *Lordiphosa* as well, but the subgenus *Scaptomyza* takes that position in my scheme). Hackman and I do agree on some very fundamental aspects of *Scaptomyza*. First, we both maintain (e.g., Hackman, 1955, 1982) that *Lordiphosa* is closely related to *Scaptomyza*, and is not a subgenus of *Drosophila* (see discussion above). Also, the subgenus *Euscaptomyza* Séguéy is "distinctly different from *Scaptomyza* s. lat." (Hackman, 1959: 5). I concur with Hackman (1959) at least in concluding that *Marquesia* and *Scaptomyza* are close relatives (he suggests them to be synonymous). In addition, Hackman (1982) maintains, as do I, that the Hawaiian subgenus *Drosophila* (*Engiscaptomyza*) Kaneshiro is closely related to *Scaptomyza*, not *Drosophila*. *Engiscaptomyza* should eventually be elevated to generic status. It was the apparent intermediacy of *Engiscaptomyza* with respect to *Drosophila* and *Scaptomyza* that forced Throckmorton to conclude that the boundaries between *Scaptomyza* and *Drosophila* were indistinct in Hawaii, and he even concluded that *Scaptomyza* originated in Hawaii, to subsequently colonize the world. Hackman and I further agree that the Hawaiian species of *Scaptomyza* are not a monophyletic group. This is at variance with Okada (1973) (fig. 553), who linked all of the Hawaiian *Scaptomyza* into a monophyletic group, with the exception of the subgenus *Exalloscaptomyza*. [This subgenus was not examined by me, but Hackman (1982) indicated that *Exalloscaptomyza* "may be a strongly differentiated off-shoot of the scaptomyzoid [endemic Hawaiian *Scaptomyza*]

branch".] Hackman did not address the question of possible relationships of the Hawaiian endemic genus *Titanochaeta* to *Scaptomyza*.

In the cladogram (fig. 542), *Titanochaeta* occupies a very plesiomorphic position, at the base of the Drosophilinae. Hardy (1965) gave descriptions of all of the species in the genus, including a generic diagnosis, and concluded that *Titanochaeta* was intermediate between endemic Hawaiian "*Drosophila*" (*Idiomyia* s.l.) and *Scaptomyza*. It is indeed an enigmatic group of flies, both for their morphological reductions as well as their highly derived tastes as larval predators of spider embryos. The male genitalia, spermathecae, and even the posterior cibarial sensilla are highly reduced. The long, thin, dense interfacetal setulae (fig. 164) would indicate a relationship in or near *Idiomyia* s.l., not with one of the Hawaiian *Scaptomyza* groups. As well, the long interfrontal setulae are similar to those of *Idiomyia* (*Ateledrosophila*). However, the reduced number and size of arisal branches, the long orbitals (fig. 245), and proximity of the anterior reclinate to the proclinate orbital (fig. 245) all suggest a close relationship to *Scaptomyza*. I am skeptical that *Titanochaeta* is a primitive drosophiline, but rather suspect it is most closely related to *Idiomyia* s.l.

GENERA INCERTAE SEDIS

With the exception of the amber fossil, *Miomyia*, I did not place the following genera. Most are represented by types or very few specimens in foreign collections: *Apacrochaeta*, *Balara*, *Drosophila* (*Chusqueophila*), *Miomyia*, *Pyrogometopa*, *Soederbomia*, *Sphyrnoceps*.

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APPENDIX 1

CHARACTER STATE MATRIX FOR GENERA OF THE DROSOPHILIDAE

Arrangement of genera is alphabetical, using nomenclature in Wheeler (1981; 1986). For each taxon entry, the first character is number 0, the last is 218. Those taxa marked with an asterisk (*) were used in the HENNIG-86 analysis; those with a cross (+) are amber fossil taxa.

**Acletoxenus indicus* Malloch:

1011110000 0000000000 0000101000 0000000000 0000100000 0000000000 0010000000 0000020000 0000000000 0000000020 0000001000 0000100000
0010111000 0000001100 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 000001?100 00000000

**Amiota (Amiota) humeralis* Loew:

1011100101 1000000000 0001101020 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000010 0000000000 0000010000
1000111000 0000000000 0000000000 0111011000 0000000000 0000000000 0000000000 0000000000 000000??00 0???0000

Amiota (Amiota) leucostoma Loew:

1011100101 1000000000 0001101020 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000010000
1000111000 0000000000 0000000000 0111011000 0000000000 0000000000 0000000000 0000000000 000000??00 0???0000

**Amiota (Phortica) variegata* (Fallén):

1010100101 1000???0?? ?00?10???? ????000000 0000000000 0000010000 0000000000 0000000000 0000000000 0100000020 0000100000 0000010000
1000111000 0000000000 0000000000 0110100000 0000000000 0000000000 0000000000 0000000000 000000??00 0?000000

Amiota (Phortica) sp.:

10?0100101 1000???0?? ?00?10???? ????000000 0000000000 0000010000 0000000000 0000000000 0000000000 0100000020 0000100000 0000010000
1000111000 0000000000 0000000000 0110100000 0000000000 0000000000 0000000000 0000000000 000000??00 0?000000

**Amiota (Sinophthalmus) picta* (Coquillett):

10?0100101 1000000000 0001100020 0000000000 0000100000 0000010000 0000000000 0000000000 0000100000 0100000020 0000100000 0000010000
1000111000 0000000000 0000000000 0110000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000

**Apenhacia crassiseta* (Hackman):

101?100100 1000000000 0001100020 0000000000 0000100000 0000010000 0000000000 0000000000 0000100000 0100000030 0000100000 0000010000
1000111000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001000 0000000000

**Ateledrosophila preapicula* Hardy:

10???0000? 0010??0?? ?00?0???? ?1?0000100 0011000000 0000100000 0000001000 0000000000 0000000000 0000020030 1000000000 0000100000
1000?0?000 0000000000 0000000000 0000000111 11?1000000 0000000000 0000000000 0000000000 100000?100 01100000

**Baeodrosophila pubescens* Wheeler & Takada:

1010000010 0000000000 0010001000 000000001? 0000100000 0000100010 ?000?00000 0000000000 0000000000 1000020031 10?1000000 0001100?00
0000110000 0000000000 0000000000 0000000000 0000000000 0000100000 0000000000 0000001100 1000001100 01000000

**Cacoxenus (Gitonides) perspicax* (Knab):

1000100001 1000000000 0000001020 0000000000 0000100000 0000010000 0001000000 0000000000 0000020000 0000000020 0000100000 0000000000
0000111000 0000000000 0000000001 1000000000 0000000000 0000000000 0000000000 0000000000 0000001000 0000000000

**Cacoxenus (Paracacoxenus) guttatus* (Hardy & Wheeler):

1000100001 1000???0?? ?00?10???? ????000000 0000100000 0000010000 0000000000 0000020000 0000000020 0000100000 0000000000
0000111000 0000000000 0000000001 1000000000 0000000000 0000000000 0000000000 0000000000 000000?000 00000000

**Calodrosophila phalerosa* Wheeler and Takada:

1010100000 00001100?1 0000002000 010000001? 0000000000 0000100000 ?000?001?0 2000000000 0000000000 0000020151 00?0000000 0000100?00
000011?000 0000000000 0000?00000 0000000000 0000000000 0000000000 0000000000 0000000000 000000???? ????0000

**Celidosoma nigrocincta* Hardy:

10???00000 0010??0?? ?00?00???? ????00001? 0011000000 0000100000 0000000100 0000000000 0000000000 0000020040 1110000000 0000100000
0000??0000 0000000000 0000000000 0000000??? ????000000 0000000000 0000000000 0000000000 0000000100 00000000

**Chymomyza amoena* (Loew):

1010000000 0000100000 0000013001 2100000000 0000000000 0000100000 0000000020 0000000000 0000000000 0000020041 0010000000 0000100000
0000000000 0000000000 0000011100 0000000000 0000000000 0000000000 0000000000 0000001000 1000001100 01000000

**Cladochaeta inversa* (Walker):

1010000000 0000000001 00000000?0 0000001000 0000000000 0000100000 0000000010 0000000000 0000000000 0000020031 1000000000 0001100000
0000110000 0000000000 1111100000 0000000000 0000000000 0000000000 0000000000 0000002000 0000001100 00000000

Cladochaeta nebulosa (Coquillett):

1010000000 0000000001 000000?0?? ????0001000 0000000000 1000100000 0000000010 0000000000 0000000000 0000020031 0000000000 0001100000
0000??0000 0000000000 1111100000 0000000000 0000000000 0000000000 0000000000 0000002000 0000001100 00000000

**Colocasiomyia stamenicola* (Carson & Okada):

1010000000 0010000000 0010000010 0000000000 0000100000 0000100000 ?00?000000 0000000000 0000000000 1000020041 1000000000 0000100?00
0000??0000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 01000000

**Dettopsomyia formosa* Lamb:

1010000000 0011171?? ?007001?0? 0100000011 0000000000 0110100000 0000000110 1000000000 1000000200 0000020051 0000010000 0100100000
0000??7000 0000000000 0000000000 0000000000 0000000000 1100000000 0000000000 0000000000 1000001100 01100000

**Diathoneura metallica* (Sturtevant):

1010000000 1000000001 0000000?11 2000001000 0000000000 0000100000 00000001?0 1000000000 0000000000 0000021131 0000000000 0001100000
0000110000 0000000002 0010000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000002000 1000001100 01110000

Diathoneura opaca (Williston):

1010000000 1000000001 0000001111 2000001000 0000000000 0000100000 00000001?0 1000000000 0000000000 0000020141 1000000000 0001100000
0000110000 0000000011 0010000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000022000 1000001100 01110000

**Dieladochaeta biseriata* Malloch:

1010000000 0110??70?? ?10?01???? ???0000011 0000000000 1000100000 0000000100 0000000000 0000000000 0000120051 0100000000 0000100000
0000??7000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 100000?100 01000000

**Drosophila (Antopocerus) adunca* (Hardy):

1011000000 0110110020 0000011000 0100000100 0000010000 0000101000 0000000000 0000000000 0000000000 0000020030 1110000000 0000100000
1000110000 0000000000 0000000000 0000000111 11?1000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Antopocerus) longiseta Grimshaw:

1011000000 0110??70?? ?00?01???? ???0000100 0000010000 0000101000 0000000000 0000000000 0000000000 0000020030 1110000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Dichaetophora) a berans* Lamb:

1010000000 0000??70?? ?00?0????? ???0000010 0000000000 0000100000 0000000000 0000000000 0000000000 0000020031 1011000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 1100000100 0000000000 0000000000 1000001100 01110000

**Drosophila (Dorsilopha) busckii* Coquillett:

1010000000 0010100000 0000001000 0100000011 0000000010 0000100000 0000000010 0000000000 0000000000 0000120031 1000000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1100001100 01100000

**Drosophila (Drosophila) achlya* Hardy:

1010000000 0010??70?? ?00?00???? ???0000000 0000000000 0000100000 0000000000 0000000000 0000000000 0000020031 1010000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) adiantola* Hardy:

1011000000 0100??70?? ?10?01???? ???0100000 0000000000 0000100000 0000000000 0000000000 0000000000 0000020030 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) araiotrichia* Hardy:

1010000000 0010??72?? ?00?00???? ???0100000 0000000000 0000100000 0000000110 0000000000 0000000000 0000020031 1000000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 100000?100 01100001

**Drosophila (Drosophila) atroscutellata* Hardy:

1011000000 00101??0?? 010?011??? ???0000100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) attigua* Hardy & Kaneshiro:

1011000000 0110??70?? ?00?01???? ???0000100 0000000000 0000100000 0000000000 0000000000 0000000000 0000020030 1110000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) basimacula* Hardy:

1010000000 0010110020 0000001000 0100000100 0000000000 0000100000 0000000000 0000000000 0000000000 0000020030 1000000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) bipoliata* Hardy:

1010000000 0000??70?? ?00?01???? ???0000000 0000000000 0000100000 0000000110 0000000000 0000000000 0000020031 1000000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

**Drosophila (Drosophila) calloptera* Schiner:

1010000000 0000110000 2000001000 0100000010 0000000000 0000100000 0000000100 0000000000 0000000000 1000120031 1110000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1100001100 01100000

**Drosophila (Drosophila) cardini* Sturtevant:

1010000000 0000110000 ?000001000 0100000010 0000000000 0000100000 0000000100 0000000000 0000000000 1000120031 1000000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 01100000

**Drosophila (Drosophila) colorata* Walker:

1010000000 0010110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000020031 1110000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1111101100 01100000

**Drosophila (Drosophila) crucigera* Grimshaw:

1111000000 00101??020 0000011000 0100000100 0000000000 0001100000 0000000000 0000000000 0000000000 0000020031 1110000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) dissita Hardy:

1010000000 0010110020 0100001000 0100000100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020030 1000000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) engyochracea Hardy:

1011000000 0110110020 0100011000 0100000100 0000000000 0001100000 0000000000 0000000000 0000000000 0000020031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) flavopilosa Frey:

1010000000 0010??0?? ?00?01???? ???0000010 0000000000 0000100000 0000000000 0000000000 0000000000 1000020041 1100000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1010101100 01100000

Drosophila (Drosophila) funebris (Fabricius):

1010000000 0010100000 1000001000 010000001? 0000000000 0000100000 0000000000 0000000000 0000000000 1000120021 1110000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000010000 1000001100 01100000

Drosophila (Drosophila) fungiperda Hardy:

1110000000 0000110020 010000?000 0100000100 0000000000 0000100000 0000000000 0000000000 0000000000 0000120031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 11?1000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) hanaulae Hardy:

1011000000 0110??2?? ?00?01???? ???0000100 0000010000 0000100000 0000000000 0000000000 0000000000 0000120040 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) hirtitarsus Hardy:

1010000000 0010??2?? ?00?01???? ???0000100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) hydei Sturtevant:

1010000000 0010100000 2100011000 010000001? 0000000000 0000100000 0000000000 0000000000 0000000000 2000020031 1010000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1010001100 01100000

Drosophila (Drosophila) immigrans Sturtevant:

1110000000 0010110000 2000001000 010000001? 0000000000 0000100000 0000000000 0000000000 0000001000 0000120021 1010000000 0000100010
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 1010001100 01100000

Drosophila (Drosophila) melanica Sturtevant:

1010000000 00001?0?? ?00?001??? ???0000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000020030 1000000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1010001100 01100000

Drosophila (Drosophila) melanoloma Hardy:

1010000000 0000??0?? ?10?01???? ???0000100 0000000000 0000100000 0000000110 0000000000 0000000000 0000020031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1111000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) mimica Hardy:

1011000000 0010??2?? ?10?01???? ???0100100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020021 1000000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) monochaeta Sturtevant:

1110000000 00001?0?? ?00?001??? ???0000000 0000000000 0000100000 0000000100 0000000000 0000001000 0010021021 1010000000 0000100010
1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1010101100 11100001

Drosophila (Drosophila) perissopoda Hardy:

1010000000 0010110020 0100011000 0100000100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020030 1000000000 0000100000
1000??000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01110001

Drosophila (Drosophila) primaeva Hardy & Kaneshiro:

1011000000 0110??0?? ?00?01???? ???00000100 0000000000 0000100000 0000000000 0000000000 0000000000 0000020030 1010000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) quinaria Loew:

1010000000 0010110000 20000?0?? ???0000010 0000000000 0000100000 0000000000 0000000000 0000000000 1000120031 1010000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 1010001100 01100000

Drosophila (Drosophila) repleta Woollaston:

1010000000 0010110000 2000001000 010000001? 0000000000 0000100000 0000000000 0000000000 0000000000 2000020021 2000000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1011001100 01100000

Drosophila (Drosophila) scolostoma Hardy:

1011000000 0110??2?? ?10?01???? ???0100100 0000000000 0000100000 0000000010 0000000000 0000000000 0000020021 0110000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) spectabilis Hardy:

1011000000 0110110020 0100011000 0100000100 0000000000 0000100000 0000000000 0000000000 0000000000 0000020031 1100000000 0000100000
1000110000 0000000000 0000000000 0000000111 1101000000 0000000000 0000000000 0000000000 1000001100 01100001

Drosophila (Drosophila) testacea Roser:

1010000000 0010110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 1000120031 1010000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 1010101100 01100000

Drosophila (Drosophila) tripunctata Loew:

1010000000 0010110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 1000120031 1010000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 1010101100 01100000

Drosophila (Drosophila) virilis Sturtevant:

1011000000 0010110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000120030 1110000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000010 1111001100 01100000

Drosophila (Dudaica) senilis Duda:

10?00000?0 7000??0?? 700?01?? 7??0000000 0000000000 0000100000 7000?00110 0000000000 0000001000 0010020031 1010000000 0000100?00
0000110000 0000000000 0000000000 0000000000 0000000000 100000?000 0000000000 0000000000 0000000000 101000???? ????????

Drosophila (Engiscaptomyza) crassifemur Grimshaw:

1011000000 0010110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0010000000 0000020031 1110000000 0000100000
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 01000000

Drosophila (Engiscaptomyza) nasalis Grimshaw:

1011000000 0010100020 0000001000 010000001? 0000000000 1000100000 0000000010 0000000000 0010000000 0000020031 1110000000 0000100000
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 01000000

Drosophila (Hirtodrosophila) sp. A:

1010000000 0000??0?? 700?01?? 7??000001? 0000000101 0000100000 0000000100 0000000000 0001000000 0000020041 1000000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1001000000 1000001130 01100000

Drosophila (Hirtodrosophila) sp. B:

1010000000 0000??0?? 700?01?? 7??0000010 0000000101 0000100000 0000000000 0000000000 0000000000 0000020031 1000000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1001100000 1000001120 01000000

Drosophila (Hirtodrosophila) duncani Sturtevant:

1010000000 0000100000 2000001000 0100000010 1000000101 0000100000 0000000010 0000000000 0010000000 0000020031 1000000000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0000000020 0000000000 1001000000 1000001100 01100000

Drosophila (Hirtodrosophila) nigrohalterata Duda:

1010000000 0000??0?? 2000001000 0110000010 0000000101 0000100000 0000000010 0000000000 0010000000 0000020031 1000000000 0000100000
1000?0000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1001000000 1000001130 01100000

Drosophila (Lordiphosa) fenestrarum Fallén:

1010000000 0110100000 0000001100 010000001? 0000000000 0000100000 0000000100 0000000000 0000000000 0000020041 1110000000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000002000 1000001100 01100000

Drosophila (Phloridosia) floricola Sturtevant:

1010000000 0000101010 0010000000 0101000010 0000001000 0000100000 0000000000 0000000000 0000000000 1000020031 1000000000 0000100100
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 1100001100 01100000

Drosophila (Phloridosia) luzii Sturtevant:

1010000000 0000101010 0010000000 0101000010 0000001000 0000100000 0000000000 0000000000 0000000000 1000020031 1000000000 0000100100
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 1100001100 01100000

Drosophila (Scaptodrosophila) lurida Walker:

1011000001 1000110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000000010 2000000000 0000100000
1000111000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 1110101100 01100000

Drosophila (Scaptodrosophila) scaptomyzoidea (Duda):

1010000000 0000000000 0000002000 0100000000 0000000000 0000100000 0000000010 0000000000 0000000000 0000000031 1010000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001100 01000000

Drosophila (Siphodora) flexa Loew:

1010000000 0000110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000010031 1010000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1100101100 01000000

Drosophila (Siphodora) sigmoides Loew:

1010000000 0000110000 2000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0000000000 2000010031 1010000000 0000100000
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1100101100 01000000

Drosophila (Sophophora) affinis Sturtevant:

1010000000 0000??0?? 700?01?? 7??0000010 0000000000 0000100000 0000000010 0000000000 0010000000 0000020031 1010000000 0000100000
0100100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001100 1100001100 01100000

Drosophila (Sophophora) melanogaster Meigen:

1010000000 0000000000 1000001000 0100000010 0000000000 0000100000 0000000010 0000000000 0000000000 1000120031 1010000000 0000100000
0100100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001100 1100001100 01100000

**Drosophila (Sophophora) takahashii* Sturtevant:

1010000000 0000000000 1000110000 0100000010 0000000000 0000100000 0000000000 0000000000 0010000000 0000120031 1010000000 0000100000
0100100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001100 1100001100 01100000

**Drosophila (Spinodrosophila) nigrosparisa* Strobl:

1111000000 1110000000 0000001000 010000001? 0000000000 1000100000 ?00?00000 0000000000 0000000000 2000020031 0000000000 0000100?00
0000100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000010001 1111101100 01100000

**Drosophila superba* Sturtevant:

1110000000 1000000001 0000100101 2000001000 0000000000 0000100000 0000000100 0000000000 0000000000 0000020021 0000000000 0001100000
0000000000 0000000013 0110000000 0000000000 0000000000 0000000000 0000000000 0000002000 100000?7100 00000000

**Drosophila xiphophora* Pipkin:

1010000000 0000??0?? ?00?01?0?? ???0000000 0000000000 0000100001 0000000000 0000000000 0000000010 0000020011 1000000000 0000100100
1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001101 00100000

Electrophorica succini Hennig+

????????? ?00??70?? ?00?00? ???0000000 0000100000 0000?00000 000?00?00 0000000000 0000000000 0000000020 0000000000 0000000?0?
?000? ????? ? ????? ? ????? ? ????? ? ????? ? ????? ? ????? ? ????? ?

**Eostegana ortalidoides* (Walker):

1001101000 0000??00? ?00010???? ???0000000 0000000000 0000000000 0000210000 0000000000 0100000000 0000000011 0000000000 0000000001
0001111001 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00000010

**Gitona bivaualis* Patterson:

1000100001 1000000000 0000100020 0000000000 0000000000 0000000000 0001000000 0000000000 0000010000 0000000020 0000100000 0000100000
0000111000 0000011100 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001000 00000000

Gitona brasiliensis Lima:

1000100001 1000??0?? ?00?10???? ???0000000 0000100000 0000000000 0001000000 0000000000 0000010000 0000000030 0000100000 0000100000
0000111000 0000011100 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001000 00000000

**Gitona distigma* Meigen:

1000100001 1000000000 0000100020 0000000000 0000100000 0000000000 0001000000 0000000000 0000020000 0000000020 0000100000 0000100000
0000111000 0000011100 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000001000 00000000

**Grimshawomyia palata* Hardy:

1010000000 0000??0?? ?00?00? ???0000010 0011000000 0000100000 0000000000 0000000000 0000000000 0000020030 0110000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 100000?7100 01100000

**Hypselothyrea (H.) guttata* Duda:

1010000000 000110200 ?000011000 0100000000 0100000000 0100100100 0000000100 2000000000 0000000200 0000021151 0000010000 0002100000
0000110000 0000000000 0000000000 0000000000 0000000000 1100000000 0000000000 0000000000 1000001100 01101000

**Jeannelopsis* sp:

1010000000 0000110000 0000000000 010000001? 0000000000 0000100000 0000000110 0000000000 0000000000 0000020041 1000010000 1000100000
0000100000 0000000000 0000000000 0000000000 0000011100 1100000000 0000000000 0000000000 1000001100 01110000

**Laccodrosophila flavescens* Wheeler:

1010000000 0000000000 0000000000 0100000000 0000000000 1000100001 0000000000 0100000001 0000000020 0000000001 1100000000 0000100100
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 ?000001101 01100000

Leucophenga (L.) maculosa (Coquillett):

1000101000 1000??0?? ?00?00? ???0000000 0000000000 0000000000 0000000001 0000000000 0000000000 0000000040 1000000001 0000100001
0000111000 1111100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00000100

Leucophenga (L.) regina Malloch:

1000101000 1000??0?? ?00?00? ???0000000 0000000000 0000000000 0000000001 0000000000 0000000000 0000000030 0000000001 0000100001
0000111000 1111100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00000100

**Leucophenga (L.) scutellata* Malloch:

1100101000 1000000000 0000000020 0000000000 0000000000 0000000000 0000000001 0000000000 0000000000 0000000020 1100000001 0000100001
0000111000 1111100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 000000?000 00000100

**Leucophenga (L.) varia* (Walker):

1000101000 1000000000 0000000020 0000000000 0000000000 0000000000 0000000001 0000000000 0000000000 0000000020 0000000001 0000100001
0000111000 1111100000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00000100

**Liodrosophila onchopyga* Okada:

1010000000 00001??2? ?00?011??? ?1?0000000 0100000000 0100100100 0000000100 2000000000 0000000200 0000021151 1010000000 0001100000
0000??7000 0000000000 0000000000 0000000000 0000000020 1100000000 0000000000 0000000000 1000001100 01111000

**Lissocephala sabroskyi* Wheeler & Takada:

1010000000 0000000000 0000003001 0100000000 0100000000 0000100010 0000000000 1000000000 0010000100 0000021120 1000000000 0001100000
0000110000 0000000000 0000000000 0000000000 0000000020 0000000000 0000000000 0000000000 0000001100 01100000

**Scaptomyza (Alloscaptomyza) muica* Hardy:

1010000000 0010000000 0000000000 010000001? 0000000000 0000100000 0000000110 0000000000 0000000000 0000020051 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 00001011?0 0000010000 0000001000 ?000001100 00000000

Scaptomyza (Alloscaptomyza) stramineifrons Hackman:

1010000000 0000???0?? ?00?00???? ?1?0000010 0000000000 0000100000 0000000110 0000000000 0011000000 0000020041 0100010000 0000100000
0000???000 0000000000 0000000000 0000000000 0000000000 00011121?0 0010010000 0000001000 ?000001100 00000000

Scaptomyza (Bunostoma) anomala Hardy:

1010000000 0000???1?? ?00?00???? ?1?000001? 0000000000 0000100000 0000000110 0000100000 0013000000 0000120051 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000111100 0000000110 0000001000 0000001100 01000000

**Scaptomyza (Bunostoma) australis* Malloch:

1010000000 0010100200 0000001000 0100000010 0000000000 0000100000 0000000110 0000000000 0013000000 0000120051 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0001112100 10100001?0 0000001000 0000001100 00000000

**Scaptomyza (Bunostoma) flavifacies* (Malloch):

1010000000 0000???2?? ?00?0000?? ?1?0000010 0000000000 0000100000 0000000110 0000000000 0013000000 0000020051 0100010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0001112120 0010000000 0000001000 1000001100 01100000

Scaptomyza (Bunostoma) palmae Hardy:

1010000000 0000100100 0000002000 0100000010 0000000000 0000100000 0000000110 0000100000 0013000000 0000120041 0000010000 0000100000
0000???000 0000000000 0000000000 0000000000 0000000000 00????????? ?????????? 0000001000 ?000001100 01000000

**Scaptomyza (Deniscaptomyza) denticauda* Malloch:

1010000000 0010100000 0000001000 0100000010 0000000000 0000100000 0000000110 0000000000 0011000000 0000020041 1100010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001112121 0001100000 0000001000 1000001100 ?????????

Scaptomyza (Deniscaptomyza) intermedia (Duda):

1011000000 0110???0?? ?00?00???? ?1?001001? 0000000000 0000100000 0000000110 0000000000 0011000000 0000120041 0100010000 0000100000
0000000000 0000000000 0000000000 0000000000 0000000000 0000000100 0000000110 0000001000 0000001100 01000000

**Scaptomyza (Deniscaptomyza) multispinosa* Malloch:

1010000000 0110100000 0000001000 010001001? 0000000000 0000100000 0000000110 0000000000 0011000000 0000120041 1100010000 0000100000
0000000000 0000000000 0000000000 0000000000 0000000000 0001000101 0000001000 0000001000 0000001100 01000000

**Scaptomyza (Euscaptomyza) chylizosoma* (Seguy):

101?100000 0000???0?? ?00?00???? ???0000010 0000000000 0000100000 0000000000 0000000000 0011000000 0000020030 1100010000 1000100000
0000???000 0000000000 0000000000 0000000000 0000000000 00????????? ?????????? 0000001000 ?000001100 ?????????

**Scaptomyza (Hemiscaptomyza) apicata* (Thomson):

1011000000 0110100000 0000001000 0100010010 0000000000 0000100000 0000000110 0000000000 0011000000 0000020041 1100010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0000111100 0000000010 0000001000 0000001100 01110000

Scaptomyza (Hemiscaptomyza) trochanterata Collin:

1010000000 0110???0?? ?00?00???? ???001001? 0000000000 0000100000 0000000110 0000000000 0011000000 0000020041 1100010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0000111100 0000000010 0000001000 0000001100 01100000

**Scaptomyza (Lauzanomyza) horaeoptera* Tsacas & Cogan:

101?000000 0010???0?? ?00?00???? ???0000010 0000000000 0000100000 0000000110 0000000000 0000000000 0000020041 0100010000 0000100000
0000???000 0000000000 0000000000 0000000000 0000000000 0000111121 0000000010 0000001000 100000?100 ?????????

**Scaptomyza (Macrosaptomyza) altissima* (Frey):

1011000000 0110100020 0000001000 0100000010 0000000000 0000100000 0000000000 0000000000 0013000000 0000120051 0110010000 0000100000
0000000000 0000000000 0000000000 0000000000 0000000000 0011101010 0000000000 0000001000 1000001100 00000000

**Scaptomyza (Mesosaptomyza) paravittata* Wheeler:

1010000000 0110100000 0000002000 010000001? 0000000000 0000100000 0000000110 0000000000 0011000000 0000020051 0110010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0001011100 0000000000 0000001000 0000001100 01000000

Scaptomyza (Mesosaptomyza) wheeleri Hackman:

1010000000 0010???0?? ?00?00???? ???001001? 0000000000 0000100000 0000000110 0000000000 0011000000 0000020051 0110010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0011112100 0000000000 0000001000 0000001100 01000000

**Scaptomyza (Parascaptomyza) pallida* (Zetterstedt):

1010000000 0010100100 0000001000 010000001? 0000000000 0000100000 0000000110 0000000000 0012000000 0000020051 0110010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0011112110 0000000000 0000001000 1000001100 01000000

Scaptomyza (Parascaptomyza) adusta (Loew):

1010000000 0010???0?? ?00?00???? ???001001? 0000000000 0000100000 0000000110 0000000000 0000000000 0000020051 0010010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0011111100 0000000000 0000001000 0000001100 01100000

Scaptomyza (Rosenwaldia) abrupta Hackman:

1010000000 0110???2?? ?00?00???? ???0000011 0000000000 1000100000 0000000110 0000000000 0011000000 0000020041 0100010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001111121 1110000000 0000001000 1000001100 01000000

**Scaptomyza (Rosenwaldia) mitchelli* Hackman:

1010000000 0110100220 0000001100 0100010011 0000000000 1000100000 0000000110 0000000000 0011000000 0000020041 0100010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001111121 1110000000 0000001000 1000001100 01000000

**Scaptomyza (Scaptomyza) graminum* (Fallén):

1010000000 0000100100 0000001000 0100000010 0000000000 0000100000 0000000110 0000000000 0012000000 0000020051 0110010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0011112110 0000000000 0000001000 1000001100 01000000

**Scaptomyza (Scaptomyza) nigrita* Wheeler:

1010000000 0110100000 0000001000 010001001? 0000000000 0000100000 0000000110 0000000000 0000000000 0000020041 0110010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0000002100 0000000000 0000001000 0000001100 01100000

Scaptomyza (Tantalia) albovittata (Malloch):

1010000000 0010?7?1?? 700?00?7?? ?7?001001? 0000000000 1000100000 0000000110 0000000000 0011000000 0000020031 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 00?7?7?7?? ?7?7?7?7?? 0000001000 ?000001100 00000000

**Scaptomyza (Tantalia) varipicta* Hardy:

1010000000 0010100100 0000001100 0100010010 0000000000 1000100000 0000000110 0000000000 0011000000 0000020041 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0001111121 0111001000 0000001000 1000001100 00000000

Scaptomyza (Trogloscaptomyza) articulata Hardy:

1010000000 0010?7?1?? 700?00?7?? ?7?001001? 0000000000 1000100000 0000000110 0000000000 0011000000 0000020031 0000010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001?12121 0111100000 0000001000 1000001100 01000000

Scaptomyza (Trogloscaptomyza) inaequalis (Grimshaw):

1010000000 0010?7?1?? 700?00?7?? ?7?001001? 0000000000 1000100000 0000000110 0000000000 0011000000 0000020031 0000010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001111121 0111000000 0000001000 1000001100 01000000

Scaptomyza (Trogloscaptomyza) intricata Hardy:

1010000000 0010?7?1?? 700?00?7?? ?7?0000010 0000000000 1000100000 0000000100 0000100000 0011000000 0000020031 0000010000 0000100000
0000100000 0000000000 0000000000 0000000000 0000000000 0001112121 0111101000 0000001000 1000001100 01000000

**Scaptomyza (Trogloscaptomyza) platyrhina* Hardy:

1011000000 0010100700 0000001000 0100010010 0000000000 1000100000 0000000110 0000100000 0011000000 0000020031 0000010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0001110101 1111001000 0000001000 0000001100 01000000

**Scaptomyza parva*:

1010000000 0000100020 0000001000 010001001? 0000000000 0000100000 0000000110 0000000000 0012000000 0000020031 1100010000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 00001?1110 0000000000 0000001000 1000001100 01000000

**Sphaerogastrella* sp:

1010000000 0111100100 0000001100 0100000000 0100000000 0110100100 0000000100 2000000000 0000002000 0000021161 ?7?0010000 0002100000
0000110000 0000000000 0000000000 0000000000 0000000010 1100000000 0000000000 0000000000 1000001100 01111000

**Stegana (Orthostegana) acutangula* (Hendel):

1000101000 0000000000 0000101020 0000000000 0000000000 0000000000 0000110000 0000000000 0000000000 0000000000 0000000011 0000000001
0001111101 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000010

Stegana (S.) vitata (Coquillett):

1000101000 0000?7?0?? 700?10?7?? ?7?0000000 0000000000 0000100000 0000200000 0000000000 0100000000 0000000010 0000000011 0000000001
0001111111 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000010

**Stegana (Steganina) coleoprata* (Scopoli):

1000101000 0010000000 0000001070 0000000000 0000000000 0000000000 0000200000 0000000000 0100000000 0000000010 0000000011 0000000001
0001111111 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000010

**Stegana (Pseudostegana) sp:*

10?01010?0 7000?7?0?? 700?0?7?? ?7?0000000 0000000000 0000100000 ?000?00000 0000000000 0000000000 0000020021 0001000011 0000100?01
0000?7?100 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00000?7?

**Styloptera alocasiae* Okada & Carson:

1010000000 0010?7?0?? 700?0?7?? ?7?000001? 0000000000 0000100000 0000000010 1000000000 0000000000 0000020041 1000010000 0100100000
0000?7?000 0000000000 0000000000 0000000000 0000000000 1100000000 0000000000 0000000000 1000001100 ?7?7?7??

**Tambourella ornata* Okada:

1010000000 00111?1?1? 700?00?7?? ?7?0000000 0100000000 0110100000 0000000?0 2000000000 0000002000 0000020061 0000010000 1002101000
0000110000 0000000000 0000000000 0000000000 0000011100 1100000000 0000000000 0000000000 100000?100 01100000

Titanochaeta ichneumon Knab:

1011000000 0000?7?0?? ?10?01?7?? ?7?0000100 0000000000 0000100000 0000002010 0000000000 0000000000 0000020030 0000000000 0000100000
0000?7?000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 00000000

**Titanochaeta swezeyi* Wirth:

1011000000 0000000000 0100010010 0000000100 0000000000 1000100000 0000002000 0000000000 0000000000 0000020031 0000000000 0000100000
0000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001100 00000000

Zaprionus multistriatus Sturtevant:

1011000000 0010???0?? ?00?00???? ???0000010 0000000000 0000100000 0000000000 0000001100 0000001000 0010020031 2000000100 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000100 0000000000 0000000010 1000001100 01100000

**Zaprionus vittiger* Coquillett:

1011000000 0010110000 ?00000???? ???0000010 0000000000 0000100000 0000000000 0000001100 0000001000 0010020041 1000000100 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000100 0000000000 0000000010 1000001100 01100000

**Zapriothrica dispar* (Schiner):

1010000010 0110???0?? ?00?00???? ???1000000 0000001000 0000100000 1000000100 0000000000 0000000020 0000020031 1000000000 0000100100
 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001101 01100000

**Zapriothrica nudiseta* Wheeler:

1010000010 0100000000 0000000000 0001000000 0000101000 0000100000 1000000100 0000000000 0000000020 0000020031 1000000000 0000100100
 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 1000001101 01100000

**Zygothrica atriangula* Duda:

1010000000 0000100000 0000000000 0110000000 0000000101 0000100000 0000000100 0000000000 0000000000 0000020031 1000000000 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 0110000000 1000001100 01100000

Zygothrica dispar (Wiedemann):

1010000000 0000?00000 ?00000???? ???0000000 0000000001 0000100000 0000000000 0000000000 0000000000 0000020031 1000000000 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 000000000? ?????00000 1000001100 01100000

Zygothrica orbitalis (Sturtevant):

1010000000 0000100000 0000000000 0110000000 0000000001 0000100000 0000000000 0000000000 0000000000 0000020031 1000000000 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 0010000000 1000001100 01100000

**Zygothrica samoensis* Malloch:

1010000000 0000000000 0000010000 0110000000 0000000001 0000100000 0000000000 0000000000 0000000000 0000020021 1000000000 0000100000
 1000110000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 0001100000 1000001100 01100000

APPENDIX 2
THROCKMORTON'S DATA MATRIX OF DROSOPHILID
GENERA

CHARACTERS:	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R		
<i>P. victoria</i> group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	
<i>P. coracina</i> group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	
<i>P. latifasciaeformis</i>	0	0	0	0	0	0	0	1	0	0	?	0	0	0	0	0	0	4	1	
<i>P. bryani</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	2	
<i>P. populi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>S. obscura</i> group	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0		
<i>S. melanogaster</i> group	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	3	0		
<i>S. willistoni</i> group	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	3	0		
<i>S. saltans</i> group	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	3	0		
<i>Chymomyza</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	5	2		
<i>Scaptomyza</i>	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	2		
<i>Dorsilopha</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	2		
<i>Titanochaeta</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1		
<i>Zaprionus</i>	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	?	2		
<i>Hirtodrosophila</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	4	2		
<i>Mycodrosophila</i>	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	4	2		
<i>D. pinicola</i>	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	4	?		
<i>D. immigrans</i>	1	1	0	0	0	0	1	0	1	2	0	1	0	0	0	0	4	2		
<i>Liodrosophila</i>	0	1	0	0	0	1	0	0	1	2	0	0	0	0	0	0	4	2		
Hawaiian <i>Drosophila</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2		
<i>D. crassifemur</i>	0	1	0	0	1	0	0	0	?	1	0	0	0	0	0	0	0	1		
<i>D. nasalis</i>	0	1	0	0	0	1	0	1	0	?	1	0	0	0	0	0	0	1		
<i>D. parva</i>	0	1	0	0	0	0	0	0	?	1	0	0	0	1	0	0	1	1		
<i>Alloscaphomyza</i>	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1		
<i>Bunostoma</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1		
<i>Exalloscaphomyza</i>	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1		
<i>Parascaphomyza</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1		
<i>Rosenwaldia</i>	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1		
<i>Tantalia</i>	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1		
<i>Trogloscaphomyza</i>	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1		
<i>Idiomya</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	4	2		
<i>Antopocerus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	2		
<i>Nudidrosophila</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	4	2		
<i>Ateledrosophila</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	2		
<i>D. aracea</i>	0	1	0	1	0	0	0	1	0	?	2	0	0	0	1	0	?	?		
<i>D. funebris</i> group	1	1	0	0	0	0	1	0	1	2	0	1	0	0	0	0	4	2		
<i>D. calloptera</i> group	1	1	0	1	0	0	0	1	1	2	0	1	1	0	0	0	4	2		
<i>D. quinaria</i> group	1	1	0	1	1	0	0	1	1	2	1	1	0	0	0	0	4	2		
<i>D. testacea</i> group	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	4	2		
<i>D. pallidipennis</i> group	1	1	0	0	0	0	1	1	?	?	0	1	1	0	0	4	?			
<i>D. sticta</i>	1	1	0	0	0	0	0	1	?	?	0	0	0	0	0	4	?			
<i>D. rubrifrons</i> group	1	1	0	0	0	0	1	1	?	2	0	1	0	0	0	4	?			
<i>D. macroptera</i> group	1	1	0	1	0	0	0	1	1	?	1	0	1	0	0	4	?			
<i>D. tripunctata</i> group	1	1	0	1	0	0	1	1	1	2	0	1	1	0	0	4	2			
<i>D. cardini</i> group	1	1	0	1	0	0	0	1	1	1	2	0	1	1	0	0	4	1		
<i>D. guarani</i> group	1	1	0	1	0	0	0	1	1	1	2	1	1	1	0	0	?	2		
<i>Phloridosa</i>	0	0	0	0	0	0	0	1	1	1	?	0	0	0	0	0	?	1		
<i>D. polychaeta</i>	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0	4	2			
<i>D. virilis</i> group	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	4	2		
<i>D. nanoptera</i> group	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	3	1			
<i>D. bromeliae</i> group	0	1	0	1	0	0	0	0	0	1	?	0	0	0	0	2	1			
<i>D. annulimana</i> group	0	1	0	0	0	1	1	0	1	2	1	1	0	0	0	4	2			
<i>D. robusta</i> group	0	1	0	0	0	1	0	0	1	0	2	1	1	0	0	0	4	1		
<i>D. melanica</i> group	0	1	0	0	0	0	1	0	0	1	2	0	1	0	0	0	3	2		
<i>Dettopsomyia</i>	0	?	?	?	?	?	?	0	0	1	2	0	1	1	0	0	2	1		
<i>D. canalinea</i> group	0	1	0	1	0	0	0	0	0	1	2	0	1	0	1	0	?	2		
<i>D. dreyfusi</i> group	0	1	0	1	0	0	0	0	0	1	2	0	0	0	0	1	?	2		
<i>D. hydei</i> subgroup	0	1	0	0	0	0	0	0	0	1	2	1	1	0	0	1	?	2		
<i>D. melanopalpa</i> subgroup	0	1	1	0	0	0	0	0	1	2	1	1	0	1	0	1	0	4	2	
<i>D. mercatorum</i> subgroup	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	4	2
<i>D. fasciola</i> subgroup	0	1	1	0	0	0	0	0	0	1	?	0	0	0	1	0	4	1		
<i>D. mulleri</i> subgroup	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	4	1		
<i>D. mesophragmatica</i> group	0	1	0	0	0	0	0	0	0	1	?	0	1	0	0	0	?	2		

APPENDIX 3

OKADA'S DATA MATRIX OF DROSOPHILID GENERA

CHARACTERS:	A	B	C	D	E	F	G	H	I	J	K	L	M	N		
Electrophortica	0	0	0	0	0	0	0	0	0	1	1	0	0	0		
Soederbomia	?	0	?	?	0	0	0	0	0	0	?	0	0	0		
Pyrgometopa	?	0	?	?	0	?	0	?	?	?	?	0	0	0		
Eostegana	0	0	0	0	1	0	0	0	0	0	1	0	0	0		
Stegana	0	0	0	0	1	0	0	0	0	0	1	0	0	0		
Amiota	0	0	0	0	1	0	0	0	0	0	1	0	0	0		
Crincosia	0	1	1	1	0	0	0	0	0	0	1	0	0	0		
Apenthecia	0	1	0	0	0	1	0	0	0	0	1	0	0	0		
Mayagueza	0	1	0	0	0	0	0	0	0	0	1	0	0	0		
Cacoxenus	0	1	0	0	1	0	0	0	0	0	1	0	0	0		
Gitona	0	1	0	0	1	0	0	0	0	1	1	0	0	0		
Acletoxenus	0	1	?	0	1	0	0	0	0	1	0	0	0	1		
Luzonimyia	0	1	1	0	1	0	0	0	0	1	1	0	0	1		
Leucophenga	0	0	0	0	1	0	0	0	0	1	1	0	0	1		
Paraleucophenga	0	0	0	0	1	0	0	0	0	0	1	0	0	1		
Pseudiaста	0	1	1	0	0	0	0	0	0	0	?	0	0	1		
Trachyleucophenga	?	0	?	0	0	0	0	0	?	?	?	0	0	1		
Pararhinoleucophenga	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
Rhinoleucophenga	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
Microdrosophila	1	0	0	0	0	1	1	1	1	1	1	1	0	1		
Hypselothyrea	1	0	0	1	1	1	1	1	1	1	0	0	0	1		
Tambourella	0	0	0	1	0	1	1	1	1	1	1	0	0	1		
Sphaerogastrella	0	0	0	1	0	1	1	1	1	1	1	0	0	1		
Liodrosophila	0	0	0	0	1	1	1	1	1	1	1	0	0	1		
Lissocephala	1	0	0	0	1	1	1	1	1	1	1	0	0	1		
Mulgravea	1	0	0	0	0	1	1	1	1	1	1	0	0	1		
Paraliodrosophila	1	0	?	?	0	?	1	?	?	1	0	0	0	1		
Calodrosophila	?	0	1	0	1	1	1	1	0	1	0	0	0	1		
Colocasiomyia	1	1	1	0	1	1	1	1	1	1	0	0	0	1		
Nesiodrosophila	1	0	1	0	0	0	1	1	1	1	1	0	0	1		
Jeannelopsis	1	0	1	0	0	0	1	1	1	1	1	0	0	1		
Mycodrosophila	0	0	0	0	0	1	1	1	0	1	1	1	1	1		
Styloptera	1	0	1	0	0	0	1	1	1	1	1	0	1	1		
Dettopsomyia	1	0	0	0	1	1	1	1	1	1	1	1	1	1		
Paramycodrosophila	1	0	0	0	0	1	1	1	0	1	1	1	1	1		
Dicladochaeta	?	1	?	0	?	1	1	?	1	?	1	?	0	0	1	
Baeodrosophila	?	1	1	?	?	?	1	1	0	?	1	1	0	0	1	
Sphyrnoceps	?	0	?	?	0	1	1	1	?	?	1	?	0	0	1	
Cladochaeta	0	0	0	0	0	1	1	1	0	1	0	0	0	1		
Miomyia	0	0	0	?	0	1	1	1	0	?	?	?	0	0	1	
Diathoneura	1	0	0	0	0	1	1	1	1	1	1	0	0	0	1	
Neotanygastrella	1	0	0	0	0	1	1	1	0	1	1	0	0	0	1	
Ateledrosophila	?	0	?	0	1	1	1	1	0	1	?	?	0	0	1	
Nudidrosophila	1	0	1	?	0	0	0	0	?	1	?	?	0	0	1	
Zygothrica	1	0	0	0	1	1	1	1	0	1	0	0	0	0	1	
Collessia	1	0	0	0	1	1	1	1	0	1	1	0	0	0	1	
Phorticella	1	0	0	0	1	1	1	1	0	1	1	0	0	0	1	
Grimshawomyia	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	
Celidosoma	?	0	0	0	1	0	1	1	0	1	?	?	0	0	1	
Protochymomyza	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	
Chymomyza	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	
Titanochaeta	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	
Balara	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Samoaia	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	
Scaptomyza	1	0	0	0	0	0	1	1	1	1	1	0	0	0	1	
Marquesia	?	0	?	?	0	0	0	1	1	0	1	?	?	0	0	1
Neorhinoleucophenga	0	0	?	?	0	0	0	1	1	?	1	?	?	0	1	1
Zaprionus	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1
Drosophila	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1
Apacrochaeta	0	0	?	?	0	0	?	1	?	0	?	?	?	0	0	1
Laccodrosophila	1	0	?	?	0	0	0	0	0	?	?	?	?	0	0	1
Pseudocacoxenus	?	1	?	?	?	0	?	?	0	1	?	?	?	0	0	1
Zapriothrica	?	1	0	0	?	1	1	1	0	?	?	?	0	0	0	1