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8 • Relicts in the Drosophilidae

(Diptera)

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So far as I know, almost all continental drosophilids have ranges that cover an area at least an order of magnitude greater than those of insular species. Also, closely related mainland species are sympatric more often than not. Assuming an allopatric model of speciation, these two facts must mean that drosophilids have considerable ability to disperse and colonize, which may explain why the endemism of drosophilids in the Caribbean region is quite low compared with many other insects, such as some carabids (see other papers in this volume). This hypothesis will be tested here, as applied to Caribbean Drosophilidae.

Fifty-eight species of Drosophilidae are endemic to the Antilles, 11 of which have yet to be described (App. 8.1). At least 12 genera and subgenera are represented in the region (68 world genera have been described for about 2500 species, and some await classification). I can discuss in detail only three groups here: *Mayagueza*, the *Drosophila repleta* species group, and *Zygothrica*. *Mayagueza* is probably the most plesiomorphic and *Zygothrica* the most recently derived of the three taxa. The decision to compare these three taxa was based on several criteria: for *Mayagueza*, because it is the only endemic genus in the Caribbean for the Drosophilidae; for the *D. repleta* species-group, because extensive research has already been done; and for *Zygothrica*, because it is a taxon I am currently studying.

Throughout the text there will be references to the age or relative age of a group. Given three species or taxa of other rank (A, B, and C), one set of relationships may be that A is the sister group to B + C. In this event, the cladogenesis between A and B + C is certainly no younger than, and may have preceded the event that gave rise to, B and C. Thus the lineage to which A belongs (and perhaps A itself) is either as old or older than either lineage B

or C. These definitions are important to understand my use of the word "relict."

A relict (or paleoendemic, or anachronism) is a narrowly endemic, living member of a relatively old group. "Old" is taxonomically subjective: it depends on genealogy and where the presumed relict lineage arises in a phylogenetic tree. Implied in the endemism of a relict lineage is extinction: the relict is a remnant surrounded by extinction, it is part of a waning lineage. In this paper I try to be explicit about the relative age of some Caribbean drosophilids. It is often difficult to ascertain whether any one species is itself a relict because of the difficulty in identifying the extinct ancestors of an endemic taxon or the extinction of the relict itself in many parts of its former range (see, e.g., many examples in Eldredge and Stanley 1984). Therefore, my use of "relict" is qualified to mean a relict *lineage* to which the endemic belongs. As I discuss later, a study of Dominican and Chiapas amber fossils (Grimaldi 1987a) has thus far provided little data to corroborate the role of inferred extinctions in present endemism patterns of Caribbean drosophilids.

Results

Mayagueza

Mayagueza, a monotypic genus, was described for a species presently known only from Mayaguez, Puerto Rico. *M. argentifera* was apparently given generic rank because of several features that it shares with various genera of lower Drosophilidae (Wheeler 1960). I will present explicit evidence for *Mayagueza* genealogy.

Mayagueza belongs to the subfamily Steganinae, whose members usually possess several more primitive traits than those in the other subfamily, the Drosophilinae. There is strong indication that the Steganinae are paraphyletic, namely, they are defined either by the possession of traits that arose well before the Drosophilidae (e.g., strong prescutellar setae and several other chaetotaxal characteristics, and the absence of "teeth" on the "egg guide" [= sternite VIII]), or by several clearly derived traits that occur sporadically in the subfamily (e.g., "pegs" on the distal costal wing vein segment). The *Pseudiasata* genus-group, to which *Mayagueza* belongs, will be designated here in the steganine confusion.

To examine the relationships of *Mayagueza*, it was necessary to study representative steganines, particularly those with pubescent arista, such as *M. argentifera* (Fig. 8-2C-E). Mâca (1980b) believed this state of the arista to be primitive, but when comparing it with several drosophilid relatives (using the taxa mentioned below), it seems obvious that the trait is a derived one for the Drosophilidae. Adults belonging to 15 and the larvae of 6 of the following genera/subgenera were examined (* indicates immature material):

Acletoxenus indicus,* *Acletoxenus* sp.* (Sumatra), *Amiota* (*Amiota*) *humeralis*, *Amiota* (*Sinophthalmus*) *picta*, *Amiota* (*S.*) *polychaeta*, *Apenthecia crassiseta*, *Cacoxenus* (*Gitonides*) *perspicax*,* *Cacoxenus* (*Paracacoxenus*) *guttatus*,* *Gitona bivisualis*, *G. brasiliensis*, *Leucophenga varia*, *Leucophenga* spp. (4, Neotropical), *Mayagueza argentifera*, *Pseudiasata pseudococcivora*,* *P. vorax*,* *Pseudiasata* spp. (2, Mexico, Trinidad), *Rhinoleucophenga obesa*,* *R. pallida*, *Rhinoleucophenga* spp. (2, Trinidad, Panama), *Stegana coleoprata*, *Stegana* sp. near *tarsalis*, *Stegana* spp. (4, Neotropical).

Many of the above taxa do not have pubescent arista, but they were included in the study to better judge steganine variation. In addition, the following papers served as references for some taxa that I did not examine, either as adults or as larvae/puparia: McAlpine (1968), Mäca (1977, 1980a, 1980b), Okada (1968), and Wheeler (1960). Gonçalves (1939) provided a good description of the habits and morphology of *Pseudiasata brasiliensis* larvae. For outgroup taxa, which were used to decide on the primitive state for characters, the following were used: *Diastata repleta*, *D. eluta* (Diastatidae); *Camilla glabra* (Camillidae); *Notiphila teres* (Ephydriidae); *Curtonotum helvum* (Curtonotidae). The published information on ephydrid immatures helped to polarize the states of immature characters at the family level for the Drosophilidae (diastatid and camillid immatures are unknown).

Figures 8-1 and 8-2 and Appendix 8.2 present some of the taxonomic characters. Based on the cladogram (Fig. 8-3), I concur with Wheeler (1960) that at least *Pseudiasata* and *Acletoxenus* are close relatives of *Mayagueza*, but *Cacoxenus* is not. *Mayagueza* is also related more closely to *Acletoxenus* than to *Pseudiasata*. Before turning to the biogeography of the flies, I will briefly discuss two interesting implications of the cladogram. First, there are at least three major clades among the Steganinae: (1) one to which belong the genera *Stegana* and *Leucophenga* which are phenetically quite distinct; (2) a large one that separates the subgenera of the large genus *Amiota*; and (3) the *Pseudiasata* genus group. More taxa and characters need to be examined before formal categories are assigned to any of the clades. Second, among the traits that appear to be homoplasious, the most interesting one is predation by the larvae. A very readable and thorough review of the habit is given in Ashburner (1981). Obligate predation by larvae has arisen four or perhaps five times among the taxa in Figure 8-3, and several more times (e.g., *Cladochaeta*, *Titanochaeta*) in all the Drosophilidae (see Figs. 8-9A, B for two of the hosts). Several African *Leucophenga* larvae feed on cercopids, *Cacoxenus perspicax* feeds on coccids, *Rhinoleucophenga obesa* is a predator of *Aclerda* scales, and *Gitona brasiliensis* predaes mostly *Orthezia* among some other scales. The existence of different prey taxa confirms that predation at these levels has appeared independently. The habits of many *Stegana* and *Amiota*, however, are unknown. True to the predatory habits of the

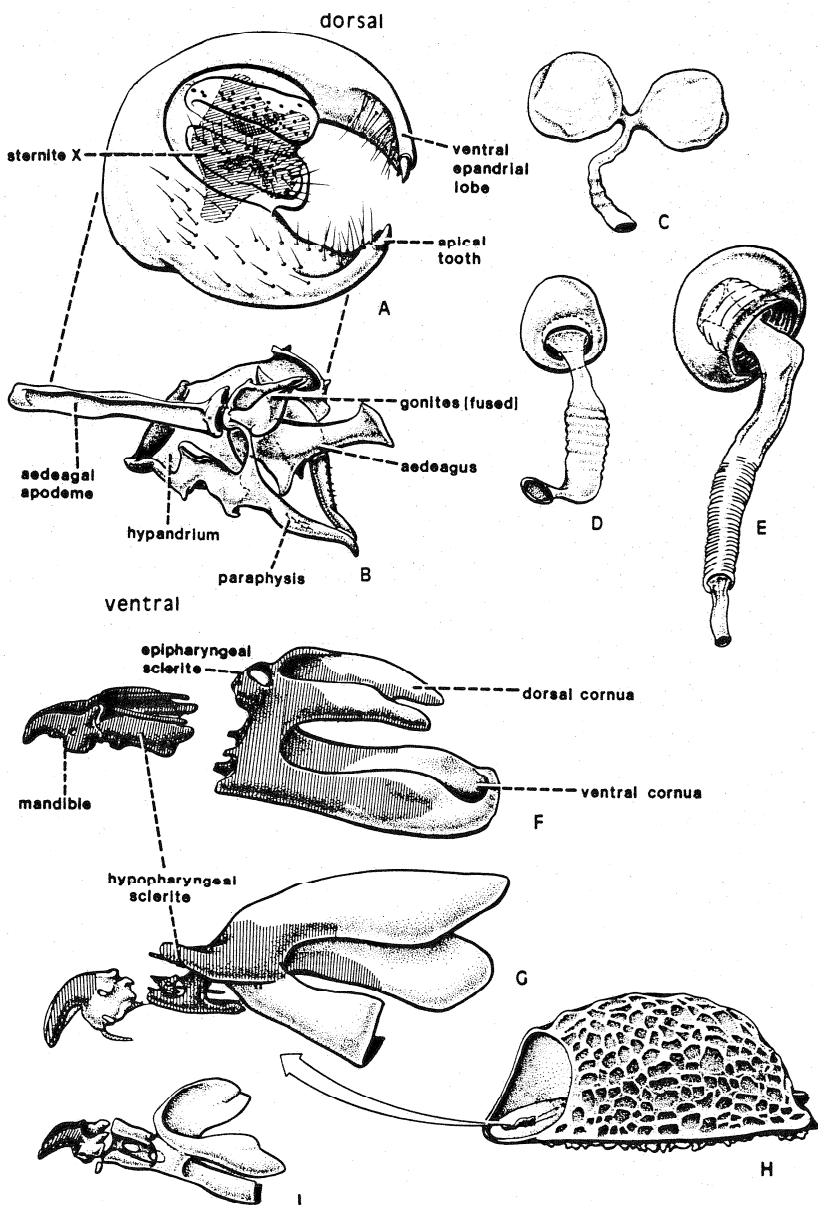


Figure 8-1. Some taxonomic characters used in the cladogram, Fig. 8-3. A, B: Male genitalia of *Mayagueza argentifera*. A, epandrium; B, genitalia. C-E: spermathecal capsules (to same scale as A, B). C, *M. argentifera* (fusion of the pair is a very unusual trait in the Drosophilidae); D, *Acletoxenus* sp. (India); E, *Amiota (Erima) crassiseta*. F, G, I: larval instar III cephalopharyngeal skeletons (extracted from puparia). F, *Cacoxenus (Gitonides) perspicax*; G, *Pseudiasata pseudococcivora*; I, *Acletoxenus* sp. (India). H: puparium of *Pseudiasata pseudococcivora*.

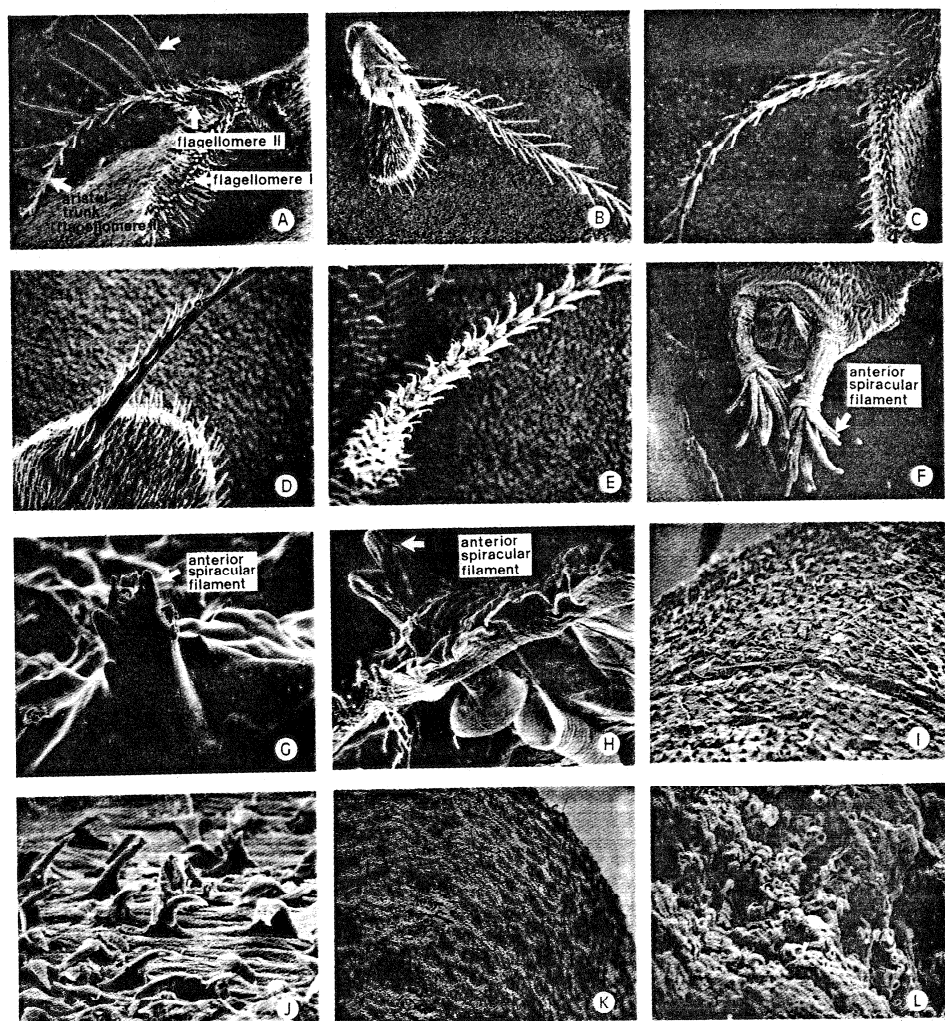


Figure 8-2. Scanning electron micrographs of some structures used for steganine phylogenetic reconstruction. A-E: antennae or portions thereof. A, *Camilla glabra* (Camillidae), 170 \times ; B, *Diastata eluta* (Diastatidae), 74 \times (short plumose); C, arista (flagellomeres II & III) of *Acletoxenus indicus* (Drosophilidae), 207 \times ; D, basal portion of arista of *Amiota* (*Sinophthalmus*) *picta* (Drosophilidae), 218 \times ; E, detail of arista of *Mayagueza argentifera* (Drosophilidae), 183 \times ; F, anterior spiracles of *Drosophila* (*Siphlodora*) *busckii*, 56 \times ; G, detail of anterior spiracle of *Pseudiatata nebulosa* pupa, 285 \times (note stubby filaments); H, anterior spiracle (also showing internal attachment of trachea and felt chamber) of *Acletoxenus* sp. (India), 659 \times ; I, dorsal puparial integument, *Cacozenus* (*Paracacoxenus*) *guttatus*, 97 \times ; J, detail of spicules, showing bifid structure, *Cacozenus guttatus*, 500 \times ; K, dorsolateral puparial surface, *Pseudiatata nebulosa*, 41 \times ; L, detail of view in K, showing poroid surface and curled (waxy?) exudate, 477 \times .

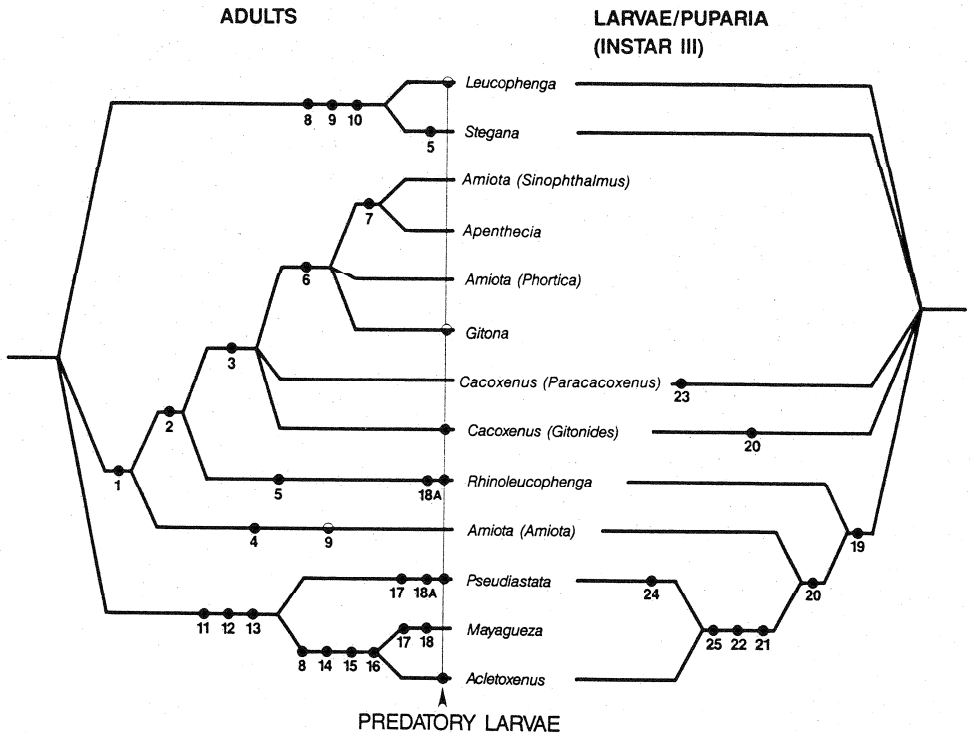
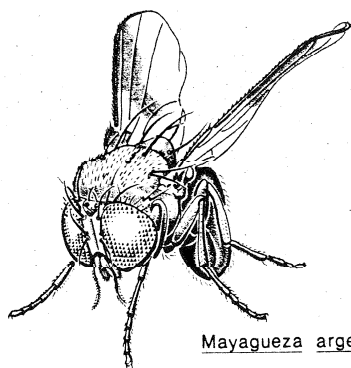


Figure 8-3. Hypothesis of phylogenetic relationships among some genera and subgenera of steganine Drosophilidae, which is based on immature characters (cladogram at right) and characters of adult morphology (left). The appearance of predatory larvae has occurred several times independently, which is indicated (bicolored circles indicate that the predatory habit is found among some of the members of that taxon).

lower Drosophilidae are the tastes of *Pseudiasata* and *Acletoxenus*: the former feeds on scales, the latter on white flies (Aleurodidae: Homoptera). It takes very little imagination to predict that when *Mayagueza argentifera* larvae are found, they will be predatory on sessile Homoptera and will share some traits of the cephalopharyngeal skeleton that presently are restricted to the *Pseudiasata* genus group.

Acletoxenus is a widespread genus, due primarily to the distribution of *A. formosus*, which occurs in Europe, the Middle East, northern Africa, south-east Asia, and northern Australia. The remaining four species are found in tropical India, southeast Asia, and Australia (Fig. 8-4), and one of these is an undescribed species from Sumatra. Together, *Mayagueza* + *Acletoxenus* is the sister group of *Pseudiasata*, which is a predominantly Neotropical group of at least ten species; *P. nebulosa* is in the eastern and south-central United States, and I have seen specimens of two undescribed species from Mexico



Mayagueza argentifera

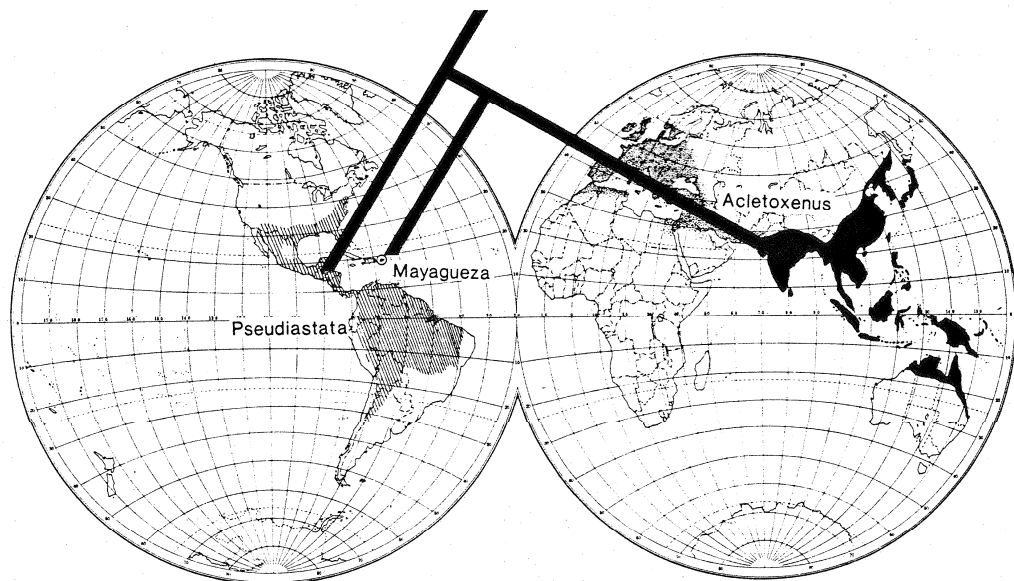


Figure 8-4. Distribution of the *Pseudiastata* genus group. *Pseudiastata* is hatched, *Mayagueza* occurs on Puerto Rico, and *Acletoxenus* spp. are in black (the range of *Acletoxenus formosus*, where it extends farther than its congeners, is stippled).

and Trinidad. Two hypotheses may account for the disjunct distribution of *Pseudiastata* genus group flies. One of them is more probable because it is supported by geologic evidence, but both presume that some African and Malagasy extinction of *Acletoxenus* sp(p). or a direct ancestor thereof has occurred.

On the one hand, dispersal of an *Acletoxenus-Mayagueza* ancestor from Puerto Rico to Africa may have left behind what is now *Mayagueza*, while also establishing *Acletoxenus*. But why would the Neotropical mainland not

be colonized several times before central (tropical) Africa? I believe that the ancestor of the *Acletoxenus-Mayagueza* clade evolved around the time of the split between the Greater Antilles and South America, an event that simultaneous with or later than the African–South American divergence about 80 Ma. Both genera may be recent additions to what are actually old and vicariant lineages.

The *Drosophila repleta* species group

The *Drosophila repleta* group is one of 22 species groups recognized in the subgenus *Drosophila*. It is a well-defined group of higher Drosophilidae, and it is distinguished among other groups in the subgenus in part by the presence of a spotted integument or elaborate maculations. With 76 described morphospecies (Vilela 1983) and 3 species yet to be described (M. Wasserman, pers. comm. 1986), this is the second largest clade endemic to the New World. Most species are found in dry habitats, where the species breed mostly in cactus necroses. The remaining species are mostly forest-edge flies that breed in flowers and fruits.

The species group has been the subject of extensive study, primarily by William Heed and his students and by Marvin Wasserman, whose work spans three decades. The evolution and especially the ecology of these flies were presented in a recent book (Barker and Starmer 1982), from which my discussion has been distilled; in a review by Wasserman (1982), and in Vilela's revision (1983).

Wasserman split the species group into nine subgroups based on cytological characters (Fig. 8-5). The characters are found in the metaphase complements and the polytene chromosomes in the larval salivary glands. The latter are huge, presumably because of immense metabolic and transcriptional activity. Arranged along the length of each polytene chromosome are bands (chromomeres) of varying widths that also occur in a sequence characteristic of one arm or a portion thereof. If inversions or their portions are shared among two or more species, that chromosomal segment is considered a synapomorphy and can be used to infer genealogy. There is little doubt that inversions are truly unique character states (one idea is that smaller inversions may actually be transposons), but deciding which inversional sequence is primitive can be difficult. If it is impossible to discover an inversion in an outgroup taxon, morphological or other criteria can be used to polarize the trend in inversional states.

Two predominant biogeographic patterns involve endemic species on the Antilles. In one, old endemics are restricted to Jamaica, Puerto Rico, and Hispaniola. In the other the insular endemics have some close relatives that are widespread, usually in the southern United States and Central America, or in Central America plus northern South America. The following is a brief

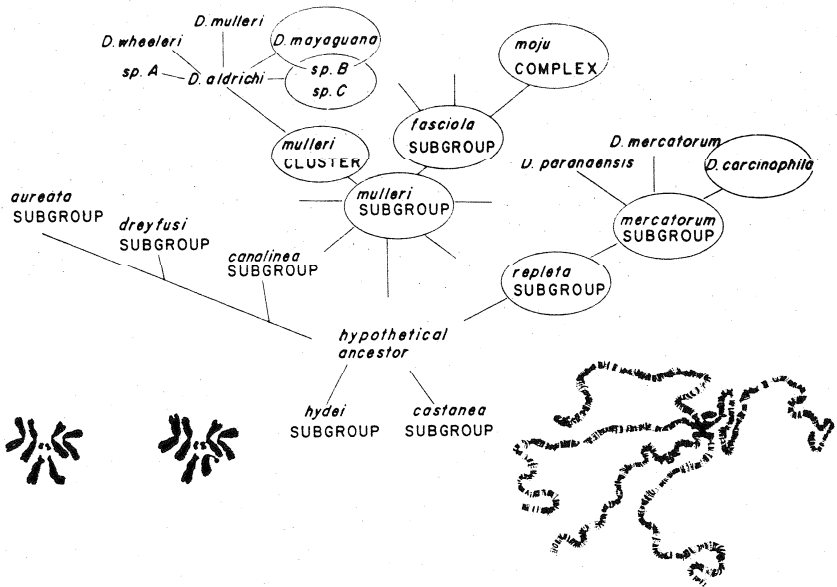


Figure 8-5. Relationships among groups in the *Drosophila repleta* species group (redrawn from Wasserman 1982). This phylogenetic tree has been constructed on polytene and metaphase chromosome characteristics. Taxa that are circled are Caribbean or have Caribbean representatives.

discussion of four endemic *repleta* lineages, three of which appear to be relatively old; the other has widespread relatives on the mainland, but the relationships are obscure.

Drosophila peninsularis, which is found in southern Florida, Puerto Rico, and Cuba (Fig. 8-6A), is one branch of a trichotomy that also involves the *repleta* and *fulvimaculata* complexes of species. This conclusion is based on cytological grounds, since Vilela (1983) places it in the *mercatorum* subgroup because of morphological resemblance. That the *repleta* subgroup probably originated before the *mercatorum* subgroup (which has one species endemic to the Caribbean) suggests *D. peninsularis* to be old indeed. Members of the *repleta* subgroup are widespread in deserts or scrub habitats abundant with cacti, such as in the southwestern United States, northern Mexico, Brazilian *caatingas*, and portions of Mato Grosso.

D. paraguattata, which occurs on Jamaica, is basal to the *moju* species complex. The other members of this complex are *D. mojuoides* (Trinidad) and *D. moju* (Costa Rica to Bolivia and southern Brazil) (Fig. 8-6B). According to Wasserman, the latter species should be separated into a Central American and a South American population. Here again is an insular endemic, *D. paraguattata*, that appears to be relatively old.

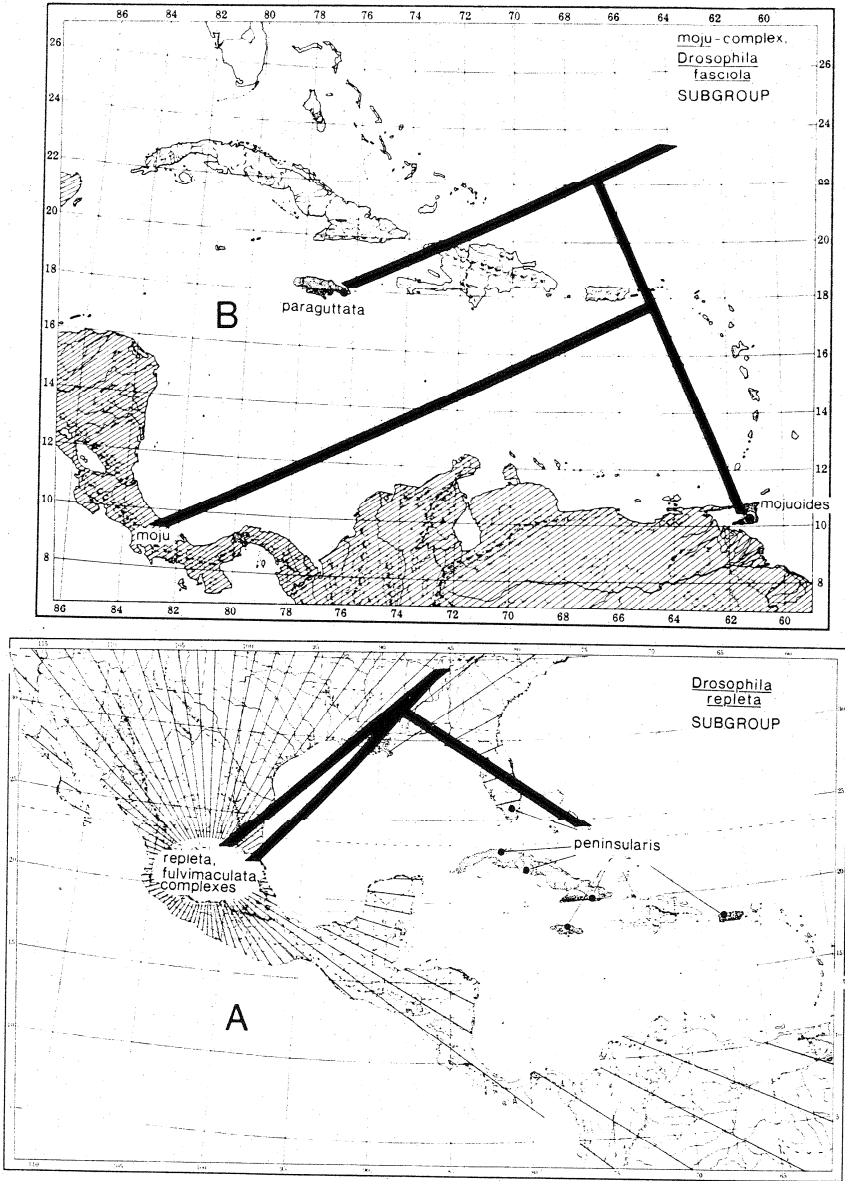


Figure 8-6. Distributions and relationships of some *Drosophila repleta* species group lineages (relationships from Wasserman 1982).

In the *mercatorum* subgroup are three species: *D. mercatorum*, *D. paranaensis*, and *D. carcinophila* (which occurs on the Bahamas, Cuba, Dominica, Grand Cayman, Jamaica, Montserrat, and Puerto Rico). *D. mercatorum* is very opportunistic in its use of hosts, facultatively parthenogenetic, and ranges over most of the southeastern United States and Central and South America, recently it has even colonized Hawaii and Africa. Curiously, there are no records or specimens of this species from the Antilles. Everywhere, its breeding sites consist mostly of decaying fruits and vegetables. The habits of *D. paranaensis* have yet to be discovered. *D. carcinophila* has specialized larvae that feed on the exudates in nephric grooves of the land crab, *Gecarcinus ruricola* (Carson 1967; Fig. 8-9E, F). Because it does not share two polymorphic inversions found in *D. paranaensis* and *D. mercatorum*, this fly seems to be the most primitive species of the *mercatorum* subgroup. The habit of crab commensalism has actually evolved three times in the Drosophilidae; the other two instances involve *Lissocephala powelli* (on Christmas Island) and *D. endobranhia* (Carson 1974). The latter species is also a Caribbean endemic (Cayman Island; perhaps Cuba, but this record is based only on larval specimens). The relationships of *D. endobranhia* are not entirely clear because it does not fit into any of the standard species-groups. Despite their highly derived tastes, the Caribbean "crab flies" appear to be recent members of nonterminal lineages.

Other insular endemics in the species group belong to the *mulleri* species cluster, which comprises *D. mayaguana* (widespread), and two new species, n.sp. 1 (Haiti, Navassa Island), and n.sp. 2 (Hispaniola, Jamaica). Wasserman and others believe that these three species and three others distributed from Nebraska to Venezuela are derived from *D. aldrichi* or a close relative thereof (Fig. 8-5). *D. aldrichi* has a very expansive range that extends from Texas to Colombia. Finally, there is an undescribed species from Jamaica that breeds well in the laboratory and has been examined morphologically and karyotypically (W. Heed, pers. comm. 1986). Like *D. endobranhia*, which will be discussed later, it shares derived features of two species groups, in this case the *repleta* and *nannopectera*.

Zygothrica

Zygothrica is the most speciose lineage of Drosophilidae in the New World (discounted here are the numerous species of *Drosophila*; this genus appears paraphyletic [see Throckmorton 1975]). Sixty-four species names presently exist, and a recent study gives descriptions of 48 additional species in a portion of the genus (Grimaldi 1987b). I currently estimate a total of about 200 species of *Zygothrica*. Seven of the species belong to an Indo-pacific clade (Samoa, east to Thailand on the Malay peninsula, and in northern Australia); members of the other clades occur from southern Mex-

ico to Bolivia and southern Brazil. Despite their diversity on the Neotropical mainland, only 14 species are found on the Caribbean islands and 9 are endemic there (Table 8-1). Species epithets given below in quotations indicate taxa to be described in my upcoming monograph on the genus.

Before I discuss the Neotropical *Zygothrica*, I will point out a distribution found in one clade of the group that closely reflects the situation in the *Pseudiasata* genus group. Two New World species, *Z. bilineata* (which is Amazonian and circumcaribbean) and *Z. "flavifrons"* (presently known only from Trinidad), are the closest relatives of the Indopacific, *samoensis*-group species. As with the *Pseudiasata* group, no African relatives exist. It is very difficult to say if the same geologic events have affected the distributions of the two unrelated groups.

All species of *Zygothrica* are known to aggregate at imbricate polypores and Tricholomataceae, particularly white fleshy ones (Fig. 8-9C). Some primitive species breed in the fungi, but most breed in fleshy bracts of flowers, principally in the Zingiberales (Fig. 8-9D), and simply retain the plesiomorphic habit of using fungi to rendezvous. During dry seasons, when fungus blooms are scarce, the aggregations of *Zygothrica* are very dense and can approach a "standing room only" situation.

My phylogenetic hypothesis on the genus is presented in Figure 8-7. It is based on the morphology of 53 species and the reproductive behavior repertoires of 7 of them. The majority of species fit well into particular clades, but the relationships among clades are not clear. I do not believe this polychotomous lineage exhibits paraphyly: the synapomorphies distinguishing the genus are distinctive for drosophilids, and behavior corroborates the morphological conclusions. Most *Zygothrica* are lowland tropical, moist/rain forest dwellers (<500 m), but a few are restricted to high altitudes (>1500 m). None of the Caribbean endemics is a highland species: only *Z. microstoma*, which is circumcaribbean, is a highland species in the Greater Antilles (Table 8-3).

Table 8-1. Nonendemic Caribbean *Zygothrica*

<i>Z. microstoma</i> Duda, 1927 (1.1, <i>microstoma</i> group):	Puerto Rico, Jamaica, southern Mexico to trans-Andean Ecuador and northern Peru
<i>Z. circumveha</i> Grimaldi, 1987 (1.2.1, <i>dispar</i> group):	Haiti, Jamaica, southern Mexico to northern Colombia
<i>Z. vitticlara</i> Burla, 1956 (1.2.2, unnamed group):	Dominica, St. Lucia, Brasil (São Paulo)
<i>Z. bilineata</i> (Williston) 1896 (2.1, <i>bilineata-samoensis</i> group):	Cuba, Dominica, Guadeloupe, Haiti, Jamaica, Martinique, Puerto Rico, St. Vincent, from Panama (Chiriqui) to Rio de Janeiro, Brasil
<i>Z. atriangula</i> Duda, 1927 (4.2.2, <i>atriangula</i> group):	Dominica, Jamaica, southern Vera Cruz (Mexico) to São Paulo, Brasil, and Cocos Is. (Costa Rica)

NOTES: Major lineage to which each species belongs is in parentheses. Information based on cladogram in Figure 8-7.

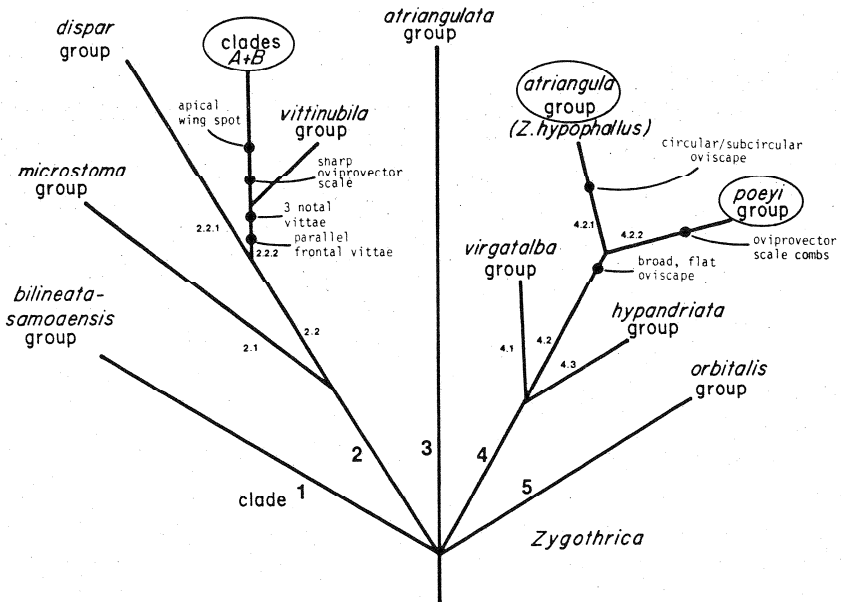


Figure 8-7. Hypothesis of phylogenetic relationships among species groups of the genus *Zygothrica*. Clade 1 is Neotropical and Indopacific in distribution, 2–5 are entirely Neotropical. Groups that are circled have Antillean representatives.

Little is known about three endemic *Zygothrica*—*Z. "palpivanna," Z. vitrea*, and *Z. "hypophallus."* Specific placement of the first two of these undescribed species, which are found on Jamaica, must await the discovery of females. *Z. "hypophallus"* is a modified member of a terminal clade that includes some very widespread species (e.g., *Z. atriangula*; Table 8-1), and is known only from St. Vincent.

Two major groups of Caribbean Drosophilidae exist. First is the *poeyi* clade, which includes *Z. poeyi*, *Z. semistriata* Wheeler, and *Z. "parasemistriata"* (note that this is not the "poeyi" of Burla 1956, which is actually *Z. laevifrons* Duda, a widespread Amazonian species). *Z. poeyi* is the sister group to the pair of other species, and it occurs from Cuba to Puerto Rico. Collections on Jamaica, Puerto Rico, and the Dominican Republic have been good, so *Z. "parasemistriata"* is probably restricted to the Haitian peninsula, assuming that the rampant deforestation in this area has not taken its toll. *Z. semistriata* is known only from southern Mexico on the Gulf Coast. The endemism pattern of the *poeyi* species group is another instance where a Greater Antillean species is the sister group to a Central American clade or species (Fig. 8-8A).

The distribution of the second *Zygothrica* clade is shown in Figure 8-8B.

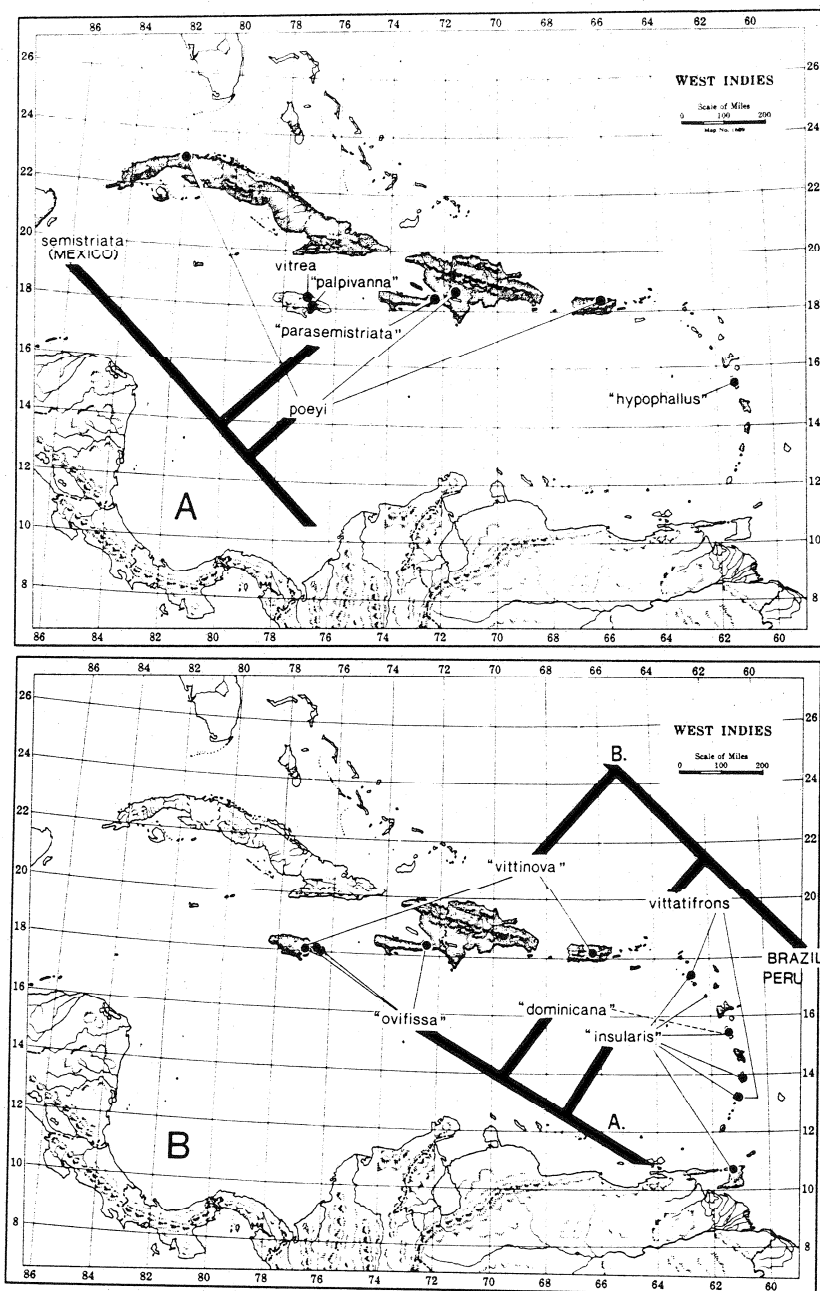


Figure 8-8. *Zythricha* distributions and relationships. A, assorted species (*Z. "vitrea"* and *Z. "palpivanna"* are as yet unplaced; *Z. "hypophallus"* belongs to the *atriangula* species group) and species of the *poeyi* species group. B, the two lineages of *Zythricha* clade 2.2.2. that occur in the Caribbean region.

The species in this group, like numerous superficially similar ones, are attractive, striped forms with apical wing spots (Fig. 8-10), and they form two main lineages (shown in Fig. 8-8B as A and B). The monophyly of A + B is supported by a trait unique in Diptera: the females possess one to three terminal, large, ramphate scales at the apex of the eversible ovipositor membrane (the oviprovectator). The scales embed themselves in the host plant tissue during oviposition, probably to anchor the female.

The distribution of clades A and B can best be described as countercurrent. Outgroup comparison places the primitive state for the distribution of this group as Amazonian. In clade A, the first divergence event is between the pair *Z. "insularis"* + n.sp. from Peru (700 m altitude) (not shown in Fig. 8-8B) and the pair *Z. "dominicana"* (on Dominica) + *Z. "ovifissa"* (on Jamaica, Haitian peninsula). Even if this distribution is not a progression up the Lesser Antilles, there is little doubt that *Z. "ovifissa"* is a relatively recent addition to the Greater Antilles.

Clade B has a distribution with an opposite direction. *Z. "vittinova"* (on Jamaica, Puerto Rico, and perhaps Hispaniola) is the most plesiomorphic member of clade B, and it is the sister group to the following set of species: *Z. vittatifrons* (St. Kitts, St. Vincent, and probably the intervening islands) + n.sp. from Brazil (São Paulo State) + n.sp. from Peru (mid-altitude). There is a problem with the interpretation that B is spreading southeastward, for it suggests that the lineage B evolved in the Greater Antilles, which A has only recently colonized. Are A + B paraphyletic? Because there appears to be no reason to revise the morphological decisions, a remaining explanation for the countercurrent distributions of clades A and B is extinction. The ancestor to A + B might have been widespread on both the mainland and the islands, given rise to each lineage in different areas, and gone extinct, since no extant and plesiomorphic fly has such a distribution.

Among the three taxa discussed in this paper, *Zygothrica* appears to have the greatest number of recent additions to the Antilles, composed of *Z. "hypophallus"* and clades A + B. The other lineages that have endemic species also have mainland relatives that appear to be more recently derived. Even though it should not be standard practice in historical biogeography to discuss which groups are not present in an area, especially where extinction is of primary concern, the absence of species belonging to the *dispar* species group (clade 2.2.1 in Fig. 8-7) is a glaring attribute of the West Indian drosophilid fauna. Except for the primitive and circumcaribbean species *Z. "circumveha,"* no others in this group are found on the islands. And this is despite the fact that some *dispar* group members are among the most common *Zygothrica*: *Z. prodispar*, for example, has the most expansive distribution in *Zygothrica* (Vera Cruz, and Mexico to Bolivia). Their absence from the islands is perplexing and may be evidence that dispersal in Caribbean Drosophilidae was not important.

Other Caribbean Drosophilidae

Three other drosophilid groups have Caribbean endemics that are cladistically basal to mainland groups. First is *D. insularis*, a member of the *willistoni* species-group. It is endemic to St. Kitts and St. Lucia. Except for *D. neoalagitans*, the other species in the group are widespread and abundant rain forest inhabitants in Central and South America. Dobzhansky (1957) mentioned that, based on morphological and chromosomal grounds, the relationships of *D. insularis* are obscure, for it possesses few of the derived traits in the group. Second, there is *D. endobranhia*, which, as noted earlier, is a perplexing species: it possesses traits of the *D. quinaria* and *D. virilis* species groups, both of which are widespread Holarctic and entirely continental groups. Third is *Paramyodrosophila nephelea* on Jamaica. There are ten other *Paramyodrosophila* species: one in the southeastern United States, seven in the Indopacific and in northern Australia, and two circum-Caribbean species that include Hispaniola and Puerto Rico in the Antillean portion of their distributions. The *Paramyodrosophila* distribution is very similar to that of the *Pseudiasata* genus group and to some *Zygothrica* that I have already mentioned.

An addition to Cuba that is probably recent is *Chymomyza microdiopsis*, and one recent to Jamaica is *C. jamaicensis* (Grimaldi 1986). Each of these two species belongs to the two main lineages in the *C. aldrichii* species group. They represent terminal clades, and the species group itself is cladistically terminal compared to the other groups in the genus (Okada 1976). The closest relative of *C. microdiopsis* is *C. exophthalma*, a species ranging from Panama to Peru. *C. guyanensis* + *diatropa* is the sister group to *C. jamaicensis*, and the range of this group is from Costa Rica to Guyana, and the southern tip of Florida (*C. diatropa*). The sister group of the *C. aldrichii* species group is the *procnemis* species group, which is most speciose in the Congo Basin and has several members in southeast Asia (*C. procnemis* is the only Nearctic representative). Since the *aldrichii* species group is entirely New World, it is certainly no older than the split between South America and Africa about 80 Ma and may be much more recent than that.

Discussion

With the exception of *Zygothrica* clade "A," Z. "hypophallus," and the two *Chymomyza*, the Antillean Drosophilidae probably appeared before the divergence in their mainland relatives. This is the pattern first elucidated by Rosen (1975:456, Fig. 20), whereby taxa from the Greater Antilles represent the sister groups to taxa from Central America + northern South America. It is apparent from the discussion of the three drosophilid taxa that these

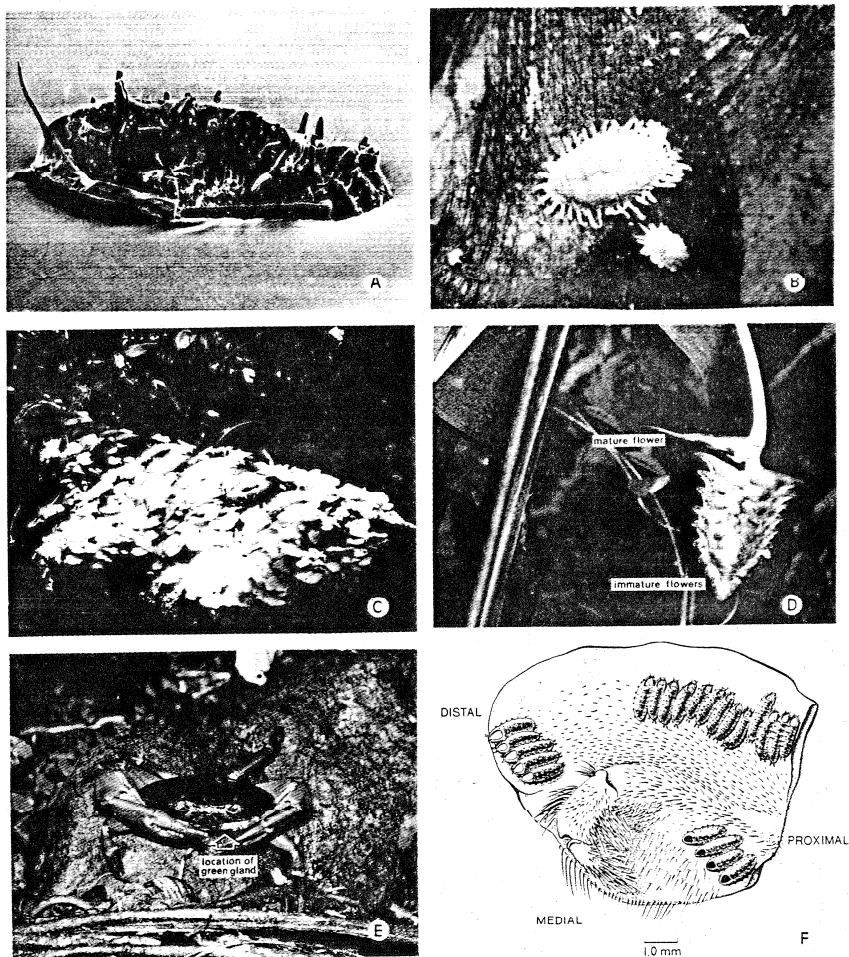


Figure 8-9. Hosts and prey of some drosophilid taxa that have Antillean species. A, scanning electron micrograph of scale ("*Aleuracanthus* sp.," according to the label data) on which an undescribed species of *Acletoxenus* from Sumatra was found feeding (82 \times). B, Pineapple mealybug, *Dysmicoccus brevipes*, on *Ctenanthe oppenheimeriana*? (photo by R. J. Gill, California Department of Foods and Agriculture). This is the reported prey of several *Pseudiastata* species. C, *Polyporus tricholoma* (Polyporaceae: Basidiomycetes) bloom on Barro Colorado Island, Panama. White fleshy polypores like this serve as rendezvous sites for probably all species of *Zygothrica* and as breeding sites for some primitive species. D, *Heliconia mariae* (Heliconiaceae: Zingiberales) inflorescence. The fleshy bracts of zingiberaceous flowers are one of the primary breeding sites of *Zygothrica*. E, Black land crab, *Gecarcinus ruricola*, at El Yunque, Puerto Rico. *Drosophila carcinophila* larvae feed on the exudate in nephric grooves of this crab (photo by J. K. Liebherr). F, Drawing of a famous specimen in the NMNH. This is the maxilliped of *Gecarcinus ruricola* taken from a specimen on Montserrat in 1894 by H. G. Hubbard. Twenty-two puparia of *Drosophila carcinophila* adhere to the inner surface, and four at the lower right have enclosed.

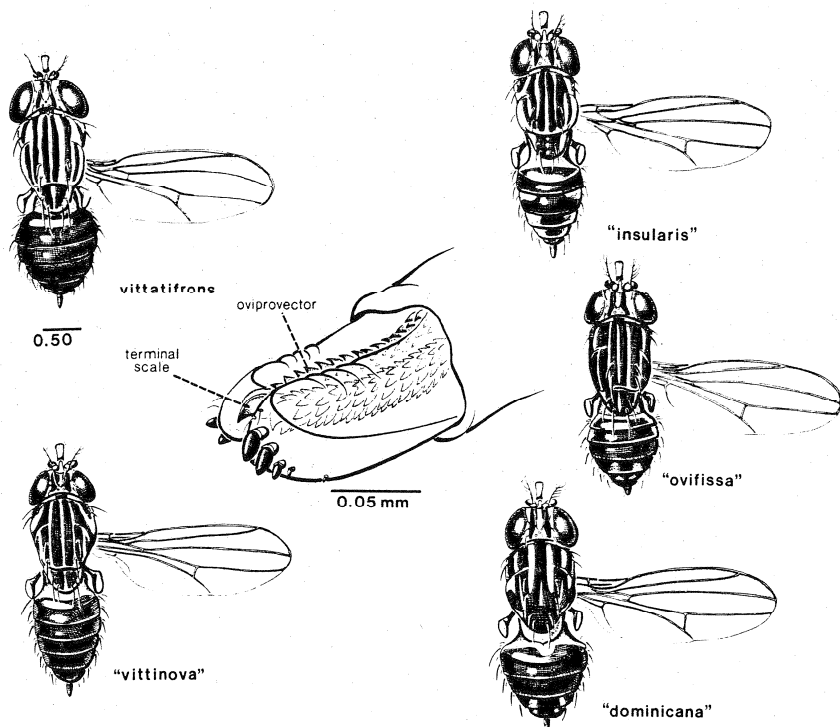


Figure 8-10. Insular Caribbean endemics of *Zygothrica* clades A+B (from Fig. 8-8B). An unusual feature that distinguishes this lineage is the possession of sharp, cleaverlike scales on the apex of an eversible ovipositor membrane (the oviprovector). Some species have apical wing spots that have become coalesced into the costal and subcostal wing cells (*Z. "dominicana," Z. "ovifissa"*).

groups have contrasting life styles: cactophilics, crab commensals, homopteran predators, flower breeders, and mycophilous forms are represented on the Antilles (Fig. 8-9). Because of such ecological diversity, any biogeographic patterns are probably due more to historical factors than to a similarity in habits.

George Gaylord Simpson (1956:12) wrote: "... waifs by this route would be highly improbable, but they would be possible, and that is all that the theory [of dispersal] demands." If chance is the currency of dispersal sweepstakes, then it seems impossible that most of the Caribbean drosophilid lineages could have founded the younger mainland lineages via dispersal. At the very least, the islands are relatively depauperate in virtually every biological respect, and therefore any flow of colonists should be from the opposite (mainland to island) direction. A vicariant origin of the plesiomorphic Carib-

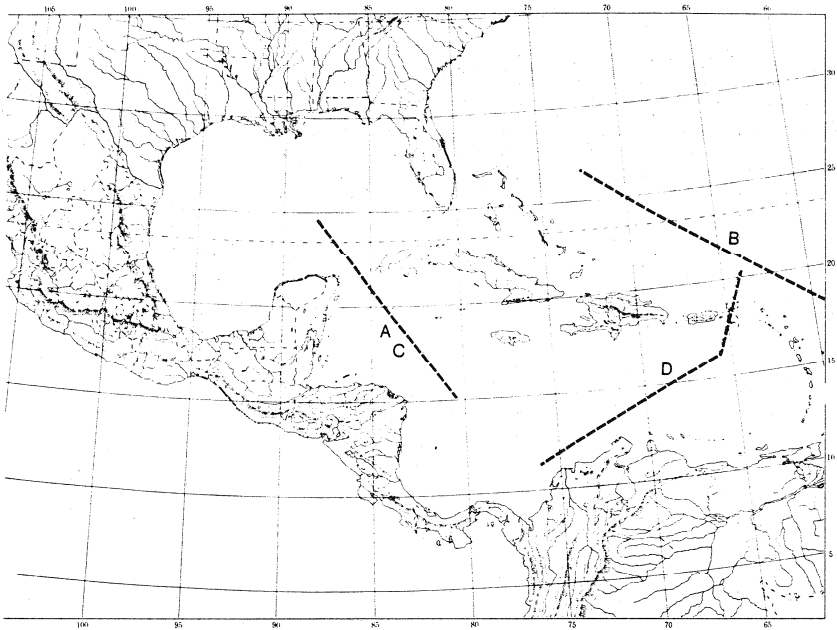


Figure 8-11. Hypothesis of vicariant events based on the distributions of *Drosophilidae* discussed in the text. A is the earliest event and represents a presumed separation of the Greater (and Lesser?) Antilles + Africa from Central America. B is the next event and is the separation of the West Indies from the west coast of Africa. C is an event involving the same land masses as in A, but at a later date and with a different type of geologic event (i.e., separation of a land bridge). D is the latest event and represents a separation of the Lesser and Greater Antilles, and of the Greater Antilles from northern South America.

bean drosophilid clades may require some equally complicated hypotheses, for example, one that assumes that ranges were at one time contiguous (i.e., that the islands have drifted or that they fused either geologically or during periods of low sea level). Using the approach established by Platnick and Nelson (1978), I present a hypothesis in Figure 8-11 for the Caribbean *Drosophilidae* which at least has geologic and biogeographic support.

Geologic evidence suggests that the Greater Antilles, and perhaps the northern Lesser Antilles, had a continental origin. Anderson and Schmidt (1983) have reviewed numerous studies and came to the conclusion that the Antilles formed from a shearing of several middle American plates beginning in the late Cretaceous (about 70 Ma). Durham (1985), whose evidence comes from marine fossils, has hypothesized that a large Caribbean plate moved through what was formerly the peninsula of southern Mexico and carried with it the portion of Central America that ranges from Honduras to Panama, Jamaica, southern Haiti, and the Lesser Antilles. This scenario

apparently represents the geologic consensus on the origins of at least the Greater Antilles (reviewed in Rosen 1985). In my study I have been unable to resolve controversy over intransland relationships (e.g., hybridization of Cuba and Hispaniola) because of the large areas of endemism. Durham (1985), however, has published the latest dates for early drifting, which are between 20 and 10 Ma. With North America, South America, and Africa joined into a predrift land mass, the Caribbean would fall at the point of their triple junction. Triple junctions are extremely active tectonically and are very likely to give contrasting dates of divergence, depending on what criteria are used. Finally, Donnelly (see chap. 2) supports the view that the Antilles not only evolved *in situ*, but were almost entirely submerged during periods in the Quaternary.

Fossils: Flies and Otherwise

Two drosophilid fossils were known prior to my recent study (Grimaldi 1987a): *Electrophortica succini* (Hennig 1965) (from Baltic amber, Eocene to early Oligocene [40–50 Ma]), and a *Neotanygastrella* (Chiapas amber, 30 Ma [Wheeler 1963]). The *Electrophortica* male possesses a pubescent arista and has a strong anterior reclinate seta, but it lacks a facial carina. Using these criteria, one can place the fossil basal to the *Pseudiasata* genus group, probably at an unresolved node from which *Pseudiasata* and *Acletoxenus* + *Mayagueza* originate. This also means that a primitive lineage (like *Pseudiasata*) formerly inhabited the Baltic region. *Neotanygastrella* is a distinctive group of flies with a distribution very similar to that of *Paramyodrosophila*, which I have already discussed. Of the 17 described species, 6 *Neotanygastrella* are Neotropical (mainland), 5 occur on the Ivory Coast, 4 are Indopacific insular, 1 is northern Australian, and another, *N. antillea*, occurs on Jamaica. *Neotanygastrella* is at least 30 million years old, but, given its Gondwanan distribution, it is probably even older. Dominican amber, which is at least early Miocene in origin (ca. 23 Ma), has thus far yielded 9 species of Drosophilidae (e.g., Fig. 8-12), representing 3 extant genera (*Chymomyza*; *Drosophila*, including 3 of its subgenera; *Scaptomyza*), and 2 extinct genera (Grimaldi 1987a). Because the genitalia could not be examined microscopically, it was not possible to place most of the species close to extant ones. It is clear, however, that the Drosophilidae were in existence when and where they could be affected by at least late Oligocene geophysical events in the Caribbean.

The abundance of fossils of animals other than flies makes extinction of Caribbean groups appear substantial. For ants, 22 of 37 genera and subgenera in Dominican amber remain on Hispaniola (Wilson 1985; see also chap. 9). Fifteen others have colonized the island since then, and 3 genera are extinct everywhere. Probably the most impressive account showing how

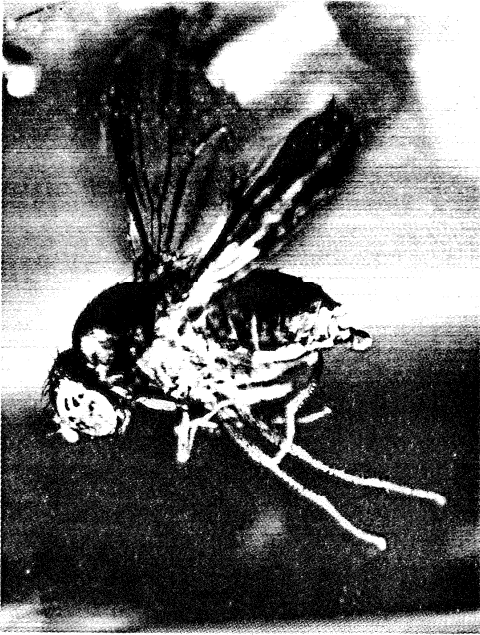


Figure 8-12. Female paratype of *Drosophila poinari* Grimaldi, fossilized in amber from the lower Miocene of the Dominican Republic (photo by G. O. Poinar, Jr.).

extinction can modify distribution is that of the Caribbean xerophilic vertebrates (Pregill and Olson 1981). Bats, owls, the extant mockingbird, *Mimus gundlachii* (on the Bahamas, Jamaica, and a fossil in Puerto Rico), caracaras, *Leiocephalus* and *Cyclura* iguanids, and meadowlarks (*Sturnella* spp.) are some taxa for which fossil evidence suggests that a wider distribution existed that usually encompassed the mainland. *Todus* (Todidae: Aves: Coraciiformes), which has 5 species, each endemic to a Greater Antillean island, once had a distribution that also included Wyoming in the Oligocene (Olson 1976). In fact, fossils show that the Todidae and another Caribbean group, the Momotidae (Coraciiformes), have a presently restricted distribution (Mourer-Chauvré 1982, Becker 1986). One figure speaks best: excluding bats, at least 75% of the Caribbean land mammals are extinct since at least the Pleistocene (Pregill and Olson 1981). At present, *Solenodon* is the largest native mammal on the Greater Antilles—a place where ground sloths (de Paula Couto 1967) and giant caviomorph rodents once roamed as well. Even though *Solenodon* is a terminal clade in the Solenodontoidea (MacFadden 1980), there is little doubt that the genus is relict because its endemism is imposed by the extinction of close relatives—the Nesophontidae, Apterodontidae, and Geolabididae. Unfortunately, for most paleontologic studies there is too little evidence to allow a comparison between insular and mainland extinctions. For example, a single fossil locality on the mainland usually

provides little data on the past distribution of the taxon to which the fossil belongs. Such a deposit would suggest a formerly wider distribution only when, first, there are taxa plesiomorphic to the fossil which lie within an area circumscribing the extant forms (e.g., within the Antilles); and second, the area has been examined for the presence of other fossils and extant taxa that show a similar biogeographic pattern, to ensure that the deposit is not an isolated case of ancient dispersal.

Other putatively relict lineages in the Caribbean are *Dugesia* flatworms (Ball 1971), *Polycentropus* caddisflies (Flint 1976), and some fishes (Rosen 1975). Among the ground beetles (Carabidae), *Antilliscaris* (Nichols 1986, 1987) and *Barylaus* (Liebherr 1986; see also chap. 6) are two genera known to have African and/or Malagasy affinities. In the Lepidoptera, groups showing Antillean-African connections are some Hesperiiidae, the nymphalids *Calisto* and *Ypthima*, *Hypanartia* and *Antanartia*, and perhaps some species in the *Papilio thoas* species-group (Shields and Dvorak 1979). Wille and Chandler (1964) described *Trigona dominicana* (Apoidea: Meliponinae) from Dominican amber fossils. They considered it to be a primitive member of the subgenus *Hypotrigona*, most closely related to three species in tropical Africa and Madagascar, but Michener (1982) considers its affinities to be Central American. Five endemic Caribbean genera of Orthoclaadiinae Chironomidae (Diptera) have relatives that are either cosmopolitan (*Antill-cladius*, *Lepurometriocnemus*), African-Holarctic (*Comptosmittia*), or Australian (*Petalocladus*) (Saether 1977, 1981, Sublette and Wirth 1972). Because few of the endemic chironomid species have a South American connection, Saether believes that vicariance and extinction have been biogeographically important in the Caribbean region. The genus *Wendilgarda* (Araneae: Theridiosomatidae) has three species: *W. mexicana* (Central America + Cuba), *W. clara* (Central America and northern South America), and *W. atricolor* (two small islands off the coast of Gabon, equatorial Africa) (Coddington 1986). Thus the African-Antillean connection is supported by ample data and fulfills predictions 2 and 4 by Rosen (1985:655). My review of these data does not necessarily imply that the Antillean fauna is an extremely ancient one, as may be the case for, say New Zealand or Tasmania. The fauna is certainly older than most people have previously realized, and the drosophilids are no exception in this regard. It is an important point to address since there is a common view that islands of continental origin harbor many relicts (Carlquist 1974), and because of the geologic controversy over the origins of the Antilles (see Donnelly, chap. 2).

It is speculative to interpret the past distributions of Caribbean Drosophilidae, but still compelling to consider why Antillean relicts may occur, at least for the fruit flies. Because of the extremely depauperate insular faunas, competitive release has been suggested dozens of times—and shown explicitly in some cases—as a reason for the success of some taxa. It is generally

believed that insect populations are not limited by competition (Strong et al. 1984), but competition has been shown to be harsh in a guild of mycophagous *Drosophila* (Grimaldi and Jaenike 1984). In other words, relatively old drosophilid lineages on the islands may have an extended existence because, perhaps, of the availability of unoccupied niches. Jaenike (1978) concluded that competition and the genetic nature of peripheral populations probably account for the distribution of several closely related *Drosophila* species on islands off the coast of Maine.

A relaxed insular regime of competitive selection may account for the distribution in Florida of three generalist *Drosophila* species: *D. tripunctata*, and two species in the *D. cardini* group, *D. cardini* and *D. acutilabella*. *D. tripunctata* occurs in eastern North America and is the only nearctic member of the large (60 + spp.) *tripunctata* species-group (only two members of the group are Antillean endemics [Table 8-1], so this is an almost entirely Neotropical mainland group). Eight *cardini* group species are Antillean, and six are on the Central and South American mainland (Heed 1962), making this more of an insular group. At about the middle of the Florida peninsula, the replacement of the two *cardini* group species by *D. tripunctata* begins: in the Everglades, only an occasional *D. tripunctata* occurs among the many *cardini* group individuals; and at Gainesville (near the panhandle), only *D. tripunctata* can be found (J. Jaenike, pers. comm.). All three species come readily to the same bait, and their replacements appear independent of any obvious ecoclines (even temperature shows no such sharp change). Perhaps the *cardini* group flies, having evolved under insular conditions, cannot contend with a competitively superior mainland lineage. Population biologists interested in mechanisms of insular evolution would do well to do some comparative biology. In particular, the derived conditions of certain features considered important in colonization and demography, such as dispersal and competitive ability and host use, can be incorporated into a cladogram of a monophyletic group having mainland and insular species. Some species in *D. willistoni* or especially *cardini*, and *repleta* species groups would be good examples for study.

Summary

Fifty-eight species of Drosophilidae belonging to 9 genera are known only from the Antilles. Thirty-eight of them occur on the greater Antilles, with 20 species occurring on Jamaica, 16 on Puerto Rico, 12 on Hispaniola, and 9 on Cuba (the latter small number is due primarily to a lack of collecting). The relationships of three lineages are discussed in detail: *Mayagueza* (a monotypic genus found on Puerto Rico) and the two most speciose drosophilid taxa in the Caribbean and Neotropical regions, which are the *Drosophila*

repleta species group and the genus *Zygothrica*. The closest relative of *Mayagueza* is *Acletoxenus*, a primarily southeast Asian genus that also has one Palearctic species. Insular endemics of the *repleta* group have their closest relatives widespread throughout Central America, and, in three of the four lineages, the insular lineages appear to have diverged before the formation of mainland taxa. This pattern is also seen in the *Zygothrica poeyi* species group, but the other main lineage of Antillean *Zygothrica* has an unusual countercurrent distribution along the Lesser Antillean arc. Hypothesized extinction of formerly widespread ancestors in some of the lineages may account for endemism, suggesting that the flies belong to relict lineages. The above three groups have contrasting life styles, which indicates that the biogeographic patterns are more an effect of historical rather than ecological factors. Ages of fossil Drosophilidae show that the family was developed enough to have been affected by at least by late Oligocene–early Miocene Caribbean tectonic movement. A hypothesis of four primary vicariance events for the Antillean Drosophilidae is presented.

Appendix 8.1: Endemic species of Antillean Drosophilidae (classification following Wheeler 1981)

Distribution data come from Wheeler (1981), from specimens that were examined at the Smithsonian Institution, from the American Museum of Natural History, and from revisions.

Subfamily Steganinae

Stegana

(*Steganina*)

horae Williston, 1896 (St. Vincent)

tarsalis Williston, 1896 (St. Vincent)

Mayagueza

argentifera Wheeler, 1960 (Puerto Rico: Mayaguez)

Subfamily Drosophilinae

Chymomyza

microdiopsis Grimaldi, 1986 (Cuba: Santa Clara Prov.)

jamaicensis Grimaldi, 1986 (Jamaica: Hardware Gap)

Diathoneura

metallica (Sturtevant), 1921 (Cuba: Bartle; Puerto Rico: Adjuntas; Dominican Republic: Cabo rojo)

Drosophila

(*Drosophila*)

Calloptera species group

ornatipennis Williston, 1896 (Cuba: throughout; Puerto Rico: Adjuntas, El Yunque, Maricao; Haiti: Jamaica, St. Vincent)

Canaline species group

paracanalinea Wheeler, 1957 (Puerto Rico: El Yunque, Rio Piedras)

Cardini species group

acutilabella Stalker, 1953 (S. Florida; Cuba: Jamaica: Hispaniola)

antillea Heed, 1962 (St. Lucia)

arawkana Heed, 1962 (St. Kitts; Guadeloupe)

bedicheki Heed & Russell, 1971 (Trinidad)

belladunni Heed & Krishnamurthy, 1959 (Jamaica: Hardware Gap)

caribiana Heed, 1962 (Martinique)

dunni Townsend & Wheeler, 1955 (Puerto Rico: Rio Piedras; St. Thomas)

ngrodunni Heed & Wheeler, 1957 (Barbados)

similis Williston, 1896 (Cuba: Bartle; Grenada; Jamaica: St. Vincent)

Flavopilosa species group

nesiota Wheeler & Takada, 1962 (Haiti: Petionville)

Tripunctata species group

mediodiffusa Heed & Wheeler, 1957 (Haiti; Jamaica; Puerto Rico: El Yunque; Cuba)

spinatermina Heed & Wheeler, 1957 (Trinidad: Pt. of Spain)

Drosophila

(*Drosophila*)

Repleta species group

repleta subgroup:

peninsularis Patterson & Wheeler, 1942 (Cuba; S. Florida; Jamaica; Puerto Rico)

mulleri subgroup: *stalker* complex

stalker Wheeler, 1954 (Cayman Is.; S. Florida; Jamaica)

richardsoni Vilela, 1983 (Dominica; Montserrat; Puerto Rico: La Paraguera, Mayaguez; Virgin Gorda*)

mulleri subgroup: *eremophila* complex

n.sp. (Dominican Republic; Haiti; Jamaica)

mulleri subgroup: *mulleri* complex

mayaguana Vilela, 1983 (Bahamas; Conception; Dominican Republic; Gr. Inagua; Gr. Cayman; Haiti; Mayaguana Is.; Tortola)

n.sp. 1 (Haiti; Nauassa Is.*)

n.sp. 2 (Dominican Republic; Haiti; Jamaica: Pt. Henderson*)

fasciola subgroup:

mojuoides Wasserman, 1962 (Trinidad)

paraguttata Thompson, 1957 (Jamaica: Bath)

mercatorum subgroup:

carcinophila Wheeler, 1960 (Gr. Cayman; Montserrat; Puerto Rico: Mona Is., Cueva los Lirios)

unplaced subgroup:

ramsdeni Sturtevant, 1916 (Cuba: Guantanamo)

Unplaced to species group

- coffeata* Williston, 1896 (St. Vincent)
endobranchia Carson & Wheeler, 1968 (Cuba?; Gr. Cayman)
verticis Williston, 1896 (St. Vincent)

(Hirtodrosophila)

- pleuralis* Williston, 1896 (St. Vincent)
prognatha Sturtevant, 1916 (Puerto Rico: Adjuntas; San Domingo)

Drosophila

(Sophophora)

Saltans species groups

- lusaltans* Magalhaes, 1962 (Puerto Rico)
milleri Magalhaes, 1962 (Puerto Rico: El Yunque)
pulchella Sturtevant, 1916 (Montserrat; St. Vincent)

Willistoni species group

- insularis* Dobzhansky, 1957 (St. Kitts: St. Lucia)
neoalagitans Wheeler & Magalhaes, 1962 (Haiti: Petitionville, Kenscoff; Jamaica: Hardware Gap)

Unplaced to subgenus

- fusca* Coquillett, 1900 (Puerto Rico: Utado)
illota Williston, 1896 (St. Vincent)
lutea (Wiedemann), 1830 (not specified)
sororia Williston, 1896 (St. Vincent)

Neotanygastrella

- antillea* Wheeler, 1957 (Jamaica: Montego Bay)

Paraliodrosophila

- antennata* Wheeler, 1957 (Jamaica: Bath)

Paramycodrosophila

- nephelea* Wheeler, 1968 (Jamaica: Hermitage, Windsor)

Zygothrica

- ** *dominicana* (Dominica)
 ** *hypophallus* (Dominica)
 ** *insularis* (Dominica; Montserrat; St. Kitts; St. Vincent; Trinidad)
 ** *ovifissa* (Haiti: Kenscoff; Jamaica)
 ** *palpivanna* (Jamaica: Hermitage)
 ** *parasemistriata* (Haiti: Kenscoff)
poeyi (Sturtevant), 1916 (Cuba: Havana; Dominican Republic: Las Abejas; Puerto Rico: Rio Piedras, Sabana)
 ** *vitrea* (Jamaica: Hardware Gap)
vittatifrons (Williston), 1896 (St. Vincent; St. Kitts)
 ** *vittinova* (Jamaica: Hermitage; Puerto Rico: Cidra)

* Marvin Wasserman, pers. comm., June 1985

** are undescribed species (Grimaldi ms.)

Appendix 8.2: Taxonomic Characters Used in the Phylogenetic Hypothesis of Some Steganinae (Fig. 8-3)

“A” is the apomorphic and “P” the plesiomorphic state of each character.

Adults

1. Genitalia, male. A: complex, hypandrium reduced to narrow arch; sternite X with complex ventroapical process.
P: hypandrium resembles shape of more proximal sternites; sternite X without processes; unadorned gonites.
2. Face. A: carinate. P: flat.
3. Arista (flagellomere 3). A: pubescent. P: short or long plumose.
4. Genitalia, male. A: aedeagus lost, or reduced to very small endophallus.
P: aedeagus robust.
5. Prescutellar setae. A: 2 or more pairs present. P: 1 pair.
6. Clypeus. A: bulbous; height at least one-half of width; protrudes in profile.
P: flat, barely visible in lateral view.
7. Leg coloration. A: tibiae with 2 dark bands each. P: tibiae unicolorous light.
8. Intraocellar setulae. A: lost. P: 1–3 (usually 2) pair present.
9. Third costal wing vein section. A: possesses blunt spines. P: blunt spines absent.
10. Spermathecal capsule. A: possesses papillae. P: glabrous.
11. Face. A: short, length much less than length of front of head. P: face about equal in length to frontal region.
12. Inner vertical setae. A: parallel, directed backward. P: convergent.
13. Ocellar setae. A: absent/greatly reduced. P: robust, length \geq length of postocellars.
14. Spermathecal capsule. A: glabrous, spherical, weakly sclerotized. P: large, heavily sclerotized, with annulations or papillae.
15. Facial and frontal regions. A: extremely narrow (width approximately equal to that of outer ocelli), inner eye margins parallel or nearly so. P: width is $\geq 3 \times$ width of outer ocelli.
16. Ventral epandrial lobe (male). A: elongate, with sclerotized and pointed end (toothlike). P: simple, rounded lobe.
17. Ocellar setae. A: convergent/cruciate. P: divergent.
18. Setae coloration. A: golden. P: black.
- 18a. Interfrontal setulae. A: numerous, cover almost entire front, 50 or more in number. P: setulae on anterior portion of front, near ptilinum; 25 or less in number.

Larvae/Puparia (Instar III)

19. Cephalopharyngeal skeleton: epipharyngeal sclerite.
A: absent/greatly reduced (fused to tentorial phragma).
P: parastomal bar distinct, with latticed process.
20. Anterior spiracles. A: reduced filament length (length \leq width), budlike.
P: prominent spiracular filaments (length $> 2 \times$ width).

21. Thoracic and abdominal spicules. A: absent (lost). P: present.
 22. Cephalopharyngeal skeleton: sclerotization. A: only anterior portion of mandible sclerotized. P: most of skeleton sclerotized, including all of mandibles and anterior bridges plus cornuas.
 23. Thoracic and abdominal spicule shapes. A: bifid. P: single point.
 24. Structure of spiculeless surface. A: poroid, (waxy?) exudate. P: smooth.
 25. Cephalopharyngeal skeleton. A: hypopharyngeal sclerite fused to tentorial phragma. P: sclerite detached, but articulates with, tentorial phragma.
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