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The Phylogeny, Ecology, and Geography of *Drosophila*

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Introduction

The genus *Drosophila* is large, diverse, and widely distributed. Its members are found from sea level to high mountains and from the tropics to the edges of the tundra. Plains, deserts, swamps, and savannas all play host to them, but woodlands and forests are their habitat of choice and their centers of greatest abundance. Within the ecosystem, the species of *Drosophila* are important in saprophytic food chains because their immature stages are dependent upon organisms causing fermentation or decay. Efficient exploitation of this food niche accounts for much of the success of the genus and for many of its patterns of geographic distribution.

In spite of its size and diversity, the genus *Drosophila* cannot be treated apart from the other members of the family Drosophilidae. Too often, genera, subgenera, and species groups arise from a single common ancestor, and to treat some and exclude others would make biogeographic

analysis impossible. It would also obscure fruitful and challenging opportunities for research that contemporary biology can profit from. The evolutionary patterns among *Drosophila* and its close relatives show only the most recent working out of a success story that began with the founding of the family. Hence, if one is to fully understand the complex ways adaptive change, opportunity, time, and accident are interwoven in the history of *Drosophila*, this deep perspective is needed. Some mention must be made of other genera of drosophilids, but limitations of space prevent a detailed treatment of such a large group. This discussion of phylogeny, ecology, and geography can only be a summary, but it should be sufficient to illustrate the knowledge accumulated to date, to introduce the resources provided by *Drosophila* and its relatives, and to expose gaps in our understanding that can be filled by careful work in many areas.

A Guide to the Literature on *Drosophila*

The monograph, *Evolution in the Genus Drosophila*, by Patterson and Stone (1952), is still the most valuable single reference to the genus *Drosophila*. I use the distributions of *Drosophila* species mostly as they are given there, with some revisions where more recent work has altered the general pattern. I also depend on this work to provide the reader with an adequate bibliography of the earlier (prior to 1950) literature, so I will touch on that only lightly. Among the most significant of the older works are those of Sturtevant (1921, 1942). The University of Texas Publications, *Studies in the Genetics of Drosophila*, edited by Patterson (1940–1957), and *Studies in Genetics*, edited by M. R. Wheeler (1962–1972), are indispensable for many major papers on the taxonomy, biology, and distribution of drosophilids. The work of Wheeler (1952, 1954) is likewise indispensable, particularly for taxonomy and distribution, but also for genetics and ecology of *Drosophila*. His major catalogs (Wheeler, 1959, 1965, 1970; Wheeler and Hamilton, 1972) provide access to the earlier and more specialized literature of drosophilid taxonomy, which, for that reason, I omit from this listing. The studies of Okada (1956, 1962, 1966b, 1968a) are invaluable references to the oriental and Asian faunas and are important also for information they provide on the ecology, immature stages, and internal anatomy of many drosophilids other than *Drosophila*. Momma (1957) and Takada (1958, 1960) list species of Hokkaido, and Takada and Lee (1958) list species of Korea. Wheeler and Takada (1964) and Wheeler and Kambysellis (1966) treat faunas of the islands of the Pacific, and Mather (1955, 1956a, 1960)

and Bock (in preparation) treat that of Australia. Hardy (1965, 1966, 1969) and Hardy and Kaneshiro (1968, 1969, 1972) describe the spectacular Hawaiian drosophilid fauna, while Carson *et al.* (1970) summarize the evolutionary biology of these forms. Burla (1951, 1954, 1956) has published much valuable work on the European and African species and on the neotropical *Hirtodrosophila* and *Zygothrica*. Lachaise (1974*a,b*), Lachaise and Tsacas (1974) and Tsacas and Lachaise (1974) provide extremely valuable work, particularly on the ecology of African species. Basden (1956), Basden and Harnden (1956), and Wheeler and Throckmorton (1960) treat arctic and subarctic faunas, and Hackman (1955, 1957) treats with north European forms. Dobzhansky and his co-workers have dealt extensively with Neotropical and Nearctic forms, and this literature is accessible through citations in Patterson and Stone (1952) and Dobzhansky (1970). Brncic (1970) summarizes the biology of Chilean species. Dobzhansky (1965) and Carson (1965) discuss cosmopolitan forms.

Phylogenetic relationships among Drosophilidae, aside from those implicit in taxonomic treatments, have been studied mostly within major groups, and the more important of this work has involved chromosome studies. Foremost among these is the work of Wasserman (1963) on species of the *repleta* group, of Patterson, Stone, and co-workers on species of the *virilis* group [reported by Stone, *et al.* (1960)], and of Dobzhansky and his co-workers on species of the *obscura* group [summarized by Dobzhansky (1970)]. Miller and his associates deal with chromosomes of species of the *affinis* subgroup (Miller and Stone, 1962; Miller and Voelker, 1968, 1969*a,b*; Miller and Sanger, 1968), Stalker (1966) with the *melanica* group, Heed and Russell (1971) with the *cardini* group, Kastritsis (1966, 1969) with the *tripunctata* and *guarani* groups, Mather (1956*b,c*, 1960) with the subgenus *Scaptodrosophila* (= *Pholadoris*), Carson and Stalker [see Carson *et al.* (1970) for references], Carson (1970, 1971), Clayton *et al.* (1972), and Yoon *et al.* (1972*a,b,c*) with Hawaiian drosophilids, Ward and Heed (1970) with the subgenus *Sordophila* and its relatives, and Brncic *et al.* (1971) with species of the *mesophragmatica* group. Stalker (1972) has published on intergroup chromosome phylogeny, Kastritsis *et al.* (1970) have commented on relationships between the *guarani* and *tripunctata* groups, and Yoon *et al.* (1972*a*) have shown intergeneric chromosome homologies.

Special studies of relationships between major groups have been made mostly by Sturtevant (1942), Patterson and Stone (1952), Nater (1953), Okada (1956, 1963*a,b*, 1966*a*, 1967, 1968*b*, 1971), and Throckmorton (1962*a,b*, 1966, 1968). Bächli (1971) has made a computer study of phenetic distances within and between the genera *Leucophenga*

and *Paraleucophenga*, but he has not yet followed this with a covariation analysis to discover the phylogenetic relationships therein.

Biogeographic studies of *Drosophila* and its relatives are rare, at least at the level of the group as a whole. The most comprehensive treatment is that of Patterson and Stone (1952), but this is more a report of distribution than of biogeography. Okada (1970) has published a faunal analysis of drosophilids in the area around New Guinea.

Fossil drosophilids are known from only two sources. Wheeler (1963) describes specimens of *Neotanygastrella* from Mexican amber of Oligocene–Miocene age. Hennig (1965) describes the genus *Electrophortica* from Baltic amber which is generally taken to be of Eocene origin.

Explanation of Tables and Figures

Table 1 is a taxonomic listing of the groups treated herein, together with their distributions and culturability. I have departed somewhat from the traditional procedure of indicating distribution by zoogeographic regions. Instead, I indicate the land masses across which the species are found. The primary purpose of biogeography is to interrelate history, ecology, and distribution of organisms, aiming toward a more complete understanding of existing ecosystems and of ecological and evolutionary theory. Movements from continent to continent are a critical feature of history. Accordingly, I am most concerned with the five continental areas of the globe, excluding Antarctica and Greenland for obvious reasons. Further aspects of distribution can be read from Figure 6. I have not been overly concerned with islands, either those of the Pacific or of the Caribbean. Their faunas mostly show relationships with those of adjacent continents, or of interconnecting island chains. The fauna of the Hawaiian Islands is rather a special case, and I will comment on it later. New Zealand has no endemic drosophilid fauna (Hennig, 1960).

With regard to distribution, I am concerned with general patterns rather than finer details of pattern (altitude, seasonality, etc.). These are very incompletely known and will be of concern later, when the overall picture is completed. In consequence, I list the distributions only by continent or by some well-known descriptive term (Holarctic, Pantropical, etc.). I include Malaysia, New Guinea, the Philippines, and so on as part of Eurasia (EA in Table 1). I have considered it necessary to exclude the widespread cosmopolitan or domestic species when listing distributions. Thus, the *melanogaster* group is listed as being found in Africa, Eurasia, Australia, and the Pacific islands (Micronesia, etc., excluding the East In-

TABLE 1. Taxonomic Listings of Groups, Distribution, Culture, and Figure where Phylogenetic Position is Shown

Group	Culture ^a	Distribution ^b	Figure
FAMILY: DROSOPHILIDAE			
Subfamily: Steganinae			
<i>Amiota</i>		WW	1, 5
<i>Amiota</i>	0		
<i>Phortica</i>	0		
<i>Electrophortica</i>	—	Baltic amber	1
<i>Gitona</i>	0	AF, EA, NW	1
<i>Leucophenga</i>	0	WW	1
<i>Oxyphortica</i>	0	EA	1
<i>Paraleucophenga</i>	0	AF, EA	1
<i>Pararhinoleucophenga</i>	0	EA	1
<i>Protostegana</i>	0	WW	1
<i>Rhinoleucophenga</i>	0	NW	1
<i>Stegana</i>		WW	1, 5
<i>Stegana</i>	0		
<i>Steganina</i>	0		
Subfamily: Drosophilinae			
<i>Chaetodrosophilella</i>	+, B	EA, PI	4, 6
<i>Chymomyza</i>	+–0, B	WW	2, 6
<i>Dettopsomyia</i>	+–0, B	WW	3
<i>Drosophila</i>			
<i>Dorsilopha</i>	+, B	EA	4, 6
<i>Drosophila</i>			
<i>annulimana</i>	+–?, B	NW	3, 6
<i>bizonata</i>	+–?, C	EA	—
<i>bromeliae</i>	±–?, B	NW	3, 6
<i>canalinae</i>	+–?, B	NW	3, 6
<i>carbonaria</i>	0	NA	3, 6
<i>cardini</i>	+, B	NW	4, 6
<i>carsoni</i>	+, B	NA	3, 6
<i>castanea</i>	+, B	NW	3, 6
<i>dreyfusi</i>	+, B	NW	3, 6
<i>funnebris</i>	+, B, C	HO	2, 6
<i>guaramunu</i>	+, B	NW	4, 6
<i>guarani</i>	+, B	NW	4, 6
<i>histrio</i>	±, B	EA	—
<i>immigrans</i>	+–0, B, C	EA, AU, PI, AF	4, 6
<i>macroptera</i>	±, B	NA	4, 6
<i>melanderi</i>	±, S	HO	4

^a Abbreviations for culture are as follows: B = banana medium, C = corn meal medium, S = special techniques; + = readily cultured, ± = difficult, 0 = not successfully cultured to date, ? = probably culturable.

^b Abbreviations for distributions are as follows: AF = Africa, EA = Eurasia, AU = Australia, PI = Pacific Islands, HI = Hawaiian Islands, NA = North America, SA = South America, WW = World-wide, PT = Pantropical, HO = Holarctic, NW = New World.

TABLE 1. Continued

Group	Culture ^a	Distribution ^b	Figure
<i>melanica</i>	+, B, C	HO	3, 6
<i>mesophragmatica</i>	+—?, B	NW	3, 6
<i>nannoptera</i>	+, B	NA	3, 6
<i>pallidipennis</i>	+, B	NW	4, 6
<i>peruviana</i>	±, B	SA	3, 6
<i>pinicola</i>	±, S	NA	4, 6
<i>polychaeta</i>	+, B	EA, PI, NW	3, 6
<i>quinaria</i>	+—?, B	HO	4, 6
<i>repleta</i>			
<i>fasciola</i>	+—±, B	NW	3, 6
<i>hydei</i>	+, B	NW	3, 6
<i>melanopalpa</i>	+, B	NW	3, 6
<i>mercatorum</i>	+, B	NW	3, 6
<i>mulleri</i>	+, B	NW	3, 6
<i>robusta</i>	+, B, C	HO	3, 6
<i>rubrifrons</i>	+, B	NA	4, 6
<i>sternopleuralis</i>	±, B, C	EA	—
<i>sticta</i>	+, B	SA	4, 6
<i>testacea</i>	±, B	HO	4, 6
<i>tripunctata</i>	+—?, B	NW	4, 6
<i>virilis</i>	+, B	HO	3, 6
<i>Engiscaptomyza</i>	?, S	HI	4
<i>Hirtodrosophila</i>			
<i>denticeps</i>	0	EA	4, 6
<i>duncani</i>	+, B	NA	4, 6
<i>hirticornis</i>	±—0, S	EA, NW	4, 6
<i>quadrivittata</i>	±—0, S	EA	4, 6
Other species	±—0, S	WW	4
<i>Phloridosa</i>	0	NW	3, 6
<i>Scaptodrosophila</i>			
<i>bryani</i>	+, B, S	AF, EA, AU, PI	2, 6
<i>coracina</i>	+, B, S	EA, AU, PI	2, 6
<i>subtilis</i>	+, B, S	EA	2, 6
<i>victoria</i>	+, B, S	HO	2, 6
Other species	?, S	AF, EA, AU, PI	2
<i>Siphlodora</i>	0	NW	4, 6
<i>Sophophora</i>			
<i>melanogaster</i>	+, C, B	AF, EA, AU, PI	2, 6
<i>obscura</i>	+, C, B	HO	2, 6
<i>populi</i>	0	NA	6
<i>saltans</i>	+, C, B	NW	2, 6
<i>willistoni</i>	+—0, C, B	NW	2, 6
<i>Sordophila</i>	+, B, S	NA	3, 6
Hawaiian drosophiloids	+—0, S	HI	4, 6
<i>Hypselothyrea</i>	0	AF, EA	2, 6

TABLE 1. Continued

Group	Culture ^a	Distribution ^b	Figure
<i>Liodrosophila</i>	±-0	EA, AU, PI	2, 6
<i>Microdrosophila</i>	±-0, S	AF, EA, AU, PI, NW	1
<i>Mycodrosophila</i>	+ -0, S	WW	4, 6
<i>Neotanygastrella</i>	0-?, S	AF, EA, PI, NW Miocene amber	4, 6
<i>Nesiodrosophila</i>	0-?, S	EA, PI	4, 6
<i>Paramycodrosophila</i>	0-?, S	EA, AU, PI, NW	6
<i>Samoaia</i>	±, B, S	PI	4, 6
<i>Scaptomyza</i>	+ -?, S	WW	4, 6
<i>Titanochaeta</i>	0	HI	4, 6
<i>Zaprionus</i>	+ -?	AF, EA, PI	4, 6
<i>Zaprionthrica</i>	0	NW	—
<i>Zygothrica</i>	0-?, S	NW, PI	4, 6
	Not placed in subfamily		
<i>Lissocephala</i>	0	PT	1, 5

dies, Hawaii, and New Zealand), even though some cosmopolitan species are found in the New World and Hawaii. When groups are indicated as being present in an area, this should not be taken as implying that they completely occupy that area, although they may do so. Hence, by world-wide I mean only that the group is represented by presumably noncosmopolitan species in Africa, Eurasia, North America, and South America. It may or may not also be present in Australia, for that fauna is poorly known, and it may be present in some islands I take no special note of, as those of the Caribbean, for example.

Culturability is shown in Table 1 by symbols (+, ±, etc.). They indicate the ease of culture, but only in a very general way, since members of a given group are not always cultured with comparable ease. The culture medium is indicated (B = banana, C = corn meal, S = special), and in some cases the probable range of culturability within the group is also shown (+-±, etc.). Recipes, general culture methods, and a key to the United States species of *Drosophila* are given by Strickberger (1962). Special methods are quite varied and depend somewhat on the investigator. The methods of Wheeler and Clayton (1965) and Speith (1972) are useful for many forms that are otherwise impossible to maintain in the laboratory.

Finally, a word needs to be said about terminology. I shall be referring to radiations, and in the figures these are represented by several, or even many, lineages arising at one level in the dendrogram. In part, or in places, this will be an evolutionarily realistic picture of diversification. Certainly there is no reason to suppose that populations do not at times fragment, effectively founding several or many independent lineages simultaneously. In other cases radiations will reflect lack of evidence as to the sequence of events by which diversification proceeded at a given time. For these, relevant character states are discovered in so many of their possible combinations that no hierarchical pattern is discernible. In some of these instances future work may discover patterns of character covariation where none are now seen. In others, true radiation, rapid diversification within a new adaptive zone, habitat, or geographical area, will remain the parsimonious inference. The radiations referred to here must be regarded as conservative indications of covariation patterns in the data. Future work may show certain branches from a radiation to be more closely related than is presently indicated; it is unlikely that they will be shown to be less closely related. Finally, neither vertical nor horizontal dimensions in the figures have significance. These were determined at the whim of the illustrator. Only sequence of diversification is to be read from the dendrograms.

Phylogeny, Ecology, and Biogeography

Origin and Early Radiations of the Family Drosophilidae

The family Drosophilidae stems from a cluster of families of Acalypterae, the Drosophiloidea (Hennig, 1958). Of these (Curtonotidae, Drosophilidae, Diastatidae, Camillidae, Ephydriidae), the Diastatidae are most closely related to the Drosophilidae (Figure 5). Members of the two major families of this radiation, the ephydriids and the drosophilids, have larval stages depending for food on organisms or organic matter in a liquid or semiliquid medium. The larval stages of many ephydriids are aquatic, but some are found in foul muds, manures, or carrion, while others mine the stems of aquatic or terrestrial plants. The diastatids are saprophagous in leafmold (Hennig, 1965), as are a considerable number of species of somewhat more distantly related families (Oldroyd, 1964). Okada (1962) has suggested that larval feeding on sap of bleeding trees was the primitive drosophilid condition, but I suspect the group was not quite so specialized in the earliest times. The drosophilids of the primitive radiations (Figure 1) are quite varied in their habits. Some species of

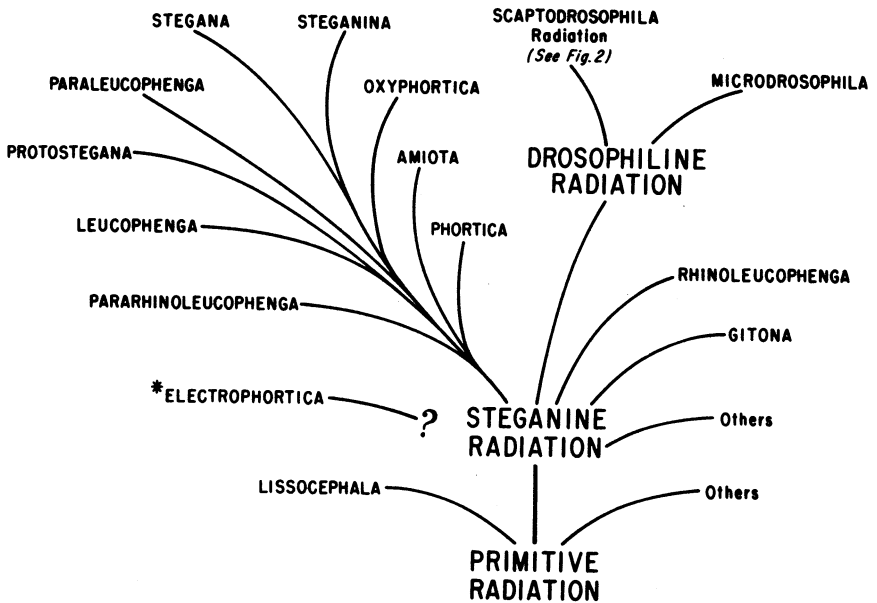


Figure 1. The early radiations of the family *Drosophilidae* showing the origin of the genus *Drosophila* from among the early drosophiline genera with the appearance of the subgenus *Scaptodrosophila* (upper right). The genus *Electrophortica* (*) is described from Baltic amber of Eocene age.

Amiota are sap feeders and some are fungivorous. Species of *Leucophenga* are fungivorous, larvae of *Stegana* are reported under bark [Morge (1956) cited by Okada (1968a)] and in flowers (Buruga and Olembo, 1971), species of *Gitona* are reported in broken plant parts, flowers, fruits, rotting cactus, and as parasites of mealybugs, a species of *Rhinoleucophenga* is parasitic on coccids, and so on. Many drosophiline species are reported in rotting leaves and decaying or fermenting fruit, as well as in fungus, sap, flowers, and pollen (Wheeler, 1952; Heed, 1957; Cole, 1969; Okada, 1956, 1962, 1968a; Pipkin, 1964). To me, this adds up to a pattern of opportunism and versatility centering around the saprophagous leafmold habit of some primitive acalypterates. It is not uncommon for drosophilids to exhibit considerable breadth in their choice of breeding site. Thus, for example, Basden (1954) reports *D. subobscura* as breeding naturally in the saps of elm, willow, and sycamore, in iris root, in toadstools, and in fermenting fruit and oak galls; this very nearly embraces all the basic food types exploited by the family, excepting only flowers and the parasitic modes of existence. It is not improbable that the earliest drosophilid was an opportunist of this sort, capable of exploiting many alternative resources but perhaps preferring one of these over the others. On present evidence it seems simplest to visualize the diversification of the *Droso-*

philoidea as being founded on the food resources of rotting leafmold, with two major lineages diverging and specializing from this. On the one hand the ephydriids exploited the wetter, more foul muds and related organic decay, with some eventual specialization on algae. On the other hand the drosophilids evolved more toward decaying leaves, fermenting vegetables and fruits, saps, and fungi, with specialization mostly on yeasts. At one time or another both have adjusted to mining tissues of plants.

The most primitive genus of drosophilids is *Lissocephala* (Figures 1 and 5). It is pantropical in distribution and provides sound evidence for the tropical origin of the Drosophilidae. The food habits of these species are not well known, but I have swept them from compost. Wheeler and Kambysellis (1966) report sweeping them from garbage, Buruga and Olembo (1971) report them on fruit, and Carson (Carson and Wheeler, 1973) discovered larvae of one of these species developing on land crabs on Christmas Island.

The major genera of the steganine radiation (*Amiota*, *Leucophenga*, *Stegana*) also have their main distributions in the tropics, and this lends support to the conclusion that the family originated there. The genus *Amiota* is world-wide in distribution, and so is *Stegana* (Table 1), with *Stegana* being proportionately less well represented in the temperate fauna than *Amiota*. *Gitona* is found in Africa, Europe, and North America, but the assignment of some of the North American species to specific genera is uncertain (McAlpine, 1968), and these may represent a group endemic to North America (Wheeler and Takada, 1971). Some of the remaining genera are also restricted to certain regions, as *Rhinoleucophenga* to the Americas, *Pararhinoleucophenga* to Taiwan, and *Oxyphortica* to New Guinea, Taiwan, and Southeast Asia.

The major steganine genera, and the minor genera associated with them (to the left in Figure 1), form a coherent lineage, sharing much, both of internal and external anatomy. Of these, *Amiota* combines more of both drosophiline and steganine attributes, and among the Steganinae it is the most generalized group. In collecting, it has been my experience that *Amiota* tends to be of the shaded forest, *Leucophenga* is more often of the brighter and less humid forest edges, savannas, and brushy meadows, and *Stegana* is of stream sides, mossy banks and logs, and humid ravines. *Oxyphortica* resembles *Leucophenga* in being found in drier and more-open places, particularly in the upper reaches of valleys or the drier valley edges. Hence, in spite of some close resemblance and overlap in food choice among the members of this kindred, resources seem generally to be partitioned along habitat boundaries, and direct competition between individuals of these genera must be limited.

Most of these species can be collected by sweeping brush and vegetation in appropriate habitats, with special attention to tree trunks, fallen logs, and mossy banks. Fungus is important also, as are slime fluxes and bleeding trees, and an aspirator is often the most convenient way to collect from these. *Leucophenga* occasionally comes to fermenting baits, or local fungus can be gathered and used as bait. Males of *Amiota* have a habit of buzzing around the head of a person walking through the woods, and then they can be netted. Basden (1954) reports obtaining good numbers of both males and females of a species of *Amiota* using fermenting apple bait placed high up in oak and chestnut trees. He also reports collection of *Stegana* near fungus, and on several occasions I have collected female *Stegana* directly off mushrooms.

Hennig (1965) describes a fossil genus, *Electrophortica*, from Baltic amber. He notes that in some keys for the family it would be in the genus *Amiota*, but it might equally well belong to the stem group for all recent species, or it could be the ancestral species itself. Baltic amber may be from Eocene times, and the presence of a drosophilid then and there is fully consistent with the conclusion one reaches from steganine distributions. These indicate dispersion at a time when tropical corridors connected Asia and North America, and the middle of the Oligocene period is very nearly the latest time when that might have been true. This fossil seems to have existed before then, and probably much before then. Depending on the reliability of dates for Baltic amber, the family Drosophilidae may be 50 million years old, or older.

The Early Drosophiline Radiations

The genus *Microdrosophila* is treated taxonomically by Okada (1968*b*). It has a world-wide distribution through the tropics, and there are several representatives in the temperate zone. The greater number of known species is from Southeast Asia and the adjacent islands. Okada (1968*a*) reports eggs, larvae, and pupae from rotting sweet potatoes and rotting bamboo leaves, and adults can be collected by sweeping brush, garbage, and rotting fruit. Some of the species can be cultured on standard *Drosophila* medium, but culture is generally difficult.

The primary distribution of the *Scaptodrosophila* radiation (Figures 2 and 6), exclusive of the *subtilis* and *victoria* groups, is in the tropics. It is probably represented in the New World by the genus *Zapriothrica*, individuals of which have been collected from flowers of *Datura* (Wheeler, 1956). As the subgenus *Scaptodrosophila*, members of this radiation are distributed through the Old World tropics from Africa to Australia and the

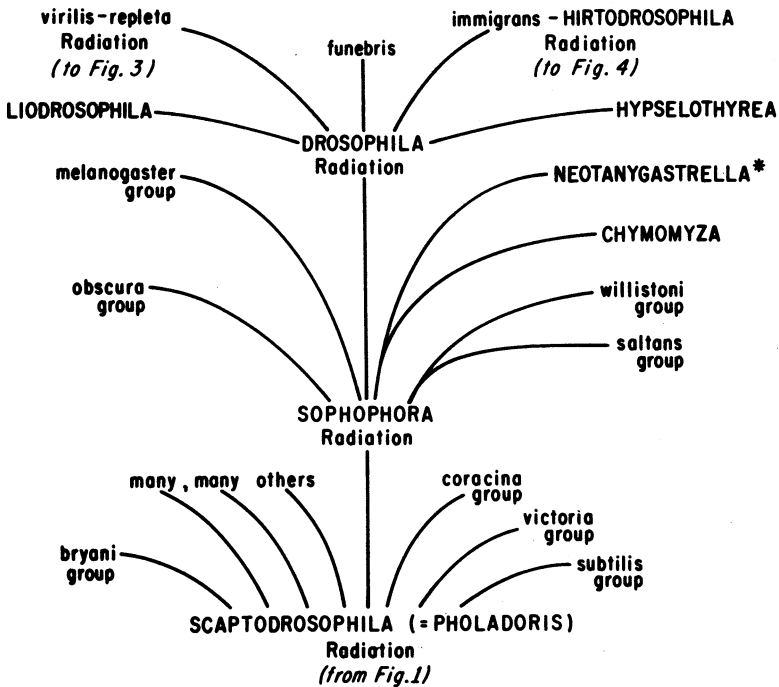


Figure 2. The early radiations of *Drosophila* and derived genera (continued from Figure 1).

Pacific, and this defines the place of origin of the genus. Although there has been a sizeable expansion of *Scaptodrosophila* into Australia [44 of 46 recognized species are regarded as endemic (I. R. Bock, private communication)], no evidence indicates that the group originated there. Much evidence points to its origin in tropical Asia (Throckmorton, unpublished).

Species of *Scaptodrosophila* are collected from tree sap, palm sap, fungus, fruit, and flowers. Okada (1968a) reared *D. throckmortoni* Okada 1973 (= *D. rufifrons* Okada 1956) from slime flux on oak and *D. coracina* from fallen leaves. Hence, the feeding diversity encountered among the steganine genera is still encountered here, but with a shift in emphasis toward more feeding on fermenting fruit. Burla (1954), Lachaise (1974a,b), and Lachaise and Tsacas (1974) describe the ecology of African species, Mather (1955, 1956a) and I. R. Bock (in preparation) discuss the Australian species, and Wheeler and Takada (1964) and Wheeler and Kambysellis (1966) list Pacific island species.

In contrast to the other species of this radiation, the *victoria* and *subtilis* groups have primary distributions in the north temperate zone. The *subtilis* group is from China and Japan, while the *victoria* group has a disjunct distribution, with species in Europe, the Middle East, and North America. The distributions of these two groups do not bear directly on the problem of the origin of the genus *Drosophila*. Anatomically they

are clearly derivative within *Scaptodrosophila*. The *victoria* group breeds on bleeding cottonwoods, and its disjunct distribution almost certainly originated at the disruption of the temperate deciduous forest in late Miocene times. Judging by present distributions, the *Scaptodrosophila* radiation occurred prior to the middle of the Oligocene period, so the *victoria* group would have arisen later than that but well prior to mid-Miocene, presumably by invasion of the temperate deciduous forest at the northern border of the Old World tropics.

Many of these species can be collected fairly easily from the standard, fermenting fruit baits, or by sweeping or aspirating from bleeding trees, fungus, or fallen fruit. Some of these species show less diurnal periodicity than is usual for *Drosophila*, tending to come to baits in the hotter parts of the afternoon and preferring fresher baits than do the better-known species (*D. melanogaster*, etc.). Some flies do well on various "instant" *Drosophila* media, and I have been able to bring otherwise recalcitrant species into culture through exposing them to a light regimen of long days and short nights. The *victoria* group in North America is reviewed most recently by Pipkin (1961). At present, the known species are concentrated in the Southwest, but one or more species do exist in the United States east of the Rockies (Wheeler, 1949; L. Throckmorton, unpublished).

The Sophophoran Radiation

This radiation (Figures 2 and 6) is comprised of the *saltans-willistoni* lineage in the New World tropics, the *melanogaster* lineage in the Old World tropics, and the *obscura* group distributed throughout the Holarctic temperate zone. It also includes isolated species such as *D. populi*, and the two genera, *Chymomyza* (world-wide) and *Neotanygastrella* (pantropical).

Although I have not myself seen *Neotanygastrella*, I include it here because two fossil specimens, tentatively assigned to this genus, are described by Wheeler (1963) from Mexican amber of Oligocene or early Miocene age. Frota-Pessoa and Wheeler (1951) and Burla (1954) regard *Chymomyza* and *Neotanygastrella* as being very close, so I include them in one lineage in the figure. I note that Burla's figure (1954, his p. 52) shows internal details that place *Neotanygastrella* closer to *D. populi* than to *Chymomyza*, so *D. populi* may be very near the stem from which these two genera arose. *D. populi* was collected over fallen cottonwood in Alaska (Wheeler and Throckmorton, 1960), and I have collected two closely related species from Taiwan. Hence, *D. populi* seems to be a northern relict of a subtropical group that was once distributed through that region. *Neotanygastrella* and *Chymomyza* are both attracted to cut tree trunks, *Chymomyza* is attracted to peeled bark of aspen, alder, fir,

pine, and birch (Wheeler, 1952; Basden, 1954). *C. amoena* breeds in acorns and *C. aldrichi* larvae have been found under aspen bark [Spieth, reported by Wheeler (1952)]. Wheeler (1963) suggests an Afro-Asian origin for the *Chymomyza* complex, with the African species representing the ancestral type that gave rise to both *Chymomyza* and *Neotanygastrella*. This suggestion is compatible with other available evidence. These genera relate through forms such as *D. populi* to Afro-Asian *Scaptodrosophila* similar to *D. bryani* or *D. latifasciaeformis*, which themselves represent the primitive group out of which the sophophoran radiation emerged. Here, as for the previous radiation, the New World lineages are derivative relative to the Old World forms, and none of the higher lineages show any indication of having been derived from them. The Old World forms, on the other hand, intergrade in many features, both with members of lower and higher radiations. Hence, parsimoniously, the sophophoran radiation can be regarded as originating in the Old World tropics. From distribution, the time for this would again be very much before mid-Oligocene times. The fossils indicate the same thing, since the sophophoran radiation must have occurred well before the Oligocene–Miocene times from which the fossils are recorded.

The *melanogaster* group, of 76 named species, is reviewed by Bock and Wheeler (1972). Aside from four widespread species, its distribution is within the tropical and subtropical regions of the Old World. In south Asia it extends from India and Nepal east to Korea, Japan, and the other islands offshore (Taiwan, Philippines, New Guinea, etc.), thence east and south to the islands of the Pacific, and then along the northern edge of Australia. Members of the group are also widespread in Africa.

There are four species of nearly cosmopolitan distribution. *D. kik-kawai* is from Asia, the Pacific islands and South America; *D. ananassae* is found in Africa, Asia, Australia, the Pacific islands, and the New World; and *D. simulans* and *D. melanogaster* are both world-wide, being excluded only from the polar regions. As noted by Bock and Wheeler, however, *D. melanogaster* is more common in colder regions, while *D. simulans* is more common in the warmer areas. From patterns of distribution it can be concluded that the *melanogaster* subgroup, including both *D. melanogaster* and *D. simulans*, arose in Africa (but see Bock and Wheeler for a less parsimonious alternative, and see Tsacas and Lachaise, 1974, for their views), and they probably coevolved with man throughout their period of coexistence with him. The *melanogaster* group itself almost surely arose in south Asia, and it has diversified and dispersed from there. While the group, or at least a *protomelanogaster* group, must have existed prior to mid-Oligocene times, its major radiation has quite obviously occurred since the New and Old World tropics became isolated from each other. A second-

ary radiation of the group has occurred in Africa, possibly starting in the late Oligocene times. Although the *melanogaster* group is represented in Australia, present evidence suggests no great amount of evolution there (I. R. Bock, private communication). In view of the history of the Australian continent, this may not be surprising. From the time when the *melanogaster* group originated in south Asia, Australia has been connected to that region only through island chains. They may not have been efficient corridors for *Drosophila* migration until quite recently, and even now, possibilities for movement across them are not great. That regardless, the subgenus *Scaptodrosophila* did achieve a greater radiation in Australia, presumably because it originated earlier and arrived there sooner.

The ecology of species in this group has not been greatly studied. The majority can be collected at fermenting fruit baits or swept over fallen fruit. Carson (1965) lists a great variety of breeding sites for widespread species of this group, including more than twenty different kinds of fruit, living flowers, potatoes, slime fluxes, mushrooms, rotting plant tissues, stale beer, and human feces. At least one endemic species of the Philippines, *D. elegans*, is collected from flowers, as was discovered by C. Kanapi (unpublished). Most of the members of this group can be cultured in the laboratory on standard media, though many of them are considerably more difficult to care for than is *D. melanogaster*.

The *saltans* and *willistoni* groups are products of a single sophophoran lineage. They are distinct from all other sophophoran groups but very close to each other, and they are derivative within the subgenus. A review of the *saltans* group by Magalhaes (1962) includes a map of distributions and a key to the species. Two species have been described since then (Mourão and Bicudo, 1967), for a total of 21 species in five subgroups. These show an orderly progression from the more primitive *cordata* and *elliptica* subgroups, through the *sturtevanti* and *parasaltans* subgroups, to the *saltans* subgroup, which is unequivocally the most derivative cluster of species. Members of the primitive subgroups are distributed from Mexico to Brazil. Most of the *saltans* subgroup species are in South America. They show a distribution pattern typical of groups that evolved on the South American continent and then spread northward after the building of the present Isthmus of Panama in the late Pliocene period, perhaps 4.5 million years ago. The evidence from distribution thus suggests origin of the *saltans* group in tropical North America, colonization of South America at least once prior to the building of the present Isthmus of Panama, diversification in South America to produce at least the *parasaltans* and *saltans* subgroups, and finally diffusion of the *saltans* subgroup northward into Central America, Mexico, and the Caribbean. Except for Pipkin's observations (1965), the ecology of these species is not

well known. Some do not come readily to bait, but *D. saltans* is reported as being bred from pineapple (Magalhaes, 1962), *D. sturtevanti* from citrus (Heed, 1957) and from fallen fruits and blossoms, and *D. pro-saltans* from fallen fruits and blossoms (Pipkin, 1965). The larvae skip, which is a habit often associated with sap-feeding forms, but in this case it may only indicate the retention of one of the characters of *Scaptodrosophila* ancestors.

The *willistoni* group (25 species) divides into three major clusters. One of these, morphologically the most primitive form, is comprised of *D. willistoni* and its siblings, a second contains only *D. fumipennis*, and the third contains all the remaining species, including the *alagitans-bo-cainensis* complex of Wheeler and Magalhaes (1962). The distribution of these clusters presents almost a reverse image of that of the *saltans* group. Here it is the primitive group that is found predominantly in South America (Spassky *et al.*, 1971). The derivative group extends from Mexico south to Argentina (Wheeler and Magalhaes, 1962). *D. fumipennis* is reported from Costa Rica south to Brazil (Wheeler, 1970). In light of these distributions, a fragile case might be made for the hypothesis that the *saltans* group originated in tropical North America while the *willistoni* group originated in South America, perhaps evolving there in isolation after an early crossing of the water gap then existing between the two continents. Subsequent crossings in both directions could complete existing patterns, and not all of these need to have been prior to the formation of the Isthmus of Panama. The most recent evolutionary event would have been the blossoming of sibling clusters in each lineage. Those of both the *saltans* and the *willistoni* groups seem to have originated in South America, but the diversification of the *willistoni* siblings seems to have been nearly complete at the time when these species moved northward into Central America, whereas the *saltans* cluster was still actively evolving at that time. Several of the *willistoni* siblings are found together in most Central American localities (Spassky *et al.*, 1971), as if an entire fauna had moved northward, but in the *saltans* cluster the pattern is more one of individual populations spreading northward, with some speciation in the process. Thus, the species *D. saltans*, with a distribution from Costa Rica to Mexico, is largely parapatric with *D. pro-saltans*, as if this were one of the most recent speciation events in that cluster, and there is apparently much less sympatry among the *saltans* siblings than among the *willistoni* siblings. The diversification of the semi-species of *D. paulistorum* (Spassky *et al.*, 1971; Dobzhansky, 1972) is apparently still continuing. One can speculate that at least part of this diversification was induced by Pleistocene events, but population shifts seem

not to have been great, and genetic differentiation seems to have been comparatively minor (Ayala *et al.*, 1974).

Only slightly more is known of the ecology of the *willistoni* group than is known for the species of the *saltans* group. These species can be collected from the standard fruit baits or by sweeping over fallen fruits. *D. sucinea*, *D. nebulosa*, *D. fumipennis*, and the *willistoni* siblings have been reared from fruits and flowers (Pipkin, 1965) and some have been swept from acorns (Heed, 1957; Pipkin *et al.*, 1966). *D. willistoni* and its closest relatives are cultured readily, but attempts to culture many of the remaining species have been unsuccessful. *D. capricorni* has been reared from flowers, and flower feeders are all difficult to rear in the laboratory.

The 23 species of the *obscura* group are distributed throughout the North Temperate Zone. Ten species are recorded from Eurasia, being distributed from North Africa, Spain, the British Isles, and Scandinavia through the Middle East to Japan and Korea. Thirteen species are from the New World, with a distribution extending from Alaska, Manitoba, and Quebec south to Florida, Mexico, Guatemala, and central South America. Although phylogenetic relationships are known for several species clusters within the group, no overall phylogeny is available. Dobzhansky and Epling (1944) and Heed *et al.* (1969) describe the relationships and distribution of *D. pseudoobscura* and its relatives in western North America. Miller (1958) outlines the distribution of the remainder of the North American species, and Sulerud and Miller (1966) give a key to these species.

The *obscura* group is most closely related to the *melanogaster* group and to the subgenus *Scaptodrosophila* of the Old World tropics. Although several species have distributions bordering or extending into the tropics, there is no indication that any of these represents ancestral links to tropical species. The available evidence suggests that the group originated from a *protomelanogaster* lineage of the Old World tropics. Following adaptation to temperate habitats, diversification occurred in the Palearctic and the group spread to North America through the temperate deciduous forest prior to mid-Miocene times. Within the Palearctic, the members of this group present no clear pattern of diversification. Somewhat more of a pattern is discernible in North America, where two relatively distinct subgroups are present. The *obscura* subgroup (5 species) is western, with a distribution from British Columbia south through the Rocky Mountains to Mexico, Guatemala, and Colombia. The *affinis* subgroup has both a western (4 species) and an eastern (4 species) branch, with one species (*D. athabasca*) having both eastern and western-northern forms. The western branch extends from Oregon south through the Rocky Mountains to

Colombia, Venezuela, Bolivia, and Haiti. The eastern cluster extends from southern Canada south to Florida and west through the Great Plains almost to the eastern face of the Rockies. In the west, *D. athabasca* extends from New Mexico north to Alaska, then east to northern Manitoba (Throckmorton, unpublished) and Quebec, and then south to Tennessee and Nebraska (Miller, private communication).

Tentatively, the New World evolution of the *obscura* group appears as follows: Either before arrival in the New World or shortly thereafter, two main types existed. Presumably both of these were western, but eventually one or more of the *affinis* subgroup types extended the distribution to the east. Ecological separation of the North American continent by grasslands of the Great Plains dates from the Miocene era, and it may have been this partial barrier that isolated the eastern and western branches of the *affinis* subgroup and that restricted the *obscura* subgroup to the West. Much of the area occupied by *D. athabasca* was covered by ice during the Pleistocene so that part of the range must have been occupied quite recently. The eastern and western-northern forms of *D. athabasca* overlap in a zone extending from Minnesota to Maine (Miller, private communication), and significant barriers to gene exchange between them have been demonstrated (Miller, 1958; Miller and Westphal, 1967; Miller and Voelker, 1968, 1969a,b). Most of the distribution of these species to the Neotropics has been at higher altitudes, and the present pattern undoubtedly represents the end result of chance colonizations, of island hopping from mountain top to mountain top over several millions of years, with just three successes (*D. azteca*, *D. tolteca*, and *D. pseudoobscura*) out of unnumbered trials. One colonization, that of Colombia by *D. pseudoobscura*, is thought to have occurred within the last few decades (Prakash, 1972).

Dobzhansky and Epling (1944, their pages 147–183) discuss paleoecology and the evolution of the *obscura* subgroup in company with the development of the western paleoflora. There is little reason to doubt that many of its chromosome inversions have persisted since Miocene times, or earlier.

As usual, the ecology of these species is by no means well known. The most important natural breeding site seems to be in sap of trees such as oak, sycamore, willow, and elm. *D. pseudoobscura* has also been reared from cactus (Heed, private communication), *D. pseudoobscura*, *D. persimilis*, and *D. affinis* from the sap of wild grape vines (Patterson and Stone, 1952), and *D. pseudoobscura* from slime flux on fir (Carson, 1965). Both *D. athabasca* and *D. algonquin* have been reared from fungi, but this is probably not an important natural breeding site for these

species (Carson and Stalker, 1951; Miller and Sanger, 1968). *D. affinis* has been reared from ripe blackberries (Miller and Weeks, 1964). *D. subobscura* has also been reared from toadstools, fermenting fruits, and so on, and probably many of these species are similarly general in their tastes. Most of the *obscura* subgroup species can be collected readily at baits and cultured fairly easily. The *affinis* subgroup species are also easy to collect, but some of them are troublesome to keep in culture for any length of time. They tend to be sensitive to propionic acid as a mold inhibitor, and they are often easier to maintain if some alternative chemical is used for the suppression of molds.

The *Drosophila* Radiation

This radiation is comprised primarily of major subradiations (Figures 2 and 6). In addition, several groups are clearly related at this point to the higher *Drosophilinae*, yet they show none of the special features of any of the well-defined lineages. *Liodrosophila* and *Hypselothyrea* are distinctive, small flies. *Liodrosophila* is the more diverse of the two, and it is distributed from South Asia to the Pacific islands. *Hypselothyrea* is from Africa and south Asia. The groups themselves are compact, but they differ as much from each other as from the other groups associated with this radiation. They can be regarded as independent lineages arising from early species of the *Drosophila* radiation. As lineages they probably existed by Oligocene times, but since they are not represented in the New World, a major part of their diversification may have occurred during the Miocene times or later, which would be consistent with their distinctiveness as groups as well as with their present distribution. Individuals of both groups are most readily collected by sweeping low shrubs, thick leafy vegetation, and tall grass in shaded areas under trees. Okada (1956) reports collecting *Liodrosophila* from tree sap, and some species of *Liodrosophila* can be cultured on standard *Drosophila* culture medium.

The *funnebris* group is also associated with this radiation. In contrast to the two previous groups, its species share derivative features with species of both major subradiations. Hence, it cannot be assigned definitely to either one. Of the six species in this group, two are Oriental, three are Nearctic, and one, *D. funnebris*, is cosmopolitan. The group's primary distribution is within the temperate zone, and its relationships are with species of the Old World tropics. As a member of the temperate deciduous forest fauna, it most probably dispersed to the New World prior to mid-Miocene times. Within the Nearctic region, *D. macrospina*

is represented by a cluster of subspecies. The form *D. macrospina macrospina* is distributed from Texas and Arizona north to Montana, east to New York, and thence south to Florida. *D. m. limpiensis* is reported from Texas, Arizona, and Mexico, while *D. m. ohioensis* is reported from Ohio, Michigan, and New York. The two species *D. subfunnebris* and *D. trispina* are distributed to California and Washington, and California and Arizona, respectively. This distribution pattern is a very common one for *Drosophila* species of the temperate deciduous forest. It will be commented upon during discussion of the next cluster of species. The Nearctic form, *D. m. limpiensis*, is reported as breeding in bracket fungus on willow (Patterson and Stone, 1952), and *D. maculnotata* of Japan is reported from bleeding trees (Okada, 1968a). The cosmopolitan *D. funnebris* is reported from fungi, walnut husks, fruit, potatoes, and onions (Carson, 1965).

The *virilis-repleta* Radiation

This radiation (Figures 3 and 6), while complex in appearance, is basically simple. The primary radiation occurred in the Old World tropics, and I have seen representatives of it from Taiwan and Luzon. Eventually it extended from the Old to the New World tropics, and since that time there have been two centers of evolution for it. Out of this radiation in the Old World tropics came at least one temperate lineage, and the *repleta* group developed out of the Neotropical branch. The *repleta* lineage has also shown considerable diversification into the temperate zone and has produced several cosmopolitan species.

The early tropical radiation is represented by a heterogeneous assemblage of groups. The two species of the *tumiditarsus* group are both Oriental. The *polychaeta* group is represented in both the New and Old Worlds. *D. polychaeta* itself is distributed from the United States through Central America to Brazil, as well as to several Pacific islands, with the last probably being the result of human transport. The ranges of other New World species are within that of *D. polychaeta*. *D. daruma* of Japan is a member of this group (Okada, private communication), and the species of this group seem mostly to be associated with fallen fruit. The *annulimana* group is wholly Neotropical, being distributed to Mexico and Brazil. One of these species, *D. gibberosa*, has been reared from fruit. The genus *Dettopsomyia* is world-wide in distribution. *D. nigrovittata* has been reported from California, but it is primarily from the Old World tropics. *D. formosa* is the only Neotropical representative. Outside of Central America it is also found on several islands of the Pacific and In-

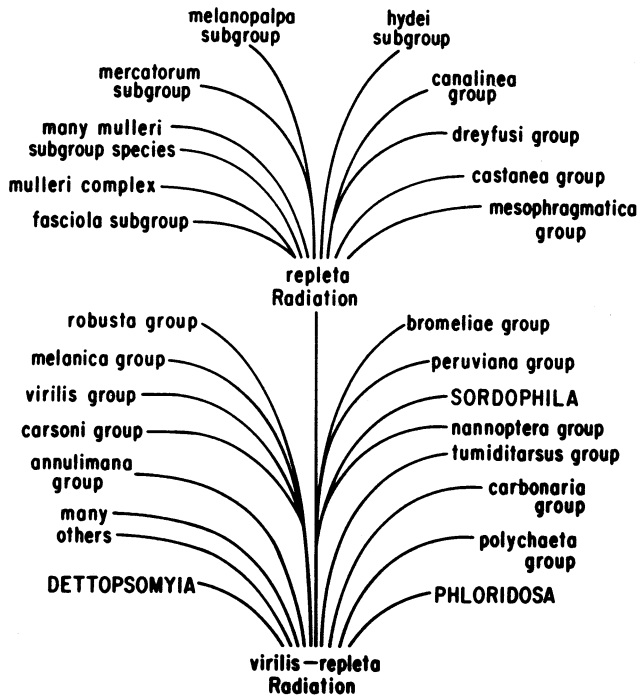


Figure 3. The virilis-repleta radiation continued from the upper left of Figure 2.

dian Oceans. It breeds in rotting banana stems and presumably was distributed through much of this region by man. The subgenus *Phloridosa* is a small cluster of flower feeders whose larvae utilize the pollen of *Datura*, *Hibiscus*, and so on. It is distributed from the southern United States south to Chile and Argentina, but it is mostly Neotropical. The *carbonaria* group contains only *D. carbonaria*, a species that breeds in bleeding mesquite, and its distribution is from the southern United States into Mexico (Patterson and Stone, 1952).

Several major temperate-forest groups emerged from the Old World limb of this radiation. Three of these now have a Holarctic distribution and one is Nearctic only. They seem to represent a single lineage that adapted to the temperate zone, diversified there, and eventually spread through the temperate deciduous forest to the New World. The *virilis*, *melanica*, and *robusta* groups are well represented in the literature of *Drosophila*, and each of these presents disjunct distribution patterns typical of groups associated with the temperate deciduous forests of the Holarctic region. The *robusta* group is comprised of eight species in the Orient and two species, *D. robusta* and *D. colorata*, in the Nearctic region. *D. robusta* breeds in the slime flux of elm (Carson and Stalker,

1951) and *D. sordidula* breeds in the sap of oak trees (Okada, 1968a). It is probable that other members of the group have similar habits. These species can be collected with standard baits, although many of them are quite rare, and most of them can be cultured on standard media.

Stalker (1966) treats the distribution and chromosome phylogeny of six North American members of the *melanica* group. Aside from these, there is one European species (Burla and Gloor, 1952) and one Oriental species (Okada and Kurokawa, 1957). Another species, *D. melanissima* of North America, may be a member of this group. In Eurasia the group's distribution is widely disjunct, although this may in part represent our lack of information regarding the *Drosophila* of central Asia. Disregarding *D. melanissima*, there are four eastern forms in North America and three species have east-west disjunct patterns. *D. melanura* shows a spotty distribution across the northern United States, *D. melanica* is scattered across the center of the continent, and *D. micromelanica* shows a comparable pattern across the south. *D. melanura* and *D. micromelanica*, together with an eastern form, *D. nigromelanica*, are phylogenetically the oldest representatives of the *melanica* group in North America (Stalker, 1966), and this disjunct pattern probably results from the fragmenting of the North American forests in Oligocene-Miocene times with the rise of the Rocky Mountains and the cooling and drying of the climate of western North America at that time. *D. melanica*, *D. paramelanica*, and *D. euronotus* exhibit a south-north-south pattern of speciation that might reflect Pleistocene changes (Stalker, 1966). Most of these species are readily cultured and can be collected with standard fermenting banana baits. Carson and Stalker (1951) report rearing *D. paramelanica* from slime fluxes on red oak, black locust, and elm. In Nebraska I have collected *D. paramelanica* in numbers from a bleed on willow where they congregated, but I did not attempt to rear them from it. *D. micromelanica* has been reared from a slime flux on oak (Heed, private communication).

The *virilis* group is discussed at length by Patterson and Stone (1952), and more recently by Stone *et al.* (1960). The group is presently comprised of twelve species; four European, one Oriental, six North American, and one cosmopolitan form, *D. virilis*. The group is divided cytologically into phylads (Stone *et al.*, 1960), and information from proteins shows the group to be comprised of two phylads that are completely consistent with the evidence from the chromosomes (Throckmorton and J. L. Hubby, unpublished). Both phylads are represented in the Nearctic and Palearctic regions. The group appears to have originated in Asia as a species of the temperate deciduous forest associated predominantly with riparian communities. This is the present habitat of most members of the *virilis* phylad, and *D. americana* has been bred from under the bark of

willow (Blight and Romano, 1953). Members of the *montana* phylad are associated mostly with riparian communities of the boreal and montane forests. One of these species, *D. lacicola*, has been bred from the rotting phloem of aspen (Spieth, 1951), and this is probably the most important breeding site for the American members of this phylad. However, Wheeler (private communication) has reared *D. flavomontana*, a North American species of the intermontane west, from slime flux on the narrow-leaved cottonwood, and *D. montana* breeds in red alder (Moorhead, 1954). Basden (1954) reports rearing *D. littoralis*, a European member of the *montana* phylad, from the stumps of recently felled sycamore in Scotland.

In North America the group shows an east-west pattern similar to that noted earlier for the *victoria*, *obscura*, *funnebris*, and *melanica* groups. Each phylad has eastern and western species, and again the pattern would reflect the disjunction of the North American forest in Oligocene-Miocene times. The present distributions of *D. montana*, *D. borealis*, and *D. lacicola* are partly or wholly in areas formerly covered by ice during the Pleistocene, and for one of these, *D. montana*, studies of proteins have shown that populations in areas formerly occupied by ice exhibit a distinct genotype. This genotype is distributed from high altitudes in the Colorado Rockies to the coastal plain in western Alaska, and it seems to represent a single "ecogenotype" that expanded from some Pleistocene refugium to occupy this broad area (Throckmorton and J.L. Hubby, unpublished). In Eurasia an east-west disjunct pattern is also seen, with *D. ezoana* in Japan and Korea, and *D. littoralis*, *D. lummei*, *D. lakovaarai* and *D. ovivororum* in Europe and Scandinavia. *D. virilis* is cosmopolitan but it was probably endemic in Asia (Patterson and Stone, 1952).

The *carsoni* group is comprised of only one species. It is represented by eastern (South Dakota to Maine) and western (New Mexico and Wyoming) populations in North America. These differ slightly morphologically, and breeding tests might disclose more than one species to be involved here. This is a rare species and nothing is known of its biology. It can be bred in the laboratory and collected on the usual baits.

Taken together, the *carsoni*, *virilis*, *melanica*, and *robusta* groups show remarkable parallels in distribution and ecology. They seem to be predominantly sap feeders, with some known from under bark near cuts or breaks and others from slime flux. Their distribution is that of the temperate deciduous forest, and there is no reason to assume other than that they achieved this distribution when the forest itself was continuous. The disjunction between Palearctic and Nearctic branches is attributed to the Miocene events that severed the Beringian connection, and the east-west disjunction within both the Palearctic and Nearctic can be attributed also to mountain-building episodes of these early periods. Since

these groups are derived from a radiation that itself occurred early enough so some of its members could reach the New World through tropical or subtropical corridors, the influence of Miocene events on intragroup distribution patterns is not at all improbable, which is not to say that parts of the patterns may not have been generated during the Pleistocene, as was noted earlier regarding late speciation events in the *melanica* group. The profound disjunctions exhibited by the groups in Eurasia, if real, may also partly reflect the severe effects of Pleistocene conditions on temperate faunas there. While it is conceivable that a series of evolutionary accidents produced all the parallels mentioned, parsimony does not permit us to take seriously such a compounding of coincidence. There can be little question that common environmental changes, effecting a common substrate, the deciduous-forest community, evoked the parallel responses exhibited by the four groups just discussed, by the *victoria*, *obscura*, and *funbris* groups mentioned earlier, and by the *quinaria*, *testacea*, and *melanderi* groups, which are yet to be discussed in connection with a higher radiation in the genus.

The remainder of the *virilis-repleta* radiation is centered in the tropics of the New World. It is comprised of the large *repleta* lineage and a smaller cluster of groups closely related to it. These latter groups are rather diverse on casual inspection, and their habits also are quite varied, but several share unique features with the *repleta* lineage and these were probably derived from a single original group in the New World. Ward and Heed (1970) have demonstrated that *D. acanthoptera* (of the monotypic subgenus *Sordophila*), *D. pachea*, and an unnamed species make up a cytological lineage that includes *D. nannopectera*. Through their courtesy I have been able to examine all these species. Morphologically, the first three comprise a tight cluster. They are very similar to each other and share several derivative features. *D. nannopectera* obviously shares a common ancestor with these, but it has no more in common with them than it does with the *bromeliae* group or *D. peruviana*. Hence, *D. nannopectera* can be regarded as the primitive representative of the lineage leading to *D. acanthoptera* and its relatives. *D. acanthoptera*, *D. nannopectera*, and the unnamed species are from dry habitats in southern Mexico, and *D. pachea* is found in the Sonoran desert of northern Mexico and Baja California. They all breed in cactus and all are fairly easy to rear in the laboratory. *D. pachea*, however, breeds only on senita cactus and requires medium that is supplemented with that cactus or with a specific sterol from it (Kircher and Heed, 1970). The *bromeliae* group is small, and I have seen only two species from it. They are collected from flowers and are distributed from Mexico through Colombia to Brazil.

They do not breed well in the laboratory, but with constant attention they can be maintained. Internally they have much in common with *D. nanoptera* and with *D. peruviana*. This latter species represents a cluster of small yellow forms of which I have seen several undescribed species. Together with the *bromeliae* group, these form a link between *D. nanoptera* and the *repleta* lineage. *D. peruviana* is from Peru and Brazil, and the undescribed species are also from South America. Pipkin *et al.* (1966) report breeding *peruviana*-like forms from flowers, and many of the flower-feeding species described by Pipkin (1964) appear to be derived from this radiation. The *flavopilosa* group of flower feeders (Wheeler *et al.*, 1962) is derived either from this radiation or from the *repleta* radiation. I have made no direct observation of these species.

The *repleta* radiation (Figure 3) includes the *castanea*, *canalineae*, *dreyfusi*, and *mesophragmatica* groups, as well as the large *repleta* group. With the exception of the *mesophragmatica* group, all of these have been shown to be related cytologically. Wasserman (1963) summarizes his work with this cluster of species, and morphological details permit the remainder of the pattern to be filled in. *D. castanea*, the sole member of its group, is distributed from Colombia and Venezuela to Mexico. It shares derivative morphological features with both the *mesophragmatica* and *peruviana* groups. The *mesophragmatica* group of eight species is reviewed by Brncic *et al.* (1971), who give the distribution and a cytological phylogeny. These are predominantly Andean species, but *D. gaucha* is also found in southern Brazil, Uruguay, and Argentina. They are collected with standard, fermenting-fruit baits and most can be cultured. The *canalineae* and *dreyfusi* groups are both distributed from Brazil to Central America, with *D. canalineae* ranging northward into Mexico. Pipkin (1965) classes these species among those preferring small, dry fruits and fallen blossoms as feeding and breeding sites.

The *repleta* group of about eighty species is comprised of five subgroups, and these are related to each other and to the *canalineae*, *dreyfusi*, and *castanea* groups through the *repleta* standard gene arrangement (Wasserman, 1963). The *canalineae* and *dreyfusi* groups share a common branch off the standard gene arrangement, the *mulleri* and *fasciola* subgroups share a second branch, the *hydei* subgroup makes up a single independent branch and so also does the *castanea* group, and the *melanopalpa* and *mercatorum* subgroups share a fifth branch. *D. peninsularis*, morphologically a member of the *mulleri* subgroup, is also a member of this last branch. Members of the *hydei* subgroup are found from the southern United States through Mexico and Central America to Colombia, Venezuela, and Peru. *D. hydei* is a cosmopolitan species. The

melanopalpa subgroup extends from Oregon and Idaho in western North America southward through Mexico and Central America to Peru and Brazil. *D. repleta* of this subgroup is cosmopolitan. The *mercatorum* subgroup is distributed from the United States through Mexico, Central America, and Colombia to Brazil, Chile, Peru, and Bolivia. *D. mercatorum* itself is also distributed to Hawaii (Carson, 1965). The *fasciola* subgroup is distributed from Arizona and Mexico to the West Indies, and to Central and South America. The *mulleri* subgroup, the largest of all, is distributed from central California, Nebraska, Tennessee, and Florida south to Argentina and Chile. *D. buzzatii* is also distributed to the Mediterranean region and Australia.

The *repleta* radiation, and the *nannoptera*, *bromeliae*, and *peruviana* groups, appear to have originated in or near present-day Mexico. On anatomical grounds, the *nannoptera* line was the earliest to branch off as a separate lineage, and these species are presently restricted to the deserts and arid lands of Mexico. Parsimony requires that this be regarded as the general area of origin for these groups, and other evidence indicates the same thing. The anatomically more-primitive species of the *hydei* subgroup (*D. bifurca*, *D. nigrohydei*) are northern species (Texas, Arizona, Mexico), and so is *D. fulvalineata*, the most primitive of the *fasciola*-subgroup species. The biology and distribution of these forms suggests that diversification occurred largely in association with the developing American deserts. It probably began in tropical or subtropical forests of North America and spread through chance colonization to secondary centers of radiation in South America. The *canalinae*, *dreyfusi*, *mesophragmatica*, *peruviana*, and *castanea* groups are forest forms and center in South America. The first four of these probably originated there, and the *castanea* and *bromeliae* groups could have originated either in North or South America. All the subgroups of the *repleta* group seem to have originated in North America, with the possible exception of that of *D. mercatorum*. Wasserman (1962a) suggests that this subgroup originated in Brazil.

The species of the *repleta* group are mostly desert forms associated with cactus (Patterson and Stone, 1952; Wasserman, 1963; Fellows and Heed, 1972), but the *fasciola* subgroup is found in wetter areas of rain and cloud forest and on banana and coffee plantations of Central and South America. *D. californica* breeds in bleeding trees (Patterson and Stone, 1952), and *D. hydei*, *D. repleta*, *D. melanopalpa*, and *D. fasciola* have been reared from fallen fruits and flowers (Pipkin, 1965). Since the morphologically and cytologically primitive member of the *fasciola* subgroup, *D. fulvalineata*, is a desert species, Wasserman (1962b) sug-

gests that the group originated as a desert form, then returned to the ancestral forest habitat. A more parsimonious alternative, consistent with the cytological, morphological, ecological, and distributional evidence, would suggest that the *fasciola* subgroup represents the primitive type out of which the *repleta* radiation evolved. The group that first invaded the desert would have included initially both forest and desert forms, and these could easily have shared the more-primitive gene arrangements presently distributed among these lineages.

This lineage, from the *nannoptera* cluster to the *repletas*, engaged in considerable ecological experimentation (forest, flowers, cactus), with at least two radiations into the desert and major expansions into both high altitudes and temperate zones. As already indicated, the lineage almost surely arrived in the New World as a member of the tropical or subtropical forest fauna, presumably by mid-Oligocene times. Its diversification partly involved colonization of South America across the Caribbean water gap (*mesophragmatica*, etc.) and partly involved ecological experimentation and adaptation to diverse food types (flowers, rotting cactus) and climates (desert, temperate) or altitudinal regions. It is reasonable to infer that much of this latter development reflects responses to environmental stress attending the development of the New World mountains and deserts during Oligocene and Miocene times. And it would equally reflect exploitation of novel opportunities presented to these species with the expansion of new ecological communities in arid regions and the flourishing of unusual plant types such as cactus. These species are readily collected and cultured, and they are among the most promising research materials available in the genus *Drosophila* today.

The *immigrans*-*Hirtodrosophila* radiation

When grasped in its entirety, this last major radiation is seen to have a basic structure very similar to that of the *virilis-repleta* radiation. It originated and diversified first in the Old World tropics, spread from there, and sent two separate lineages (*tripunctata* and *Hirtodrosophila*) to the New World tropics. Then, from both of these centers the temperate zone was entered, with the major impetus for this coming from the Old World. A similar dominance of the Old World was seen in the *virilis-repleta* radiation, and the reason seems simple. In the Old World, and particularly in east Asia, the tropical and temperate forests intergrade on a wide front. This provides abundant and continuing opportunity for tropical faunas to spread into and master temperate environments. In the New World the situation is different. As climatic and altitudinal zonation

became more pronounced in Oligocene and Miocene times, the tropics were more and more isolated from temperate North America by deserts that developed across what is now northern Mexico. The progenitors of the *tripunctata* radiation depended for their living on fungus and on flowers and fruits fermenting slowly on the humid forest floor. The expanding deserts crowded them southward. The species of the *virilis-repleta* radiation, on the other hand, responded to the growing deserts by adjusting to them, a circumstance encouraged by their utilization of oozing saps and rotting parts of still-living plants (rot pockets of cactus, for example). Hence, they continued to occupy a large part of arid southwestern North America, but since they had specialized so much toward cactus, they did not have efficient entry into the temperate deciduous forest. Those forms, of the *melanica*, *robusta*, and *virilis* groups, for example, came eventually from Asia, as did comparable forms of the *quinaria*, *melanderi*, and *testacea* groups from this radiation.

The *immigrans*, *denticeps*, and *pinicola* groups make up a complex that forms the core of the higher Drosophilinae. The *melanderi* group and the subgenus *Siphlodora* are very close to these, so close in fact that it is difficult to make sharp distinctions among them for characters of phylogenetic significance at this level. On many other characters they are easily distinguished, and the extremes of this radiation are sharply separate from each other. Figure 4 exaggerates the closeness of some of these groups, particularly those near *Hirtodrosophila*, and at the same time it underemphasizes the similarities of *immigrans*, *denticeps*, and so on.

According to Wilson *et al.* (1969) the *immigrans* group contains about 70 "nominal" species, which they assign to five subgroups plus a sixth that contains species of uncertain relationships. This group is part of a larger cluster of about 100 species, the taxonomy of which remains confused. Various generic and subgeneric names have been applied to some of the more conspicuous phenotypes, but the entire cluster is, in reality, a close-knit lineage little justifying the nomenclatural industry expended on it. Except for one cosmopolitan species (*D. immigrans*), the *immigrans* group is distributed in Africa, the Seychelles, south Asia north to Japan, Australia, and the Pacific islands. In Southeast Asia it intergrades broadly with related lineages, both of its own radiation and of earlier radiations, so it must be regarded as originating there. The genus *Zaprionus* predominates in Africa, where there are 25 species, and several more species of dubious relationship are found elsewhere. The seven species of *Samoaia* are endemic to Samoa (Wheeler and Kambysellis, 1966). The genus *Chaetodrosophilella* is small and is found in Southeast

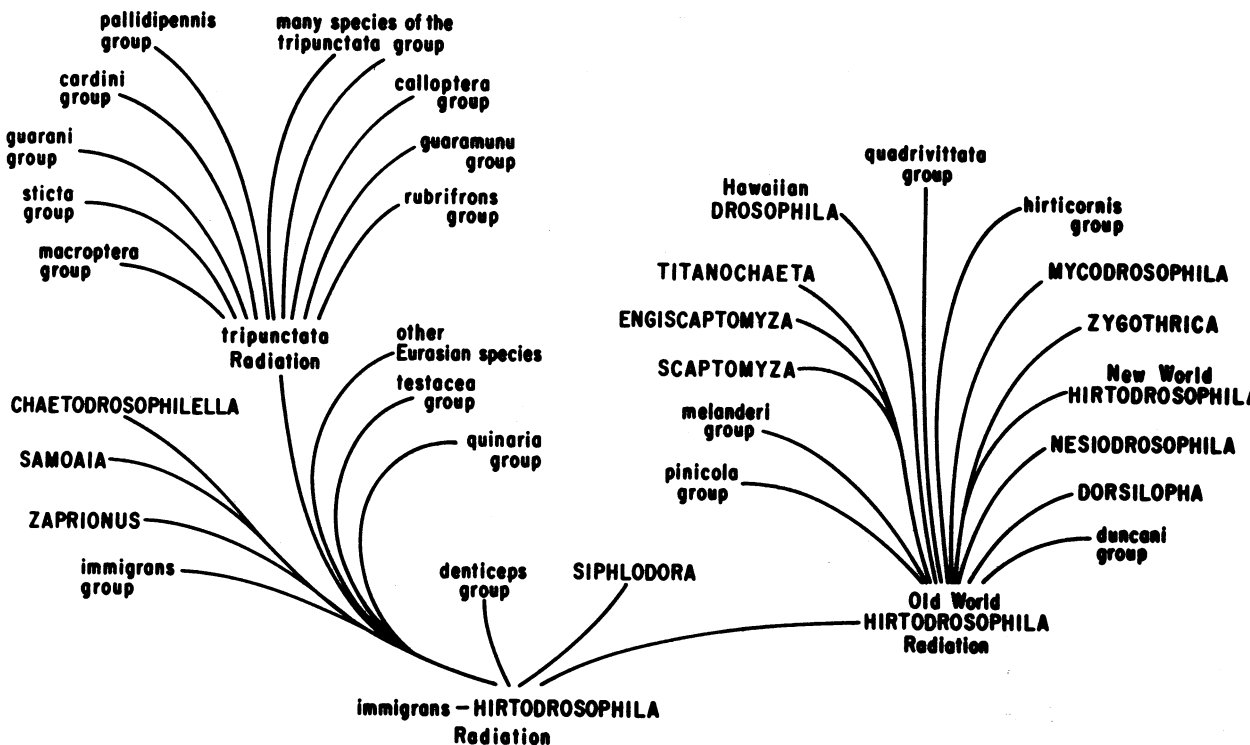


Figure 4. The *immigrans*-*Hirtodrosophila* radiation continued from the upper right of Figure 2.

Asia and the Pacific islands. Where the ecology of the species is known, species of the *immigrans* cluster are associated with fungus, fallen fruit, flowers, tree sap, slime flux, or rotting vegetables and leaves. Many of them cannot be cultured, even though they come to fruit baits and are swept over fallen fruit. Together with species of the *melanogaster* group they make up the greater part of the drosophilid fauna in parts of the Old World tropics (Bock and Wheeler, 1972).

The *tripunctata* radiation centers in the New World tropics, and individuals from it make up a large part of collections from South and Central America. The *tripunctata* group itself is comprised of nearly 60 species, and it seems to be related to the other groups of this cluster, very much as the genus *Drosophila* is related to the higher Drosophilinae. That is to say, it is the group out of which, at different times and at different levels, other groups arose. On cytological grounds Kastriitis *et al.* (1970) drew attention to a relationship of this sort among the *tripunctata*, *guaramunu*, and *guarani* groups, and distribution and morphology point to a similar relationship for the remaining ones. This evolutionary pattern is also observed among groups of the *repleta* radiation, and it is seen also

among those of the *Hirtodrosophila* radiation. The major treatments of the *tripunctata* group are by Frota-Pessoa (1954), Heed and Wheeler (1957), Pipkin and Heed (1964), and Kastritsis (1966). It is distributed from the eastern United States to Mexico, Central America, the West Indies, and South America, with perhaps its highest concentration of species being in Brazil, where it ranks second only to the *willistoni* group in population densities (Frota-Pessoa, 1954). The species of this group have diverse feeding habits. Some are fungivorous, some are sap-feeding, and some are ground-feeding forms associated with fallen flowers, small fruits, and decaying pulpy vegetation (Heed, 1957; Heed and Wheeler, 1957; Patterson and Stone, 1952; Pipkin, 1965). The group originated in the New World tropics, but whether in North or South America remains uncertain. The one United States species, *D. tripunctata*, is derived from the south, and it represents the single, successful colonization of the eastern deciduous forest by this group. Taken together, the Caribbean and the deserts of northern Mexico have been very effective barriers to a northward dispersion of the *tripunctata* radiation.

The *cardini* group is summarized by Heed and Russell (1971). They divide the group into continental and island clusters, each of eight species. The continental subgroup is distributed from Georgia, Texas, Mexico, and the West Indies south to Chile and Brazil. The island subgroup is from the West Indies, except for *D. acutilabella*, which also extends northward into Florida. Heed (1957) reports some of these species from fallen fruits and fungus, and Pipkin (1965) classifies some of them as utilizing fleshy fruits for feeding and breeding sites. The *rubrifrons* and *macroptera* groups are both North American, with the first being distributed from New Mexico and Arizona south into Mexico and the second from Colorado and Texas south to Guatemala. The two groups together comprise no more than a dozen species. Heed (private communication) has reared both *D. macroptera* and *D. rubrifrons* from fungus. The *calloptera*, *guarani*, *guaramunu*, *pallidipennis*, and *sticta* groups are also small, with fewer than two dozen species all told. Species of the *calloptera* group are most distinctive, with dark, patterned bodies and patterned wings. *D. sticta* is not greatly different from species of the *tripunctata* group. Both of these groups are part of the ground-feeding fauna associated with fallen flowers and fruits (Pipkin, 1965). The *calloptera* and *pallidipennis* groups are distributed from Mexico through Central America to Peru and Brazil, the *sticta* group is from Colombia and Central America, and the *guarani* and *guaramunu* groups are found from Mexico to Brazil.

When species of this radiation are better known it is probable that a pattern of distribution and evolution similar to that for the *saltans* group

will be evident. The ancestors of the radiation were members of the tropical fauna that arrived in the New World prior to mid-Oligocene times. Mountain building and desert formation fragmented former continuous distributions, leaving the species of the *rubrifrons* and *macroptera* groups scattered and isolated from Mexico north to the Colorado Rockies. The remaining groups all have a conspicuously southern distribution. They may well have originated in South America and spread northward with the building of the Isthmus of Panama in Pliocene times. Species of the *cardini* group can be cultured with relative ease. They have skipping larvae, whatever that signifies, and so also do several other species of this radiation. Some members of the other groups can be cultured readily but many cannot. When problems of culturing these species are solved they will provide outstanding materials for studying evolutionary ecology.

The temperate limb of this radiation evolved out of some Eurasian species having features in common with the *immigrans*, *denticeps*, *pinicola*, and *melanderi* groups. As representatives of this evolutionary level I have seen *D. sternopleuralis*, *D. bizonata*, *D. histrio*, and *D. confusa*, all from Japan. Some of these have more in common with the *quinaria* section, some more with *Hirtodrosophila*, and they can hardly be regarded as an evolutionary unit. Regardless of that, they serve my present purpose very well, for they provide a strong link to the *quinaria* group and support the conclusion that it originated in the Old World.

The *quinaria* group is comprised of 25 species, 4 from Europe (Burla, 1954; Basden, 1954), 5 from the Orient (Okada, 1956), and 16 from North America (Patterson and Stone, 1952; Wheeler, 1960). This distribution is exactly that noted previously for the species of the temperate forest, and the resemblance is further enhanced by the distribution of the North American species. Nine of these are western, with an overall range from Alaska to Mexico. Only one of these, *D. subquinaria*, extends very much north of southern Canada and, like *D. athabasca* of the *obscura* group and *D. montana* of the *virilis* group, it achieved this distribution through expansion northward with the retreat of the continental glaciations of the Pleistocene.

There are two groups of predominantly eastern forms. One of these is an evolutionary lineage comprised of *D. palustris*, *D. subpalustris*, and *D. guttifera* (possibly also *D. deflecta*, which I have not seen). These are distributed from Nebraska, Manitoba, and Ontario south to Texas and Florida. *D. quinaria* ranges from Manitoba and Quebec south to Missouri and Virginia. Its nearest relatives are among the western forms. Likewise *D. recens* and *D. falleni* represent northeastern extensions of the western

types, with the first ranging from North Dakota and Ontario east to Quebec and Maine, and the second ranging from British Columbia and Quebec south to Colorado, Texas, and Alabama. Most of the species breed in fungus or in rotting vegetation (Patterson and Stone, 1952; Basden, 1954; Okada, 1956, 1968a). *D. palustris* and its relatives breed in decaying water plants such as *Sagittaria* (Patterson and Stone, 1952). *D. transversa* has been reared from meat and mushroom baits placed into vole burrows (Hackman, 1963).

The *testacea* group is small. *D. putrida* is from eastern North America, where it ranges from Ontario south to Texas and Florida. In North America *D. testacea* ranges from Alaska south to Washington and California and east to Quebec and the southern Appalachians. It is also found in Europe and Japan. *D. putrida* is reported from fungi, and Okada (1968a) has reared *D. testacea* from fallen leaves.

The *melanderi* group is derived from the *Hirtodrosophila* radiation, but since it is part of the temperate fauna it is convenient to deal with it now. One species of the group, *D. mankinoi*, is Oriental and three are North American. Two of the latter are from the eastern United States and one, *D. melanderi*, is western, ranging from Alaska and Oregon east to Montana and Minnesota. Spieth recently reared *D. melanderi* from fungi, and through his courtesy I was able to examine some of these individuals. The group is very near the *pinicola* group and to *Hirtodrosophila*, particularly species of the American southwest such as *D. orbospiracula*. *D. pinicola* and *D. flavopinicola* of the *pinicola* group were also recently provided me by Spieth. The *pinicola* group is known only from western North America, where it ranges from southern California to British Columbia. These species are fungivorous (Spieth, private communication). Again, these groups exhibit the disjunct patterns of the temperate forest species, and they reinforce the conclusion presented earlier that the temperate forest fauna originated, in all its varied lineages, prior to mid-Miocene times.

Before turning to the remainder of the *Hirtodrosophila* radiation, two smaller groups should be discussed. The subgenus *Siphlodora* is comprised of three species, one of which (*D. sigmoides*) is distributed through southeastern North America from Illinois and New York south to Texas and Alabama. The other two are distributed from Mexico and the West Indies south to Brazil. *D. sigmoides* has been reared from inflorescences of *Tripsacum* (Butler and Mettler, 1963). *D. sigmoides* combines characteristics of both the *tripunctata* and the *Hirtodrosophila* radiations. The subgenus is closest to the *denticeps* group, which is placed by Okada in the subgenus *Hirtodrosophila*. *D. denticeps* itself is a leaf miner (Okada

1968a), and it is quite possible that some species of the subgenus *Siphlodora* are also. The *denticeps* group of four species is reviewed by Okada (1971). This group is distributed from Nepal to Taiwan and Japan. I have seen one species from Japan and at least two from Taiwan, including one undescribed form. The group is at least as close to the *immigrans* cluster, *D. histrio*, and *D. confusa*, as it is to the more typical *Hirtodrosophila*. Thus, the subgenus *Siphlodora*, together with the *pinicola* and *melanderi* groups already mentioned, provides the link to the remainder of this radiation.

The subgenus *Hirtodrosophila* is treated most recently by Burla (1956) and Okada (1967). It is divided into eight species groups and, as usual, some of the more conspicuous phenotypes have been segregated out as subgenera or genera (Figure 4). In his review of the Old World *Hirtodrosophila*, Okada notes 27 Palearctic, 11 Oriental, 7 Australian, and 4 Ethiopian forms, for a total of 42 species. Within the Palearctic some species have invaded the Far North, and Hackman (1969) has described one species, *D. subarctica*, from northern Finland. There is an overlap of three species between the Palearctic and Oriental regions and of three species between the Oriental and Australian regions. There are, in addition, a great number of undescribed species. In one visit to Taiwan I obtained data on a minimum of 36 species of *Hirtodrosophila* and this was by no means all that were there. In the New World there are 27 Neotropical species, with three of these extending into Florida or Texas. Of the ten Nearctic species, three are southwestern (Texas, New Mexico, Arizona, Mexico) and four are distinctly northern. Taken together, these latter range from Nebraska and Ontario east to Rhode Island, then south to Alabama and Texas. *D. duncani*, of the eastern United States, is morphologically the most primitive species in the subgenus. The *Hirtodrosophila* are fungivorous, except for *D. denticeps*, which is a leaf-mining species.

The genus *Zygothrica* is from the New World tropics, with some species endemic to Samoa (Wheeler and Kambysellis, 1966). On the basis of external morphology, *Zygothrica* is very close to *Hirtodrosophila* (Burla, 1956), and internal morphology shows it to be derived from the New World types. The adults are numerous over fungi. Dr. Alan Young sent me a collection he had made over one fungus in Costa Rica, and out of it I sorted 31 species. Wheeler (1970) lists only 59 species of *Zygothrica* from the entire New World, so it appears that there is a large job of description remaining here also. Pipkin *et al.* (1966) report rearing *Zygothrica* from flowers, so for some species the larval feeding site may be quite different from that of the adults.

The subgenus *Dorsilopha*, with its single species, *D. busckii*, is world-wide in distribution, but species very close to it exist in Southeast Asia, and its origin is almost certainly there. It breeds in a great variety of rotting vegetables as well as in fungus (Heed, 1968). The genus *Nesiodrosophila* is from Southeast Asia, the Pacific islands, and Africa (Wheeler and Takada, 1964; Okada, 1970). There is no report of its biology. *Paramycodrosophila* is from South Asia, the Pacific islands, and the New World, where five species are distributed from the southern United States to the West Indies and Central America. These three groups, plus the typical *Hirtodrosophila* (excluding the *denticeps* and *confusa* groups) comprise a tight cluster that is most probably a phylogenetic unit.

The genus *Mycodrosophila* is world-wide in distribution, though its species are predominantly tropical (only two of the ten New World species have distributions entirely north of Mexico). Its species are fungivorous. The genus *Scaptomyza* is also world-wide in distribution, from Africa to arctic Norway in the Old World, and from Argentina and Chile to Alaska in the New World (Basden, 1956; Hackman, 1959; Wheeler and Takada, 1966). Its species are predominantly miners of fresh leaves, though they occasionally breed in fruit, and Hawaiian *Scaptomyza* have been reared from flowers, fungus, slime flux, leaves, stems, and fruit (Heed, 1968).

The endemic Hawaiian drosophilids are a large, complex, and fascinating group. The biology of these species is reviewed by Carson *et al.* (1970). They are comprised of two major lineages, the so-called drosophiloids (*ca.* 340 species) and the scaptomyzoids (*ca.* 140 species). Hardy estimates a total endemic drosophilid fauna of nearly 700 species, of which one-third would be scaptomyzoids. There are five endemic drosophiloid genera in addition to *Drosophila* (*Antopocerus*, *Ateledrosophila*, *Celidosoma*, *Grimshawomyia*, *Nudidrosophila*), and the genus *Drosophila* has one endemic subgenus, *Engiscaptomyza*. There is one endemic genus of scaptomyzoids in addition to *Scaptomyza* (*Titanochaeta*) and six endemic subgenera of *Scaptomyza* (*Alloscaptomyza*, *Bunostoma*, *Exalloscaptomyza*, *Rosenwaldia*, *Tantalia*, *Trogloscaptomyza*). Some species of *Bunostoma* are found also in the Marquesas, Samoa, and Australia, and *Rosenwaldia* has been reported from the Marquesas. One species of *Trogloscaptomyza* is reported from Tristan da Cunha (Hackman, 1959). Heed (1968) summarizes their ecology as follows: Among drosophiloids, species of the genus *Antopocerus*, and the bristle-tarsi, fork-tarsi, and spoon-tarsi groups, mine fermenting leaves exclusively; those of the light-tip-scutellum group are fungivorous; and some species of the picture-wing, modified-labellum, and ciliated-tarsi groups are polyphagous on leaves,

stems, and flowers. Most drosophiloids are from higher altitudes in areas of low light intensity and high humidity. Among species of scaptomyzoids, those of the subgenus *Exalloscapteromyza* breed in flowers and those of *Titanochaeta* breed on spider eggs. Species of *Trogloscapteromyza* are polyphagous and overlap ecologically with the polyphagous drosophiloids, although they tend to utilize substrates in fresher condition. To some extent the scaptomyzoids choose the drier and more exposed habitats of higher light intensity, but they broadly overlap drosophiloids within habitats also. The major evolutionary pattern is one of dispersion from the oldest island (Kauai) to the younger ones (Oahu, Molokai-Maui-Lanai, Hawaii) and of pronounced, single-island endemism. The Maui complex has the greatest number of drosophiloids (160), followed by Hawaii (98), Oahu (84), and Kauai (44). A minimum of 22 interisland founder events was postulated by Carson *et al.* (1970) to account for the distributional and cytological patterns seen among about 100 picture-winged species studied up to that time. The major factors responsible for these patterns seem to be the low variety of usable foods, the dissection and isolation of habitats through volcanic and meteorological activity, and the infrequent successful colonization of adjacent islands.

It has been suggested that the Hawaiian drosophilids originated in East Asia (Throckmorton, 1966). Investigations since that time have tended to confirm this (Throckmorton, unpublished; Okada, 1967, 1971). They arise from among the cluster of species groups and genera already discussed, and this cluster is distributed in Asia from the northern subtropics to the cold temperate region. Some representatives of these lineages are also found in the New World (the *melanderi* and *pinicola* groups and *Siphlodora*). These latter are specialized in one way or another, however, giving small probability that they were themselves ancestral to the Hawaiian drosophilids. The highest concentration of related types is in the northern subtropics of East Asia, and it is most probable that the Hawaiian lineages derive from there by some more-or-less direct route. Populations with the requisite genotypes were in existence in that region by Miocene times at the latest, so they were easily available to colonize the Hawaiian chain during the Pliocene times when the present high islands developed, or they could have colonized earlier islands of the central Pacific before the existing Hawaiian Islands emerged.

The problem of the origin of the drosophiloid and scaptomyzoid lineages of Hawaii remains unresolved. It is possible that two introductions to Hawaii were involved, and there is no reason to postulate more than that. However, the Hawaiian drosophiloid and scaptomyzoid lineages intergrade conspicuously for internal morphology (Throckmorton,

1966), behavior (Spieth, 1966), genitalia (Takada, 1966; Kaneshiro, 1969), and external morphology [Hardy, in Carson *et al.* (1970)]. All of this is presumptive evidence for the origin of *Scaptomyza* in Hawaii and its subsequent dispersal from there to achieve its present world-wide distribution. The parsimonious inference from the evidence, in its present state, still favors the origin of all Hawaiian drosophilids from a single introduction. This would have come from subtropical Southeast Asia and from among such related species groups as those including *D. histrio*, *D. confusa*, *D. denticeps*, and so on.

Insofar as culture is concerned, the species of the *Hirtodrosophila* radiation are a heterogeneous lot. Forms such as *D. busckii*, *D. duncani*, and so on can be cultured readily on standard media. So can several species of *Mycodrosophila* and *Scaptomyza*. Many others (the Hawaiian drosophiloids, *D. pinicola*, *D. melanderi*, etc.) can be cultured with special media or special techniques (Wheeler and Clayton, 1965; Spieth, private communication).

Generalizations and Hypotheses

The family Drosophilidae is one of two major lineages that emerged from a small radiation of acalypterate diptera saprophagous in leafmold. The other major lineage, the ephydrids, specialized toward wetter substrates and aquatic habitats. The Drosophilidae apparently gained their own ascendancy through specializing on organisms causing fermentation. This gave them access to a great variety of substrates in a variety of habitats, and presumably to a variety of fermenters, bacteria as well as yeasts. The history of the family is a history of the mastering of this niche complex as it has been accomplished through the last fifty million years or so and over the major continents of the globe.

Originally, the Drosophilidae were probably associated with slowly fermenting leaves and other fleshy plant parts on the humid forest floor and probably also with sap and broken and damaged parts of living plants themselves. It is unlikely that they "saw" a sharp boundary among these, especially if they were oriented more toward fermentation *per se* than toward some specific plant product. This was a relatively austere existence since breaks and other damage may have been infrequent and small, or highly periodic in occurrence (after storms, etc.), and the saps and tissues exploited were not rich in carbohydrates. This provided a step, however, toward exploitation of fleshy fungi, and that transfer was made several times in the history of the family. The first major entrance into such an association was made among the Steganinae by the founders of the *Leu-*

cophenga lineages, and many other and later groups accomplished such a transfer also. The major evolutionary line continued, however, in the fermentation mode, and by the time of the origin of the Drosophilinae, some lines had the capacity to move into richer fermentation sites such as fruits. The first considerable exploitation of these was by the *Scaptodrosophila*. The utilization of fleshy fruits contributed to small expansions of *Scaptodrosophila* and to much larger radiations of sophophorans and the *immigrans* complex. That is, the later radiations have most conspicuously exploited fruits. The utilization of the fleshy fungi promoted the flourishing *Hirtodrosophila* line, together with the genera, subgenera, etc., associated with it. Both of these together enabled the flies to invade the temperate zone in force, as it were, since they could use enriched saps and plant tissues of deciduous forest trees, and the fleshy fungi themselves reach into the arctic and so provide avenues of advance out of the tropics that can be utilized by many species.

Only two major patterns, components of a larger and more inclusive pattern, were generated during the evolution of the Drosophilinae. The sophophoran radiation developed these in almost diagrammatic clarity and can be recalled by way of example. The first pattern is that of the primary tropical disjunction. For sophophorans this involves the *melanogaster* group (ca. 80 species) in the Old World tropics and the *saltans-willistoni* lineage (ca. 50 species) in the New World. A more limited secondary pattern of only certain subgroups of the *melanogaster* group and of the related *fima* group is seen in Africa, and only individual species of Asian subgroups are found in Australia. The second major pattern is seen in the New and Old World disjunctions among the temperate-forest species and in their secondary east-west disjunctions within Eurasia and North America. For the *obscura* group (ca. 22 species) this is seen in the distribution of approximately 5 species to Europe, 2 to East Asia, 10 to the western United States, and 5 to the eastern United States.

The complete pattern closely matches Cenozoic continental and vegetational histories. The older tropical disjunctions involve species groups, subgenera, and genera. The more recent temperate disjunctions involve species subgroups and species. The partial African disjuncts involve species groups, subgroups, and species, which is consistent with the late establishment of contacts with Africa during Oligocene times and the development of the present connection during the Pliocene. Even now, the drosophilid faunas of Asia and Africa are partially isolated by the deserts of the Middle East. The minor radiation into Australia is compatible with its relatively recent approach to Southeast Asia and to the continued presence of a water gap there. The somewhat blurred patterns in the New

World seem to reflect secondary radiations into South America across the Caribbean water gap, evolution in isolation for a time, and a subsequent partial merging of North and South American faunas with the establishment of the Isthmus of Panama in late Pliocene times.

This overall pattern is repeated five times in more or less detail, but always sufficiently to be identified. Simplifying somewhat for the sake of brevity, the five occurrences appear as follows. The first is the *Scaptodrosophila* radiation, with *Scaptodrosophila* in the Old World tropics, *Zaprionothrica* in the New, and the *victoria* group of *Scaptodrosophila* showing the temperate disjunct patterns. The second is the sophophoran radiation with the *melanogaster* group in the Old World tropics, the *saltans-willistoni* lineage in the New, and the *obscura* group showing the temperate disjunctions. The third is the *virilis-repleta* radiation, with a nondescript cluster of species, species groups, genera, and subgenera in the Old World tropics, the *repleta* radiation in the New, and the *virilis*, *melanica*, and *robusta* groups showing the temperate-forest patterns. The fourth is the *immigrans* radiation, with the *immigrans* cluster in the Old World, the *tripunctata* radiation in the New, and the *quinaria* group disjunct through the temperate forests. The fifth and last is the *Hirtodrosophila* radiation, with the Old World tropical *Hirtodrosophila* and related groups, the New World tropical *Hirtodrosophila* and *Zygothrica*, and the *melanderi*, *pinicola*, and related groups involved in the temperate disjunct patterns.

At some time representatives of each of these radiations spread through the tropics between the New and Old Worlds, and these movements may have been quite widely separated in time; at least there is no reason to suppose that they were synchronous. There is some evidence for a partial restriction of the passage through Beringia, particularly for members of the earliest drosophiline radiations. Both the *Scaptodrosophila* and the sophophoran radiations are represented in the New World by lineages attributable to a single founder each (realizing that the present data are incomplete and appearances may be misleading). The higher radiations all give evidence of greater heterogeneity among the New World founders. As a single example, at least five lineages appear to have been represented among the founders of the radiation of the *virilis-repleta* cluster in the New World tropics. Of all the groups involved, *Scaptodrosophila* and *Sophophora* show the tightest affinity to the tropics. Only one species of each was involved in founding the temperate lineages, but several or many species from each of the higher radiations accomplished this adjustment to temperate habitats. It may be that Beringia never offered more than a warm, temperate avenue to the New World

during the time of evolution of *Drosophila* and related genera. Hence, the genus *Drosophila* might have arisen as late as the late Eocene, but not a great deal later. Alternately, *Drosophila* can have originated much earlier, but *Scaptodrosophila* and *Sophophora* may have been minor elements of early faunas and relatively fewer existed to explore the Beringian passage. The limits of the continental shelf in the region of Beringia do not permit this passage to have ever been broad, and optimum conditions for *Drosophila* may have been either infrequent or short-lived. Intermittent closings of the land bridge by a water gap may not have been trivial so far as tropical drosophilids were concerned, and a filtering effect might be inevitable, even granting optimal conditions for tropical species.

The development of temperate faunas may have taken place during a relatively shorter interval and in a more nearly coordinated fashion. The time at which this began cannot be fixed at present. It does seem that the temperate deciduous forest itself came into being rather rapidly during the mid-Tertiary times, and only shortly before it was fragmented by mountain-building episodes (Graham, 1972). If that is true, it seems plausible to suppose that the temperate drosophilid fauna expanded with it. Evidence from the *Drosophila* groups themselves suggests this. The *victoria*, *obscura*, *virilis-melanica-robusta*, and *quinaria* clusters are distinctive and clearly distinct from their tropical relatives. Each group is quite homogeneous and seems to be derived from a founder that had diverged to a characteristic type before diversifying to the cluster of species seen today (in contradistinction to the pattern seen for the *repleta*, *tripunctata* and *Hirtodrosophila* radiations). Each of these founders could have developed in response to some local climatic, altitudinal, or biotic conditions within, or at the northern borders of, the tropical forest. Then they could have marked time, preadapted as it were to temperate forests that did not exist or, if they did exist, that were too limited in distribution to permit much diversification within them. There is a rough parallel between the distinctness and homogeneity of a group and the relative age of the radiation from which it was derived. Thus, the *victoria* group, from the earliest radiation, is sharply distinct from other *Scaptodrosophila* and is very homogeneous. The *obscura* group, from the second radiation, is moderately distinct from other sophophorans and is moderately homogeneous. From later radiations, the *virilis-melanica-robusta* cluster and the *quinaria* group are each distinct, but both overlap close relatives in certain important features and both are considerably more heterogeneous internally than are the *victoria* and *obscura* groups. Thus, the *victoria* founder may have arisen early and existed for a long time as an isolated specialist. The *obscura* founder may have arisen later, existed a shorter

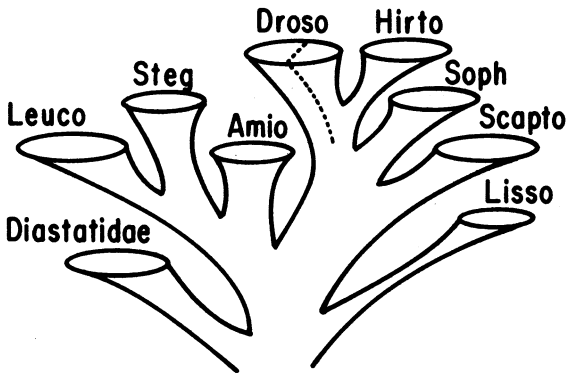
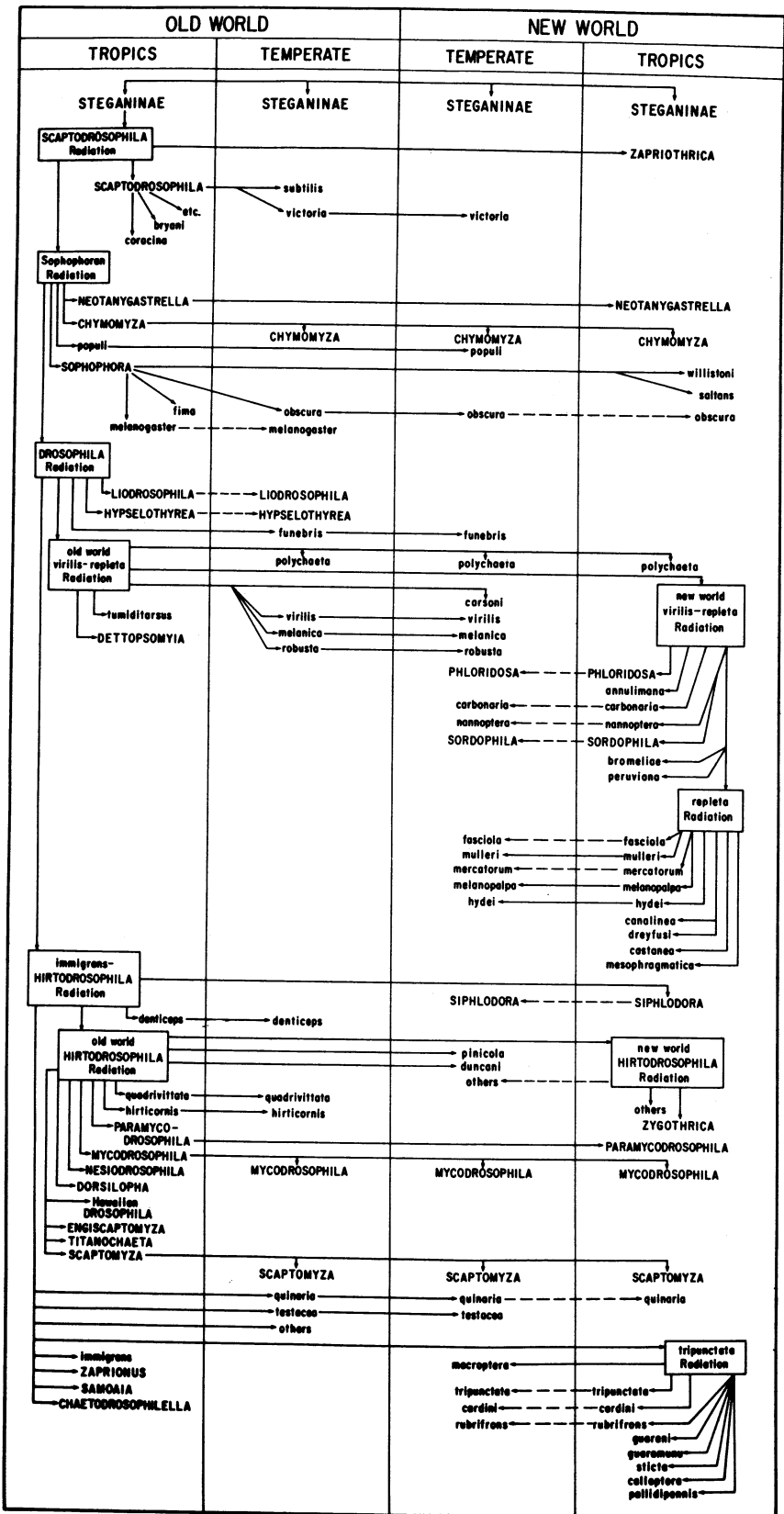


Figure 5. The basic skeleton of the family *Drosophilidae* as it most probably existed by the middle of the Oligocene age. Abbreviations are as follows: *Leuco* = *Leucophenga*, *Steg* = *Stegana*, *Amio* = *Amiota*, *Droso* = subgenus *Drosophila*, *Hirto* = subgenus *Hirtodrosophila*, *Soph* = subgenus *Sophophora*, *Scapto* = subgenus *Scaptodrosophila*, *Lisso* = *Lissocephala*.

time before expanding with the temperate forest, etc. Hence, in spite of different times of origin, the five major temperate radiations may have begun diversification nearly at the same time, and the patterns we now see would have developed in consequence.

The parallels and consistencies, both internal and external, from successive radiations are too compelling to be dismissed as accidental or convergent. They reflect in great detail the disjunctions of tropical and temperate floras and of continental relationships during the Cenozoic era; these seem to have influenced each radiation in the same manner and to the same degree, as if the effects were being felt simultaneously by the members of all radiations. Nearly 600 drosophiline species are involved in the tropical disjunctions (*ca.* 60 African, 190 Eurasian, 340 Neotropical) and almost 150 species contribute to the temperate disjunctions (*ca.* 40 European, 35 East Asian, 30 western North American, 20 eastern North American). It is difficult to avoid the conclusion, or to argue otherwise, that the five successive radiations of *Drosophilinae* occurred before the end of the Eocene age. The individual branches would not have existed then as the fully diversified groups we see today, but at least the basic skeleton of the family, as it is shown in Figures 5 and 6, would have been elaborated. Subsequent to this, the tropical disjunctions occurred in the early Oligocene times, the temperate faunas developed and spread up to the

Figure 6. A flow diagram of the phylogeny and distribution of the higher *Drosophilidae*. Solid lines indicate major occupations of a zone. Dashed lines indicate only minor incursions.



time of the temperate-forest disjunction in mid-Miocene age, and the final details of present-day patterns were added by speciation events within local regions during the Pliocene and Pleistocene ages, and on into recent times.

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