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Pathways of Evolution in the Genus *Drosophila* and the Founding of the *Repleta* Group[1]

Lynn H. Throckmorton *(1982)*

Department of Biology
University of Chicago
Chicago, Illinois

I Introduction

When the biogeography of the *repleta* group was last treated (Throckmorton, 1975), it was not possible to present either the evidence for, or the theoretical basis of, conclusions that were reached. For a group being so actively investigated, it is desirable that this information be available, but space still limits what can be provided. Only token examples of the data can be given here, but the method of biogeographical analysis is summarized. In addition, some new evidence is in hand, justifying a slightly different perspective on the *repleta* group and its nearest relatives from what was seen before. The results of this reinterpretation are also presented.

The discussion is organized according to the following plan. *First,* requirements for biogeographical analysis are sketched out, indicating what is needed before a large-scale biogeographical study is begun. *Second,* phylogenetic relationships among the major groups of the Drosophilidae are shown, together with the kind of evidence from which they were inferred, and the method used for phylogenetic analysis is indicated briefly. *Third,* the method of biogeographical analysis is given in some detail, with small extracts from the data illustrating the kind of information that supports

the most important biogeographical conclusions. *Fourth*, data from paleoecology is integrated with ecological data from extant species to show how observed biogeographical patterns justify conclusions regarding the time and place of origin of the *repleta* group. And, finally, brief note is taken of the information still needed to further refine our understanding of the group's origin and affinities.

II Requirements for Biogeographical Analysis

More and more, it is apparent that evolutionary study cannot be provincial, and this is especially true for studies of systematics and biogeography. Evolutionary changes in a group may be largely conditioned by properties of the lineage from which it sprang, distribution patterns on one continent may contradict rather than complement those on another, and patterns that seem simple when viewed from local perspective may appear quite otherwise, and much more complex, when seen in world view. Regional studies may not even be able to treat with species authoritatively, much less with species complexes or species groups. Thus it is, that biogeographical analysis, even of the compact and geographically coherent *repleta* group, must encompass most of the family Drosophilidae and much of its distribution throughout the world.

There are four requirements for a thoroughgoing biogeographical analysis: (1) a phylogeny, derived from intrinsic properties of individuals from the entire group which *includes* the group of primary interest, (2) knowledge of the distribution of all species, species complexes, and species groups within this larger group, (3) knowledge of the ecological requirements of all species of the larger group, and (4) knowledge of the paleoecology of the regions throughout which the presentday species are distributed and through which their ancestral forms may have dispersed.

This is a formidable list of requirements, and it is rarely fulfilled. At present, knowledge of drosophilid distribution and ecology is poor, our knowledge of seasonal and altitudinal relationships within faunas is virtually nonexistent, and the basic taxonomic treatment of major faunas is still very incomplete (e.g., Rocha Pité and Tsacas, 1979). Paleoecology itself will probably never be as informative as hope would have it, and historical detail on past plant associations, their distributions, and their spatial and temporal changes, will surely come slowly. Answers are, accord-

ingly, limited by available data. They will change as the data change. On a positive note, however, there is reason to expect that future revisions of drosophilid biogeography will not be extreme. Major new discoveries from Africa (Tsacas, 1979, 1980) and Australia (Bock, 1976, 1977, 1979, 1980a; Bock and Parsons, 1975, 1978) provide data complementing and reinforcing patterns seen earlier. This important new information adds tremendously to our understanding of drosophilid evolution, but it shifts the biogeographical pattern hardly at all.

III Phylogenetic Relationships

A phylogeny is already available for the major genera and subgenera of the Drosophilidae (Throckmorton, 1962, 1965, 1966, 1975). The evidence upon which it is based comes from attributes of a variety of anatomical features of the eggs, pupae, and adults, and from both males and females. Data are derived from more than 40 genera and subgenera of drosophilids, and from more than 50 species groups, just of the genus *Drosophila*. Nearly two-thirds of the data are published (Throckmorton, 1962, 1966), and significant unpublished information is presented herein.

Figure 1 shows the overall structure of the family, indicating the relative positions of major genera, subgenera, and so on. The central problem in phylogenetic analysis is always determining direction of evolution, and this can be done objectively only by reference to "outside" groups (Throckmorton, 1962, 1968). My earliest publications on the phylogeny of *Drosophila* (Throckmorton, 1962, 1965) were limited because too few data from the earliest radiations in the family were available. Other families of diptera were used as outside groups, and they turned out to be somewhat too distant. Since then, I have accumulated data on an assortment of steganine genera, and this has allowed correction of some early mistakes (compare Throckmorton, 1965, 1975). It also confirmed the placement of the Steganinae as an early radiation of the family, out of which sprung the Drosophilinae, the genus *Drosophila*, and ultimately, the *repleta* group.

Figures 2 and 3 illustrate some of the features contributing to this conclusion. They are intended, first to show the relatively pronounced anatomical change that has occurred during the evolution of the family, which readily
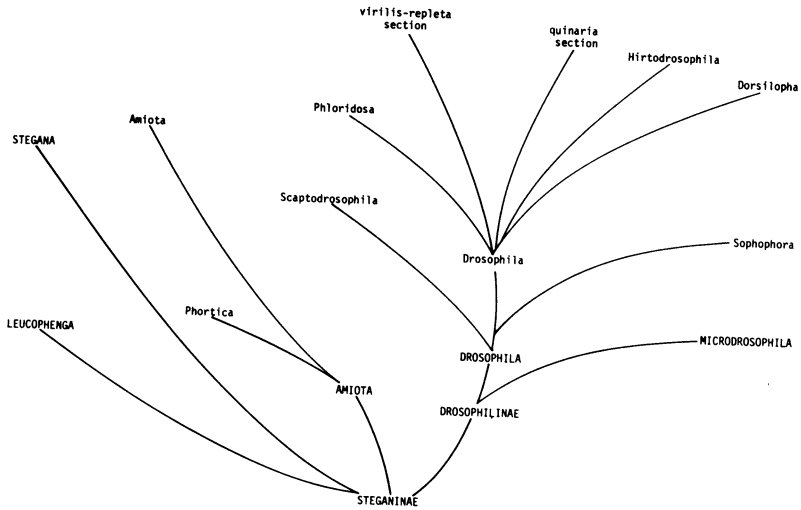
FIGURE 1. *Phylogenetic relationships of major groups within the family Drosophilidae. Names in upper-case letters, other than those of subfamilies, are of genera. Only the first letter is capitalized for names of subgenera.*

permits assessing direction of evolution; and second, taking together the features shown in both figures, to illustrate covariation of character states, which is the analytical evidence for phylogeny (Throckmorton, 1978). Thus, the uniqueness of particular character states among *Drosophila* is readily seen by contrast to states among the Steganinae. And, if space permitted, the uniqueness of steganine character states could be seen in contrast to states among other families of diptera. When unique states of different characters tend to "agree" on specific partitions among groups, as they do in the examples shown, clusters of species appear, and these are inferred to derive from a unique common ancestor. It will be recognized, of course, that the branching pattern in the figures is derived from consideration of the complete data set, and not just of the features illustrated.

For the phylogeny of the family, this brief summary must suffice. It shows the kind, but not the extent, of the basic data. Only key features of phylogenetic analysis are given, since method is treated extensively elsewhere (Throckmorton, 1962, 1965, 1968, 1978).
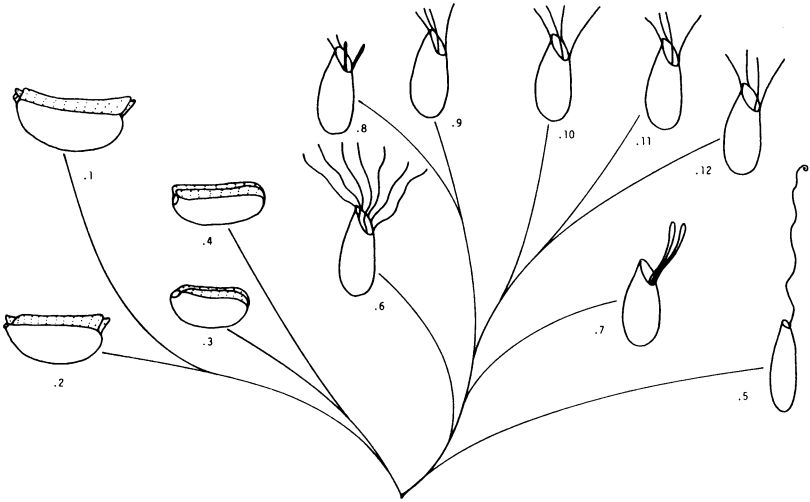
FIGURE 2.   Eggs of species from the taxa shown in Figure
1.   Names are as follows: .1 Stegana nigrifrons, .2 Leuco-
phenga ornata, .3 Amiota (Phortica) variagata, .4 Amiota
(Amiota) clavata, .5 Microdrosophila urashimae, .6 Drosophila
(Scaptodrosophila) nitithorax, .7 D. (Sophophora) simulans,
.8 Dettopsomyia nigrovittata, .9 D. (Drosophila) aldrichi,
.10 D. (Drosophila) cardinoides, .11 D. (Hirtodrosophila)
pictiventris, .12 D. (Drosophila) busckii.

IV   Biogeography

Once a phylogeny is available, the basic procedures of
biogeographical analysis are simple. One lineage at a time,
known distributions of major species complexes are plotted
on the world map. Working back from derivative groups, con-
nections are drawn between the geographical areas they occupy
until the base of a lineage is reached. When all individual
lineages are mapped, the bases of lineages are then connected
to each other in accordance with their phylogenetic relation-
ships. When the bases of phylogenetically close lineages
plot into the same geographical region, the lineages are
presumed to have arisen there in the temporal sequence indi-
cated by the phylogeny. When the bases of phylogenetically
close lineages plot into widely separate areas, it is neces-
sary to infer the routes or means by which ancestral popula-
tions achieved this distribution, and how the disjunction
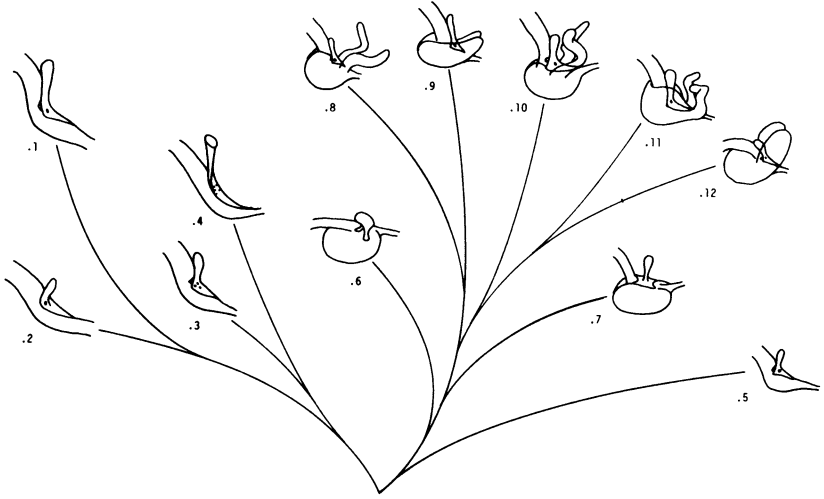was established. The combined information from distribution

*FIGURE 3.   Ejaculatory bulbs of species of representa-
tive genera and subgenera of drosophilids.   Names are as in
Figure 2.*

and phylogeny produces biogeographical patterns. To deter-
mine how and why these originated, recourse is made to the
known ecology of extant groups, and to paleoecology. Ex-
planations that emerge may permit inferences regarding prob-
able timing of events, the separation of certain lineages,
and so on.

The use of this method to discover the place of origin
of the genus *Drosophila* is illustrated in Figure 4. Since
phylogenetic analysis has already shown that the subgenus
Scaptodrosophila represents the earliest radiation in the
genus, attention can be given only to it. The derivative
ends of its known lineages are found in South America, in
North America, in temperate Asia, and in Australia and
Africa. Types most nearly like the primitive for the sub-
family (Fig. 3.5) are mostly in Southeast Asia (Fig. 4.1),
although the type seen in Africa (Fig. 4.4) is only slightly
more derivative. Types known from South America and Africa
differ sharply (compare Figs. 4.4 and 4.10), and the connect-
ing forms between them are seen on the northern continents
(Figs. 4.7-4.9). They trace back through intermediate types
(Fig. 4.5) to primitives in tropical Asia, and the African
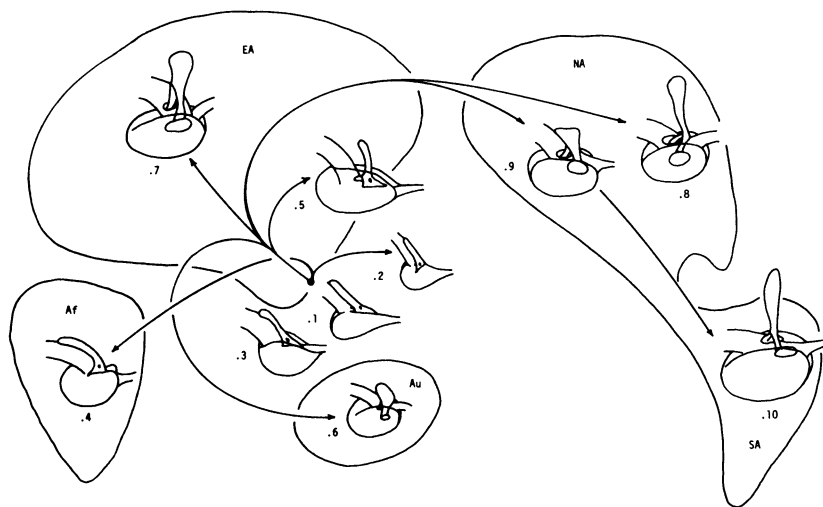type seems to be derived along another route. Hence, in its

FIGURE 4. *Geographical patterns illustrating evidence that the genus Drosophila originated in Southeast Asia. These examples are of ejaculatory bulbs from species of the subgenus Scaptodrosophila. Species names are as follows: .1 dorsocentralis, .2 coracina, .3 bryani, .4 latifasciae-formis, .5 subtilis, .6 lativittata, .7 pattersoni, .8 casteeli, .9 victoria, .10 D. sp. of the victoria group.*

evolution, the subgenus *Scaptodrosophila* appears to have radiated outward, along several lines, from Southeast Asia. Again, it must be emphasized that this conclusion rests on other features also, but the ejaculatory bulbs show the pattern in its most diagrammatic state and so have been chosen to illustrate here.

Figure 5 illustrates the basic biogeographical pattern seen at least five times within the genus *Drosophila*. It shows examples from the sophophoran radiation, which follows next after *Scaptodrosophila* in the evolution of the genus. Ejaculatory bulbs are used again since it is easy to see, both their resemblances to primitive types, and their ad-vances relative to them. From this radiation, the *melano-gaster* group dominates tropical Asia and Africa, and it has made its way to Australia (Bock, 1980b). In Central and South America, this radiation is represented by the *saltans* and *willistoni* groups. It can be noted that in both the New and Old World tropics, the sophophoran radiation began from
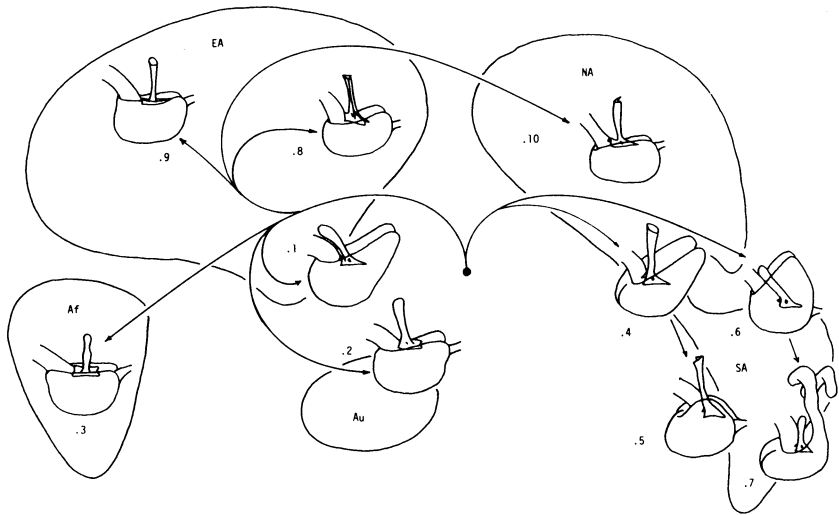
FIGURE 5. *The basic biogeographical pattern seen in the genus Drosophila. It is illustrated here with ejaculatory bulbs from species in the subgenus Sophophora. Species names are as follows: (melanogaster gp.) .1 ananassae, .2 pseudo-takahashii, .3 melanogaster; (saltans gp.) .4 emarginata, .5 prosaltans; (willistoni gp.) .6 willistoni, .7 capricorni; (obscura gp.) .8 bifasciata, .9 subobscura, .10 algonquin.*

basically similar types (compare Figs. 5.1, 5.4 and 5.6), which are themselves most similar to primitive types from the subgenus *Scaptodrosophila* (compare Fig. 5.1 and Figs. 4.1-4.5). In contrast, the North American temperate forest members of this radiation share their characters, not with Central and South American forms, but with species from temperate Asia (Figs. 5.8-5.10). And these species themselves show their closest ties with species of the *melanogaster* group, mainly from Asia and Africa (compare Figs. 5.8-5.10 and Figs. 5.2-5.3). On the one hand, there is continuity through the temperate zone, and on the other, tropical disjunction, with the temperate and tropical forms intergrading in the Old, but not in the New, World. And the temperate forms are derivative to at least some of the Old World tropical species. Which is to say, the sophophoran lineage became distributed throughout the tropics, split into New and Old world branches, and the *obscura* group of the north temperate zone originated from the Old World lineage.

When this pattern was first observed (Throckmorton, 1975), it was a temptation to attribute it to continental drift, as Tsacas (1979) has done. He proposes that *Sophophora* arose on the southern supercontinent prior to the separation of Africa and South America during Cretaceous times. However, when phylogeny is considered as well as distribution, both of *Sophophora* and of related groups, this conclusion is not supported by presently available evidence. It is the derivative members of the *melanogaster* group and its relatives that are found in Africa, and the *saltans-willistoni* lineage itself is derivative to other sophophorans. The Oriental region has forms showing characters which tend to intergrade with types from *Scaptodrosophila*, so it is here the group must be inferred to have originated. One can, of course, hypothesize that the group originated elsewhere, disappeared there, and primitive types remain only in Southeast Asia. But one cannot contradict an observation (primitive groups exist in Southeast Asia) with a hypothesis (they might have existed at one time elsewhere). Hence, parsimoniously, *Sophophora* arose in the tropics of Asia.

A similar pattern of tropical disjunction and north temperate continuity is seen for all the major radiations of the higher *Drosophila* (Throckmorton, 1975). Of the groups illustrated in Figure 1, it is most evident for *Sophophora* and *Hirtodrosophila*, and for the *quinaria* section of the subgenus *Drosophila*. It is somewhat less clear for the *virilis-repleta* section, apparently because very few representatives of this radiation are yet recognized as such from tropical Asia. Until additional evidence forces reevaluation, this pattern is most readily interpreted within the context of events of the Cenozoic Era. Among all of the groups, tropical origin is always clearly evident. Support is not equally strong for an origin in the Old, as opposed to the New, World, and some of the higher radiations may have originated in the New World. This does not affect the major question, however, which is that of accounting for disjunctions in so many tropical radiations.

As is well-known now (e.g., Pearson, 1978), in the early Tertiary the climate was mild. About 60 million years ago the southern continents were still mostly separate from the northern ones. India was an island drifting toward eventual collision with Asia, Australia was drifting eastward and northward, and Southeast Asia was probably a mass of island arcs and continental fragments aggregated in a

very complex fashion. In North America the Rockies were not
yet high, tropical forest extended northward at least to mid-
continent, and wet subtropical or warm temperate forest ex-
tended through Alaska and into east Asia. The Oligocene saw
the continued rise of the Rocky Mountains, the Alps, and the
Himalayas and climates of the northern land masses cooled. A
relatively pronounced change occurred about 30 million years
ago (Wolfe, 1978). During this period a flora of arid lands
began to expand to occupy much of southwestern North America.
A relatively cool, mixed mesophytic forest replaced tropical
or subtropical vegetation in Beringia, inaugurating the dis-
junction of tropical forests that remains to the present day.
By middle Miocene, about 20 million years ago, a diversified
broad-leaved forest probably extended from Japan through
Alaska into Oregon. Mean temperatures in Beringia continued
to decline, and by late Miocene time (7-10 million years ago)
there was a disjunction of the mesophytic forest, and coni-
fers began to occupy the uplands near the Bering Land Bridge
(Graham, 1972; Daubenmire, 1978; Pearson, 1978; Wolfe, 1978).

V   The Origin of the *Repleta* Group

Granting the inference that the genus originated in
tropical Asia, and given the evidence that all its major
radiations were founded in both the New and Old Worlds by
tropical lineages, it seems necessary to conclude that the
major lineages of *Drosophila* themselves arose before
tropical connections between the New and Old Worlds were
broken; i.e., before 30 million years ago, more or less. A
fossil is known from Baltic amber (Hennig, 1965) establish-
ing that drosophilids were in European forests by about 40
million years ago. A fossil is also known from amber of
Chiapas, Mexico (Wheeler, 1963), so drosophilids were on the
North American continent by about 30 million years ago. Ac-
cordingly, when all available information is combined, it is
consistent with, and supports, the inference that the ances-
tral lineage of the *virilis-repleta* radiation in the New
World tropics was in place in tropical North America by about
30 million years ago. There is no ground even to speculate on
how much before then they appeared. A somewhat later time
might be permitted, depending on the ecological requirements
of the forms involved, but 20 million years ago (middle Mio-
cene) is probably the latest time members of a major tropical
radiation might have passed between the northern continents,
and even this is quite improbable, given current views of
Tertiary climates (e.g., Pearson, 1978). Possible long-

distance dispersals could be considered, but since a corridor existed at a reasonable time, and since a number of lineages made the passage, that does not seem called for.

Figure 6 shows the major lineages of the *virilis-repleta* radiation in the New World. This has been changed from the earlier version (Throckmorton, 1975) by data obtained from *D. melanissima*, a species of the eastern deciduous forest of North America, and not available to me earlier. It proves to connect the *annulimana* group and the *robusta* group. The *melanica* group is shifted farther from the *robusta* group and into a closer relationship with the *nannoptera, bromeliae,* and *peruviana* groups, as shown in the figure. Since both the *annulimana* group and the *nannoptera* cluster are known only from the New World, this now places the origin of both the *melanica* and *robusta* groups there.
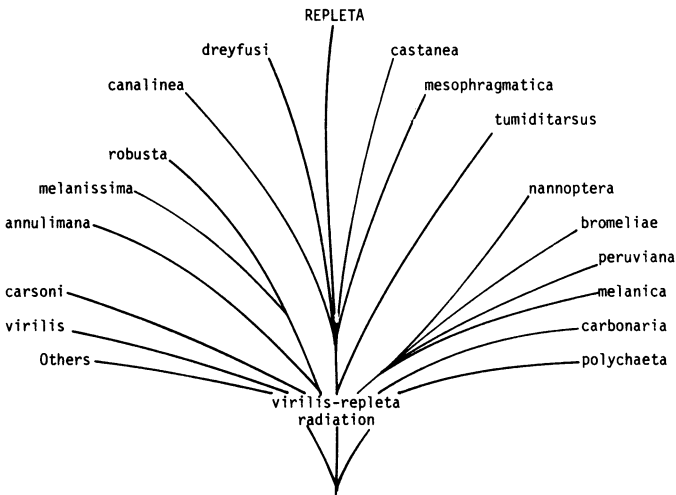

FIGURE 6. The phylogenetic structure of the virilis-repleta radiation. The names are those of species groups. "Others" refers to species I have observed in the Orient but for which little information is available. They are clearly members of this radiation, but they have not yet been placed into species groups. Of the tropical or semitropical forms, only the polychaeta group is represented by both New and Old World species. However, polychaeta itself is nearly cosmopolitan and was probably introduced by man into the New World.

So far as is known, only one Eurasian species, *D. tumiditarsus*, shows a possible relationship to the *repleta* group, but chromosomally it is not close (Wasserman, personal communication). Thus, the evidence indicates that the *repleta* lineage (including the *canalinea* group, etc.) originated from forms that were already established in the New World. This lineage may share a New World common ancestor with other New World lineages, but the present evidence from phylogeny does not require this (or exclude it). The *virilis-repleta* radiation in the New World began from species of the tropical forest. Whether the ancestor of the *repleta* group itself was a forest species which "became" a "repleta", began diversifying in the forest, and subsequently moved into arid habitats, or whether it first moved into arid habitats and became a repleta there, is difficult to determine. Its closest relatives, the *castanea, canalinea, dreyfusi* and *mesophragmatica* groups, are forest forms, for the most part, and apparently primitive members of the *repleta* group are at least facultative forest forms breeding in fallen fruit (see Throckmorton, 1975, p. 446). Parsimoniously, this permits the inference that the founder of the *repleta* group was a forest form, not necessarily of the wet forest, which "became" a repleta while still associated with forest habitats. The evidence for this, however, is not strong. To clarify the point further, it will be necessary to establish more firmly just which species are nearest to the bases of the different branches within the *repleta* group, and this will require much additional cytological and anatomical study. Then it will be necessary to determine the breeding sites, and the degree of polyphagy, of these species. This is also a formidible, but crucial, undertaking.

Determining the place of origin of the *repleta* group encounters somewhat the same problems as were met when considering the ecology of its founders. Earlier (Throckmorton, 1975), the known primitives from the major branches of the group showed distributions centering in and around Mexico That still has not changed, and, parsimoniously, the place of origin of the group must still be regarded as Mexico. However, if different species prove to be primitive, and if their distributions are different, this conclusion may change. At the present time, and on anatomical grounds especially, the major separation within the *repleta* group is between the *hydei* subgroup on the one hand and the remaining subgroups on the other, with the *fasciola* subgroup being most primitive among the latter forms. (For example,

see Throckmorton, 1962, and compare its Figures 17.1-17.8 to
Figures 4.1-4.4 of this paper.) Both the *canalinea* and *drey-*
fusi groups appear closest to the *hydei* subgroup. The *cas-*
tanea and *mesophragmatica* groups are closest to each other
and somewhat more distant from the *repleta* group. Conse-
quently the members of the *fasciola* subgroup take on unusual
importance with respect to the origin of the group, as do
members of the *hydei* subgroup and their relatives. Sene
(personal communication) has found a number of new *fasciola*
species from South America. Their features, when fully
known, may be decisive evidence for the location and ecology
of the founders of the *repleta* group, or at least for that
branch of the group that includes the *mulleri* complex and its
cytological derivatives. It is not inconceivable that the
repleta group had two (or more) "foundings", and the origin
of the *hydei* branch might profitably be treated as a separate
problem until it proves otherwise.

As was shown earlier, evidence indicates that the an-
cestors of the *repleta* group were in the New World by at
least 30 million years ago, and they almost surely arrived
there from Asia by way of Beringia. How long before then
they might have arrived cannot be said, and exactly when a
true "repleta" emerged from the ancestral radiation is
equally uncertain. There has clearly been much independent
evolution within the group on both the North and South Ameri-
can continents. The water gap between North and South
America existed from Eocene to Pliocene times (Pearson, 1978)
but it may not have been much of a barrier to *Drosophila*.
Arid conditions that might have provided habitats for an-
cestors of the *repleta* group were already present in northern
South America by the late Cretaceous (Pearson, 1978), and
they appeared in southwestern North America by Oligocene
times, or earlier (Daubenmire, 1978). Hence, by 30 million
years ago, the stage was surely set for the appearance of
the *repleta* group, if they had not already appeared by then.
Still, a great amount of evolution or diversification does
not seem to have occurred within the *repleta* group before 30
million years ago, or at least some of them should have "re-
turned" to Asia through the same corridor that brought them
to North America. There is no evidence that that happened.
This could be explained as due to limitations on the move-
ments of their cactus hosts, but since some species of the
repleta group have been reared from bleeding trees, fallen
fruits and flowers (cf. Throckmorton, 1975, p. 446) this can-
not be the whole story. Most probably, the major evolution

within the group has occurred during the last 30 million years, especially during Miocene times when floras of arid lands seem to have been well developed.

VI   Further Needs

While a great deal can already be said about the origin of the *repleta* group, much information is still needed at almost all levels. The accuracy of conclusions relating to this group depends heavily on the completeness of understanding of evolution of the genus as a whole. Refining our present knowledge requires more facts, especially about the members of the *virilis-repleta* radiation, both in Asia and in Africa. Almost surely, species exist in Southeast Asia, knowledge of which would enable us to more sharply delineate the evolutionary history of the entire radiation. And knowing that there are no close relatives of the *repleta* group in Africa would reinforce present conclusions of the group's origin on a northern continent. Timing of the origin of the group depends surprisingly heavily on our knowledge, not only of paleoecology, but also of the ecology of present species. If the founder of the group were a high altitude species, for example, the conditions for its passage to the New World might be quite different from those envisioned by the present treatment, which necessarily equates "tropical" with "warm". Hence, major efforts are needed to obtain more complete data on all attributes of species of the group. Anatomical, cytological and ecological data all complement each other, and they must be gathered, not just from species of the *repleta* group, but from their close relatives as well.

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