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Historical Biogeography of the *Drosophila melanogaster* Species Subgroup

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INTRODUCTION

Whereas there has been increasing interest in the eight members of the *melanogaster* species subgroup of *Drosophila*, no comprehensive survey exists of the biogeography and ecology of these species in the Afrotropical region.

The purpose of the present work is twofold: to summarize the available biogeographic and ecological information concerning these eight species and to propose a historical reconstruction of the distribution pattern of the *melanogaster* species subgroup.

The drosophilid fossil fauna is too poorly known (Loew, 1850; Cockerell, 1923; Hennig, 1965; Wheeler, 1963; Poinar, 1984) to be a guide to phylogenetic relationships within the family, let alone individual species

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groups. Only by the study of extant species can their relationships be inferred. The construction of a hypothesis of genealogical relationships is made difficult because ancestors may be extinct. In addition, the rooting of any phylogenetic tree, such as that proposed for the *melanogaster* species subgroup (Ashburner *et al.*, 1984; Lemeunier and Ashburner, 1984) necessarily requires assumptions that cannot be rigorously justified.

The eight species of this subgroup differ most from one another in male genitalia, ecologically, and by the patterns of polymorphism of their populations. With regard to the objectives of the present work, it is worth stressing that the *melanogaster* subgroup provides species with very different ecological habits. *Drosophila erecta* (Tsacas and Lachaise, 1974) and probably *D. orena* (Tsacas and David, 1978) are localized and specialist species, whereas *D. teissieri* (Tsacas, 1971) and *D. yakuba* (Burla, 1954) are generalist and widespread on the African mainland. In the *melanogaster* complex, *D. sechellia* (Tsacas and Bächli, 1981) and possibly also *D. mauritiana* (Tsacas and David, 1974) are specialist insular species, whereas *D. melanogaster* (Meigen, 1830) and *D. simulans* (Sturtevant, 1920) are opportunistic human commensals with an exceptional colonizing ability that has allowed them to spread all over the world. However, it is clear that *D. melanogaster* and *D. simulans* have achieved their cosmopolitan status by very different genetic characteristics (Hyytia *et al.*, 1985).

Although based on considerable biogeographic, ecological, reproductive, and genetic evidence, the evolutionary pathway proposed below remains speculative. However, it provides a general hypothesis of patterns of speciation in the *D. melanogaster* species subgroup that leads to testable predictions. An attempt is also made to relate the distribution of these species to the paleogeographic events of Africa.

BIOGEOGRAPHIC AND ECOLOGICAL EVIDENCE

The Biogeography of the Species

Drosophila melanogaster and Drosophila simulans

The fact that *D. melanogaster* and *D. simulans* are now cosmopolitan species does not, of course, imply that they were and are always sympatric. The geographic distributions of the two species in Africa, based on all the records for this region, are summarized in Fig. 1. There is a

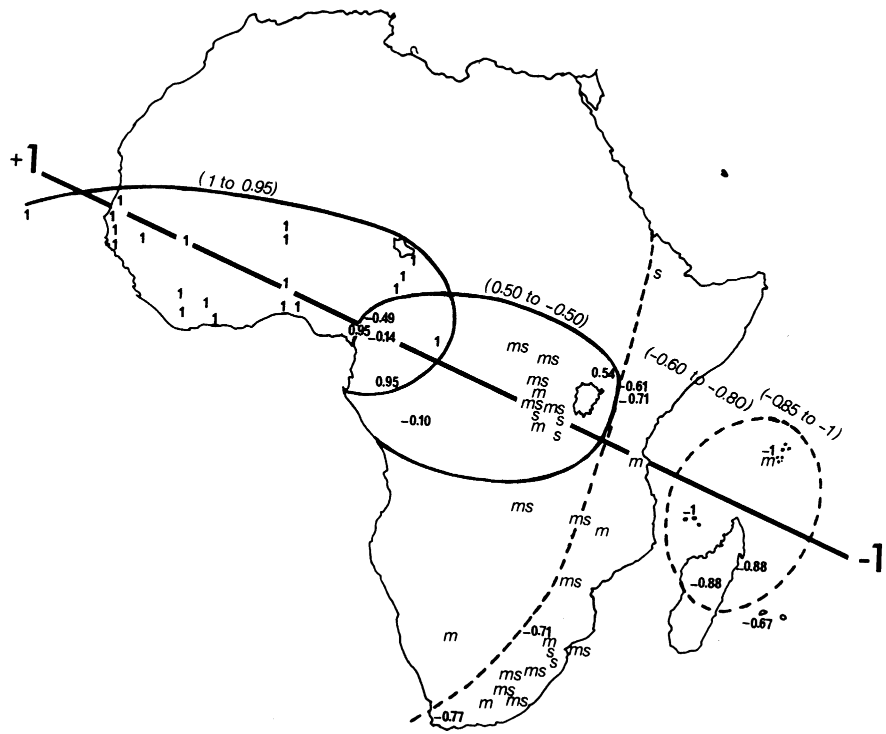


FIG. 1. Present-day distribution of the two cosmopolitan species *Drosophila melanogaster* (m) and *D. simulans* (s) in the Afrotropical region, showing a striking west–east differentiation. The map is made using the ratio (m − s)/(m + s), which ranges between +1 (*D. melanogaster* occurs alone) and −1 (*D. simulans* occurs alone) through zero (the two species coexist with equal population sizes). Only the most reliable values based on large samples are indicated. The letters are used to plot those records where the presence of either *D. melanogaster* (m) or *D. simulans* (s) or both (ms) is reported without any indication of their relative frequencies. Most values (+1) and (−1) in the Kivu–Adamaoua montane corridor to the east of the Congo basin should be considered as provisional, due to the very limited amount of reliable data. From this numerical shift, a situation arises where *D. melanogaster* inhabits western and central Africa, while *D. simulans* inhabits central and eastern Africa and the western Indian Ocean. At the scale of the overall species range within the Afrotropical region, the western populations of *D. melanogaster* are allopatric with regard to the eastern populations of *D. simulans*, while populations of the two species are sympatric in centroequatorial Africa. Note, however, that this large area is comprised of a mosaic of discontinuous habitats and either sympatry or allopatry may occur for the two species at the local level (see Fig. 10h for comparison).

striking west/east differentiation in their respective ranges, confirming Tsacas' (1979) prediction.

In the west of the Afrotropical region *D. melanogaster* is widespread and very abundant, can be found in both wild and domestic habitats, and can breed in native host plants, whereas *D. simulans* is exceedingly rare and has appeared only sporadically, and then in domestic coastal habitats.

In the east, including the easternmost mainland, Madagascar, Mascarene, Comoro, and Seychelles, the situation is just the reverse: *D. melanogaster* is rare, occasionally being found in domestic coastal habitats, whereas *D. simulans* is widespread and abundant and is sometimes confined to wild habitats, for example, in upland forest in the Seychelles (450 m) and in submontane rainforest on Mt. Ambre in northernmost Madagascar.

The most spectacular characteristic of the Afrotropical distribution of *D. simulans* is the sharp disappearance of this species to the west of the Cameroon mountains. In spite of intensive study over a 30-year period [from the work of Burla (1954) to that of Lachaise and Tsacas between 1970 and 1983 (Lachaise and Tsacas, 1983)] no more than 12 individual *D. simulans* have been collected anywhere in west Africa. These few specimens are all from harbors, of Lagos, Abidjan, and Dakkar, and have not led to the establishment of any permanent populations. They were clearly accidental, sporadic, and ephemeral introductions (they are therefore not reported on the distribution maps).

This fact corresponds to a major biogeographic break, already reported by some authors, most recently by Mayr and O'Hara (1986) for plants and animals.

By contrast, *D. melanogaster* is ubiquitous and can be very abundant everywhere in west Africa. Although basically a domestic species, as in other areas of the world, *D. melanogaster* displays in west Africa "less domestic" ecological features. When *D. melanogaster* is found, for example, deep within the evergreen rainforest of Taï (in the southwesternmost Ivory Coast) there is always a remnant, albeit sometimes tenuous, of former human activity. The presence of a small *D. melanogaster* population in the wild open highland of Mt. Nimba (1300–1400 m) in the Guinean mountains is also worth noting, although some human activity is assumed from evidence of montane grassland burning, presumably by iron miners.

One of the us (L. T.) recently had the opportunity to study museum material collected between 1934 and 1957 for the Musée Royal de l'Afrique Centrale (Tervuren, Belgium) in the mountains of east upper Zaïre. Several records of *D. melanogaster* are labeled "on *Lobelia* inflorescences in montane forests." This association with *Lobelia* is reported from two distant locations, in north Kivu (2300 m) in the vicinity of Lubero (to the west of Lake Edward) and further north on Mt. Bughera (2200 m) between the Kibali–Ituri rivers on the western edge of Lake Mobutu (Albert). Were these data reliable, they would provide a promising lead, since they would represent the only evidence for the occurrence of *D. melanogaster* on a native plant (host plant?) in a wild montane habitat in Africa. However, the altitude appears very low for *Lobelia* (Thulin, 1984) and we do not know whether or not the collection sites showed domestic features. About 100 *D. melanogaster* males and females were also recorded from Uvira in east Kivu in northern Tanganika Lake on the araceous floating plant *Pistia stratiotes* ("water salad").

One point to stress for all these records is that, although possibly introduced by humans, *D. melanogaster* has at least retained the ability to maintain permanent populations in wild habitats after human activity has ceased. In Taï, the species breeds in the native host plants available within the rainforest (see below). It seems, therefore, that in west Africa *D. melanogaster* populations can occur in seminatural habitats.

The recent origin of a population of *D. melanogaster* in the eastern Afrotropical region has been directly shown for that in the city of Victoria, Mahé (the major island of the Seychelles Archipelago). With respect to allozyme frequencies and ethanol tolerance this population closely resembles those of temperate regions (David and Capy, 1982). With respect to morphological traits it resembles those of North Africa (see also Capy *et al.*, 1983).

Evidence of sporadic introduction of *D. melanogaster* to Mauritius, the stronghold of *D. mauritiana*, was also observed. *Drosophila melanogaster* was found to be exceedingly rare in Mauritius in the 1986 survey (only four individuals were collected); in contrast numerous individuals were caught in the previous year (1985 survey), but exclusively in warehouses at Port Louis harbor. Interestingly, this has resulted in the production of natural hybrids. This was confirmed by the examination of the progeny of a wild-caught female (David *et al.*, 1987). Both the polytene chromosome banding pattern of F_1 larvae and the production of only sterile female offspring showed that the female was a hybrid from the cross of a *D. melanogaster* female with a male very likely to have been *D. mauritiana*, considering the absence of *D. simulans* there (S. Aulard, personal communication).

Despite few data from many areas (e.g., the wide geographic region of the central Congo basin, with the Chad–Sudan region to the north and the Angola–Zambia region to the south), there is increasing evidence that *D. melanogaster* is native in the west (from west Africa to the Rift), where *D. simulans* is an invader, and vice versa in the east. Our contention is that in recent historical time, i.e., Pleistocene, the geographic ranges of *D. melanogaster* and *D. simulans* were completely disjunct. Hence, the two cryptic species are assumed to have been allopatric species in the Afrotropical region, and indeed to some extent they remain so.

Drosophila erecta

Drosophila erecta has been recorded from the south and mid Ivory Coast: Yalé at the bottom (400 m) of Mt. Nimba at the border of Guinea, Taï and Sakré on the Cavally River at the border of Liberia, Lamto and Tabouatien on the Bandama River, Grand-Bassam on the coast (Lachaise and Tsacas, 1974, 1983; Rio *et al.*, 1983), from the Sudanese zone near Zaria in north Nigeria (Tsacas, 1979), from the mountains of the Bamiléké and Adamaoua plateaux, from a location close to Yaoundé in Cameroon, and from the Boko district in the Congo (Vouidibio, 1985) (Fig. 2).

A complete 15-year census of *D. erecta* records, made from 1970 to 1984 over its entire geographic range, includes only 674 adult individuals reared from *Pandanus* syncarps and less than 1000 flies collected by sweeping. Therefore *D. erecta* appears to be a rare species. Except in the Lamto savannas in the Ivory Coast, however, no comprehensive survey of the population dynamics of *D. erecta* has been made, mostly due to the difficulty of access of many of the swampy habitats of *Pandanus*.

The data on *D. erecta* breeding sites are all based on records made in the forest and preforest zones in the Ivory Coast, where the three extant strains were collected. Of the two series of ecological observations made, one is a continuous 14-month survey for 1970–1971 in the preforest area of Lamto (Lachaise and Tsacas, 1974; Rio *et al.*, 1983); the other is a 4-year survey (from 1980 to 1983), with discrete checking every month, in four distant localities in southern and mid-Ivory Coast: Grand Bassam, Lamto, Taï, and Sakré (Rio *et al.*, 1983). From these surveys it is clear that *D. erecta* is closely associated with the screwpine *Pandanus* (Monocots: Pandanaceae).

Recent studies of the genus *Pandanus* in west and central Africa have shown that several species have been included under the name *Pandanus candelabrum* [K. -L. Huynh (1984 and in preparation) for the descriptions of the new species].

Drosophila erecta has been reared from the syncarps of at least three *Pandanus* species (two monosyncarpic, the other polysyncarpic) in the Ivory Coast. *Drosophila erecta* depends on those *Pandanus* species that produce large, fleshy syncarps. These are the species found in west and central Africa. Many other *Pandanus* species, for instance, from the Indian Ocean region, produce syncarps of large, woody drupes. These ap-

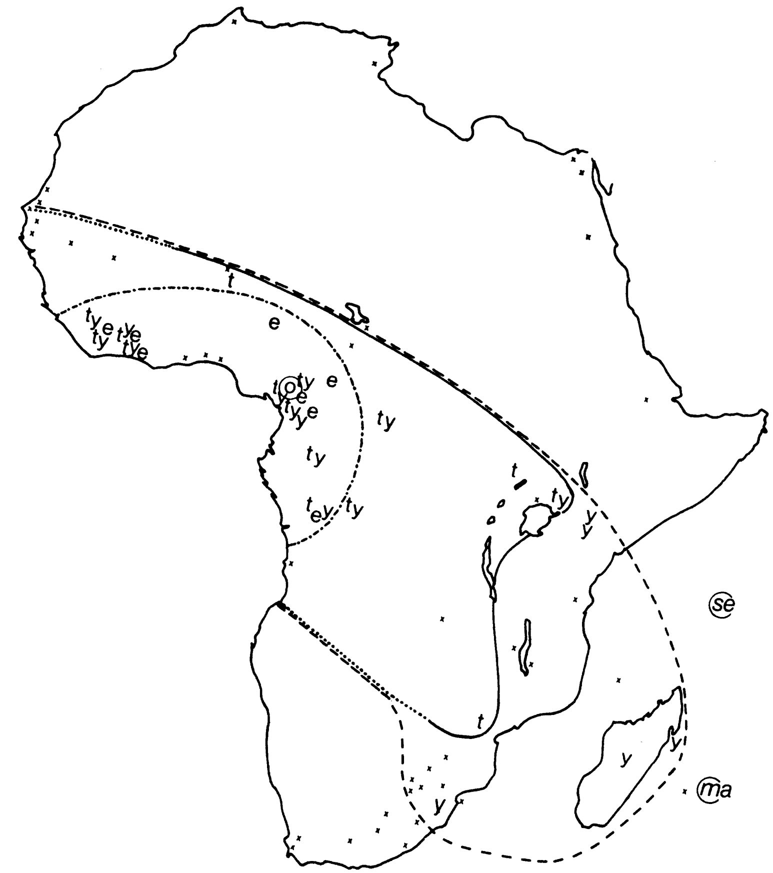


FIG. 2. Present-day geographic distribution of the six species of the *Drosophila melanogaster* subgroup endemic to the Afrotropical region. e, *D. erecta*; o, *D. orena*; t, *D. teissieri*; y, *D. yakuba*; se, *D. sechellia*; ma, *D. mauritiana*; ×, localities surveyed where the four species were not found.

pear to be unsuitable for *Drosophila* breeding. Due to the ecological requirements of its host plants, *D. erecta* appears as a swamp or stream side dweller.

The specialization of *D. erecta* to *Pandanus* is generation-dependent. It appears as a "seasonal specialization." Those generations coincident with the maturity of *Pandanus* fruit are strictly and obligatorily dependent on *Pandanus* for breeding. They show large population sizes. By contrast, those starved of *Pandanus* fruits exhibit a more opportunistic behavior and a very low population size.

It is interesting that a unique pattern of cuticular hydrocarbons is observed in the females of *D. erecta*. This is the only species of the *melanogaster* subgroup to possess particularly long-chain molecules. These may be a particularly efficient intraspecific mate recognition signal favoring sex encounters, especially during long-term demographic bottlenecks, when *Pandanus* fruits are unavailable (Jallon and David, 1987).

It must be stressed that the breeding of *D. erecta* in host plants other than *Pandanus* has only very rarely been demonstrated (two males reared from *Ficus* sp. and a palm fruit, respectively, in Lamto). Certainly, the population sizes of *D. erecta* oscillate, with peaks coinciding with the fruiting of *Pandanus*. Although it is possible that the several months between the availability of *Pandanus* fruits could be spanned by female *D. erecta* delaying their ovarian maturity, we consider that it is more probable that alternative host plants are used for breeding. When *Pandanus* fruits are available, *D. erecta* clearly prefers these to the absolute exclusion of other potential host plants, whatever their availability.

In the west Cameroon mountains there is good evidence that the altitudinal range of *Pandanus* does not exceed 800 m [in the Bamiléké plateau (R. Letouzey, personal communication)]. We have recorded *D. erecta* at 1100 m at Mangoum near Foumbot, at 1300 m in the Kounden periforest savannas, and up to 2000 m in the submontane forests of Bafut N'Guemba on Mt. Lefo. Further north, a few males were caught at 1000 m near Tizong Lake, close to Ngaoundéré in the Adamoua plateau, and further east at 800 m in N'Kolbisson near Yaoundé (Fig. 3). The question arises as to how *D. erecta* can successfully maintain populations at these high altitudes in the absence of its host plant. In view of the host-plant switching reasonably assumed to occur in the Ivory Coast lowlands, it can be suggested that, in the west Cameroon mountains, those generations of *D. erecta* coincident with the production of mature syncarps of *Pandanus* are confined to lower altitudes, whereas those starved of *Pandanus* fruits disperse and forage randomly, especially toward higher altitudes. Two males were swept on Mt. Lefo on *Eucalyptus* and the immature fruit of a rubiaceous plant, respectively. Alternatively, different host-plant races of *D. erecta* may exist in different regions of west Africa. Only further field work in the west Cameroon can settle this question.

Drosophila orena

Drosophila orena has been found only once (in 1975) and then only at Bafut N'Guemba, Mt. Lefo (2000 m) (Tsacas and David, 1978; Tsacas *et al.*, 1981). Mount Lefo is one of the volcanoes emerging from the Bamiléké plateau [the Bamenda-Banso block of Moreau (1966)] in west Cameroon (Fig. 3). In spite of an intensive 2-week investigation on Mt. Lefo, the species is known from fewer than ten wild-caught males and only one

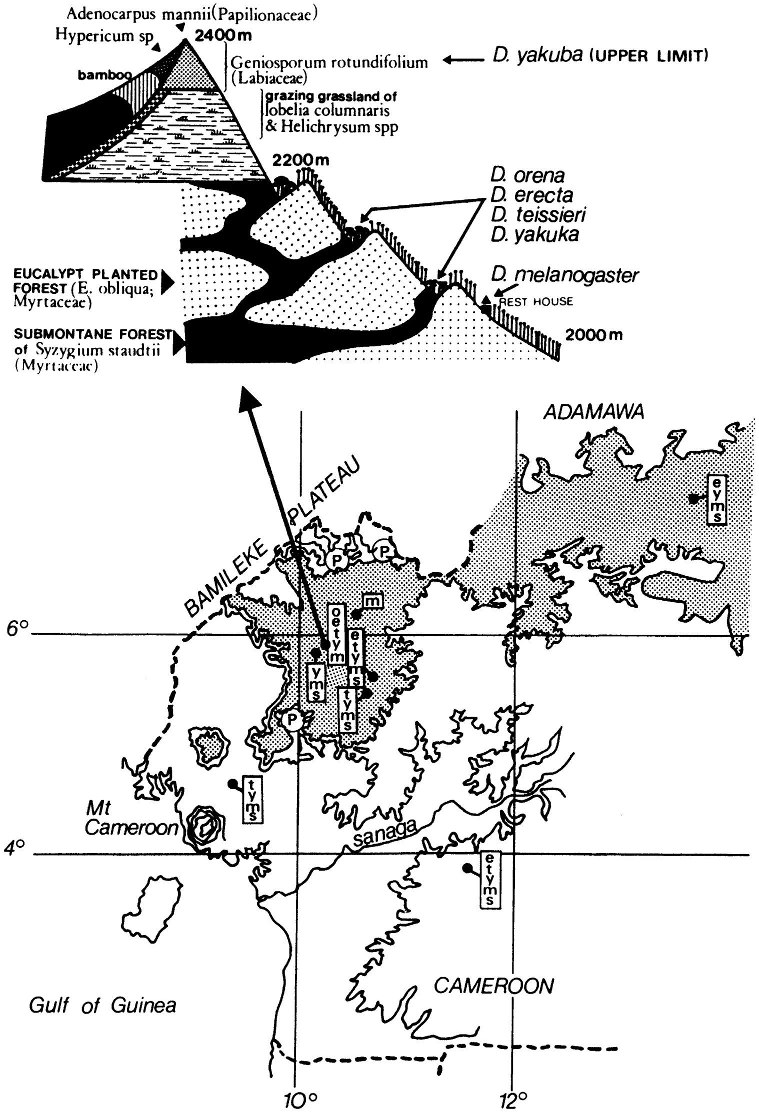


FIG. 3. Six of the eight species of the *Drosophila melanogaster* species subgroup have been recorded in the west Cameroon mountains. The cooccurrence of the species in various localities is indicated in boxes. e, *D. erecta*; m, *D. melanogaster*; o, *D. orena*; s, *D. simulans*; t, *D. teissieri*; y, *D. yakuba*. Altitudes over 1000 m are shown by shaded areas. P indicates the upper limit (800 m) of the altitudinal distribution of *Pandanus* spp. To the south of the Bamileke plateau *Pandanus* patches were recorded between 700 and 800 m at the bottom of the Manenguba volcano in the Mbo plain to the north of Nkongsamba; to the north of the Bamileke Plateau other locations are known around Nkambe between 450 and 750 m, more especially in the Tsalé Valley (Letouzey, personal communication). Above is a schematic environmental drawing of the unique locality where *D. orena* was found, Bafut Nguemba on Mt. Lefo at 2100 m in elevation in the Bamileke plateau.

female (from which the single extant strain was founded). The forest reserve of Bafut N'Guemba displays a very peculiar feature (Fig. 3), with the valley bottom occupied by primeval wet submontane rainforest and the slopes and peaks (between 1500 and 2000 m) by eucalypt forest (*Eucalyptus obliqua*; Myrtaceae) planted in the last century (Letouzey, 1968).

The few adult flies caught in the wild suggest that *Drosophila orena* is strictly confined to the submontane forest, characterized by another myrtaceous plant, *Syzygium staudtii*, and the abundance of various epiphytic plants, such as *Usnea*. *Drosophila orena* shares this habitat with about 40 other drosophilid species, among which are its close relatives *D. erecta*, *D. yakuba*, *D. teissieri*, and, near the forest lodge, *D. melanogaster*.

The ecology of *D. orena* is completely unknown. The difficulty of breeding this species on standard laboratory media and its delayed maturity suggest that it may be a specialist species.

Since similar submontane forest relicts exist on different uplands of the Bamiléké plateau, it can be reasonably inferred that the geographic range of *D. orena* extends over them. Recent field investigations in the Kenyan mountains have failed to find *D. orena*. The mountains in between, i.e., north Adamaoua, north Kivu, and the Mitumba corridor, are unexplored.

Drosophila teissieri and *Drosophila yakuba*

Strikingly, the geographic ranges of *Drosophila teissieri* and *D. yakuba* are similar, extending from eastern Guinea in northwest Africa to Zimbabwe in the southeast. On the African mainland *D. teissieri* is apparently absent to the south of a line defined by the Namib and Kalahari Deserts and the Zambeze River, while *D. yakuba* is known further south in Swaziland (McEvey *et al.*, 1988) (Fig. 2).

However, there is also clear evidence of a west–east differentiation of the geographic ranges of these two species, with that of *D. teissieri* being more western and that of *D. yakuba* more eastern. *Drosophila teissieri* does not cross the eastern Rift, whereas *D. yakuba* is widespread in east Africa and is also found in the center of Madagascar (Tsacas, 1979; Tsacas *et al.*, 1981). We can now add new records indicating its presence further east, on Ste-Marie Island (to the east of Tamatave).

The biogeographic distinction between these two related sibling species appears more evident when their relative abundance is taken into account. To the westernmost end of their geographic range (e.g., in the Mt. Nimba submontane forest within the Guinean mountains) *D. teissieri* is far more abundant than *D. yakuba* (Fig. 4).

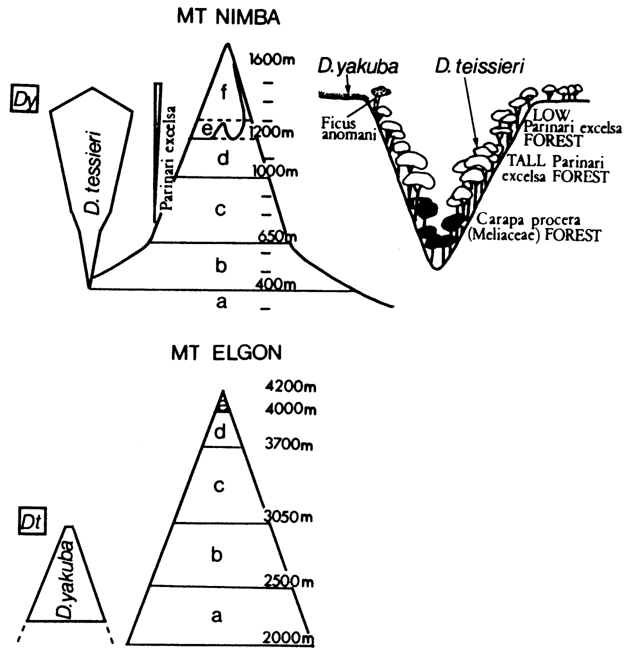


FIG. 4. Altitudinal ranges of *Drosophila teissieri* and *D. yakuba* on Mt. Nimba in the Guinean mountains and on Mt. Elgon in Kenya. The two species exhibit a somewhat reverse distributional pattern in the western and eastern mountains. (Above) Mt. Nimba is the only place in Africa where *D. teissieri* is significantly more abundant than *D. yakuba*. The absolute number of *D. teissieri* collected increases with altitude and with the approximate frequency of its main breeding site, *Parinari excelsa* (Rosaceae). The open lowland species *D. yakuba* is exceedingly rare in the submontane forest and reappears in the *Loudetia* montane grassland. (a) Lowland mesophilous forest, including second growth vegetation; (b) lower altitude evergreen rainforest; (c) transitional forest; (d) *Parinari excelsa* submontane forest; (e) *Loudetia arundinaceae* montane grassland; (f) *Loudetia kagerensis* montane grassland. (Above, right) Ravine *Parinari* forest, habitat of *D. teissieri* at the contact of the montane grassland [botanical features after Schnell (1952)]. (Below) Mt. Elgon: *D. yakuba* is widespread in the domestic area around 2200 m and is present in both the *Diospyros* forest between 2300 and 2500 m and at 3000 m at the upper limit of the bamboo. Its presence in between, in the *Podocarpus* submontane forest between 2500 and 3000 m, is not established. The only male of *D. teissieri* ever found in Kenya was caught at 3000 m. (a) *Diospyros abyssinica* forest; (b) *Podocarpus*–bamboo submontane forest; (c) Ericaceous zone; (d) *Senecio johnstonii* and *Lobelia deckenii elgonensis* zone; (e) *Senecio brassica* and *Lobelia telekii* zone.

By contrast, in the east, e.g., in the Kenya highlands, the reverse is true; *D. yakuba* is widespread and abundant, while *D. teissieri* is exceedingly rare. We have recently found the former species in Nairobi (1.700 m), at the base of Mt. Kenya (1950 m), and at various elevations on Mt. Elgon (up to 3000 m). Only one isolated male of *D. teissieri* was found in Kenya, at 3000 m on Mt. Elgon (Fig. 5). It is worth noting that

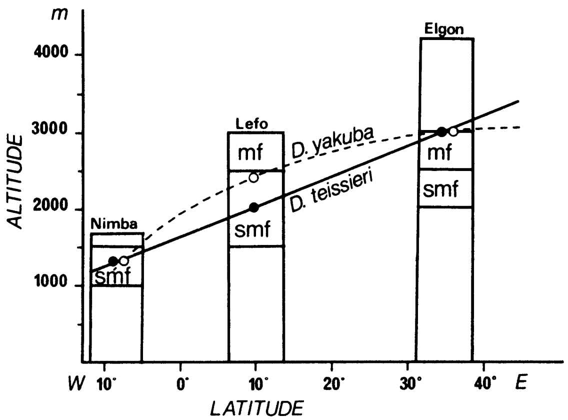


FIG. 5. Upper limit of the altitudinal range of *Drosophila teissieri* and *D. yakuba* in the Guinean mountains (Mt. Nimba), in the Bamileke Plateau in west Cameroun mountains (Mt. Lefo), and in Kenya mountains (Mt. Elgon). smf, Submontane forest; mf, montane forest.

this male is the only record of *D. teissieri* from east Africa other than the two females collected by H. E. H. Paterson on Mt. Selinda in Zimbabwe (~1000;–1200 m), from which the type strain was founded.

These two closely related species display a striking ecological divergence. The diagram in Fig. 6 illustrates the forest–savanna boundary

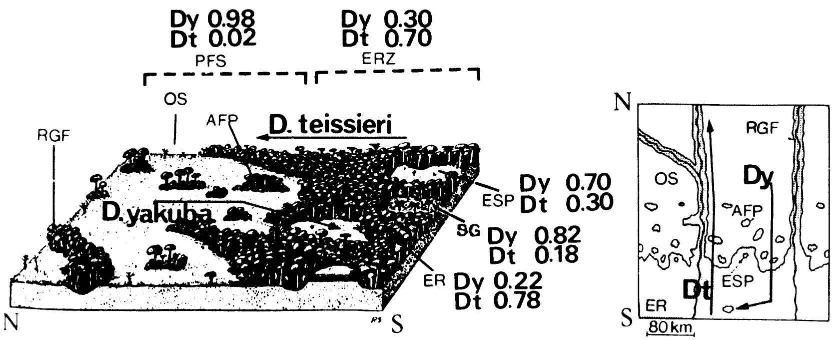


FIG. 6. Habitat partitioning of *Drosophila teissieri* and *D. yakuba* in the environmental discontinuities at the forest–savanna border in the Ivory Coast. PFS, Preforest savannas of Lamto (Guinean savannas of mid-Ivory Coast); ER, evergreen rainforest of Taï (southwestern Ivory Coast); ESP, enclosed savanna patch; AFP, advancing forest patch; OS, open savannas; RGF, riparian gallery forest; SG, second growth vegetation in forest areas. The relative frequencies of the two sibling species are given for the different environmental patches. Diagrammatic background after (left) Schnell (1971) and (right) Hopkins (1974).

in west Africa, and more especially in the Ivory Coast. *Drosophila teissieri* is chiefly a forest species, while *D. yakuba* is basically an open field species. The ratio of their abundances (*D. teissieri*/*D. yakuba*) is 0.70/0.30 in the forest and 0.02/0.98 in the savanna.

The border between the savanna and forest is not, of course, a precise line. These habitats interpenetrate, for example, along riverine forests and in patches of savanna and clearings within the forests. As a result, the distributions of *D. teissieri* and *D. yakuba* overlap extensively; frequently these species are found together, with a marked abundance of one or other species, depending on the particular habitat.

Drosophila sechellia and Drosophila mauritiana

Drosophila sechellia and *D. mauritiana* are two insular endemics in the Indian Ocean living in the Seychelles and Mauritius, respectively.

The Seychelles Archipelago, which extends over some hundreds of kilometers to northeast Madagascar, is comprised of some 30 old granitic islands and some 60 coralline islets of various ages (Stoddart, 1984). Very few of them have been surveyed. *Drosophila sechellia* was collected on three small islands, Praslin, Cousin, and Frigate. On each of them *D. sechellia* is strictly associated for breeding with the fruits of the rubiaceous shrub *Morinda citrifolia*, which is widespread all around the Indopacific area. *Morinda citrifolia* is assumed to originate from southeast Asia, but the date of its introduction to the Seychelles is unknown [see Lemeunier and Ashburner (1984) for alternative hypotheses concerning the origin of the association of *D. sechellia* with *Morinda*].

Drosophila mauritiana is restricted to the volcanic island of Mauritius located at about 900 km to the east of Madagascar and less than 200 km to the northeast of La Réunion (David and Tsacas, 1975). However, a few rare individuals of this species were recently collected by M. Solignac (1985) in Rodriguez, some 500 km to the east of Mauritius. Although confined to a very restricted home range, *D. mauritiana* is, paradoxically, an abundant, broad-niched, opportunistic, and domestic species (David *et al.*, 1987). *Drosophila mauritiana* is widespread all over Mauritius; from sea level to about 700 m, and has been repeatedly collected since 1974. The breadth of its ecological niche can be indirectly appreciated by the proportion of samples yielding *D. mauritiana*. In the 1985 survey, *D. mauritiana* was found in 49 of 50 collecting sites throughout the island, using banana bait, and in 1986 in 17 of 23 sites investigated. However, its present ecological status may be quite recent, since almost all identified resources were introduced fruits. In this respect *D. mauritiana* is ecologically quite similar to its cosmopolitan relatives *D. melanogaster* and

D. simulans, while strongly differing from its insular sibling *D. sechellia* (Louis and David, 1986). The opportunistic abilities of *D. mauritiana* are also shown by its capacity to use unfamiliar resources, such as banana, while its domestic habit is strengthened by its capacity to enter human constructions, as does *D. melanogaster*. In this respect, *D. mauritiana* could be considered as more domestic than its cosmopolitan sibling *D. simulans*, which is, in other geographic places, more reluctant to enter buildings. Therefore, the endemic insular *D. mauritiana* might potentially be a colonizing species. It is probable that the few individuals collected on Rodriguez Island were introduced by humans.

Drosophila simulans is widespread on the Seychelle and the Mascarene islands, but is not found on islands on which *D. sechellia* or *D. mauritiana* occur. Hence, in the Indian Ocean the three sibling species are comprised of completely allopatric insular populations. Note that *D. simulans* occupies large islands, like Mahé in the Seychelles, and Madagascar or La Réunion in the Madagascar–Mascarene region, to the west or the south of smaller, neighboring islands inhabited by *D. sechellia* or *D. mauritiana*.

The Breeding Sites

In studying this subgroup there is one very difficult problem: how to reconstruct the natural distributions, especially those of species such as *D. melanogaster* and *D. simulans* that have been so much affected by humans. One way to approach this question is to examine their natural breeding sites. Areas where *D. melanogaster* and *D. simulans* are found breeding in natural resources are likely to be within their natural distribution.

Of the 45 families, 90 genera, and 146 species of host plants that have been shown to be exploited as breeding sites by at least one species of drosophilid in the tropical African mainland, 29 families, 45 genera, and 63 species have yielded at least one of the species of the *D. melanogaster* subgroup (Table I).

It is obvious that our knowledge of the breeding sites of these species is very incomplete. With the exception of a single record from Ethiopia (*D. simulans*), all of the data are from collections in west and west-central Africa. Unfortunately the records of Buruga and Olembo (1971) from Uganda are not useful, since they did not distinguish between *D. melanogaster* and *D. simulans*. Very few breeding sites are known for *D. mauritiana* and none for *D. orena*.

However, some conclusions can be made from the data. It is clear

TABLE I. Check-List of the Host Plants Used As Breeding Sites by at Least One of the Closely Related Species of the *Drosophila melanogaster* Subgroup in the Tropical African Mainland[a]

		D. erecta	*D. simulans*			*D. melanogaster*		*D. melanogaster + simulans*	*D. teissieri*		*D. yakuba*	
		W	W	C	E^1	W	C	E^2	W	C	W	C
Mangifera indica	Anacardiaceae	·	·	Int	·	·	Int	Int	·	Int	·	Int
Spondias cytherea	Anacardiaceae	·	·	·	·	·	·	·	·	·	·	Int
Spondias mombin	Anacardiaceae	·	·	·	·	Int	·	·	·	·	Int	·
Annona sp.	Annonaceae	·	·	·	·	·	·	Nat	·	·	·	·
Landolphia dulcis	Apocynaceae	·	·	·	·	Nat	·	·	·	·	·	·
Unidentified	Araceae	·	·	·	·	·	·	·	Nat	·	Nat	·
Dacryodes sp.	Burseraceae	·	·	·	·	Nat	·	·	Nat	·	·	·
Ananas comosus	Bromeliaceae	·	·	·	·	·	·	Int	·	·	·	·
Rhipsalis sp.	Cactaceae	·	·	·	·	·	·	Int	·	·	·	·
Detarium senegalense	Caesalpiniaceae	·	·	·	·	Nat	·	·	·	·	Nat	·
Carica papaya	Caricaceae	·	·	·	·	·	Int	Int	·	Int	·	·
Quisqualis indica (flower)	Combretaceae	·	·	·	·	·	·	Int	·	·	·	·
Cucurbita sp.	Cucurbitaceae	·	·	·	·	Int	·	·	·	·	·	·
Drypetes chevalieri	Euphorbiaceae	·	·	·	·	·	·	·	Nat	·	Nat	·
Manihot esculenta	Euphorbiaceae	·	·	·	·	·	Int	·	·	·	·	·
Caloncoba welwitchii	Flacourtiaceae	·	·	·	·	·	·	·	·	·	·	Nat
Gossypium hirsutum	Malvaceae	·	·	·	·	·	·	Int	·	·	·	·
Guarea cedrata	Meliaceae	·	·	·	·	·	·	·	·	·	Nat	·
Artocarpus utilis	Moraceae	·	·	·	·	·	·	Int	·	·	·	·
Artocarpus sp.	Moraceae	·	·	·	·	·	Int	·	·	Int	Int	Int
Ficus elasticoides	Moraceae	·	·	·	·	·	·	·	·	·	Nat	·
Ficus exasperata	Moraceae	·	Nat	·	·	Nat	·	·	·	·	Nat	·
Ficus kamerunensis	Moraceae	·	·	·	·	Nat	·	·	·	·	Nat	·

(*continued*)

TABLE I. (*Continued*)

		D. erecta	*D. simulans*			*D. melanogaster*		*D. melanogaster + simulans*	*D. teissieri*		*D. yakuba*	
		W	W	C	E[1]	W	C	E[2]	W	C	W	C
Ficus lutea	Moraceae	·	·	·	·	·	·	·	·	·	Nat	·
Ficus lyrata	Moraceae	·	·	·	·	·	·	·	Nat	·	Nat	·
Ficus macrosperma	Moraceae	·	·	·	·	Nat	·	·	·	·	Nat	·
Ficus mucuso	Moraceae	·	·	·	·	·	·	Nat	·	·	Nat	·
Ficus ovata	Moraceae	·	·	·	·	·	·	Nat	·	·	Nat	·
Ficus polita	Moraceae	·	·	Nat	·	·	·	·	·	·	·	Nat
Ficus saussureana	Moraceae	·	·	·	·	Nat	·	·	·	·	·	·
Ficus sur	Moraceae	·	·	·	·	Nat	·	·	·	·	Nat	·
Ficus thonningii	Moraceae	·	·	·	·	·	Nat	·	·	Nat	Nat	·
Ficus sp. A (Congo)	Moraceae	·	·	·	·	·	Nat	·	·	·	·	·
Ficus sp. B (Ethiopia)	Moraceae	·	·	·	Nat	·	·	·	·	·	·	·
Musanga cecropioides	Moraceae	·	·	·	·	·	Nat(*)	·	·	·	·	·
Treculia africana (flower)	Moraceae	·	·	·	·	·	·	Nat	·	·	·	·
Musa sapientum	Musaceae	·	·	·	·	·	Int	·	·	·	·	·
Psidium guajava	Myrtaceae	·	·	·	·	·	Int	Int	·	Int	·	Int
Averrhoa carambola	Oxalidaceae	·	·	·	·	·	·	Int	·	·	·	·
Borassus aethiopum	Palmaceae	·	·	·	·	·	·	·	·	·	Nat	·
Phoenix reclinata	Palmaceae	·	·	·	·	Nat	·	·	·	·	·	·
Pandanus nov. sp. A (Lamto)	Pandanaceae	Nat	·	·	·	·	·	·	·	·	·	·
Pandanus nov. sp. B (Gd. Bass.)	Pandanaceae	Nat	·	·	·	Nat	·	·	·	·	·	·
Pandanus nov. sp. C (Taï)	Pandanaceae	Nat	·	·	·	·	·	·	·	·	·	·
Maesopsis eminii	Rhamnaceae	·	·	·	·	·	·	Nat	·	·	·	·
Eriobotrya japonica	Rosaceae	·	·	·	·	·	·	Int	·	·	·	·
Hirtella sp.	Rosaceae	·	·	·	·	·	·	·	·	·	Nat	·
Parinari excelsa	Rosaceae	·	·	·	·	·	·	·	Nat	·	Nat	·
Rubus steudneri	Rosaceae	·	·	·	·	·	·	Int	·	·	·	·
Coffea arabica	Rubiaceae	·	·	·	·	·	Nat(*)	·	·	·	·	·
Coffea canephora	Rubiaceae	·	·	·	·	·	·	Nat	·	·	·	·
Nauclea sp.	Rubiaceae	·	·	·	·	·	·	·	·	·	Nat	·
Citrus maxima	Rutaceae	·	·	·	·	·	·	·	·	Int	·	·
Gambeya taiensis	Sapotaceae	·	·	·	·	·	·	·	·	·	Nat	·
Manilkara obovata	Sapotaceae	·	·	·	·	Nat	·	·	·	·	·	·
Tieghemella heckelii	Sapotaceae	·	·	·	·	Nat	·	·	Nat	·	Nat	·
Cyphomandra betacea	Solanaceae	·	·	·	·	·	·	Int	·	·	·	·
Solanum incanum (flower)	Solanaceae	·	·	·	·	·	·	Nat	·	·	·	·
Solanum gilo	Solanaceae	·	·	·	·	·	·	Nat	·	·	·	·
Lantana camara (flower)	Verbenaceae	·	·	·	·	·	·	Int	·	·	·	·
Aframomum sanguineum (flower)	Zingiberaceae	·	·	·	·	·	·	Int	·	·	·	·
Costus spectabilis (flower)	Zingiberaceae	·	·	·	·	·	·	Nat	·	·	·	·
Phaeomeria sp.	Zingiberaceae	·	·	·	·	·	Int	·	·	·	·	·

[a] Data from west Africa: Ivory Coast (W), Central Africa: Cameroon and Gabon (C*), and East Africa: Ethiopia (E[1]) after Lachaise and Tsacas (1983) and Couturier *et al.* (1985); from Congo (C) after Vouidibio (1985); and from Uganda (E[2]) after Buruga and Olembo (1971). These latter data, which do not separate *D. melanogaster* and *D. simulans* from one another (mel. + sim.), are not involved in the comparative analysis summarized in Table II. This series of host plants includes 29 families, 45 genera, and 63 species, including one additional genus and species (*Momordica charantia*, Cucurbitaceae) from the Ivory Coast not reported here, since it provided only unidentified females of the *D. melanogaster* subgroup. Note also that *D. sechellia*, which breeds exclusively in some Seychelles islands on the fruits of *Morinda citrifolia* (Rubiaceae), is not included. Here "Nat" or "Int" under W (or C or E) does not mean that the host-plant species is "native" (or "introduced") in west Africa (or central or east Africa), but that this native host plant is exploited by *Drosophila* as a breeding site there. Hence, reading a column gives an idea of the ratio of native versus introduced host plants used in the different geographic areas.

that the diversity of host plants used as breeding sites varies greatly from one species to another, ranging from the specialist habit of *D. sechellia* and *D. erecta* to the generalist habits of *D. melanogaster* and *D. yakuba*.

The apparently strict association of *D. sechellia* with *Morinda citrifolia* (Rubiaceae) might be an example of the rare one-to-one relationship between a drosophilid and a host plant. The evidence that *D. sechellia* is a specialist species comes from the fact that it exploits *M. citrifolia* more efficiently than does *D. malerkotliana*, a highly opportunistic colonizing species, which is its only serious competitor on Cousin Island. Of the flies caught on *Morinda* (i.e., *D. sechellia* and *D. malerkotliana*), 54% were *D. sechellia*, yet of the flies reared from *Morinda* fruits, 87% were *D. sechellia* (Louis and David, 1986).

It could, of course, be argued that the specialization of *D. sechellia* to *Morinda* is due to the lack of any other suitable resources, rather than because this host plant uniquely supplies the requirements for larval growth. Thus a distinction should be made between trophic specialization in default of resource diversity and trophic specialization in spite of resource diversity, a contrast that is somewhat similar to that of ecological monophagy versus coevolved monophagy (Gilbert, 1979).

The contrast between *D. sechellia* and *D. erecta* is of interest. *Morinda* fruits throughout the year in a habitat lacking other significant resources. *Pandanus* fruits periodically in a habitat that includes many other resources suitable for breeding. Wiklund (1982) argued that specialization and generalization are relative concepts and, from an adaptationist standpoint, a specialized usage of host plants should be expected when one plant consistently gives a higher number of surviving offspring than others. As long as the most suitable host plant is abundantly available, all other potential host plants would be avoided, regardless of their abundance. In the laboratory, *D. sechellia* and *D. erecta* have similar demographic parameters. Fecundity is relatively low (<20 eggs/day), preadult development takes about 9 days, and longevity is between 30 and 40 days for both species (Lachaise, 1983; Louis and David, 1986; Payant, 1988).

Drosophila sechellia also strongly differs in ecological habit from its insular allopatric relative *D. mauritiana*, a generalist, domestic species with a broad ecological niche. *Drosophilia mauritiana* breeds in a great variety of sweet, fermenting resources, most of which are introduced plant species. It is suggested that the demographic expansion that accompanies the present domestic status of this species occurred in the last 500 years, since the first human colonization of Mauritius (David *et al.*, 1987). The reason for this suggestion is that the island was previously covered by forests. These only remain in the southwest, where they have been preserved from clearing and plantation of sugar cane. Sugar cane extends over 80% of the cultivated area. Interestingly, *D. mauritiana* was the most abundant species at Rivière des Galets, a place with a remnant portion of indigenous forest. Hence, it is assumed that in historical times *D. mauritiana* was restricted to a few native fruits and survived as a relatively small population. The sole natural breeding site of *D. mauritiana* to be recognized is, curiously, *Morinda citrifolia*. However, these data may be misleading. *Drosophila mauritiana* breeds in completely rotten *Morinda*, not in fresh fruits, as does *D. sechellia*. When completely rotten, *Morinda* fruit is exploited by a great diversity of generalist species. Moreover, only a few rare individuals of *D. mauritiana* have been reared from *Morinda*. Therefore, it seems unlikely that *Morinda* is a significant, primitive resource for *D. mauritiana* (David *et al.*, 1987).

TABLE II. Number of Host-Plant Taxa Shared by the Larvae of the Three Closely Related Species *Drosophila melanogaster, D. teissieri,* and *D. yakuba* in the Afrotropical Region[a]

Drosophila species	Host-plant taxa		
	Families	Genera	Species (native/introduced)
D. melanogaster	15	19	25 (16/9)
D. teissieri	10	11	12 (7/5)
D. yakuba	12	16	27 (22/5)
D. melanogaster/teissieri	7	7	7 (3/4)
D. melanogaster/yakuba	8	7	11 (7/4)
D. teissieri/yakuba	7	8	9 (6/3)
D. melanogaster/teissieri/yakuba	5	5	5 (2/3)

[a] The comparative analysis is based on an array of 20 host-plant families, 29 host-plant genera, and 45 host-plant species, including 34 native and 11 introduced items (see the check-list in Table I).

The extent to which the three generalist species *D. melanogaster*, *D. teissieri*, and *D. yakuba* overlap with regard to the host plants exploited by their larvae is shown in Table II. It appears that the three species share one host-plant family in four, one host-plant genus in six, and only one host-plant species in nine. Pairwise comparisons further separate quite evenly the species from one another, suggesting some possible resource partitioning (Fig. 7).

However, if resource partitioning were to result from competitive displacement, one would expect strong ecological divergence in those habitats where the species live sympatrically. Unfortunately, there are very few ecological studies at the local level from which comparisons can be made. One is from the evergreen rainforest of Taï, in the southwestern

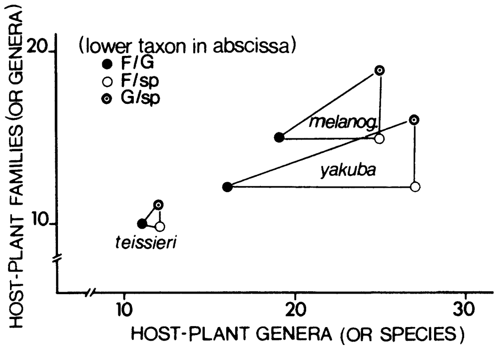


FIG. 7. Number of host-plant families (or genera) plotted against number of host-plant genera (or species) utilized as breeding sites by the more generalist species of the *Drosophila melanogaster* subgroup species in the Afrotropical region. *Drosophila teissieri* exploits significantly fewer plants than its two other relatives with an equal number of families, genera, and species. *Drosophila melanogaster* differs from *D. yakuba* in utilizing a greater number of host-plant families and genera, while the later species exploits a greater number of host-plant species than the former.

Ivory Coast, where *D. erecta*, *D. melanogaster*, *D. teissieri*, and *D. yakuba* are sympatric (Table III). The tendencies observed at the wider level are strengthened locally. *Drosophila yakuba* exploits twice as many host-plant species as breeding sites as does *D. melanogaster*. Similarly, *D. melanogaster* uses twice as many host plants as does *D. teissieri*. Hence, the host-plant pattern of *D. teissieri* appears to be significantly narrower than that of its closest relative, *D. yakuba*. Moreover, *D. teissieri* only exploits host plants that are also used either by *D. yakuba* or by *D. melanogaster*. *Drosophila melanogaster* has only one breeding site not also exploited by either *D. teissieri* or *D. yakuba*. In contrast, *D. yakuba*, the species that displays the widest local host-plant pattern, breeds in eight host-plant species not used by either of its two siblings.

From all over the Afrotropical region, of the 27 host-plant species from which *D. yakuba* has been bred, 22 (i.e., 81%) were native. Of the 25 host-plant species known to be used as a larval resource by *D. melanogaster*, 16 were native (64%). This is an unexpectedly high ratio for such a domestic species. In Taï, all the host plants from which any *Drosophila* species of the *melanogaster* subgroup, including *D. melanogaster*, have been reared are native.

UNEQUIVOCAL VERSUS EQUIVOCAL PHYLOGENETIC RELATIONSHIPS

As a preliminary to any consideration of the relationships between species within the *melanogaster* subgroup it is necessary to consider whether or not the species clustered around *D. melanogaster* have characters that enable them to form a natural group.

TABLE III. Example of Resource Sharing by the Sympatric, Closely Related Species of the *Drosophila melanogaster* Subgroup in One Locality, the Evergreen Rainforest of Taï in the Southwestern Ivory Coast[a]

Host plant		*D. erecta*	*D. melanogaster*	*D. teissieri*	*D. yakuba*	Undetermined females
Landolphia dulcis	Apocynaceae	—	L	—	—	—
Unidentified	Araceae	—	—	L	L	—
Detarium senegalense	Caesalpiniaceae	—	L	—	L	—
Momordica charantia	Cucurbitaceae	—	—	—	—	L
Oldfieldia africana	Euphorbiaceae	—	—	A	A	—
Pentadesma butyracea	Guttiferae	—	—	A	A	—
Parkia sp.	Mimosaceae	—	—	A	—	—
Ficus elasticoides	Moraceae	—	—	—	L	—
Ficus kamerunensis	Moraceae	—	L	A	L	—
Ficus lyrata	Moraceae	—	L	L	L	—
Ficus mnacrosperma	Moraceae	—	L	A	L	—
Ficus mucuso	Moraceae	—	A	A	L	—
Ficus ovata	Moraceae	—	—	—	L	—
Ficus saussureana	Moraceae	—	L	L	—	—
Ficus sur	Moraceae	—	A	—	L	—
Ficus vogeliana	Moraceae	—	—	A	A	—
Pandanus nov. sp.	Pandanaceae	L	A	—	—	—
Hirtella sp.	Rosaceae	—	—	—	L	—
Parinari excelsa	Rosaceae	—	—	—	L	—
Gambeya taiensis	Sapotaceae	—	—	—	L	—
Tieghemella heckelii	Sapotaceae	—	L	L	L	—
Mushrooms	—	—	—	—	L	—

[a] Number of host-plant taxa: investigated locally, 29 families, 46 genera, 61 species; used as a breeding sites by any Drosophilidae, 15 families, 22 genera, 35 species; on which adults of the *D. melanogaster* subgroup were caught (A), 11 families, 13 genera, 20 species; used as breeding sites by any *D. melanogaster* subgroup relatives (L), 7 families, 9 genera, 16 species. [From records reported in Couturier *et al.* (1985).]

Classification of natural groups is discovered *a posteriori*, and is not created by taxonomists *a priori* (Mayr, 1969). The objective of a classification is that it is *explanatory* and has a *predictive* value. This explains why our understanding of the *melanogaster* subgroup as a natural group changes when new species are found. At a time when only *D. melanogaster* and *D. simulans* were known, they were classed together in the "*melanogaster* subgroup" by Hsu (1949) on the basis of "genital arch with large process on posterior margin; one clasper, primary teeth long and somewhat irregularly arranged." Since then, a number of related species have been discovered that do not conform to this morphological definition. Therefore, the definition of the *melanogaster* subgroup has been gradually modified (Bock and Wheeler, 1972; Bock, 1980). It is clear that the *melanogaster* subgroup cannot be defined on the basis of any single morphological character, but only by a combination of characters.

Even though there is a great deal of genetic data allowing species comparisons within the *melanogaster* subgroup, there is very little appropriate data involving outgroup species of closely related subgroups that could provide genetic criteria for assessing the identity of the *melanogaster* subgroup. The little amount of data available [metaphase karyotypes and preliminary results dealing with homologies of polytene chromosome banding sequences (Lemeunier and Ashburner, 1984, and unpublished results; Lemeunier *et al.*, 1986)] does not allow us to decide whether the *melanogaster* subgroup is monophyletic with respect to other subgroups (e.g., *takahashii*, *suzukii*, *ficusphila*, *elegans*, *eugracilis*). Mayr (1969) stressed that evolutionary classifications should explain the joint attributes of taxa, the gaps separating taxa, and the hierarchy of categories. Doubtless, the ten species subgroups admitted within the large *melanogaster* group correspond to taxa of very unequal value. Some species within the *montium* or within the *ananassae* subgroups may well be more distantly related to each other than species of the *melanogaster* and *takahashii* subgroups.

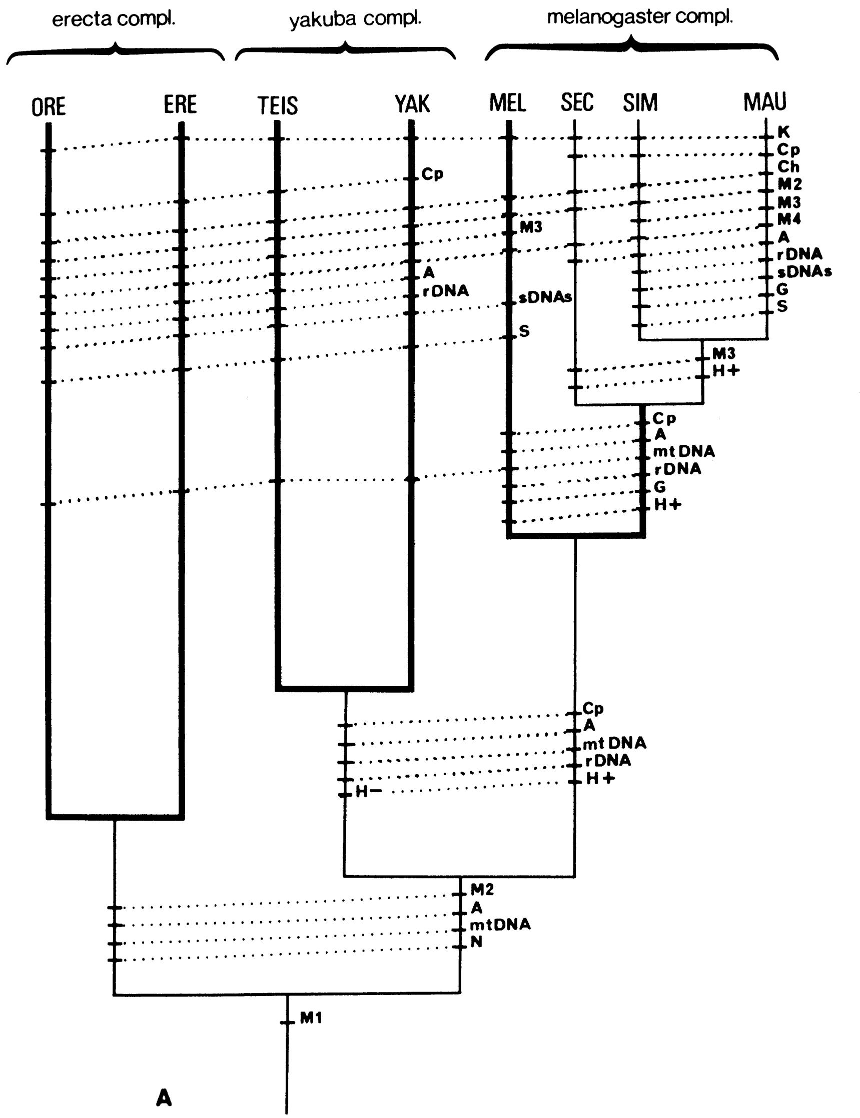
Nevertheless, although the *melanogaster* species subgroup still remains elusive as a taxon, there is strong *a posteriori* evidence of relatedness of the eight species. Figure 8 summarizes the congruence of phylogenetic data concerning these eight species from a considerable variety of characters (e.g., morphological, cytological, biochemical, molecular, and behavioral). Difficulties have appeared due to confusion resulting from the dual function of characters in classification and identification (Fig. 9) and from incomplete information from the eight species. Additional characters could have been used for uniting species within a lineage, but were omitted because they have not yet been studied in one or the other lineages and therefore could not account for the between-lineage branching.

The data presented here give consistent evidence about the relatedness of the extant species and controversial evidence about the branching pattern and ancestry. Two basic phylogenetic trees can be proposed which differ in only the first dichotomy (Figs. 8A and 8B). Both trees are monophyletic. In the two phylogenies it is assumed that the parental taxon expired when it gave rise, by splitting, to two daughter taxa. But the possibility that one of the lineages has not strongly diverged from the parental taxon and that the others have budded off from it cannot be refuted. Such a phylogenetic pattern was suggested by Throckmorton (1975) for the evolution of the entire family Drosophilidae.

The most equivocal part of the phylogeny concerns the first dichotomy, which unites the *D. teissieri* + *yakuba* species pair with either the *melanogaster* species complex (*D. melanogaster* + *sechellia* + *simulans* + *mauritiana*) (tree A) or the *D. orena* + *erecta* species pair (trees B). Most characters used in tree B are dubious and do not clearly refute tree A, while those used in tree A strongly support the relevant branching and refute tree B. In particular, the most convincing criterion supporting tree B is the number of fixed autosomal inversion differences used under a cladistic approach (Lemeunier and Ashburner, 1984). But when presented as an unrooted framework, as Lemeunier and Ashburner (1976) formerly did, the chromosomal relationships are consistent with tree A as well. Hence, *a posteriori* weighting of characters explains why tree A is most widely accepted today. Consistently data from morphology, allozymes and two-dimensional electrophoresis and mitochondrial DNA and nuclear transplantation relate the *D. teissieri* + *yakuba* species pair to the *melanogaster* complex (see references in the legend of Fig. 8). Except for morphology, these data strongly refute a monophyly for the *D. teissieri* + *yakuba* species and the *D. orena* + *erecta* species pairs. Hence, what was originally termed the *yakuba* complex (*D. orena* + *erecta* + *teissieri* + *yakuba*) has no sound basis; there is no morphological evidence and very weak genetic evidence for it.

Therefore, we propose reducing the *yakuba* complex to the *D. teissieri* + *yakuba* species pair and elevating the *D. erecta* and *orena* species pair to the level of a third independent species complex, the *erecta* complex.

The major unequivocal conclusion to be derived from the two phylogenetic trees shown in Fig. 8 is, indeed the consistent occurrence of three main lineages even though the *yakuba* and *melanogaster* lineages appear to some extent to be more closely related. It should be noted that the phylogenetic framework proposed by Lemeunier and Ashburner



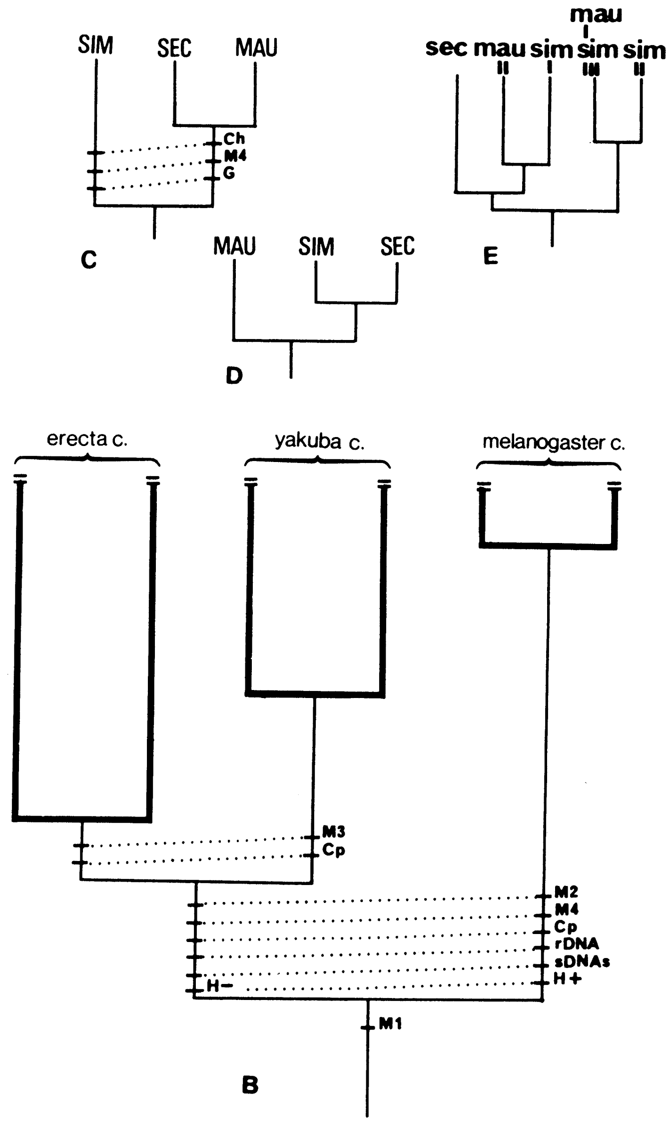


FIG. 8. Congruence of phylogenetic data concerning Afrotropical *Drosophila* of the *melanogaster* species subgroup from (M1) original combination of morphological characters involving sexual dimorphism of coloration, sex comb, clasper, (M2) morphology of male genitalia and posterior tergites and sternites (Tsacas and Bocquet, 1976; Lemeunier *et al.*, 1986), (M3) cyst length (Joly, 1987), (M4) sex comb teeth (Tsacas, 1971; Bock and Wheeler, 1972; Tsacas and David, 1974, 1978; Tsacas and Lachaise, 1974; Coyne and Kreitman, 1986), (K) metaphase karyotype (Lemeunier *et al.*, 1978; Lemeunier and Ashburner, 1984), (C) polytene chromosome banding sequences (Lemeunier and Ashburner, 1976, 1984), (Ch) distribution of centric heterochromatin of metaphase chromosomes (Lemeunier *et al.*, 1978), (A) allozymes and two-dimensional electrophoresis (Eisses *et al.*, 1979; Gonzales *et al.*, 1982; Daïnou *et al.*, 1986; Cariou, 1987; Ohnishi *et al.*, 1983), (mtDNA) mitochondrial DNA (Solignac *et al.*, 1986), (rDNA) ribosomal DNA and histone gene family orga-

FIG. 8 (*Continued*) nization (Coen *et al.*, 1982; Roiha *et al.*, 1983), (sDNAs) distribution of satellite DNA sequences (Barnes *et al.*, 1978; Cseko *et al.*, 1979; Strachan *et al.*, 1982), (G) unique DNA sequences (Langley *et al.*, 1982; Ashburner *et al.*, 1984; Cohn *et al.*, 1984; Coyne and Kreitman, 1986), (rRNA) 5S ribosomal RNA repeat (Samson and Wegnez, 1984, 1987), (N) nuclear transplantation (Santamaria, 1975), (H) hybridization relationships (David *et al.*, 1974; Coyne and Kreitman, 1986; Lachaise *et al.*, 1986), (S) courtship songs (Cowling and Burnet, 1981; Cobb *et al.*, 1985, 1986). Unequivocal phylogenetic relationships are shown by heavy lines and equivocal relationships by thin unbroken lines. When one kind of data lie on the same horizontal dotted line, this indicates similarity, whereas if data lie on slanting dashed lines, this shows a difference. For example, a character that is the same in all taxa will lie on a single horizontal line through the whole tree, whereas variation is indicated by sloping lines.

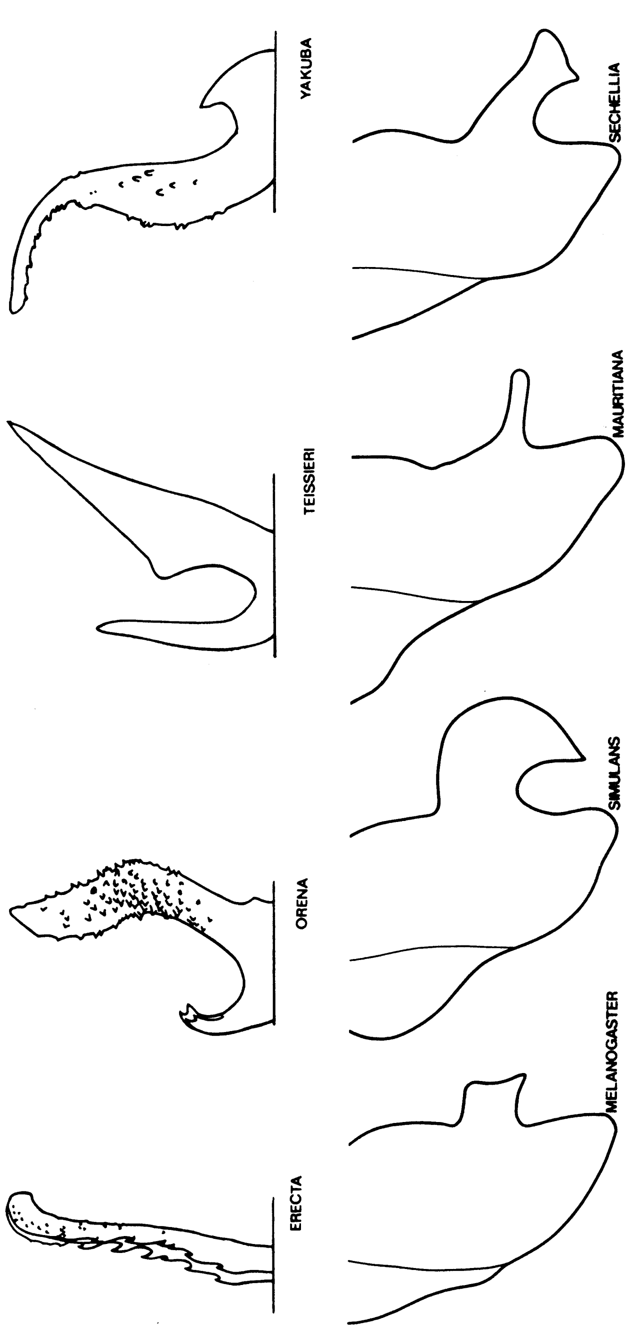


FIG. 9. Some of the major identification characters for the eight closely related species of the *Drosophila melanogaster* subgroup. The shape of the phallus (above, in lateral view) is a highly species-specific character in both the *erecta* and *yakuba* species complexes, while the shape of the posterior process of the genital arch (below, in lateral view) is the only reliable and easily visible character for the identification of the species of the *melanogaster* complex. With a little practice these characters, together with the shape of the anal plates, can be used for species diagnosis without any dissection.

(1976) on the basis of polytene chromosome banding sequences is fully consistent with such a three-lineage pattern. Data from polytene chromosomes, allozymes and 2-D electrophoresis, and mitochondrial and ribosomal DNAs and reproductive relationships strongly support the general contention that *D. teissieri* and *D. yakuba* form a monophyletic group and the *melanogaster* complex another.

Within the *melanogaster* complex, in view of concordance of chromosomal, allozymic, mtDNA, rDNA, unique DNA sequence, and hybridization data, there is general agreement for separating *D. melanogaster* from the three *D. "simulans*-like" species. In contrast, the relationship of *D. simulans* to *D. sechellia* and *D. mauritiana* has been the subject of several studies without any clear consensus of conclusions [e.g., Fig. 8, tree A (Lachaise *et al.*, 1986; Joly, 1987); tree C (Coyne and Kreitman, 1986); tree D (Cariou, 1987)]. The reason for this is that these three species, which are chromosomally homosequential and produce hybrids (including fertile females) when intercrossed, are very close to one another. Hence, only one or two characters (of rather dubious phylogenetic significance) can be used for uniting either *D. simulans* with *D. mauritiana*, *D. simulans* with *D. sechellia*, or *D. sechellia* with *D. mauritiana*. Note, however, that allozymic data equally support the two former species pairings, but soundly refute the latter (Cariou, 1987). Therefore, no character appears on tree D even though it is as plausible as the others. Mitochondrial data (Fig. 8, tree E) complicate the situation still more because of introgression between species (Solignac and Monnerot, 1986).

As a result of all these considerations, and although some uncertainties remain, there is in general a good and quite striking congruence between the numerous sets of characters considered. Only one point remains strongly conflicting and enigmatic: *D. teissieri* and *D. yakuba* are mitochondrially indistinguishable from one another, in contrast with a substantial divergence of their nuclear genomes (Solignac *et al.*, 1986). These authors invoked either introgression (but the two species do not hybridize) or quantum speciation: from a chromosomally polymorphic ancestral population, they assumed different gene arrangements could have been fixed, each with an allelic composition peculiar to it, but sharing the same mitochondrial genome.

PALEOBIOGEOGRAPHIC INFERENCES

Mayr and O'Hara (1986) stated that all currently observed distributional patterns are the result of an interplay of historical and ecological factors, and to invoke ecological explanations to the exclusion of historical ones is unwise. The approach to reconstructing past distributions requires a test of whether or not dispersal has affected distributions, and, if so, by how much. With that objective we have attempted to compare the genealogical and distributional data with a "geological genealogy." Alternative theories of historical biogeography have been proposed for explaining the evolution of distribution patterns of biotas.

Dispersal Tracks, Vicariance Biogeography, and the Refuge Theory

The *dispersal theory* was initially based on the reconstruction of centers of origin from which species dispersed over long distances. These centers of origin were assumed to have had a more or less fixed position relative to one another on the surface of the earth (Simpson, 1965). From there a stepwise dispersal occurred, involving founder populations, to differentiate into new species in descendant areas independent of geological events. Croizat *et al.* (1974) criticized the concept of "center of origin," and its corollary, dispersal of species, as conflicting with the principles of common ancestry and vicariance (allopatry). Therefore, they proposed instead to use the concept of "dispersal track" to define the distribution of a species or a monophyletic group (individual tracks); generalized tracks include the coincident individual tracks of several species or groups.

Vicariance theory assumes that biotas and distribution patterns originate through the continued geological fragmentation (subdivision, vicariance) of a formerly continuous distribution area, followed by extensive differentiation of successively isolated portions of the fragmented biota (Croizat *et al.*, 1974). Continental drift and vertical movements of the earth during the Tertiary are considered to be the main historical causes of biotic differentiation, through the formation of effective barriers between portions of a previously continuous biota, which becomes increasingly subdivided during the course of time. Under this rather static (nondynamic) theory of biotic history the significance of faunal and floral active dispersal is considered to have been small (Haffer, 1982). The dispersal theory and the vicariance theory are both based on the allopatric (geographic) speciation model, i.e., speciation by the "founder effect" according to the dispersal theory and by "subdivision" according to the vicariance theory (Haffer, 1982). Vicariance was originally rather strictly defined as the separation of the geographic range of a widespread ancestral species due to geological (tectonic) causes alone. Considering that vicariance requires no more than the development of temporary barriers

leading to the fragmentation of the range of parent species and subsequent differentiation of daughter populations in geographic isolation, many authors have given a broader sense to vicariance: a vicariant event is any geophysical, climatic, or ecological phenomenon that results in the disruption or fragmentation of a formerly continuous distribution and hence leads to allopatric speciation (Platnick and Nelson, 1978; Pregill, 1981; Haffer, 1982; Cracraft, 1986). Among the various possible causes of range fragmentation are vegetational shifts resulting from climatic reversals, leading to the formation of (ecological) "refuges."

The *Pleistocene refuge theory* was first explicitly expounded by Haffer (1969) for the American tropics, using distribution patterns of Amazonian birds to solve the apparent paradox of allopatric speciation and the lack of conspicuous orographic, vegetational, or climatic barriers in vast areas of tropical lowlands covered with forests and savannas. It has been subsequently applied to a number of organisms, including South American *Drosophila* (Spassky *et al.*, 1971; Winge, 1973). One of the interesting aspects of the refuge theory is its ability to combine the seemingly incompatible biogeographic models based on dispersal and vicariance (Haffer, 1982). Haffer stressed that "refuge" is an interpretive term referring to climatology, pedology, geomorphology, palynology, and other phenomena.

Refuge theory assumes that forest and nonforest areas changed continuously in their distribution during the geological past, breaking up into isolated blocks and then expanding and coalescing as climatic conditions change. Under this theory, plant and animal populations isolated in the more or less restricted forest and nonforest "refuges" during adverse climatic phases either became extinct, survived without much change, or, more often, differentiated to the taxonomic level of subspecies or species. Opportunities for range expansion during favorable periods led to extensive passive dispersal through continuous habitat zones and to sympatry of species spreading from different refuges. The many zones of secondary contact, with and without hybridization, document areas where dispersal was halted due to the encounter of a biologically similar population (Haffer, 1982). If at this time a refuge population of an ancestral species had evolved a new specific mate recognition system (Paterson, 1985), it could disperse widely in the now-continuous habitat before its extensive range was fragmented during the next adverse climatic phase (Haffer, 1982).

The refuge theory does not propose that all speciation has taken place in refuges, nor that all extant species are Quaternary in age (Haffer, 1982); nor does it predict that all contact zones should have been established at the same time (Mayr and O'Hara, 1986). Rather, it attempts to explain the latest and likely most effective of the series of differentiation events beginning during the late Tertiary period.

Fragmentation of the African Tropical Forest and the Refuge Theory

The refuge theory has been applied to African lowland tropical forests to explain the distribution of extant species of mammals, birds, reptiles and amphibians, and butterflies (Booth, 1958; Moreau, 1963, 1966; Carcasson, 1964; Schiotz, 1967; Laurent, 1973; Hamilton, 1976; Diamond and Hamilton, 1980; Grubb, 1982; Mayr and O'Hara, 1986). There is some agreement in recognizing three lowland forest refuge areas in west and west central Africa: the upper Guinea forest, the west lower Guinea forest (in the area of Gabon) and the east lower Guinea (or east Congo) forest (eastern Zaïre). It can be noted that the Taï rainforest in southwestern Ivory Coast, from which so many strains of *D. melanogaster*, *D. teissieri*, *D. yakuba*, and *D. erecta* originate, lies precisely in the heart of the putative upper Guinea forest refuge.

Endler (1982) rejects the refuge theory, in view of predictions about contact zones that would not be borne out by the evidence. Endler's basic arguments have been refuted by Mayr and O'Hara (1986); who conclude that strong support for the refuge hypothesis comes from the existence of many taxa endemic to those particular forest areas that have been postulated as refuges and from fragmented taxa that are still allopatric, never having come into secondary contact. Although Livingstone (1982) does not reject the possibility of Pleistocene refuges, he stresses the lack of stratigraphic evidence for the existence of even a single forest refuge:

> Fragmentation of the African tropical forest is more than a speculative fancy. Our forest is divided today into two great blocks and many smaller fragments. The topography, climate, and geological history of Africa make forest refuges very likely features of the late Quaternary evolutionary milieu. We have some fossil information on range changes of forest trees. And yet, I would be unwilling to undertake the specification and location of a single Pleistocene forest refuge in Africa.

Livingstone (1982) stressed that there were not prolonged periods of alternating dry and wet climates. Rather, constantly changing climatic patterns may have occurred, with no trend prevailing for more than a few thousand years. Haffer (1982) was led to a similar conclusion, but assumed that, even though the changes in the distribution of forest and nonforest vegetation occurred, refuges may represent areas of relative habitat con-

tinuity and average survival of certain groups of animals and plants through time.

During the Pleistocene (and especially in the last 1 million years) successive alternation of glacial and interglacial periods have led to the alternate confluence and isolation of montane forests in equatorial Africa (Moreau, 1966; Cerling *et al.*, 1977; Livingstone, 1982). There is clear evidence, from Ruwenzori, Mt. Elgon, Cherangani, Mt. Kenya, Kilimanjaro, and the mountains of the Tanganyka–Zambian border and northeast Angola, of a downward shift in vegetation belts from the high mountains during the maximum of the last glaciation (Bakker, 1964; Coetzee, 1964, 1976; Morrison, 1968; Hedberg, 1969; Flenley, 1977; Hamilton, 1982). This may have lowered the critical boundary of the montane zones from 1500 to 500 m, leading to the communication of now isolated regions some 9000–14,000 years ago (Maley, 1986). The precise nature and extent of this shift remain conjectural, especially with respect to the vegetational connections between the mountains in the eastern block (Hedberg, 1969).

However, irrespective of the real causes of the lowering of the montane glacier and vegetation belts, it is clear from changes in lake levels, sand dunes, and glacial moraines and from palynological evidence (Cerling *et al.*, 1977; Livingstone, 1982) that crucial climatic episodes and hence ecological changes, took place repeatedly in the whole Afrotropical mainland during the Pleistocene and that these resulted in major evolutionary steps in the radiation of many animals.

Several examples from the present-day distributions of plants and animals clearly indicate a previous contiguity of regions that are now isolated. For example, the upland floras of the Cameroon plateau and the Fouta Djalon-Loma-Nimba massifs in the Guinean mountains, which are at present separated by a very extensive low-lying area, were probably connected at some stage(s) during the Pleistocene (Bakker, 1967; Schnell, 1977; Maley and Livingstone, 1983). Wider east–west connections between the east African highlands, west Cameroon mountains, and the Guinean mountains in west Africa (Loma, Nimba) are attested to by the occurrence in these montane blocks of disjunct populations of plants, such as *Leucas deflexa* and *Mimulopsis solmsii* (Schnell, 1977).

The distribution of some mountain birds and other organisms in the isolated highland regions of east Africa has been explained on the hypothesis that these regions were in contact in Pleistocene times (Moreau, 1963). There is, however, a view that glacial periods were too dry for montane forest to have spread into areas at present occupied by lowland forest (Diamond and Hamilton, 1980). If it is true that periods of glacial maxima, such as that between 15,000 and 20,000 years ago, were too dry for the spread of montane floras and faunas toward lower altitudes, there have also been cold and dry phases (e.g., 15,000–20,000 years ago) and cold (or cool) and wet phases (e.g., prior to 20,000 years ago, and 9000–14,500 years ago) during which montane vegetation could well have spread to the lowlands and established connections between mountains (J. Maley, personal communication).

Significant evidence is also provided by montane species of Drosophilidae (Tsacas *et al.*, 1981). Connections within the eastern block (Ruwenzori–Elgon) and between this and the Bamileke plateau in Cameroon are all the more probable in view of the occurrence of closely related allopatric species in the *Drosophila dentissima* group (Tsacas, 1980) and in the subgenus *Scaptomyza* (*Euscaptomyza*) (Tsacas, 1972).

From the evidence of the upland floras and drosophilid faunas it is likely that migrations from the east African montane area took place during subpluvial conditions, possibly along the southern rim of the Congo basin via Angola [assumed by J. Maley (personal communication) to have been an important turntable] and then across Cameroon via the Mayombe hills.

Further west, a connection between the Bamileke plateau and Mt. Nimba in the Ivory Coast and Guinea is strongly suggested by the present-day disjunct distribution of the populations of two montane *Drosophila*, *D. adamsi* and *D. lamottei* (Tsacas *et al.*, 1981), to take examples in *Drosophila* only. It can be reasonably inferred that the isolation of these *Drosophila* populations cannot be of great age.

In summary, we will assume that great vegetational–climatic changes throughout the Pleistocene provided repeated opportunities for allopatric speciation to occur even though the timing of the events is questionable, except for the recent Quaternary.

An Ancestor Originating from Asia (Fig. 10a)

The *melanogaster* species subgroup is one of the ten species subgroups of the large *melanogaster* species group (141 species). Eight of the subgroups are represented in the Oriental region, where 91 species exist, including 72 Oriental endemics. India alone, where eight subgroups are present, has 41 species, including 21 endemics. In view of this diversity, it is generally assumed that the Oriental region is the center of origin of the *melanogaster* species group (Bock and Wheeler, 1972; Throckmorton, 1975; Bock, 1980; Tsacas, 1984; Lemeunier *et al.*, 1986). The *melanogaster* group extends over three adjacent biogeographic regions (Afrotropical, Australasian, East Palearctic) very unevenly, each having its own endemics. The Afrotropical region harbors 36 species,

among which 26 are endemics. The major point to emphasize here is that of the three species subgroups significantly represented in Africa (*melanogaster*, *montium*, *ananassae*), only one is endemic in the Afrotropical region, that is, the *melanogaster* species subgroup (assuming that the distribution of the two cosmopolitan species *D. melanogaster* and *D. simulans* is very recent). There is also chromosomal evidence indicating close relationships between the *melanogaster* species subgroup and its Oriental *takahashii* and *eugracilis* sister-subgroups (Lemeunier and Ashburner, 1984, and unpublished results). Hence, both diversity and chromosomal affinity criteria support the assumption that the origin of the ancestor of the *melanogaster* subgroup was Oriental.

The crucial question is whether the *melanogaster* species subgroup resulted from geological (tectonic) vicariant events or from dispersal tracks. The vicariance model agrees with the fact that the *melanogaster* species subgroup inhabits one biogeographic region, while its sister-subgroups (*takahashii*, *suzukii*, *ficusphila*, *elegans*, *eugracilis*) nearly all inhabit the adjacent Oriental region (including India). However, there is no consistent geological evidence (i.e., involving plate tectonics as an active biogeographic mechanism) of an ancient biogeographic subdivision of an ancestral biota that could have resulted in such a vicariance. Rather, the tendency is for plate collision, for example, the collision of India with the Asian plate around 20 million years ago (MYA). There are no data justifying the assumption that the ancestral origin of the entire *melanogaster* species group was in India. Instead, the affinities between the *suzukii* subgroup and a Palearctic outgroup, the *obscura* species group (Hsu, 1949; Okada, 1954), suggests a southeast Asian origin for the *melanogaster* group. In view of these diversity criteria, the hypothesis of major geological vicariant events for explaining the origin of both the *melanogaster* species group and, at a lower taxonomic level, the *melanogaster* species subgroup is generally refuted.

As far as the distribution patterns of extant species in rapidly evolving groups of animals such as *Drosophila* are concerned, geological events related to continental drift during the cretaceous or Tertiary are often too old to be considered as explanations (Haffer, 1982).

It is more likely that the *melanogaster* subgroup is the ultimate outcome of a succession of repeated "vicariant" events caused by climatic or ecological shifts within continental biotas, alternating with westward dispersals across mainlands. Assuming that the proto-*melanogaster* founder population arrived in Africa as a consequence of the evolution of Asian, Indian, and Arabian continental biotas, the age of the arrival of this ancestor into Africa may have coincided with the major geologic event that occurred in the early Miocene (around 17–20 MYA). At that time

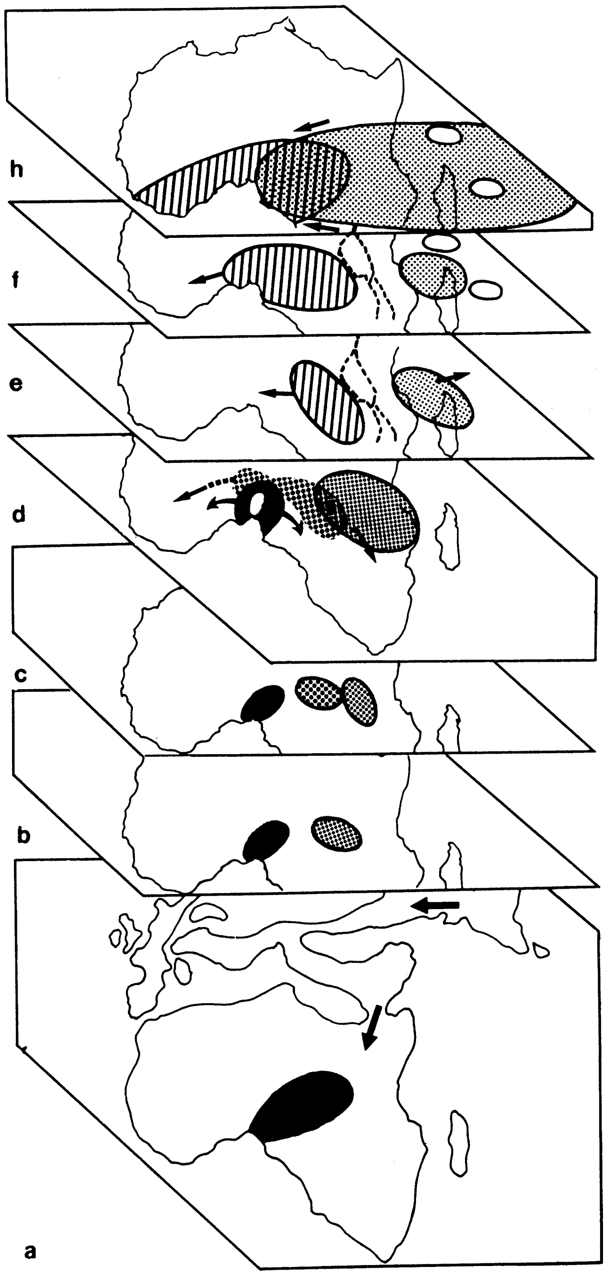


FIG. 10(a–h). A paleobiogeographic reconstitution of the evolutionary pathway of the *Drosophila melanogaster* subgroup species in the Afrotropical region. (a) Arrival of an Asiatic immigrant, which

the final closure of the Tethys Sea occurred between the Afro-Arabian and Eurasian plates (Coppens, 1984; Rögl and Steininger, 1984; Dercourt *et al.*, 1985). The closure of the Tethys Sea between the Indo-Pacific and the Middle East was accompanied by violent tectonic events, increased relief, and more diversified climates and vegetation (Axelrod and Raven, 1978; Grove, 1983). The path was open for the most important migration between Eurasia and Africa and resulted in a striking faunal change, as attested, for example, by the breakdown of the formerly strict endemism of the African mammal fauna (Thenius, 1972; Corynden and Savage, 1973; Ginsburg, 1979; Mein, 1979; Pickford, 1981; Thomas, 1984; de Bonis *et al.*, 1985). Throughout the early to middle Miocene an intermittent corridor between Arabia and Asia Minor permitted a series of waves of migration between the adjoining continents (Rögl *et al.*, 1978). Vertebrate fossils further indicate that the east African fauna became endemic precisely from the early to late Miocene, around 10–11 MYA, constituting the so-called "proto-Ethiopian" community (Thomas, 1984), which preceded the classic "Ethiopian" fauna that settled from the late Miocene to the Plio-Pleistocene (around 7 MYA).

A colonization of Africa earlier than 17–20 MYA would imply transoceanic immigration. Were this to have occurred, then the fact that the *melanogaster* subgroup is the only one of the ten species subgroups of the *melanogaster* group to be endemic in Africa (Tsacas, 1984) would not be so easily explained.

Splitting of the Primeval Trunk into Two Branches (Fig. 10b)

We suggest that the ancestral stock divided into two population groups, possibly localized on the northwest and the northeast of the Congo

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forms the stem of the *D. melanogaster* subgroup in Africa, possibly benefiting from the first terrestrial connection between the Afro-Arabic plate and Eurasia in the middle Miocene. (b) The primeval trunk splits, giving rise to the *D. orena–erecta* stem to the northwest of the Congo basin and to the stem ancestral to the other species somewhere to the east of the Congo basin. (c) The eastern stem splits again, separating the ancestor of the *D. melanogaster* species complex from that of the *D. teissieri–yakuba* species pair. (d) Differentiation of *D. orena* and *D. erecta*, possibly in west Cameroon mountains, and further spread of *D. erecta* alone to the west–west central regions; west–east extension of the *D. teissieri–yakuba* ancestor, resulting in the divergence of the two species along environmental gradients (western rainforests versus eastern savannas, respectively) with isolation by distance; the eastern branch ancestral to the *D. melanogaster* species complex occupies a vast zone from the east of the Congo basin to the Indian Ocean. (e) The continuously increasing aridification of the Rift, with a major arid phase around 2.5 MYA, results in the removal of native eastern populations and the separation of those isolated in Western forests from those isolated in the Indian Ocean islands. *Drosophila melanogaster* will emerge from the western stock and the *D. simulans*-like species from the eastern stock. (f) Westward dispersion of *D. melanogaster* in equatorial Africa and differentiation of the *D. simulans*-like species in the Indian Ocean. [See subsequent figure for part (g).] (h) The restored contact between *D. simulans* and *D. melanogaster* creates a vast zone of long-term sympatry between the two species in centroequatorial Africa.

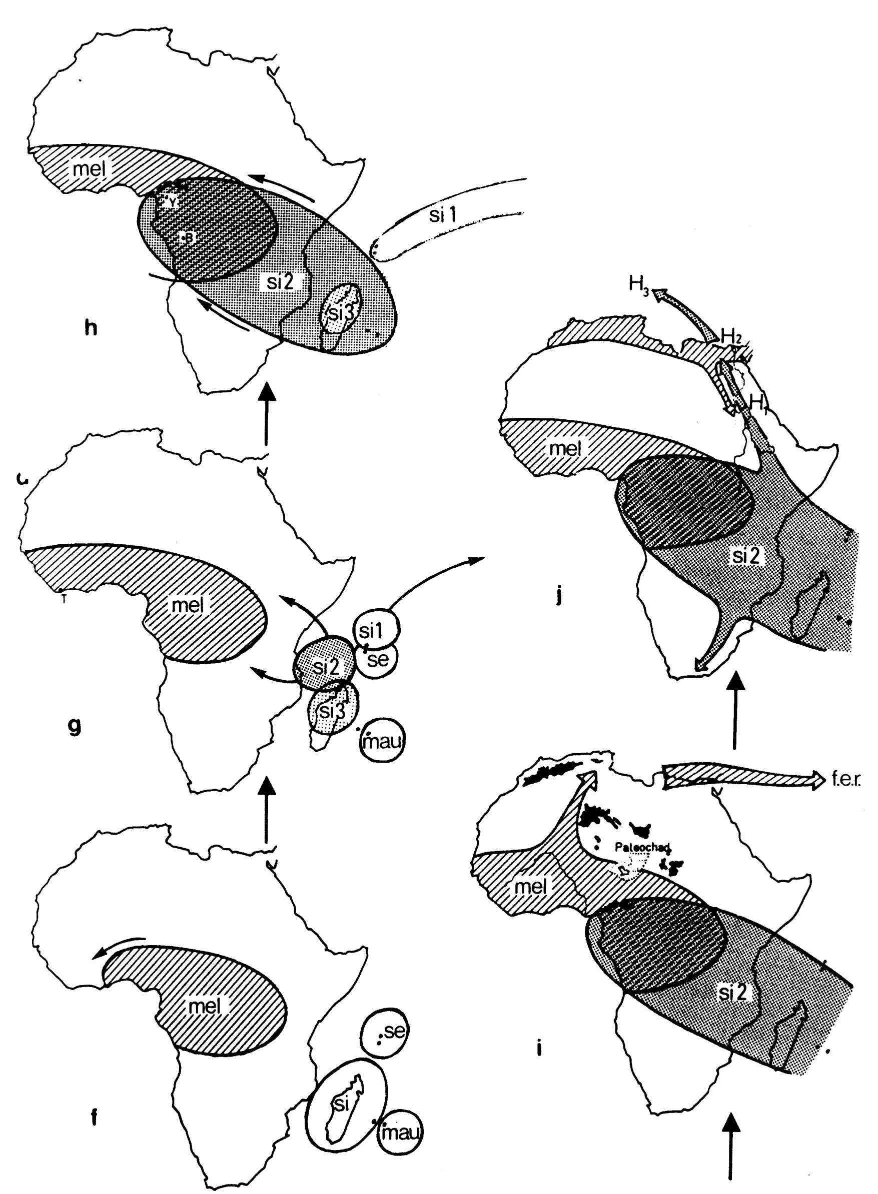

FIG. 10(f–j). (f) Complete vicariance of the four sibling species of the *Drosophila melanogaster* complex in the Afrotropical region in late Pleistocene. West and west-central Africa are the historic home ranges of *D. melanogaster*, while the western Indian Ocean is the historic home range of the *D. simulans*-like species. (g) Differentiation of the three *D. simulans* races and further expansion of the Indo-Pacific race (Si1) and the future cosmopolitan race (Si2) that colonizes first the African mainland (T: Taï). The Malagasy race (Si3) remains confined to its original area. (h) Immigrant

basin, respectively. The former lead to the *D. erecta–orena* lineage, the latter to the six other species.

The early separation of the *D. erecta–orena* lineage is based on several arguments: First, transplantation of nuclei between embryos of *D. teissieri*, *D. yakuba*, *D. simulans*, and *D. mauritiana* leads to embryonic development when made into embryos of *D. melanogaster*, but not when made into those of *D. erecta* (Santamaria, 1975). Second, the highly polymorphic amylase locus shows alleles common to five species, *D. teissieri*, *D. yakuba*, *D. melanogaster*, *D. simulans*, and *D. mauritiana*, but not to *D. erecta* or to *D. orena*. Moreover, *D. erecta* and *D. orena* possess a very slow species-specific allele different from those of any of the six other species (Daïnou, 1985; Daïnou *et al.*, 1987). Third, a restriction map analysis of mtDNA (Solignac *et al.*, 1986) shows that *D. erecta–D. orena* are relatively far apart from the six other species.

The localization of the two branches of the subgroup on either side of the Congo basin is assumed in view of the west–east allopatry of most of the species that have derived from each of them. That is, *D. erecta* and *D. orena* live to the west of the Congo basin only, whereas the *D. simulans*-like species are chiefly confined to the east. Assuming that the first split of the ancestral stock was an allopatric (vicariant) event, it can perhaps be correlated with the fragmentation of the Congolese forest. This may have resulted from the redistribution of Kalahari sand over this forest. From the Namib and extending north across the Zaïrean cuvette, there is an enormous area of stabilized dunes. The deposits are difficult to date with certainty, but late Cenozoic (Livingstone, 1982) or mid-Pleistocene (Moreau, 1966) conditions were severe enough to permit drifting of sand to extend from what is now the southern hemisphere subtropical arid belt into the zone of equatorial humidity (Livingstone, 1982).

The Three-Root Stage (Fig. 10c)

It would appear that soon after the separation of the *D. erecta–orena* lineage, the eastern branch split in its turn, separating the *D. teissieri–*

populations of the cosmopolitan *D. simulans* race restore contact with native populations of *D. melanogaster* in centroequatorial Africa, resulting in a vast zone of "historic sympatry" (Y: Yaoundé; B: Brazzaville). (i) The northward dispersal of *D. melanogaster* across the Saharan zone occurred in late Pleistocene prior to that of *D. simulans* and emerged from the westernmost *D. melanogaster* populations that had never been in contact with *D. simulans* before. Differentiation of the Far East race (f.e.r.) of *D. melanogaster*. (j) Late northward and southward dispersion of *D. simulans* from the easternmost *D. simulans* populations that had never before been in contact with *D. melanogaster*. The Nile and Mediterranean island track is marked by geographic pockets of natural hybridization (H_1 Kom Ombo; H_2, Abu Sir; H_3, Lipari) between the newly dispersing *D. simulans* and the previously arrived *D. melanogaster* ("modern sympatry").

yakuba and *D. melanogaster–simulans* lineages. Then, presumably, the *D. melanogaster* species subgroup comprised three independent ancestral forms that have all subsequently disappeared.

The argument that there was a tripartite evolutionary stage is based on the comparison of the between-group versus the within-group genetic distances calculated from allozyme frequencies (Cariou, 1987). The species groups are recognized on the basis of chromosomal affinities (Lemeunier and Ashburner, 1976). The Nei genetic distances from various authors are given in Table IV. The between-group distances range from 0.8 to 1.6 for the comparison between the *D. yakuba–teissieri* and the *D. melanogaster–simulans–mauritiana–sechellia* lineages, it is around 0.9–1.6 between the latter lineage and the *D. erecta–orena* pair, and around 1.1–1.9 between the *D. teissieri–yakuba* and *D. erecta–orena* pairs. This strongly suggests that the three lineages (i.e., *D. erecta–orena*, *D. teissieri–yakuba*, and *D. melanogaster–simulans–mauritiana–sechellia*), emerged at about the same time from a common root, rather than in a stepwise fashion. Phylogenetic relationships based on genetic distances obtained by two-dimensional electrophoresis similarly suggest a three-lineage pattern (Ohnishi *et al.*, 1983). Coen *et al.* (1982) also proposed a three-rooted phylogenetic tree, on the basis of ribosomal DNA and histone gene family organization.

A correlation between genetic distance and divergence time can be extrapolated from the observed relationship between genetic distance of Hawaiian species of *Drosophila* and the sequential ages of the Hawaiian islands that the *Drosophila* presumably colonized (Carson, 1976; Carson and Yoon, 1982).

On the basis of different appraisals of the mutation rate and from the sequences of their alcohol dehydrogenase genes, Ashburner *et al.* (1984) and Bodmer and Ashburner (1983) proposed four possible estimates of the divergence times for *D. orena* and *D. melanogaster*, i.e., 37, 15, 6, and 2 MYA. *A posteriori* reconsideration of all the data suggests that 6–15 MYA is more likely to be correct.

The *Drosophila erecta–Drosophila orena* Divergence May Have Occurred in the West Cameroon Mountains (Fig. 10d)

The antiquity of the *D. erecta–orena* divergence has long been a matter of conjecture. Although the *D. erecta–orena* ancestor represented an early stage in the evolutionary sequence, *D. erecta* and *D. orena* may have become separated more recently. The hypothesized phylogeny of Lemeunier and Ashburner (1984), based on a cladistic analysis of polytene

TABLE IV. Genetic Distances between the Eight Species of the *Drosophila melanogaster* Subgroup Based upon Allozymes[a]

Species pair	Cariou (1987)	Eisses *et al.* (1979)	Gonzales *et al.* (1982)	Ohnishi *et al.* (1983)
mel–sim	0.55	0.32	0.40	0.69
mel–mau	0.50	0.32	0.56	0.96
mel–se	0.62	—	—	—
mel–yak	0.94	1.10	—	1.47
mel–tei	1.01	0.81	—	1.65
mel–ere	1.63	1.10	—	1.31
mel–ore	1.14	—	—	—
sim–mau	0.30	0.32	0.20	0.49
sim–se	0.28	—	—	—
sim–yak	1.00	0.95	—	1.31
sim–tei	1.24	1.10	—	1.47
sim–ere	1.50	0.95	—	1.65
sim–ore	1.01	—	—	—
mau–se	0.32	—	—	—
mau–yak	0.88	1.28	—	1.31
mau–tei	1.24	0.95	—	1.31
mau–ere	1.59	1.10	—	1.65
mau–ore	1.07	—	—	—
se–yak	1.27	—	—	—
se–tei	1.36	—	—	—
se–ere	1.51	—	—	—
se–ore	1.27	—	—	—
yak–tei	0.39	0.59	—	0.86
yak–ore	1.40	1.28	—	1.47
yak–ore	1.12	—	—	—
tei–ere	1.54	1.50	—	1.87
tei–ore	1.47	—	—	—
ere–ore	1.03	—	—	—

[a] The first and the third data sets are estimates from the allele frequencies according to Nei (1972), while the other two are based upon the most common allozymes. mel, *D. melanogaster*; sim, *D. simulans*; mau, *D. mauritiana*; se, *D. sechellia*; yak, *D. yakuba*; teis, *D. teissieri*; ere, *D. erecta*; ore, *D. orena*.

and mitotic chromosomes, is consistent with a recent age for the *D. erecta–orena* differentiation. Four inversions are synapomorphic for *D. erecta* and *D. orena*, while three autosomal inversions, which are assumed to be autapomorphic, may have appeared during the most recent evolution of *D. orena*. The exceptional karyotype of *D. orena* has a massive addition of heterochromatin (Lemeunier *et al.*, 1978) and hence, of satellite DNA sequences (Barnes *et al.*, 1978; Strachan *et al.*, 1982). This might also represent an autapomorphic character that appeared subsequent to the differentiation of *D. orena*, rather than related to the supposed relict status of the species, as previously suggested by Lemeunier and Ashburner (1984).

The genetic distance between the two species of the *erecta* complex based on allozyme data (Table IV) is, however, fairly high (1.03) compared to the distance between species within either the *yakuba* or *melanogaster* complexes, suggesting an older split. The divergence between *D. erecta* and *D. orena* appears to be the most ancient within the subgroup. A study of the differentiation of satellite DNAs led to a similar conclusion (Strachan *et al.*, 1982).

Whatever the age of the *D. erecta–orena* divergence, the range of *D. orena*, which comprises submontane relictual forest in the Bamileke plateau in west Cameroon, and the confinement of *D. erecta* to west and equatorial Africa, including the Cameroon mountains (where it is sympatric with *D. orena*), suggest, as the most parsimonious hypothesis, that the emergence of the two cryptic species occurred in these highlands. This also weakens the hypothesis that it occurred 37 MYA, a time that would place the species in the late Oligocene, in other words, prior to the origin of these mountains.

In the late Miocene, around 11–12 MYA, the tectonic calm of Africa broke. In the late Miocene, the high volcanoes of the Bamileke plateau were only beginning to pile up (Furon, 1968). Considering that volcanic activity was particularly intense in this area during the Plio-Pleistocene, corresponding to 6–7 MYA, this presumably represents the earliest date for the emergence of *D. orena* consistent with the divergence time from *D. erecta* as inferred from allozymes (Cariou, 1987).

It is of course conceivable that *D. orena* already existed in the area to which it is now confined prior to the period of mountain building, simply taking refuge in the mountainous areas as they became habitable. A similar situation may have occurred in the Hawaiian islands, where, on molecular evidence, drosophilines existed some 40 MYA, well before the oldest extant island (Beverley and Wilson, 1985).

The Refuge Theory Possibly Valid for the *Drosophila teissieri–Drosophila yakuba* Differentiation (Fig. 10d)

The following discussion concerns two problems: first, the nature of the initial *D. yakuba–teissieri* divergence, and second, the subsequent evolution of *D. teissieri*. The males of *D. teissieri* and *D. yakuba* have very different genital morphologies (Tsacas and Bocquet, 1976) and at least 16 autapomorphous chromosomal inversions separate them (Lemeunier and Ashburner, 1984). Molecular data are ambiguous with respect to the question of the age of the *D. teissieri–yakuba* split. On one hand, the genetic distance between these species based on allozymes is fairly high, around 0.5, yet only half that between *D. erecta–orena* and no more than that between *D. melanogaster* and *D. simulans* (Table IV). Interpretation of satellite DNA (Strachan *et al.*, 1982) and ribosomal and histone gene families (Coen *et al.*, 1982) also suggests that the *D. teissieri–yakuba* split is more, not less, recent than that between *D. erecta* and *D. orena*. On the other hand, a very recent origin would be suggested from the mtDNAs of these species, which appear remarkably similar (Solignac *et al.*, 1986).

The distribution patterns of *D. teissieri* and *D. yakuba* suggest that they are species adapted to forests or savannas, respectively, and that they may have evolved in the morphoclimatic domains with which they are presently associated. Therefore, it is tempting to assume that pre-*D. teissieri–yakuba* populations were isolated in the more or less restricted forest or nonforest "refuges" during adverse climatic phases [see the discussion of refuge theory in Haffer (1982)]. This adaptation to different habitats resulted in the differentiation of the specific mate recognition system (Paterson, 1985) of at least one of the refuge populations of the ancestral species. In view of the present-day geographic distribution of *D. teissieri* and *D. yakuba*, it is undeniable that long-distance dispersals occurred after speciation, resulting in wide and overlapping geographic ranges all over tropical Africa. It is likely that *D. teissieri* invaded the forested vegetation networks within the savanna morphoclimatic domain, while *D. yakuba* invaded the open formation vegetation networks within the forest domains. Thereby, the two species came into secondary contact with previously conspecific populations of other refuges and, ultimately, reestablished partial sympatry. A quite similar zoogeographic scenario was proposed by, for example, Heyer and Maxson (1982) to explain the distributional patterns of some Amazonian frogs. However, the antiquity of *D. teissieri* and *D. yakuba* dispersals is a matter of conjecture. They may be of various ages. Evidence for the antiquity of the west–east spread

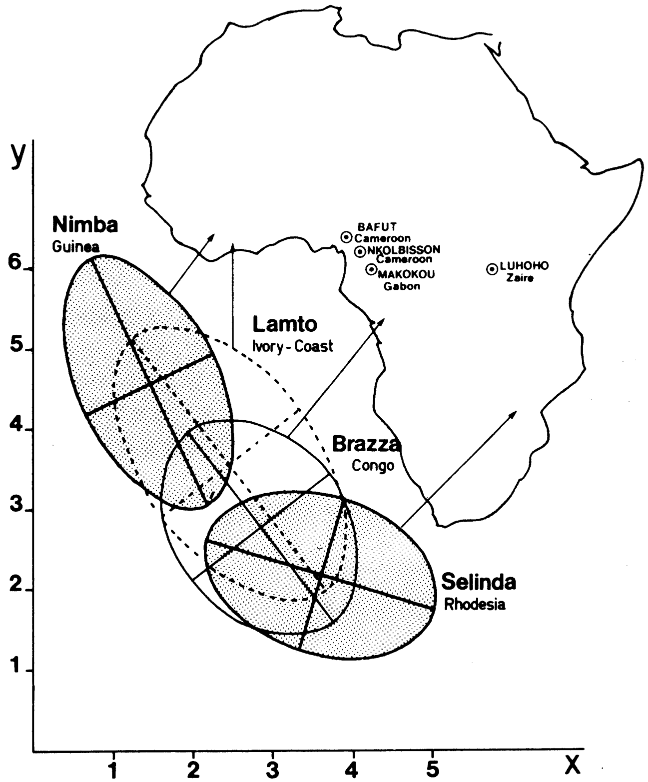

FIG. 11. Clinal differentiation of male anal plates in *Drosophila teissieri* throughout its range in Africa. Equal-probability ellipses constructed on the major axis include 95% of the variability of the populations investigated. Ellipses of four populations are plotted here to clarify the figure. Those of other populations would be placed similarly in the axis of the cline in intermediate positions.

of *D. teissieri* is seen in the striking clinal differentiation of the morphology of its male genitalia (Lachaise *et al.*, 1981). In a group of organisms where species identification on the basis of male genitalia is a dogma, the case of *D. teissieri* is unique. The geographic differentiation of male genitalia allows populations from various origins to be distinguished (Fig. 11). On the basis of the common diagnostic criteria, and without data from intermediate populations, the Mt. Nimba (Guinea/Ivory Coast) population would probably have been made one subspecies (at least) and the Mt. Selinda (Zimbabwe) population another. The *D. teissieri* populations involved in the morphological cline show some, albeit noncorrelated, differences of polytene chromosome inversions. All between-strain crosses

yield fertile hybrids and no statistically significant behavioral isolation could be detected, except for a weak tendency for assortative mating when the Nimba and Selinda populations are involved. Hence, there is clear evidence that gene flow has not prevented spatial differentiation and is not as strong a dedifferentiating factor as has often been supposed. Endler (1977) argued that geographic differentiation can be strong with respect to a locus responding to a selection gradient, even though there may be a continual and uninterrupted flow of genes among the component populations.

Whether the genitalia cline in *D. teissieri* is smooth or step is unclear. The cline may be steeper than it seems in Fig. 11. It is presently impossible to assess whether it results from primary or secondary intergradation. Primary intergradation is defined as character gradients between two geographic forms that have always been in contact, while secondary intergradation refers to two geographic forms that at one time diverged in isolation (Endler, 1977). This author further assumed that repeated fragmentation and concomitant interruption or reduction of gene flow may accelerate the differentiation process, but is not necessary for population differentiation and speciation. Hence, it is not necessary to postulate paleoclimatological refugia to explain existing geographic patterns; they can be explained on the basis of environmental gradients and dispersal patterns that continue today. However, we can disregard neither the refuge theory nor the river theory (Haffer, 1982) for explaining the origin and maintenance of the *D. teissieri* cline. In that respect it is worth noting that the Nimba and Selinda types are not characteristic of isolated montane populations. The Nimba type, for example, is widespread from upland submontane forests, around 1300 m, on Mt. Nimba to the lowland rainforest of Taï, some 220 km to the southeast. But the Lamto type, some 300 km distant to the east, does differ from the Nimba type. What happens in between is unknown. We cannot refute the idea that large rivers act as geographic barriers for certain ecologically restricted species. For forest species like *D. teissieri*, which avoid flying across very small open spaces in forest, we may expect large rivers (representing much larger and more insulated spaces), such as the Sassandra, which flow between Mt. Nimba and Lamto, to act as barriers limiting the extent of gene flow.

In summary, we speculate that the species of the *erecta* and *yakuba* complexes may have been distinct at a time when the *melanogaster* complex began to differentiate. The greater divergence between the *erecta* and *yakuba* complex species and within each of these two complexes in comparison with that in the *melanogaster* complex is also seen in their inability to cross-hybridize, both among themselves or with members of the *melanogaster* complex (Lemeunier *et al.*, 1986).

The 2- to 3-MYA Rift Aridification: A Plausible "Vicariant" Event Resulting in *Drosophila melanogaster* and the Ancestor of the Three *Drosophila simulans*-like Species (Fig. 10e)

The suggestion is made that the first speciation event in the *melanogaster* complex began by a "vicariant" event resulting in the fragmentation of the ancestral biota of the "pre-*melanogaster* population" (this name is used here for the common ancestor of the four *melanogaster* complex species). This vicariant event may have been the major climatic change that is assumed to have occurred in Africa about 2.5 MYA (Coppens, 1984). For example, the rich pollen microflora of Pliocene diatomites in the Ethiopian highlands provides evidence for the existence of an ericaceous belt some 1000 m below its present altitude, indicative of a much cooler climate than now (Bonnefille, 1983).

Renewal of tectonic activity of the Rift Valley, with the formation of step faults, backward-tilting blocks, and calderas (King, 1978; Grove, 1983), would have, to some extent, separated periequatorial Africa into western and eastern regions (Coppens, 1984). Wet airflows borne from above the Gulf of Guinea have continued to water the entire region between the Atlantic Ocean and the Rift Valley, but are stopped by the walls of the western Rift Valley. The forest that is assumed by some authors (Flenley, 1977) to have stretched from the Atlantic Ocean to the Indian Ocean, either as continuous rainforest or as a forest-wooded savanna mosaic, would have shrunk drastically in the eastern region following the Rift uplift (Andrew and Van Couvering, 1975).

The westward shift of the rainforest, which probably started in the mid-Miocene when the Tethys closure changed the airflow and hence rainfall patterns, increased during the late Pliocene and early Pleistocene, with a major arid phase at about 2.5 MYA. The general implications of this shift for both fauna and flora have been discussed by Coppens (1984). As the region to the east of the Rift became more arid, with the establishment of savanna and steppe environments, it seems probable that the continuous distribution of the pre-*melanogaster* population (from the Congo basin to the Indian Ocean) was split. In particular, we suggest that this led to the extinction of the pre-*melanogaster* population from the arid region between the western rift escarpment and the Indian Ocean. As a result, there was the complete separation of a western forest-dwelling population (possibly in some coastal forests of Mozambique) that may have further dispersed to the climatically milder islands of the Indian Ocean.

These two population groups, subject to very different ecological conditions, evolved independently from one another. It is probable that the populations in the eastern islands were, to a large extent, smaller than and diverged more rapidly from the ancestral pattern. An allopatric differentiation of *D. melanogaster*, confined to the equatorial African forests, and its eastern relative (either pre-*simulans* or *D. simulans sensu stricto*), localized to some coastal forests of east Africa or some major Indian Ocean islands, could then have occurred.

The origin of the four species of the *melanogaster* complex cannot be explained wholly by the vicariance model. The rift aridification could have been the "vicariance" event resulting in both *D. melanogaster* and the ancestor of the three *D. simulans*-like species. However, to explain the origin of these three species, there must have been, in addition, subsequent oversea dispersal to the old Indian Ocean islands followed by founder effects resulting in speciation. Thus, vicariance and dispersal are compatible in such a case, as argued by MacFadden (1981).

Using extensive congruence among the spatial and temporal histories of bird lineages in Australia, Cracraft (1986) similarly argued that an aridity gradient increase from the late Miocene onward may have been one of the factors governing the origin and evolution of continental biotas.

Of the four species of the *melanogaster*-complex, three, *D. simulans*, *D. mauritiana*, and *D. sechellia*, are far more closely related to each other than to *D. melanogaster*, a conclusion that can be consistently drawn from studies of their chromosomes (Lemeunier and Ashburner, 1984), allozymes (Table IV), repetitive and unique DNA sequences (Strachan *et al.*, 1982), mtDNA (Solignac *et al.*, 1986), response to parasitoids (Carton and Kitano, 1981), courtship behavior (Cobb *et al.*, 1986), and reproductive isolation (Lachaise *et al.*, 1986).

The major chromosomal difference between *D. melanogaster* on one hand and *D. simulans*, *D. mauritiana*, and *D. sechellia* on the other is the inversion In(3R)a$^+$ of *D. melanogaster*. The presence of this inversion in an outgroup species, the Oriental *D. eugracilis* (F. Lemeunier and M. Ashburner, unpublished results), implies that it is ancestral. However, we cannot know whether or not the population that gave rise to the present-day species of the *D. melanogaster* complex was monomorphic for In(3R)a [i.e., In(3R)a$^+$ arising in *D. melanogaster sensu stricto* at a time coincident with its speciation] or polymorphic for both chromosomes.

The ecophysiological traits of present-day populations of *D. melanogaster* and *D. simulans* differ, and do so in such a way that could suggest either a montane origin of *D. melanogaster* or an origin when climatic conditions were cooler than now found in equatorial Africa (Cohet *et al.*, 1980). For example, *D. melanogaster* is more tolerant than *D. simulans* to extreme temperatures (both high and low) and to desiccation (McKenzie, 1975; Stanley *et al.*, 1980).

Oversea Dispersal, Founder Effect, and Speciation within the *Drosophila simulans* Lineage without Novel Chromosomal Rearrangements (Fig. 10f)

The three extant species of the *simulans* lineage are chromosomally homosequential and very closely related, and all possible crosses between them yield fertile female (but sterile male) F_1 hybrids. Within this lineage *D. simulans* and *D. mauritiana* appear to be less isolated from each other than either is from *D. sechellia*. Crosses between *D. sechellia* females and *D. simulans* males are very difficult to achieve and *D. sechellia/mauritiana* F_1 males have atrophied testes. By contrast, *D. simulans/mauritiana* F_1 males have well developed (though aspermic) testes (Lachaise *et al.*, 1986). Finally, the introgression of genes between *D. simulans* and *D. mauritiana* is more complete, as seen by the increase in fertility of hybrid males, in the cross *D. simulans/mauritiana* than that of *D. simulans/sechellia* (David *et al.*, 1976; Lachaise *et al.*, 1986) [though see Coyne (1984, 1985) for somewhat contradictory results to these]. Solignac and Monnerot (1986) provide evidence of a recent introgression of mitochondrial DNA of *D. simulans* from Madagascar into *D. mauritiana*.

Coyne and Kreitman (1986) reviewed the relationships of the species of this lineage with data on genital morphology (Coyne, 1983), hybrid sterility (Coyne, 1984, 1985), and *Adh* gene sequence. It is clear that there can as yet be no unambiguous hypothesis of the relationship between these species. However, Coyne and Kreitman (1986) point to parallel morphological and behavioral changes in the two insular species, *D. mauritiana* and *D. sechellia*, suggesting that these diverged independently, but in a similar manner, from an older *D. simulans* migrant. Similarly, Solignac and Monnerot (1986) suggest from mtDNA data that the two island endemic species were probably founded by *D. simulans* propagules that evolved faster than the main bulk of *D. simulans* populations. However, there are a very few criteria that provide clear evidence that *D. simulans* is the closest of these species to *D. melanogaster*, in support of the hypothesis that it is the ancestral species. For example, after C-banding, the chromosomes of *D. sechellia* appear more similar to those of *D. mauritiana* than to those of *D. simulans* or *D. melanogaster* (Lemeunier and Ashburner, 1984).

Therefore, the possibility remains that the parental line was a pre-*simulans* and that *D. simulans* has not strongly diverged from it. *Drosophila sechellia* and *D. mauritiana* would have sequentially budded off from this lineage. But the chronology of the speciation events between the three extant *simulans*-like species is still conjectural. Hence, it would be unwise to discount the idea that *D. simulans* may well be the most recently evolved species of the *melanogaster* complex.

Coyne and Kreitman (1986) concluded that *D. sechellia* is more recently derived from *D. simulans* than is *D. mauritiana*. The *Adh* gene sequences of *D. simulans* and *D. sechellia* code for identical proteins. Yet, *D. mauritiana* and *D. simulans* are reproductively (Lachaise *et al.*, 1986) and phenetically (Joly, 1987) closer to one another than either is to *D. sechellia*, which lies nearer to *D. melanogaster*. Although *D. mauritiana*, *D. simulans* and *D. sechellia* make a monophyletic group with respect to *D. melanogaster*, *D. sechellia* appears to have strongly diverged from the *D. mauritiana-simulans* pair. Therefore, the relationship between the ability to hybridize and morphological similarity, and degree of relatedness is ambiguous.

From allozymic data, Cariou (1987) proposed a third phylogenetic tree—*D. mauritiana* emerging prior to *D. simulans* and *D. sechellia*—but stressed that these data equally support the prior differentiation of *D. sechellia*. In contrast, allozymic data refute the hypothesis that *D. simulans* arose first. Otherwise, the 5S RNA genes of *D. simulans* and *D. sechellia* are very close, but that of *D. mauritiana* has not yet been sequenced (Samson and Wegnez, 1983, 1987).

Coyne and Kreitman (1986) raise the possibility that some of the evolutionary parallels seen between the two insular species may be attributable to similar pools of genetic variation as well as to similar selection pressures. If so, were the pre-*simulans* population to have been polymorphic for In(3R)a and In(3R)a$^+$, then the fixation of the inversion in all species of the lineage may well reflect this.

The extent to which ecological conditions on the Seychelles and on Mauritius are similar is, however, debatable. The Seychelles Archipelago consists of a large number of Precambrian granitic islands (Stoddart, 1984)—granites from Praslin and Mahé were dated 654 and 532 million years, respectively (Furon, 1968)—of which all except the larger support a poorly diversified flora with respect to species producing fruits suitable for the breeding of *Drosophila*. On the other hand, the volcanic island of Mauritius is much younger: three volcanic deposits are recognized, from upper Cretaceous, Tertiary, and Pleistocene (Furon, 1968). Mauritius possesses a very diverse flora, including a number of *Drosophila* host plants that are endemic to the Mascarenes, such as *Ficus* spp. (Berg and Van Heusden, 1985). It is interesting that *Morinda citrifolia*, the host plant of *D. sechellia*, is present in Mauritius but apparently not significantly exploited by *D. mauritiana* (David *et al.*, 1987).

The only common feature of the Seychelles and Mauritius would appear to be their insularity. Moreover, there are marked differences in reproductive strategy between *D. sechellia* and *D. mauritiana*, which suggest rather different events in the adaptation of these species to their habitat. In the Seychelles, *M. citrifolia* is the sole abundant, predictable breeding site for *Drosophila*. The adaptation of *D. sechellia* to *M. citrifolia* is accompanied by a marked reduction in the number of ovarioles per female, less than half the number seen in either *D. simulans* or *D. mauritiana*. This relationship is not necessarily causal (Lachaise *et al.*, 1986).

However, J. Coyne (personal communication) argues that insularity alone may well account for the similarities in the *D. simulans–sechellia* and *D. simulans–mauritiana* divergences. Furthermore, he says that the absence of predators or competitors alone, both resulting from island colonization, may account for a significant amount of parallel evolution, particularly in those characters responding to sexual selection.

The route of the migration of *D. simulans*, or pre-*simulans*, from the east African mainland to the islands of the Indian Ocean presumably occurred via Madagascar. This is because the prevailing surface winds are easterly or southeasterly between about 1 and 10° south and the Tropic of Capricorn, whereas the major drift currents in the Mozambique channel run from northeast to southwest. Both the avifauna of the Comoro Islands (Moreau, 1966) and the insect fauna of Aldabra (Cogan *et al.*, 1971) show affinities and these congruent distributions suggest origins from or via Madagascar.

We conclude that while the number and sequence of events leading to the differentiation of the four *melanogaster* complex species cannot be rigorously determined, the data are consistent with their origin by the late Pleistocene from eastern populations of pre-*melanogaster* isolated during the period of Pliocene aridity.

Three *Drosophila simulans* "Races" (Fig. 10g)

On the basis of differences in mitochondrial DNA pattern, three geographically isolated groups of populations of *D. simulans* are recognized (Baba Aïssa and Solignac, 1984; Solignac and Monnerot, 1986): a "Malagasy race" has remained confined to its origin area, an "Indo-Pacific race" that spread out the Seychelles to colonize New Caledonia and Hawaii, and a "cosmopolitan race" endowed with an exceptional colonizing ability. The mtDNA polymorphism may either result from independent evolution within isolated populations of *D. simulans* or by segregation from a common polymorphic population.

In view of the similarity in mtDNA sequences (Baba Aïssa and Solignac, 1984), the low level of chromosomal polymorphism (Ashburner and Lemeunier, 1976), the low level of allozyme polymorphism (Hyytia *et al.*, 1985), and low variation of morphological traits (Hyytia *et al.*, 1985) observed in most populations of cosmopolitan *D. simulans*, it may be suggested that this species passed through a dramatic bottleneck early in its colonization. Colonization presumably began by the invasion of continental east Africa from the offshore islands.

Equatorial Africa Is Presumably the Historic Zone of Secondary Contact between *Drosophila melanogaster* and *Drosophila simulans* (Fig. 10h)

Our hypothesis is that the populations of *D. simulans* now found in continental Africa originated by dispersal to east Africa from Madagascar and the islands of the Indian Ocean. The westward expansion of *D. simulans* that presumably occurred after the arid conditions east of the Rift ameliorated, brought *D. simulans* into contact with large autochtonous populations of *D. melanogaster*. This expansion has been stopped by the Cameroon cordillera. Yet, and perhaps since the late Pleistocene, *D. melanogaster* and *D. simulans* have continued to evolve in sympatry over a large area of forest in equatorial west Africa, between the western escarpment of the Rift and the Cameroon cordillera.

This has led to the striking situation, still visible in the biogeographic distribution of the two species (Fig. 8h, to be compared to Fig. 1), where, to the east of the Rift, *D. simulans* lived in the absence of *D. melanogaster*, while to the west of the Cameroon mountains, *D. melanogaster* lived in the absence of *D. simulans*. In between there was an extensive contact zone between the two species.

This ancient sympatry in equatorial Africa is a unique historic situation that should be clearly distinguished from the widespread sympatry elsewhere in the world that resulted from very recent colonizations. If any reinforcement of sexual isolation between *D. melanogaster* and *D. simulans* ever occurred, then one would expect it to have resulted from this historic long-term sympatry, rather than from more recent sympatry elsewhere in the world. However, the possibility that reinforcement of sexual isolation has actually occurred between *D. melanogaster* and *D. simulans* is low. No hybrids have been found in equatorial Africa; nor did Henderson and Lambert (1982) find significant deviation from random mating of worldwide populations of *D. melanogaster*. Their study clearly showed stability in sexual behavior in a large expanded population.

It is also of interest to point out that strains of *D. simulans* collected in the Cameroon (Yaoundé) and Congo (Brazzaville) differ from those from other Afrotropical areas (Ethiopia, Kenya, Tanzania, South Africa, Comoro, Madagascar, Seychelles) in the pattern of their cuticular hydrocarbons (Luyten, 1982, 1983; Jallon and David, 1987). The cuticular hydrocarbons are thought to act as pheromones that elicit male courtship (Jallon, 1984).

Perhaps, being the smaller, the migrant *D. simulans* population of equatorial Africa may have drifted in their sexual signal traits relatively quickly.

The Northward Migration of *Drosophila melanogaster*: The Trans-Saharan Route (Fig. 10i)

The idea that the worldwide spread of *D. melanogaster* began by the crossing of what is now the desert belt of Africa, long before historic times, was suggested by David *et al.* (1976) and David and Tsacas (1981).

The hypothesis is that in the Pleistocene, *D. melanogaster* was confined to west and equatorial Africa and that a northward spread across the Sahara occurred during the late Pleistocene or Holocene periods. There is paleoclimatological evidence that suitable conditions for such a spread have frequently occurred during this period, most recently 9500–6500 years ago. Moreover, there is evidence that other groups of organisms, both plant and animal, have similarly spread.

Evidence for an extended wet period in the Saharan region comes from the lacustrine deposits of Central Ahaggar, formed contemporaneously with the last diatomites of Paleochad (Delibrias and Dutil, 1966; Maley, 1977*a*). At approximately 9500–8000 years ago, therefore, humid conditions existed in the southern and central Sahara at least, and probably also in the northern Sahara.

Holocene paleoclimates have been reconstructed from the lacustrine deposits of Paleochad by Maley (1977*b*). He concludes that tropical depressions occurred over the Tibesti plateau between 8000 and 6500 years ago, with probably two principal rainy seasons per year. Between 10,000 and 5000 years ago a more xerophytic Mediterranean flora occupied the mountains in the south, including Aïr and Tibesti (Quézel, 1965), suggesting a communication to the north. This contact is also attested by the survival of Mediterranean relict species in the central Saharan massifs. There is evidence, therefore, of floral exchange between the Mediterranean and Afrotropical region across the Sahara, and not only along the Atlantic coast corridor (Moreau, 1966).

Evidence that vertebrate species characteristic of the Afrotropical fauna have repeatedly been able to cross the Sahara until about 5000 years ago is seen from fossils from the Magrab and Sahara (Delibrias and Hugot, 1962; Moreau, 1966). We see, therefore, abundant evidence that conditions for the northward migration of *D. melanogaster* from tropical Africa to the Mediterranean existed repeatedly during late Pleistocene and Holocene periods. The date of this migration, or migrations, cannot be determined, but was presumably at least 9500–6000 years ago, the time when the last climatically suitable window existed.

Drosophila melanogaster from the eastern Palearctic region constitute a morphological race (David *et al.*, 1976; Watanabe and Kawanishi, 1976; David and Tsacas, 1981). This is presumably a consequence of an early migration from the Mediterranean region toward the east. Subsequently, *D. melanogaster* colonized the entire world (except, of course, for extreme latitudes and altitudes). This will have occurred within historical times both from the historical homeland (tropical Africa) and from secondary dispersion sites [the Mediterranean region (and hence Europe) and the Middle and Far East]. Indeed, this process of colonization continues, as witnessed by the recent spread of *D. melanogaster* to North America (Sturtevant, 1920), New Guinea (I.R. Bock, personal communication), and the Seychelles (David and Capy, 1982).

The situation to the south of the line that joins the Namib–Kalahari Deserts and the Zambeze River is still poorly understood. Nevertheless, the Zambeze seems to have been an isolating barrier even for flying animals such as birds (Moreau, 1963, 1966) and butterflies (Carcasson, 1964). In view of the tropical origin of most South African butterflies, the middle part of the Zambeze Valley failed to be such an effective barrier at some times during the upper Pleistocene (Bakker, 1967). Accordingly, a southward migration of *D. melanogaster* populations from equatorial Africa toward South Africa might have occurred during temporal windows of the late Pleistocene.

The Northward Migration of *Drosophila simulans*: The Nile Route? (Fig. 10j)

Drosophila simulans shows markedly less geographic differentiation than *D. melanogaster* for chromosomal, allozymic, quantitative, and physiological characters (Hyytia *et al.*, 1985; Singh *et al.*, 1987 and references therein). Several hypotheses can be invoked to explain the apparent contradiction between the similarity of the ecological success of these species and the differences in their genetic variation. One is that the worldwide colonization of *D. simulans* is more recent than that of *D. melanogaster* (Nei *et al.*, 1975; Singh *et al.*, 1986). This hypothesis is supported by the absence of clearly differentiated races of *D. simulans* similar to the Far East race of *D. melanogaster* (David *et al.*, 1976). Singh *et al.* (1986) further argue that this hypothesis is testable by investigating mitochondrial DNA polymorphism. If mtDNA variations were to be neutral, and if *D. simulans* has indeed gone through a recent bottleneck, one would expect to observe reduced mtDNA variation in *D. simulans*, as for allozymes, in comparison to *D. melanogaster* (Hale and Singh, in preparation).

We suggest that *D. simulans* spread from east Africa via a Nile route. This is suggested by the putative geographic home range of *D. simulans* to the east of the African mainland and from the occurrence of natural hybrids between *D. simulans* and *D. melanogaster* along that route. Mourad and Mallah (1960) collected females in the wild in both Kom Ombo in upper Egypt, to the north of Aswän, and in Abu Sir in lower Egypt, to the west of Alexandria on the Mediterranean coast. A few larval progeny, examined cytologically, proved to be hybrids between the two species. The females were clearly inseminated in their natural habitats by heterospecific males.

Another collection of *D. melanogaster/simulans* hybrids from nature is from the Lipari Islands, north of Sicily. There, Sperlich (1962) found that 5% of wild-caught females gave sterile, unisexual progeny, which morphologically were typical species hybrids. A wild-living hybrid female was also recently found in southern France and recognized by her hybrid *Adh* electrophoretic pattern (J. R. David, unpublished results).

The occurrence of natural *D. melanogaster/simulans* hybrids in the Nile Valley and Mediterranean suggests a failure of premating isolation barriers. This could be explained were these *D. simulans* populations to have derived from the parental *D. simulans* population east of the Rift Valley, a population not yet in contact with *D. melanogaster* and therefore one whose premating isolation from *D. melanogaster* had not yet been reinforced. Although tenuous, this argues for a natural migration of *D. simulans* from east Africa by the Nile Valley.

Major changes affected the hydrographic regime of the Nile in the late Pleistocene, although the details of these are controversial (Butzer and Hanzen, 1968; De Heïnzelin, 1967; Wendorf and Said, 1967; Williams and Adamson, 1974). Between 17,000 and 8000 years ago a widespread wet phase is assumed for the region between the Ethiopian plateaux and the Nubian highlands and the Red Sea, although the Sudan, which separates these, remained arid (Maley, 1981).

Later (8000–6100 years ago) there is evidence, from sediments and pollen, of climatic and vegetational change, indicating a wet period, in the hyperarid core of eastern Sahara (Ritchie *et al.*, 1985). There is evidence in northwest Sudan for a relatively deep lake, surrounded by savanna woodland, with a wet tropical climate (annual monsoon rainfall at least 400 mm) between these dates. From 6000 to 4500 years ago conditions became drier, with a reduction of rainfall from 300 to <100 mm/year. This led to the replacement of the tropical Sudano-Sahelian savannas by *Acacia*-thorn savanna and scrub grassland. The lake appears to have dried up at about 4500 years ago and, with increasing aridity, was covered by aeolian sediments.

In this connection, one might wonder how long reestablished sympatry between *D. melanogaster* and *D. simulans* would have to have lasted for premating barriers to have been achieved. Our estimate for this period is more than 6500–5000 years, a time that we suspect to be the minimum age that should be attributed to the spread of *D. melanogaster* and *D. simulans* from the Afrotropical mainland toward Eurasia and hence corresponding to the minimum age of the older modern sympatries. Having said this, we should not discount the possibility that *D. simulans* spread from the Afrotropical region only in very recent times. As for *D. melanogaster*, there is evidence of a continuing spread of *D. simulans*, most dramatically its recent colonization of Japan (Watanabe and Kawanishi, 1976). However, Casares and Carracedo (1985) found that sexual isolation was notably higher between allopatric than sympatric Japanese populations of *D. melanogaster* and *D. simulans*. In addition to refuting the hypothesis of reproductive character displacement, this suggests that only a short time may be required for divergence in sexual isolation to be achieved.

CONCLUDING REMARKS AND SUMMARY

In view of the ecological and biogeographic characteristics of the cryptic species summarized here and genetic evidence from the literature, pathways of evolution in the *D. melanogaster* species subgroup are tentatively proposed. Similar historical reconstitutions have been made for the evolution of Hawaiian *Drosophila*, the timing of which has greatly benefited from the possibility of dating past events, using the age of the islands as a clue (Carson, 1976; Carson and Yoon, 1982), for the evolution of the *repleta* group, showing how the observed biogeographic patterns can justify conclusions regarding the time and place of the origin of the species (Throckmorton, 1982*a*), and for the evolution of the *virilis* species group, by the inference of areas of prior distribution (Throckmorton, 1982*b*).

Considering the eight species of the *melanogaster* subgroup, isolines of equal species number, drawn on a distributional map of these species in Africa show a concentric pattern, with the largest number of species in central equatorial Africa (Fig. 12). We suspect that the diversity of the

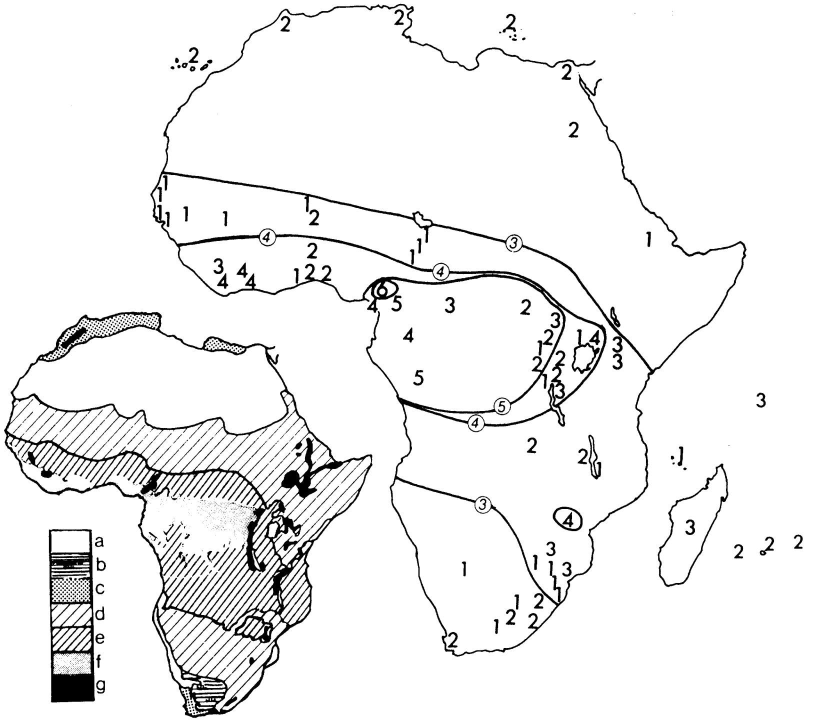

FIG. 12. Species richness of the *Drosophila melanogaster* species subgroup in the Afrotropical region. The ranges of equal species number are indicated. The large numbers show what is known, and the isolines of equal species number accompanied by small encircled numbers show what is expected. The Congo basin and Madagascar regions are very poorly known. The vegetational boundaries of the large biomes are shown at bottom left: (a) desert; (b) Karroo; (c) Macchia, Mediterranean vegetation and temperate grassland; (d) bushveld, grassland of Sahelian or Sudanese type and steppe; (e) forest–savanna mosaic of Guinean type and dry deciduous savanna woodland; (f) tropical lowland rainforest; (g) montane and temperate forest.

fauna in Madagascar and the Congo basin is underrepresented due to lack of collections in these regions. There is a clear correlation of species richness with relative rainfall and hence with vegetation. There is a relatively sharp change in species richness across the forest–savanna boundary. Similarly, outliers of high richness are in areas of high rainfall. The distribution of these species in Africa today is clearly determined in part by vegetational–climatic factors. This cannot, however, be the entire story, since neither the distribution of *D. orena* nor that of *D. simulans* corresponds to any large-scale climatic discontinuity.

There are four major lines where the boundaries of two or more species of the *melanogaster* subgroup coincide. It can be reasonably expected that the geographic range of *D. erecta* extends further west to Guinea and further east and south over some western parts of the Zairean cuvette. The southern border of the Sahara desert limits the *D. teissieri* and *D. yakuba* ranges to the north, and the Namib–Kalahari–Zambeze line those of *D. erecta* and *D. teissieri* to the south. The eastern Kenya rift appears as a major barrier to the distribution of *D. teissieri* and also *D. melanogaster* to the east. Note that for *D. melanogaster* the central core of its distribution is indeed to the west of the eastern rift even though outlying isolated populations resulting from very recent introductions may be found on the east. The fourth major line is the volcano "archipelago" of the Cameroon rift, which is peculiar in that on one hand it is the western border of the central core of *D. simulans* and on the other hand it is in itself the range of *D. orena*. Hence, the west Cameroon mountains where six species ranges overlap appears to have played a very complex role in the historical biogeography of the species: both a center of endemism for montane species and a geographic barrier or secondary contact zone for lowland species.

It is of interest to emphasize that the three major Sahelian, eastern Rift, and Namib–Kalahari–Zambeze lines delineate clear-cut faunal regions within the entire Drosophilidae family, while the Cameroon mountain line does not. The drosophilid fauna of west and west central Africa is generally the same, while greatly differing from the southern African and east African ones. The latter was recently shown to comprise more particularly a number of endemic species complexes related to Palearctic groups, such as the *obscura* and *quinaria* species groups (M.-L. Cariou, D. Lachaise, and M. Ashburner, unpublished results).

The *melanogaster* species subgroup shows a high degree of endemism. Three species (*D. sechellia, D. mauritiana, D. orena*) are restricted to very small regions and *D. erecta* to a somewhat larger one. After Endler (1982), we can recognize centers of endemism or diversity, a faunal region (Grubb, 1982) being the maximum area of distribution of endemics within one center. The west Cameroon center of endemism is also seen for drosophilids of other groups, e.g., *D. matilei*, *D. ngemba*, and *D. quatrou* (*dentissima* species group) and *Scaptomyza deemingi* (*Euscaptomyza*) (Tsacas, 1972). In the Indian Ocean the distribution of drosophilids provides evidence for two centers of endemism, in the Mascarenes (Réunion, Mauritius, Rodriguez) and in the islands of the northern Seychelles Archipelago (David and Tsacas, 1975; Tsacas *et al.*, 1981).

Species endemic to each local center (i.e., *D. orena* in western equatorial Africa, *D. sechellia* and *D. mauritiana* in Seychelles and Mauritius) have their closest relatives (i.e., *D. erecta* and *D. simulans*, respectively) in the same or close area. The nonendemic taxa (*D. melanogaster–simulans*, *D. teissieri–yakuba*) show a strong west–east differentiation in their ranges between the western and eastern centers of endemism.

From these considerations we can superimpose an area cladogram that is based on the most plausible phylogenetic tree (Fig. 13). There is some general congruence between the two. Hence, differentiation of most

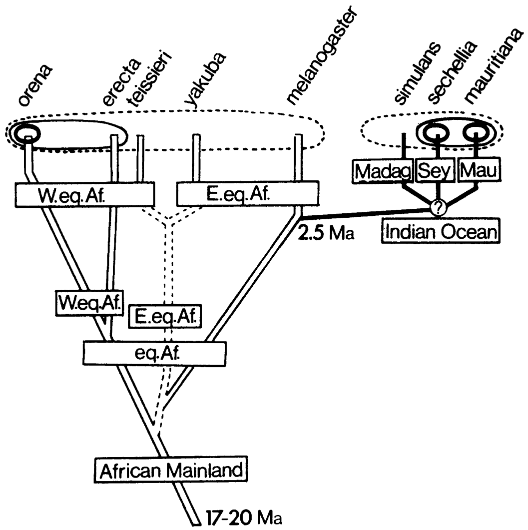

FIG. 13. Area cladogram superimposed on the most plausible phylogenetic tree of the *Drosophila melanogaster* species subgroup (see Fig. 8). The evolutionary pathway stops at some time in late Pleistocene, when *D. melanogaster* and *D. simulans* presumably were allopatric in the Afrotropical region. W.eq.Af., Western equatorial Africa; E.eq.Af., eastern equatorial Africa; Madag, Madagascar; Sey, Seychelles; Mau, Mauritius. Note that the *D. teissieri–yakuba* and *D. melanogaster*–pre-*simulans* (or *D. simulans*) divergences are assumed to have been to some extent concomitant and both late compared to the *D. orena–erecta* divergence. Also, no preference is given to particular chronologies of speciation events in the three *D. simulans*-like species.

mainland species (e.g., *D. teissieri–yakuba* or *D. melanogaster*–pre-*simulans* or *D. simulans*) is assumed to have occurred through range fragmentation and hence from vicariance. There is some consensus for the fragmentation and reconstruction of the west African rainforest during Pleistocene due to climatic–vegetational cycles (Moreau, 1963; Livingstone, 1975; Maley, 1986). Vicariance and discontinuous distributions are related to the possible former occurrence of forest refuges. *Drosophila orena*, which is a montane forest taxon, is irrelevant to the problem of the refuge hypothesis because it has never been suggested that the mountain forms evolved in lowland forest refuges (Mayr and O'Hara, 1986). In contrast, long-distance oversea dispersal of propagules resulting in founder effects did occur in the ancestral population of the *D. simulans*-like species inhabiting peripheral areas of eastern African mainland and adjacent groups of islands.

Assuming that most of the eight extant species originated during the Pleistocene, then the entire early differentiation in the *melanogaster* subgroup, i.e., the origin of the ancestral line, may have taken place during a fairly long interval in the preceding late Tertiary period.

We propose that prior to the mid-Miocene, when the Afro-Arabian continent was isolated from the rest of the world, no *melanogaster* subgroup species were to be found in Africa. No faunal exchange via a continental path was possible throughout the Paleocene, as suggested by the endemic mammal fauna (Rögl and Steininger, 1984). Further, we suggest that as a consequence of the contact between Afro-Arabia and Eurasia (17–20 MYA), a population of primeval *D. melanogaster* immigrated into Africa, possibly into the equatorial zone, and that from this event there originated a center of speciation and dispersal of the subgroup. The historical biogeography of the *melanogaster* subgroup exemplifies Müller's (1973) statement that during the evolution of a taxon, the center of origin and the center of dispersal can become widely separated from each other.

In the late Pleistocene *D. melanogaster* was confined to the west of the Rift Valley, including the Kivu mountains, whereas the ancestor of the *simulans* lineage was confined to the east of the Rift, including the islands of the Indian Ocean. *Drosophila melanogaster* populations are therefore assumed to be native to the west of the Rift Valley and those of *D. simulans* and its relatives to the east. The absence of *D. simulans* from west Africa seems then to be due primarily to the fact that it was probably allopatric to *D. melanogaster* during most of the late Pleistocene. These distributions are perhaps due to a coincidence in the time the western and eastern faunal regions differentiated with the time of the split between *D. melanogaster* and pre-*simulans*. We suggest that this was some 2.5 MYA, at the same time of major tectonic activity in the Rift and the subsequent spread of the arid zone over east Africa, a date that matches the estimates of Stephens and Nei (1985) of the time of divergence, i.e., 2.0–3.5 MYA, between *D. melanogaster* and either *D. simulans* or *D. mauritiana*.

From these considerations it follows reasonably that the northward migrations of the two cosmopolitan species have followed different routes, a western, possibly across western Sahara, for *D. melanogaster*, and an eastern, possibly along the Nile, for *D. simulans*. Interestingly, a quite similar hypothesis is suggested by Summers Smith (in press) for sparrows.

The exact time (or times) that *D. melanogaster* spread northward from its historical home range in west equatorial Africa cannot be determined. There is a strong presumption that it was at least 9500–6500 years ago. In view of the extensive genetic differentiation of present-day populations of *D. melanogaster*, it may well have been considerably earlier, in the late Pleistocene.

We predict that close relatives of *D. melanogaster*, were they to exist, would be found in the Congo Basin and that new sibling species of the *D. simulans* lineage may well await discovery in Madagascar or the surrounding islands.

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