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32. Breeding-Sites in Tropical African Drosophilids

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I. Introduction

Ephemeral plants and ephemeral plant tissues are generally claimed to escape from the selective pressure of insect herbivores to a larger extent than do predictable plants and plant tissues, since it is difficult for herbivores to locate ephemeral food resources (Feeny, 1975, 1976; Rhoades and Cates, 1976). Hence, according to the phenological characteristics of their host-plants, i.e. either annual, herbaceous perennial, deciduous woody perennial or evergeen woody perennial plants, drosophilid populations display dispersal characteristics and demographic traits which are attuned to the temporal and spatial patchiness of the plants used as larval resources. Furthermore, the generalization that emerges from the biochemical coevolutionary theory of community structure initiated by Feeny (1975, 1976) and Rhoades and Cates (1976) is that most plants contain a double defensive system, with tissue predictability and availability as a food resource to herbivores being the main determinant of the defense type employed. Plant species which are "hard to find" by insect herbivores display defensive phenotypes, like specific toxins, which are diverse and qualitative. In contrast, plant species which are "bound to be found" appear to have evolved quantitative defenses involving unspecific digestibility-reducing substances or properties. Such spatial or temporal patchiness, supplemented by diverging chemical defensive systems, pose ecological barriers (and has posed evolutionary barriers) to host-plant shift and host-plant switching in herbivorous drosophilid species.

Although most resources of drosophilids are plant tissues, many of them come from other insects as well, since commensalism and predation have evolved in addition to herbivory in African drosophilids. These host insects or prey insects have their own population genetics (polymorphisms), life histories, phenologies, and population dynamics, which affect those of the drosophilid populations whose larvae feed upon them. Moreover, the evolutionary responses to interspecific interactions feed back on the interactions themselves, thereby affecting the species composition and structure of ecological communities (Futuyma, 1979).

As a result, both specialization and generalization have evolved in tropical African drosophilids as effective adaptive strategies. Since many fundamental aspects of population ecology are illustrated in other chapters of this volume, we will mainly focus attention upon the question of resource selection and the respective evolutionary advantages of being specialists or generalists.

II. The African Fig-Breeding Drosophilids

In the tropical African region the entire *Lissocephala* genus and the endemic *fima* species group of *Drosophila* have evolved a close association with endemic figs (*Ficus* spp., Moraceae). From only 19 fig species—out of a total of 90 recognized in Berg *et al.*'s (1983) flora of Moraceae—35 narrowly restricted fig-breeding drosophilids are already known. These fig-dependent drosophilids represent a major evolutionary pathway peculiar to the tropical African drosophilid fauna (Lachaise *et al.*, 1982).

Drosophilids breeding in figs are known from other parts of the world. In El Salvador, ten species involving three genera (*Diathoneura*, *Drosophila* and *Stegana*) were reared from *Ficus* by Heed (1957); in Californian fig orchards, *Drosophila melanogaster* commonly lay many eggs in the edible fig *Ficus carica* L. (Miller and Phaff, 1962); in Australia, one species of *Liodrosophila* has been bred out of rainforest figs (Bock and Parsons, 1981). However, there is no evidence that the American and Australian fig-breeding species are dependent upon *Ficus* and they probably exploit figs opportunistically. Nothing like strict fig dependence and broad endemic adaptive radiation related to fig evolution has been found anywhere except Africa. However, similar conditions favoring such evolution occur in Borneo and New Guinea where figs (Corner, 1958, 1965, 1976), fig wasps (Wiebes, 1963) and drosophilids (Okada, Chapter 6, Volume 3a) are highly diversified. Until recently the geographical range of the genus *Lissocephala* was assumed to be paleotropical. In the Oriental and Australian regions six species are at present included in the genus *Lissocephala*. One of them, *L. powelli* from Christmas Island in the Indian Ocean, breeds as an obligatory commensal in the nephric pad region of the branchial chamber of land crabs (Carson and Wheeler, 1973; Carson, 1974). Another, *L. metallescens*, living in the Australian rainforest, is attracted to mushroom (*Agaricus campestris*) baits in considerable numbers (Bock and Parsons, 1981). However, there is strong evidence (Tsacas *et al.*, 1981) to suggest that the genus *Lissocephala* is endemic to tropical Africa and that the Oriental and Australian species should be placed in a different genus. This specialization of *Lissocephala* on *Ficus* and the evolutionary radiation in this drosophilid genus are peculiar to tropical Africa as far as we know.

Recently, Lachaise *et al.* (1982) have proposed a tentative historical explanation of how the association with fig has arisen, at least for *Lissocephala*. This includes 19 species in the genus *Lissocephala* and 16 species in the *Drosophila fima* species group which is also unequivocally endemic to this region. Species of *Lissocephala* only breed in immature figs. Most, but not all, *fima* group species are fig breeders, but are confined to post-mature figs. Speciation in *Lissocephala* is hypothesized to have proceeded from convergent evolution with the obligatory pollinating fig wasps. The *Lissocephala* radiation seems to have been an evolutionary by-product of the fig/fig wasp co-speciation; this genus, probably the oldest within the family Drosophilidae, has a long evolutionary history on the African continent. Hence, *Lissocephala* speciation is assumed to represent a fundamentally different evolutionary event than speciation within the *fima* species group. The processes whereby either new *Lissocephala* species or new *fima* group species have come into existence are not adequately known but the underlying deterministic mechanisms are thought to require behavioral adaptations in the former taxon that are not required in the latter one.

For pollination of figs, small chalcidoid Hymenoptera of the family Agaonidae are absolutely necessary. There are about 900 species of figs in the Old and New World tropics and, with only very rare exceptions where strict specificity appears to break down (Wiebes, 1979), there is clear evidence of a one-to-one relationship between species of fig and wasp (Wiebes, 1963, 1966; Ramirez, 1970). As White (1978) says: "It seems impossible to avoid the conclusion that the speciation of *Ficus* and of the agaonid has been concomitant, i.e., that each incipient species of *Ficus* has evolved in parallel with an incipient species of wasp". This provides an exceptionally sophisticated evolutionary situation and, hence, the possible parallel evolution of some African drosophilids with the fig wasp system is of particular interest.

The life histories of figs form the object of an abundant literature. Detailed synthetic articles include Wiebes (1977, 1979), Galil (1977), Janzen (1979a) and Valdeyron and Lloyd (1979). A summary of the major facts borrowed from these articles, and which are needed for understanding fig drosophilid biology, is presented below.

A. THE ORIGIN OF THE FIG SYCONIUM

The fig syconium is a hollow urn-shaped receptacle bearing several hundreds of female florets and fewer male florets on the inner surface (Fig. 1). The sheltered inflorescence of *Ficus* is assumed to be derived from a hypothetical pre-*Ficus* plant with open inflorescences (Berg, 1977). The pre-agaonid is suspected to have been a pollen-feeding gall-maker (Ramirez, 1976) or a gall-producing parasite of the pre-*Ficus* (Wiebes, 1979). This latter author argued that the symbiosis of figs and wasps made possible, and thus antedated, the special form of the syconium. An alternative proposal would be that a wide array of phytophagous insects may have exerted such strong selective pressure on this inflorescence that the pre-fig evolved a flask-like inflorescence independently of the pre-agaonid. However, between the necessities for pollination by insects and those of defense against phytophagous insects, natural selection could only retain a trade-off: a fig.

To protect the immature receptacle against herbivore attack, diverse defense systems (physical as well as chemical) evolved in figs. The receptacular structure of the fig is an anti-phytophagous insect barrier in itself. The hard and thick woody pericarp developed in, for example, *Ficus macrosperma* and *F. vallis-choudae*, and the hairy exocarp of *F. saussureana* may also act as a defense against herbivores. These morphological defenses are often coupled with chemical defenses as in other plant–insect systems

(Ehrlich and Raven, 1965; Feeny, 1975; Rhoades and Cates, 1976). Among the various chemicals in different species of figs are alkaloids and tannins in *Ficus indica* Hochst. ex Walp. and *F. sycomorus* L. ssp. *gnaphalocarpa* (Miq.) Berg (Persinos and Quimby, 1967); tannins in *F. bracteata* (Vellayan, 1981); sterols and ascorbic acid in *F. sur* (=*F. capensis* Forsskål) (Watt and Breyer-Brandwijk, 1962); steroids, sapogenin, psoralen, bergapten and several sterols in *F. carica* L. (Athnasios *et al.*, 1962; El-Sayed El-Kholy and Monem Shaban, 1966); flavonol glucosides and several sterols in *F. bengalensis* L. (Sankara Subramanian and Nair, 1970); triterpenoids in *F. nitida* L. (Elgamal *et al.*, 1975); and polyphenols in *F. mysorensis* Heyne (Bhansali *et al.*, 1978). Efficient chemical protection of the immature fig against herbivores probably comes also from a derivative of latex which soaks the receptacular wall of most figs and contains ficin, a powerful protease (Janzen, 1979a). Thus, the defensive chemistry of figs is probably comprised both of a diverse array of toxic chemicals and a digestibility-reducing system. Although the fig has evolved anti-phytophagous insect defenses, the evolutionary processes have left a small gap in this defense, the ostiole (the "Achilles' heel" of the fig) which is protected only by a series of

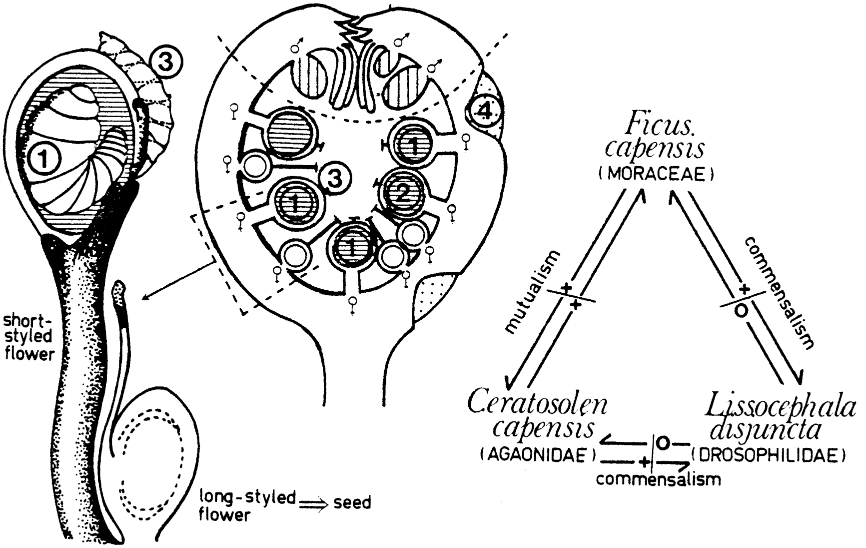


FIG. 1. (Left) Breeding site partitioning within the syconium of *Ficus sur* Forsskål (=*F. capensis* Thunberg) (Moraceae) in the Guinean pre-forest savannahs of Lamto in the Ivory Coast. 1: Pollinating fig-wasp *Ceratosolen capensis* (Agaonidae, Agaoninae); 2: *Sycophaga* sp. (Agaonidae, Sycophaginae); 3: *Lissocephala disjuncta* (Drosophilidae); 4: *Zaprionus collarti*, *Drosophila malerkotliana* and *Drosophila yakuba* (Drosophilidae). (Right) Interrelationships between fig, fig wasp and fig drosophilids (after Lachaise, 1979b).

appressed and tightly imbricated bracts to allow the pollinator to enter. The ostiole constitutes a selective filter that must admit appropriate gametes but retard the passage of detrimental organisms (Janzen, 1979a).

B. REPRODUCTIVE BIOLOGY OF FIGS

Complex symbiotic interrelationships and co-adaptations have evolved in the syconium and wasp. For successful reproduction, the fig wasps are dependent upon the ovaries of the short-styled flowers, while those flowers whose long styles exceed the length of the female fig wasp ovipositor give rise to fig seeds (Galil and Eisikowitch, 1968; Janzen, 1979b, c). Entering the syconium through the tightly interlocked ostiolar bracts (Fig. 1) requires highly specific behavioral and morphological adjustments in the wasps. A few female wasps enter the fig ostiole and manage to reach the cavity, losing their wings and most parts of the antennae in the process. They start ovipositing through the pistils of the female flowers and in doing so pollinate the stigmas.

Several weeks separate maturation of the female flowers (female phase) and that of the staminate flowers (male phase). The inter-floral phase is assumed by Ramirez (1974) to be very constant for each species of fig and varies with the species of the developing agaonids inside the fig. One generation of wasps brings pollen to the syconium and the next one breeds there during the interfloral period and takes out pollen. Hence, the coordination of pollen maturation with the emergence of the second generation of adult waps at the male phase is required for successfül pollen transfer (Galil, 1977). The strongly modified wingless male wasps emerge from their galls first and thrive in the high concentration of carbon dioxide in the syconial cavity—up to 10% in figs of *Ficus religiosa* L. (Galil *et al.*, 1973b). The males locate female-containing gall-shaped flowers, cut them open, and impregnate the females while they are still within the galls (Fig. 2, f and g). Before dying within the fig cavity where they were born and which they will never leave, the fig male wasps perform a final function by boring exit holes (Fig. 2, h) for the females through the syconial wall (Galil and Eisikowitch, 1968). As carbon dioxide escapes and the internal atmosphere equilibrates with the external, the females widen the fertilization holes and emerge from their galls. Before leaving they approach the anthers, which have only now reached maturation and fill their "pockets" or "corbiculae" with pollen (Galil and Eisikowitch, 1969; Ramirez, 1969; Galil *et al.*, 1973a; Galil, 1977).

In addition to its effect on the activation of the female wasps, the depletion of carbon dioxide also affects the postsexual development of the fruits. Inhibition of yeast growth is also removed and the process of alcoholic fermentation increases.

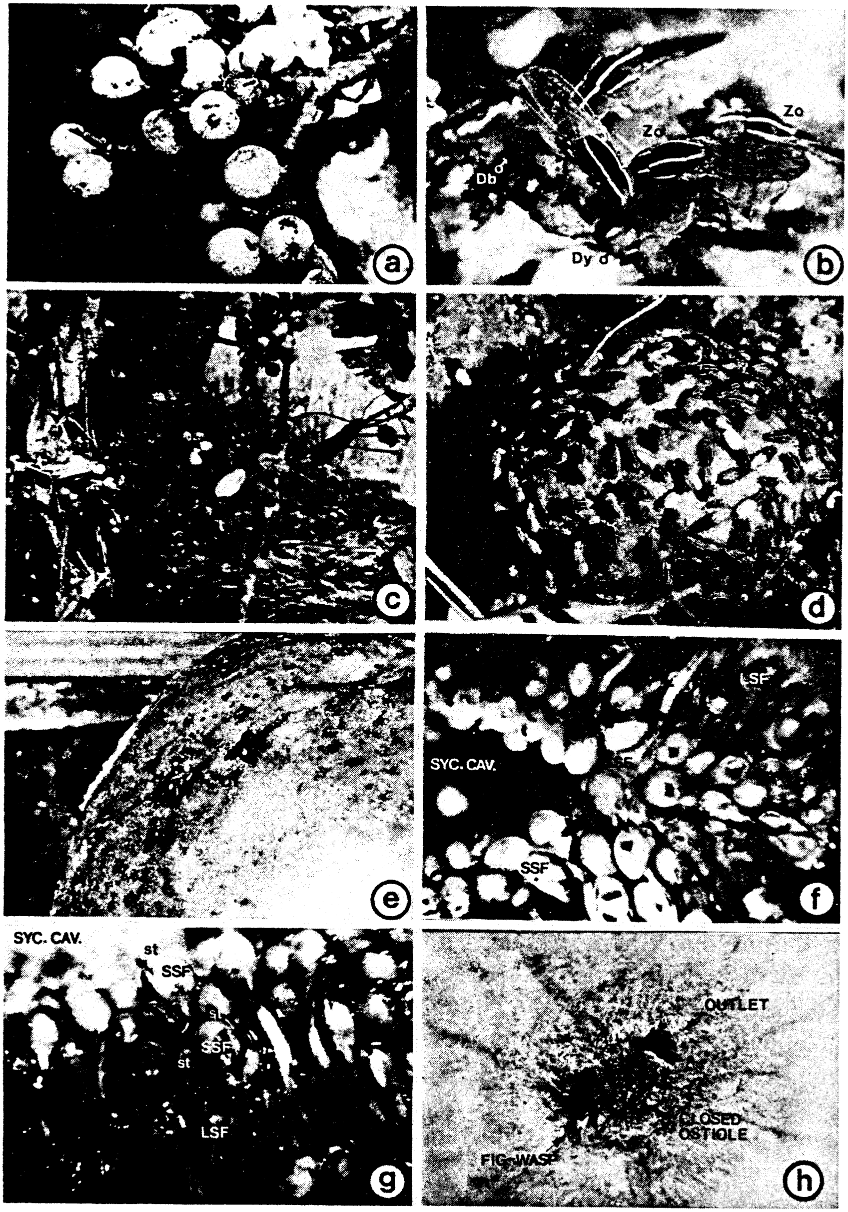


FIG. 2. (a) Immature fig cluster in *Ficus sur* Forsskål. (c): Cauliflory in *F. sur*, the fig-clusters are composed of syconia in different stages of maturation providing a substrate patchiness availability for fig-drosphilids. (b) and (d): Species packing on the fallen figs of *F. sur*; Db: *Drosophila bocqueti*, Dy: *D. yakuba*, Zo: *Zaprionus ornatus*. (e): *Drosophila fima* (Df) on fallen figs in *F. sur*. (f) and (g): pistillate flowers in *Ficus vallis-choudae*; SSF: short styled flower, LSF: long styled flower, st: style, SYC.CAV: syconial cavity. (h): Two exit holes bored by the male agaonid wasps beside the ostiolar area in *F. vallis-choudae* (Photographs from the Guinean Zone of the Ivory Coast after D. Lachaise, except (b) which is after H. Antoine).

C. THE FIG-BREEDING DROSOPHILIDS: FROM MONOPHAGY TO OPPORTUNISM

All African species of the genus *Lissocephala* and all species of the *Drosophila fima* species group breed in figs of the endemic species of the Afrotropical genus *Ficus*. Thirty-five known species of drosophilids depend strictly on figs. Their specificity to the different host-*Ficus* species varies according to the particular fly species.

Nineteen *Lissocephala* species are so far known in the tropical African region, associated with 17 fig species (Tsacas and Chassagnard, 1977, 1981; Tsacas and Lachaise, 1979; Lachaise *et al.*, 1982). We suspect there to be many more species of *Lissocephala* for at least 90 species of fig occur in continental Africa, nearly 60 of them being known from Cameroon and 40 from Gabon (Berg, 1983). The strict association between *Lissocephala* and *Ficus* has been observed from the Sudanese savannahs to Uganda in continental Africa and also from Reunion Island. It has been found in lowland Sudanese savannahs (Senegal), lowland Guinean savannahs (Ivory Coast), lowland evergreen rainforests (Ivory Coast, Cameroon, Gabon, Uganda), second growth vegetation (Ivory Coast, Uganda, Reunion), montane savannahs (Kounden plateau, 1500 m, Cameroon) and montane evergreen rainforests (Tonkoui, Nimba, 300–1400 m, Ivory Coast).

The second endemic fig-breeding drosophilid group, the *Drosophila fima* species group, is composed of sixteen species (*abron*, *abure*, *akai*, *alladian*, *dyula*, *fima*, *iroko*, *kulango*, *aloma*, *dimitra*, *microralis*, *petitae*, *sycophaga*, *sycophila*, *sycovora*, *tychaea*). Burla (1954), who created the *fima* group, described the eight former species to which Tsacas and Lachaise (1981) added the eight latter ones (Fig. 2c). The *fima* species group has a wide distribution throughout the mainland from Sahel to South Africa and from Guinea to Uganda, but is apparently lacking from Seychelles, Comoro, Madagascar and Mascarene. Although the larval habit of a few species is still not known, all adults that have been reared were bred from figs, emphasizing the close dependence of these African drosophilid taxa upon the genus *Ficus*. Twelve of the 16 *fima* group species were bred from 13 fig species. The breeding sites of the four remaining *Drosophila* species are still unknown, though adults of *D. iroko* were observed in abundance on fruits of *Tieghemella heckelii* (Sapotaceae) in the evergreen rainforest of Taï (Ivory Coast). Nevertheless, the adults of *iroko* are found along with the other fig drosophilids. *D. kulango* is the only species of the *fima* group in Taï that breeds in the fruits of another moraceous plant (*Treculia africana*) in addition to *Ficus*. Of the *fima* group species only *Drosophila fima* has been successfully bred for many generations on standard laboratory medium although *D. abron* has been maintained with difficulty for four or five generations. *D. abron* has been bred only from figs, while *fima* has been bred (once) from the fruits of *Hirtella* sp. (Rosaceae) and *Nauclea* sp. (Rubiaceae), in addition to a large number from figs. These observations suggest that some of the *fima* group species are not necessarily fig dependent, though generally being fig associated. Although the *fima* group as a whole displays a close association with *Ficus* and most of the relevant species are strictly restricted to figs for breeding, some of them have retained the ability to exploit, occasionally, a few other resources. The *Drosophila fima* group species show considerable sympatry. Thus, 13 species cohabit the evergreen rainforest of Taï where six species were reared separately from either *Ficus mucuso*, *F. vogeliana* or *F. lyrata*. In Gabon, eight species were reared from the same fig cluster in *F. subsagittifolia*. In pre-forest savannahs in the Ivory Coast, adults of ten species were found on the same host (*F. sur*). Hence, there appears to be no preference for fig species among the *fima* group species. Except possibly, the strict association between *Drosophila sycovora* and *F. vogeliana* that new records suggest (Tsacas and Lachaise, personal communication). However, this does not preclude oviposition exclusion between species on the same syconium (Table I).

In addition to the essentially obligate fig-breeding drosophilids, there are many facultative fig-breeders displaying greater or lesser preferences for figs (Fig. 2, b and d). These include the genus *Zaprionus* (mainly *Z. collarti*, *Z. sepsoides*, *Z. ornatus*), and, within the genus *Drosophila*, the *ananassae* subgroup (*D. malerkotliana* and *D. ananassae*), the *melanogaster* subgroup (mainly *D. melanogaster* and *D. yakuba*), and the *montium* subgroup (mainly *D. bakoue*, *D. bocqueti*, *D. greeni* and *D. nikananu*). All three of these subgroups belong to the *melanogaster* group. Species of the subgenus *Scaptodrosophila* rarely breed in figs and those of the subgenus *Drosophila* have never been reared from figs in Africa. A total of 56 drosophilid species have been reared from 19 fig species. Adults of 86 species—including the 56 bred from figs—have been caught on these species of *Ficus*.

D. HOW THE ASSOCIATION WITH FIGS MAY HAVE ARISEN

Lachaise *et al.* (1982) put forward the hypothesis that the genus *Lissocephala* appeared on the African continent, where it has undergone a bursting speciation owing to a convergent evolution with the obligatory pollinating, and highly host-specific, fig wasps. The fig/fig wasp symbiosis is suspected to have started in the Cretaceous, more than 100 million years ago (Wiebes, 1963; Galil, 1977), although unquestionable fossil fig wasps are only known from the Miocene of Colorado (Brues, 1910). Because of a set of plesiomorphic ("primitive") characteristics the genus *Lissocephala* is considered by Throckmorton (1975) to be the most primitive genus of

TABLE I. Number of taxa of host-Ficus (species, groups, sections, sub-genera) wherefrom specialist fig-breeding *Lissocephala* and *Drosophila* were bred. The overall host-plant array concerns 20 fig species from tropical Africa. When the number of fig species providing additional *Lissocephala* or *Drosophila* species as adults only exceeds that providing fly species as larvae, it is mentioned in parentheses as the relevant names.

Drosophilids	Host-Figs	Species	Groups	Sections	Sub-genera
Lissocephala					
juncta group					
africana	vogeliana	1	1	1	1
ambigua	sur	1	1	1	1
diola	sycomorus	1	1	1	1
disjuncta	sur, vogeliana	2	1	1	1
juncta	sur, vallis-choudae	2	1	1	1
linearis	asperifolia, ovata	2	2	2	2
sanu group					
couturieri	sur, exasperata, lutea	3	3	3	3
lachaisei	vogeliana, thonningii, lutea, unidentified sp.	4	4	2	2
lebou	sycomorus	1	1	1	1
melanosanu	kamerunensis	1	1	1	1
pulchra	ovata, unidentified sp.	2	1	1	1
sanu	sur, vogeliana, kamerunensis, natalensis, thonningii	5	3	2	2
taiensis	mucuso, sur, elasticoides, lutea, ovata	5	4	2	2
ungrouped species					
horea	kamerunensis	1	1	1	1

nigroscutellata	vogeliana, macrosperma	2	2	2	2
nigrothyrea	sur, vogeliana	2	1	1	1
unipuncta	natalensis, lutea, ovata	3	3	1	1
sp. I	vogeliana	1	1	1	1
sp. II	ovata	1	1	1	1
Drosophila					
fima group					
abron	mucuso, sur, vogeliana, exasperata, elasticoides, saussureana, lutea, macrosperma, ovata, recurvata, lyrata, subsagittifolia, (polita)	12(13)	7	3	3
abure	mucuso, lutea, macrosperma, ovata, recurvata, lyrata	6	5	2	2
akai	mucuso, sur, vogeliana, elasticoides, saussureana, lutea, macrosperma, ovata, lyrata, subsagittifolia, (polita)	10(11)	5	2	2
alladian	mucuso, sur, vogeliana, macrosperma, ovata, subsagittifolia, (polita)	6(7)	3	2	2
aloma	subsagittifolia, (sur, kamerunensis, recurvata, lyrata)	1(5)	1(4)	1(2)	1(2)
dyula	(mucuso, sur, kamerunensis, recurvata, lyrata)	0(5)	0(4)	0(2)	0(2)
fima	mucuso, sur, vogeliana, elasticoides, saussureana, macrosperma, lyrata, subsagittifolia, (vallis-choudae, polita)	8(10)	5	2	2
iroko	(mucuso, sur, polita)	0(3)	0(2)	0(2)	0(2)
kulango	lyrata, subsagittifolia, (mucuso, sur, polita)	2(5)	1(3)	1(2)	1(2)
petitae	subsagittifolia, (macrosperma, lyrata)	1(3)	1(2)	1	1
sycophaga	kamerunensis	1	1	1	1
sycophila	subsagittifolia, (mucuso, sur, recurvata, lyrata)	1(5)	1(3)	1(2)	1(2)
sycovora	(vogeliana)	0(1)	0(1)	0(1)	0(1)

Drosophilidae. Tsacas (1979) further suggested, from biogeographical arguments, that the ancestors of the *Sophophora* subgenus of *Drosophila* occurred before the separation of Africa and South America in late Cretaceous. Therefore, the genus *Lissocephala* probably has a long history on the African continent.

The evolution of figs has not in any way been dependent on *Lissocephala* and the various species of fig can simply be regarded as so many niches available for *Lissocephala* speciation. However, if speciation in *Lissocephala* has not been involved in the coevolutionary process between figs and pollinating fig wasps, it nevertheless seems to have been an evolutionary by-product of that coevolution.

Species of the *fima* group almost always oviposit on the genus *Ficus*, without regard to fig species. As Ehrlich and Raven (1965) and Janzen (1968) have stressed for other plant–insect associations, by bridging the defensive system of a particular fig species, these fig-breeding *Drosophila* may have spread to the entire genus *Ficus*. However, some of the *fima* group species (*abron*, *fima*, *kulango*) appear to remain restricted to figs though being potentially able to breed in other fruits. The restriction to figs may be related to the theoretical expectations of Levins and MacArthur (1969): as the probability of failure to find an acceptable plant in a unit of time increases, "monophagy" may be optimal when higher and higher proportions of unsuitable host plants are present. Similarly, Rausher (1980) showed that the oviposition preference in the wild involves both host-plant abundance and host-plant suitability for growth and survival of the juvenile stages. Host-selection by the ovipositing females of the *fima* species group may involve the trophic properties of the decaying syconium and the high predictability of the whole multi-species fig community.

The balance between specialization and generalization on figs may well be determined by such probability considerations involving toxicological or digestibility-reducing defensive systems (Feeny, 1975; Rhoades and Cates, 1976). There is strong evidence, however, that specialization on figs has evolved differently in *Lissocephala* and in the *fima* species group.

E. THE FIG WASP-LIKE *LISSOCEPHALA*: AN HYPOTHESIS OF EVOLUTIONARY CONVERGENCE

The outer wall of the young immature syconium is unsuitable for all drosophilids, and for most other organisms. Therefore, the colonization of figs by drosophilids begins inside the syconial cavity. Hence, only members of the genus *Lissocephala* which are able to gain entry into this cavity can exploit early immature figs. Each African fig species harbors a particular combination of *Lissocephala* species, and different fig species may have some *Lissocephala* species in common. For instance *Ficus vogeliana*, from the evergreen rainforest of Taï in southwestern Ivory Coast, yielded seven *Lissocephala* species. Both *F. ovata* from Taï and *F. lutea* from Adiopodoumé yielded four *Lissocephala* species, and *F. kamerunensis* in Taï yielded three. Comparing those pairs of fig species from which the same number of *Lissocephala* species were reared, the overlap is three common species out of seven in *Ficus vogeliana* and *F. sur*, and one common species out of four in *F. ovata* and *F. lutea*. Different *Lissocephala* species can cohabit within a syconium inasmuch as they oviposit sequentially as the immature syconium develops (Fig. 3). Each fig species yields successively both *Lissocephala* species with narrow host-fig specificity and species with a broader host-fig specificity. The former differ then from one *Ficus* species to another whereas the latter do not. The later the oviposition the less is the number of host-figs. For example, in *Ficus sur* of Lamto, six *Lissocephala* species replace one another in the order *disjuncta*, *juncta*, *couturieri*, *ambigua*, sp. nov., *sanu* (Fig. 4). Species such as *L. disjuncta* invade the fig in the earliest successional stage while those such as *L. sanu* oviposit in the latest stage of immature phase of the fig. Recently, we recognized different species groups within the genus *Lissocephala* (Tsacas and Lachaise, 1979). The *juncta* group contains species with a restricted number of host-figs, most often only one. The assumption of a possible one-to-one relation between the species of *Lissocephala* and the species of fig comes from the discovery of new species of the *juncta* group as new *Ficus* are investigated. Whether the relation between some species of *Lissocephala* and some species of figs is one-to-one is not, however, yet known. Anyway, the *sanu* group contains species utilizing a broad array of host-figs. Each *Ficus* harbors members of both the *juncta* group and the *sanu* group (and other still undefined species groups). The *juncta* group species precede those of the *sanu* group in the succession.

Tsacas and Lachaise (1979) showed that the number of species of *Lissocephala* is positively correlated with the number of individuals in a single fig receptacle. Further, the number of species and species groups cohabiting a common syconium apparently increases as the *Lissocephala* are less closely related (Fig. 3). Coexistence is achieved by temporal (Fig. 4) as well as spatial patchiness of the oviposition sites (Fig. 5).

We observed that the species of *Lissocephala* display marked changes in chorionic protection according to the species group. The *juncta* group species (*diola*, *disjuncta*) show strongly modified egg chorion features, whereas the *sanu* group species (*couturieri*, *lebou*, *sanu*) have a smooth egg chorion, similar to that of the generalist *Drosophila* species (except for the

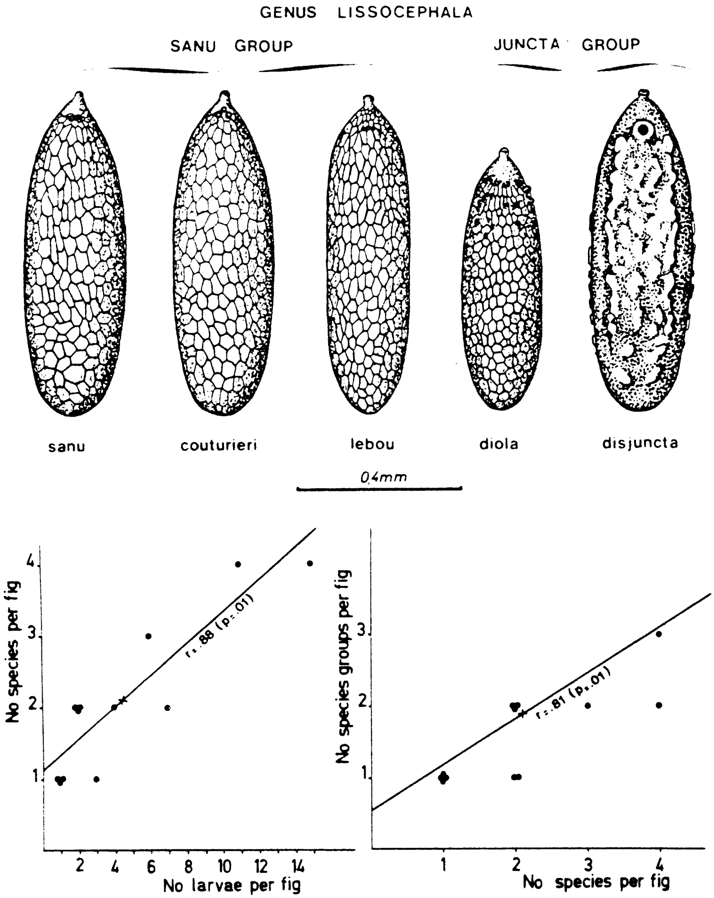


FIG. 3. (Upper) Smooth eggs in the less fig-specific *Lissocephala* species and protected eggs in the more specific ones. (Lower left) Regression of the number of species of *Lissocephala* cohabiting a single fig receptacle on the number of *Lissocephala* individuals breeding there; (Lower right) Regression of the number of *Lissocephala* species groups coexisting per fig on the number of *Lissocephala* species (after Tsacas and Lachaise, 1979).

lack of filaments) (Fig. 3). In the *sanu* group species the chorion is thin and shows the characteristic *Drosophila* network of cellular hexagons, whereas the outlines of the network of hexagons are blended by anastomosis of their rims in the eggs of *Lissocephala diola*, which have in addition protuberances and tubercules, and become entirely blurred in those of *L. disjuncta* which have a striking "corrugated iron" appearance (Fig. 6). The strongly protected eggs are those which are directly inserted between the ostiolar bracts, and it is assumed that the chorionic differentiations are protective

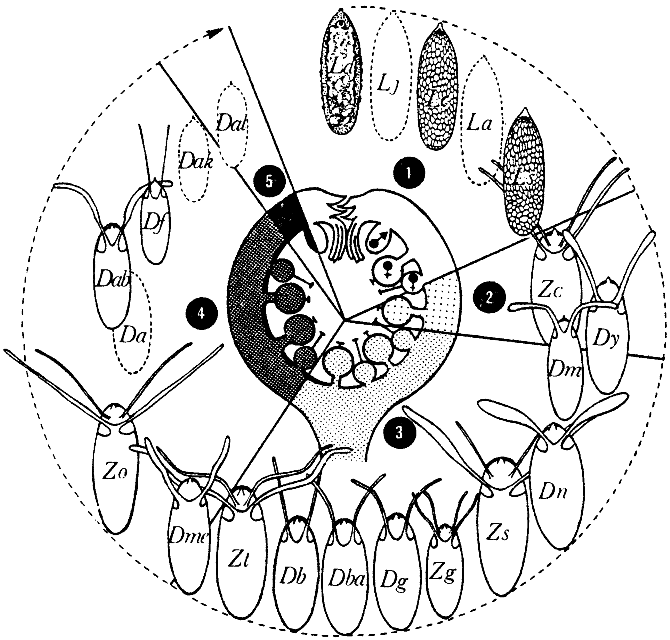


FIG. 4. Ecological succession in fig-breeding drosophilids in *Ficus sur* Forsskål in the Ivory Coast. Successional stages of the syconium: 1. floral immaturity (female-interfloral-male phases); 2. floral maturity on the tree; 3. fallen syconium, early post-sexual period; 4. decaying receptacle; 5. late decaying period, drying receptacle. The successive ovipositing fig drosophilids are represented by their characteristic eggs. Ld: *Lissocephala disjuncta*; Lj: *L. juncta*; Lc: *L. couturieri*; La: *L. ambigua*; Ls: *L. sanu*; Zc: *Zaprionus collarti*; Dy: *Drosophila yakuba*; Dm: *Drosophila malerkotliana*; Dn: *Drosophila nikananu*; Zs: *Zaprionus sepsoides*; Zg: *Z. ghesquierei*; Dg: *Drosophila greeni*; Dba: *D. bakoue*; Db: *D. bocqueti*; Zt: *Zaprionus tuberculatus*; Dme: *Drosophila melanogaster*; Zo: *Zaprionus ornatus*; Da: *Drosophila abure*; Dab: *D. abron*; Df: *D. fima*; Dak: *D. akai*; Dal: *D. aloma*,; *D. sycophila* and *D. petitae* (after Lachaise *et al.*, 1982).

devices preventing squashing of the egg due to the bract pressure (Lachaise *et al.*, 1982). These findings are in accordance with the suggestion of Kambysellis (1973, 1974) that the chorion pattern in drosophilid eggs is adaptive. The *Lissocephala* with protected eggs also appear to be those species with the narrowest host-specificity. It can be suggested that the egg chorion feature has a predictive value both with regard to the number of host-figs exploited and with regard to the oviposition period in the fig succession. Therefore, we further suspect that the smooth-egg *Lissocephala* species with a broad array of host-figs (*L. sanu*) may oviposit outside the ostiole as do other smooth-egg *Drosophila*.

Those *Lissocephala* which breed inside the syconial receptacle gain entry through the ostiolar filter and apparently cause neither damage to the fig

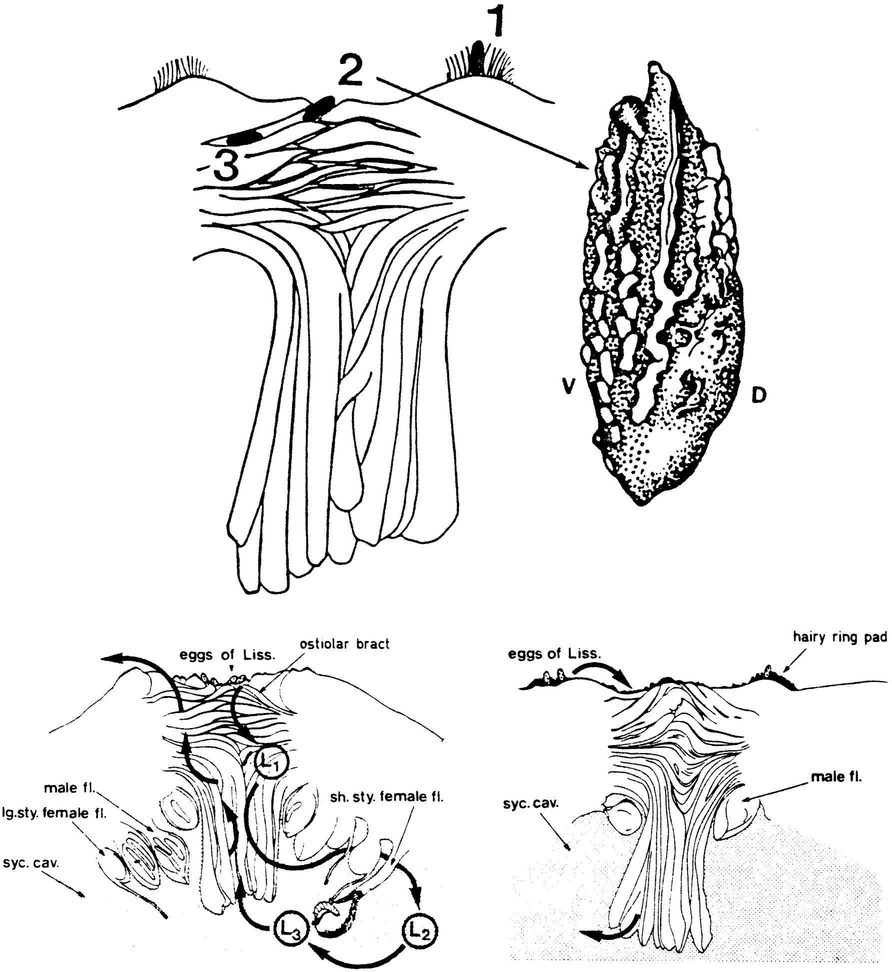
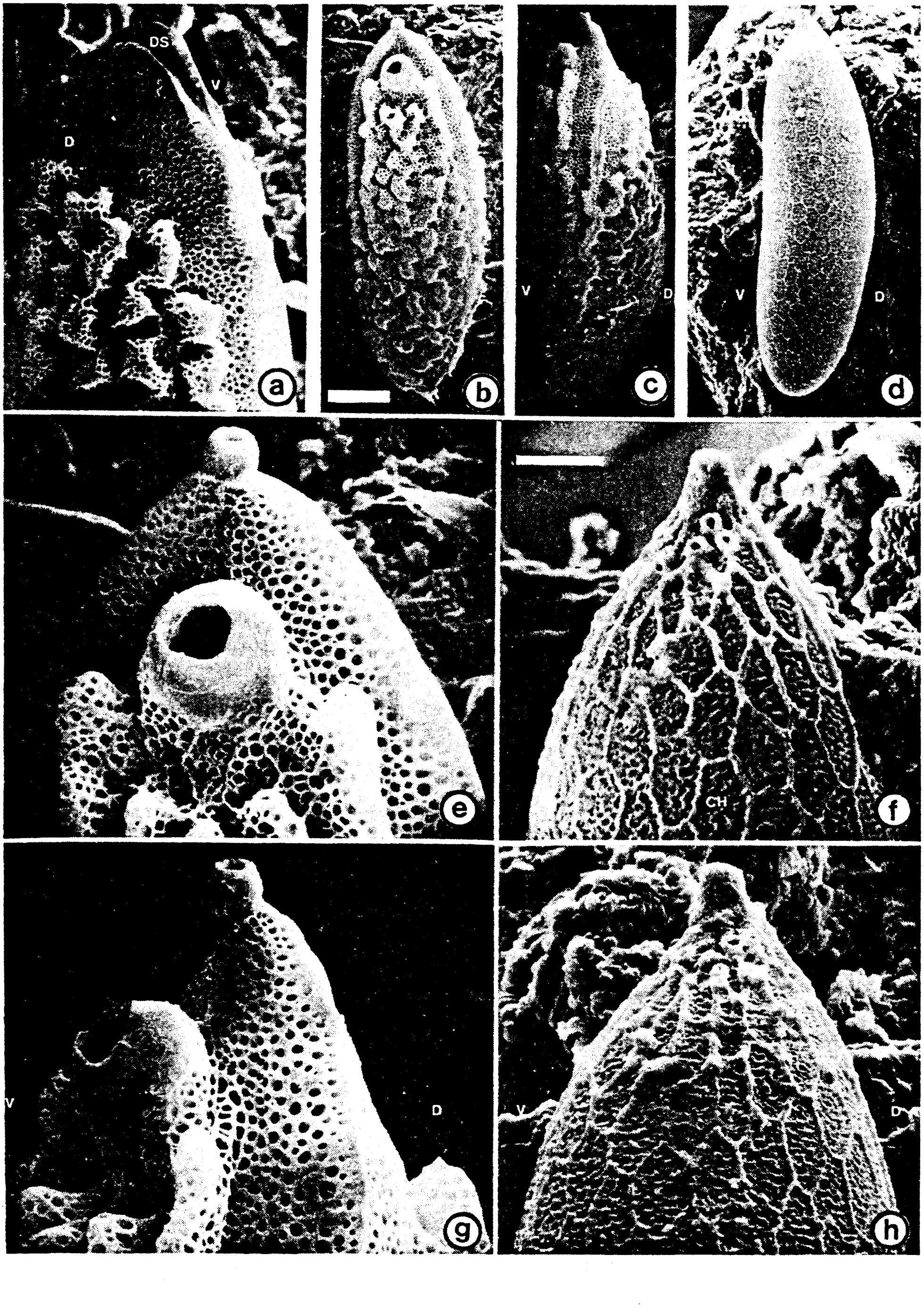


FIG. 5. (Upper left) Schematic drawing of fig-ostiole showing the different micro-oviposition sites in *Lissocephala* species. 1: *Lissocephala juncta* in *Ficus vallis-choudae*; 2: *L. disjuncta* in *F. sur*; 3: unindentified *Lissocephala* in *F. exasperata* (after Lachaise *et al.*, 1982). (Upper right) Lateral view of *L. disjuncta* egg; V: Ventral; D: Dorsal. (Lower) Real situation in "2" (left) and "1" (right) (after Lachaise, 1977).

FIG. 6. *Lissocephala* eggs (scanning electron microscopy); (a) *L. disjuncta* hatched egg in dorsal view showing the thickness and the rigidity of the chorion on both sides of the dehiscent split (DS); (b) and (e) *L. disjuncta* sculptured egg, ventral view; (c) and (g) *L. disjuncta* sculptured egg, lateral view; (d) and (h) *L. couturieri* smooth egg, lateral view; (f) *L. couturieri* smooth egg, ventral view. Scale bar for (a,e,f,g,h): 0·05 mm; Scale bar for (b,c,d): 0·10 mm. D: Dorsal; V: Ventral (after Lachaise *et al.*, 1981).


DS
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inflorescence nor to the pollinating fig wasp larvae whose development has come to an end. Many other characteristics of the life histories of fig wasps and fig flies are similar. Both ovipositing and pollinating fig wasp and the first ovipositing *Lissocephala* of the juncta group are attracted to the fig ostiole at the same receptive stage (female phase of the fig). Both the adult fig wasp and the first instar *Lissocephala* larvae gain entry at the same period into the syconial cavity, forcing their way through the ostiolar bracts. For both incoming female fig wasps and *Lissocephala* larvae the ostiolar bracts act as a series of air-locks precluding exchange of the inner atmosphere with that outside (Fig. 5). In the syconial cavity the drosophilid larvae develop outside the flowers in synchrony with the new generation of fig wasp larvae which are within the flowers, their similar development times matching the interfloral span (Fig. 1). Pignal, Lachaise and Couturier (personal communication) isolated yeast cultures from both the immature syconia of *Ficus lyrata*—directly picked up in the canopy of the Taï rainforest—and the digestive tract of *Lissocephala* larva living within these closed syconia, thereby showing the role of yeast in the diet of *Lissocephala* larvae. Whether the introduction of yeasts into the previously sterile syconium is due to the pollinating female fig wasps (Phaff and Miller, 1961), to *Lissocephala* or to both is still unknown. Finally both the mature third instar *Lissocephala* larvae and the newly emerged female fig wasps leave the receptacle at the male syconial phase. In most figs, the syconium remains closed during the entire floral development. At maturation the only exits available are those tunnels—e.g., two in *F. vallis-choudae*, six in *F. elasticoides* and one in many other species—bored by the male agaonid wasps. In a few fig species, such as *Ficus exasperata*, a natural opening of the ostiole occurs at male phase, forming a natural exit for the escape of the agaonids (Fig. 2h). In response to the fig inflorescence enclosure, the ovipositing fig wasp has developed behavioral mechanisms which enable it to penetrate these imbricated bracts, and *Lissocephala* larvae, by mimicking the behavior of the fig wasps, also gain entry to the immature receptacle of the fig by this means. Lachaise *et al.* (1982) suggest that the *Ficus*-specific *Lissocephala* species have attributes that match those of the obligatory pollinator fig wasp, thereby countering the host's protective devices. In the less specific *Lissocephala* the relation with the fig wasp is less evident. The entry is delayed in the interfloral phase and the exit may occur when the fig has fallen down to the ground.

F. ECOLOGICAL SUCCESSION IN FIGS AND OVIPOSITING FIG DROSOPHILIDS

Fig-breeding drosophilids are specialized to a particular period of the successional stages of the fig. The *Lissocephala* species oviposit in the green immature syconium while the *Drosophila fima* group species oviposit in late ripe fallen figs. Opportunistic *Drosophila* and *Zaprionus* species oviposit in

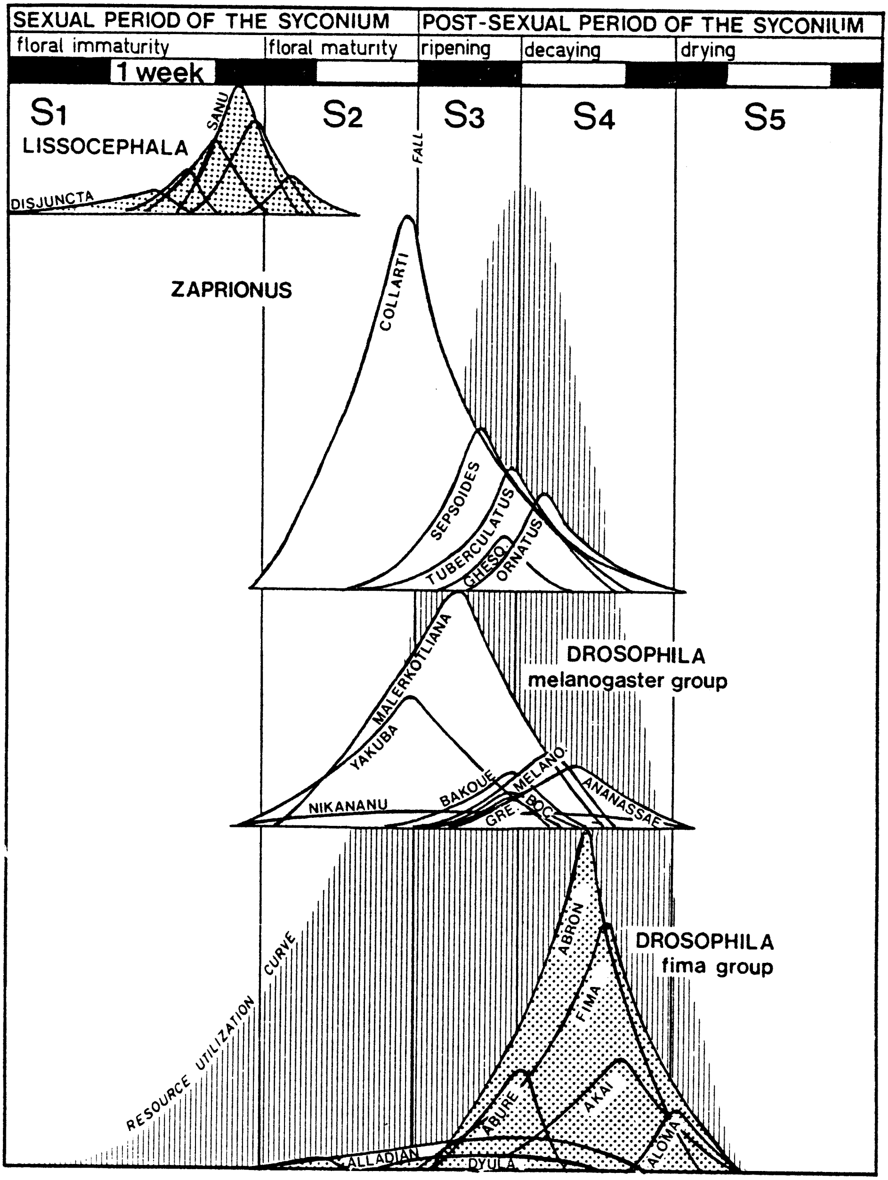


FIG. 7. Idealized diagram of the temporal distribution of eggs of the different drosophilid groups over the course of fig development. This is a composite representation of the sequence observed in different fig species, in which the sequence is quite similar. The hatched asymmetrical bell-shaped curve represents the resource utilization curve of the drosophilid community based on the total number of eggs of all species together. Dotted diagrams underline the essentially obligate fig-breeding species (after Lachaise *et al.*, 1982).

the intervening period, separating both specialist groups. The last *Drosophila* emerge from the dry remains of the receptacle on the ground (Figs 4 and 7). In addition to morphological defenses against herbivores, the fig is assumed to contain a "double or multibarrelled" chemical defensive system. We suggest that figs utilize toxins in their immature stage, owing to the protective requirements for seed setting, and use generalized digestibility-reducing systems, like tanning, subsequent to floral maturation, so as to protect against seed predation. The basic assumption of the occurrence of toxins in immature syconia comes from the very small number of insects, generalists as well as specialists (i.e. pyralid moth, fig weevil), feeding on the receptacle wall off immature figs. Significantly, no drosophilids exploit early syconia as a larval food supply. By gaining entry to the fig cavity like the fig wasp, *Lissocephala* larvae override the toxicological barrier of early immature figs. Such behavior does not imply the need of any detoxification mechanisms since that *Lissocephala* larvae feed on yeast, and not on the plant tissues. By contrast, fig specialization may have evolved in the *fima* group species, probably because all postfloral syconia, regardless of the fig species, display similar digestibility-reducing systems and, therefore, provide a highly predictable resource. Conversely, specialization might not have evolved in the receptacular wall of early immature syconia as a food resource for drosophilid larvae, probably because the toxin defensive pattern may differ in different species of figs, and herbivore specialization requires high predictability in plants and plant tissues (Rhoades and Cates, 1976). Generalist species of drosophilids breed in mid-succession where the presumably decreasing gradient of toxin concentration and the increasing gradient of digestibility-reducing substance are assumed to cross.

The expectations mentioned above are supported by the evidence that the specialization pattern in the succession is similar in all fig species, even though the succession of the ovipositing drosophilid species may be more or less truncated. Owing to the ability to recognize clearly equivalent successional stages in different fig species, it was possible to gather information bearing on the actual number of eggs in a sort of pre-competitive universal succession (Fig. 7). This is somewhat theoretical (pre-competitive) since it is made from a series of completely realized (post-competitive) successions observed in different fig species with varying succession length. The entire process of fig receptacle succession takes from 8 to 15 weeks depending upon the particular fig species. The striped asymmetrical bell-shaped curve corresponds to the total number of eggs laid by all the species of drosophilid pooled together, i.e. the resource utilization curve of the drosophilid community (Lachaise *et al.*, 1982).

Generally, a high carbon dioxide content in the internal atmosphere of fruits inhibits ripening, whereas its depletion promotes ripening (Burg and

Burg, 1965). If the green immature syconium is pierced before complete floral development, for instance by larvae of the fig weevil, depletion of inner atmosphere will result in an early and abortive fall and the death of the fig microcosm. Thus, depletion of carbon dioxide separates two different events in the life history of the fig, each of them resulting in a resource gradient. The composition and diversity of the fig-breeding drosophilid community breeding in the outer exocarpic wall change drastically with the successional changes in the syconium. The modification of the environment is caused by the fly species themselves which require preparation of their substrate by the earlier species, making the succession order obligatory. Therefore, this order of ovipositing species is constant whatever the duration of the succession and, apparently, independent of the fig species.

G. POPULATION TRAITS OF BEHAVIOR OF FIG-BREEDING DROSOPHILIDS IN RELATION TO TRAITS OF FIGS

According to Feeny (1975), plant species which are rare, ephemeral, or both, are assumed to be "hard to find" by insect herbivores. Chemical defenses of such plants are likely to be diverse and qualitative (toxins). Plant species which are abundant or persistent, or both, are, by contrast, "bound to be found" by insects both in ecological and evolutionary time; such plants appear to have evolved quantitative barriers (e.g., large amounts of unspecific chemicals such as tannins). Both kinds of anti-herbivore defensive strategies are expected to represent divergent evolutionary barriers, accounting for the achievement of generalization, as well as specialization, as best adaptive strategies in phytophagous insects. Rhoades and Cates (1976) further argued that escape in space and time is more effective against specialist herbivores than against generalist herbivores, because specialist herbivores have no alternative food source. For a generalist herbivore, on the other hand, the predictability and availability of any individual resource is of less consequence, since a generalist can opportunistically utilize whatever resource happens to be available. Lachaise *et al.* (1982) discuss this ecological situation of fig-breeding drosophilids in the light of the ideas of Feeny and of Rhoades and Cates. Some consideration of the phenology and predictability of fig production is therefore required to understand the strategies of resource utilization of the flies. A detailed discussion of fig phenology can be found in Janzen (1979a and exhaustive references therein). Due to the strict dependence of figs for pollination by specific agaonid fig wasps, fig species have evolved demographic features which favor the continuous development of these symbionts all year round in the tropics. Usually, there is in every fig population a continuous production of figs. Hence, in any particular area, some fig trees of the same species are always in a receptive stage. A fig population may be found with syconia in all phases of development, although on any one tree all syconia are roughly of the same stage (Ramirez, 1970; Janzen, 1979). Few studies (Hill, 1967a; Medway, 1972; Morrison, 1978; Janzen, 1979a) show how often a single tree fruits. Janzen (1979) concludes that most studies show that there are fig-trees in fruit somewhere in the population throughout the year. Such a study has been conducted in the lowland evergreen rainforest of Taï in southwestern Ivory Coast by Lachaise and Couturier (personal communication) with the aim of determining the availability and predictability of a multi-fig species community as a larval food resource for drosophilids.

1. Habitat patchiness

Fig species may live in somewhat different habitat patches. For example, *Ficus sur* Forsskål is typically a savannah fig-tree and is absent from evergreen rainforests (Fig. 2, b and c). Therefore it only occurs within forested areas in old fallow lands or plantations. There it cohabits with *F. kamerunensis* Mildbraed and Burret and *F. ovata* Vahl. *F. elasticoides* De Wildeman, *F. saussureana* A. P. de Candolle, *F. lyrata* Warburg, *F. macrosperma* Mild. and Bur. and *F. polita* Vahl live in primary forest. *F. vogeliana* Miquel is confined to Marantaceae swamps within semi-deciduous or evergreen rainforests. *F. asperifolia* Miquel is characteristically a riparian fig-tree, growing in easily flooded habitats; its branches usually hang above water and their mature receptacles usually drop into water. Accordingly, the late fig-succession is generally curtailed, accounting for the absence of the *fima* group of *Drosophila* from this fig species (Table I). Other species of fig such as *F. exasperata* Vahl, *F. lutea* Vahl, *F. mucuso* Ficalho, *F. recurvata* De Wildeman are located in second growth patches. These habitat preferences provide strong habitat-patchiness for the most specific *Lissocephala* or for *Drosophila sycovora*.

2. Resource predictability

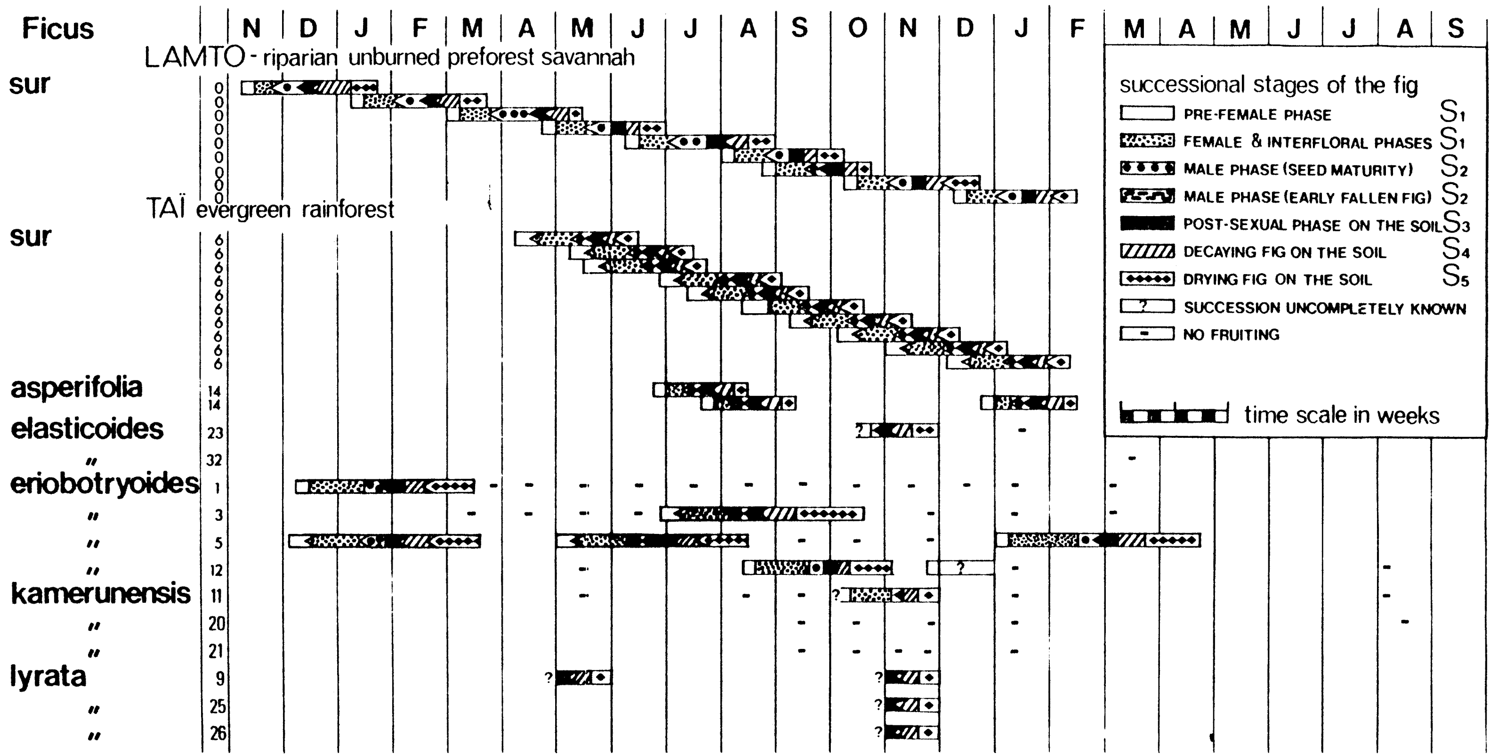
These species of fig display quite different demographic strategies, from continuous to discontinuous fruiting, with a variable number of fruiting cycles per year. Continuous fruiting within a single fig-tree occurs in both *Ficus sur* and *F. vogeliana* and may occur periodically in *F. asperifolia*. Figure 8 shows, for some examples of individual trees, how the successive fruitings are or are not linked with one another. Only the link between immature periods is important for the demographic attributes of both figs and pollinating fig wasps. But the overlap of immature and post-mature successional stages is of concern for the changes in fig drosophilid community and the demographic attributes of flies. A broad overlap occurs in *F. sur* so that each tree produces 13 fruiting cycles per year in the evergreen rainforest clearings. There is an unexpected decrease in fruiting overlap in this species living in unburned preforest savannah areas. Indeed, in the Lamto savannah, where denser populations exist, each individual tree shows only eight continuous fruiting cycles. Though all are continuously fruiting, the trees in the same locality usually show asynchronized development. Moreover, in the open grass savannahs of Lamto, which are burned every year, the fruiting periods may be drastically reduced in number and completely separated. *Ficus vogeliana* seems to fruit continuously five times a year. In these three species of fig the opportunity often occurs for emerging fig drosophilids to find a receptive stage on the same tree.

The opposite strategy is a single fruiting cycle per year with asynchrony in fruiting between trees yet strongly synchronous fruiting within trees. This strategy is seen in *F. ovata*, and may be the rule in *F. kamerunensis* and *F. thonningii* in June–July–August suggesting some yearly periodicity, at least in the second growth habitat of Adiopodoumé (Ivory Coast). For these fig-trees the chances are that when one tree is in fruit, few others in the vicinity will also be in fruit. The population of specialist fig drosophilids will therefore be divided among a low number of fruit-bearing trees. Consequently, specialist fig drosophilids will be more densely packed, thereby favoring sex encounters in rare species. This implies that the most specific *Lissocephala* must be extremely efficient at locating their fig trees. In contrast, only medium range search flights are required in those *Lissocephala* species, like *L. sanu*, and other fig *Zaprionus* and fig *Drosophila* species which can exploit any fig.

Other demographic patterns exist in other fig-species, which may show two or more disjunct fruitings per year. The fruiting periods may vary greatly from one year to another; selection has favored both predictability at the population level, by promoting lack of periodicity, and unpredictability at the individual level. Thus, *F. macrosperma* has two fruitings annually and *F. recurvata* at least two widely separated fruitings per year.

3. *Resource availability*

Since the time of the substrate succession, from early immature inflorescence to the dry remains of the receptacle on the ground, varies greatly from 7–8 weeks in *F. asperifolia* and *F. thonningii* to 14–15 weeks in *F. macrosperma* and *F. saussureana*, the question arises as to whether the former support fewer fig drosophilid species than the latter. This might result from the exclusion of some members within the different groups or from niche


Ficus
N D J F M A M J J A S O N D J F M A M J J A S
LAMTO - riparian unburned preforest savannah
sur
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0
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TAÏ evergreen rainforest
sur
6
6
6
6
6
6
6
6
6
6
asperifolia
14
14
elasticoides
23
"
32
eriobotryoides
1
"
3
"
5
"
12
kamerunensis
11
"
20
"
21
lyrata
9
"
25
"
26
?
successional stages of the fig
PRE-FEMALE PHASE S_1
FEMALE & INTERFLORAL PHASES S_1
MALE PHASE (SEED MATURITY) S_2
MALE PHASE (EARLY FALLEN FIG) S_2
POST-SEXUAL PHASE ON THE SOIL S_3
DECAYING FIG ON THE SOIL S_4
DRYING FIG ON THE SOIL S_5
SUCCESSION UNCOMPLETELY KNOWN
NO FRUITING
time scale in weeks

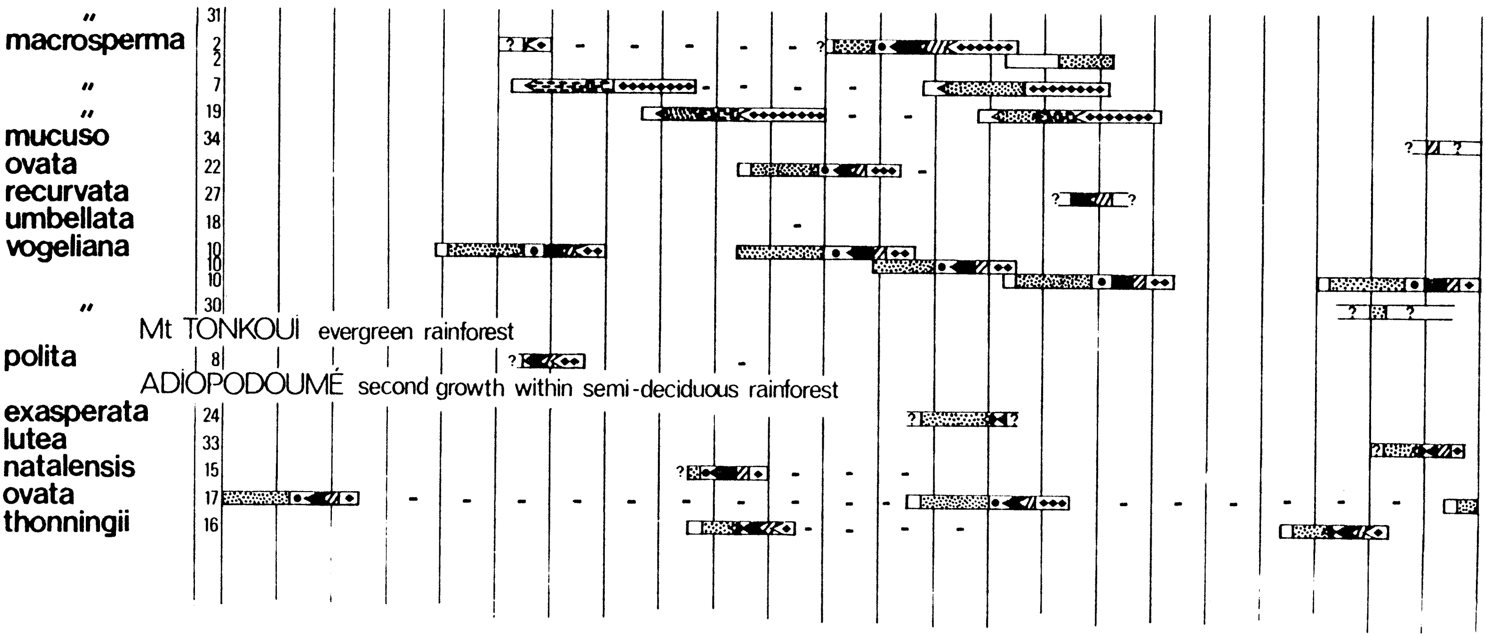


FIG. 8. Fig phenology on the Ivory Coast during a 23-month period from November, 1977, to September, 1979. Every fruiting is figured by the successional stages of the syconia involving fig-breeding drosophilids. The numbers correspond to different fig trees. Hence if one fig species may be represented by several trees, one fig may be plotted on different lines to show the intra-tree fruiting overlap (after Lachaise and Couturier, personal communication). Note: *eriobotryoides* = *saussureang*.

compression. The data remain insufficient to settle this problem, but the varying duration of the fig successions and change in the ratio of immature to post-mature stages provides fruitful material for devising testable hypotheses in competitive displacement. Figure 8 gives the phenology of the figs simultaneously available to fig drosophilids in different localities. At each fruiting the relative durations of the different successional stages are figured. Vertically, each column gives a crude idea of how the spatial fig-tree patchiness is at a given time. Although the recording of trees is limited, the sample of emerging fig drosophilids is equivalent to the sample of figs. Hence it is possible to correlate the number of different successional stages available at each time in a given habitat to the relative proportion of fig drosophilid species (Fig. 9). These correlations emphasize further the constancy of the nutritional specializations of the flies or the fly groups to one or more successional stages. Were competitive displacements a reality they should be expected to increase or decrease species packing, either by niche compression/release or by species invasion/exclusion, rather than to allow one successional group to replace another.

4. Demographic implications of fig-dependence in drosophilids

In view of those aspects of the biology and phenology of figs we have described, the specialization gradient involving fig-breeding drosophilids is expected to have demographic implications. Most importantly the absence of continuous fruiting within a tree results in the drosophilids having to disperse.

In order to verify the demographic implications of fig-dependence, Lachaise (1979a, 1983) showed experimentally that the greater the degree of specialization on *Ficus*, the more delayed is the reproductive effort and the lower is the fecundity (Fig. 10). Thus, generalist drosophilid species (e.g., *D. malerkotliana*) which exploit figs, among many other resources in a fine-grained manner, show a reproductive pattern with short adult immaturity and high fecundity. High reproductive effort is concentrated in a few age classes. In contrast, specialist fig drosophilids exhibit long adult immaturity and lower fecundity. Considering the degree of host-fig dependence, different demographic patterns exist. Thus, in the *fima* group, represented in Fig. 10 by *Drosophila fima*, the period of adult sexual immaturity is shorter than in *Lissocephala* species but longer than in all other species of *Drosophila* or *Zaprionus*. Since all ripe fallen figs are favorable to the *fima* group species, regardless of the host-fig species, search flights between suitable fig-trees are doubtless shorter than in most *Lissocephala*. The species of *Lissocephala* delay reproductive effort as the degree of their

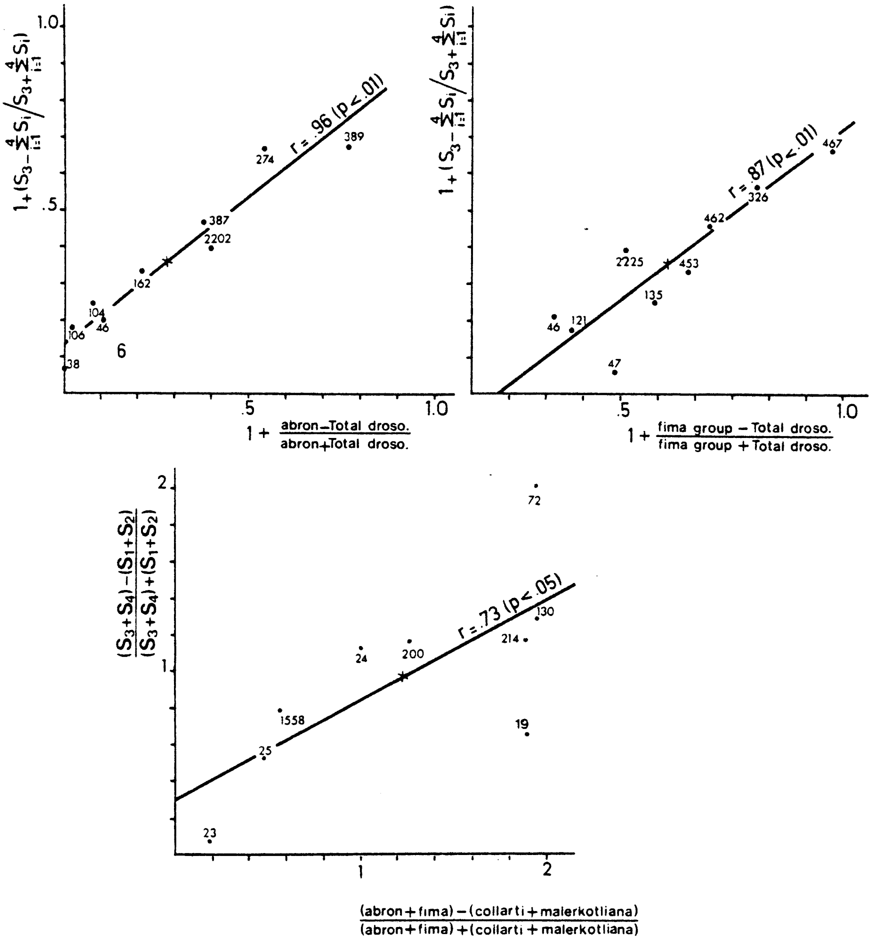


FIG. 9. Specialization of fig-breeding drosophilids to different successional stages of the fig: regression of successional stages (two-week samples) of the fig on the abundance of fig drosophilids reared from these (see Fig. 8).

host-fig specificity increases. In *L. disjuncta* adult sexual immaturity is about six times longer than the mean time of immaturity of the fig *Drosophila* or *Zaprionus* species.

As discussed above the most highly fig-specific *Lissocephala* species, which breed inside the closed immature fig cavity, display demographic features which tend to match those of the obligatory pollinator fig wasp. Owing to their common specificity to the same host-fig, these *Lissocephala* and the wasps probably display similar flight behavior and flight ranges. Joseph (1966), Ramirez (1970) and Janzen (1979) give evidence that agaonid

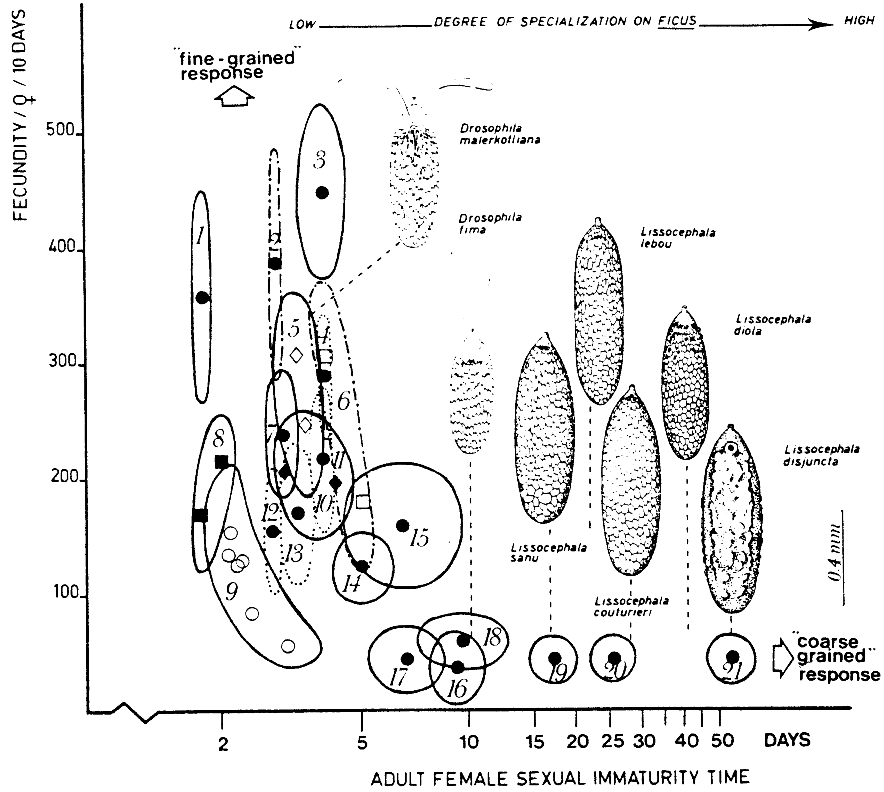


FIG. 10. Hyperbolic relationship between fecundity and the maximal time during which the reproductive effort can be delayed ($\log_2$ scale) in 21 drosophilid species living in southern Ivory Coast. These are represented by clouds which include the intraspecific variability. Each point within a cloud represents the mean value per population given with the 95% confidence limits. (1) *Drosophila melanogaster*; (2) *Zaprionus ghesquierei*; (3) *D. iri*; (4) *Z. sepsoides*; (5) *D. malerkotliana*; (6) *D. tsacasi*; (7) *D. greeni*; (8) *D. yakuba*; (9) *D. teissieri*; (10) *D. bakoue*; (11) *D. burlai*; (12) *D. nikananu*; (13) *D. erecta*; (14) *Z. collarti*; (15) *Z. tuberculatus*; (16) *Lissocephala sanu*; (20) *L. couturieri*; (21) *L. disjuncta*. The eggs figured are those of species of the fig drosophilid community living on *Ficus sur* on the Ivory Coast. Two additional eggs (*Lissocephala lebou* and *L. diola*) of the fig drosophilid community living on *Ficus sycomorus* s.sp. *gnaphalocarpa* in Senegal are included for comparison (after Lachaise, 1979a).

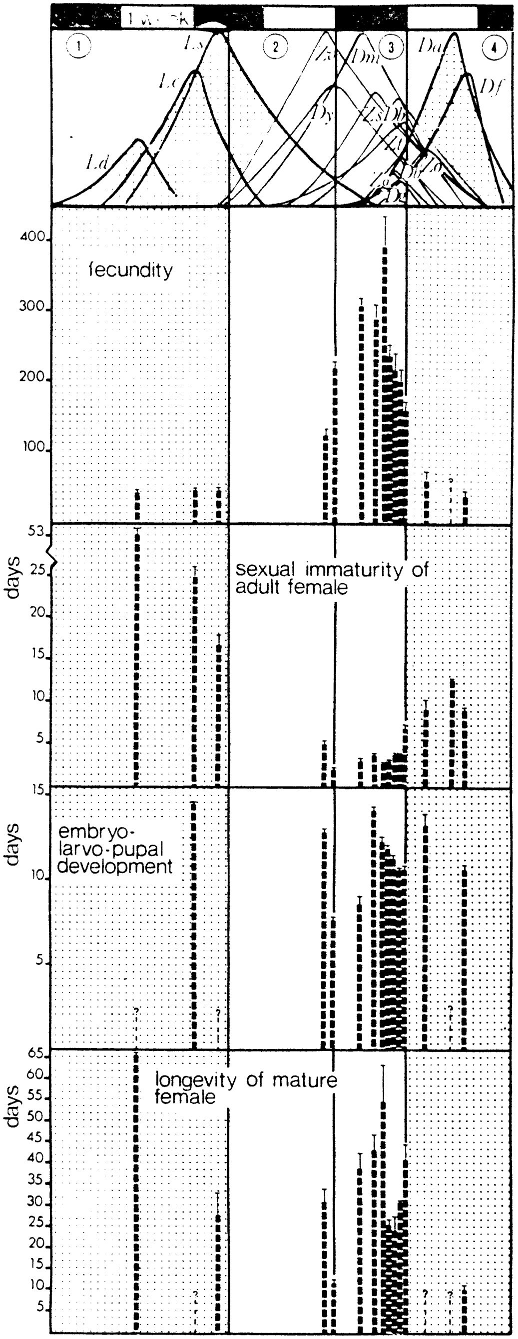
fig wasps may move distances of many kilometers between individual fig trees. These demographic strategies of both specific *Lissocephala* and fig wasps are assumed to be of the same kind. For example, the delayed reproduction which is seen in *Lissocephala* (Lachaise, 1979a) is also suggested by Janzen (1979) for the wasps: ". . . newly emerged fig wasps may have the behavioral trait of having to fly or otherwise delay before they can (will) attempt to enter a receptive fig". Because of limiting food supply, or of a physiological inability to exploit resources in excess, any organism has a certain and limited amount of time, matter and energy available to devote to foraging, growth, maintenance and reproduction (Cody, 1966; Levins, 1968; Pianka, 1974). The way in which a drosophilid species allocates these resources among various conflicting demands depends on the degree of specialization of the fly population and of its response to host-plant patchiness and predictability. Delaying reproduction allows resources to be diverted toward search flights for more adequate breeding sites. The greater the interpatch search time expected, the more delayed will be the reproductive effort (Pianka, 1974). Specialist herbivores must allocate time and energy to a search for their host plant. The more ephemeral the resource, the greater will be herbivore mortality during the search (Rhoades and Cates, 1976).

Regarding their degree of specialization on *Ficus*, fig fly species exploit the changing environmental mosaic of rainforests or savannahs in either a fine-grained or in a coarse-grained manner (Wiens, 1976).

In response to their dependence on *Ficus* and to their host's patchy distribution, drosophilid species have evolved different demographic strategies. In Afrotropical drosophilids, as in some Neotropical butterflies (Gilbert and Singer, 1973, 1975), dispersal characteristics of populations are attuned to local patchiness. Female *Lissocephala* spend the greater part of their immature adult life-span in searching for suitable *Ficus* patches containing figs in the appropriate receptive immature stage. Much energy is thus expended in flying between patches. *Ficus* patches can be regarded as "islands" in a "sea" of unsuitable habitats (Janzen, 1968, 1973).

The specialist drosophilid species which exploit both early and late fig successional stages display similar demographic traits, i.e. low reproductive rate and long sexual immaturity as adult females. Thus, they differ fundamentally from the generalist species which colonize opportunistically the medium-succession and which show a short adult immaturity period and a high reproductive rate. The duration of pre-adult development, and longevity of mature females, appear to be uncorrelated with the successional stages (Fig. 11). Clearly, early and late successional stages furnish a poorer food supply than intervening stages. The causes and major trends of the demographic traits of successive fly species might also, therefore, be found in the nutritional qualities of the changing substrate.

The amount of the resources allocated to host-plant search activities will depend on the relationship between the cost of such diversion versus the benefit derived from it. The less frequent a host-plant, the less benefit will be gained from the diversion of energy to search for it. Reciprocally, the


1 week
①
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Ls
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Da
Df
Lo
fecundity
400
300
200
100
sexual immaturity of adult female
days
53
25
20
15
10
5
embryo-larvo-pupal development
days
15
10
5
?
longevity of mature female
days
65
60
55
50
45
40
35
30
25
20
15
10
5

more renewable and predictable a host-plant, the more likely an organism will be to increase its fitness by diverting some of its resource in searching for it (Pianka, 1974; Rhoades and Cates, 1976). This is probably also the reason why most fig-dependent drosophilids are not restricted to any single species, since mixed communities provide abundant, constant and, hence, predictable resources. Furthermore, it should be borne in mind that those *Lissocephala* species which presumably divert resources from reproduction *per se* to host plant search flight are also those which allocate resources to egg protection (Fig. 10).

III. The Breeding Site Arrays in Africa

In this section we will present as complete a picture as possible of the array of breeding sites used by tropical African drosophilids.

Table II summarizes all the presently available data on breeding sites of

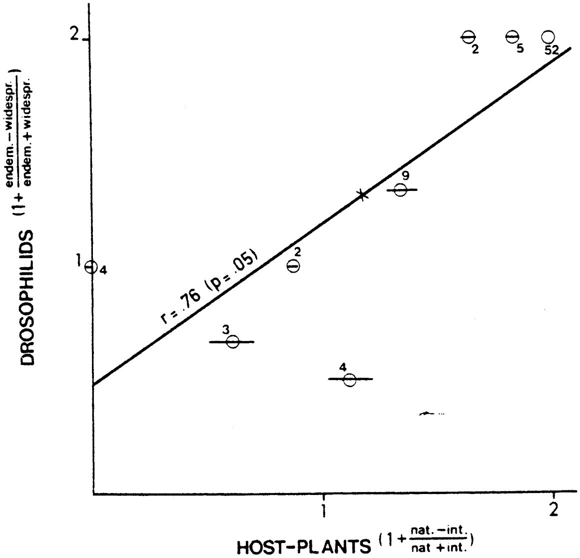

FIG. 12. Regression of the proportion of endemic species of drosophilids on the proportion of native host-plants in tropical Africa. The host-plants of the 81 species of drosophilids involved are mentioned in Table II. The numbers near the points give the number of drosophilid species in each class defined by the proportion of native host-plants and introduced ones.

FIG. 11. Demographic properties of the fig drosophilids reared from different successional stages of *Ficus sur* in the Ivory Coast. Dotted diagrams underline the fig-dependent species (see legends of Fig. 4 and 7).

TABLE II. Compilation of the breeding sites of drosophilids in the tropical African region. Origin: nat. = native; int. = introduced. Habitats: ERF = evergreen rainforest; SDF = semi-deciduous forest; SWF = swamp forest; SF = secondary forest; F = non characterized forest; RFG = semi-deciduous riparian forest gallery; FG = forest gallery of temporary tributaries; SG = second growth vegetation; F/S = forest/savannah mosaic; S = savannah; GV = grassveld; P = plantation; BG = botanical garden; DA = domestic area; CSA = costal sand area; CSL = costal salt-lake water. *Ficus* names after Berg *et al.* (1983). References are given on p. 288.

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
FRUIT BREEDERS					
Drosophila erecta (SG *Sophophora*; *melanogaster* group; *melanogaster* subgroup)					
Pandanus candelabrum	nat.	Pandanaceae	Lamto, Ivory Coast	FG	26
Pandanus candelabrum	nat.	Pandanaceae	Taï, Ivory Coast	RFG	31
Pandanus candelabrum	nat.	Pandanaceae	Sakré, Ivory Coast	SWF	31
Pandanus candelabrum	nat.	Pandanaceae	Gd-Bassam, Ivory Coast	CSL	31
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Drosophila melanogaster (*melanogaster* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	DA	41
Spondias mombin	int.	Anacardiaceae	Mt Tonkoui, Ivory Coast	SG	9
Landolphia dulcis	nat.	Apocynaceae	Taï, Ivory Coast	ERF	9
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Cucurbita sp.	int.	Cucurbitaceae	Bouaké, Ivory Coast	DA	22
Manihot esculenta	int.	Euphorbiaceae	Yakayaka, Congo	P	41
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	P	41
Ficus sp.	nat.	Moraceae	Dimonika, Congo	P	41
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	22
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24

Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	DA	23, 24
Musanga cecropioides	nat	Moraceae	Makokou, Gabon	SF	16
Psidium guajava	int.	Myrtaceae	Brazzaville, Congo	P	41
Phoenix reclinata	nat.	Palmaceae	Lamto, Ivory Coast	FG	22
Pandanus candelabrum	nat.	Pandanaceae	Gd-Bassam, Ivory Coast	CSL	31
Coffea arabica	nat.	Rubiaceae	Bankuop, Cameroon	DA	22
Manilkara obovata	nat.	Sapotaceae	Lamto, Ivory Coast	RFG	18
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Drosophila sechellia (*melanogaster* subgroup)					
Morinda citrifolia	nat.	Rubiaceae	Cousin, Seychelles	CSA	43
Drosophila simulans (*melanogaster* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	DA	23, 24
Ficus sp.	nat.	Moraceae	Ataye Riv., Welo, Ethiopia	—	45
Drosophila melanogaster+*D. simulans* (not distinguished from one another)					
Mangifera indica	nat.	Anacardiaceae	—, Uganda	P	4
Annona sp.	nat.	Annonaceae	Arua, Uganda	S	4
Rhipsalis sp.	int.	Cactaceae	—, Uganda	—	4
Carica papaya	int.	Caricaceae	—, Uganda	P	4
Ananas comosus	int.	Bromeliaceae	—, Uganda	P	4
Artocarpus utilis	int.	Moraceae	—, Uganda	P	4
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	—, Uganda	SF	4
Psidium guajava	int.	Myrtaceae	Makerere, Uganda	BG	4
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Maesopsis eminii	nat.	Rhamnaceae	Nabugabo, Uganda	F	4
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	4
Rubus steudneri	nat.	Rosaceae	Makerere, Uganda	BG	4

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Coffea canephora	nat.	Rubiaceae	—, Uganda	P	4
Cyphomandra betacea	int.	Solanaceae	Makerere, Uganda	PG	4
Solanum gilo	nat.	Solanaceae	Makerere, Uganda	BG	4
Aframomum sanguineum	nat.	Zingiberaceae	Nabugabo, Uganda	F/S	4
Drosophila teissieri (*melanogaster* subgroup)					
Mangifera indica	int.	Anacardiaceae	Dimonika, Congo	P	41
unidentified	nat.	Araceae	Taï, Ivory Coast	ERF	9
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Drypetes chevalieri	nat.	Euphorbiaceae	Mt Nimba, Ivory Coast	ERF	22
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	P	41
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Psidium guajava	int.	Myrtaceae	Brazzaville, Congo	P	41
Parinari excelsa	nat.	Rosaceae	Mt Nimba, Ivory Coast	ERF	22
Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Drosophila yakuba (*melanogaster* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	9
unidentified	nat.	Araceae	Taï, Ivory Coast	ERF	9
Detarium senegalense	nat.	Caesalpiniaceae	Adiopodoumé, Ivory Coast	SG	9
Drypetes chevalieri	nat.	Euphorbiaceae	Mt Nimba, Ivory Coast	ERF	22
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Artocarpus sp.	int.	Moraceae	Adiopodoumé, Ivory Coast	SG	9
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	SG	41

Ficus sp.	nat.	Moraceae	Dimonika, Congo	SG	41
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Psidium guajava	int.	Myrtaceae	Dimonika, Congo	P	41
Borassus aethiopum	nat.	Palmaceae	Lamto, Ivory Coast	S	19
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Parinari excelsa	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Nauclea sp.	nat.	Rubiaceae	Adiopodoumé, Ivory Coast	SG	9
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Drosophila bakoue (*melanogaster* group; *montium* subgroup)					
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Coffea arabica	nat.	Rubiaceae	Bankuop, Cameroon	DA	22
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Drosophila bocqueti (*montium* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	23
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Artocarpus sp.	int.	Moraceae	Adiopodoumé, Ivory Coast	SG	9
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	SG	41
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Cissus dinklagei	nat.	Vitaceae	Makokou, Gabon	ERF	16
Drosophila burlai (*montium* subgroup)					
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Hugonia macrophylla	nat.	Linaceae	Mt Nimba, Ivory Coast	ERF	22
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Hirtella sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Nauclea pobeguinii	nat.	Rubiaceae	Taï, Ivory Coast	SWF	9
Citrus grandis	int.	Rutaceae	Dimonika, Congo	P	41
Pancovia bijuga	nat.	Sapindaceae	Lamto, Ivory Coast	RFG	18

Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22
Drosophila diplacantha (*montium* subgroup)					
Pentadesma butyracea	nat.	Guttiferae	Taï, Ivory Coast	ERF	9
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Nauclea pobeguinii	nat.	Rubiaceae	Taï, Ivory Coast	SWF	9
Drosophila greeni (*montium* subgroup)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Ficus asperifolia	nat.	Moraceae	Taï, Ivory Coast	RFG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Drosophila megapyga (*montium* subgroup)					
Cissus dinklagei	nat.	Vitaceae	Makokou, Gabon	ERF	16
Drosophila nikananu (*montium* subgroup)					
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Drosophila seguyi (*montium* subgroup)					
Mangifera indica	int.	Anacardiaceae	—, Uganda	P	4
Carica papaya	int.	Caricaceae	—, Uganda	P	4
Artocarpus utilis	int.	Moraceae	—, Uganda	BG	4
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	Budongo, Uganda	SDF	4
Ficus asperifolia	nat.	Moraceae	Mpanga, Uganda	RFG	4
Psidium guajava	int.	Myrtaceae	Makerere, Uganda	BG	4
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	4
unidentified	int.	Rosaceae	Mulago, Uganda	—	4
Cyphomandra betacea	int.	Solanaceae	Makerere, Uganda	BG	4
Solanum gilo	nat.	Solanaceae	Makerere, Uganda	BG	4
Solanum verbascifolium	nat.	Solanaceae	Kyambogo, Uganda	—	4
Drosophila tsacasi (*montium* subgroup)					
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Psidium guajava	int.	Myrtaceae	Lamto, Ivory Coast	SG	18
Chytranthus sp.	int.	Sapindaceae	Banco, Ivory Coast	ERF	22
Drosophila ananassae (*melanogaster* group; *ananassae* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Mangifera indica	int.	Anacardiaceae	—, Uganda	P	4
Annona senegalensis	nat.	Annonaceae	Lamto, Ivory Coast	F/S	18
Landolphia dulcis	nat.	Apocynaceae	Taï, Ivory Coast	ERF	9
Landolphia hirsuta	nat.	Apocynaceae	Lamto, Ivory Coast	F/S	18

unidentified	nat.	Araceae	Taï, Ivory Coast	ERF	9
Crescentia cujete	int.	Bignoniaceae	Lamto, Ivory Coast	SG	18
Ananas comosus	int.	Bromeliaceae	—, Uganda	P	4
Rhipsalis sp.	int.	Cactaceae	—, Uganda	—	4
Carica papaya	int.	Caricaceae	—, Uganda	P	4
Artocarpus utilis	int.	Moraceae	—, Uganda	P	4
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Staudtia gabonensis	nat.	Myristicaceae	Makokou, Gabon	ERF	16
Psidium guajava	int.	Myrtaceae	Brazzaville, Congo	P	41
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Borassus aethiopum	nat.	Palmaceae	Lamto, Ivory Coast	S	18
Pandanus candelabrum	nat.	Pandanaceae	Lamto, Ivory Coast	FG	31
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Rubus steudneri	int.	Rosaceae	Makerere, Uganda	BG	4
Nauclea pobeguinii	nat.	Rubiaceae	Taï, Ivory Coast	SWF	9
Nauclea sp.	nat.	Rubiaceae	Adiopodoumé, Ivory Coast	SG	9
Rothmannia whitfieldii	nat.	Rubiaceae	Taï, Ivory Coast	ERF	9
Cyphomandra betaceae	nat.	Solanaceae	Makerere, Uganda	BG	4
Aframomum sanguineum	nat.	Zingiberaceae	Nabugabo, Uganda	F/S	4
Drosophila malerkotliana (*ananassae* subgroup)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Spondias cytherea	int.	Anacardiaceae	Dimonika, Congo	P	41

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
unidentified	nat.	Araceae	Taï, Ivory Coast	ERF	9
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Pentadesma butyracea	nat.	Guttiferae	Taï, Ivory Coast	ERF	9
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Artocarpus sp.	int.	Moraceae	Adiopodoumé, Ivory Coast	SG	9
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	SG	41
Ficus sp.	nat.	Moraceae	Dimonika, Congo	SG	41
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20, 21
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus thonningii	nat	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Musa sapientum	int.	Musaceae	Dimonika, Congo	P	41
Psidium guajava	int.	Myrtaceae	Dimonika, Congo	P	41
Psidium guajava	int.	Myrtaceae	Lamto, Ivory Coast	SG	18
Pandanus candelabrum	nat.	Pandanaceae	Lamto, Ivory Coast	FG	26
Pandanus candelabrum	nat.	Pandanaceae	Gd-Bassam, Ivory Coast	CSL	31
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Nauclea latifolia	nat.	Rubiaceae	Lamto, Ivory Coast	F/S	18
Nauclea sp.	nat.	Rubiaceae	Adiopodoumé, Ivory Coast	SG	9
Citrus sp.	int.	Rutaceae	Dimonika, Congo	P	41

Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Solanum sp.	?	Solanaceae	Dimonika, Congo	SG	41
Drosophila abron (*fima* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	23, 24
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus recurvata	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25
Drosophila abure (*fima* group)					
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus recurvata	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Drosophila akai (*fima* group)					
Momordica charantia	nat.	Cucurbitaceae	Mpanga, Uganda	ERF	4

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	4
Aframomum sanguineum	nat.	Zingiberaceae	Nabugabo, Uganda	F/S	4
Drosophila alladian (*fima* group)					
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Drosophila aloma (*fima* group)					
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25

Drosophila dyula (*fima* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	23, 24
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Drosophila fima (*fima* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	23, 24
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Nauclea sp.	nat.	Rubiaceae	Taï, Ivory Coast	ERF	9
Drosophila kulango (*fima* group)					
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9, 24
Drosophila sycophaga (*fima* group)					
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Drosophila sycophila (*fima* group)					
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Drosophila petitae (*fima* group)					
Ficus subsagittifolia	nat.	Moraceae	Makokou, Gabon	ERF	25
Drosophila busckii (SG. *Dorsilopha*)					
Mangifera indica	int.	Anacardiaceae	—, Uganda	P	4
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Coffea canephora	nat.	Rubiaceae	—, Uganda	P	4
Drosophila framire (SG. *Scaptodrosophila*)					
Artocarpus utilis	int.	Moraceae	—, Uganda	SG	4
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	—, Uganda	SF	4
Psidium guajava	int.	Myrtaceae	Makerere, Uganda	BG	4
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	4
Drosophila lambi (SG. *Scaptodrosophila*)					
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Treculia africana	nat	Moraceae	Taï, Ivory Coast	ERF	9
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	4
Drosophila latifasciaeformis (SG. *Scaptodrosophila*)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Landolphia dulcis	nat.	Apocynaceae	Taï, Ivory Coast	ERF	9
Crescentia cujete	int.	Bignoniaceae	Lamto, Ivory Coast	SG	18

Artocarpus sp.	int.	Moraceae	Adiopodoumé, Ivory Coast	SG	9
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Musa sapientum	int.	Musaceae	Dimonika, Congo	P	41
Borassus aethiopum	nat.	Palmaceae	Lamto, Ivory Coast	S	19
Phoenix reclinata	nat.	Palmaceae	Lamto, Ivory Coast	RFG	22
Pandanus candelabrum	nat.	Pandanaceae	Lamto, Ivory Coast	RFG	26
Pandanus candelabrum	nat.	Pandanaceae	Gd-Bassam, Ivory Coast	CSL	31
Pandanus candelabrum	nat.	Pandanaceae	Taï, Ivory Coast	RFG	31
Pandanus candelabrum	nat.	Pandanaceae	Sakré, Ivory Coast	SWF	31
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Drosophila mokonfim (SG. *Scaptodrosophila*)					
Ficus asperifolia	nat.	Moraceae	Taï, Ivory Coast	RFG	23, 24
Drosophila sp. cf. *pugionata* (SG. *Scaptodrosophila*)					
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	Budongo, Uganda	SDF	4
Averrhoa carambola	nat.	Oxalidaceae	Makerere, Uganda	BG	4
Drosophila fraburu (SG. *Drosophila*)					
Pandanus candelabrum	nat.	Pandanaceae	Sakré, Ivory Coast	SWF	31
Drosophila iri (SG. *Drosophila*)					
Pandanus candelabrum	nat.	Pandanaceae	Taï, Ivory Coast	RFG	31
Drosophila nasuta (SG. *Drosophila*)					
Mangifera indica	int.	Anacardiaceae	Brazzaville, Congo	P	41
Spondias cytherea	int.	Anacardiaceae	Dimonika, Congo	P	41
Artocarpus sp.	int.	Moraceae	Dimonika, Congo	P	41
Musa sapientum	int.	Musaceae	Dimonika, Congo	P	41

Table II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Psidium guajava	int.	Myrtaceae	Dimonika, Congo	P	41
Citrus grandis	int.	Rutaceae	Dimonika, Congo	P	41
Citrus reticulata	int.	Rutaceae	Dimonika, Congo	P	41
Drosophila pruinosa (SG. *Drosophila*)					
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	4
Drosophila sp. aff. *pruinosa* (SG. *Drosophila*)					
Turraeanthus africanus	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Drosophila repleta (SG. *Drosophila*)					
Ananas comosus	int.	Bromeliaceae	—, Uganda	P	4
Coffea canephora	nat.	Rubiaceae	—, Uganda	P	4
Citrus grandis	int.	Rutaceae	Dimonika, Congo	P	41
Solanum lycopersicum	int.	Solanaceae	—, Uganda	F	4
Liodrosophila sp.					
Ficus asperifolia	nat.	Moraceae	Taï, Ivory Coast	RFG	23, 24
Zaprionus armatus Collart					
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Zaprionus collarti Tsacas 1980 (=*vittiger* auctoris non Coquillett 1902)					
Mangifera indica	int.	Anacardiaceae	Arua, Uganda	P	2
Spondias dulcis	int.	Anacardiaceae	Eala, Zaïre	P	5

Spondias mombin	int.	Anacardiaceae	Mt Tonkoui, Ivory Coast	SF	9
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	9
Annona sp.	int.	Annonaceae	Arua, Uganda	BG	2
Polyalthia sauveolens	nat.	Annonaceae	Makokou, Gabon	ERF	16
Rollinia sieberi	int.	Annonaceae	Eala, Zaïre	—	6
Landolphia dulcis	nat.	Apocynaceae	Taï, Ivory Coast	ERF	9
Landolphia hirsuta	nat.	Apocynaceae	Lamto, Ivory Coast	F/S	18
Rauvolfia sp.	nat.	Apocynaceae	Eala, Zaïre	—	6
Crescentia cujete	int.	Bignoniaceae	Lamto, Ivory Coast	SG	18
Ananas comosus	int.	Bromeliaceae	—, Uganda	P	—
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Carica papaya	int.	Caricaceae	—, Uganda	P	4
Uapaca sp.	nat.	Euphorbiaceae	Eala, Zaïre	F	6
Pentadesma butyracea	nat.	Guttiferae	Taï, Ivory Coast	ERF	9
Persea americana	int.	Lauraceae	Makerere, Uganda	BG	4
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Malpighia sp.	int.	Malpighiaceae	Eala, Zaïre	—	6
Turraeanthus africanus	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Turraeanthus africanus	nat.	Meliaceae	Mt Nimba, Ivory Coast	ERF	22
Bellutia sp.	int.	Melastomataceae	Eala, Zaïre	—	6
unidentified liana	nat.	Menispermaceae	Mt Nimba, Ivory Coast	ERF	22
Artocarpus utilis	int.	Moraceae	—, Uganda	P	4
Artocarpus communis	int.	Moraceae	Entebbe, Uganda	BG	2
Artocarpus sp.	int	Moraceae	Adiopodoumé, Ivory Coast	SG	9
Dorstenia sp.	nat.	Moraceae	Eala, Zaïre	—	6
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20, 21
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus asperifolia	nat.	Moraceae	Taï, Ivory Coast	RFG	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus polita	nat.	Moraceae	Mt Tonkoui, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	2, 4
Ficus mucuso	nat.	Moraceae	Budongo, Uganda	SDF	2, 4
Ficus asperifolia	nat.	Moraceae	Mpanga, Uganda	RFG	4
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Staudtia gabonensis	nat.	Myristicaceae	Makokou, Gabon	ERF	16
Psidium guajava	int.	Myrtaceae	Eala, Zaïre	—	6
Psidium guajava	int.	Myrtaceae	Lamto, Ivory Coast	SG	18
Psidium guajava	int.	Myrtaceae	Makerere, Uganda	BG	2
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	2, 4
Pandanus candelabrum	nat.	Pandanaceae	Gd Bassam, Ivory Coast	CSL	31
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	2
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Parinari excelsa	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Rubus steudneri	int.	Rosaceae	Makerere, Uganda	BG	2
unidentified	?	Rosaceae	Mulago, Uganda	—	2
Coffea canephora	nat.	Rubiaceae	Nabugabo, Uganda	F/S	2, 4
Coffea canephora	nat.	Rubiaceae	Eala, Zaïre	—	6
Nauclea latifolia	nat.	Rubiaceae	Lamto, Ivory Coast	S	18
Nauclea sp.	nat.	Rubiaceae	Adiopodoumé, Ivory Coast	SG	9
Citrus sinensis	int.	Rutaceae	Eala, Zaïre	P	6

Citrus sp.	int.	Rutaceae	Eala, Zaïre	P	6
Pancovia bijuga	nat.	Sapindaceae	Lamto, Ivory Coast	RFG	18
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Malacantha alnifolia	nat.	Sapotaceae	Lamto, Ivory Coast	S	18, 22
Manilkara obovata	nat.	Sapotaceae	Lamto, Ivory Coast	RFG	18
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Cyphomandra betacea	int.	Solanaceae	Makerere, Uganda	BG	2, 4
Solanum campylacanthum	nat.	Solanaceae	Makerere, Uganda	BG	2
Solanum gilo	nat.	Solanaceae	Makerere, Uganda	BG	2
Solanum verbascifolium	nat.	Solanaceae	Kyambogo, Uganda	—	2
Solanum sp.	nat.	Solanaceae	Budongo, Uganda	F	2
Lantana camara	int.	Verbenaceae	Kyambogo, Uganda	—	2
Cissus dinklagei	nat.	Vitaceae	Makokou, Gabon	ERF	16
Aframomum sanguineum	nat.	Zingiberaceae	Nabugabo, Uganda	F/S	2, 4
Dendrophilum sp.	?	?	Eala, Zaïre	—	6
Phoenix reclinata	nat.	Palmaceae	Lamto, Ivory Coast	FG	22
Zaprionus inermis					
Musa sapientum	int.	Musaceae	Dimonika, Congo	P	41
Zaprionus ghesquierei					
Mangifera indica	int.	Anacardiaceae	Arua, Uganda	P	2, 4
Spondias mombin	int.	Anacardiaceae	Adiopodoumé	SG	9
Polyalthia sauveolens	nat.	Annonaceae	Makokou, Gabon	ERF	16
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Carica papaya	int.	Caricaceae	Makerere, Uganda	BG	2
Uapaca sp.	nat.	Euphorbiaceae	Eala, Zaïre	F	6
Persea americana	int.	Lauraceae	Makerere, Uganda	BG	2, 4
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Dorstenia sp.	nat.	Moraceae	Eala, Zaïre	—	6
Ficus ovata	nat.	Moraceae	Makerere, Uganda	BG	2, 4

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Musa sp.	int.	Musaceae	Arua, Uganda	P	2
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	2, 4
Cocos romanzoffiana	—	Palmaceae	—, Zaïre	—	14
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Coffea canephora	nat.	Rubiaceae	Eala, Zaïre	P	6
Citrus sinensis	int.	Rutaceae	Eala, Zaïre	P	6
Citrus sp.	int.	Rutaceae	Eala, Zaïre	P	6
Pancovia bijuga	nat.	Sapindaceae	Lamto, Ivory Coast	RFG	18
Gambeya perpulchra	nat.	Sapotaceae	Mt Nimba, Ivory Coast	ERF	22
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Cyphomandra betacea	int.	Solanaceae	Makerere, Uganda	BG	2, 4
Solanum gilo	nat.	Solanaceae	Makerere, Uganda	BG	2
Zaprionus neglectus Collart					
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Zaprionus ornatus (*vittiger* complex)					
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	9
Polyalthia sauveolens	nat	Annonaceae	Makokou, Gabon	ERF	16
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24

Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Staudtia gabonensis	nat.	Myristicaceae	Makokou, Gabon	ERF	16
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Cissus dinklagei	nat.	Vitaceae	Makokou, Gabon	ERF	16
Zaprionus proximus (*vittiger* complex)					
Cussonia sp.	nat.	Araliaceae	Nairobi, Kenya	—	7
Zaprionus sepsoides (*tuberculatus* complex)					
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	9
Spondias mombin	int.	Anacardiaceae	Mt Tonkoui, Ivory Coast	SG	9
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Pentadesma butyracea	nat.	Guttifereae	Taï, Ivory Coast	ERF	9
Hugonia sp.	nat.	Linaceae	Banco, Ivory Coast	ERF	22
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Turraeanthus africanus	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20, 21
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus sp.	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Treculia africana	nat.	Moraceae	Taï, Ivory Coast	ERF	9
Pandanus candelabrum	nat.	Pandanaceae	Taï, Ivory Coast	RFG	31
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9
Parinari excelsa	nat.	Rosaceae	Taï, Ivory Coast	ERF	9

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Nauclea pobeguinii	nat.	Rubiaceae	Taï, Ivory Coast	SWF	9
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Zaprionus sexvittatus					
Acokanthera sp.	?	Apocynaceae	Nairobi, Kenya	—	7
Zaprionus tuberculatus (*tuberculatus* complex)					
Spondias mombin	int.	Anacardiaceae	Mt Tonkoui, Ivory Coast	SG	9
Spondias mombin	int.	Anacardiaceae	Adiopodoumé, Ivory Coast	SG	9
Landolphia hirsuta	nat.	Apocynaceae	Lamto, Ivory Coast	F/S	18
Santiria trimera	nat.	Burseraceae	Mt Nimba, Ivory Coast	ERF	22
Dacryodes sp.	nat.	Burseraceae	Banco, Ivory Coast	ERF	22
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	9
Artocarpus sp.	int.	Moraceae	Adopodoumé, Ivory Coast	SG	9
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20, 21
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus saussureana	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Budongo, Uganda	SDF	4
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Guarea cedrata	nat.	Meliaceae	Banco, Ivory Coast	ERF	22
Hirtella sp.	nat.	Rosaceae	Taï, Ivory Coast	ERF	9

Parinari sp.	nat.	Rosaceae	Banco, Ivory Coast	ERF	22
Parinari excelsa	nat.	Rosaceae	Mt Nimba, Ivory Coast	ERF	22
Uncaria sp.	nat.	Rubiaceae	Taï, Ivory Coast	ERF	9
Pancovia bijuga	nat.	Sapindaceae	Lamto, Ivory Coast	RFG	18
Gambeya taiensis	nat.	Sapotaceae	Taï, Ivory Coast	ERF	9
Tieghemella heckelii	nat.	Sapotaceae	Banco, Ivory Coast	ERF	22
Zaprionus.(undistinguished species of the *tuberculatus* complex)					
Mangifera indica	int.	Anacardiaceae	Makerere, Uganda	BG	4
Spondias dulcis	int.	Anacardiaceae	Eala, Zaïre	—	6
Rollinia sieberi	int.	Annonaceae	Eala, Zaïre	—	6
Acokanthera sp.	?	Apocynaceae	Nairobi, Kenya	—	7
Cussonia sp.	?	Araliaceae	Nairobi, Kenya	—	7
Uapaca sp.	nat.	Euphorbiaceae	Eala, Zaïre	F	6
Malpighia sp.	int.	Malpighiaceae	Eala, Zaïre	—	6
Bellutia sp.	int.	Mellastomataceae	Eala, Zaïre	—	6
Dorstenia sp.	nat.	Moraceae	Eala, Zaïre	—	6
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	Makerere, Uganda	BG	4
Psidium guajava	int.	Myrtaceae	Eala, Zaïre	P	6
Psidium guajava	int	Myrtaceae	Makerere, Uganda	BG	2, 4
Averrhoa carambola	int.	Oxalidaceae	Makerere, Uganda	BG	2, 4
Phytolacca dodecandra	nat.	Phytolaccaceae	Buto, Uganda	F/S	2, 4
Eriobotrya japonica	int.	Rosaceae	Makerere, Uganda	BG	2, 4
unidentified	int.	Rosaceae	Mulago, Uganda	—	2, 4
Coffea canephora	nat.	Rubiaceae	Kawanda, Uganda	SG	2, 4
Citrus sp.	int.	Rutaceae	Eala, Zaïre	P	6
Murraya exotica	int.	Rutaceae	Eala, Zaïre	P	6
Cyphomandra betacea	int.	Solanaceae	Makerere, Uganda	BG	2, 4
Solanum gilo	nat.	Solanaceae	Makerere, Uganda	BG	2, 4
Solanum verbascifolium	nat.	Solanaceae	Kyambogo, Uganda	—	2, 4
Solanum sp.	nat.	Solanaceae	Budongo, Uganda	SDF	2, 4

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Cola acuminata	nat.	Sterculiaceae	Eala, Zaïre	—	6
Aframomum sanguineum	nat.	Zingiberaceae	Makerere, Uganda	BG	2, 4
unidentified *Drosophila* and *Zaprionus*					
Ficus carica	int.	Moraceae	Cilaos, Reunion	P	12
Lissocephala africana (*juncta* group)					
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Lissocephala ambigua (*juncta* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	21
Lissocephala diola (*juncta* group)					
Ficus sycomorus	nat.	Moraceae	Dakar, Senegal	DA	23, 24
Lissocephala disjuncta (*juncta* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	21
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Lissocephala juncta (*juncta* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	21
Ficus vallis-choudae	nat.	Moraceae	Lamto, Ivory Coast	F/S	21
Lissocephala linearis (*juncta* group)					
Ficus asperifolia	nat.	Moraceae	Taï, Ivory Coast	RFG	23, 24

Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus ovata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Lissocephala sp. Z (*juncta* group)					
Ficus exasperata	nat.	Moraceae	Brazzaville, Congo	—	41
Ficus polita	nat.	Moraceae	Brazzaville, Congo	—	41
Lissocephala couturieri (*sanu* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	21
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Detarium senegalense	nat.	Caesalpiniaceae	Taï, Ivory Coast	ERF	23, 24
Lissocephala lachaisei (*sanu* group)					
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus sp.	nat.	Moraceae	Brazzaville, Congo	—	41
Lissocephala lebou (*sanu* group)					
Ficus sycomorus	nat.	Moraceae	Dakar, Senegal	DA	23, 24
Lissocephala melanosanu (*sanu* group)					
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Lissocephala pulchra (*sanu* group)					
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus sp.	nat.	Moraceae	Brazzaville, Congo	—	41

Table II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Lissocephala sanu (*sanu* group)					
Ficus sur	nat.	Moraceae	Lamto, Ivory Coast	F/S	20, 21
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Nauclea pobeguinii	nat.	Rubiaceae	Adiopodoumé, Ivory Coast	SWF	23, 24
Lissocephala taiensis (*sanu* group)					
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus elasticoides	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Lissocephala horea (ungrouped species)					
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Lissocephala nigroscutellata (ungrouped species)					
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Lissocephala nigrothyrea (ungrouped species)					
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24

Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Lissocephala unipuncta (=*punctipennis* Duda) (ungrouped species)					
Ficus ovata	nat.	Moraceae	Entebbe, Uganda	BG	4
Ficus mucuso	nat.	Moraceae	Budongo, Uganda	SDF	4
Ficus lutea	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Lissocephala sp. H (ungrouped species)					
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Lissocephala sp. I (ungrouped species)					
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Lissocephala spp. (unidentified females)					
Ficus sur	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus macrosperma	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus vogeliana	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus mucuso	nat.	Moraceae	Taï, Ivory Coast	SF	23, 24
Ficus lyrata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus kamerunensis	nat.	Moraceae	Taï, Ivory Coast	SG	23, 24
Ficus ovata	nat.	Moraceae	Taï, Ivory Coast	ERF	23, 24
Ficus exasperata	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus thonningii	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus natalensis	nat.	Moraceae	Adiopodoumé, Ivory Coast	SG	23, 24
Ficus ludens	nat.	Moraceae	Salazie, Reunion	—	12
Ficus sp.	?	Moraceae	Grande Terre, Reunion	—	12
Ficus sp	?	Moraceae	Mayotte, Reunion	—	12
Ficus sp.	?	Moraceae	—, Reunion	—	12

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
? *Scaptomyza* sp.					
Solanum sp.	nat.	Solanaceae	Budongo, Uganda	SDF	4
FLOWER BREEDERS					
Drosophila melanogaster+*D. simulans* (not distinguished from one another)					
Quisqualis indica	int.	Combretaceae	—, Uganda	—	4
Gossypium hirsutum	int.	Malvaceae	—, Uganda	—	4
Treculia africana	nat.	Moraceae	—, Uganda	—	4
Solanum incanum	nat.	Solanaceae	—, Uganda	—	4
Lantana camara	int.	Verbenaceae	Kyambogo, Uganda	—	4
Aframomum sanguineum	nat.	Zingiberaceae	—, Uganda	—	4
Costus spectabilis	nat.	Zingiberaceae	—, Uganda	S	4
Drosophila bakoue (SG. *Sophophora, melanogaster* group/*montium* subgroup)					
Markhamia sp.	nat.	Bignoniaceae	Kounden, Cameroon	F/S	22
Drosophila seguyi (*montium* subgroup)					
Costus spectabilis	nat.	Zingiberaceae	—, Uganda	S	4
Drosophila ananassae (*ananassae* subgroup)					
Rothmannia whitfieldii	nat.	Rubiaceae	Taï, Ivory Coast	ERF	9
Aframomum sanguineum	nat.	Zingiberaceae	—, Uganda	—	4

Drosophila sp.aff. *ananassae* (*ananassae* subgroup)					
Ipomoea tricolor	int.	Convolvulaceae	—, Uganda	—	4
Gossypium hirsutum	int.	Malvaceae	—, Uganda	—	4
Hibiscus rosa-sinensis	int.	Malvaceae	—, Uganda	P	4
Drosophila aterrima complex (SG. *Scaptodrosophila*)					
Ipomoea digitata	int.	Convolvulaceae	Lamto, Ivory Coast	F/S	18
Ipomoea involucrata	?	Convolvulaceae	Taï, Ivory Coast	SG	9
Ipomoea sp.	?	Convolvulaceae	Sambava, Madagascar	CSA	42
Gossypium sp.	?	Malvaceae	Taï, Ivory Coast	SG	9
Hibiscus esculentus	nat.	Malvaceae	Dimonika, Congo	P	11, 41
Hibiscus sp.	nat.	Malvaceae	Dimonika, Congo	P	11, 41
Drosophila sp.aff. *mokonfim* (SG. *Scaptodrosophila*)					
Aframomum sanguineum	nat.	Zingiberaceae	—, Uganda	—	4
Drosophila flavohirta (SG. *Sophophora*; *melanogaster* group; *flavohirta* subgroup)					
Eucalyptus grandis	int.	Myrtaceae	Central Transvaal, S.Af.	GV	44
Eucalyptus paniculata	int.	Myrtaceae	Central Transvaal, S.Af.	GV	44
Drosophila dyaramankana (subgenerically unplaced species)					
Aframomum sanguineum	nat.	Zingiberaceae	—, Uganda	—	4
Drosophila sp.aff. *dyaramankana* (subgenerically unplaced species)					
Aframomum sanguineum	nat.	Zingiberaceae	—, Uganda	—	4
Drosophila sp.B aff. *dyaramankana* (subgenerically unplaced species)					
Kaempferia aethiopica	nat.	Zingiberaceae	Lamto, Ivory Coast	FG	18

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Drosophila spinipes (subgenerically unplaced species)					
Crinum jagus	nat.	Amaryllidaceae	Taï, Ivory Coast	SWF	9
Aframonum danieli	nat.	Zingiberaceae	Taï, Ivory Coast	ERF	9
Costus afer	nat.	Zingiberaceae	Taï, Ivory Coast	SG	9
Drosophila suma (subgenerically unplaced species)					
Ipomoea tricolor	int.	Convolvulaceae	—, Uganda	SG	4
unidentified *Drosophila* spp.					
Culcasia angolensis	?	Araceae	Banco, Ivory Coast	ERF	46
Culcasia scandens	?	Araceae	Taï, Ivory Coast	RFG	46
Culcasia tepoensis	?	Araceae	Grabo, Ivory Coast	SDF	46
Costus albus	nat.	Zingiberaceae	—, Uganda	SG	4
Zaprionus badyi					
Crinum sanderianum	nat.	Amaryllidaceae	Mt Nimba, Ivory Coast	FG	22
Crinum jagus	nat.	Amaryllidaceae	Lamto, Ivory Coast	RFG	22
Rothmannia whitfieldii	nat.	Rubiaceae	Lamto, Ivory Coast	RFG	18
Zaprionus neglectus					
Crinum jagus	nat.	Amaryllidaceae	Taï, Ivory Coast	SWF	9
Pentadesma butyracea	nat.	Guttiferae	Taï, Ivory Coast	ERF	9
Rothmannia whitfieldii	nat.	Rubiaceae	Taï, Ivory Coast	ERF	9

Zaprionus tuberculatus (*tuberculatus* complex)					
Costus spectabilis	int.	Zingiberaceae	—, Uganda	S	4
Zaprionus sp. (*tuberculatus* complex)					
Spathodea campanulata	nat.	Bignoniaceae	—, Uganda	—	4
Gossypium hirsutum	int.	Malvaceae	—, Uganda	—	4
Treculia africana	nat.	Moraceae	—, Uganda	—	4
Zaprionus ornatus (*vittiger* complex)					
Rothmannia whitfieldii	nat.	Rubiaceae	Lamto, Ivory Coast	RFG	18
Zaprionus sp. (*vittiger* complex)					
Ipomoea tricolor	int.	Convolvulaceae	—, Uganda	SG	4
Passiflora sp.	int.	Passifloraceae	—, Uganda	—	4
Costus spectabilis	nat.	Zingiberaceae	—, Uganda	S	4
Kaempferia aethiopica	nat.	Zingiberaceae	Lamto, Ivory Coast	FG	18
Zaprionus vrydaghi					
Costus afer	nat.	Zingiberaceae	Budongo, Uganda	SDF	2
Costus afer	nat.	Zingiberaceae	Mabira, Uganda	SDF	2
Costus afer	nat.	Zingiberaceae	Dimonika, Congo	SG	41
Costus afer	nat.	Zingiberaceae	Taï, Ivory Coast	SG	9
Costus sp.	nat.	Zingiberaceae	Makokou, Gabon	SG	42
Stegana proximata					
Erythrina abyssinica	nat.	Papilionaceae	—, Uganda	—	4
FUNGUS BREEDERS					
Drosophila seguyi (*melanogaster* group; *montium* subgroup)					
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
Drosophila ananassae & *D.* sp.aff. *ananassae* (*melanogaster* group; *ananassae* subgroup)					
Favolus sp.	—	Polyporaceae	—, Uganda	—	4
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
Drosophila sp.aff. *mokonfim* (SG. *Scaptodrosophila*)					
unidentified	—	—	—, Uganda	—	4
Drosophila busckii (SG. *Dorsilopha*)					
Agaricus sp.	—	Agaricaceae	—, Uganda	—	4
Drosophila pruinosa (SG. *Drosophila*)					
unidentified	—	—	—, Uganda	—	4
Drosophila sp.aff. *akabo* (SG. *Hirtodrosophila*)					
Favolus sp.	—	Polyporaceae	—, Uganda	—	4
Leucophenga buxtoni					
unidentified	—	—	Lamto, Ivory Coast	RFG	22
Leucophenga proxima					
Ganoderma sp.	—	—	—, Zaïre	SG	14
unidentified	—	—	Eala, Zaïre	—	8
unidentified	—	—	Lamto, Ivory Coast	RFG	22
unidentified	—	—	Taï, Ivory Coast	ERF	9

Leucophenga perargentata					
unidentified	—	—	Taï, Ivory Coast	ERF	9
unidentified *Leucophenga* spp.					
Favolus sp.	—	Polyporaceae	—, Uganda	—	4
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
Mycodrosophila ditan & *M.* sp.aff. *ditan*					
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
Mycodrosophila fracticosta & *M.* sp.aff. *fracticosta*					
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
Mycodrosophila kabakolo					
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
Mycodrosophila nigerrima & *M.* sp.aff. *nigerrima*					
Polyporus sp.	—	Polyporaceae	—, Uganda	—	4
LEAF MINERS AND STEM BORERS					
Gitona pauliani Séguy					
Phytolacca dodecandra	nat.	Phytolaccaceae	Tsimbazaza, Madagascar	BG	34
Phytolacca dodecandra	nat.	Phytolaccaceae	Addis Ababa, Ethiopia	—	39
Gitona ethiopica					
Phytolacca dodecandra	nat.	Phytolaccaceae	Addis Ababa, Ethiopia	—	39

TABLE II (*cont.*)

Host-plant species	Host origin	Host-plant family	Locality, country	Habitat	References
DECAYING TRUNK, BRANCH AND TUBERCULOUS ROOT BREEDERS					
Drosophila melanogaster (*melanogaster* group; *melanogaster* subgroup)					
Manihot esculenta= manioc-retted tubercule	int.	Euphorbiaceae	Ngoko, Nto, Bu Konzo, Congo	SG	40
Drosophila malerkotliana (*ananassae* subgroup)					
Manihot esculenta= manioc-retted tubercule	int.	Euphorbiaceae	Dimonika, Congo	SG	41
Drosophila fraburu (SG. *Drosophila*)					
Manihot esculenta= manioc-retted tubercule	int.	Euphorbiaceae	Ngoko, Nto Bu Konzo, Congo	SG	40
Manihot esculenta (id.)	int.	Euphorbiaceae	Dimonika, Congo	SG	41
Drosophila iri (SG. *Drosophila*)					
Manihot esculenta= manioc-retted tubercule	int.	Euphorbiaceae	Ngoko, Nto Bu Konzo, Congo	SG	40
Elaeis guineensis	nat.	Palmaceae	Mt Nimba, Ivory Coast	P	22
Drosophila nasuta (SG. *Drosophila*)					
Manihot esculenta= manioc-retted tubercule	int.	Euphorbiaceae	Ngoko, Nto Bu Konzo, Congo	SG	40

Drosophila saba (SG. *Scaptodrosophila*)					
Elaeis guineensis= parenchyme of cut trunk	nat.	Palmaceae	Dimonika, Congo	SG	41
Zaprionus ghesquierei					
Elaeis guineensis= decaying cut trunk	nat.	Palmaceae	—, Zaïre	SG	14
Zaprionus inermis					
Elaeis guineensis= parenchyme of cut trunk	nat.	Palmaceae	Dimonika, Congo	SG	41
ANIMAL ORGANIC MATTER BREEDERS					
Drosophila melanogaster (*melanogaster* group; *melanogaster* subgroup)					
Sheath of *Deborrea malgassica* (Lepidoptera, Psychidae)			—, Madagascar	—	30
Drosophila latifasciaeformis (SG. *Scaptodrosophila*)					
Dead caterpillars of Thaumetopoeidae			Lamto, Ivory Coast	F/S	22
unidentified *Drosophila* sp.					
Faeces of caterpillars in head capsule of the cotton plant			Maroua, N. Cameroon	S	17
Gitona gossypii					
Faeces of insect in head capsule of the cotton plant			—, Mozambique	—	33

TABLE II (*cont.*)

Host-plant species	Locality, country	Habitat	References
COMMENSAL BREEDERS WITHIN SOLITARY BEE NESTS			
Cacoxenus apidoxenus (SG. *Gitonides*)			
Pollen/nectar provision of *Chalicodoma mephistolica* (SG. *Callomegachile*) (Apoidea, Megachilidae)	Bambey, Senegal	S	36
Idem of *Chalicodoma kamerunensis kamerunensis* (SG. *Callomegachile*) (Apoidea, Megachilidae)	Foumbot, W-Cameroon	F/S	36
Idem of *Chalicodoma cincta cincta* (SG. *Gronoceras*) (Apoidea, Megachilidae)	Bambey, Senegal	S	36
Idem of *Chalicodoma cincta cincta* (SG. *Gronoceras*) (Apoidea, Megachilidae)	Adiopodoumé, Ivory Coast	SG	36
Idem of *Chalicodoma cincta cincta* (SG. *Gronoceras*) (Apoidea, Megachilidae)	NKolbisson, Cameroon	SG	36
COMMENSAL BREEDERS WITHIN CERCOPID SPITTLE MASSES			
Leucophenga decaryi (=*Ptyelusimyia decaryi* Séguy)			
Ptyelus goudoti (Homoptera, Cercopidae) on *Mimosa delicatula* (Mimosaceae)	—, Madagascar	—	32
Leucophenga sp.aff. *sema*			
Ptyelus flavescens (Homoptera, Cercopidae) on *Milletia dura* (Papilionaceae)	—, Uganda	—	29
Leucophenga proxima			
Ptyelus grossus (Homoptera, Cercopidae) on *Cajanus cajan* (Papilionaceae)	Ife-Ife, Nigeria	BG	27
Ptyelus grossus (Homoptera, Cercopidae) on *Spathodea campanulata* (Bignoniaceae)	Ife-Ife, Nigeria	BG	27

Poophilus adustus (Homoptera, Cercopidae) on *Cajanus cajan* (Papilionaceae)		Ife-Ife, Nigeria	BG	27
Poophilus adustus (Homoptera, Cercopidae) on *Aspilia africana* (Compositae)		Ado-Ekiti, Nigeria	SG	27
PREDATORS AND PARASITES OF HOMOPTERA				
Amiota sp. Tsacas				
Perkinsiella saccharioidea	Delphacidae on sugar cane	St Marie, Reunion	P	12
Peregrinus maidis	Delphacidae on maize	La Bretagne, Reunion	P	12
Saccharicoccus sacchari	Pseudococcidae on sugar cane	La Bretagne, Reunion	P	12
Cacoxenus frontalis (SG. *Gitonides*)				
Aspidoproctus bouvieri	Margarotidae on Cassia siamea	Lukolela, Zaïre	—	5
Cacoxenus perspicax (SG. *Gitonides*)				
Dysmicoccus boninsis	Pseudococcidae on Ananas	—, Mauritius	P	1
Planococcus citri	Pseudococcidae on Rose Laurel	St-Gilles, Reunion	P	12
Pseudococcus brevipes	Pseudococcidae on Ananas	—, Mauritius	P	28
Pseudococcus filamentosus	Pseudococcidae on —	—, Zaïre	—	13
Saccharicoccus sacchari	Pseudococcidae on —	—, Reunion	—	10
Saccharicoccus sacchari	Pseudococcidae on —	—, Mauritius	P	1, 10
Saccharicoccus sacchari	Pseudococcidae on —	—, Somalia	—	36
AQUATIC PREDATORS OF SIMULID AND CHIRONOMID LARVAE				
Drosophila cogani (SG. *Drosophila*; *simulivora* group)				
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Wowe Riv., Kumba, W-Cameroon		37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Mungo Riv., Kumba, W-Cameroon		37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Blackwater, Kumba, W-Cameroon		37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Kobe Riv., Kumba, W-Cameroon		37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Menge Riv., Kumba, W-Cameroon		37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)		Bille Riv., Kumba, W-Cameroon		37

TABLE II (*cont.*)

Host-prey species	Locality, country	References
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)	Okia Riv., Kumba, W-Cameroon	37
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)	Firestone, Liberia	37
Drosophila gibbinsi (*simulivora* group)		
Larvae of Chironomids and Simuliids (Diptera)	Nile Riv., Jinga, Uganda	35
Larvae of Chironomids and Simuliids (Diptera)	Shooters Hill, Natal, S-Africa	37
Larvae of Chironomids and Simuliids (Diptera)	Ruzizi Riv., Bugarama, Rwanda	15
Drosophila sp.cf. *gibbinsi* (*simulivora* group)		
Larvae of Chironomids and Simuliids (Diptera) (presumed)	Kimoro, Madagascar	37
Drosophila libellulosa (*simulivora* group)		
Eggs of the dragonfly *Malgassophlebia aequatoris*	Baté Riv., Makokou, Gabon	38
Drosophila simulivora (*simulivora* group)		
Young larvae of *Simulium damnosum* (Diptera, Simuliidae)	Blackwater, Kumba, W-Cameroon	37

* References: 1. Box, 1953; 2. Buruga, 1976; 3. Buruga, unpublished results; 4. Buruga and Olembo, 1971; 5. Collart, 1935; 6. Collart, 1937a; 7. Collart, 1937b; 8. Collart, 1939; 9. Couturier, Lachaise and Tsacas, unpublished results; 10. David and Tsacas, 1975; 11. David and Vouidibio, unpublished results; 12. Etienne, unpublished results; 13. Ghesquière, 1934; 14. Ghesquière, in litt., in Lepesme, 1947; 15. Gouteux, 1976; 16. Hladik and Lachaise, unpublished results; 17. Jacquemard and Tsacas, unpublished results; 18. Lachaise, 1974; 19. Lachaise, 1975; 20. Lachaise, 1976; 21. Lachaise, 1977; 22. Lachaise, 1979a; 23. Lachaise, Couturier and Tsacas, unpublished results; 24. Lachaise *et al.*, 1982; 25. Lachaise and Michaloud, unpublished results; 26, Lachaise and Tsacas, 1974; 27. Medler and Adenuga, 1969; 28. Moutia and Mamet, 1946; 29. Odhiambo, 1957; 30. Paulian, in Séguy, 1951; 31. Rio *et al.*, 1983; 32. Séguy, 1932; 33. Séguy, 1933a, b; 34. Séguy, 1951; 35. Smart, 1937; 36. Tsacas and Desmier, 1976; 37. Tsacas and Disney, 1974; 38. Tsacas and Legrand, 1979; 39. Tsacas and Teshome, 1981; 40. Vouidibio, 1977; 41. Vouidibio, unpublished results; 42. Lachaise, unpublished results; 43. David, unpublished results; 44. Tsacas and Johannsmeier, unpublished results; 45. Tsacas, unpublished results; 46. Knecht, unpublished results.

African drosophilids. Ten categories are recognized: A. fruit breeders; B. flower breeders; C. fungus breeders; D. leaf miners and stem borers; E. decaying trunk, branch and tuberculous root breeders; F. commensal breeders within cercopid spittle mass; G. commensal breeders within solitary bee nests; H. predators of Homoptera; I. aquatic life and predation in the *simulivora* group species; J. decaying animal organic matter breeders.

Clearly, the African endemic drosophilids, like the Hawaiian endemics (Heed, 1968; Montgomery, 1975) and Australian endemics (Bock and Parsons, Chapter 7, Volume 3a), have highly diversified larval habits and are not the homogeneous group of saprophagous organisms commonly assumed. So many adaptive pathways have evolved in mainland Africa that many quite unexpected breeding sites might well remain to be found.

To stress the colonizing abilities of species, Table II specifies whether the host-plants used by fruit-breeders and flower-breeders are native or introduced. Figure 12 shows a remarkable correlation between flies and host-plants, i.e. those flies which are widespread also breed (or only breed) in introduced host-plants. The term "widespread" includes widespread, paleotropical, pantropical, subcosmopolitan and cosmopolitan species (see Parsons and McDonald, 1978; David and Tsacas, 1981). Similarly, Parsons (1977b) found in Australia that resources in rainforests are fully utilized by endemic species, so preventing colonization by cosmopolitan species. Furthermore, few endemic species have emerged from rainforests, emphasizing that suitable resources probably do not occur outside their historic habitats for species not coming to fruit bait.

Species with high colonizing abilities, such as *D. melanogaster*, *D. simulans*, *D. busckii*, *D. latifasciaeformis* and *Z. collarti*, invade indifferently both introduced and native host-plants; their abilities to tolerate a permanent host switch is due to their opportunistic behavior. By contrast, endemic species breeding only in native host-plants display both a more specialist behavioral pattern.

A. FRUIT-BREEDERS

Plant species whose fleshy fruits are not colonized by any drosophilid are rare in the tropics. In contrast to temperate areas, where fruits are relatively rare and ephemeral (Carson, 1971; Begon, 1975 and Chapter 17, Volume 3b), tropical Africa and other tropical zones appear to be characterized by an "unlimited" supply of fruit available for drosophilids. Fruits may be both so highly productive and predictable a resource that species packing is a major feature of the tropics. If competitive displacements occur, they doubtless rarely lead to competitive exclusion from the resource patch including a number of food items; so that the question to be raised is rather that of food item partitioning.

Many tropical fruits support species packing of drosophilids because of the length of time they remain favourable to larval growth. Southwood (1976) stressed that the significance of this duration stability was dependent on the relationship between the organism's generation time (τ) and the length of time the substrate remains suitable (H): "In those species where τ/H approaches unity, one generation cannot affect the resource of the next; there will be no evolutionary penalty for overshooting the carrying capacity of the habitat. Those species are then exploiters, opportunists. Conversely, for those animals that occupy long-lived habitats where the carrying capacity (K) is fairly constant, significant overshooting will lower K, and will adversely affect subsequent generations".

Thus, some African fruits last no longer than one *Drosophila* generation (e.g., *Cissus*, *Coffea*, *Psidium*, *Spondias* or *Staudtia*), whereas some others may, potentially, support many consecutive generations (e.g., *Anonidium*, *Artocarpus*, *Borassus* or *Pandanus*). However, as was discussed in the first section, due to the foraging behavior of the larvae, each generation makes the substrate unsuitable for the next one.

1. Seasonal specialization in Drosophila erecta

Drosophila erecta is one of the eight closely related species of the *melanogaster* subgroup living in the Afrotropical region. Its narrow association with the screw-pine *Pandanus candelabrum* (Monocots, Pandanaceae), previously seen in Lamto in the pre-forest Ivory Coast (Lachaise and Tsacas, 1974), is now confirmed by new records from the southern Ivory Coast (Rio *et al.*, 1983). The geographical range of *erecta* includes the Ivory Coast, Nigeria, Cameroon and Congo, thereby matching the

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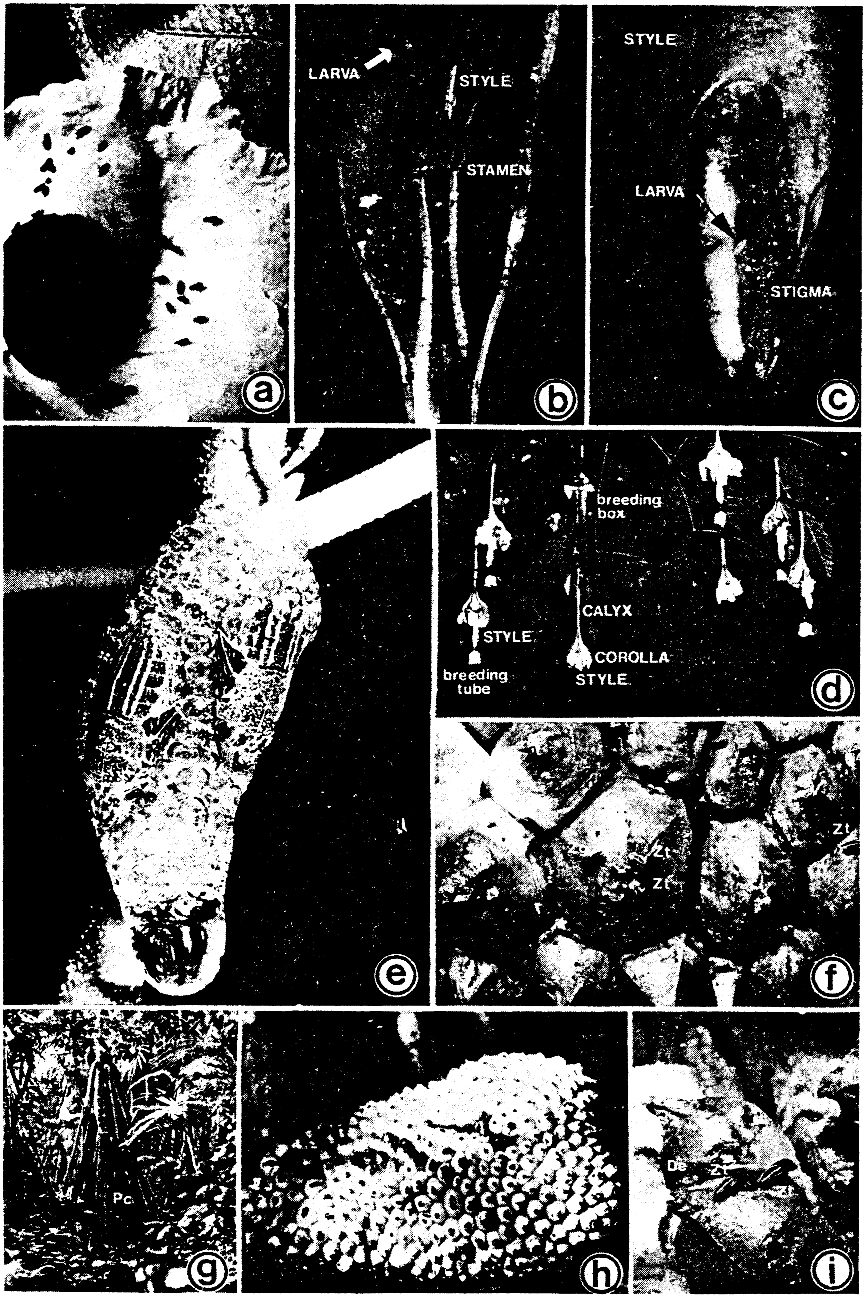
FIG. 13. (a) Packing of adults of the *Drosophila aterrima* species complex within the corolla of *Hibiscus rostellatus* (Malvaceae). (b) Larvae of *D. aterrima* species complex within the corolla of *Ipomoea digitata* (Convolvulaceae). (c) Larvae of *Zaprionus badyi* on the myophilous stigma of *Rothmannia whitfieldii* (Rubiaceae) in the riparian forest gallery of the River Bandama. (d) Flowers of *R. whitfieldii* and breeding methods. (e) Spittle-mass of the spittle-bug *Ptyelus grossus* (Fab.) (Cercopoidea, Aphrophoridae) yielding two last instar larvae head down; the spittle-mass which drips unceasingly is a common breeding site for *Leucophenga proxima*. (f) Hexagonal figures due to appressing of the drupes which make the infrutescence of *Pandanus candelabrum* (Pandanaceae). (g) Stilt roots of *P. candelabrum* (Pc) in the forest gallery of a temporary tributary of the River Bandama. (h) General view of the entire infrutescence. (i) Drupes loosing in an older stage. De: *Drosophila erecta*; Zg: *Zaprionus ghesquierei*; Zt: *Zaprionus tuberculatus*. (Photographs after D. Lachaise from the Guinean zone of the Ivory Coast, except (e) which is after M. Boulard).


LARVA
STYLE
STAMEN
b
a
STYLE
LARVA
STIGMA
c
breeding box
CALYX
STYLE
breeding tube
COROLLA
STYLE
d
e
Zt
Zt
Zt
Zt
f
Pc
g
h
De
Zt
Zt
i

Guineo-congolese distribution of its host plant. Neither the fly nor the *Pandanus* extend to the east over the Rift Valley.

The *erecta–Pandanus* association is perennial but not permanently obligatory. The records on *erecta* lead to the concept of "seasonal specialization". Rather than a species status, specialization appears to be a generation-dependent allocative option. Those generations appearing when *Pandanus* fruits are available are strictly and obligatorily dependent on *Pandanus* for breeding, whereas those starved of *Pandanus* fruit show, all things considered, a more opportunistic behavior. Rare and isolated individuals of *erecta* can occasionally be caught in sites of *Pandanus* devoid of fruits, as was observed in Lamto and Taï in the Ivory Coast and on the Kounden plateau in Cameroon (Rio *et al.*, 1983). Regarding the very low level of population size in those generations starved of *Pandanus*, one can expect that the energetic cost paid by the transitional generations is high. The extension of the host plant range might result in an appreciable increase in metabolic costs, for example by tolerating a greater range of defensive chemicals present in a wider array of host plants. This probably explains why the specialization strategy has been selected and since maintained.

The populations of *P. candelabrum* live in swampy riparian habitats (Fig. 13g). Generally, *Pandanus*-patches show a coarse-grained distribution that involves a similar discrete distribution in the populations of *erecta*. Moreover, considering that *erecta* has also greater sensitivity to dessication and high temperatures than other *melanogaster* subgroup species (Stanley *et al.*, 1980), one can expect between-population migration and then gene flow to be limited. Nevertheless, no differences have been seen between populations, at least at the chromosomal and reproductive levels (Rio *et al.*, 1983).

The decaying fruit of *Pandanus* may remain suitable for drosophilids as a larval resource for about two months. However, due to the changes of the substrate, the ovipositing species of flies replace one another as was shown for figs. *Drosophila erecta* oviposits in the early decaying fruit while *D. latifasciaeformis*, the most colonizing *Scaptodrosophila* on the Ivory Coast, lay eggs in the late successional stages. Within the same syncarp of *Pandanus* some drupes evolve more rapidly than others. This provides a micro-mosaic of drupes in different stages of decay (Fig. 13, f and h). From this a remarkable within-fruit substrate patchiness may occur that allows intra-resource partitioning between *erecta* and *latifasciaeformis* in medium succession.

Synchronism in the phenology of fruit production in *P. candelabrum* was observed during four consecutive yearly cycles (from 1980 to 1983) in four distant localities in southern Ivory Coast (Grand-Bassam, Lamto, Taï and Sakré) separated respectively by 186, 275 and 408 km. Concomitant rearing of *erecta* was obtained from the syncarpic fruits of the different geographic patches of *Pandanus* (Rio *et al.*, 1983). Overall between-patch synchronism in fruiting in the southern Ivory Coast provides a short-term predictability for the benefit of four to five consecutive generations of *erecta*. When this short-term predictability has worn away, the strict specialization pattern of the fly is no longer maintained. However, continuation of the status of specialist at the species level is likely to be accounted for by long-term predictability due to yearly periodicity in *Pandanus* fruiting. Consequently, the prerequisite promoting the evolution of seasonal monophagy in *erecta* is met. Hence, it can be more clearly understood why specialization, as an issue of an evolutionary pathway, does not necessarily lead to a dead end.

2. *The association of* Drosophila sechellia *with* Morinda citrifolia

The second of the eight species of the *melanogaster* species-subgroup to provide a highly specialized larval habit is the newly described *D. sechellia* (Tsacas and Bächli, 1981). The species is only known from the granitic small island of Cousin in the Seychelles archipelago. After David (personal communication), who collected *sechellia*, the assumption can be made that its range is larger and very likely includes at least Cousine and Aride islands, which display similar ecological features. On Cousine islet, *sechellia* is strictly restricted to the fruits of the Indian mulberry tree, *Morinda citrifolia*, for breeding. This rubiaceous plant also grows on Cousine and Aride islands.

The Indian mulberry tree is a small tree or shrub growing to 6 meters in height. Due to the striking adaptation for dispersal of its seeds—by floating in sea-water—*M. citrifolia* shows a wide geographical range throughout south eastern Asia, from India to China, Australia and the Pacific islands. It is worth noting that no species of *Drosophila* were found to inhabit the fruits of *M. citrifolia* at a few places around Varanasi in the gangetic lowland in north eastern India (Gupta, personal communication).

On Cousin islet in the Seychelles the *Morinda* tree grows on granitic sand conglomerated with guano, making dense bushes in the neighbourhood of the sea. *M. citrifolia* produces composed fruits with a smell like decaying cheese which are very conducive to *sechellia* breeding. Of 1458 adult flies emerging from *Morinda* fruits, David (personal communication) obtained 1275 *sechellia* and 183 individuals of the widespread and expanding *D. malerkotliana*. This author further indicates that the specialization of *sechellia* to *M. citrifolia* is also simply evidenced by comparing the fly species found on three adjacent traps baited, respectively, with *Morinda*, banana and coconut palm cabbage. The results clearly show that *sechellia* concentrates almost exclusively on *Morinda*, whereas *malerkotliana* frequents any of the three baits indifferently.

Finally, David (personal communication) emphasizes that neither *D. simulans* nor *D. melanogaster* live on Cousin islet, and that *sechellia* is lacking in the large Mahé island where *simulans* and *melanogaster* are locally present in wild or domestic areas respectively.

3. *Adaptive radiation of* Scaptodrosophila *on palm-trees*

The subgenus *Scaptodrosophila* has achieved a wide adaptive radiation on palm-trees in tropical Africa (Burla, 1954, 1955; Lachaise, 1975, 1979a). Thirteen species belonging to this subgenus, ten of which are endemic, were found feeding on all parts of palm trees: fruits, sap-exudations, palm-cabbage, decaying trunk mold. *Drosophila latifasciaeformis*, *D. bangi* and *D. saba* were found on "Rônier" palm-tree (*Borassus aethiopum*), on oil-palm tree (*Elaeis guineensis*) and on different *Raphia* palm-trees. Burla (1954) found the following species together on *Raphia* in the southeastern Ivory Coast: *saba*, sp. aff. *pugionata* (as *pugionata*), *latifasciaeformis*, *senufo*, *anyi*, *bangi*, *uebe*, *mbettie*, *framire*, *triangulifer*, *eoundo* (as *brunnea*), *agamse* and *lambi*.

Species of *Scaptodrosophila* may produce large swarms on palm-trees. Thus, Burla (1954) noticed large numbers of *agamse* on oil-palm trees and Lachaise (1975) stressed that 99% of the multi-species drosophilid community, adults as well as larvae, living on Rônier palm-tree belonged to a single expanding species, *latifasciaeformis*. Because little attention has been focused on African *Scaptodrosophila*, only *latifasciaeformis* has been found to breed in the fruits of its host-palm tree; the breeding-sites of the twelve other palm-tree *Scaptodrosophila* species are still conjectural.

Lachaise (1975) estimated that 10^5 drosophilid larvae, mainly *latifasciaeformis*, were produced per year for a female palm-tree bearing 100 fruits. This is nearly the same production as on *Ficus sur* bearing 3000 fruits ($75 \cdot 10^4$ larvae) (Lachaise, 1976). Both trees share the same habitats in the Guinean pre-forest savannahs in the Ivory Coast. Since palm-trees fruit once a year and *Ficus sur* continuously eight times a year, the production is respectively 10^5 and $6 \cdot 10^6$ larvae per tree per year, assuming constant production and mortality. The densities of both trees change greatly from one habitat-patch to another. In forested savannah, where both trees are at a relatively high density, i.e. 5·45 female palm-trees per hectare (Vuattoux, 1970) and 30 fig-trees per hectare (Menaut, 1971 and personal communication), the overall production of drosophilid larvae per hectare might be around 10^8 larvae. Due to the differences in density, palm-trees appear far less productive than fig trees in forested savannahs. However, since fig trees are absent from open grass savannahs, which are burned every year, palm-trees are probably as productive in the pre-forest grove of the

Ivory-Coast. In Rônier palm-groves *D. latifasciaeformis* acts as an invader of the monoculture. Of 176,388 specimens of 105 species, recorded in a 2000 hectare area within a palm grove during a four-year period, 95,156 specimens, i.e. 54%, were *D. latifasciaeformis* (Lachaise, 1979a).

Borassus displays unpredictable and asynchronous between-tree fruiting (Portères, 1964–1965; Vuattoux, 1968), so that *Borassus* fruits have a high predictability as a larval food resource for *D. latifasciaeformis* throughout the year. Therefore, the Lamto population of this opportunistic *Scaptodrosophila* species behaves as a specialist in contrast to the forest populations.

B. FLOWER-BREEDERS

In view of the chapter by Brncic on flower-breeding drosophilids (see Chapter 33), we will only report data involving the African species and will present some new unpublished records on those species.

1. *African* Hibiscus-*breeding drosophilids*

The genus *Hibiscus* (Malvaceae), a genus of two hundred species in the world, is most richly represented in mainland Africa and Madagascar. Letouzey (1970) reported the occurrence of 50 native *Hibiscus* species from Africa, mainly living in the Sahelian and Sudanese zones.

Hibiscus-breeding drosophilids provide a remarkable ecological convergence in the tropics. Cook *et al.* (1977) found a new species of *Scaptodrosophila*, *D. hibisci* which was associated with flowers of two *Hibiscus* species in tropical Australia. Larvae and pupae were found in one of them. Since native *Hibiscus* species occur mainly in northern Australia other host-*Hibiscus* are likely to be found.

In the evergreen rainforest of Dimonika in Congo, David and Vouidibio (personal communication) found two sibling species of *D. aterrima* whose larvae coexist within the flowers of the native *Hibiscus esculentus* and other unidentified *Hibiscus*. Hence, with *D. aterrima sensu stricto*, which Burla (1954) found as adults within *H. sumatrensis* (*sic.* probably *H. surratensis*!) in the southern Ivory Coast, a complex of three flower-breeding sibling species, at least, exist under the term *aterrima*. It is a matter of conjecture whether the adults of the *aterrima*-like species found by Buruga and Olembo (1971) within *H. rosa-sinensis* flowers in Uganda and by Lachaise (1974, 1979a) in *H. rostellatus* and *H. asper* in the Ivory Coast belong to one of these three species or to further species (Fig. 13a).

In eastern Zaïre, around Kivu-lake, Graber (1957) collected adults of two closely related *Scaptodrosophila* species, *D. ebenea* and *D. pseudoebenea*, from the large flowers of *Hibiscus ludwigii*. Occasional non-*Scaptodrosophila* were recorded from *Hibiscus*, e.g. *D.* sp. aff. *ananassae*, *D. melanogaster* and *D. simulans* on *H. rosa-sinensis* (Buruga and Olembo, 1971) and *D. teissieri* and *Mycodrosophila* sp. on *H. rostellatus* (Lachaise, 1974).

In most *Hibiscus*, e.g. *H. ludwigii* and *H. esculentus*, the flowers are ephemeral, lasting not more than one or two days. As the flower grows older during the day, it turns bronze and then red before dropping at nightfall. Burla (1954) and Lachaise (1974) observed that a population of 50 flies of *Drosophila aterrima* or a similar species lets itself become entrapped within the flower as it quietly closes and fades at nightfall. As suggested by Cook *et al.* (1977) this implies that any resource utilization must begin soon after colonization on the day that the flowers are open, and that the colony of a flower is stable throughout the day. As suggested by Graber (1957) the females may await the fall of the flower they inhabit before ovipositing. Further larval development occurs in the decaying fallen flowers, so that the time the resource remains suitable for drosophilids is extremely short. Since Graber (1957) found adult flies of *D. aterrima*, *D. ebenea* and *D. pseudoebenea* to have intestines full of pollen, it appears likely, as stressed by Cook *et al.* (1977), that fresh *Hibiscus* flowers provide courting and feeding sites for the adults, as well as a resource suitable for larval development once the flowers begin to decay.

It is unlikely that African flower-breeding *Scaptodrosophila* display host-specificity, or even host-dependence, for *Hibiscus*. The adaptive breeding site shift to *Hibiscus* in many parts of the world is due to the great number of *Hibiscus* species available as resources in all tropical areas rather than to the suitability of this breeding site. The flowering time is very restricted in the course of the year and a strictly *Hibiscus*-dependent fly population could not survive the year around. Similarly, Cook *et al.* (1977) emphasized that Australian *Hibiscus* flowers were short-lived resources, maintaining populations for from one week to three months. This implies a continuous process of colonization and raises the problem of what resources, if any, are utilized when *Hibiscus* are not flowering. Burla (1954), in the Ivory Coast, reported the continuous breeding-site transfer of *D. aterrima* from *Hibiscus* to *Ipomoea* flowers and vice versa.

Furthermore, Couturier *et al.* (1983) showed that the species of the *aterrima* complex also breed within the tubular-like flowers of the cotton (*Gossypium*) and within *Ipomoea*-like Tubiflorales.

2. *African Tubiflorale-breeding drosophilids*

The Tubiflorales are an order of gamopetalous dicots with tubuliform corolla which provide suitable breeding sites for drosophilids. Indeed, flower breeding drosophilids have been bred from five Tubiflorale families:

Convolvulaceae (*Ipomoea*), Solanaceae (*Cestrum*, *Datura*, *Solanum*), Bignoniaceae (*Markhamia*, *Spathodea*) and Acanthaceae (*Aphelandra*, *Thunbergia*) mainly in the Afrotropical and the Neotropical regions (see Brncic this volume, and references therein).

In tropical Africa the great flower bindweeds of the genus *Ipomoea* yield approximately the same flower-breeding species that exploit *Hibiscus* flowers, so that *Ipomoea* and *Hibiscus* appears to substitute for one another indifferently as a fly resource. Drosophilids have been found within the flowers of four *Ipomoea* species (*I. digitata*, *I. involucrata*, *I. tenuirostris* and *I. tricolor*). Of these only *I. involucrata* is native, the others being introduced. In the Ivory Coast adults of the *D. aterrima* species complex were found within the flowers of *I. involucrata* in the evergreen rainforests of Banco by Burla (1954) (as "*I. involvuata*") and of Taï by Couturier *et al.* (1983), and of *I. digitata* in the Lamto savannahs by Lachaise (1974) (Fig. 13b). Larvae were found in *I. involucrata* from Taï and in *I. digitata*. In Uganda, Buruga (personal communication) found adults of the *aterrima* complex within the flowers of *I. tricolor*.

Buruga (1976) also bred *Zaprionus collarti* from *I. tricolor* and Burla (1954) mentioned a *Zaprionus* close to *Z. neglectus* in the flowers of *I. digitata* near Abidjan.

In the vicinity of the Kivu-lake, Graber (1957) recorded adults of *Drosophila suma* in *I. tenuirostris* (reported as *I. gracilior*). In Uganda, Buruga and Olembo (1971) also mentioned the occurrence of *D.* sp. aff. *ananassae*, *D. lambi*, *D. seguyi*, *D. suma* and one species of the *Zaprionus vittiger* complex in *I. tricolor*, but the presence of their larvae in the flowers is somewhat equivocal.

Among other Tubiflorales that host drosophilids are the flowers of Solanaceae. Burla (1954) recorded adults of *D. aterrima* within *Datura* sp. flowers in southern Ivory Coast and Buruga (personal communication) those of sibling species of the *aterrima* complex from the trumpet-shaped flowers of the small tree *Datura candida* in Uganda. There Buruga and Olembo (1971) also found *D. melanogaster* (or *simulans*) in the native *Solanum incanum*.

The Bignoniaceae are mainly trees or shrubs native to tropical Africa and produce large tubuliform flowers (10–12 cm) in the genera *Spathodea* and *Markhamia*. The "African tulip tree" *Spathodea campanulata* is a small tree living in wet rainforest and in old grove areas (Letouzey, 1970). Its fiery red flowers grow in circular groups, around closely crowded buds. These buds develop a few at a time thus ensuring blooms the year around. *S. campanulata* is, therefore, a relatively predictable breeding site for flower-breeding drosophilids. Buruga (1976) bred members of the *Zaprionus tuberculatus* complex in Uganda from these flowers (reported as *S. nilotica*).

The yellow flowered *Markhamia* grow in forests or peri-forest savannahs and is frequent in old groves (Letouzey, 1970). Once they fall to the ground large quantities of decaying *Markhamia* flowers provide a suitable resource for drosophilids. In the Kounden plateau (1400 m) in Cameroon Lachaise (1979a) recorded that adults of *Drosophila bakoue*, *burlai*, *latifasciaeformis*, *pruinosa*, *simulans* and *triangulifer* and of *Neotanygastrella* sp. B visit these flowers, but only *bakoue* was found to breed there. Notice that no "*Bignonia*"-breeding drosophilids are true flower-breeding flies. Attention should be focused on the evolutionary significance of those drosophilids which breed in fresh flowers and those which exploit fallen ones.

The last Tubiflorale to yield adult drosophilids from its flowers is *Thunbergia* sp, a genus which is a widely cultivated plant in Africa and Asia. This lianescent plant blooms almost continuously and produces funnel-shaped flowers of five lobes in which adult *Drosophila suma* were found feeding by Graber (1957) in eastern Zaïre.

3. *African Zingiberale-breeding drosophilids*

The Zingiberales include families (Strelitziaceae, Zingiberaceae, Cannaceae, Marantaceae, Musaceae) whose fleshy flowers are among the most favourable for drosophilid breeding. The adaptive radiation of flower-breeding drosophilids on these monocots in the Neotropical region is one of the most fascinating of co-adaptations between drosophilids and flowers (Pipkin, 1964, 1966; Pipkin *et al.*, 1966; see Brncic, in Chapter 33). Referring only to Zingiberales, Pipkin *et al.* (1966) bred *Drosophila* from the flowers of 13 *Heliconia* species, 5 *Calathea*, 3 *Costus* or *Dimerocostus* and 1 *Hedychium*. These authors emphasized the occurrence of a remarkable gradient of host-specificity, and discussed its bearing on the evolutionary history of both drosophilid and host.

The African Zingiberales from whose flowers drosophilids were reared all belong to the family Zingiberaceae. The members of this family may bear compact inflorescences apically to leaf-like stems, but most usually the inflorescences grow directly from the rhizome rising in spikes or panicles which appear to emerge from the earth. The most remarkable record is the strict association of the black-winged *Zaprionus vrydaghi* and the high-stemmed inflorescences of *Costus* spp. This plant–drosophilid association is assumed to be strict since it was encountered in second-growth patches within the semi-deciduous forests of Budongo and Mabira in Uganda (Buruga, 1976), the Dimonika rainforest in Congo (Vouidibio, personal communication), the Taï rainforest in the Ivory Coast (Couturier *et al.*, 1983) and the Makokow rainforest in Gabon (Lachaise, personal communication. Moreover, this black-winged *Zaprionus*, which is constant (possibly perennial) on *C. afer* inflorescences, has so far not been found anywhere else.

In Taï, this *Zaprionus* shares this inflorescence with a flower-breeding *spinipes*-like *Drosophila*.

Couturier *et al.* (1983) showed that one fresh inflorescence can support at least several successive generations of *Zaprionus vrydaghi* owing to the long flowering duration. The compact inflorescence borne apically by a two–three meter high stem is composed of about 30–40 appressed flowers which blossom successively. The eggs are laid externally at the bottom of the immature flowers in a permanent area of decaying tissues in which larvae breed. Owing to the lack of pupae on the fresh inflorescence, pupation is suggested to occur in the soil beneath the flower. The newly emerged adult colonizes the newly blossoming flower and so forth. The mature flower is mainly a shelter and probably a feeding site for the adults.

Larval development within decaying tissues of vegetables is fundamentally different from larval development within flowers of *Hibiscus* or Tubiflorales. Another example comes from W. M. Wheeler (1942) who reported that H. von Ihering bred a neotropical species of *Drosophila* from larvae living in matter derived from the decomposition of vegetable excrescences in an internode of *Cecropia adenopus* (Moraceae). These larvae are more closely related ecologically to fruit-breeders or scavengers than to true flower-breeders.

Also noteworthy is the association of a *D. dyaramankana*-like species with this latter kind of stemless flower. Burla (1954) found adults of *D. dyaramankana* in the flowers of *Aframomum cuspidatum* in southern Ivory Coast, and Buruga and Olembo (1971) reared *D. dyaramankana* and a sibling species of *dyaramankana* in those of *A. sanguineum* in Uganda. These latter authors noticed that flowers collected in the wild forests or forest/savannah mosaic yielded only *dyaramankana*-like species while flowers obtained from cultivated areas supported additional species. Lachaise (1974) bred *dyaramankana*-like species from the fresh flowers of *Kaempferia aethiopica*, which grows at ground level in the hygrophilic gallery forests of temporary streams in the pre-forest Ivory Coast.

Occasionally adults of other *Scaptodrosophila*, e.g. *D. aterrima*, *D. lambi*, *D.* sp. aff. *mokonfim*, have been found in different *Aframomum*, *Costus*, *Kaempferia* and *Musa* (see Table II). Four *Zaprionus* species have been bred from native *Costus* flowers; Buruga and Olembo (1971) reared members of the *Z. tuberculatus* and *Z. vittiger* complexes from *C. spectabilis* Lachaise (1974) also reared a species of the *Z. vittiger* complex from the flowers of *Kaempferia aethiopica*.

4. Eucalyptus-*breeding* Drosophila flavohirta

The saligna gum *Eucalyptus grandis* (Myrtaceae) is the most commonly grown eucalypt in South Africa and the main source of honey in that country. Unnatural declines in honey production from this eucalypt have occurred since the mid-1970s resulting in detrimental economic consequences for bee-keeping. From this recognition, investigations were made in order to find which factors might have an effect on the nectar secretion. Tsacas and Johannsmeier (personal communication). These authors stress that climatic factors were not responsible for the fluctuations in honey production. By contrast, there is both circumstantial and positive evidence that the diminished honey yields were due, to a greater or lesser extent, to the presence in the flower cups of larvae of *Drosophila flavohirta* Malloch, a "rare" species of the *melanogaster* group whose geographical range was formerly restricted to Australia.

Tsacas and Johannsmeier (loc. cit.) indicate that flowers with *Drosophila* larvae contain no nectar, whereas adjacent flowers of the same inflorescence may be full of nectar if free of larvae. They therefore assume the larvae to develop on the secreted nectar within the flower cup. This probably represents the first clear evidence of a nectar feeding habit in *Drosophila* larvae. Between three to ten small larvae can be found in a single saligna flower; however, only one of them appears to develop successfully to maturity. Puparia were found either in the cup of withered flowers or adhering to the filaments.

Both young and old eucalypt trees yield larvae and adults of *D. flavohirta*. According to the localities or the periods of the year the larval infestation varies from 0 to 70% of the total number of flowers examined. Adult flies were sometimes observed in large numbers in areas where larvae were not found.

In addition to the records in Central Transvaal on *Eucalyptus grandis*, Tsacas and Johannsmeier (loc. cit.) report the occurrence of *flavohirta* larvae in the flower cup of a single *E. paniculata* flowering at the same time, and of a few adult flies sitting on a flower of *E. elata*. By contrast, no flies were found in *E. maculata* flowers. No insects are found when the flower becomes dry. Outside Central Transvaal, a very small number of adults of *flavohirta* were found on *E. cladocalyx* in the Cape Peninsula.

Though *flavohirta* has been observed to fly actively at relative low temperatures (ca. 12°C), colder temperatures probably prevent flies from breeding. In the warmest region surveyed in central Transvaal, *E. grandis* flowers early in the season. When flowering ends, weather conditions and the occurrence of potential alternative host plants are still conducive to fly breeding, accounting for the presence of a high size of the population throughout the flowering season. In the coldest region surveyed, one of grassveld planted to wattles and eucalypts, breeding seems possible only for a short period at the start of flowering. The breeding is then interrupted by low temperatures and by the lack of alternative host plants.

Regarding the Australian origin of both the host-*Eucalyptus* and *flavohirta*, Tsacas and Johannsmeier (loc. cit.) stress the interest of the finding of *flavohirta* associated with *Eucalyptus* in South Africa. Though *flavohirta* is known from only a few specimens in Australia, it is widespread and is associated with *Eucalyptus* blossom (Bock, 1976). It is worth noting that the fly body coloration, which is unique within the *melanogaster*-group, may be an adaptation to camouflage for predator avoidance, since it is almost the same color as the flowers of the *Eucalyptus* species on which it feeds (Bock, 1980). Considering that very few collections seem to have been made from *Eucalyptus* flowers in Australia, the species may not be rare in that region where it is native (Bock, personal communication).

Hence, *Drosophila* associated with *Eucalyptus* appears to show a situation which has some of the characteristics of that involving the resource-specific *D. buzzatii*, which extended its geographical range together with its host-plant, the cactus genus *Opuntia* (Carson and Wasserman, 1965). However, it is more difficult to explain how the eucalypt *Drosophila* immigration in South Africa proceeded, since *Eucalyptus* were probably not introduced as flower-cups. For the *buzzatii–Opuntia* association the colonizing process is clearer inasmuch as *buzzatii* can breed in both cladodes and fruits. Owing to the introduction of *Eucalyptus* throughout the world, *flavohirta* may likely be found in other biogeographical regions. This example illustrates the possible role of man in the actual biogeographical range of some species.

D. flavohirta is clearly closely allied to the *melanogaster* species-group (Bock, 1976). However, probably due to its adaptation to flower-breeding, *flavohirta* appears to represent a specialized offshoot of the main *melanogaster* group phylogenetic line. Though rare, the flower-breeding specialization has appeared twice within the *melanogaster*-group, since it is also known in those members of the *elegans*-subgroup living in the oriental biogeographical region. The monospecific *flavohirta*-subgroup and the *elegans*-subgroup are not particularly closely related and they represent independent adaptive events to flower breeding.

5. *Flower-breeding* Zaprionus

Flower-breeding habits have evolved within the genus *Zaprionus* as in the genus *Drosophila*. African *Zaprionus* species provide a broad array of flower-dependency, from those species which exploit decaying fallen flowers as often as any other decaying fruit (*Z. collarti*) to those which have strict flower-dependency (*Z. badyi* and *Z. vrydaghi*).

Graber (1957) reported that two endemic Cucurbitaceae, *Momordica runzorica* and *M. foetida*, live sympatrically on the slopes of volcanoes lying in the Upper Rift of central Africa. Though these species differ only slightly in their inflorescences, they are assumed, by this author, to support different flower-breeding drosophilids. *M. runzorica* is only visited by *Zaprionus momorticus* whereas *M. foetida* is only visited by *Drosophila momortica*. Both flies lay eggs within the male flowers before they wither and larval development occurs in decaying fallen flowers. Such a host-plant partitioning involving two closely related sympatric plants is very interesting and requires confirmation.

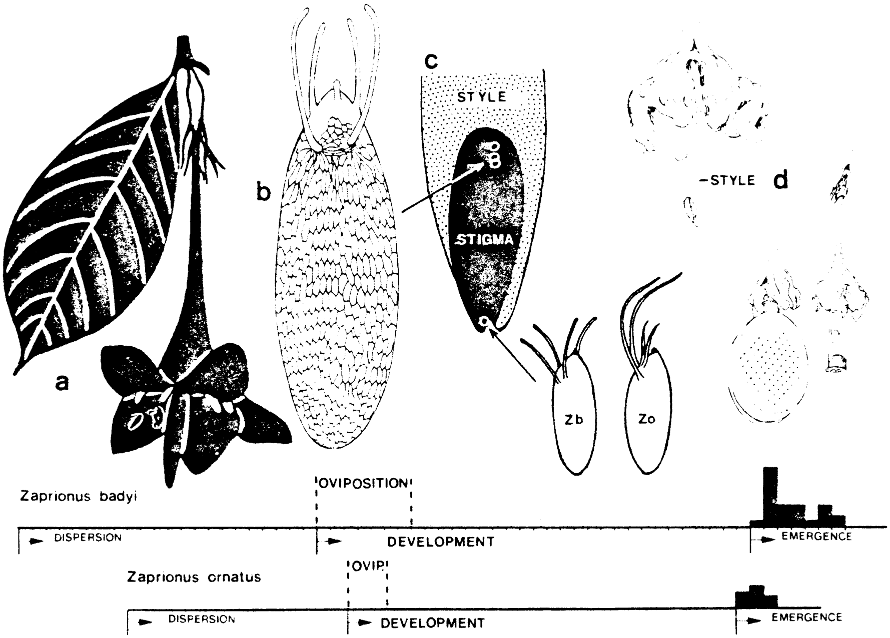


FIG. 14. Flower-breeding *Zaprionus* in the Ivory Coast. (a) Flower of *Rothmannia whitfieldii* (Rubiaceae); (b) egg of *Zaprionus badyi*; (c) eggs of *Zaprionus* on the myophilous stigma of *R. whitfieldii*; (d) drosophilid breeding methods on the tree (after Lachaise, 1979a).

Lachaise (1974) found two co-existing *Zaprionus* species, *Z. badyi* and *Z. ornatus*, simultaneously sharing the same flowers of the Rubiaceae *Rothmannia whitfieldii*. This small tree lives in the riparian semi-deciduous gallery forest of the Bandama river in the pre-forest areas of the Ivory Coast. Flowering occurs from February to April, and the plant is easily located by its heavy, fruity fragrance. The large flowers are solitary on short stalks at the ends of the branchlets (Fig. 13d). Each has a tubular calyx covered with rusty-brown hairs and five narrow lobes, a trumpet-shaped corolla with five lobes, and a massive, club-shaped hanging style with apical stigmas. Both

Zaprionus breed in the fleshy style on the living flower (Fig. 14). Eggs are not laid in any place on the style but accurately on the apical stigmas (Fig. 13c). In view of the relative lengths of the sexual immaturity time in adult females (Fig. 14) *Z. badyi* is expected to be more specialized than *Z. ornatus*, inasmuch as extrapolation can be made from what was known from fig-breeding drosophilids. (In Lachaise's former paper *Z. ornatus* was not distinguished from the sibling species of the *Z. vittiger* complex.) This assumption of different degrees of specialization has some confirmation: *Z. badyi* has also been reared from the flower of the Amaryllidaceae *Crinum sanderianum* in swampy areas of the Nimba mount bottom (Lachaise, 1979a). It appears, therefore, as a strict flower-breeding *Zaprionus*. In contrast, *Z. ornatus* was shown (Table II) to breed also in fruits (*Ficus*, *Spondias*, *Polyalthia*, *Staudtia*, *Gambeya* and *Cissus*).

Moreover, characteristics of the eggs support this assumption: those of *Z. badyi* have four short filaments as also found by Graber (1957) in the flower-breeding *Z. momorticus*. By contrast, the eggs of *Z. ornatus* have four long filaments, as do other fruit-breeding *Zaprionus*.

Though *Zaprionus* larvae were only seen feeding on the stigma, they may exploit the entire massive style, inasmuch as they are able to feed on the plant tissues. If such is the case, the style of *Rothmannia* provides a large amount of a relatively long-lived food supply. This may then support the larval growth of two *Zaprionus* species in so far as both species lay few eggs on the same stigma. However, since *Z. badyi* was shown to breed in fresh flowers and *Z. ornatus* in decaying fruits and fallen flowers, the overlapping oviposition period observed might also be part of an ecological succession whose early stages (fresh flowers on the tree) are exploited by *Z. badyi* and whose late stages (withering flowers on the tree and fallen flowers) are exploited by *Z. ornatus*.

In the evergreen rainforest of Taï *Zaprionus neglectus* breeds frequently in February in the flowers of *Rothmannia whitfieldii* (Couturier *et al.*, 1983). Twenty eggs of *Zaprionus* were counted on a single style, all of them located in the gelatinous stigma where the larvae are also found. In addition, *Drosophila ananassae* was bred from more ripened styles of this plant.

In Taï *Zaprionus neglectus* also breeds frequently within the flowers of *Crinum jagus* (Amaryllidaceae) which grows abundantly in swampy areas. The eggs are laid on the base of the staminate peduncles and on the base of the corolla (Couturier *et al.*, loc. cit.).

6. *Host-flower specificity and reproductive strategies*

Except for *Zaprionus vrydaghi*, strictly associated with high-stemmed *Costus*, no relatively strict host-flower "specificity" has definitely been proved to occur among African flower-breeding drosophilids, since the association of one fly species to one flower genus or species is inconclusive from the few available records. Those species which are obligatory flower-breeders, e.g. the *aterrima* species complex and *Z. badyi*, certainly use several host-plant genera. Moreover, most records from flowers involve fly species (see Table II) which exploit decaying fallen flowers opportunistically. Hence, most African flower-breeding drosophilids are polyphagous, depending upon a broad array of host-plants. Host-specificity cannot evolve in host-plants with short blossoming periods. Predictability is a consequence of repeatability, and continuous blossoming is the first condition of host-specificity.

Kambysellis and Heed (1971) described the highly diverse female reproductive systems of the Hawaiian drosophilids stressing the causal factors operating to adjust reproductive rates in various environments. They convincingly showed that the flower niche supports species with a low reproductive potential in contrast to the stem niche or leaf niche and discussed how the reproductive physiology of the various species had been adapted to the carrying capacity of these niches. Kambysellis and Heed's conclusions have been supported by all subsequent work and are consistent with the scattered observations dealing with flower-breeding drosophilids, not only in Africa, but in every other region of the world [see Wheeler *et al.*, 1962; Brncic, 1966 (in Chile); Pipkin *et al.*, 1966 (in Panama, Colombia and Trinidad); Okada, 1975 (in Java and Taiwan); Cook *et al.*, 1977 (in Australia); Hunter, 1979 (in Colombia); Burla, 1954; Lachaise, 1979c; and David and Vouidibio, personal communication (in Africa)].

Flower-breeding drosophilids have in common a low reproductive potential, few ovarioles, few concurrent mature eggs, and they lay few eggs on the same flower. Owing to the low carrying capacity and the poor nutrient value of flowers as a larval food resource, such a reproductive strategy appears highly adapted to exploitation of flowers.

Contrary to the assumptions of Pipkin (1964) and Hunter (1979), a lack of filaments in eggs cannot be used as a phylogenetic characteristic. Indeed, on the contrary, the absence of filaments has been proved to be an adaptive characteristic associated with oviposition in flowers, such that this characteristic has evolved in flower-breeding drosophilids of three genera (*Drosophila*, *Drosophilella*, *Scaptomyza*) and in three subgenera of *Drosophila* (*Drosophila*, *Phloridosa*, *Scaptodrosophila*). As a corollary, all species belonging to these taxa which are not associated with flowers for reproduction have filament-bearing eggs. Furthermore, closely related species may have very different egg filament patterns consequent on the type of breeding-site used. For instance in African species of the subgenus *Scaptodrosophila*, the egg of the flower-breeding *aterrima* is filament-less, while that of the fruit-breeding *latifasciaeformis* has six filaments.

This allows for a prediction of breeding site from egg filament structure (see the discussion in Lachaise, 1979c). Since egg filaments have a respiratory function (Hinton, 1959, 1969), they appear to be only necessary in those eggs which are laid in oxygen poor media, such as fermenting fruit or sap. In contrast, for those eggs which are simply laid on the surface of flowers, respiratory exchanges can occur through the chorion of the body of the egg and filaments are unnecessary. Further evidence for the adaptive nature of egg filaments can be found in the eggs of species with intermediate ovipositing behavior. For example, though being strict flower-breeders, females of the African species *Zaprionus badyi* lay their eggs in the fleshy style of *Rothmannia*. That the eggs are partly submerged in this medium, may account for the occurrence of four short-filaments. Short egg filaments can be found in other strict African flower-breeding *Zaprionus* such as *Z. momorticus*. All fruit-breeding *Zaprionus* have eggs with four long filaments.

Notice, however, that Pipkin *et al.* (1966) also provide strong arguments supporting the adaptive nature of egg filaments. Like Kambysellis and Heed (1971) they showed that flower-breeding flies may be ovoviviparous and stressed that filaments are not then needed. Paradoxically, still further evidence can be found in the long egg filaments of the neotropical flower-breeding *D. mcclintockae* and in the oar-shaped filaments of *D. hansoni*. Pipkin *et al.* (loc. cit.) showed that these provide a mechanism for the attachment of the egg to the floral hairs of the host-plants.

7. *Co-adaptation of flowers and pollinating drosophilids*

So far there has been little attention given to the role of flower-feeding drosophilids in pollination ecology. However, this aspect of flower–fly association has evolutionary implications for plant–drosophilid co-adaptations in the tropics.

Free (1970) reported that drosophilids may be effective in the pollination of certain field crops such as guayale, the composite *Parthenium argentatum*. In New Guinea, Essig (1973) assumed that pollination of *Nypa* palm-tree flowers was due to drosophilids which use the *Nypa* inflorescences as feeding–breeding sites. In Cameroon De Miré (1971) emphasized a relationship between the fruiting rate and the frequency of visiting cacao flowers by *Drosophila*, ceratopogonids and ants. In this study, one *Scaptodrosophila*, *D. triangulifer*, was assumed to have carried out about 43% of the fertilizations. In cacao plantations in the vicinity of Yaoundé in Cameroon, Massaux *et al.* (1976) showed that many drosophilids (*Drosophila bocqueti*, *D. eoundo*, *D. lambi*, *Zaprionus armatus*, *Z. ghesquierei*, *Z. tuberculatus*) had pollen-bearing teguments (see the mean number of pollen grains borne per fly in Table III). Since it is usually assumed that about 35 pollen grains are required to ensure cacao-flower fertilization all the drosophilids mentioned above are potential pollinators. Drosophilids were shown to have more cacao pollen than all other insects except aphids. The pollination efficiency of these drosophilids would be related to morphological structures favoring pollen transport and to their permanent presence in cacao-plantations the year round. According to Massaux *et al.* (loc. cit.) their larvae would live in leaf mould, cacao-pods and decaying wood; however, except for cacao-pods, these breeding sites appear somewhat speculative.

TABLE III. Amount of cacao pollen grains carried per fly (after Massaux *et al.*, 1976)

	Samples	Mean	% of Variation Coefficient
Drosophila bocqueti	9	63·0	20
Zaprionus spp.	9	62·3	62
Drosophila lambi	9	55·8	32
Drosophila eoundo	9	49·5	22
Drosophila sp.	2	46·5	4
Drosophila sp.	2	36·0	31
Drosophila sp.	3	32·0	36
Drosophila triangulifer	9	19·8	49

None of the cases reported above suggest a specific adaptation of the plant for pollination by drosophilids comparable to what occurs in Asclepiadaceae flowers living in South Africa (Agnew, 1976). This author reported an exciting case of co-adaptation between the myophilous small, leafless xerophytic Stapeliad *Caralluma schweinfurthii* and certain species of pollinating drosophilids. The plant is a small, jointed, procumbent perennial consisting of soft fleshy stems growing up to 5 or 6 cm above the soil. Though the fly–plant interraction has been studied under semi-natural conditions, it should be pointed out that the plant species and the pollinating drosophilids are widely distributed in central and south-central Africa.

Five species of *Drosophila* (*D. immigrans*, *melanogaster*, *simulans*, *punctatonervosa*, and the *Drosophila repleta* species group) and two species of *Zaprionus* (*Z. tuberculatus* and *Z. collarti*) were deceptively attracted to the stapeliad flowers, which chemically mimic the natural breeding substrate. Then, Agnew (loc. cit.) reported the first instance of myophily involving drosophilids. According to Faegri and van der Pijl (1966), myophilous flowers are those which are adapted for pollination by flies and exhibit a complex of characteristics associated with this adaptation. *Caralluma* Stapeliads were shown by Agnew (1976) to provide the syndrome of myophily: (a) chemical mimicry of the drosophilid breeding substrate; (b) positive attraction of potential pollinators; (c) capture of four different species (*immigrans*, *melanogaster*, *simulans*, *collarti*) carrying pollinia; (d) features of the flower indicative of myophily; and (e) correspondence between flowering time and peak drosophilid activity.

Drosophilids were efficiently attracted at dawn and dusk to the flowers, which emitted a strong odor of over-ripe fruit. No insects other than drosophilids were observed to be attracted to the flower. There was no differential attraction between the sexes of the visitors, and both males and females appeared to be equally capable of acting as carriers of pollinia. Attachment of the pollinaria (pollinia plus associated structures) to the proboscis of the fly takes place while the fly is tapping with the proboscis on the corona. In one case, two pairs of pollinia were attached to a single fly. None of the captured specimens with pollinia had them attached anywhere but on the proboscis, where the corpusculum and retinacula (or translator arms) were affixed to the shaft of the proboscis.

Actual pollination (that is, release of the pollinia) was not observed. Agnew (loc. cit.) suggested that there must be a time delay between picking up the pollinia and their release in order to minimize the likelihood of self-pollination. He concluded that his observations do not necessarily establish that any or all of the visitors are the actual pollinators where the plant grows naturally. The fact that several drosophilid species can pick up pollinia support the viewpoint that the stapeliad plant may be adapted, not to a specific pollinator, but to a group of similar sized or closely related species. In contrast to *Drosophila immigrans*, *melanogaster* and *simulans*, most *Zaprionus* species are restricted to Africa and may well be effective pollinators in the wild.

This expectation of Agnew is supported by similar observations of many pollinia-laden *Zaprionus* in the riparian semi-deciduous forest of Lamto and in the evergreen rainforest of Taï (Lachaise, 1979a). Further, in the lowland evergreen rainforest of Kumba in southwestern Cameroon, Lachaise (personal communication) collected five *Zaprionus* specimens (four *Z. collarti* and one *Z. tuberculatus*) all carrying one pollinia on the side of the abdomen on the second, third or fourth segment.

Agnew (1976) stressed that while drosophilids are deceived into investigating the stapeliad flowers, oviposition does not take place. Hence, wastage of eggs does not occur and thus the deception is not counter-selective to responsive insects. This suggests that the co-adaptation is a long standing one.

Lachaise (1979a) argued that a second example of a myophilous-plant was the Rubiaceae *Rothmannia whitfieldii* in whose style two co-existing *Zaprionus* species breed in the Ivory Coast. It was mentioned above that the *Zaprionus* eggs were not laid in any place on the style but in the apical stigma. In contrast to the major part of the style, the stigma is gelatinous in appearance and consistency and has strong similarities to fermentative fruit-tissues (Fig. 13c). Furthermore, the swollen portion of the style clearly sticks out of the corolla, making the sigma fully apparent. The hanging habit of the flower may allow the corolla to be protected without hiding the stigma. These structures strongly evoke adaptations evolved to attract drosophilids, which could thereby be involved in the pollinating process. Further evidence is needed to prove this.

C. FUNGUS-BREEDERS

Adaptive radiations on fungi have occurred twice in tropical Africa at the generic level: *Leucophenga* and *Mycodrosophila* are both unequivocally fungus-associated genera, even though some *Leucophenga* are known to breed in cercopid spittle-masses (see below). Both of these genera are world-wide in their distribution, though predominant in the tropics, and include fungus-breeding species in every biogeographical region (Heed, 1957; Throckmorton, 1975; Bock and Parsons, Chapter 7, Volume 3a).

Lepesme (1947, quoting Ghesquière) reported that *Leucophenga proxima* was bred from *Ganoderma* parasitizing the oil-palm tree *Elaeis guineensis* in Zaïre. *L. proxima* was also reared from unidentified fungi in Zaïre by Collart (1939), in the Lamto pre-forest savannahs of the Ivory Coast by Lachaise (1979a) and in the rainforest of Taï in the southwestern Ivory Coast by Couturier *et al.* (1983). Several unidentified *Leucophenga* species were bred from *Favolus* and *Polyporus* in Uganda by Buruga and Olembo (1971). From unidentified fungi growing in riparian gallery forests in Lamto 114 individuals of *Leucophenga buxtoni* were bred (Lachaise, 1979a) while 585 individuals of *L. perargentata* were bred from a cluster of fungi on felled tree trunks in the rainforest of Taï (Couturier *et al.*, loc. cit.). The density of fungus-breeding *Leucophenga* larvae appears strikingly high with respect to the amount of available food. The ratio of the biomass of *Leucophenga parargentata* produced on the biomass of resource shared is probably the largest known for drosophilids in tropical Africa.

Furthermore, in the rainforest of Banco, in the southern Ivory Coast, Burla (1954) collected adults of *Leucophenga guro*, *L. halteropunctata* Duda, *L. proxima*, *L. sema* and *L. subvittata* on fungi on felled tree trunks. In riparian forest galleries of Lamto, Lachaise (1975, 1979a) observed that *Leucophenga proxima* and *L. buxtoni* occupy, all the year round, the undersides of the leaves of the underwood Graminaceae *Streptogyna* *gerontogaea* and *Olyra latifolia*. Since both species have been shown to breed in fungi, and not on grasses, this may indicate a lek behavior resembling that observed by Spieth (1968, 1973) in Hawaii, and Parsons (1977a) and Parsons and Bock (1976, 1977) in Australia.

Adults of *Leucophenga* have occasionally been found feeding on sap exudation in Japan (Okada, 1962) and Africa (Lachaise, 1975). Moreover, Okada (loc. cit.) described for *Leucophenga* and *Amiota* a special habit of flying which appears to be adapted to their feeding and resting on vertical tree trunks. Accordingly it can be concluded that the breeding and adult feeding sites of *Leucophenga* are separated, in contrast to other tropical African drosophilids.

Mycodrosophila appear to form a more biologically homogeneous genus than *Leucophenga*, though little attention has been paid to them in Africa. However, species of *Mycodrosophila* show strong evidence of being narrowly restricted to fungi for reproduction and feeding. Although there are few published records, it is rare to find soft fungi in tropical Africa without *Mycodrosophila*.

Buruga and Olembo (1971) reared *Mycodrosophila ditan*, *M.* aff. *ditan*, *M. fracticosta*, *M. nigerrima*, and a species near *M. nigerrima* from *Polyporus* in Uganda. Burla (1954) caught five *Mycodrosophila* species, *M. adyala*, *M. atie*, *M. fracticosta*, *M. gaku* and *M. kabakolo*, which were feeding on fungi in the rainforest of Banco in the southern Ivory Coast. In the evergreen rainforest of Taï in the same country, Couturier *et al.* (1983) caught three species of *Mycodrosophila* in the same conditions.

Within the genus *Drosophila* few African species use fungi widely as larval food supply except, perhaps, the subgenus *Hirtodrosophila*, in contrast to the situation in the palearctic region (Shorrocks, Chapter 18, Volume 3b; Shorrocks and Charlesworth, 1980). Burla (1954) recorded *D. akabo*, *D. sanyi* and *D. vina* on fungi on felled trees in the Banco rainforest, and Buruga and Olembo (1971) reared a species near *D. akabo* from *Favolus* in Uganda. Those *Drosophila* species which utilize soft fungi as breeding sites and the undersides of bracket fungi as lek territories in Australian rainforests also belong to the subgenus *Hirtodrosophila* (Parsons, 1977a,b; Parsons and Bock, 1976, 1977). Indeed, the majority of Australian *Hirtodrosophila* species have been collected in the vicinity of soft fungi (Parsons, personal communication).

D. LEAF MINERS AND STEM BORERS

Drosophilids that use leaves as a larval food source are rare in tropical Africa, in contrast to the situation in Hawaii (Montgomery, 1975). Nevertheless, two species of *Gitona* were found to be leaf miners and stem borers of Phytolaccaceae, a family closely related to Caryophyllaceae and Chenopodiaceae, in both continental eastern Africa and Madagascar. Séguy (1951) reported the occurrence of *Gitona pauliani*, whose larvae mine the leaves of the Endod plant *Phytolacca dodecandra* (reported as *P. abyssinica*) in Madagascar. Tsacas and Teshome (1981) found that the larvae of *G. pauliani* and a second species, *G. ethiopica*, mine the soft stems and leaves of *Phytolacca dodecandra* in Ethiopia. *P. dodecandra* is a dioecious liane living in post-farming bush in peri-forest savannahs, and is widespread in tropical and South Africa and in Madagascar (Letouzey, 1970). Tsacas and Tshome (loc. cit.) suggested that the geographical range of *G. pauliani* matches that of *P. dodecandra*. *Gitona pauliani* is therefore expected to be found in West Africa.

Phytolacca dodecandra is of interest as a host-plant for drosophilids due to the high rate of saponins yielded by its fruits and, probably, also its leaves (Rodriguez and Levin, 1976; Harborne, 1977). Saponins are a group of non-nitrogenous terpenoid toxins which act as repellents or feeding deterrents for many insects (e.g. Scarabaeoidea), molluscs and fishes (Rodriguez and Levin, loc. cit. and references therein). The metabolic effects of saponins on phytophagous insects have been postulated to be the result of inhibited sterol assimilation or proteinase inhibition (Beck and Reese, 1976 and references therein).

Evidence of such adaptation to saponin poisoning is also shown in the behavior of *Zaprionus tuberculatus* (or a closely related species of the *tuberculatus* species complex) whose larvae feed on the fruits of *Phytolacca dodecandra* in the Buto forest in Uganda (Buruga and Olembo, 1971; Buruga, 1976). The attention of pathobiologists has been focused, in Ethiopia, on leaf-mining *Gitona* because of an indirect implication in the extension of bilharzia. Aklilu Lemma (1970) stressed the strikingly high molluscicidal potency of the fruits of the Endod plant (*Phytolacca dodecandra*) which, therefore, represents a potential means of reducing or even eradicating Schistosomiasis, a human disease that is endemic to Ethiopia. These plants are used to suppress the populations of snails which are the intermediary hosts of the Trematode *Schistosoma*. Ghiday (1971) reported that "future plans for developing the Awash Valley of Ethiopia, include a far-reaching snail control programme for preventing the spread of Schistosomiasis. Therefore, it was considered important to investigate the possibility of mass producing Endod for self-help molluscicidal purposes. Because *Gitona* species seriously attack *Phytolacca dodecandra* they are of grave concern in the struggle against schistosomiasis. Accordingly, the control of bilharzia requires elimination of *Phytolacca*-dependent *Gitona*. A good knowledge of the life-histories of *Gitona* species is therefore needed. Thus, Ghiday (1971) made a preliminary study of the pre-imaginal stages of the "Endod fly" (egg, larva and pupa) which develop on or within the plant stem.

The extension of the range of *Gitona pauliani* was, presumably, coincident with the spread of its host plant from a centre in East Africa.

The larval habit of *Gitona pauliani* is somewhat similar to that of the Palearctic leaf mining *Scaptomyza*. These species are known to mine the leaves of many genera belonging to such families as Amarantaceae and Salsolaceae which are, anatomically, also closely related to Phytolaccaceae (Séguy, 1951).

Nothing is known in Africa regarding the larval habits of species of *Scaptomyza*. However, it can be pointed out that adults of *Scaptomyza* (*Scaptomyza*) *santahelenica* were caught on *Senecio prenanthiflora* in Saint Helena Island (Tsacas and Cogan, 1976). In this connection, it can be reported here that *Drosophila altissima*, a species of montane *dentissima* group, was found on *Senecio brassiciaeformis* (or *S. aberdarica*) on Mount Kinangop in Kenya (Tsacas, 1980). This species, which has been found as high as 3961 meters, is the highest drosophilid in the world.

In the high volcanic mountains of Bafut Nguemba (Western Cameroon) the sub-montane forest gives place to a grazing-meadow with *Lobelia* and *Helichrysum* above 2000 meters and then, at 2400 meters, to an ungrazed grass area with dense cover of *Geniosporum rotundifolium*. This Labiaceae supports an abundant population of adult *Scaptomyza*, e.g. 187 individuals were caught on less than 20 square meters (Tsacas and Lachaise, personal communication).

E. Decaying Trunk, Branch and Tuberculous Root Breeders

Nothing exists in tropical Africa similar to the remarkable adaptive radiation on decaying fibrous bark, layered wood or parenchymatous stems that has occurred in the picture-winged *Drosophila* living in Hawaii (Heed, 1968, 1971; Montgomery, 1975). This may be accounted for by a much greater amount of fruit available as a larval resource in Africa, in contrast to Hawaii. Owing to the high productivity, predictability and superior nutritive value of fruits, in comparison to any kind of wood larval resource, such an adaptive radiation had little opportunity to evolve in Africa.

Despite these considerations a few species have been found to utilize a woody resource in tropical Africa. Thus, *Zaprionus ghesquierei* in Zaïre (Ghesquière, in litt., in Lepesme, 1947), and *Z. inermis* and *Drosophila saba*, a species of the subgenus *Scaptodrosophila*, in the Congo (Vouidibio, personal communication) were shown to breed occasionally in decaying trunks of cut oil palm trees *Elaeis guineenis*. Also, Collart (1937a) mentioned that adults of *Z. armatus* and *Z. collarti* were found on decaying trunks of *Ficus* in Zaïre, but larvae were not recorded. It is noteworthy that all of these five species have also been reared from fruits.

Of greater interest are the sibling species *Drosophila iri* and *D. fraburu* which mainly breed in retted tuberculous roots of the manioc *Manihot esculenta* (Euphorbiaceae). This has been observed in several localities in the Congo by Vouidibio (1977). Manioc has tuberculous roots which are used as a major food source by the local people. However, these tubercules contain hydrocyanic acid and they require retting to be edible. Once softened and skinless, the manioc wastes make a suitable and highly nutritive larval food supply for drosophilids.

In addition three other species (*D. melanogaster*, *D. malerkotliana* and *D. nasuta*) have been reared from retted manioc by Vouidibio (loc. cit.).

Retting occurs in man-made ponds which are usually connected with the stream. *D. iri* has been reared from a number of substrates that have been partially immersed in water, for example infrutescences of *Elaeis* and *Pandanus* (Lachaise, 1979a; Rio *et al.*, 1983). In the western Ivory Coast, Rio *et al.* (1983) reared large numbers of *D. iri* from partially immersed infrutescences of *Pandanus candelabrum*. In this region, the screw-pine population grows in an area liable to flooding. In forested mountains in the vicinity of Yaoundé (Cameroon) *D. iri* was only swept above temporary streams flowing through the dark underwood (Tsacas *et al.*, 1981). Likewise, Tsacas and David (personal communication) recorded *D. iri* in the Seychelles on the fruits of a Jaquier (*Artocarpus* sp., Moraceae) which were partially immersed by a coastal stream.

Thus, *Drosophila iri* shows a strong habitat preference for water-dependent resources (and shelters), as has been shown for some Japanese species by Beppu (1979). Tsacas and Legrand (1979) suggest that the larval habit of species like *D. iri* may have been the first step within the evolutionary pathway that led to an aquatic larval life and predation, as occurs in the *simulivora* group.

F. COMMENSAL BREEDERS WITHIN CERCOPID SPITTLE MASSES

Though most African and Malagassy *Leucophenga* species are clearly fungus breeders, three of them show the remarkable larval habit of developing in the spittle-masses of spittle-bug nymphs. These are Homoptera of the family Cercopidae which suck the sap of the plant. The froth which surrounds the nymphs is produced by the nymphs themselves by forcing air into a fluid exuded from the anus. The foamy secretion is widely assumed to protect the cercopid nymphs from dessication and may also afford them some degree of protection from predators. Hence, cercopid associated *Leucophenga* larvae may be similarly protected.

In Madagascar, larvae of *Leucophenga decaryi* (reported as *Ptyelusimyia decaryi*), develop in the excreta produced by the cercopid *Ptyelus goudoti*, which grows on *Mimosa delicatula* (Séguy, 1932). In Uganda, a *Leucophenga* species close to *L. sema* breeds within the abundant frothy fluid secreted by *Ptyelus flavescens*, which uses the Leguminosae tree *Milletia dura* (Odhiambo, 1958). In Nigeria larvae of *Leucophenga proxima* live in spittle masses of *Ptyelus grossus* (Fig. 13e) on stems of pigeon pea, *Cajanus cajan* and *Spathodea campanulata* or in spittle masses of *Poophilus adustus* on the Compositae *Aspilia africana* (Medler and Adenuga, 1969).

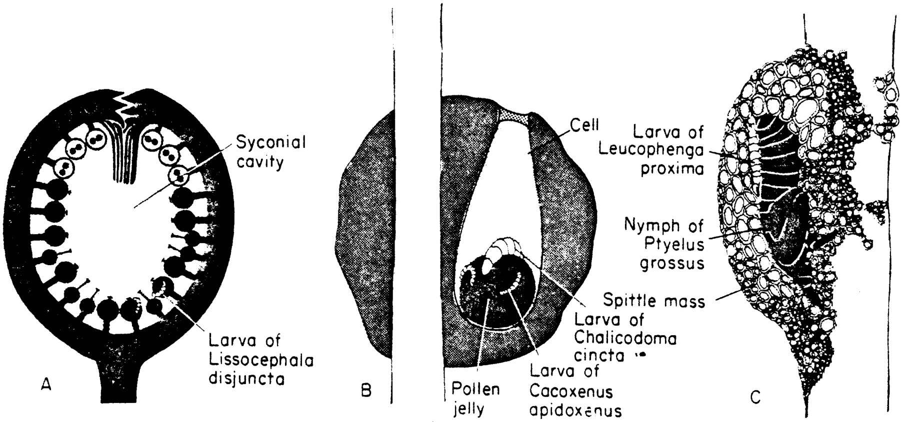


FIG. 15. Three examples of protected breeding-sites used by specialist drosophilids in tropical Africa. (A) *Lissocephala disjuncta* breeding within the closed fig cavity of *Ficus sur*; (B) *Cacoxenus apidoxenus* breeding within the solitary bee nest of *Chalicodoma cincta*; (C) *Leucophenga proxima* breeding within the spittle mass of the cercopid *Ptyelus grossus*.

The association with cercopid nymphs has evolved at least three times in Africa within the genus *Leucophenga* (Fig. 15). It is noteworthy that the commensal cercopids are mainly *Ptyelus* exploiting Leguminosae. The African and Malagassy *Ptyelus* species are gregarious spittle bugs, i.e. a coalescence of the individual spittle masses making a frothy muff around the plant stems. These large foamy masses drip unceasingly to such a degree that puddles of water occur at the foot of the plants (Fig. 13e). By associating with these gregarious spittle bug nymphs, rather than with solitary species, *Leucophenga* larvae are protected against dessication when a cercopid nymph moves to a new feeding place on the plant.

A similar ecological adaptation to the spittle masses of cercopids has also occurred in the New World (Ainslie, 1906; Lamb, 1919; Baerg, 1920; Williams, 1923, 1931; Clausen, 1940; Wheeler, 1952; Bennett, 1965). There, three species of the neotropical and nearctic genus *Clastopteromyia* use the same larval habitat. Their commensal cercopids all belong to the genus *Clastoptera* (see Ashburner, Chapter 10, Volume 3a, for more detailed information).

Such an adaptive convergence in both the new and old world is an example of "ecological equivalence": "the products of convergent evolution, organisms that have evolved independently and yet occupy roughly similar niches in various communities in different parts of the world" (Pianka, 1974). Both *Leucophenga proxima* (Medler, and Adenuga, 1969) and *Cladochaeta inversa* larvae (Wheeler, 1952) show hook bearing ventral pseudo-legs, which favor attachment to the spittle bug nymph when it is moving. These morphological adaptations are not seen in fungus-breeding *Leucophenga*. Such a similar phenotypic response provides evidence that it is an evolutionary convergence *per se*. *Leucophenga* and *Clastopteromyia* evolving independently of one another under similar environmental conditions have responded to similar selective pressures with nearly identical adaptations.

It is difficult to conceive that a species has evolved a morphological differentiation in relation to a peculiar type of breeding site which would be used only occasionally. *Leucophenga proxima* is clearly a fungus-breeder (see above) and the specific identification of this species in cercopid spittle masses must remain in doubt, especially as it predates Bächli's (1971) thorough revision of African *Leucophenga*.

The demographic implications of this larval habit are not known. Bennett (1965) recorded that the larval development of *Clastopteromyia* was completed in 18–20 days and the pupal stage in about 8–9 days. This development time would thus last about one month. This is exceptionally long and might be due to the very low nutritive value of the spittle.

G. COMMENSAL BREEDERS WITHIN SOLITARY BEE NESTS

Tsacas and Desmier (1976) found in Senegal, in the Ivory Coast and in Cameroon one species of *Cacoxenus* (subgenus *Gitonides*), *C. apidoxenus*, which lives in a close commensal association within the arboreal nests of solitary bees (Fig. 15). This life history is strikingly similar to that of the palearctic *Cacoxenus (Cacoxenus) indagator* (Séguy, 1934, 1950; see chapter 10 by Ashburner in volume 3a for details). The solitary bees supporting development of *Cacoxenus apidoxenus* in West Africa belong to two subgenera of *Chalicodoma*: the subgenus *Callomegachile* with *C. mephistolica* in Senegal and *C. kamerunensis* in Cameroon; and the subgenus *Gronoceras* with *C. cincta cincta* in the Ivory Coast and in Cameroon.

Cacoxenus apidoxenus appears to be associated with the entire genus *Chalicodoma*, a genus whose species are either mason or resin bees. The aerial mud-nests consist of one or several cells in which the *Chalicodoma* bees store a mixture of pollen and nectar. The eggs of *C. apidoxenus* are laid either on this pollen jelly or on the walls of the cell before it is closed. The drosophilid larvae are assumed to feed on the pollen jelly *per se* and to be commensals of, rather than predators of, the bee larvae.

Although nothing is known of the demographic strategies of these bee-dependent drosophilids, it is to be expected that their reproductive effort is greatly delayed (in order to allow ovipositing females to discover unclosed solitary bee-nests), that their fecundity is low and that they lay eggs in several bee nests. Tsacas and Desmier (1976) pointed out that the bee-nests transported to France yielded only four to five *Cacoxenus* adults per cell.

Tsacas and Desmier (loc. cit.) and Tsacas *et al.* (Chapter 5, Volume 3a). emphasize that if adults of *Cacoxenus* are able to tolerate such different climatic conditions as those that occur in the Sahel and in the rainforests, then their pre-adult stages must develop under remarkably constant conditions. An adaptive strategy involving a metabolic cost can have evolved only insofar as the individual fitness of the progeny is thereby greatly enhanced. Once inside the closed bee-nest the few drosophilid larvae find an excess of food and efficient shelter. *Cacoxenus* larvae then have broken away from intraspecific competition, predation risk and environmental instability. The wide geographic range of *C. apidoxenus*, coincident with that of its host, stresses the success of such an adaptive strategy.

H. PREDATORS OF HOMOPTERA

Many Homoptera secrete honey-dew which renders them attractive for ovipositing females of drosophilids and suitable as a food source for their predaceous larvae.

Adults of *Leucophenga proxima* and of *Zaprionus* belonging to both the *vittiger* species complex and the *tuberculatus* species complex have been caught while visiting honey-dew produced by colonies of the coccid *Leucanium africanum*, which use *Coffea* as a host-plant in Zaïre (Collart, 1937a and 1939). One adult of L. proxima was also recorded on honey-dew secreted by Leucaninae developing on *Cassia siamea* in Zaïre (Collart, 1939). There is no evidence that either *Zaprionus* or *Leucophenga* are able to oviposit and breed within the sugary secretion of Homoptera.

In contrast the subgenus *Gitonides* of the genus *Cacoxenus* widely exploits the colonies of scale insects or mealy bugs as breeding sites in the pantropical region (see Ashburner, Chapter 10, Volume 3a). The mealy bugs of the family Pseudococcidae are among the least specialized of the superfamily Coccoidea and cause damage to a wide variety of plants. These coccids are easily transported on plant material and this accounts for the world-wide distribution of species such as *Saccharicoccus sacchari*. The larvae of the drosophilid *Cacoxenus (Gitonides) perspicax*, which predate this mealy bug have spread with its coccid-prey in Africa, Asia, New Guinea, North-eastern Australia and Hawaii (Tsacas and Desmier, 1976).

In Africa *Cacoxenus perspicax* breeds on the pseudococcid *Saccharicoccus sacchari* in Somalia (Séguy, 1933), Mauritius Island (Box, 1953; David and Tsacas, 1975) and Reunion Island (David and Tsacas, 1975). Other pseudococcids are also used as prey by *C. perspicax*, e.g. *Pseudococcus filamentosus* in Zaïre (Ghesquière, 1934), *Pseudococcus brevipes* (Moutia and Mamet, 1946) and *Dysmicoccus boninsis* (Box, 1953) both colonizing pineapples (*Ananas comosus*) in Mauritius and *Planococcus citri* damaging rose-laurel (*Nerium oleander*) in Reunion Island (Etienne, personal communication).

Another member of the *Gitonides* subgenus, *Cacoxenus frontalis* has larvae which predate *Aspidoproctus bouvieri* in Zaïre (Collart, 1935). This scale-insect, which grows on *Cassia siamea*, belongs to the Margarotidae, another family of Coccoidea which produces waxy secretions.

An undescribed species of *Amiota* whose larvae predate *Saccharicoccus sacchari* on sugar cane in Reunion Island has been found by Etienne (personal communication). Etienne discovered that this *Amiota* species also predates Delphacidae, such as *Perkinsiella saccharicida* colonizing sugar cane and *Peregrinus maidis* colonizing maize in Reunion Island. These Delphacidae are Fulgoroidea pests which greatly damage sugar food crops in the tropics. *Perkinsiella* is a vector of the "Fidji virosis" and the *Amiota* species could possibly be used, in addition to mirid bugs and mymarid wasps, for the biological control of these pests. Tsacas (personal communication) has noticed *Amiota* species visiting sugar cane in the Upper Volta, but the larval habitat is unknown.

I. AQUATIC LIFE AND PREDATION IN THE *SIMULIVORA* GROUP SPECIES

The *simulivora* species group (Tsacas and Disney, 1974) includes seven closely related tropical African species: *Drosophila gibbinsi*, *D. cogani*, *D. simulivora*, *D. libellulosa* and three still undescribed new species from East Africa (Tsacas, personal communication). The main feature of the life history of this group is the adaptation of their larvae to an aquatic life (Fig. 16).

Of the seven species one, *D. libellulosa*, lives in a very peculiar aquatic environment—the egg-mass of a dragonfly species (Tsacas and Legrand, 1979). In contrast, the six other species live in running water (Smart, 1937; Tsacas and Disney, 1974; Gouteux, 1976; Tsacas, personal communication).

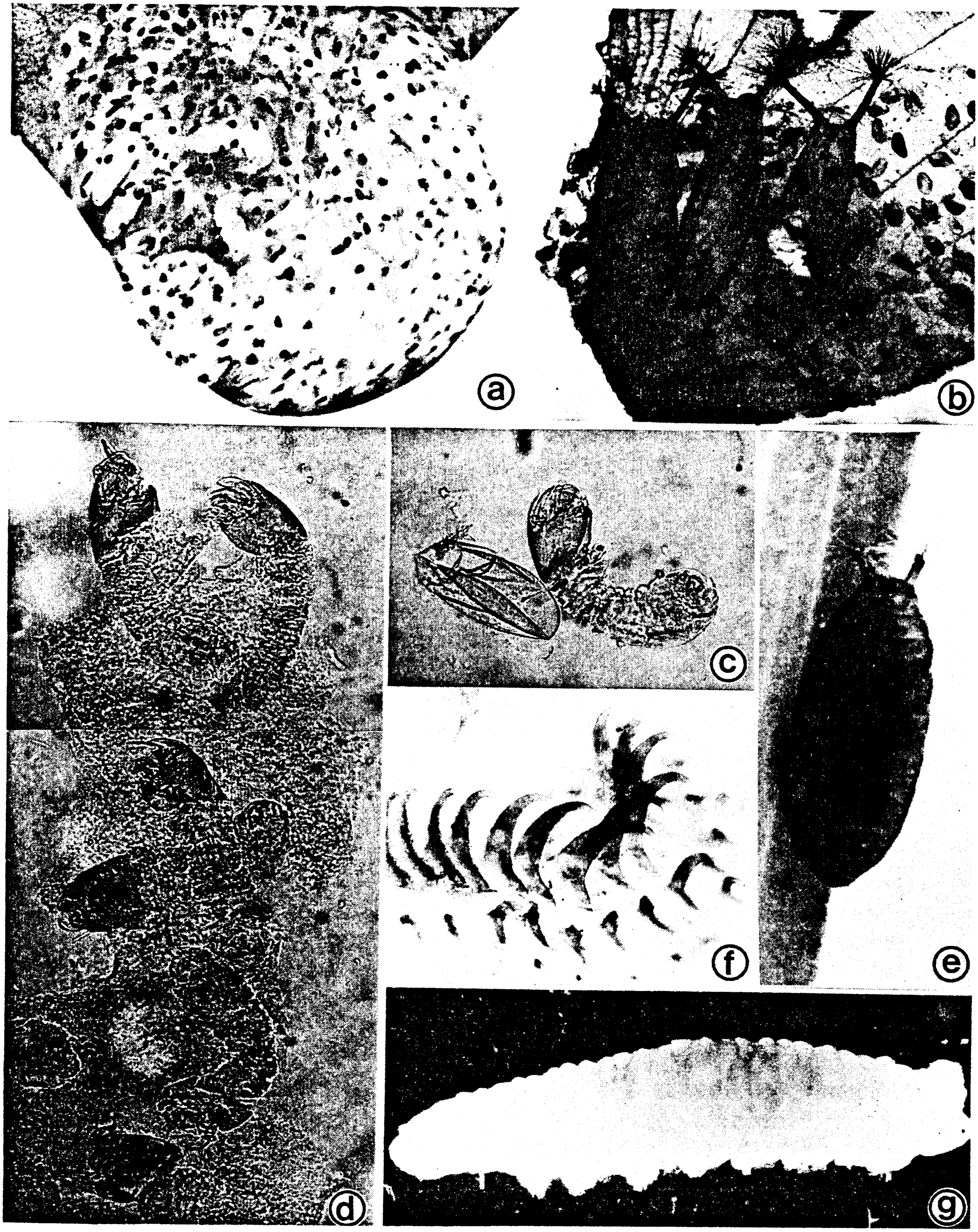
The shift from aerial life to life in rapid running water involves extreme physiological and morphological changes. The conditions of life within egg-masses of dragonflies and in running water are not fundamentally different. In both cases the larvae live in a liquid, either jelly or water, and these therefore require similar respiratory adaptations. All the larvae of the *simulivora* species group have the same type of respiratory spiracles, and this is clearly a similar response to the same selective pressure.

The use of aquatic environments by larvae makes the ultimate evolutionary step toward specialization in the *simulivora* group species. *Drosophila libellulosa* represents an intervening evolutionary step between species with terrestrial larvae and species with larvae preying on aquatic insects. Therefore, Tsacas and Legrand (1979) suggest that the ability of the larvae to become predators preceded the adaptation to aquatic life.

All species of the *simulivora* group have a similar diet, i.e. they prey on the eggs of dragonflies or on the eggs and the first and second instar larvae of *Simulium* and chironomids (Smart, 1937; Tsacas and Disney, 1974; Disney, 1975; Gouteux, 1976) (Fig. 16,c and d). In Cameroon, the river that is the main breeding site for the *simulivora* group species is the only site that also continuously supports a large population of *Simulium damnosum* (Disney, 1975). This emphasizes the possible role of these aquatic drosophilid larvae in the biological control of *S. damnosum.*

Evolution toward predation has taken place through adaptive morphological changes in larvae. The dorsal fusion of the mouth hooks of all the four species is probably a feeding adaptation to suck and swallow newly hatched prey larvae. No other example of a dorsal fusion of the mouth hooks is known in drosophilids (Tsacas and Disney, 1974). The occurrence of an interectosomal plate, which bounds the ectosomal sclerites, further underlines the predatory habits of the larvae of the *simulivora* group species. Carnivorous larvae tend to have a greater number of sclerites in their mouthparts. To attach to leaves hanging above fast running water, the larvae display strongly sclerotinized ventral hooks (Fig. 16, e,f,g). The morphological adaptations of the aquatic species are seen in *D. libellulosa* but are less highly developed.

Drosophila libellulosa larvae live in Gabon feeding on the eggs of the dragonfly *Malgassophlebia aequatoris* Legrand. Egg laying has not been observed directly but probably occurs either in the dragonfly egg-mass itself or next to it. According to Legrand (1979) egg-laying of the drosophilid occurs very soon after oviposition by the dragonfly. The egg of *D. libellulosa*,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which is the only egg of the *simulivora* species group whose morphology is known, displays two short filaments (Tsacas and Legrand, 1979). The number of *D. libellulosa* larvae varies, but may be great enough to succeed in destroying all the host eggs.

The infestation rate of Odonata egg-masses is strikingly high: of 30 egg-masses studied, 13 (43·3%) were attacked by *D. libellulosa*. Full larval and pupal development occurs within the gelatinous egg-mass. The drosophilid larvae lie fully within the mucus surrounding the eggs on which they feed, leaving only the chorions (Fig. 16a). Pupation occurs at the borders of the egg-mass in such a way that the spiracles and the anterior part of the pupa remain outside. Thereby, the emerging adult has no contact with the mucus, which could damage it (Fig. 16b).

The duration of larval development of the drosophilid matches that of the embryonic development in *M. aequatoris*. From egg hatching to emerging adult, the larval and pupal development time in *D. libellulosa* lasts around 18 days under laboratory conditions.

J. DECAYING ANIMAL ORGANIC MATTER BREEDERS

In contrast with many families of *Diptera*, drosophilids rarely exploit decaying animal organic matter as a larval food supply (see the few known cases in Ashburner, Chapter 10, Volume 3a).

Séguy (1951), quoting Paulian, reported that, in Madagascar, larvae of *D. melanogaster* perhaps breed within sheaths of the Psychid Lepidoptera *Deborrea malgassica*. Jacquemard and Tsacas (personal communication) observed that larvae of *Drosophila melanogaster*, *D. latifasciaeformis*, *D. lambi* and *Zaprionus collarti* in the dry Sudanese savannahs of northern Cameroon develop on the faeces of the *Diparopsis watersi* caterpillars (Lepidoptera, Noctuidae) which breed in the head capsule of cotton plants.

Owing to the restricted availability of breeding-sites in the Sahel, the cotton crops play a major role in supporting populations of drosophilids. It is noticeable that here several of the most common species, and especially *D. melanogaster*, colonize the peculiar breeding site of decaying organic matter enclosed in the head capsules of cotton. No true specialists are recorded, and

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FIG. 16. Aquatic or semi-aquatic life and predation in the *Drosophila simulivora* group species. (a) Larvae of *Drosophila libellulosa* within the hydrated egg-mass of the dragonfly *Malgassophlebia aequatoris*; (b) pupa of *D. libellulosa* on the egg-mass of *M. aequatoris* (photographs after L. Tsacas and J. Legrand, 1979), (c) simuliid egg and larvae found in the stomach of *Drosophila simulivora* larva; d: gut contents (*Simulium* larvae) of *D. simulivora* larvae (photographs after L. Tsacas and R. H. L. Disney, 1974); (e) pupa of *D. simulivora* attached on leaf hanging above fast running water; (f) sclerotinized hooks on the ventral pads of *D. simulivora* larva; (g) larva of *D. cogani* with ventral pads (photographs after L. Tsacas).

the three that are found are generalists with opportunistic behavior and high colonizing abilities. These recent observations support the conclusions of Séguy (1933b) that *Gitona gossypii*, which was also reared from head capsules of cotton plants in Mozambique, is breeding in close association with a phytophagous insect, probably a lepidopteran larva.

Finally, Lachaise (1979a) has observed, in preforest savannahs of the Ivory Coast, that the invading *Scaptodrosophila* species, *D. latifasciaeformis* bred opportunistically in cadavers of caterpillars of *Thaumetopoeidae* which were probably killed by a virus disease and were still hanging in a mass on a branch of *Ficus sur*. In these savannahs *D. latifasciaeformis* breeds mainly in the fruits of the Rônier palm tree *Borassus aethiopum* and this shows the abilities of such an opportunistic species to realize rapid host switching, thereby accounting for its great colonizing power.

It can finally be stressed that most known cases of drosophilid larvae developing in decaying animal organic matter involve larvae of Lepidoptera.

IV. Conclusion

The African tropics are notable for the speciation and further wide adaptive radiation of many taxa, e.g., the genus *Lissocephala* and the *Drosophila fima* species group on native figs, the *Drosophila simulivora* species group with their carnivorous larvae living in aquatic or semi-aquatic environments, the *Drosophila aterrima* species complex on flowers, and many others. These radiations are reflected by the fact that 80% of African drosophilids are endemic species (Tsacas *et al.*, Chapter 5, Volume 3a).

Some drosophilids, e.g. certain *Lissocephala*, are assumed to have evolved a close association with their host-plant (*Ficus*) while others, e.g. *Drosophila latifasciaeformis*, show rapid changes in breeding site (e.g., from palm-tree fruits to decaying organic matter).

Tropical African drosophilids display a great range of breeding strategies from phytophagous habits to predation. Moreover, in plant-feeding species many specialization patterns exist, varying from monophagous species, which may be dependent on a single or a restricted number of host plant species (e.g., certain *Lissocephala* species, *Zaprionus vrydaghi*, *Drosophila sechellia* and *D. erecta*) to polyphagous species which may breed on plants from many different families (e.g., *Drosophila yakuba*, *D. bocqueti* or *D. malerkotliana*). By bridging the defensive system of a particular plant species an insect species may spread to other plant species with the same defense system. Thus, some fig-breeding drosophilids may have thereby spread to the entire genus *Ficus*.

The *simulivora* group radiation is undoubtedly the most fundamental evolutionary shift, since it involves both a change from terrestrial to aquatic life and a change from a phytophagous diet to a predaceous one. Mayr (1963) has pointed out that such fundamental shifts are only possible to the carrier of a highly unlikely combination of characteristics, and that this is the reason for the infrequency of such shifts.

The second point to be emphasized deals with the ecological equivalents found in different biogeographical regions. Unrelated drosophilids, most usually belonging to different genera, which evolved independently of one another under similar environmental conditions have in many cases responded to similar selective pressures with nearly identical adaptations. Thus the tropical African *Drosophila libellulosa*, which develops within dragonfly egg-masses, fills a very similar ecological niche to that of the neotropical *Zygothrica* sp., which breeds within frog egg-masses (Villa, 1977). It is probable that drosophilids whose larvae live within egg-masses of insects or amphibia, feeding on their eggs or embryos, are more frequent than is usually expected. Indeed, Lachaise and Couturier (personal communication) recently reared ephydrid flies from the arboreal egg-masses of rhacophorid frogs and chloropid flies from the arboreal egg-masses of the dragonfly *Tetrathemis* sp. (Libellulidae) in the evergreen rainforest of Taï. Both fly families are closely related to Drosophilidae within the Drosophiloidea super-family.

Many other pairs of such independently evolved "ecological equivalents" exist. Thus the larval habits of tropical African *Leucophenga*, which breed within spittle masses of *Ptyelus*, are strikingly close to those of the neotropical and nearctic *Cladochaeta*, which breed within spittle-masses of *Clastoptera*.

The tropical African monophagous *Zaprionus vrydaghi*, whose larvae exploit the native Zingiberales, is equivalent ecologically to the neotropical monophagous flower-breeding *Drosophila* species which exploit the neotropical Zingiberales. Tropical African *Drosophila* species of the *aterrima* complex, which breed preferentially in Convolvulaceae flowers are ecological equivalents of the Hawaiian *Exalloscaptomyza* species which breed exclusively in Convolvulaceae flowers (Heed, 1968; Kambysellis and Heed, 1971). Further, *Drosophila (Scaptodrosophila) bangi* which exploits the sap-exudate of palm trees in tropical Africa, occupies a similar ecological niche as do the many closely related picture-winged *Drosophila* of the *grimshawi* subgroup in Hawaii (Montgomery, 1975).

The tropical African *Gitona pauliani* and *Gitona ethiopica*, which are leaf-miners of Phytolaccaceae, have a similar ecological niche to the palearctic leaf-mining *Scaptomyza* which attack Amarantaceae and Salsolaceae. Here it must be said, however, that leaf-mining *Scaptomyza* may also occur in Africa.

There is a second category of "ecologically equivalent species" which comprises related species. Thus, for instance, *Drosophila aterrima* in tropical Africa and *D. hibisci* in Australia are two closely related species of the subgenus *Scaptodrosophila* which both breed within *Hibiscus* flowers or similar tubiflorales. In such a case the similarity in the larval habits may not be due to any evolutionary convergence, but may rather depend on the proper process of speciation.

An intermediate category is provided by the genus *Cacoxenus*, in which the same larval habits have evolved in two different subgenera in the tropical African and palearctic regions. Thus, *Cacoxenus apidoxenus*, which colonizes the solitary bee nests of *Chalicodoma* in Africa belongs to the subgenus *Gitonides*, while *C. indagator* which colonizes the nests of *Osmia*, *Chalicodoma* and *Anthophora* in Europe, belongs to the subgenus *Cacoxenus*. The other known *Cacoxenus* of both subgenera display different larval habits.

The final category deals with entire (or nearly entire) genera or subgenera, with different species in the different biogeographical regions, but whose larval habits are similar. Thus, the genera *Mycodrosophila*, *Leucophenga* and the subgenus *Hirtodrosophila* display fungus-breeding habits on a world-wide basis. Similarly, *Chymomyza* species exploit fresh tree-stumps, sections of freshly cut trees and peeled areas on tree trunks in both the Nearctic and Afrotropical regions.

An important feature of tropical environments, with regard to the reproductive strategies of drosophilids, is the occurrence of larval resources which may remain suitable for drosophilid development for strikingly long periods of time, e.g. from one to three months in fig species, or from one to two months in *Pandanus* infrutescences. The long duration of certain resources allows the occurrence of successional gradients, i.e. species replacements occur as the long-lived substrates become older. Hence, the importance in the tropics of ecological successions at one resource level has led to foraging strategies absent or reduced in temperate drosophilids.

Another important feature of tropical African drosophilid communities is the occurrence of specialization gradients both with regard to the array of different resources available and to the different successional stages of a particular resource. Then, intra-resource partitioning may add to inter-resource partitioning to account for considerable species packing. Furthermore, species may be generalists with respect to the array of resources used and specialists for a definite and equivalent successional stage in each of them.

The wide occurrence of specialists in tropical African drosophilids raises a question which is discussed by Pianka (1974): if the only currency of natural selection is differential reproductive success and if specialization involves becoming less abundant, why have organisms become specialized at all? Holmes (1976) wonders whether or not specialization is a dead end and argues that specialized structures, or groups of animals, may have retained an evolutionary potential. As far as the insect's choice of food is concerned Levins and MacArthur (1969) assumed that either monophagy or polyphagy may be favored depending on the proportion of an extended diet that would be unsuitable if chosen, versus the difficulty in finding the most suitable food. These authors suggest that the strategy which is adopted is that which maximizes the expected production of offspring in the face of uncertainty due to failure in distinguishing between quite different plants. Hence monophagy may remain optimal when higher and higher proportions of unsuitable foods are present. Thus, if a female has a 50% chance of locating a food on a restricted diet, she should remain restricted and not extend her diet unless more than 30% of the extended diet items are suitable (see arguments in Levins and MacArthur, loc. cit.).

Such thresholds of specialization are illustrated within the *fima* species group. Species like *Drosophila fima* or *D. abron* remain restricted to *Ficus* though both species are potentially able to breed in other fruits. As Feeny (1975) has argued: "At least in a qualitative way, therefore, a variety of possible adaptive advantages can be seen to accrue to insects with narrow host plant ranges. The persistence of many species of rather general feeding habits, however, prompts one to ask whether or not at least in some circumstances specialist feeders may remain specialists not because this is their optimal strategy but because once they have become specialists they have little evolutionary opportunity to reverse the process."

A similar example occurs in *Drosophila erecta* which specifically breeds in the fruits of *Pandanus candelabrum*. When screwpines are fruiting, *D. erecta* is strictly monophagous and develops large populations. When no *Pandanus* are in fruit, *D. erecta* is expected to become more polyphagous, but then, the population level is remarkably low, showing that an extension of the host plant range might result in an appreciable increase in metabolic cost, for example by tolerating a greater range of defensive chemicals present in a wider array of host plants. Furthermore, Levins (1968) and MacArthur (1972) emphasize that specialization in resource use is likely to be favored in species faced with relatively constant or abundant resources. In contrast more generalized species or genotypes are expected to be favored when resources are rare and unpredictable. Thus, Futuyma (1979) argues that "the overlap in resource use between genotypes is favored by avoiding competition, but it is likely to increase insofar as the unpredictability of resources favors generalized genotypes".

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