THE DROSOPHILIDAE ASSOCIATED WITH TROPICAL AFRICAN FIGS

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In the tropical African region the entire drosophilid genus *Lissocephala* and *Drosophila fima* species group have evolved a close association with endemic figs (*Ficus* spp., Moraceae). We previously described the biology of a few of these fig-dependent drosophilids (Lachaise, 1977). We report here on a further investigation in evergreen rainforests, mainly in western Africa, that has yielded information bearing on 19 fig species harboring 35 fig-breeding drosophilids. The information shows that these fig-dependent drosophilids represent a major evolutionary pathway of the tropical African drosophilid fauna.

Small chalcidoid Hymenoptera of the family Agaonidae are absolutely necessary for fig pollination. 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." 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 needed for understanding the biology of fig drosophilids follows.

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). This inflorescence is assumed to be derived from an open inflorescence in a pre-*Ficus* ancestor (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). Wiebes (1979) argued that the symbiosis of figs and wasps made possible, and thus antedated, the special form of the syconium. Phytophagous insects may have exerted such strong selective pressure on this inflorescence that the pre-fig evolved a flask-like inflorescence.

Figs have diverse physical and chemical defenses against herbivore attack. The receptacular structure of the fig is itself a barrier to phytophagous insects. 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 be defenses against herbivores. These morphological defenses are often coupled with chemical defenses, as in other plants (Ehrlich and Raven, 1965; Feeny, 1975; Rhoades and Cates, 1976), including alkaloids, tannins, flavonol glycosides, triterpenoids, polyphenols and probably others. The most efficient chemical protection of the immature fig against herbivores probably comes from a derivative of latex which soaks the receptacular wall of most figs and contains ficin, a powerful protease (Janzen, 1979a). The fig's "Achilles' heel" is the ostiole, an entry into the syconium protected only by a series of appressed and tightly imbricated bracts. The ostiole is a

FIG. 1. 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 in the early postfloral period; 4. decaying receptacle; 5. late decaying period, drying receptacle. The circle portions are not proportional to time. 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*.

selective filter that must admit appropriate pollinators but retard the passage of detrimental organisms (Janzen, loc. cit.).

Reproductive Biology of Figs

Complex symbiotic interrelationships and coadaptations 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's ovipositor give rise to fig seeds (Galil and Eisikowitch, 1968; Janzen, 1979b, 1979c). 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 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 interfloral 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 wasps at the male phase is required for successful 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 cut open the female-containing gall-shaped flowers and impregnate the females while they are still within the galls. Before dying within the fig cavity where they were born and which they will never leave, the male fig wasps bore exit holes 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 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.

MATERIALS AND METHODS

The results upon which this paper is based come from a four year study in which drosophilids were reared from 19

fig species, mainly from the Ivory Coast. These included 11 *Ficus* species in the evergreen rainforest of Taï at the border of Liberia (*mucuso, sur, vogeliana, asperifolia, kamerunensis, elasticoides, saussureana, macrosperma, ovata, recurvata, lyrata*); five species in Adiopodoumé on the side of the laguna within the evergreen rainforest belt surrounding Abidjan (*exasperata, natalensis, thonningii, lutea, ovata*); two species in the pre-forest savannas of Lamto in the Guinean zone (*sur, vallis-choudae*); and one species in the evergreen rainforest covering Mount Tonkoui (*polita*). In addition, records come from *Ficus sycomorus* living in a dry semi-domestic area in Dakkar in Senegal and also from *F. subsagittifolia* living in the dense evergreen rainforest of Makokou in Gabon. In order to present as complete a picture as possible of fig drosophilids, we include a few records reported from Uganda, i.e., from *Ficus mucuso* in Budongo, *F. ovata* in Entebbe and *F. asperifolia* in Mpanga (Buruga and Olembo, 1971) and from one unidentified fig species in La Réunion (J. Etienne, pers. comm.).

The fig species were identified according to the fundamental work of C. C. Berg (in press). Due to much synonymy, many well-known fig species are given unfamiliar names (Table 1).

Several hundreds of figs were collected at every successional stage of sexual and postfloral maturation and eggs of drosophilids were censused exhaustively in each of them. The age of the sexual period of the syconium can be easily determined owing to the clear definitions of the four immature phases, prefemale, female, interfloral and male, given by Galil and Eisikowitch (1968). Owing to the species-specific features of many drosophilid eggs, most could be identified before getting adults. Nevertheless, all the eggs were reared to adulthood on the figs either for differentiating species with rather similar eggs and/or for verification of the early identification. A good deal of data comes only from rearing adults (250 fig samples) whose eggs were not classified, either because the eggs have no known species-spe-

cific feature or because the chorionic envelope was eaten by a predator after hatching. The results take all these records into account.

RESULTS

As a result of our work, 19 species in the genus *Lissocephala* and 16 species in the *Drosophila fima* group are now known, i.e., more than twice the number known previously. Although the larval habit of a few species is still not known, all adults were bred from figs, thereby emphasizing the close dependence of these African drosophilid taxa upon the genus *Ficus*. The 19 *Lissocephala* species were bred from 17 fig species and 12 of the 16 *fima* group species were bred from 13 fig species (Table 1). The breeding sites of the four remaining *Drosophila* species are still unknown though adults of *D. iroko* were observed in abundance on fruits of the "Makoré" *Tieghemella heckelii* (Sapotaceae) in the evergreen rainforest of Taï. Nevertheless, the adults of *D. iroko* are found with the other fig drosophilids. *Drosophila 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*. 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 kinds of resources.

The strict association between *Lissocephala* and *Ficus* has been observed from the Sudanese savannas to Uganda in continental Africa and also from Réunion Island. It has been found in lowland Sudanese savanna (Senegal), lowland Guinean savanna (Ivory Coast), lowland evergreen rainforest (Ivory Coast, Cameroon, Gabon, Uganda), second growth vegetation (Ivory Coast, Uganda, Réunion), montane savannas (Kounden plateau, 1,500 m, W. Cameroon) and montane evergreen rainforest (Tonkoui, Nimba, 300–1,400 m, Ivory Coast). Similarly, the *fima* species group has a wide distribution throughout the mainland

TABLE 1. *Number of narrowly or strictly restricted (*) and facultative fig-breeding drosophilid species from 19 tropical African fig species. Without parentheses: species bred from syconia; in parentheses: species swept on syconia. Fig identification, synonymies and classification after Berg (1982).*

	Lissocephala*			Drosophila					All drosophilids pooled
	juncta* group	sanu* group	ungrouped* species	S. gen. Sophophora fima* group	Sophophora melanogaster group	Scaptodrosophila	Zaprionus	Others	
Genus *Ficus*									
Subgenus *Sycomorus*									
mucuso Ficalho		1 (1)	1 (1)	6 (8)	3 (3)	2 (2)	4 (4)		17 (19)
sur Forsskål (=*capensis* Thunberg)	3 (3)	3 (3)	1 (1)	5 (10)	9 (13)	1 (10)	5 (9)	– (8)	27 (57)
sycomorus L. ssp. *gnaphalocarpa* (Miquel) C. C. Berg	1 (1)	1 (1)							2 (2)
vallis-choudae Delile	1 (1)			– (1)	– (3)	– (1)	– (1)		1 (7)
vogeliana (Miquel) Miquel	2 (2)	2 (2)	3 (1)	6 (8)	2 (5)	– (2)	2 (4)	– (1)	17 (25)
Subgenus *Ficus* (section *Sycidium*)									
asperifolia Miquel	1 (1)				2 (2)	1 (1)	1 (1)	1 (1)	6 (6)
exasperata Vahl		1 (1)		1 (1)	6 (6)		1 (1)		9 (9)
Subgenus *Urostigma* (Section *Galoglychia*)									
thonningii group									
kamerunensis Mildbraed & Burret		2 (2)	1 (1)	1 (8)	4 (11)	– (5)	– (5)	– (4)	8 (36)
natalensis Hochstetter (=*leprieuri* Miquel)		1 (1)	1 (1)		2 (2)		3 (3)		7 (7)
thonningii Blume (=*dekdekena* (Miquel) A. Richard)		2 (2)			5 (5)		2 (2)		9 (9)
barteri group									
elasticoides De Wildeman		1 (1)		3 (3)	4 (4)		3 (3)		11 (11)
lutea group									
saussureana A. P. de Candolle				3 (3)	4 (7)	– (1)	3 (3)		10 (14)
lutea Vahl (=*vogelii* (Miquel) Miquel)		3 (3)	1 (1)	4 (4)	1 (1)		3 (3)		12 (12)
ottoniifolia group									
macrosperma Mildbraed & Burret			1 (1)	5 (6)	8 (9)		2 (3)		16 (19)
ovata Vahl	1 (1)	2 (2)	2 (2)	4 (4)	7 (7)	3 (3)	6 (6)		25 (25)
polita Vahl			– (3)	– (7)	– (4)	– (2)	1 (4)		1 (20)
trichopoda group									
recurvata De Wildeman (=*goliath* A. Chevalier)				2 (7)	– (3)	– (1)	– (2)		2 (13)

TABLE 1. Continued.

| | Lissocephala* | | | Drosophila | | | | | | All drosophilids pooled |
	juncta* group	sanu* group	ungrouped* species	S. gen. fima* group	Sophophora melanogaster group	Scaptodrosophila	Zaprionus	Others	
conraui group									
lyrata Warburg	6 (6)		1 (1)	6 (6)	5 (5)		1 (1)		13 (13)
subsagittifolia Mildbr. ex. Berg			– (2)	8 (8)	– (1)	1 (2)			10 (13)
The 19 fig species together	6 (6)	7 (7)	6 (6)	12 (16)	14 (16)	5 (12)	6 (11)	– (12)	56 (86)

from Sahel to South Africa and from Guinea to Uganda, but is apparently lacking from Seychelles, Comoro, Madagascar and Mascarene.

In addition to the essentially obligate fig-breeding drosophilids there are many facultative fig-breeders displaying greater or lesser preferences for figs. 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 *Ficus* (Table 1).

A Common Successional Pattern

Fig-breeding drosophilids are specialized to a particular period of the successional stage. 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 the intervening period, separating both specialist groups. The last *Drosophila* emerge from the dry remains of the receptacle on the ground (Fig. 1). The specialization pattern in the succession appears to be similar regardless of the fig species, although the succession of the ovipositing drosophilid species may be truncated. Figure 2 presents an 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 entire process of fig receptacle
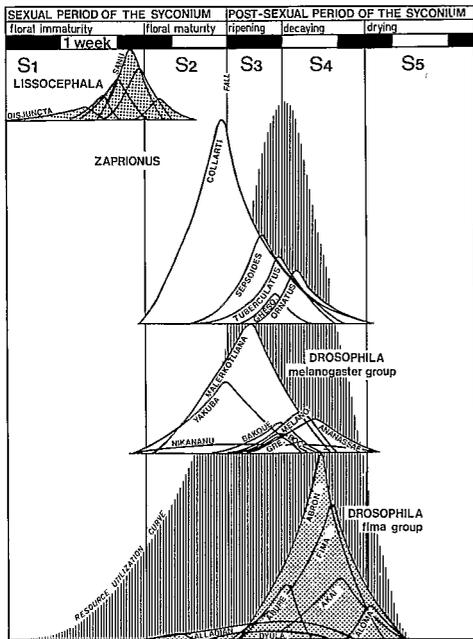
FIG. 2. Change in the relative frequencies of eggs laid by narrowly or strictly (dotted) and facultative (white) fig-breeding drosophilid species in the course of the floral and postfloral life-spans of the *Ficus* syconium in 12 African fig species pooled together.

succession takes from 8 to 15 weeks depending upon the particular fig species. 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 pooled together. The processes involved in host selection by ovipositing female are assumed to be different in *Lissocephala* and *Drosophila fima* species group, which will be discussed separately.

Lissocephala: an Hypothesis of Evolutionary Convergence

The outer wall of the young immature syconium is unsuitable for all drosophilids and also for most other organisms. Therefore, the succession begins inside the syconial cavity. Hence, only members of the genus *Lissocephala* which are able to enter the cavity take part in the first succession. 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,* also in Taï, yielded three. Three of the seven species in *Ficus vogeliana* and *F. sur* are shared, and one of the four in *F. ovata* and *F. lutea* is held in common. Different *Lissocephala* species may be able to cohabit within a syconium by ovipositing sequentially as the immature syconium develops. Each fig species yields both *Lissocephala* species with narrow host-fig specificity and species with a broader specificity. In *Ficus sur* of Lamto, six *Lissocephala* species replace one another in the order *disjuncta, juncta, couturieri, ambigua,* sp. nov., *sanu* (Fig. 1). 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 findings of new species of the *juncta* group as novel *Ficus* are investigated. However, the statement of host-specificity in so diversified a genus requires a good deal of further data to be definitive. 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.

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
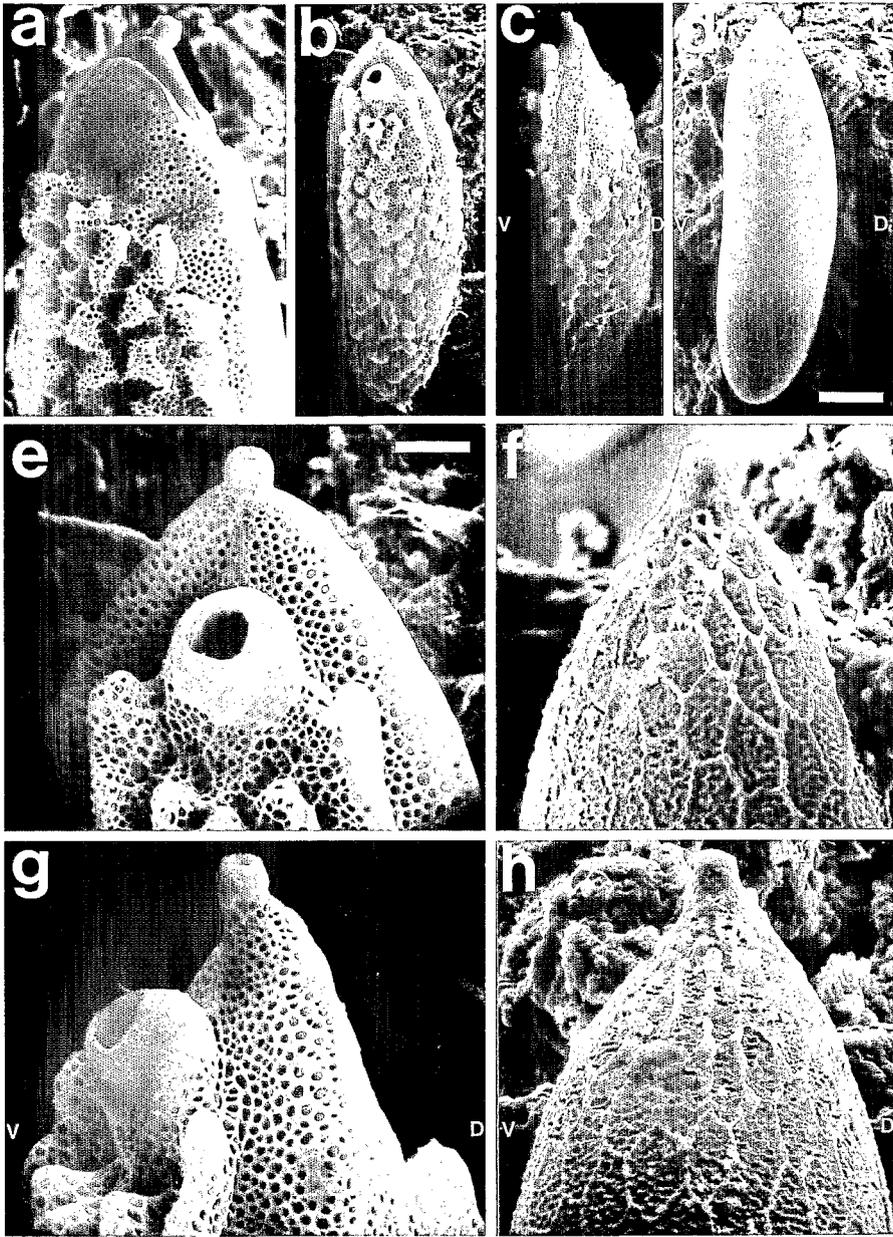
FIG. 3. *Lissocephala* eggs (scanning electron microscope); a: *L. disjuncta* hatched egg in dorsal view showing the thickness and the rigidity of the chorion on both sides of the dehiscent split; b and e; *L. disjuncta* sculptured egg, ventral view; c and g: *L. disjuncta* sculptured egg, lateral view; d and h: *L. couturieri* smooth egg, lateral view; f: *L. couturieri* smooth egg, ventral view. Scale bar for aefgh: .05 mm; Scale bar for bcd: .10 mm.—D: dorsal; V: ventral.

the lack of filaments. In the *sanu* group species the chorion is thin and has the characteristic *Drosophila* network of cellular hexagons. The eggs of *Lissocephala* *diola* have a network of hexagons which blend by anastomosis of their rims; in addition there are protuberances and tubercules. The expanding rims become entire-
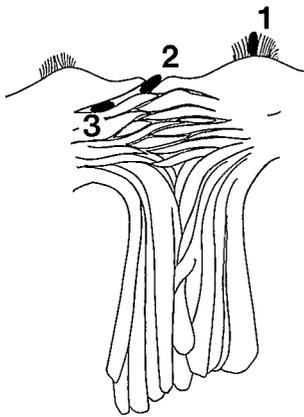
FIG. 4. Schematic drawing of fig-ostiole showing the different micro-oviposition sites in *Lissocephala* species. 1: *Lissocephala juncta* in *Ficus vallis-choudae*; 2: *L. disjuncta* in *F. sur*; 3: unidentified *Lissocephala* in *F. exasperata*.

ly blurred in eggs of *L. disjuncta* which have in addition a striking "corrugated iron" appearance (Fig. 3). The micro-oviposition site is well established for only a few *Lissocephala* species; it appears to differ slightly from one species to another. Different eggs were found either at the border of the ostiolar area, or between the superficial bracts of the ostiole, or else more deeply inserted within the ostiolar bush (Fig. 4). The strongly protected eggs are those which are directly inserted between the ostiolar bracts and we assume the chorionic differentiations to be protective devices preventing squashing of the egg due to the bract pressure. These findings are in accord with the suggestion of Kambysellis (1973, 1974) that the chorion pattern in drosophilid eggs is adaptive. The *Lissocephala* with protected eggs appear to be also those species with the narrowest host-specificity.

Those *Lissocephala* which breed inside the syconial receptacle gain entry through the ostiolar filter and apparently cause neither damage to the fig inflorescence nor to the fig wasp larvae. Many other characteristics of the life histories of fig wasps and fig flies are similar. Both fig wasp and *Lissocephala* 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. 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. Finally, both the third instar *Lissocephala* larvae which are ready to pupate 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 the tunnels 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. We hypothesize that the *Ficus*-specific *Lissocephala* species have attributes that match those of the obligatory pollinator fig wasp, thereby countering the host's protective devices.

Later Drosophilid Succession in Figs

Once carbon dioxide depletion has occurred, the new generation of fig wasps escapes and the *Lissocephala* larvae drop to the ground for pupation and ripening of the receptacle begins. Yeast for the first time begin to grow and the process of alcoholic fermentation starts. A new association of drosophilid species, comprising *Zaprionus collarti, Z. sepsoides, Drosophila yakuba* and *D. malerkotliana,* invades the maturing receptacle while it still hangs in the trees, laying eggs in the outer exocarpic wall. Typically the concentration of sugar and the products of alcoholic fermentation increase as the succession proceeds. These changes may bring about the succession of species. Once fallen to

the ground, the decaying fig undergoes further successional stages which are exploited, sequentially, by new invading species, e.g., different *Zaprionus* species (*Z. tuberculatus, Z. ghesquierei*) and *Drosophila* of the *melanogaster* species group (*D. bakoue, D. bocqueti, D. greeni* and *D. melanogaster*). The order of ovipositing species seems independent of the duration of the succession and, apparently, of the fig species. The fallen fig is like any other fruit and at this stage harbors the maximum density and maximum species diversity. This stage is a "window" for many opportunistic species. In fact, African species which never use figs are rare. After this "window" period, the resource becomes rapidly unsuitable for the opportunistic *Zaprionus* and *Drosophila*; then come the species of the *Drosophila fima* group (Fig. 2).

The Fig-breeding fima *Species Group*

The *Drosophila fima* group species show much sympatry. Thus, 13 species cohabit in the evergreen rainforest of Taï where six species were reared separately either from *Ficus mucuso, F. vogeliana* or *F. lyrata*. In Gabon, eight species were reared from the same fig cluster in *F. subsagittifolia*. In pre-forest savannas in the Ivory Coast adults of ten species were found on the same host (*F. sur*). Hence, there appears to be no fig species preference among the *fima* group species. Of the *fima* group species only *Drosophila fima* has been successfully bred indefinitely on standard laboratory medium; *D. abron* was maintained with difficulty for four or five generations. It is of interest that *D. abron* has been bred only from figs. In contrast, *D. fima* was reared once from fruits of *Hirtella* sp. (Rosaceae) and *Nauclea* sp. (Rubiaceae). These arguments suggest that some of the *fima* group species are not obligatorily fig-dependent, though generally being fig-restricted.

DISCUSSION

Drosophilids breeding in figs are known from other parts of the world (Heed, 1957; Miller and Phaff, 1962; 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, 1981) are highly diversified. Until recently the geographical range of the genus *Lissocephala* was assumed to be paleotropical. In the Oriental and Australian regions 12 species are at present included in the genus *Lissocephala*. 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. The specialization of *Lissocephala* on *Ficus* is peculiar to tropical Africa, as far as known.

We hypothesize *Lissocephala* has undergone a burst of speciation owing to a convergent evolution with the obligatory pollinating fig wasps which are highly host-specific. The fig wasp symbiosis is thought 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 Drosophilidae. Tsacas (1979) further suggested from biogeographical arguments that the ancestors of the *Sophophora* subgenus of *Drosophila* occurred before separation of Africa and South America in late Cretaceous. Therefore, the genus *Lissocephala* is thought to have 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 be regarded as

so many niches available for *Lissocephala* speciation. Thus speciation in *Lissocephala* may be a by-product of the coevolutionary process between figs and pollinating fig wasps.

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 association with figs requires behavioral adaptations in the genus *Lissocephala* that are not required in the *fima* species group. Thus, the evolutionary histories differ fundamentally between these guilds of fig-breeding drosophilids.

SUMMARY

The fig-breeding drosophilids of tropical Africa include 19 species in the genus *Lissocephala* which appears to be endemic to the tropical African region and 16 species in the *Drosophila fima* species group which is unequivocally endemic to this region. The *Lissocephala* species are strictly restricted to immature figs for breeding, whereas the *fima* group species are confined to post-matured figs though

some of the latter are not obligatory fig-breeding species.

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.

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