

10. Entomophagous and other Bizarre Drosophilidae

MICHAEL ASHBURNER

*Department of Genetics
University of Cambridge
Cambridge, England*

I. Introduction	395
II. Taxonomic Treatment	396
A. The Genus <i>Lissocephala</i>	396
B. The Subfamily <i>Steganinae</i>	398
C. The Subfamily <i>Drosophilinae</i>	408
III. Conclusion	418
Acknowledgements	421
References	421

I. Introduction

There can be little doubt that the Drosophilidae are, in the main, adapted to feed and breed on decaying and fermenting vegetable matter, themselves substrates for the growth of bacteria, yeasts and other fungi. Yet many species have become specialized to quite different resources. The leaf mining *Scaptomyza* and the species breeding in living flowers are well known. Those species whose lives have become intimately bound with those of other insects and animals are less well known and have, in the past, been comparatively ignored by students of drosophilid biology. This review is devoted to these species.

This review, will perforce, be somewhat anecdotal in its style. This is because the serious scientific study of most, though not all, of the species to be discussed has hardly begun. This is not to under-rate the contributions of the authors upon whom I rely; the problems stem from the facts that many of the studies of the more bizarre drosophilids have been done incidental to other work and, often, at times or under conditions not conducive to proper study. Moreover many of the bizarre species are difficult, or have so far proved to be impossible, to culture in the laboratory.

The literature on the bizarre drosophilids is exceptionally scattered

through both professional and amateur journals and my task would have been virtually impossible without access to E. B. Basden's unrivalled collection of offprints. Since my acquaintance with most of the material to be reviewed is second-hand many of the problems raised will be treated at rather a superficial level. I apologize for this, but I hope that the advantage of having, for the first time, a reasonably comprehensive review of bizarre drosophilids will outweigh this disadvantage and, I hope, stimulate further research.

II. Taxonomic Treatment

A. THE GENUS *LISSOCEPHALA*

Throckmorton (1975) considers that the tropical genus *Lissocephala* is the most primitive of the drosophilids (see Tsacas and Lachaise, 1979 for discussion). Species of the genus are known from the Australian, Oriental and Afro-Tropical regions and, until recently, nothing was known of their biology. Now, however, it is quite clear that the Afro-Tropical radiation of *Lissocephala* has occurred through a very close, and fascinating, association of the flies and various species of fig (*Ficus*) (see Lachaise, 1977; Tsacas and Lachaise, 1979). The only reason for including this genus in this review is the discovery, by Carson and Wheeler (1973; see also Carson, 1974) of a species of *Lissocephala* associated with land crabs on the Indian Ocean island of Christmas Island. The breeding-site of this species, *L. powelli*, recalls that of *D. carcinophila* and *D. endobranhia* from the Caribbean (see Section II, C, 2, ii).

Two species of land crab are, on Christmas Island, the main hosts of *L. powelli*—*Gecaroidea humei* (Wood—Mason) and *Birgus latro* L. The incidence of infection may be very high, reaching 100%, for example, in the case of *B. latro*. The female fly lays her eggs at the base of the second antennal segment and along the edge of the crab's carapace, above the mouth parts. The association of fly and crab is clearly one of commensalism. On hatching the larvae are to be found "in the hairs at the apical end of the third maxillipeds . . . this area is continually saturated by fluid excreted from the green gland" (Carson and Wheeler, *loc cit*). The larvae presumably feed upon micro-organisms which themselves grow in a substrate provided by the crab's excreta. On completion of their larval development the animals leave their hosts and pupariate in the sand.

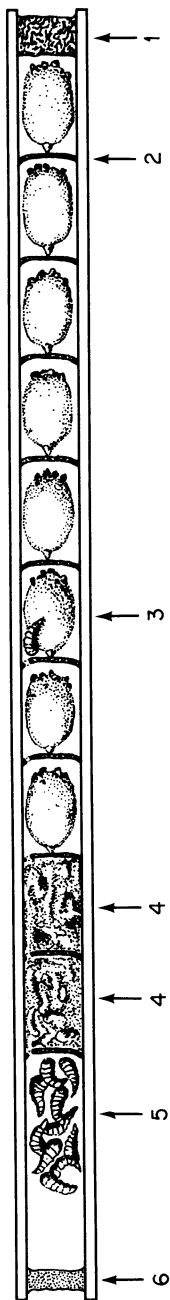


FIG. 1. A nest of *Osmia rufa* parasitized by larvae of *Cacoxenus indagator* (from Juillard, 1947). The base of the nest (1) is closed with a mud plug. Eight cells are occupied by pupal *Osmia*, each attached by its anterior end to the partition wall (2) separating the cells. In the cell marked (3) a single *Cacoxenus* larva has transversed backwards from the more distal cells by breaking through the partitions as it did so. The cells marked (4) are full of *Cacoxenus* larvae and their excrement. Ten larvae are found (5) in the vestibule behind the plug (6) that closes the end of the nest.

B. THE SUBFAMILY STEGANINAE

1. The genus *Acletoxenus*

This small genus of elegant flies, established in 1864 by Loew, is allied to *Cacoxenus* and *Gitona*. Four species have been described. One, *A. formosus*, is known from Europe, Israel (Basden, 1966), the Canary Islands (Duda, 1935) and Australia (presumably introduced, Bock, 1981), and three (*A. indicus*, *A. mejerei* and *A. quadristriatus*) are from the Oriental region. There is every reason to believe that further species are to be found in South East Asia and Australasia: indeed Clausen and Berry (1932) mention a further species from Java.

in the Australian National Insect Collection.

A. formosus is a very striking fly, with a shiny jet black dorsum, pale yellow pleura and a bright yellow scutellum (see Collin, 1902, for a coloured plate and Jenkinson's, 1901, account of this specimen's capture at his home in Cambridge). Our knowledge of the biology of *Acletoxenus* comes from scattered accounts of *A. formosus* in the European literature, from the paper on *A. indicus* by Clausen and Berry (1932) and from that refuge of the desperate, museum labels.

TABLE I. The known associations of *Acletoxenus* species and their Aleurodidae prey

Species	Prey	Locality
<i>A. formosus</i>	<i>Siphoninus philyreae</i> (Haliday)	Europe (Germany, Great Britain, Greece, Bulgaria, Italy) ¹
	<i>S. immaculatus</i> (Haeger)	Great Britain ²
	<i>Aeurotrachelus jelinekii</i> (von Frauenfeld)	Germany ³
<i>A. indicus</i>	<i>Aleyrodes proletella</i> (L.)	Italy ⁴
	<i>Aleurocanthus woglumi</i> (Ashby)	Java, ?Malaysia, ?Sri Lanka ⁵
<i>A. quadristriatus</i>	<i>A. citriperdus</i> (Quaintance and Baker)	Java ⁵
	<i>Aleurodes</i> sp.	India ⁶
<i>Acletoxenus</i> sp.	<i>Aleurodicus destructor</i> (Mackie)	Australia (Thursday Is.) ⁷
	<i>A. woglumi</i> (Ashby)	Sumatra ⁵
	<i>A. citriperdus</i> (Quaintance and Baker)	Sumatra ⁵

References: 1. Walker (1853), von Frauenfeld (1867, 1868), Gautier (1922), Golfari (1937), Mentzelos (1967), Pelov and Trenchev (1973). 2. Varley, in Mound and Halsey (1978). 3. von Frauenfeld (1868). 4. Silvestri (1934). 5. Clausen and Berry (1932). 6. Malloch (1929). 7. Duda (1936).

The larval stages of *Acletoxenus* predate Aleurodidae. The known associations of host and predator are listed in Table I. The female fly deposits her eggs singly upon leaves infested with white-fly, adjacent to late-stage white-larvae or pupae, according to Clausen and Berry (1932). The eggs are apparently glued to the leaf (see Riley and For-gash, 1967, for an account of the egg glue of *D. melanogaster*). The first stage of larvae are white (*A. indicus*, Clausen and Berry, 1932) or orange (*A. formosus*, G. Varley, *in litt.*) but turn green by the third instar. In the case of *A. formosus*, at least, this pigment is in the fat body, the cuticle remaining white and translucent (M. Ashburner, unpublished observations). Neither the nature, nor origin, of the pigment is known, though it is reasonable to conclude that it is derived from the plants on which the white-fly are feeding.

The larvae of both *A. indicus* and *A. formosus* are covered with a mucilagenous slime (von Frauenfeld, 1867; Clausen and Berry, 1932; and other authors). It is not known whether this slime is derived from the larva's salivary glands or from its dermal glands. However, as a consequence of this stickiness the larvae collect debris, including eggshells of their white-fly prey.

The larvae are very sluggish, probably never leaving the leaf upon which they started life (Clausen and Berry, 1932). *A. formosus* larvae, predated the white-fly *Siphoninus immaculatus* (Haeger) on the underside of old leaves of *Hedera helix* L. in Oxford, England, make tracks through the sooty-moulds (see Section III) that grow on the infested leaves (G. Varley, *in litt.*).

Puparium formation occurs on the leaf, the puparium being firmly glued to its substrate. In Europe the life cycle of *A. formosus* has been found to be between 12 (von Frauenfeld, 1867) and 27 (Pelov and Trenchev, 1973) days.

In Europe *A. formosus* is an important predator of *Siphoninus phillyreae* (Haliday), itself a pest of, for example, the pear (*Pyrus communis* L.) (see Gautier, 1922; Silvestri, 1934; Golfari, 1937; Mentzelos, 1967; Pelov and Trenchev, 1973). Pelov and Trenchev (1973) estimate that each *Acletoxenus* larva consumes some 30 to 40 white-fly puparia in its life and some attempt, though futile, has been made to use *A. formosus* for the biological control of white-fly (Vayssiere, 1953). Indeed Clausen and Berry (1932) twice imported *A. indicus* into Cuba, from South East Asia, for the control of *Aleurocanthus woglumi* Ashby, a pest of *Citrus*, but without lasting effect. The reasons for the failure of *Acletoxenus* to act as agents for white-fly control are not clear, though extensive parasitism by Hymenoptera (Clausen and Berry, 1932; Mentzelos, 1967; Pelov and Trenchev, 1973) may have been a factor.

2. *The genera Gitona and Cacozenus*

It is convenient to consider these related genera together. The classification of *Gitona*, *Cacozenus* and of the genera *Paracacozenus* and *Gitonides* (now subgenera of *Cacozenus*) has recently been revised by Tsacas and Chenon (1976; see also McAlpine 1968).

The ten described species of the genus *Gitona* are to be found in the Palaearctic and Afro-Tropical regions. Their biology is very poorly known and the only justification for their inclusion here is the suspicion that some species may be predacious.

The single European species of *Gitona*, *G. distigma*, is frequently quoted as an example of an aphidophagous species. The evidence for this statement is, to say the least, slender, and the manner in which it has become accepted into the literature an object lesson. Loew (1847) reared adult *G. distigma* from the flower heads of the Composite *Sonchus arvensis* L., the larvae pupating within the flower heads. Later Schiner (1864) also reared this species from *Sonchus* and from the flower heads of another composite, *Onopordon acanthium* L., and L. Tsacas (*in litt.*) informs me that this fly has been reared from *Sonchus oleraceus* L. in France. As far as I am aware these are the only primary accounts of the biology of *G. distigma*, all others (Scholtz, 1849; Kaltenbach, 1874; Brauer, 1883; Townsend, 1893; Knab, 1914; Seguy, 1933a, 1934, 1951; Duda, 1935) being derivative. It is to Knab (1914) that we owe the suggestion that the larvae are aphidophagous for, after quoting Loew (1847), he writes "As plant lice are known to occur in large numbers on the upper part of this plant [i.e. *Sonchus*] (vide Kaltenbach, p. 397) there is every reason to believe that the larvae of *Gitona* prey upon these" (Knab 1914:165). Kaltenbach (1874) lists three species of aphid and one psyllid from *Sonchus arvensis*. Were *Sonchus* uniquely infected by "plant lice" then there would be some grounds for taking this speculation more seriously.

Another species of *Gitona*, *G. gossypii* was described by Seguy (1933b) from the damaged head capsules of the cotton plant, *Gossypium*. Presumably on the basis of Knab's speculation concerning the larval habits of *G. distigma*, Seguy (1951) writes of the larvae of *G. gossypii*, that "se developpement probablement aux depends d'une autre larve d'insecte saprophage" but here again, I can discover no evidence that this is so.

The known North American species of *Gitona* are probably not predators: two, *G. americana* and *G. bivisualis*, have been reared on standard *Drosophila* medium, and *G. americana* and a third species, *G. sonotia*, are known to feed on decaying vegetable matter from cacti

(Wheeler, 1952 and *in litt.*). Furthermore two Afro-Tropical species, *G. pauliana* and *G. sp.* are known to be leaf miners as larvae (Seguy, 1951; Tsacas and Teshone, personal communication).

Two species described as *Gitona*, that is *G. brasiliensis* and *G. fluminensis*, do have larvae that predate Homoptera: however it is very likely that these are not *Gitona* at all, but *Rhinoleucophenga*, and I will deal with them under that genus.

The genus *Cacoxenus* assuredly includes predatory species. Two, previously described in the separate genus *Gitonides*, predate Homoptera. These are *C. (Gitonides) frontalis*, found but once predated *Aspidoproctus bouvieri* Vayssiere (Margarotidae) in Zaire (Collart, 1935)

TABLE II. Insects known to be predated by *Cacoxenus (Gitonides) perspicax*. All are Homoptera, Pseudococcidae, with the exception of *Peregrinus* which is Homoptera, Delphacidae.

Prey	Distribution
<i>Brevannia rehi</i> (Lindiger)	India (7, 8)
<i>Chorizococcus rostellum</i> (Hoke)	Hawaii (16)
<i>Dysmicoccus boninsis</i> (Kuwana)	Hawaii (1), Mauritius (2)
<i>D. brevipes</i> (Cockerell)	Hawaii (1), Mauritius (21)
<i>Gigantococcus maximus</i> (Newstead)	Nigeria (19)
<i>Laminicoccus pandani</i> (Cockerell)	Hawaii (1), Zaire (20)
<i>Nipaeococcus viridis</i> (Newstead)	India (4), Hawaii (1)
<i>N. filamentosus</i> (Cockerell)	Hawaii (5)
<i>Palmicultor palmarum</i> (Ehrhorn)	Hawaii (1)
<i>Phenacoccus saccharifolii</i> (Green)	India (6)
<i>Planococcus citri</i> (Risso)	Comores (22)
<i>Pseudococcus</i> sp.	Hawaii (3), Philippines (3)
<i>P. longispinus</i> (Targ.)	Hawaii (1)
<i>Saccharicoccus sacchari</i> (Cockerell)	Hawaii (1), Mauritius (2, 9), Reunion (9), Somalia (10), Sri Lanka (11), India (12), Papua New Guinea (13), Philippines (14, 15)
<i>Peregrinus maidis</i> (Ashmead)	India (17)
"Mealy aphid"	Australia (4)
undetermined	Formosa (18)

References: 1. Hardy (1965). 2. Box (1953). 3. Knab (1914). 4. Malloch (1924b). 5. Fullaway (1920). 6. Ali (1963). 7. Ayyar (1938). 8. Manjunath (1968). 9. David and Tsacas (1975). 10. Seguy (1933a). 11. Rujendra (1974). 12. Puttarudriah (1954). 13. Szent-Ivany and Ardley (1963). 14. Uichanco and Villanueva (1932). 15. Goseco (1932). 16. Beardsley (1957). 17. Malloch (1924a). 18. Duda (1924). 19. L. Tsacas (personal communication). 20. Ghesquiere (1934). 21. Moutia and Mamet (1946). 22. J. Etienne (personal communication).

and *C. (Gitonides) perspicax*, a well known predator of scale insects, particularly those on sugar cane and rice.

It is surprising that, in view of the economic importance of the plant hosts of the scale insects predated by *C. perspicax*, very little indeed is known of the biology or life history of this fly. The larvae of *C. perspicax* "live in the tight roll of the leaf axis of the sugar-cane and other grasses" (Hardy, 1965) where they are protected against predation by ants and are in a relatively humid environment (see Dick, 1969). Indeed this is just the environment of the victims of *C. perspicax* though predation of species that live on the leaf lamina [e.g. *Phenacoccus saccharifolii* (Green)] is known (Ali, 1963). Beardsley (1960) notes that the larvae of *C. perspicax* tend not to migrate far in search of foods but to "remain feeding on mealy bugs at a single node".

The insects upon which *C. perspicax* is known to feed are listed in Table II. Tsacas and Chenon (1976) point out that the distribution of *C. perspicax* is co-extensive with that of *Saccharicoccus sacchari* (Cockerall), with the notable exception of the Americas, where the scale insect, but not the drosophilid, is found. However this drosophilid is also known from Western Australia, where sugar-cane is not grown (Bock, 1981).

Presumably this distribution has been very markedly affected by man. There is some evidence that *C. perspicax* can result in a significant biological control of sugar-cane scale insect pests (e.g. Rujendra, 1974) and for this reason, if no other, further studies of the biology of this species would appear to be well justified.

Two other species of *Cacoxenus* are of great interest, they are *C. (Cacoxenus) indagator* and *C. (Gitonides) apidoxenus*. Though belonging to different subgenera (Tsacas and Chenon, 1976) the similarities in the biology of these two species are so marked that they may be considered together.

Cacoxenus (Cacoxenus) indagator was described from Europe by Loew (1858), and his correspondent, Dr. Schultz of Breslau, clearly recognized the extraordinary association of this fly with certain species of solitary bee. The details of this association were first described in detail by Giraud (1861) but we owe most of our more recent knowledge to two papers by Juillard (1947, 1948). *C. indagator* is a nest parasite of many species of solitary bee (Table III) in Europe. The study of its biology is aided by the fact that its host species can be induced to colonize artificial nests in the field (see Levin, 1957; Free and Williams, 1970; Raw, 1972; and Tasei, 1972). The nest building habits of *Osmia coerulescens* (L.) in south-western France have been described by Tasei (1972): the female *Osmia* provisions, with pollen and nectar, a series of cells within a hollow tube, such as a drinking straw. It takes

TABLE III. Known host bees of *Cacoxenus indagator* in Europe and *C. apidoxenus* in West Africa

<i>C. indagator</i>	<i>Anthophora plumipes</i> (Pallas)	Hamm (1932)
	<i>Chalicodoma pyreniaca</i> (Lep.)	Seguy (1934)
	<i>Chalicodoma pyropeza</i> Pz.	Giraud, in Seguy (1934)
	<i>Osmia coerulescens</i> (L.)	Juillard (1947), Richards (1932), Vachal, in Seguy (1934)
	<i>Osmia cornuta</i> Latr.	Juillard (1947), Seguy (1934)
	<i>Osmia emarginata</i> Lep.	Giraud (1861), Mik (1892)
	<i>Osmia fulviventris</i> Pz.	Richards (1932), Raw (1972)
	<i>Osmia rufa</i> (L.)	Richards (1932), Juillard (1947), Seguy (1934)
	<i>Osmia ventralis</i> Pz.	Krober (1912)
	<i>C. apidoxenus</i>	<i>Chalicodoma cincta</i> Fab.
<i>Chalicodoma kamerunensis</i> Friese		Tsacas and Chenon (1976)
<i>Chalicodoma mephistophelica</i> Gribodo		Tsacas and Chenon (1976)

the bee about 20 separate visits (over a period of three hours) to provision each cell and to deposit within it a single egg. The cell is then closed off with a partition made from a paste of leaves of a plant [in Tasei's study, of *Malva moschata* L. (Malvaceae)] mixed with saliva. A linear array of cells is constructed within the nest and the open end finally sealed with a strong plug of masticated leaves (Tasei, 1972) or mud (Juillard, 1947). Whilst the bee constructs and provisions her nest the adult female *Cacoxenus* "tourbillant devant d'orifice, attendant une occasion propice pour entrer" (Juillard, 1947). When the propitious moment arrives the *Cacoxenus* enters the nest and lays several eggs in an uncompleted, yet provisioned, cell (up to 22 larvae have been found in a single cell; Juillard, 1948) (Fig. 1).

The drosophilid larvae, on hatching, first eat the supplies so provisionally stored for her progeny by the bee. What happens next is, in detail, unclear: either the bee larva (which has also hatched by this time) dies of starvation, and may then be eaten by the fly larvae (Raw, 1972) or the larval *Cacoxenus* actually preys upon the living larval *Osmia* (Juillard, 1948). Since, according to both Juillard (1948) and Raw (1972), both *Cacoxenus* and *Osmia* can complete their development within one cell it would appear that the former is the most usual occurrence, the *Osmia* only surviving when "left" enough food by the *Cacoxenus*.

Both host bees and *Cacoxenus* are univoltine species, at least in northern Europe. The fly over-winters as a prepupa or pupa. Before doing so, however, the larvae use their very well developed mouth-hooks (Meijere, 1944) to pierce the partitions that separate the bee

cells and migrate distally to the penultimate cell of the nest. To break through the intercellular partitions requires the co-operative effort of several larvae, and the type of effort expended can be seen if *Cacoxenus* third instar larvae are imprisoned within a small gelatine capsule (G. Varley, *in litt.*).

In the spring following the year of their birth the flies and bees complete their development. The adult *Cacoxenus* have, now, a problem: they are quite unable to effect an exit from the nest, through the terminal closure. For this they rely totally upon the single *Osmia* remaining in the terminal cell—this cell is never attacked by the *Cacoxenus*: if all of the bee larvae are removed from a nest, which is then reassembled, then the adult flies are trapped and die within (Juillard, 1947). The lives of the fly and bee must, therefore, be closely synchronized.

The third instar larvae of *Cacoxenus* have been described by Meijere (1944). The most surprising fact is that they, unlike the known larvae of all other Drosophilidae, are metapneustic, that is to say the anterior spiracles are non-functional. Another remarkable fact concerning larval *Cacoxenus* is that their excreta form extraordinarily, and long, ribbon like filaments that eventually fill the infested cells.

A species of the related subgenus *Cacoxenus* (*Gitonides*) has recently been discovered in West Africa to have a life-style very similar to that of *C. (Cacoxenus) indagator*. This species is *C. (Gitonides) apidoxenus* and it lives in close association with the arboreal nests of a number of solitary bees (Table III) (Tsacas and Chenon, 1976). The bee larvae, in cells infested by *C. apidoxenus*, die and Tsacas and Chenon suggest three possible reasons why this is so: (i) starvation, (ii) attack by the fly larvae and (iii) infection by bacteria or yeast introduced by the female *Cacoxenus* in the act of oviposition. Although the nests of the bees infested by *C. apidoxenus* are globular, rather than linear, this species has the same problem as *C. indagator* in effecting an exit of the newly emerged adult flies: indeed the problem is solved by precisely the same trick—the terminal cell is left uninfested so that its inhabitant can make an exit hole, both for itself and the fly. Since, incidentally, the infestation rates of *Osmia* by *C. indagator* can be very high this adaptation also means that infestations do not cripple the bee populations.

In addition to *C. indagator*, itself perhaps a complex of species (Hardy and Wheeler, 1960; Hackman, 1969) and *C. apidoxenus* several other species of this genus have been described from India, Australasia, Europe, Africa and North America but almost nothing is known of their biology. The North American *Cacoxenus (Paracacoxenus) guttatus* passes its larval stage in the cankers of the rust fungus *Cronartium comandrae* Peck on the Lodgepole Pine (*Pinus contorta* Douglas var. *latifolia* Engelm)

(Powell, 1971; Powell *et al.*, 1972), and the Palearctic *Cacoxenus* (*Gitonides*) *vlasavi* has been found in the burrows of ground-squirrels (*Citrellus* (Duda, 1935), a habitat recalling that of *Camilla* (*Camillidae*) (Basden, 1961). More predatory species probably remain to be recognized: for example L. Tsacas (*in litt.*) informs me of a species near *Cacoxenus* (*Gitonides*) *frontalis* which is recorded as "ex *Steatococcus* sp" in Nigeria.

3. The genus *Pseudiastata*

The eight described species of this Neotropical genus are related to those of the genus *Cacoxenus* (Sabrosky, 1951; Hardy, 1959; Wheeler, 1960). Their larvae are predacious on coccids. Indeed, several attempts have been made to use *Pseudiastata* for the biological control of coccids, especially of the pineapple [*Ananas cosmos* (L.) Merr] pest *Dysmicoccus brevipes* (Cockerell). In view of this potential it is surprising that the only detailed account of the biology of this genus is that of Goncalves (1939), and this is far from complete, though Lima (1937) and Figueiredo (1938) do include a little biological information in their papers.

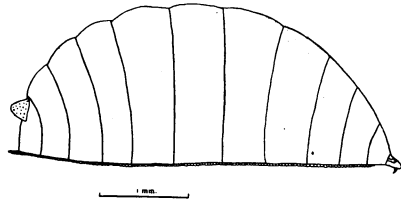


FIG. 2. Larva of *Pseudiastata brasiliensis* (from Goncalves, 1939).

According to Goncalves (1939) the predation of *D. brevipes* by *P. brasiliensis* is aided by subterranean tunnels made by ants (principally *Solenopsis saevissima* Forel) when the host coccid is feeding upon the roots of the grass *Eriochloa punctata* (L.) Desv. The larvae of *Pseudiastata* attack, in the main, the adult female coccids and are remarkably voracious (see also Carter, 1935). The larvae of *Pseudiastata* are hemispherical (Fig. 2) (Sabrosky, 1951, describes them as "molluscoid" in shape) and have an epidermis thrown into reticulate folds with many dermal glands (Goncalves, 1939).

Various species of *Pseudiastata* were introduced, from Central America, into Hawaii with a view to controlling *D. brevipes* on pineapple. Most accounts (e.g. Fullaway, 1933 and Carter, 1935) consider that the species introduced was *P. nebulosa*, a North American species,

though, in fact, it would appear that at least three different species (*P. brasiliensis*, *P. pseudococcovora* and *P. vorax*) were introduced to Hawaii sometime between 1924 and 1935 (see Hardy, 1965). All of the introductions failed, presumably because too little attention was paid to the host preferences of the different species of fly (Beardsley, cited in Hardy, 1959) or due to parasitism by Chalcids (Carter, 1935).

There is circumstantial (i.e. museum label) evidence that a species of the subgenus *Hyalistata* may predate Psyllids (Wheeler, 1960).

4. The genera *Leucophenga*, *Rhinoleucophenga* and *Amiota*

These remaining steganine genera will be considered here together for, in each instance, we have only tantalizing glimpses of the biology of those flies of relevance to the subject of this review.

At least three species of *Leucophenga* are known to have larvae which associate with the spittle produced by gregarious larval Cercopidae (Homoptera) (see Williams, 1931). They recall the habits of the larval *Cladocheata* (see Section II, C, 1). *Leucophenga* is a very large genus (after

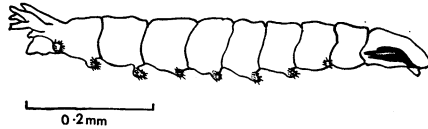


FIG. 3. Third instar larva of *Leucophenga proxima* showing the ventral spines (from Medler and Adenuga, 1969).

Drosophila and *Scaptomyza* the largest in the family Drosophilidae) predominantly tropical in its distribution. Remarkably little is known of the biology of any species; they are generally considered to breed in fungi and rotting vegetation (see Lachaise, 1974). However three Afro-Tropical species, *L. decaryi*, *L. proxima* and an undescribed species near *L. sema*, are known to develop in cercopid spittle masses. *L. decaryi* was described (as *Ptyelusimyia decaryi*) from the spittle of *Ptyelus goudoti* Bennett in Malagasy (Seguy, 1932), and the other two species from spittle of cercopids in Nigeria (Medler and Adenuga, 1969) and Uganda (Odhiambo, 1958) respectively.

Larvae of *L. proxima* are found, in Nigeria, in the spittle masses of both *Ptyelus grossus* Fabricius and *Poophilus adustus* (Walker). The association of fly and cercopid is one of inquilism, the cercopid nymphs being unharmed by the presence of the drosophilid larvae in their spittle masses. In a manner similar to the larvae of *Cladochaeta* those of *Leuco-*

phenga attach themselves to the dorsal surfaces of the cercopid nymphs, and this is probably an adaptation for phoresy, since disturbed cercopid nymphs abandon their spittle masses and would, otherwise, leave their drosophilid guests behind to desiccate. The ventral surfaces of the larvae of *Leucophenga proxima* are adapted to attaching to the nymphs, with "pseudolegs" covered with chitinous hooks (Fig. 3); at least the larvae of those Japanese species of *Leucophenga* described by Okada (1968) do not possess similar pseudolegs. The cercopid associated *Cladochaeta inversa* shows a similar adaptation (Sturtevant 1942; Wheeler, 1952).

The extent to which the association between *L. proxima* and cercopids is obligatory is unclear. Collart (1939) reared *L. proxima* from fungi in Zaire but found the adults in association with the honey-dew of species of *Lecanium* (Homoptera:Coccoidea).

In the genus *Rhinoleucophenga* one species, *R. obesa*, has been reported to predate the coccid *Aclerda takahashii* Kuwana as larvae (Lima, 1935). Wheeler (1970) questions the occurrence of this North American species in Brazil, as reported by Lima, and there the matter must rest. However there are two species described in the genus *Gitona* that should probably be considered to be *Rhinoleucophenga* (Wheeler, Chapter 1; Basden, 1966). They are *G. brasiliensis* and *G. fluminensis* of South America. Larvae of both predate coccids (Lima, 1950). *G. brasiliensis* has a fairly wide Neotropical distribution (Wheeler, 1961) and a description of its biology has been published by Beingolea (1965).

At least six species of the coccid genus *Orthezia* are devoured by larval *G. brasiliensis* in Peru. The female fly lays her eggs on the back of the prey and the first instar *Gitona* penetrate the wax "marsupial" of the scale insect [in *Orthezia* the eggs are "protected between wax plates secreted from the end of the abdomen" (Imms, 1957)]. At first the fly larvae eat the egg mass of the scale-insect but eventually they devour the whole of their prey until just its cuticular exoskeleton remains. The *Gitona* larva then pupariates within its prey's remains.

So far undescribed species of *Amiota* have been found to predate three species of Homoptera on Reunion Island: *Saccharicoccus sacchari* (Cockerell) (Pseudococcidae), *Peregrinus maidis* (Ashmead) and *Perkinsiella saccharicida* Kirkaldy (both Delphacidae). These three species are all pests of sugar-cane (J. Etienne, personal communication).

The last species to be considered in this section is perhaps the most enigmatic and least known. It is *Amiota xyleboriphaga*, whose life cycle is, in some manner, associated with the wood beetle *Xyleborus fornicatus* Eichhoff, a pest of tea (*Camellia sinensis* (L.) O. Kunze) in Sri Lanka. The presence, in the tunnels of this beetle, of a fly was, apparently, first noted by Rutherford in 1914. It is presumably the same species

that was later described by Senior-White (1921, see also Jepson, 1921). According to Senior-White, Jepson had seen the larvae of *A. xyleboriphaga* "eat a pupa of the beetle, tunnelling completely inside, and sucking it dry in about twenty minutes". Labels on specimens of *A. xyleboriphaga* in the British Museum (London) are splendidly uninformative, for example, "bred from *X. fornicatus* in tea" (B. Cogan, *in litt.*). The status of *A. xyleboriphaga* as a predator must, however, be questioned in the light of the fact that *Xyleborus* is a typical ambrosia beetle, living in symbiotic association with fungi that grow in the beetle's tunnels (for reviews see Graham, 1967; Francke-Grosmann, 1967). These fungi [*Monacrosporidium* (Ascomycete; Moniliaceae) in the case of *X. fornicatus*] often produce sweet smelling esters and attract many inquilines to the galleries. It would not, therefore, be surprising were re-investigation to show that *A. xyleboriphaga* was mainly dependent on the beetle's fungi, rather than the beetle itself.

C. THE SUBFAMILY DROSOPHILINAE

1. *The genus Cladochaeta*

"One hot July day, while annoying some of those amphibious infants [the larvae of spittle bugs (Cercopidae)] by poking into their unpleasant habitations, I noticed some small dipterous larvae that were apparently enjoying life under the same conditions as the hemipter that built the foam. These flies were evidently able to go through the life cycle among the bubble, for the little pupae were there, glued to the leaves by the drying froth" (Ainslie, 1906). Thus heralds the discovery of the flies now known under the name *Cladochaeta*. Ainslie himself considered the flies he found to be *Drosophila sigmoides* but it was Sturtevant (1921) who pointed out that this was a misidentification for *D. inversa*, a species later taken by Malloch (in Malloch and McAtee, 1924) to be the type of the genus *Clastopteromyia*. In a subsequent revision Frota-Pessoa (1947) united Malloch's *Clastopteromyia* (shown by Wheeler and Takada, 1971, to be a synonym of *Cladochaeta*) and Duda's genus *Diathoneura* though this has not always been accepted (Wheeler, 1952; Wheeler and Takada 1971). Both genera are predominantly Neotropical in their distribution though *C. inversa* is found as far-north as Quebec and a species has been attributed to *Diathoneura* from Nepal (Okada, 1966).

All three species of *Cladochaeta* (i.e. *C. inversa*, *C. paradoxa* and *C. sturtevanti*) known in their pre-adult stages have larvae that are inquilines of cercopid nymphs. Having said this it should be pointed out that

several authors have, in the past, considered the relationship between drosophilid and cercopid to be a predatory one. For example Williams (cited by Lamb, 1918) writes of the larval *C. paradoxa* that their heads "were buried in the abdomen of the *Clastoptera* nymphs, the head usually being inserted between the dorsal abdominal plates" (see also Baerg, 1920 and Williams, 1923, 1931) (Fig. 4.). Wheeler (1952, also quoting Sturtevant) also considers that the drosophilid larvae predate the cercopids, since larvae removed from the spittle died.



FIG. 4. A larval *Cladochaeta* associated with a nymph of *Clastoptera* (from Baerg, 1920).

On the other hand Baerg (1920) and Bennett (1965) formed the opinion that the relationship was one of inquilinism. Both of these authors draw attention to the fact that the fly larvae only attach themselves (by well developed ventral hooks; Sturtevant 1942; Wheeler, 1952) to the cercopid nymphs when the latter are disturbed. As with the species of *Leucophenga*, discussed above (see Section II, B, 4), this has obvious advantages for the fly larva, for if the cercopid leaves its spittle when disturbed the fly larva will follow. Bennett (1965) reared eggs of *Cladochaeta* to pupae outside spittle.

The spittle masses of the cercopid nymphs are the products of the nymph's Malpighian tubules (see Marshall, 1966; Weaver and King, 1954; Hagley, 1965). They are rich in mucopolysaccharides, sugars and amino acids from the plant sap upon which the nymph is feeding. The spittle masses are by no means sterile and are contaminated by bacteria

(Wilson and Dorsey, 1957). There would appear to be little reason why they should not provide food for the development of a drosophilid.

The host specificity of *Cladochaeta* species is not known. According to Baerg (1920) *C. inversa* was common on spittle masses of *Clastoptera obtusa* (Say) (on *Alnus* sp.) but was absent from spittle masses of *C. proteus* (on *Cornus* sp.) nearby. It would appear that in the Eastern United States of America *C. obtusa* is the main host of *Cladochaeta inversa* but that in California the main host is *C. lineaticollis* Stal (Wheeler, 1952). In Trinidad several host species have been recorded by Bennett (1965) and the genus has been considered for the biological control of some pests of *Theobroma*. Host specificity may, of course, reflect the composition of the spittle, itself dependant upon the plant upon which the cercopid feeds, as well as on the species of cercopid *per se*.

Pipkin (1965; Pipkin *et al.*, 1966) collected various species of *Cladochaeta* in Central America under conditions suggesting that their larvae were flower breeders: for example she regularly collected adult flies over fallen fruits and flowers and bred a fly from the fallen fruit of *Clusia* sp. In view of these studies it must remain uncertain to what extent members of this genus are exclusively adapted to living in association with cercopid nymphs.

2. *The genus Drosophila*

Relatively few species of *Drosophila* have departed far from the typical larval habits of the genus. In fact only the two species of flies whose larvae are associated with land crabs (and these are probably micro-organism feeders) and the very specialized *simulivora* species group, whose larvae are carnivores, warrant inclusion here.

(a) *The simulivora species group*

The *simulivora* species group was established by Tsacas and Disney (1974) for a number of Afro-Tropical species (four have been described) the larvae of which are both predatory and either truly aquatic or semi-aquatic. The relationships of this homogeneous group of species within the subgenus *Drosophila* are unclear, though there is a suggestion of a relationship to the *polychaeta* species group, whose members are fungal feeders.

The first species to be described in what is now recognized as the *simulivora* species groups was *D. gibbinsi*, described from material collected in the River Nile in East Africa (Aubertin, 1937). The larvae of this species were described in an accompanying paper by Smart (1937) and Smart noted not only their adaptation to aquatic life but also the

fact that their guts contained the head capsules of chironomids (but see Disney, 1975, who restudied Smart's material and found the guts to include remains of both chironomids and simuliids). Nothing else was heard of *D. gibbinsi*, or anything like it, until Disney's discovery of two closely related species in West Africa (Tsacas and Disney, 1974) and Gouteux's rediscovery of *D. gibbinsi* itself (Gouteux, 1976). Subsequently a fourth species was discovered in the Gabon.

With respect to their larval habitats the four known species of the *simulivora* group are either truly aquatic and carnivorous, living on eggs and young larvae of simuliids and chironomids (i.e. *D. gibbinsi*, *D. cogani* and *D. simulivora*), or semi-aquatic living in the gelatinous egg masses of Odonata and carnivorous, feeding on the eggs of the dragonflies (i.e. *D. libellulosa*).

Tsacas and Legrand (1979) suggest that *D. libellulosa* represents an intermediate evolutionary step between terrestrial ancestors and the truly aquatic species. Certainly two of the most obvious larval adaptations of the three aquatic species, their anterior spiracles and their ventral hooks, are far less well developed in *libellulosa* than in the other three species (Fig. 5).

The anterior spiracles of the three aquatic species are quite remarkable, in both their size and in the number of their feather like papillae (Fig. 5). Presumably these anterior spiracles act as tracheal gills (Smart, 1937). In *D. simulivora* each anterior spiracle possesses nearly 100 papillae.

The second marked adaptation of the *simulivora* group larvae are the extensively developed rows of large sclerotized ventral hooks on the abdominal segments (Fig. 5). Each segment carries three double rows of hooks; in *D. cogani* lateral rows face anterior and the medial rows face posterior-wards (in *D. gibbinsi* the opposite is true). Tsacas and Disney (1974) point out that a similar adaptation also occurs in larval Empididae, another group which feeds on larval Simuliidae, and they suggest that the hooks help the larvae to move and retain a firm "foot-hold" in the fast streams in which they live (see discussion in Smart, 1937).

All known members of the *simulivora* species group are carnivorous as larvae. In West Africa, at least, the eggs and young larvae of Simuliidae and Chironomidae appear to be the chief diet of all species except *D. libellulosa*. All species have rather special mouth parts, for example in the three aquatic species there is an extra sclerite and the mouth hooks are fused dorsally (both unique features in the Drosophilidae) (Tsacas and Disney, 1974, Gouteux, 1976).

The habits of the larval *D. libellulosa* are, as far as is known, re-

stricted to the egg masses of *Malgassophlebia aequatoris* Legrand (Odonata) (Legrand, 1979). These egg masses are not aquatic, but are to be found on vegetation bordering forest streams. There is a remarkable parallel between this habitat and those of the *Zygothrica* species feeding on frog's eggs in Central America (see below, Section II, C, 4). Indeed Tsacas and Legrand (1979) suggest that amphibian egg masses may be an alternative habitat for *D. libellulosa*. The entire development of the larvae occurs in the egg masses, the eggs being consumed and the animals pupating within the egg jelly.

The three truly aquatic species complete their entire larval development in water. Oviposition has never been observed, yet even *D. melanogaster* will oviposit on water (Yoon and Fox, 1965) and egg laying would not appear to be any major problem for these species. Pupation occurs in air or just below the air-water interface (Gouteux, 1976) the larvae adhering to a suitable leaf (Smart, 1937: incidentally

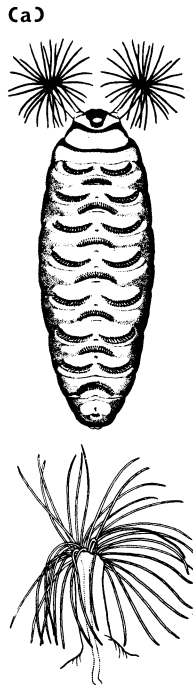
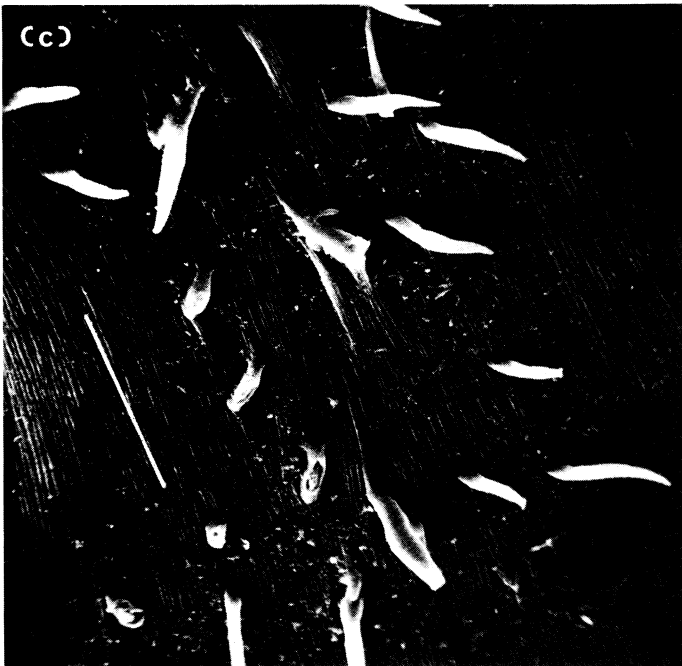


FIG. 5. (a) Pupa of *Drosophila gibbinsi* showing the rows of ventral hooks and the anterior spiracles (from Smart, 1937). (b) and (c) Scanning electron micrographs of the ventral hooks of (b) *D. simulivora* and (c) of *D. libellulosa* (from Tsacas and Legrand, 1979).



this paper appears to be the first that correctly attributes to the larval salivary gland of *Drosophila* its function, i.e. the production of the puparial glue, see Fraenkel and Brookes, 1953). Whether or not eclosion can occur below the water line is unknown; perhaps the flies only eclose when the water level drops. In the case of *D. libellulosa* the pupae are orientated within the egg jelly in such a way that eclosion occurs without the flies becoming trapped in the egg's jelly.

It is very unlikely that we know the full extent of the *simulivora* radiation, for example L. Tsacas (*in litt.*) informs me of two undescribed species from East Africa. *D. libellulosa* is known only from the Gabon, *D. cogani* and *D. simulivora* from West Africa (Liberia, Camerouns) and *D. gibbinsi* from Uganda, Rwanda, Natal and, perhaps, from Malagassy (though this may be a fifth species). The extent to which the species display prey specificity (see Tsacas and Disney, 1974; Disney, 1975) is also unknown. In view of the opinion of Tsacas and Disney (1974) that these species may be useful for the biological control of *Simulium damnosum* Theobald, an important vector of human disease in Africa, further studies of these species are obviously desirable.

(b) *Crab associated Drosophila*

The association of *Lissocephala powelli* and land crabs on Christmas Island has already been mentioned in this review. In addition to this species there are also two *Drosophila* that have evolved a remarkably similar adaptation (Carson, 1974). The association of *Drosophila* and land crabs was first noted by Hubbard (1895) but it is only recently that we have learnt very much more about these interesting flies. The two species concerned are the *repleta* species group member *D. carcinophila* (Wheeler, 1960) and the *virilis-quinaria* section species *D. endobranhia* (Carson and Wheeler, 1968).

Both *D. carcinophila* and *D. endobranhia* are found in the Caribbean and both are associated with the land crab *Gecarcinus ruricola* (L.) though not sympatrically. The larvae of *D. carcinophila* live in the nephric groove of the crab, a "microorganism-laden urinal" (Carson, 1974), whilst the larvae of *D. endobranhia* are found in the nephric groove only in the first instar, they then migrate into the gill chambers of the crab. The two species also differ in the site their larvae choose for pupariation, those of *D. carcinophila* pupariate on the crab's third maxilliped (Fig. 6) whilst those of *D. endobranhia*, like the larvae of *Lissocephala powelli*, leave their host to pupariate in the soil.

The adults of both *D. carcinophila* and *D. endobranhia* (but not of *L. powelli*) are also associated closely with their host crabs (Carson, 1967, 1974).

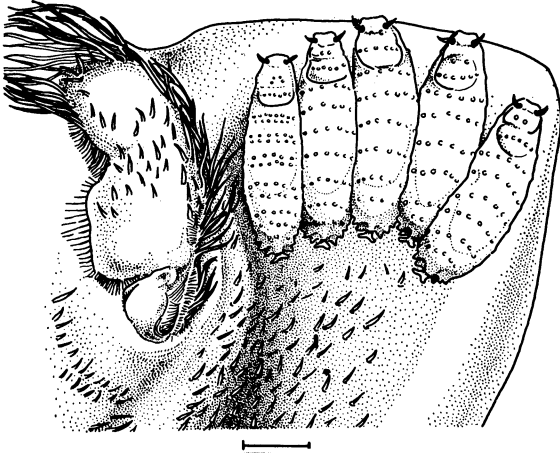


FIG. 6. Pupae of *Drosophila carcinophila* on the third maxilliped of *Gecarcinus ruricola* (from Carson, 1967).

It is truly remarkable that three species of drosophilid have adapted to a similar commensal association with land crabs. The fact that the excretory products of the crabs provide an ideal, and to the flies, accessible, site for the culture of microorganisms is certainly one contributory factor.

(c) *A miscellany*

It seems worthwhile to record examples of bizarre habitats of otherwise "conventional" *Drosophila* under this heading. The rather non-discriminating habits of *D. busckii* are well known (see Sturtevant, 1921; Okada and Sasakawa, 1956). However the occurrence of larval *D. busckii* in the head of a Hottentott, arriving in Germany from South West Africa (Schulze, 1912), and in the scum covering formalin-preserved fish in a Zoology Department (M. Ashburner, unpublished observations; see also Sturtevant, 1912) are peculiarly nasty habitats even for this fly.

True myiasis by species of *Drosophila* is, fortunately, rare—I can find only the observations of Escher-Kundig (1902) of *D. phalerata* larvae being bred from a postoperatively infected breast tumor of a 50 year old Turk.

Two species, *D. busckii* and *D. repleta*, are said to parasitize the larvae of Lepidoptera (Bonnamour 1921; see also Seguy, 1933a, 1951; Mages, 1956). Attempts to repeat Bonnamour's observation, of the parasitism of larval *Pieris brassicae* L. by *D. busckii*, failed, though the fly larvae

did breed very well on the caterpillar's artificial diet (M. Ashburner and C. Redfern, unpublished observations). Lachaise (Volume 3) reviews the known examples of drosophilids developing in the cadavers of Lepidoptera.

3. *The genus Titanochaeta*

This genus, probably related to *Scaptomyza* (Hardy, 1965), is endemic to the Hawaiian islands. All eleven described species would appear to predate, as larvae, the eggs of the endemic Hawaiian spider family Thomisidae (Carson, 1971). Very little has been learnt of their biology since their discovery by Knab in 1914 (see also Swezey, 1929). According to Carson (1971) the female fly lays a few eggs within the spider's egg mass, which is then completely devoured by the larvae which pupariate within the remains of the egg sac (Wirth, 1952).

4. *The genus Zygothrica*

The sixty or so species of this genus are predominantly Neotropical in their distribution, though several species have recently been described from South-East Asia and a few are known from the Pacific islands. Very little is known of their biology though most species are thought to be fungus breeders (Burla, 1956; Takada, 1976). One, presumably aberrant, species has larvae which feed upon the eggs and early embryos of tree frogs (Villa, 1977, 1978). The egg masses of several species of frog are apparently infested, though in Nicaragua *Centrolenella fleischmanni* (Boettger) is the chief host. This, and other frogs whose eggs are prey, lay their egg masses attached to leaves, rather than being aquatic.

The female *Zygothrica* (the species studied by Villa is either *Z. pleurostrigata*, known from Brazil, or a very similar species, M. R. Wheeler *in litt.*) lays her eggs below the surface of the gelatinous egg mass and the larvae, on hatching, devour the frog embryos. It is very important that the flies synchronize their egg laying with that of the frogs since by the time the frogs have developed to the tadpole stage they are able to ward off attack by the drosophilid larvae (Fig. 7). Villa (1978) suggests that the drosophilid have found species of frog for which their own life cycle is pre-adapted; the developmental period of the chief host, *C. fleischmanni*, being the longest of all species studied by Villa. The fate of the *Zygothrica* in the dry season, when the frogs do not breed, is unknown (a similar problem faces *D. libellulosa* in the Gabon, Tsacas and Legrand, 1979).

In addition to *Zygothrica* near *pleurostrigata* Villa (1978) also describes

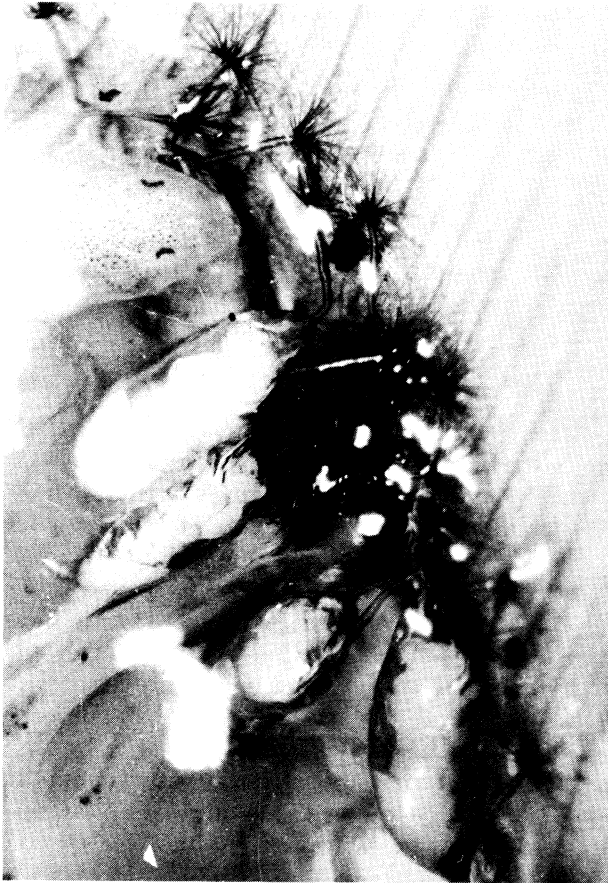


FIG. 7. Pupae of the frog fly *Zygothrica* sp. in the egg jelly mass of *Centrolenella fleischmanni*. Note surviving frog tadpole upper left and the anterior spiracles of the pupae (compare these with those of *D. gibbinsi* in Fig. 5(a) (from Villa, 1978).

a species of *Leucopsis* whose larvae have a very similar habitat in *Centrolenella* spp. egg masses. This too is a drosophilid!—a member of the subgenus *Drosophila* (Villa, 1980). It may coexist with the *Zygothrica* sp. in an egg mass. Whilst the *Zygothrica* sp. pupate within the egg jelly those of the *Drosophila* species leave the egg mass to pupate. The pupae of the *Drosophila* sp. are not, like those of the *Zygothrica* sp., adapted to a “semi-aquatic” pupal life. The *Zygothrica* sp. pupae have very long anterior spiracular horns [with an anterior horn index, i.e. the ratio length of pupa without anterior spiracles to length of anterior spiracles (Okada, 1968), of about 1.5 (compare with an index of 12

for *D. melanogaster*)], with over 20 long filaments which spread out on the jelly surface (Villa 1978). The pupae of *D. libellulosa* also have a very low horn index (about 4), their aquatic *simulivora* group relatives having indices between 8 and 9.

III. Conclusion

The known associations between species of the family Drosophilidae and other animals are summarized in Table IV. Assuredly many others remain to be discovered but for this to happen *Drosophila* biologists will either have to broaden the scope of their collecting methods or rely upon the serendipity of other entomologists.

The commensal association of drosophilids and other animals are perhaps best seen in the case of the crab-flies. All the three species which have, quite independently, evolved an association with land crabs remain, like members of the family in general, microorganism feeders (the same may be true for the cercopid-associated flies). Indeed Wallace (1978) so successfully adapted a laboratory strain of *Drosophila virilis* to a not dissimilar habitat, plastic "felt" soaked in decomposing human urine, that, after one year, these flies were unable to grow on standard laboratory *Drosophila* medium. However the adaptation of the crab-flies to their hosts must require much more than an adaptation to a crab's discharges as a food source; it must, of course, involve the evolution of a complete behavioural repertoire.

It is interesting that in the other associations that may be regarded as commensal, i.e. of *Cacoxenus indagator* and *C. apidoxenus* with bees, the larval nutrition is also not unexceptional for drosophilids, i.e. pollen. Many of the flower-breeding *Drosophila*, for example *D. flavopilosa*, have pollen-feeding larvae.

Amongst the predatory species of the family one fact stands out very strongly. That is the close association between many steganine genera and Homoptera and, moreover, with species of Homoptera which produce copious exuvates, such as waxes and honey-dew.

The honey-dew of the Homoptera are excretory products rich in sugars and amino acids (Gray, 1952; Ewart and Metcalfe 1956). The accumulation of these exuvates on the leaves of the infested plants leads, especially in the tropics but also in temperate regions, to the growth of what are commonly known as "sooty-moulds" (Hughes, 1976). These are saprophytic fungi, often of the Ascomycete genus *Capnodium* (Leach, 1940; Viennot-Bourgin, 1949; see also Dick, 1969). In Europe the so-called "black yeast", *Aureobasidium pullulans* (Hyphomycetes), is also a common growth on honey-dew contaminated

TABLE IV. A summary of the association of *Drosophilidae* and other animals

"Host".		Fly	Type of association ^a	
Crustacea:	Eucarida	<i>Lissocephala powelli</i>	commensal	
		<i>Drosophila carcinophila</i>	commensal	
		<i>D. endobranchia</i>	commensal	
Insecta:	Homoptera:	Cercopidae	<i>Leucophenga</i> spp.	commensal
			<i>Cladochaeta</i> spp.	commensal
			<i>Cacoxenus perspicax</i>	predatory
	Delphacidae	<i>Amiota</i> sp.	predatory	
		Psyllidae	<i>Pseudiastata</i> sp. ?	?
	Aleyrodidae	<i>Acletoxenus</i> spp.	predatory	
	Ortheziidae	<i>Rhinoleucophenga</i>	predatory	
		"American <i>Gitona</i> " ^b	predatory	
	Pseudococcidae	<i>Cacoxenus perspicax</i>	predatory	
		<i>Amiota</i> sp.	predatory	
		<i>Pseudiastata</i> spp.	predatory	
	Hymenoptera:	Apoidea	<i>Cacoxenus</i> spp.	commensal/predatory
	Coleoptera:	Scolytidae	<i>Amiota xyleboriphaga</i>	predatory?
	Diptera:	Chironomidae	<i>Drosophila simulivora</i> sp.	predatory
			group	
Simuliidae		<i>Drosophila simulivora</i> sp.	predatory	
Odonata:	Libellulidae	group		
		<i>Drosophila simulivora</i> sp.	predatory	
Archnida:	Araneida	<i>Titanochaeta</i> spp.	predatory	
Amphibia:	Anura	<i>Zygothrica</i> spp.	predatory	

^aI use these terms in their colloquial senses: see Starr (1975) for a discussion of the classification of the types of association between different organisms. "Commensal" is, in Starr's terminology, "an exhabitational symbiosis, in which the exhabiting symbiont feeds on surplus food captured by the exhabited (substrate) symbiont" and "predation" is "an exhabitational antagonistic, nutritionally dependant, necrotrophic symbiosis, with behavioural overtones". ^bSee Page 407.

leaves. Both the honey-dew itself and the moulds growing on it may well provide food for adult drosophilids (see Collart, 1939). Indeed *Aureobasidium* has been isolated from the crops of wild caught *Drosophila* (Begon, 1973) and the sooty-moulds have been found to be eaten by other flies (Yamamoto, 1951). Although I know of no drosophilid whose larvae feed on sooty-moulds or *Aureobasidium* the fact that many drosophilids have leaf-mining larvae should not be forgotten when considering the origin of those species whose larvae now predate the Homoptera.

The predation of Homoptera by drosophilids (paralleled, inci-

dentially, in the families Cecidomyiidae, see Nijveldt, 1969, and Chamaemyiidae) is aided by the fact that the prey are both gregarious in habit and relatively immobile.

True parasitism is unknown in the Drosophilidae. However, I cannot end this review without drawing attention to the family *Cryptochaetidae*, still considered by some modern dipterists (e.g. Oldroyd, 1964) to be included within the Drosophilidae. Some 25 species have been described in this family and all appear to be endoparasites of monophlebine coccids (*Margarodidae*), yet another Homopteran association. The majority of species are Afro-Tropical in their distribution, although nine are known from the Oriental region and Japan, three from Australia and two from Europe. An Australian species, *C. iceryae* (Williston) was introduced to California in the last century, and subsequently to many other regions, for the biological control of the *Citrus* pest *Pericleria purchasi* (Maskell). The Californian introductions were dramatically successful (see Smith and Compere, 1916; Thorpe, 1930; Debach, 1974).

Our knowledge of the biology of *Cryptochaetum* stems largely from three studies by Thorpe (1930, 1934, 1941) of *C. iceryae*, of the European *C. grandicorne* and of various African species. The adult female fly oviposits directly into the haemocoel of an immature scale insect host. The first instar larvae of the fly are quite extraordinary, they lack mouth parts, a functional gut, a tracheal system and show little evidence of segmentation. They apparently absorb nutrients from their host through their very thin cuticle. They, and subsequent instars, possess two remarkable "tails" which, by the second instar become heavily invested with tracheae: these tails function as tracheal gills [similar "tails" are seen in some larval *Conopidae*, internal parasites of *Bombus* spp. (de Meijere, 1904)]. By the second instar mouth hooks have developed but the gut remains closed until the final instar. Only in the last instar does the parasite devour its host, leaving only the cuticle through which the anterior spiracles are forced at puparium formation. Adult *Cryptochaetum* feed on honey-dew (Clausen, 1940).

Amongst the drosophilids only *Gitona brasiliensis* approaches the degree of adaptation to true endoparasitism seen in the *Cryptochaetidae*. However this statement must be tempered by our almost complete ignorance of the biology of many other predators, for example of *Cacoxenus perspicax*.

Remarkably "unusual" habitats have been colonized independently by quite different drosophilids. The example of the three crab-associated flies has already been discussed but, in addition, there are the two quite different groups (*Leucophenga* and *Cladochaeta*) associated with cercopid

spittle masses, two quite different groups (*Drosophila* and *Zygothrica*) associated with the gelatinous egg masses of dragon flies and frogs and the several genera which predate Homoptera. The study of the genetic mechanisms that have allowed these adaptations to occur will be fascinating.

ACKNOWLEDGEMENTS

I am very grateful to several colleagues for reading and commenting on a draft of this review and for providing me with information—Drs. Ian Bock, Hampton Carson, Daniel Lachaise, Lynn Throckmorton, Leonardis Tsacas and Marshall Wheeler. Dr. Wheeler has had to suffer my persistent inquiries and to him I owe especial thanks. I am also very grateful to Dr. Roger Blackman and his colleagues at the British Museum (Natural History), London, for help with the nomenclature of species from non-drosophilid taxa. I thank Dr. J. Villa for a copy of his thesis and for original photographs, and Dr. L. Tsacas for the original of Figure 5(b and c). Dr. B. Cogan has also been most helpful in answering my queries concerning specimens in the British Museum. I thank Dr. George Varley for live material of *Acletoxenus* and for information about this fly and the Oxford Scientific Film Unit for live material of *Cacoxenus*. Dr. H. Hudson was kind enough to teach me about sooty-moulds. Although this review could not have been written without this help I remain solely responsible for its content.

References

(Those marked with an asterisk have not been seen in the original).

- AINSLIE, C. N. (1906). Guests of spittle insects. *Can. Ent.* **38**, 44.
- ALI, S. M. (1963). A preliminary note on the natural enemies of sugar-cane mealy-bug, *Pseudococcus saccharifolii* (Green) in Bihar (India) *Indian J. Sugarcane Res. Dev.* **7**, 131–132.
- AUBERTIN, D. (1937). A new species of *Drosophila*, *D. gibbinsi* sp.n., from Uganda (Diptera). *Proc. Roy. Ent. Soc. Lond. B.* **6**, 169.
- AYYAR, T. V. R. (1938). The rice mealy-bug in South India. *J. Mysore Agric. Exp. Union.* **17**(4), 179–188.
- BAERG, W. J. (1920). An unusual case of parasitism on *Clastoptera obtusa* Say (Hemip., Cercopidae; Dip., Drosophilidae). *Ent. News* **31**, 20–21.
- BASDEN, E. B. (1961). Notes on the Camillidae (Diptera) in Strobl's collection and on the Biology of *Camilla*. *Not. Ent.* **XLI**, 124–129.
- BASDEN, E. B. (1966). Systematics of Drosophilidae. In: "Institute of Animal Genetics, University of Edinburgh, Research Report 1962–1965". University of Edinburgh.
- BEARDSLEY, J. W. (1957). *Trionymus rostellum* Lodbell in Hawaii (Homoptera: Pseudococcidae). *Proc. Hawaiian Ent. Soc.* **XVI**, 209–211.

- BEARDSLEY, J. W. (1960). Observations on sugar cane mealybugs in Hawaii. *In: Proc. Int. Soc. Sugar Cane Technologists*, Tenth Congress: 954-961. Elsevier, Amsterdam.
- BEGON, M. (1973). Preliminary observations on the yeasts associated with *Drosophila obscura* and *D. subobscura*. *Dros. Inf. Serv.* **10**, 128-129.
- BEINGOLEA, O. (1965). Notas sobre *Orthezia olivicola* n.sp. (Hompt: Ortheziidae), plaga del Olivo en el Peru. *Rev. Peruana Ent.* **8**, 1-44.
- BENNETT, F. D. (1965). Observations on the role of *Clastopterymyia* spp. inhabitants of spittle-masses of *Clastoptera* spp. in the West Indies. *Commonwealth Inst. Biological Control, Tech. Bull.* **5**, 98-100.
- BONNAMOUR, S. (1921). Note sur deux Diptères parasites nouveaux de la Piéride du chou (*Drosophila rubrostriata* Beck et *Phora chlorogaster* Beck). *Bull. Soc. Ent. Fr.* **1921** (15), 217-219.
- BOCK, I. R. (1981). Drosophilidae of Australia. V. Remaining genera and synopsis (Insecta; Diptera). *Aust. J. Zool.* (in press).
- BOX, H. E. (1953). List of sugar-cane insects. Commonwealth Institute of Entomology, London. 101 pp.
- BRAUER, F. (1883). Die Zweiflügler des Kaiserlichen Museums zu Wien. III Systematische Studien auf Grundlage der Dipteren-larven nebst einer Zusammensetzung von Beispielen aus der Literatur über dieselben und Beschreibung neuer Formen. *Denkschrift. Kaiserl. Akad. Wissenschaft., Math.-Naturwiss. Class* **47**, 1-100.
- BURLA, H. (1956). Die Drosophiliden-Gattung *Zygothrica* und ihre Beziehung zur *Drosophila*-untergattung *Hirtodrosophila*. *Mitt. Mus. Berlin* **32**, 189-321.
- CARSON, H. L. (1967). The association between *Drosophila carcinophila*. Wheeler and its host, the land crab *Gecarcinus ruricola* (L.). *Am. Midl. Nat.* **78**, 324-343.
- CARSON, H. L. (1971). The ecology of *Drosophila* breeding sites. Harold L. Lyon Arboretum Lecture No. 2, University of Hawaii Press, Honolulu. 28 pp.
- CARSON, H. L. (1974). Three flies and three islands: Parallel evolution in *Drosophila*. *Proc. natl. Acad. Sci. U.S.A.* **71**, 3517-3521.
- CARSON, H. L. and WHEELER M. R. (1968). *Drosophila endobranchia*, a new Drosophild associated with land crabs in the West Indies. *Ann. Ent. Soc. Am.* **61**, 675-678.
- CARSON, H. L. and WHEELER, M. R. (1973). A new crab fly from Christmas Island, Indian Ocean (Diptera: Drosophilidae). *Pacific Insects* **15**, 199-208.
- CARTER, W. (1935). Studies on the biological control of *Pseudococcus brevipes* (Ck1.) in Jamaica and Central America, *J. econ. Ent.* **28**, 1037-1041.
- CLAUSEN, C. P. (1940). "Entomophagous Insects". Mc-Graw Hill, New York. 680 pp.
- CLAUSEN, C. P. and BERRY, P. A. (1932). The citrus blackfly in Asia and the importation of its natural enemies into Tropical America. *United States Department of Agriculture, Technical Bull.* No. 320. 58 pp.
- COLLART, A. (1935). *Gitona frontalis* n.sp., parasite de Coccides au Congo Belge (Diptera: Drosophilidae). *Bull. Musée Roy.d'Hist. nat. Belg.* **11**(18), 1-8.
- COLLART, A. (1939). Revision des *Leucophenga* africains décrit par C. F. Adams (Diptera, Drosophilidae). *Bull. Musée Roy.d'Hist. nat. Belg.* **15**(21), 1-18.
- COLLIN, J. E. (1902). Note on *Acletoxenus syrphoides*, Frauenfeld. *Ent. Mon. Mag.* **2nd Ser.** **38**, 1-3.
- DAVID, J. and TSACAS, L. (1975). Les Drosophilidae (Diptera) de l'île de la Réunion et de l'île Maurice. *Beitr. Ent.* **25**, 245-254.
- DEBACH, P. (1974). "Biological Control by Natural Enemies". University Press, Cambridge. 323 pp.

- DICK, J. (1969). The mealy-bugs of sugar-cane. In: "Pests of Sugar-cane." (Editors: J. R. Williams, J. R. Metcalfe, R. W. Mungomery and R. Mather). Elsevier, Amsterdam. pp 343-365.
- DISNEY, R. H. L. (1975). *Drosophila gibbinsi* larvae also eat *Simulium*. *Trans. Roy. Soc. trop. Med. Hyg.* **69**, 365-366.
- DUDA, O. (1924). Beitrag zur Systematik der Drosophiliden unter besonderer Berücksichtigung der Paläarktischen und Orientalischen Arten (Dipteren). *Arch. Naturgesch.* **90**(A3), 172-234.
- DUDA, O. (1935). *Drosophilidae*. In: "Die Fliegen der Paläarktischen Region", (Editor E. Lindner), 58 g. E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nagele) G.M.B.H. Stuttgart. 118 pp.
- DUDA, O. (1936). Weitere neue afrikanische und orientalische akalyptrate Musciden (Diptera) des British Museum. *Ann. Mag. Nat. Hist.* 10th Series **18**(105), 337-351.
- ESCHER-KUNDIG, J. (1902). (No title, Report of Meeting on 6 July 1902) *Mitt. Schweiz. Ent. Gess.* **10**, 446-448.
- EWART, W. H. and METCALFE, R. L. (1956). Preliminary studies of sugars and amino acids in the honeydew of five species of coccids feeding on Citrus in California. *Ann. Am. Ent. Soc.* **49**, 441-447.
- FIGUEIREDO, E. R. (1938). A moscas *Pseudiasata brasiliensis*, predadora da cochonilha *Pseudococcus brevipes*. *O Biologico* **4**, 206-207.
- FRAENKEL, G. and BROOKES, V. J. (1953). The process by which the puparia of many species of flies become fixed to a substrate. *Biol. Bull. (Woods Hole)* **105**, 442-449.
- FRANCKE-GROSMANN, H. (1967). Ectosymbiosis in wood inhabiting insects. In: "Symbiosis", (Ed. S. M. Henry). Vol. II, pp. 142-205. Academic Press, New York and London.
- FREE, J. B. and WILLIAMS, E. H. (1970). Preliminary investigations on the occupation of artificial nests by *Osmia rufa* L. (Hymenoptera; Megachilidae). *J. Appl. Ecol.* **7**, 559-566.
- FROTA-PESSOA, O. (1947). Revisão do gênero *Clastopteryomyia*. *Sum. brazil. biol.* **1**(12), 181-241.
- FULLAWAY, D. T. (1920). Natural control of scale insects in Hawaii. *Proc. Hawaiian Ent. Soc.* **IV**, 237-246.
- FULLAWAY, D. T. (1933). Report of Entomologist. *Hawaii Forestry and Agric.* **30**, 55-59.
- GAUTIER, C. (1922). Un Aleurode parasite du Poirier et du Frene, *Trialeurodes inaequalis* n.sp. (Hemiptera, Aleurodidae). *Ann. Soc. Ent. Fr.* **91**, 337-350.
- GHESQUIERE, J. (1934) *L'Elaeis guineensis* Jacq. est-ile africain ou americain? *Rev. Bot. appl.* **XIV**(153), 340.
- GIRAUD, J. (1861). Fragments Entomologiques. *Verhandl. Kaiser-Königl. zool.-bot. Gesell. Wien.* **XI**, 447-494.
- GOLFARI, L. (1937). Contributia alla conoscenza dell Entomofauna del Pero (*Pirus communis* L.). *Boll. Ist. Ent. Bologna.* **9**, 206-249.
- GONCALVES, C. R. (1939). Biologia de uma *Pseudiasata* depredadora de *Pseudococcus brevipes*. *Physis (Rev. Soc. Argentina Cienc. Nat.)* **XVII**, 103-112.
- GOSECO, F. P. (1932). The pink mealy-bug, *Trionomyus sacchari* Ckll. as a pest of sugar-cane in the Philippines. *Sugar News* **13**, 201-206.
- GOUTEUX, J-P (1976). Nouveau gite, données éthologiques et morphologiques pour une *Drosophile* aquatique du groupe *simulivora* Tsacas and Disney 1974: *Drosophila*

- gibbinsi* Aubertin 1937 (Diptera: Drosophilidae). *C. R. Acad. Sci. Paris Ser. D.* **282**, 2191–2194.
- GRAHAM, K. (1967). Fungal-insect mutualism in trees and timber. *Ann. Rev. Entomol.* **12**, 105–126.
- GRAY, R. A. (1952). Composition of honeydew excreted by Pineapple mealy-bugs. *Science* **115**, 129–133.
- HACKMAN, W. (1969). Some Helcomyzidae, Opomyzidae, Sphaeroceridea, Diastatidae, Drosophilidae, Scatophagidae and Hibboboscidae (Diptera) collected in Southern Spain, with description of a new species of *Acantholeria*. *Ent. Meddelelser.* **37**, 161–181.
- HAGLEY, E. A. C. (1965). Site of feeding of the frog-hopper. *Report Tate and Lyle Central Agric. Res. Stn. Trinidad 1965*, 408–413.
- HAMM, A. H. (1932). Diptera (Milichiidae) bred from the nest of the bee *Anthrophora pilipes* F. *Proc. Ent. Soc. Lond.* **6(III)**, 81–82.
- HARDY, D. E. (1959). A review of the genus *Pseudiasata* Coquillett (Drosophilidae, Diptera). *Proc. Hawaiian Ent. Soc.* **17**, 76–82.
- HARDY, D. E. (1965). The Insects of Hawaii **12**, Diptera: Cyclorrhapha II Series Schizophora Section Acalyptera I Family Drosophilidae. University of Hawaii Press, Honolulu.
- HARDY, D. E. and WHEELER, M. R. (1960). *Paracoxenus*, new genus, with notes on *Coxenus indagator* Loew (Diptera: Drosophilidae). *Ann. Ent. Soc. Am.* **53**, 356–359.
- HUBBARD, H. G. (1895). (Meeting report, November 1st, 1894). *Proc. Ent. Soc. Washington.* **III**, 183–185.
- HUGHES, S. J. (1976). Sooty moulds. *Mycologia* **68**, 693–820.
- IMMS, A. D. (1957). "A General Textbook of Entomology". Ninth edition revised by O. W. Richards and R. G. Davis. Methuen and Co., London. 886 pp.
- JENKINSON, F. (1901). *Ent. Month. Mag.* **37**, 300.
- JEPSON, F.-P. (1921). Shot-hole borer investigations. *Tropical Ag. Peradeniya.* **56(1)**, 23–30.
- JUILLARD, C. (1947). *Coxenus indagator* Loew (Dipt. Drosophilidae). Contribution à la biologie d'une parasite d'*Osmia rufa* L. *Mitt. Schweiz. Ent. Gesell.* **20**, 587–593.
- JUILLARD, C. (1948). Le comportement des larves de *Coxenus indagator* dans les nids de l'*Osmia rufa*. *Mitt. Schweiz. Ent. Gesell.* **21**, 547–554.
- KALTENBACH, J. H. (1874). Die Pflanzenfeinde aus der Klasse der Insekten. Julius Hoffman, Stuttgart. 848 pp.
- KNAB, F. (1914). Drosophilidae with parasitic larvae. *Insector Inscitiae Menstruus* **2(11)**, 165–169.
- KROBER, O. (1912). Beitrag zur Biologie der Drosophilinae. *Zeit. wissenschaft. Insektenbiol.* **8(6-7)**, 235–236.
- LACHAISE, D. (1974). Les drosophilides des savanas préforestières de la région tropical de Lamto (Cote-d'Ivoire). V. Les régimes alimentaires. *Ann. Soc. Ent. Fr. N.S.* **10**, 3–50.
- LACHAISE, D. (1977). Niche separation of African *Lissocephala* within the *Ficus* community. *Oecologia* **31**, 201–214.
- LAMB, C. G. (1918). On a parasitic *Drosophila* from Trinidad. *Bull. Ent. Res.* **9**, 157–162.
- LEACH, J. L. (1940). "Insect Transmission of Plant Diseases". McGraw-Hill, New York and London. 615 pp.
- LEGRAND, J. (1979). Morphologie, Biologie et Ecologie de *Malgassophlebia aequatoris*,

- n.sp., nouveau *Tetratheminae* du Gabon (*Odonata: Libellulidae*) *Rev. fr. Ent.* (N.S.) **1**, 3-12.
- LEVIN, M. D. (1957). Artificial nesting burrows of *Osmia lignaria* Say. *J. econ. Ent.* **50**, 506-507.
- LIMA, A. DA C. (1935). Um Drosophilideo predador de Coccideos. *Chacaras e Quintaes* **5(1)**, 61-63.
- LIMA, A. DA C. (1937). Outras moscas cujas larvas sao predadoras de Coccideos. *Chacaras e Quintaes* **5(1)**, 179-182.
- LIMA, A. DA C. (1950). Duas espécies de *Gitona* predadoras de Coccideos do género *Orthezia* (Diptera: Drosophilidae). *Arthropoda* **1**, 247-253.
- LOEW, H. (as Low, H.) (1847). Mittheilungen über die Verwandlungsgeschichte einiger Insekten and uber ihren Haushalt auf Pflanzen. In: Allgemeine deutsche Naturhistorische Zeitung, Editor, C. Tr. Sachse. 2nd year, 4th Part: 289-301. Arnoldische Buchhandlung, Dresden and Leipzig.
- LOEW, W. (1858). Ueber *Cacoxenus indagator*, nov. sp und seine Verwandten. *Wiener Entomolog. Monatschrift*. July 1858, **2(7)**, 213-222.
- LOEW, H. (1864). *Gitona formosa*, eine neue deutsche Art. *Wein. Entomolog. Monatschrift*. **8(11)**, 366-369.
- MAGES, L. (1956). Un nouveau parasite des abeilles. *Gazette Apicole* **57**, 86.
- MALLOCH, J. R. (1924a). Two Drosophilidae from Coimbatore. *Mem. Dept. Agric. India. Entomological Series* **8(6)**, 63-65.
- MALLOCH, J. R. (1924b). Notes on Australian Diptera No. IV. *Proc. Linn. Soc. New South Wales* **43**, 348-359.
- MALLOCH, J. R. (1929). Exotic Muscaridea (Diptera). XXV. *Ann. Mag. Nat. Hist.* 10th Series. **3(17)**, 545.
- MALLOCH, J. R. and MCATEE, W. L. (1924). Flies of the family Drosophilidae of the District of Columbia region, with keys to genera, and other notes of broader application. *Proc. Biol. Soc. Wash.* **37**, 25-42.
- MANJUNATH, T. M. (1968). New records of some parasites and predators of the rice mealy-bug, *Ripersia oryzae* (Green) (Hemiptera: Pseudococcidae). *Current Sci.* **37(12)**, 354-356.
- MARSHALL, A. T. (1966). Spittle-production and tube building by cercopoid larvae (Homoptera). IV. Mucopolysaccharide associated with spittle-production. *J. Insect Physiol.* **12**, 635-644.
- MCALPINE, J. F. (1968). An annotated key to Drosophilid genera with bare or micro-pubescent aristae and a revision of *Paracacoxenus* (Diptera: Drosophilidae). *Can. Ent.* **100**, 514-532.
- MEDLER, J. T. and ADENUGA, A. O. (1969) Observations on larvae of *Leucophenga proxima* Adams (Diptera: Drosophilidae) living in spittle-masses of *Ptyelus grossus* F. (Homoptera: Cercopidae). *Bull. Ent. Soc. Nigera* **2**, 51-53.
- MEIJERE, J. C. H. DE (1904). Beitrage zur kenntnis der Biologie und der Systematischen verwandtschaft der Conopiden. *Tijd. Ent.* **46**, 144-225.
- MEIJERE, J. C. H. DE (1944). Over de Metamorphose van *Metopia leucocephala* Rossi, *Cacoxenus indagator* Löw, *Palloptera saltuum* L., *Paranthomyza nitida* Mg. en *Hydrellia nigripes* Zett. (Dipt.). *Tijd. Ent.* **86**, 57-61.
- *MENTZELOS, I. A. (1967). Contribution to the study of entomophagous insects of *Siphonius phylliraea* Halliday (= *inaequalis* Gautier) (Aleyrodidae) on pear trees in Central Macedonia. *Rep. Pl. Prot. Agric. Res. Station, Thessaloniki*. No. **3**, 92-102.
- MIK, J. (1892). Dipterologische Miscellen (2. Serie, II). *Wien. Ent. Zeit.* **XI**, 181-186.

- MOUND, L. A. and HALSEY, S. H. (1978). "White-fly of the World". British Museum (Natural History) and John Wiley and Sons, London. 340 pp.
- MOUTIA, L. A. and MAMET, R. (1946). A review of twenty-five years of economic entomology in the island of Mauritius. *Bull. Ent. Res.* **36**, 439-472.
- NIJVELDT, W. (1969). "Gall midges of Economic Importance". Vol. VIII Miscellaneous. Crosby Lockwood, London. 221 pp.
- ODHIAMBO, T. (1958). Drosophilidae (Dipt.) breeding in Cercopid (Hem.) spittle masses. *Ent. Monthly Mag.* **94**, 17.
- OKADA, T. (1966). Diptera from Nepal. Cryptochaetidea, Diastatidae and Drosophilidae. *Bull. Brit. Mus. (Nat. Hist): Entomol. Suppl.* 6. 129 pp.
- OKADA, T. (1968). Systematic study of the early stages of Drosophilidae. Bunka Zugeisha, Tokyo. 188 pp.
- OKADA, T. and SASAKAWA, M. (1956). Leaf-mining species of Drosophilidae (Diptera). *Akita* **V**, 26-28.
- OLDROYD, H. (1964). "The Natural History of Flies". Weidenfield and Nicolson, London. 324 pp.
- PELOV, V. and TRENCEV, G. (1973). (*Siphonius phillyrea* Hal. and its entomophages). *Rastitelna Zashchita* **21(11)**, 26-27 (In Bulgarian).
- PIPKIN, S. B. (1965). The influence of adult and larval food habits on population size of Neotropical ground-feeding Drosophila. *Am. Mid. Nat.* **24**, 1-27.
- PIPKIN, S. B., RODRIGUEZ, R. L. and LEÓN, J. (1966). Plant host specificity among flower-feeding Neotropical Drosophila. (Diptera: Drosophilidae). *Am. Nat.* **100**, 135-156.
- POWELL, J. M. (1971). The arthropod fauna collected from the Comandra blister rust, *Cronartium comandrae*, on Lodgepole Pine in Alberta. *Can. Ent.* **102**, 908-918.
- POWELL, J. M., WONG, H. R. and MELVIN, J. C. E. (1972). Arthropods collected from stem rust cankers of the hard pines in Western Canada. Northern Forest Research Center, Edmonton, Alberta: Information Report NOR-X-42. 19 pp.
- PUTTARUDRIAH, M. (1954). The status of the mealy-bug on sugar-cane with special reference to Mysore State. *Indian J. Ent.* **16**, 1-10.
- RAW, A. (1972). The biology of the solitary bee *Osmia rufa* L. (Megachilidae). *Trans. Roy. Ent. Soc. London* **124**, 213-229.
- RICHARDS, O. W. (1932). Some breeding and habitat records of British Diptera. *J. Ent. Soc. South England.* **1(1)**, 11-14.
- RILEY, R. C. and FORGASH, A. J. (1967). *Drosophila melanogaster* eggshell adhesive. *J. Insect. Physiol.* **13**, 509-517.
- *RUJENDRA, A. (1974). The biology and control of *Saccharicoccus sacchari* Ck11. (Hom: Pseudococcidae), the pink mealy-bug on sugar-cane in Sri Lanka. *Ceylon J. Sci. Bio. Sci.* **11**, 23-28.
- RUTHERFORD, A. (1914). Some notes on *Xyleborus formicatus* Eichh. (Shot-hole borer). *The Tropical Agriculturist (Columbo)*. **42**, 220-222.
- SABROVSKY, C. W. (1951). Two new species of *Pseudiatata* (Dipt., Drosophilidae) predacious on the Pineapple mealy-bug. *Bull. Ent. Res.* **41**, 623-627.
- SCHINER, J. R. (1864). Fauna Austriaca. Die Fliegen (Diptera). Part III Carl Gerold's Sohn, Vienna.
- SCHOLTZ, H. (1849). Ueber den Aufenthalt der Diptern während ihrer ersten Stände. *Z. Entomologie herausgegeben v. dem verein f. schlesuche Insekten zu Breslau* **1(9)**, 9-20.
- SCHULTZE, P. (1912). Entwicklung von *Drosophila rubrostriata* Becker in Formol: ein Beitrag zur Kenntnis der Lebensweise de Drosophilalarven. *Zoöl. Anz.* **39**, 199-202.

- SEGUY, E. (1932). Une Drosophilide commensal d'un cercopide de Madagascar. *Encycl. Entomol. Ser. B. II Diptera*, **VI**, 93-94.
- SEGUY, E. (1933a). Une nouvelle espèce de *Gitona* (Dipt.) de la Somalie italienne et note sur les Drosophiles parasites. *Boll. Soc. Ent. Ital., Ann.* **LXV**(8), 187-190.
- SEGUY, E. (1933b). Contributions à l'étude de la faune du Mozambique. Voyage de M. P. Lesne (1928-1929). 13^e Note. Dipteres (2^e Partie). *Mem. Estud. Mus. Zool. Univ. Coimbra 1933 Ser. I*, **67**, 1-78.
- SEGUY, E. (1934). Contributions à l'étude des Mouches Phytophages de l'Europe Occidentale. II. *Encycl. Ent. Diptera. Ser. B.* **VII**, 167-264.
- SEGUY, E. (1951). Un Drosophilide Phytophage nouveau. *Mem. Inst. Scientifique de Madagascar. Ser. A.* **VI**(2), 399-405.
- SENIOR-WHITE, R. A. (1921). New Ceylon Diptera. *Spolia Zeylonica* **XI**, 381-395.
- SILVESTRI, F. (1934). Compendio di Entomologia applicata. 1. Portici. 488 pp.
- SMART, J. (1937). On the larva and pupa of *Drosophila gibbinsi* Aub. *Proc. Roy. Ent. Soc. London B* **6**, 170-172.
- SMITH, H. S. and COMPERE, H. (1916). Observations on the *Lestophonus*, a Dipterous parasite of the cottony cushion scale. *Monthly Bull. Calif. State Com. Horticult.* **5**(10), 384-390.
- STARR, M. P. (1975). A generalized scheme for classifying organismic associations. In: "Symbiosis", Symp. Soc. Experimental Biol. **XXIX**, 1-20. University Press, Cambridge.
- STURTEVANT, A. H. (1921). "The North American species of *Drosophila*". Carnegie Institution of Washington Pub. No. 301. 150 pp.
- STURTEVANT, A. H. (1942). The classification of the genus *Drosophila*, with descriptions of nine new species. *Univ. Texas. Publ.* **4213**, 5-51.
- SWEZEY, O. H. (1929). Notes on the egg parasites of insects in Hawaii. *Proc. Hawaiian Ent. Soc.* **7**, 282-292.
- SZENT-IVANY, J. J. H. and ARDLEY, J. H. (1963). Insects of *Saccharum* spp. in the Territory of Papua and New Guinea. *Proc. Int. Soc. Sug. Cane Technol.* **11**, 690-694.
- TAKADA, H. (1976). Distribution and population constitution of *Drosophila* in South-East Asia and Oceania. II. The genus *Zygothrica* with descriptions of three new species. *Kontyu* **44**, 65-72.
- TASEI, J.-N. (1972). Observations préliminaires sur la biologie d'*Osmia* (*Chalcosmia*) *coerulescens* L., (Hymenoptera, Megachilidae), pollinisatrice de la Luzerne (*Medicago sativa* L.). *Apidologie* **3**, 149-165.
- THORPE, W. H. (1930). The biology, postembryonic development and economic importance of *Cryptochaetum iceryae* (Diptera, Agromyzidae) parasitic on *Icerya purchasi* (Coccidae, Monophlebini). *Proc. Zool. Soc. Lond.* **LX**, 929-971.
- THORPE, W. H. (1934). The biology and development of *Cryptochaetum grandicorne* (Diptera), an internal parasite of *Guerinia serratulae* (Coccidae). *Quart. J. Micr. Sci.* **77**, 273-304.
- THORPE, W. H. (1941). The biology of *Cryptochaetum* (Diptera) and *Eupelmus* (Hymenoptera) parasites of *Aspidoproctus* (Coccidae) in East Africa. *Parasitology* **XXX**, 149-188.
- THROCKMORTON, L. (1962). The problem of phylogeny in the genus *Drosophila*. *Univ. Texas Pub.* **6205**, 207-343.
- THROCKMORTON, L. (1975). The phylogeny, ecology and geography of *Drosophila*. In: "Handbook of Genetics", Vol. 3. (Editor, R. C. King), Plenum, New York.
- TSACAS, L. and CHENON, R. D. DE (1976). Taxinomie et biogéographie des "genres" *Cacoxenus*—*Paracacoxenus*—*Gitonides*—*Gitona* (Dipt., Drosophilidae) et biologie d'une

- nouvelle espèce africaine commensale d'Apoidae (Hymenoptera). *Ann. Soc. Ent. Fr. (N.S.)* **12**, 491–507.
- TSACAS, L. and DISNEY, R. H. L. (1974). Two new African species of *Drosophila* (Diptera, Drosophilidae) whose larvae feed on *Simulium* larvae (Dipt., Simuliidae). *Tropenmed. Parasit.* **25**, 360–377.
- TSACAS, L. and LACHAISE, D. (1979). La radiation africaine des *Lissocephala* inféodés aux *Ficus* (Diptera, Drosophilidae). *Ann. Soc. Ent. Fr. (N.S.)* **15**, 589–603.
- TSACAS, L. and LEGRAND, D. (1979). Les pontes d'Odonates, gîte larvaire nouveau pour une Drosophile africaine inédite: *Drosophila libellulosa*, n.sp. (Odonata: Libellulidae: Diptera: Drosophilidae). *Rev. Fr. Ent. (N.S.)*, **1**, 13–22.
- TOWNSEND, C. H. T. (1893). A general summary of the known larval food-habits of the Acalyptrate Muscidae. *Can. Ent.* **25**, 10–16.
- UICHANCO, L. B. and VILLANUEVA, F. E. (1932). Biology of pink mealy-bug of sugar-cane, *Trionymus sachari* (Cockerell) in the Philippines. *Philip. Agric.* **21**, 205–276.
- VAYSSIERE, P. (1953). Rapport de la Commission pour les recherches sur la lutte biologique contre les ennemis des cultures. C. R. de l'Assemblée générale de l'Union Int. des Sciences Biologiques, Nice 1955., 12 pp.
- VIENNOT-BOURGIN, G. (1949). "Les Champignons Parasites des Plantes Cultivées". 2 vols. Masson et Cie, Paris. 1850 pp.
- VILLA, J. (1977). A symbiotic relationship between frog (Amphibia, Anura, Centrolenidae) and fly larvae (Drosophilidae). *J. Herpetology* **11**, 317–322.
- VILLA, J. (1978). Symbiotic relationships of the developing frog embryo, with special reference to fly larvae. Ph.D. Thesis, Cornell University, Ithica, New York.
- VILLA, J. (1980). "Frogflies" from Central and South America with notes on other organisms of the Amphibian egg microhabitat. *Brenesia* **17**, 49–68.
- VON FRAUENFELD, G. R. (1867). Zoologische Miscellen. XIV. *Acletoxenus syrphoides*. *Verhand. Kaiser.-Konigl. zool.-bot. Gesell. Wien.* **18**, 150–153.
- VON FRAUENFELD, G. R. (1868). Zoologische Miscellen. XV. Ueber Gattung und Artrecht von *Acletoxenus syrphoides*. *Verhand. Kaiser.-Konigl. zool.-bot. Gessel. Wien.* **18**, 897–899.
- WALKER, F. (1853). *Diptera Britannica* **2**, 243.
- WALLACE, B. (1978). The adaptation of *Drosophila virilis* to life on an artificial crab. *Am. Nat.* **112**, 971–973.
- WEAVER, O. R. and KING, D. (1954). Meadow spittle-bugs. *Ohio Agric. Exp. Stat. Res. Bull.* **741**, 99 pp.
- WHEELER, M. R. (1952). The Drosophilidae of the Nearctic region, exclusive of the genus *Drosophila*. *Univ. Texas Publ.* **5204**, 162–218.
- WHEELER, M. R. (1960a). A new genus and two new species of Neotropical flies (Diptera: Drosophilidae). *Entomol. News.* **LXXI**, 207–213.
- WHEELER, M. R. (1960b). A new subgenus and two new species of *Pseudiasata* Coquillett (Diptera: Drosophilidae). *Bull. Brooklyn Ent. Soc.* **55**, 67–70.
- WHEELER, M. R. (1961). Some Drosophilidae (Diptera) from the Galapagos Islands. *Ann. Ent. Soc. Am.* **54**, 570.
- WHEELER, M.R. (1970). A catalogue of the Diptera of the Americas South of the United States. Fasc. 79 Family Drosophilidae. Museo de Zoologica, Universidade de Sao Paulo, Sao Paulo. 65 pp.
- WHEELER, M. R. and TAKADA, H. (1971). Male genitalia of some representative genera of American Drosophilidae. *Univ. Texas Publ.* **7103**, 225–240.
- WILLIAMS, C. B. (1923). A frog-hopper damaging Cocoa in Panama. *Bull. Ent. Res.* **13**, 271–274.

- WILLIAMS, C. B. (1931). Entomology in the Tropics. *Tropical Agriculture (Trinidad)* **VIII**, 119-123.
- WILSON, H. A. and DORSEY, C. K. (1957). Studies on the composition and microbiology of insect spittle. *Ann. Ent. Soc. Am.* **50**, 399-406.
- WIRTH, W. W. (1952). Two new spider egg predators from the Hawaiian Islands (Diptera:Drosophilidae). *Proc. Hawaiian Ent. Soc.* **14**, 415-417.
- YAMAMOTO, W. (1951). Studies on the dissemination of sooty moulds by insects. *Mem. Hyogo Prefectural Univ. of Agric., Phytopath. Ser. No. 1* **1(2)**, 1-50.
- YOON, S-B. and FOX A. S. (1965). Permeability of premature eggs from *Drosophila* collected with the 'ovitron'. *Nature, Lond.* **206**, 910-913.