

BEHAVIORAL CONVERGENCES AMONG  
FRUIT-HUSK MOSQUITOES

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Animals have often independently evolved analogous traits in response to similar selection pressures in different localities. Examination of the habitats of these species may reveal common features of their environments that prompted evolution of the shared traits (Alcock 1979). Although the evolutionary convergence of distinct taxa is a widely accepted principle, most examples in the literature concern morphological similarities among birds or mammals of differing phylogenetic ancestries (e.g., Mayr 1963, MacArthur 1972). The convergence of behavioral traits has received less attention because behaviors are more tedious to inventory and comparative studies are fewer.

Because of their limited and stereotyped repertoires, insects ought to provide excellent material for studying behavioral convergences. Obvious convergences have appeared in unrelated social insects such as ants and termites. Within single families, similar behavioral traits may have evolved independently, such as the stutter-trill acoustic signal which is found in three distinct subfamilies of Gryllidae (Alexander 1962, T. Walker, pers. comm.). For the family Culicidae, medical entomology has fostered the accumulation of sufficient natural history information to permit a contrast of behaviors which occur in divergent genera.

In the course of studies in Africa and South America (Lounibos 1978, 1980, Lounibos and Machado-Allison 1983), my attention was drawn to certain behavioral similarities among mosquitoes which had evolved, apparently independently, to occupy water-containing fruit husks. Here I will compare ovipositional and larval behaviors which have been observed among two or more unrelated mosquitoes inhabiting fruit husks in the Neotropical, Afrotropical, and Oriental Regions, and I will suggest that these specializations have evolved independently in different biogeographic zones in response to similar selective forces of the husk microhabitat.

## THE MOSQUITOES

The mosquito genera *Trichoprosopon*, *Eretmapodites*, and *Armigeres* are confined, respectively, to the Neotropical, Afrotropical, and Oriental Regions and presently have no geographical overlap (Fig. 1). Most species<sup>1</sup> oviposit in plant-held waters such as treeholes, leaf axils, fallen leaves, or fruits. Members of these three genera are the most abundant, albeit not the exclusive, mosquito inhabitants of water-containing fruit husks.<sup>2</sup> From his observations in the Old World tropics, Mattingly (1969) suggested that only husks and shells containing unpolluted fluid are used by mosquitoes other than *Eretmapodites* or *Armigeres*. In husks containing *Trichoprosopon*, *Eretmapodites*, or *Armigeres*, individuals of these genera far outnumbered

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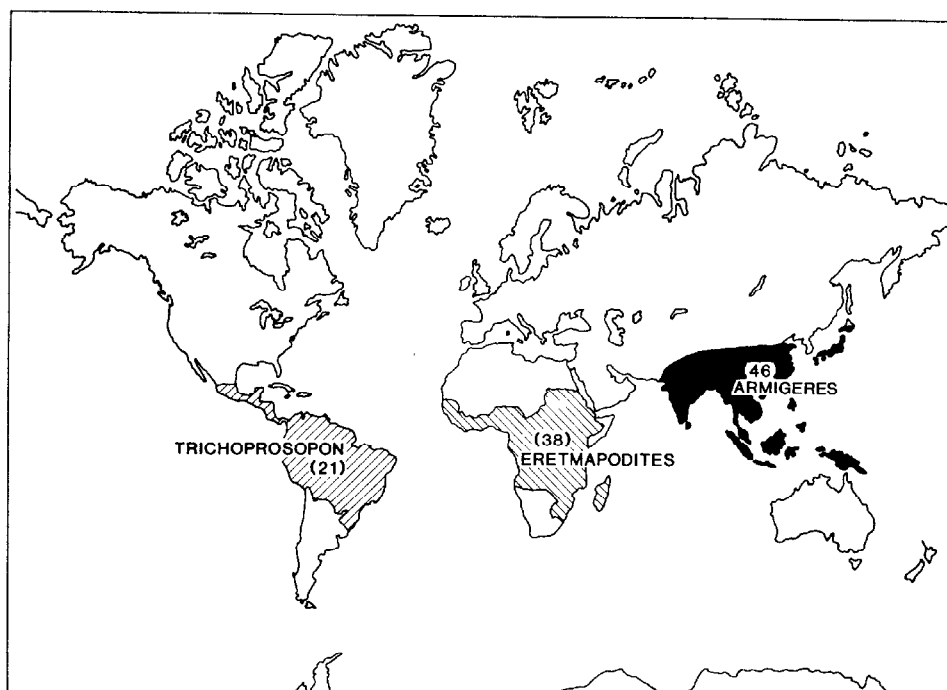


Fig. 1. The geographic distributions of the three mosquito genera specialized for the occupancy of water-containing fruit husks in their immature stages. Numbers of recognized species in each genus and records of countries of occurrence were derived from Knight and Stone (1977), Knight (1978), and Zavortink (1979).

the fruit occupants from other mosquito genera (Machado-Allison and Alvarado unpublished, Raymond et al. 1976, Bick 1951).

#### THE HUSK MICROHABITAT

To provide a habitat for larval mosquitoes, fruits must be gnawed, partially eaten, cut, or broken and dropped in a position to catch and hold rain water. In East and West Africa, monkeys and baboons are important consumers of the fruits with fleshy endocarps which subsequently offer a habitat for species of the *Eretmapodites chrysogaster* (*s.l.*) group (Raymond et al. 1976, Lounibos 1978) (Fig. 2A). Husks harboring *Eretmapodites* held 65 ml or less of fluid (Lounibos 1980), and their availability in native African forests was both seasonal and patchy (Raymond et al. 1976). The irregular occurrence of husks may explain why fruit "specialists" such as *E. subsimplicipes* also oviposit in alternative containers such as fungus cups, leaves, and snail shells on the forest floor (Lounibos 1980).

Fruits that are cultivated and/or used by man provide important habitats for species of *Trichoprosopon*, *Eretmapodites*, and *Armigeres*. Coconut shells and cacao husks are the commonest examples (Figs. 2B, C). In a wet cacao husk, but less often in a coconut shell, the medium contains decaying fruit. The culicid fauna of husks may be regulated, in part, by the contribution of fruit exudate to the medium. Species of *Trichoprosopon*, *Eretmapodites*, and *Armigeres* appear to be specially adapted to the viscous ooze (*vide* Lounibos 1978) produced by the breakdown of fleshy endocarp.

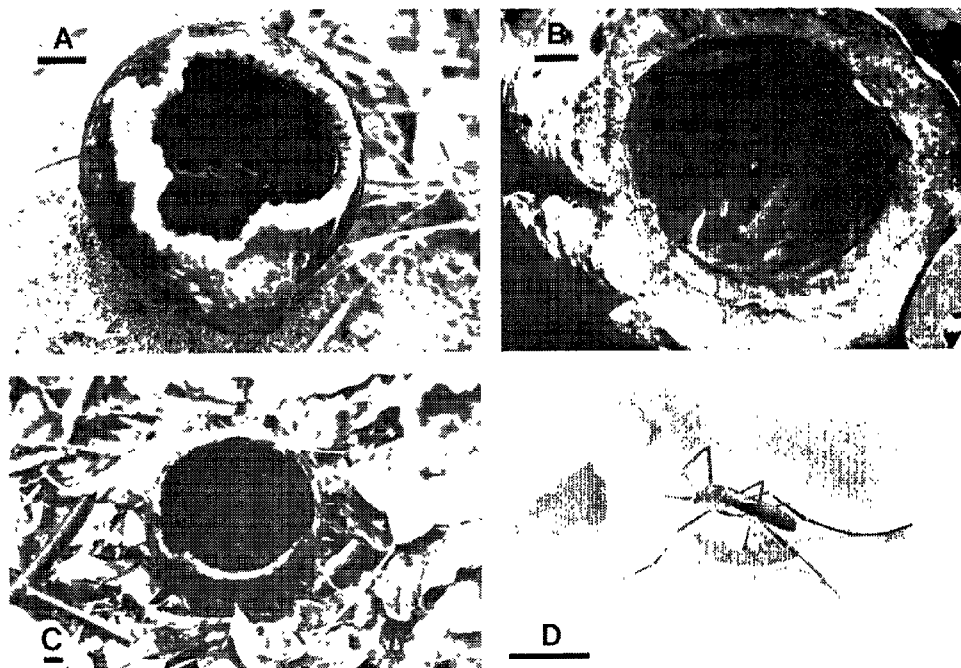


Fig. 2. A-C. Discarded fruit husks inhabited by larval mosquitoes. A. *Strychnos spinosa* husk which contained *Eretmapodites subsimplicipes* at the Kenya coast. B. *Theobroma cacao* husk which contained *Trichoprosopon digitatum* on a plantation in eastern Venezuela. C. *Cocos nucifera* shell which contained *E. subsimplicipes* and *Aedes aegypti* at the Kenya coast. D. Female *T. digitatum* brooding eggs in a cacao husk. Scale bars (approx.): A-C = 2.0 cm; D = 5.0 mm.

Fruits cultivated by man on plantations are more regularly spaced than the patchily distributed fruits of tropical forests. Presumably, the specialist mosquitoes of cacao plantations, such as *E. chrysogaster* in West Africa (Mattingly, cited in Hopkins 1952) or *T. digitatum* in the Caribbean (Aitken et al. 1968, Lane 1953), in evolutionary time first inhabited native, uncultivated fruits prior to exploiting the habitat bonanzas of plantations. In the Neotropics, *Theobroma cacao*, the source of commercial chocolate, grew wild and co-occurred with *T. digitatum* long before it was sown on plantations (Van Hall 1932).

#### THE CONVERGED SPECIALIZATIONS

##### CHEMICAL STIMULATION OF OVIPOSITION

Among mosquito genera which ordinarily do not inhabit fruits, chemical factors which cue oviposition have been identified for species of *Culex* (e.g. Ikeshoji 1966), *Aedes* (e.g. Kalpage and Brust 1973), and *Wyeomyia* (Istock et al. 1983). The stimulatory chemicals may be bacterial metabolites in the oviposition medium (Ikeshoji et al. 1967), may be derived from mosquito larvae or pupae (Kalpage and Brust 1973), or from the plant parts that create the microhabitat (Istock et al. 1983). The available information suggests that mosquitoes that oviposit in small, discrete water bodies, such as fruit husks, are more likely to be cued by a chemical.

Members of all three fruit-inhabiting genera respond to oviposition chemicals. In oviposition choice experiments, *T. digitatus* preferred fluid from cacao husks to fluid derived from *Alocasia* axils, an available habitat not used by this species (Lounibos and Machado-Allison 1983). On the Kenya coast, one or more chemicals derived from wild fruits stimulated oviposition by *E. subsimplicipes*, but *Eretmapodites quinquevittatus*, which eschews fruit husks in nature, preferred pure spring water for oviposition (Lounibos 1978). Although species of *Armigeres* have not been tested directly for responsiveness to oviposition stimulants from fruits, in the laboratory *A. kuchingensis* showed a strong preference for oviposition in polluted water (Thomson 1941). To date, there is no evidence whether oviposition stimulants from fruits are unique to this microhabitat.

#### EGG CARRYING AND BROODING

Post-ovipositional, maternal care has been recorded in six species of *Armigeres* and one species of *Trichoprosopon*. Strickland (1917) was the first to observe fertile eggs attached to the hind legs of adult *Armigeres flavus*, a Malaysian species whose larvae inhabit coconut shells and bamboo internodes. He suggested that egg carrying enabled females to deposit their progeny as newly hatched larvae into inaccessible habitats or where eggs might be subject to "some danger". Egg carrying by *A. flavus* was confirmed by Barraud (1934) who presumed that females introduced eggs or incompletely hatched larvae by poking their hind legs through small holes in bamboo nodes.

Macdonald (1960) indicated four additional Malaysian *Armigeres*, *A. annulitarsis*, *A. balteatus*, *A. inchoatus*, and *A. magnus*, that also carry eggs on their hind legs. Mattingly (1971b) added *A. traubi* to the list of *Armigeres* known to exhibit this maternal behavior. Because two egg-carrying Malaysian species occur frequently in open containers, Macdonald (1960) contested the notion that egg carrying had evolved for exploiting inaccessible habitats, but he offered no alternative hypothesis to account for this behavior. Egg batches attached to the hind legs of *Armigeres* have been discovered on females attacking man as well as on pinned museum specimens (Macdonald 1957, Mattingly 1971a).

Females of *T. digitatum* from Venezuela brood their egg rafts in cacao husks (Fig. 2D) from oviposition until egg hatch (Lounibos and Machado-Allison 1983), a period requiring 26-30 hours at 26-29°C (Aitken et al. 1968). Although oviposition behavior of this species was described by Pawan (1922), post-ovipositional egg attendance was not recognized until Aitken et al. (1968) noted its occurrence in a laboratory colony. Lounibos and Machado-Allison (1983), after demonstrating that rafts in nature were almost always guarded by females, conjectured that brooding behavior evolved to protect eggs from predation or desiccation. Rafts that were not guarded were observed to break up, and eggs floated to the sides of husks where they could be stranded and more subject to desiccation or predation. The eggs of neither *T. digitatum* nor egg-carrying *Armigeres* are resistant to desiccation (Lounibos, unpublished, Macdonald 1960).

It may simply be a coincidence that the only records of post-ovipositional egg attendance by mosquitoes occur in two fruit-inhabiting genera, *Armigeres* and *Trichoprosopon*. More likely, some property of this micro-

habitat or containers in general has promoted the independent evolution of egg carrying among *Armigeres* and brooding by *T. digitatum*.

#### LARVAL FRUGIVORY AND CARNIVORY

Three general modes of feeding behavior: filtering, browsing, and predation are recognized for larval mosquitoes (Surtees 1959). Larvae of all three genera of fruit specialists are adapted for both browsing and facultative predation.

Knight (1971) compared the larval mandible of all but three of the known mosquito genera. Among these, members of 18 genera have mandibular teeth less prominent than the fruit-husk species (Fig. 3); these mosquitoes are generally characterized as filter-feeders (Bates 1949). In the evolutionary transition from filter feeding to predation,<sup>3</sup> the mandibular teeth are known to increase in size and sclerotization (Harbach 1977). The mandibular teeth of species from ten other genera,<sup>4</sup> known as facultative or obligate predators (Bates 1949), are equally well-developed as in species of fruit specialists. (Fig. 3).

*Armigeres* are as well suited for browsing the inner walls of fruits as for carnivory. Lounibos (1978) suggested that frugivory by larvae permitted

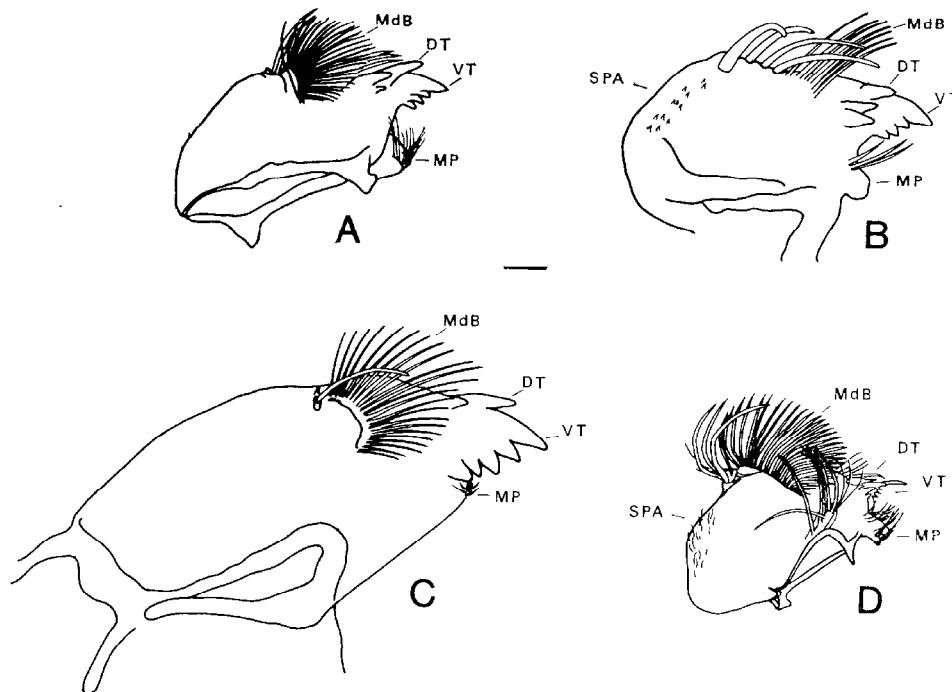


Fig. 3. Mandibles of fourth instar larvae of A. *Armigeres subalbatus* from southern Japan, B. *Eretmapodites subsimplicipes* from eastern Kenya, C. *Trichoprosopon digitatum* from eastern Venezuela, D. *Culiseta melanura* from Florida, USA. A. and D. are redrawn from Knight (1971) and B. and C. are drawn from larvae collected from fruit husks by this author. Certain structural details have been omitted to emphasize the relative sizes of the mandibular teeth. Abbreviations (after Knight 1971): DT = dorsal teeth; MdB = mandibular brush; Mp membranous process; SpA = spinose area; VT = ventral teeth. Scale bar = 0.05 mm.

the maintenance of the extraordinary densities of *E. subsimplicipes* found in African *Saba* and *Strychnos* fruits. Venezuelan cacao husks support densities of *T. digitatum* comparable to *E. subsimplicipes* in native African fruits and, like *E. subsimplicipes*, *T. digitatum* larvae rasp the fruit endocarp with their mandibles (Lounibos, unpublished).

Predation has been confirmed among larvae of various species of *Armigeres* (Tanaka et al. 1979, Bates 1949), *Eretmapodites* (Haddow 1946, Lounibos 1980), and *Trichoprosopon* (Arnett 1950, Zavortink 1979, Seifert and Barrera 1981). While laboratory studies have concentrated on predation upon other species of culicid prey (Haddow 1946, Lounibos 1980), in nature fruit-husk *Armigeres* (Bick 1951), *Eretmapodites* (Lounibos 1978), and *Trichoprosopon* (Seifert and Barrera 1981) occur most commonly only with conspecifics, and most predation may be assumed to be intraspecific (although Haddow (1946) regarded *E. chrysogaster* as resistant to attack by members of its own species). In bracts of *Heliconia aurea*, uniform-aged cohorts of larvae are maintained by larger *T. digitatum* preying upon smaller conspecifics (Seifert and Barrera 1981). The common occurrence of *T. digitatum* belonging to a single instar in cacao husks (Machado-Allison and Alvarado, unpublished) may be the product of stage-specific cannibalism.

#### LIFE AND LOCOMOTION IN MUCILAGE

The capacity to grow and metamorphose in a viscous, fetid, and anaerobic medium is shared by fruit husk inhabitants of all three genera. In New Guinea, Bick (1951) noted great concentrations of *Armigeres breinli* and *Armigeres milnensis* in minute amounts of "putrid, semi-liquid material" in coconut shells. In parts of China, favored breeding sites of *Armigeres obturans* (= *subalbatus*) are tubs of fermenting urine used by farmers for fertilizer (Feng 1937-38). Even when the fruit medium occupied by *E. subsimplicipes* evaporates to a mucilaginous sludge, larvae continue to thrive (Lounibos 1978). In Panama, Galindo et al. (1951) observed the capacity of *T. digitatum* larvae to endure desiccation and fluid too polluted for other species.

Facilitating movement through their semi-aquatic medium, members of all three fruit-husk genera are capable of sinuous crawling uncharacteristic of larval mosquitoes. Mattingly (1969) commented on the convergence of this locomotory behavior among *Eretmapodites* and *Armigeres*: "In both cases the larvae swim with a remarkable vibratory 'shimmying' motion, possibly adaptive to progress through a viscous medium." Among *Armigeres*, specific citations of crawling by larvae include *A. theobaldi* on *Curcuma* flowers (Chari 1940), and *A. breinli* whose larvae in coconut husks have "an eel-like movement whereby they are able rapidly to burrow into the semi-liquid filth on which they appear to feed" (Paine and Edwards 1929). Hopkins (1952) documented crawling of larvae of a Ugandan species of *Eretmapodites* and West African *E. quinquevittatus*. *T. digitatum* larvae are capable of crawling in cacao husks (Lounibos, unpublished). *Eretmapodites* larvae also tend to remain appressed to the bottom of a container even after all fluid has been poured out (Hopkins 1952). I have observed the tenacious adherence of larvae of *E. subsimplicipes* inhabiting fruit husks in Kenya as well as *T. digitatum* in Venezuelan cacao husks.

The 'shimmying' swimming motion used by larvae was stated by Mattingly (1969) to extend to *Eretmapodites* and *Armigeres* pupae. Further, pupae of fruit-husk genera are unusually sedentary, remaining submerged on their sides for long periods on the bottom of a container; this has been observed both among Ugandan *Eretmapodites* (Haddow 1946) and *T. digitatum* from Venezuela (Lounibos, unpublished).

#### THE EVOLUTION OF FRUIT-HUSK ADAPTATIONS

Fruit-husk inhabiting *Trichoprosopon*, *Eretmapodites*, and *Armigeres* are presumed to represent "grades", sets of species that share a level of evolutionary organization attained repeatedly by diverged lines (Futuyma 1979). The evidence for independent evolution of adaptations to fruit husks is circumstantial yet persuasive. Unlike cosmopolitan genera such as *Aedes*, *Culex*, or *Anopheles*, there is no present-day geographical overlap among *Trichoprosopon*, *Eretmapodites*, or *Armigeres*. The tribe Sabethini, which includes *Trichoprosopon*, is almost exclusively neotropical (Knight and Stone 1977). Although *Eretmapodites* and *Armigeres* are both placed in the tribe Aedini, the culicid fauna of the Afrotropical and Oriental Regions are very distinct with few species occurring in both regions (Mattingly 1962), supporting the hypothesis of independent evolution of these faunas. Independent, parallel evolution of various traits within one insect family is well documented for the Drosophilidae where chromosomal arrangements have allowed independent reconstruction of phylogenies (e.g., Throckmorton 1975).

An objective of studying behavioral convergences is resolution of the selective pressures that promoted parallel and independent evolution. Behaviors described in this paper are not necessarily direct adaptations to fruit husks, but may have existed as pre-adaptations that allowed species to exploit the habitat. Regardless, two properties of the husk microhabitat were probably important in either shaping common courses of adaptation or influencing pre-adapted colonists. Firstly, fruit husks, like many small vessels occupied by mosquitoes, provide a transient and patchy habitat, and these properties of containers may have contributed to the evolution of egg attendance to protect against desiccation, and responsiveness to chemical stimuli to locate the irregularly distributed microhabitat. Secondly, and more specific to fruit husks, is the odoriferous and viscous medium which probably fostered the invasion by pre-adapted mosquitoes or the evolution *per se* of responsiveness to ovipositional chemicals, larval frugivory, crawling larvae, and recumbent pupae.

Some groundwork in mosquito behavior and evolution has been laid because of the relevance of these insects to human health. Hopefully the comparisons and conjectures of this paper made possible by medical entomology will provide ideas for and be tested by future research.

#### SUMMARY

Three genera of mosquitoes, *Trichoprosopon*, *Eretmapodites*, and *Armigeres*, contain species which are specialized for colonizing water-containing fruit husks. Behavioral specializations include: responsiveness to a chemical oviposition stimulant in fruits; post-ovipositional maternal care of eggs;

larval frugivory; facultative cannibalism; crawling larvae and recumbent pupae in their fetid, viscous, and anaerobic media. *Trichoprosopon*, *Eretmapodites*, and *Armigeres* are confined, respectively, to the Neotropical, Afrotropical, and Oriental Regions where, it is argued, behaviors common to fruit husk inhabitancy evolved independently.

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#### APPENDIX

<sup>1</sup>The sabethine genus *Trichoprosopon* currently is composed of 21 species (Zavortink 1979). Mention of the genus in this paper refers solely to *T. digitatum*, the best-known species (Zavortink 1981). *Eretmapodites*, the only culicid genus restricted to the Afrotropical Region (Edwards 1941), now embraces 38 species (Knight and Stone 1977, Knight 1978). Most records of fruit inhabitancy refer to members of the *E. chrysogaster* complex of 12 species, which includes *E. subsimplicipes* (Gillett 1972). At last count, 46 species were included in *Armigeres* (Knight and Stone 1977). Species from both subgenera, *Armigeres* and *Leicesteria*, have been found in fruits.

<sup>2</sup>In Africa, species of *Aedes*, *Culex*, and *Toxorhynchites* also have been recorded as occupying fruits of the Loganiaceae and Apocynaceae (Raymond et al. 1976, Lounibos 1980), and on islands in the Pacific, *Tripteroides* and *Aedes* species may be found in coconut shells and rat-gnawed cacao husks (Baisas and Ubaldo-Bagayon 1952, Laird 1956). In eastern Venezuela one species of *Culex* occasionally occurs in the cacao husks ordinarily occupied by *T. digitatum* (Machado-Allison and Alvarado, unpublished).

<sup>3</sup>Filter (plankton) feeding is not necessarily the primitive mode among larval Culicidae. Harbach (1977) considers it equally likely that browsers (scavengers) are primitive and gave rise to both filter feeders and predators.

<sup>4</sup>The genera whose larval mandibles as depicted by Knight (1971) are comparable in size and form to fruit-husk mosquitoes: *Aedes* (*Mucidus*), *Culex* (*Lutzia*), *Heizmannia*, *Limatus*, *Malaya*, *Phonomyia*, *Sabethes*, *Topomyia*, *Tripteroides*, and *Zeugnumyia*.

#### LITERATURE CITED

- AITKEN, T. H. G., J. O. HINGWAN, R. MANUEL, AND H. HOSEIN. 1968. Laboratory colonization of *Trichoprosopon digitatum* (Rondani) (Diptera: Culicidae). *Mosquito News* 28: 445-54.
- ALCOCK, J. 1979. *Animal behavior: an evolutionary approach*. Sinauer, Sunderland, Mass.
- ALEXANDER, R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution* 16: 443-67.
- ARNETT, R. H. 1950. Notes on the distribution, habits, and habitats of some Panama culicines (Diptera: Culicidae). *J. N. Y. Ent. Soc.* 58: 99-115.
- BAISAS, F. E. AND A. UBALDO-BAGAYON. 1952. Notes on Philippine mosquitoes, XVI. Genus *Tripteroides*. Manila Bureau of Printing.
- BARRAUD, P. J. 1934. *Fauna of British India, Diptera, Vol. V: Family*



- Culicidae, Tribes Megarhinini and Culicini. London: Taylor and Francis.
- BATES, M. 1949. The natural history of mosquitoes. MacMillan, N. Y.
- BICK, G. H. 1951. The ecology of the mosquito larvae of New Guinea. Pac. Sci. 5: 392-431.
- CHARI, M. O. T. 1940. *Armigeres theobaldi* breeding in *Curcuma* flowers. J. Malar. Inst., India 3: 263-64.
- EDWARDS, F. W. 1941. Mosquitoes of the Ethiopian region. III. Culicine adults and pupae. British Museum, London.
- FENG, L.-C. 1937-38. A critical review of the literature regarding the records of mosquitoes in China. II. Subfamily Culicinae, tribes Megarhinini and Culicini. Pek. Nat. Hist. Bull. 12: 285-318.
- FUTUYMA, D. J. 1979. Evolutionary biology. Sinauer, Sunderland, Mass.
- GALINDO, P., S. J. CARPENTER, AND H. TRAPIDO. 1951. Ecological observations on forest mosquitoes of an endemic yellow fever area in Panama. Amer. J. Trop. Med. 31: 98-137.
- GILLETT, J. D. 1972. Common African mosquitoes and their medical importance. Heinemann Ltd., London.
- HADDOW, A. J. 1946. The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites*, Theobald. Bull. Ent. Res. 37: 57-82.
- HARBACH, R. E. 1977. Comparative and functional morphology of the mandibles of some fourth stage mosquito larvae. Zoomorphologie 87: 217-36.
- HOPKINS, G. H. E. 1952. Mosquitoes of the Ethiopian Region I.—Larval bionomics of mosquitoes and taxonomy of culicine larvae. British Museum (NH), London.
- IKESHOJI, T. 1966. Studies on mosquito attractants and stimulants. III. The presence in mosquito breeding waters of a factor which stimulates oviposition. Jap. J. Exp. Med. 36: 67-72.
- IKESHOJI, T., T. UMINO, AND S. HIRAKOSO. 1967. Studies on mosquito attractants and stimulants. Part IV. An agent producing stimulative effects for oviposition of *Culex pipiens fatigans* in field water and the stimulative effects of various chemicals. Jap. J. Exp. Med. 37: 61-9.
- ISTOCK, C. A., K. TANNER, AND H. ZIMMER. 1983. Habitat selection by the pitcher-plant mosquito, *Wyeomyia smithii*: behavioral and genetic aspects. IN J. H. Frank and L. P. Lounibos (eds.) Phytotelmata: terrestrial plants as hosts of aquatic insect communities. Plexus, Medford, N. J.
- KALPAGE, K. S. P. AND R. A. BRUST. 1973. Oviposition attractant produced by immature *Aedes atropalpus*. Environ. Ent. 2: 729-30.
- KNIGHT, K. L. 1971. Comparative anatomy of the mandible of the fourth instar mosquito larva (Diptera: Culicidae). J. Med. Ent. 8: 189-205.
- KNIGHT, K. L. 1978. Supplement to a catalog of the mosquitoes of the world (Diptera: Culicidae). Ent. Soc. Amer., College Park, Maryland.
- KNIGHT, K. L. AND A. STONE. 1977. A catalog of the mosquitoes of the world (Diptera: Culicidae). Ent. Soc. Amer., College Park, Maryland.
- LAIRD, M. 1956. Studies of mosquitoes and freshwater ecology in the South Pacific. Bull. R. Soc. N. Z. 6: 1-213.
- LANE, J. 1953. Neotropical Culicidae. Univ. of Sao Paulo, Brazil.
- LOUNIBOS, L. P. 1978. Mosquito breeding and oviposition stimulant in fruit husks. Ecol. Ent. 3: 299-304.
- LOUNIBOS, L. P. 1980. The bionomics of three sympatric *Eretmapodites* (Diptera: Culicidae) at the Kenya coast. Bull. Ent. Res. 70: 309-320.
- LOUNIBOS, L. P. AND C. E. MACHADO-ALLISON. 1983. Oviposition and egg

- brooding by the mosquito, *Trichoprosopon digitatum*, in cacao husks. Ecol. Ent. 8 (In press.)
- MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, N.Y.
- MACDONALD, W. W. 1957. Malaysian Parasites. XVI. An interim review of the non-anopheline mosquitoes of Malaya. Stud. Inst. Med. Res. Malaya. 28: 1-34.
- MACDONALD, W. W. 1960. Malaysian parasites. XXXVIII. On the systematics and ecology of *Armigeres* subgenus *Leicesteria* (Diptera, Culicidae). Stud. Inst. Med. Res. Malaya 29: 110-53.
- MATTINGLY, P. F. 1962. Towards a zoogeography of the mosquitoes. Syst. Assoc. Publ. 4: 17-36.
- MATTINGLY, P. F. 1969. The biology of mosquito-borne disease. American Elsevier, N. Y.
- MATTINGLY, P. F. 1971a. Mosquito eggs. XIII. Genus *Armigeres* Theobald Mosq. Syst. News. 3: 122-29.
- MATTINGLY, P. F. 1971b. Mosquito eggs. XIV. Genus *Armigeres* Theobald (continued) and *Aedes* subgenus *Alanstonea* Mattingly. Mosq. Syst. News. 3: 130-37.
- MAYR, E. 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass.
- PAINE, R. W. AND F. W. EDWARDS. 1929. Mosquitos from the Solomon Islands. Bull. Ent. Res. 20: 303-16.
- PAWAN, J. L. 1922. On the eggs and oviposition of *Psorophora (Janthinosoma) posticata*, Wied. (Culicidae). Bull. Ent. Res. 12: 481-2.
- RAYMOND, H. L., M. CORNET, AND P. Y. DIENG. 1976. Etudes sur les vecteurs sylvatiques du virus amaril. Inventaire provisoire des habitats larvaires d'une forêt-galerie dans le foyer endémique du Senegal oriental. Cah. ORSTOM serie Ent. Med. Parasitol. 14: 301-6.
- SEIFERT, R. P. AND BARRERA, R. 1981. Cohort studies on mosquito (Diptera: Culicidae) larvae living in the water-filled floral bracts of *Heliconia aurea* (Zingiberales: Musaceae). Ecol. Ent. 6: 191-7.
- STRICKLAND, C. 1917. A curious adaptation of habit to its environment of a Malayan mosquito. J. Straits Br. Asiatic Soc. 75: 39.
- SURTEES, G. 1959. Functional and morphological adaptations of the larval mouthparts in the subfamily Culicinae (Diptera) with a review of some related studies by Montchadsky. Proc. R. Ent. Soc. London (A) 34: 7-16.
- TANAKA, K., K. MIZUSAWA, AND E. S. SAUGSTAD. 1979. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Contrib. Ameri. Ent. Inst. 16: 1-987.
- THOMSON, R. C. M. 1941. Studies on the behaviour of *Anopheles minimus*, Part IV. The composition of the water and the influence of organic pollution and silt. J. Malar. Inst., India 4: 63-102.
- THROCKMORTON, L. H. 1975. The phylogeny, ecology, and geography of *Drosophila*. IN R. King (ed.) Handbook of genetics, Vol. 3: Invertebrates of genetic interest. Plenum, N. Y.
- VAN HALL, C. J. J. 1932. Cacao. MacMillan, London.
- ZAVORTINK, T. J. 1979. Mosquito studies. XXXV. The new sabethine genus *Johnbelkinia* and a preliminary reclassification of the composite genus *Trichoprosopon*. Contrib. American Ent. Inst. 17: 1-61.
- ZAVORTINK, T. J. 1981. Species complexes in the genus *Trichoprosopon*. Mosq. Syst. 13: 82-5.

