

## ECOLOGICAL ASPECTS OF MOSQUITO EVOLUTION (\*)

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Some years ago I was asked to contribute a paper on the evolution of arthropod disease vectors to the annual symposium of the British Society for Parasitology. The task seemed too formidable and I declined. Instead I submitted a paper on the evolution of arthropod-borne diseases regarded as ecological systems (Mattingly, 1965). It seems appropriate on this occasion to pursue the theme a little further in the direction originally requested. I shall try therefore to elucidate some of those ecological factors which have influenced the evolution of the vectors themselves and in particular my own group, the mosquitos. In the absence of a fossil record morphology alone can provide only questions, never answers. However, by asking the right questions and seeking to answer them in ecological terms we may, I think, hope to arrive, at least, at a more coherent picture of the mosquitos as a whole, something sadly lacking at the present time.

*The Mosquito Egg*

The central role of the egg stage in mosquito ecology cannot be too strongly emphasised, standing as it does in the doorway between the generations and between the aerial and sub-aerial environment of the adult and the aquatic environment of the larva and pupa. At the same time it is the site of genetic recombination with all that this implies for evolution and it provides an amplifying factor, offsetting depletions of the adult population, without which survival of the species would be hazardous indeed.

Initiation of egg production by the taking of a bloodmeal is the key factor in mosquito-borne disease. Without it transmission would simply not occur. In the next phase of its development also the egg plays a dominant

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ecological role, imposing on the mother profound changes in physiology and behaviour affecting the whole pattern of her life. Yet, paradoxically, when the egg achieves physical independence it is the mother who assumes the dominant role, determining where it shall be laid and what shall be the environment against which the embryo or diapausing larva has to be protected and in which the next generation will develop.

#### SUBFAMILY TOXORHYNCHITINAE

The interplay between the evolution of maternal behaviour and the evolution of the egg is well seen in *Toxorhynchites* Theobald (Fig. 1), the only genus in this subfamily.

Adults of both sexes are specialized for nectar feeding while on the wing. They are unable to take blood. The breeding places are container habitats. They include tree holes, bored and cut bamboos, leaf axils, flower bracts and artificial containers. The eggs are projected on the wing while the mother

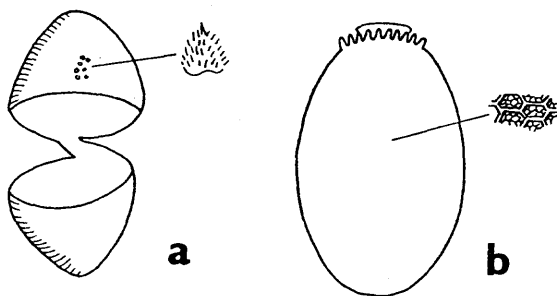


Fig. 1. - Toxorhynchitine eggs. a. *T. splendens* (Wiedemann), after Banks (1908), b. *T. brevipalpis* Theobald, after Muspratt (1951).

hovers over the centre or, in the case of vertical tree holes at the edge, of the breeding place (Paine, 1934, Williams et al., 1961), seemingly an extension of the feeding behaviour or vice versa. The egg shell (chorion) is thin, colourless and highly elastic. When projected the eggs bounce around the interior of the breeding place before coming to rest on the water surface. The chorion is hydrophobic and its surface is increased, in some cases, by numerous small, rugose papillae (Fig. 1 a) so that the eggs float with almost none of their surface submerged. Being colourless they are very conspicuous. Dehiscence is either spiral, as in the figure, longitudinal or transverse,

depending on the species. Of these various modes the spiral is known elsewhere only in one genus of subfamily Sabethinae (1) (Fig. 2 b) and the longitudinal only in two genera of Sabethinae (Fig. 2 a, c) and one small and seemingly very primitive genus of Anophelinae (Fig. 5 d). In all other known mosquitos dehiscence is transverse, allowing emergence of the larva by detachment of a small apical cap.

Summarising the situation in *Toxorhynchites*, the absence of any sclerotized inner chorion is a unique, possibly primitive, feature. In conferring elasticity it may, however, have some adaptive value in relation to the mode

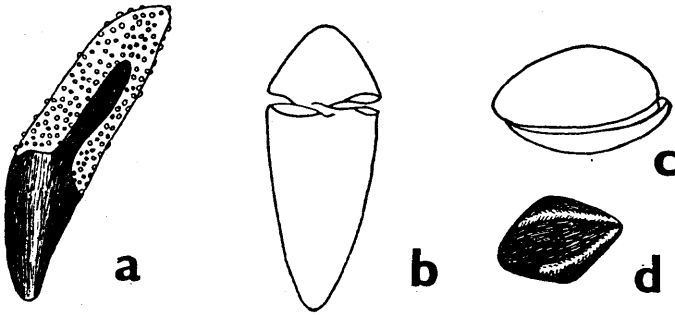


Fig. 2. Sabethine eggs. a. *Trichoprosopon digitatum* (Rondani), after Aitken et al. (1968) b. *Wyeomyia smithii* (Coquillett), after Barr & Barr (1969), c. *Maorigoeldia argyropus* (Walker), after Graham (1929), d. *Sabethes chloropterus* (Humboldt), after Galindo (1958).

of oviposition and might, therefore, be secondary. Oviposition on the wing, known elsewhere only in the Anophelinae and one genus of Sabethinae, may also be primitive but projection of the eggs, as opposed to simply dropping them on the water, seems likely to be a specialized feature.

#### SUBFAMILY SABETHINAE

Apical dehiscence is known in only one species of *Toxorhynchites* (Fig. 1 b) and in this case its advantages are offset by the fact that the egg floats with the anterior end uppermost. In the sabethine *Trichoprosopon digitatum* (Fig. 2 a), which has a hydrophobic outer chorion ornamented with rugose papillae, the

(1) This is sometimes treated as a tribe of subfamily Culicinae but I prefer on this occasion to treat all four major groups of mosquitos, for simplicity, as subfamilies.

eggs though floating vertically are inverted and hatching takes place downwards below the water line. This is achieved by rupture of the outer chorion and protrusion of the strongly sclerotized, hydrophilic inner chorion.

The outer chorionic cap is split longitudinally along three axes. Individual eggs become attached to one another at these points forming an open hexagonal reticulum on the water. This may help to keep them vertical but it seems a much less efficient arrangement than the close hexagonal packing without preferred axes of attachment, found in the rafts of various culicine genera.

Interestingly the sabethine *Wyeomyia smithii* (Fig. 2b) seems to foreshadow in a primitive fashion a quite different mode of oviposition found in other culicine genera. In this case the dorsal surface of the egg is hydrophilic and the ventral surface hydrophobic. Consequently eggs stranded at or a little above the meniscus come to lie with a film of air between the ventral surface and the wall of the plant pitcher in which the larvae develop. At the same time a film of water is drawn over the hydrophilic dorsal surface forming a temporary gill or plastron. In container breeding species belonging to the culicine genus *Aedes* Meigen and its relatives the egg is laid above the meniscus and glued to the substrate while further protection is provided by the development of a waterproofing inner chorion and serosal cuticle affording protection from desiccation for upwards of a year or more (Harwood & Horsfall, 1959). *W. smithii* shows no such resistance to desiccation.

In *Sabethes chloropterus* (Fig. 2d), as in *Toxorhynchites*, the eggs are projected on the wing while the mother hovers outside the very small tree holes serving as breeding places. During oviposition the abdomen is tucked forward between the legs and the eggs are fired like bullets from a gun to distances up to 10 cm (Galindo, 1957, 1958). These eggs differ greatly from those of *Toxorhynchites*, having, apparently, no outer chorion, only the sclerotized, hydrophilic inner chorion, and sinking on laying. They seem most easily derivable from those of the *Tr. digitatum* type, by loss of the outer chorion.

Taking the Sabethinae as a whole we find each of the more distinctive toxorhynchitine features, ornamentation of outer chorion, spiral or longitudinal dehiscence, projection of eggs on the wing, in a different genus. It seems easier to suppose that each of these genera has specialized in a different direction from a primitive proto-toxorhynchitine stock than that *Toxorhynchites* has evolved all of them independently. Our knowledge of both subfamilies is very imperfect, only a handful of species being known from each. Further knowledge may lead us to revise our ideas. It is interesting, however, that we also seem to see foreshadowed in a crude form in the Sabethinae two of the major culicine modes of oviposition.

## SUBFAMILY ANOPHELINAE

The eggs of the tree hole breeding *Anopheles plumbeus* group (Fig. 3 a) were characterized by Christophers & Barraud (1931) as « probably of primitive type ». In so far as they lack the typical anopheline float (compare, e.g., Fig. 3 c, d) this is probably true. Very interestingly the more recently discovered egg of *An. wilsoni*, usually considered the most primitive species of subgenus *Cellia* (Evans, 1938), proves to be of intermediate type (Fig. 3 b).

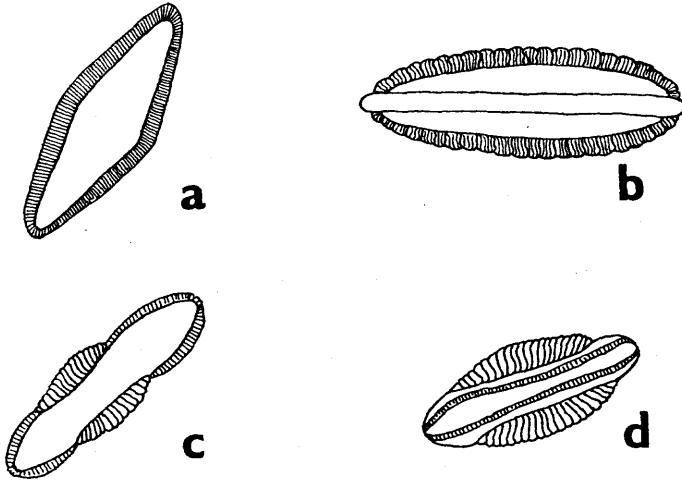


Fig. 3. Anopheline eggs. a. *An. (Anopheles) plumbeus* Stephens, after MacGregor (1921), b. *An. (Cellia) wilsoni* Evans, after Gillies (1955), c. *An. (Anopheles) maculipennis* Meigen, after Peus (1942), d. *An. (Cellia) gambiae* Giles, after Gibbins (1933).

In this species there is a continuous, finely striated, peripheral frill, recalling that of *An. plumbeus* but differing in being divided into a series of chambers as in the typical anopheline float.

If we accept that the type of structure found in *An. wilsoni* represents the forerunner of the frill and float of more typical anophelines then we are driven to the conclusion that there must have been a progressive reduction of the float not only in the subgenera *Anopheles* and *Cellia* but, in parallel, in each of the series of *Cellia*: *Neomyzomyia*, *Myzomyia*, *Pyretophorus*, *Neocellia*, *Cellia*, *Paramyzomyia* (Mattingly, 1969 a and see Gillies & De Meillon, 1968 and Reid, 1968). As a corollary we might expect to find in some series at least eggs which have lost the float altogether and in fact each of the series

does include one or more species in which the float is lacking. The picture presented by these eggs is not, however, altogether simple. Some certainly seem to have lost the float secondarily but in others the condition may be primitive.

In one section of Series *Paramyzomyia* (Fig. 4 a) the frill has been lost as well as the float and it seems that this is a secondary specialization. The eggs sink shortly after they are laid and are protected by the masses of filamentous

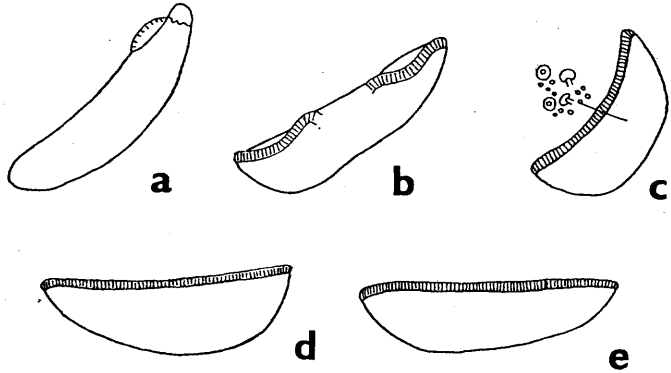


Fig. 4. Eggs of *Anopheles* and *Mimomyia*. a. *An. cinereus* Theobald, after De Meillon (1933); b. *An. multicolor* Cambouliou, after Foley (1912) and Guy (1959); c. *An. nili* (Theobald), after Evgene (1938); d. *An. murphyi* Gillies & De Meillon, original; e. *Mim. chamberlaini* (Ludlow), after Mer & Tampi (1959).

green algae on which the larvae feed (Patton, 1905, Puri, 1931, De Meillon, 1947, Aitken, 1953). In the other section of *Paramyzomyia* *An. multicolor* (Fig. 4 b) has retained only the frill, the overall appearance suggesting rather strongly that a float was originally present and has since been lost. In contrast to this the eggs of *An. nili* (Fig. 4 c), belonging to the same primitive series as *An. wilsoni*, have a rounded shape and chorionic ornamentation reminiscent of *Toxorhynchites*, both, I would think, primitive features.

The eggs of the remaining species all resemble very closely those of the culicine genus *Mimomyia* (Fig. 4 d, e and see Fig. 5), which would suggest that they must be primitive. The pattern is, however, a very simple one as could, in my opinion, have been arrived at, in some cases at least, by secondary loss of the float. This seems clearly to be the case in *An. sachari* (Fig. 5 a), a member of the *An. maculipennis* complex which develops a small float during winter and loses it in the summer (Theodor, 1925, Mer, 1933, Pringle, 1954), a reminder that we are dealing with environmental effects (

the female and not merely with the egg per se. (For other comparable effects see Matheson & Hurlbut, 1937, Hurlbut, 1938, Lawlor, 1940, Otsuru & Ohmori, 1960, Deane & Causey, 1943). The curious relict species *An. concolor* (Fig. 5 b), on the other hand, may well be primitive though there are some indications that it is related to the *An. maculipennis* complex (Reid & Knight, 1961). Other species with a similar type of egg (*An. danalicus* Corradetti (Mara, 1948), *An. ludlowae* (Theobald) (Urbino, 1936), *An. apoci* Marsh (Pringle,

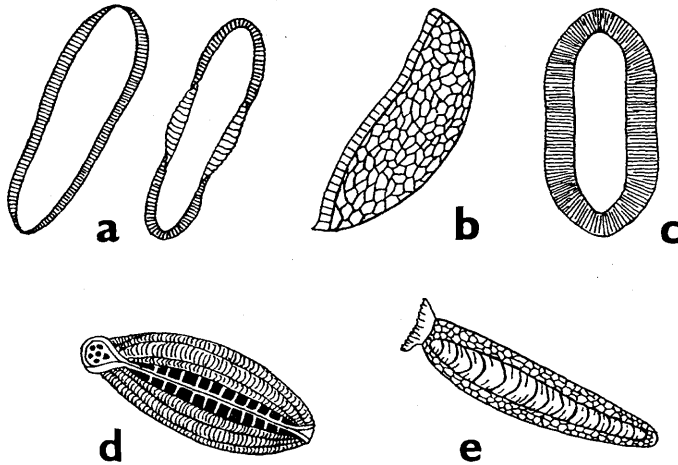


Fig. 5. Anopheline eggs. a. *An. sacharovi* Favre, after Peus (1942) and Falleroni (1926), b. *An. concolor* Edwards, after Vincke & Leleup (1949), c. *An. apoci* Marsh, after Pringle et al. (1960), d. *Chagasia fajardoii* (Lutz), after Causey et al. (1945), e. *Bironella hollandi* Taylor, after Belkin et al. (1945).

1954, Pringle et al., 1960), *An. murphyi* Gillies & De Meillon (1968), *An. superpictus* Grassi (Theodor, 1925) are associated in varying degrees with coastal or desert environments. In these the loss of the float may be an adaptation to saline breeding places. The function of the anopheline « float » appears to be stabilization rather than the enhancement of buoyancy (Trensz, 1933, Newkirk, 1955). In *An. apoci* (Fig. 5 c), and sometimes in *An. superpictus*, there is a very broad frill tending to turn outwards. The rather similar frill found in *An. plumbeus* and its allies may have arisen under quite different environmental constraints since tree hole water is said to have an exceptionally low surface tension (Ramsden, 1920).

It is not possible to discuss here the further problems raised by the eggs of Neotropical *Anopheles* or those of the primitive anopheline genera *Cha-*

*gasia* (Peryassù, 1908, Galvao e Barretto, 1939, Causey et al., 1944, 1945) and *Bironella* Theobald (Lee & Woodhill, 1944, Belkin et al., 1945, Dumbleton, 1946). It is hoped that enough has been said to indicate the types of problem which arise when considering a large and comparatively well studied genus (The eggs of some 200 species of anophelines have been described).

#### SUBFAMILY CULICINAE

This is the largest and most diverse of the subfamilies. Only one generalization is possible which is that, despite, some statements to the contrary, none of its members is known to oviposit on the wing (Mattingly, 1969). The most primitive mode of oviposition in the Culicinae would seem to

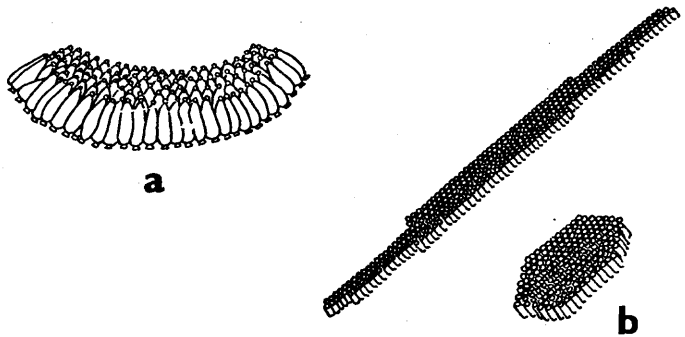


Fig. 6. - Culicine eggs rafts. a. *Culex pipiens* Linnaeus, after Christophers (1945), b. *Mansonia (quillettidia)* spp., after Gillett (1961).

the deposition of eggs singly on the water surface as in all known members of the other subfamilies. It apparently occurs as a regular mode only in a few genera *Mimomyia* (Menon, 1938, Menon & Tampi, 1959) and *Hodgesia* Theobald (McCrae & Sempala, 1969) and in some species of *Uranotaenia* Lyell (De Meijere, 1910, Bohart & Ingram, 1946, Mattingly, 1970). With these exceptions the various genera of Culicinae have evolved two main modes of oviposition, namely deposition of the eggs on the water surface in closely compacted rafts (Fig. 6) and deposition of the eggs, either singly or in groups, on a solid substrate in close proximity to the water or, in *Psorophora* Robineau-Desvoidy and some *Aedes*, in depressions in the ground exposed to subsequent flooding.

Interestingly, the raft forming mode is found in five different genera: *Uranotaenia* (Belkin & McDonald, 1956, Mattingly, 1970 b), *Culex* Linnaeus (Christophers, 1945, Newkirk, 1955, Iltis & Zweig, 1962, Hinton, 1968, Mattingly, 1970 a), *Culiseta* Felt (Owen, 1942, Christophers, 1945, Frohne, 1953, 1954, Dobrotworky, 1954, 1962, 1965, Wallis + Whitman, 1968), *Armigeres* Theobald (Macdonald, 1960) and *Mansonia* Blanchard (Gillett, 1961, Wharton, 1962) but in none of these does it characterize the entire genus. In every case one or more subgenera employ alternative modes of oviposition. As to whether raft formation is a primitive culicine mode or whether it has been evolved independently on a number of occasions remains an open question. An interesting intermediate condition is found in *Culex* subgenus *Neoculex* Dyar in which the eggs are compacted into typical *Culex* rafts but these are laid above the water line and only fall into the water when hatching takes place (Knab, 1904, Callot, 1943, Dobrotworsky, 1956, 1965).

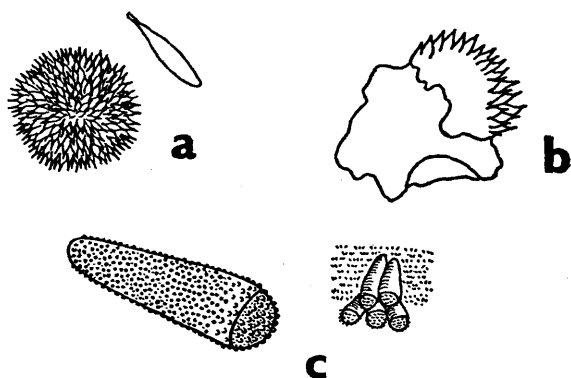


Fig. 7. - Eggs laid on aquatic plants. a. *Mansonia annulifera* (Theobald), original, b. *Culex abominator* Dyar & Knab, after Coad (1913), c. *Ficalbia minima* (Theobald), after Iyengar (1935).

In *Mansonia* subgenus *Mansonioides* Theobald (Fig. 7 a) the eggs are laid in closely compacted rosettes on the under surface of floating plants below the water line (Burton, 1960, Laurence, 1960). In *Culex* subgenus *Melanocion* Theobald (Fig. 7 b) they are laid in somewhat similar masses but above the water line on the upper surface of duckweed fronds or the emergent stems or leaves of grasses (Coad, 1913, Arnett, 1948). This might possibly be regarded as a specialization of the raft forming habit found elsewhere in both genera. *Ficalbia* Theobald (Fig. 7 c) also lays its eggs on aquatic plants but differs from both the other genera in laying them singly and on the

under side of floating plants but above the water line (Iyengar, 1935) affinities appear to be with *Mimomyia* with which it was formerly thought to be congeneric (Mattingly & Grjebine, 1958, Mattingly, 1957).

As already noted, the distinctive mode in *Aedes* and related genera is deposition of the eggs away from the water surface. Aside from the case *Neoculex*, mentioned above, the only other genus in which this occurs is *Orthopodomyia* Theobald (Fig. 8 a). This belongs, however, to quite a different stock having affinities with *Mimomyia* (Mattingly & Grjebine, 1958) and showing interesting resemblances to *Anopheles* and *Toxorhynchites*. The breeding places are container habitats, chiefly tree holes (Zavortink, 1968). The eggs s

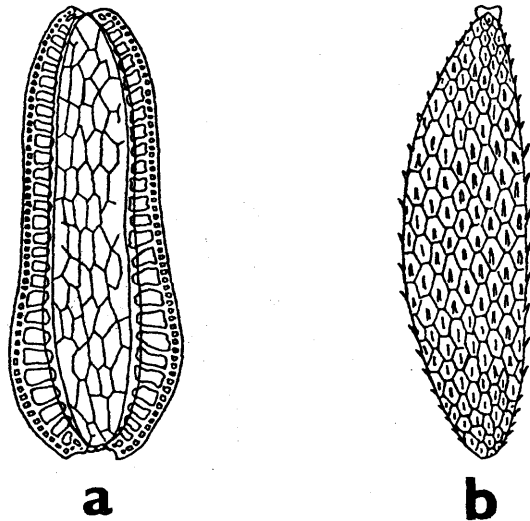


Fig. 8. - Eggs of *Orthopodomyia* and *Psorophora*. a. *O. pulchripalpis* (Rondani), after Marshall (1938). b. *Ps. ferox* (Humboldt), after Mitchell (1907).

most easily derivable from the *Mimomyia* type, or a more elaborate precursor in the manner suggested for *Anopheles* but in this case the 'floats' take form of an elaborate peripheral flange serving, apparently, for attachment to the walls of the breeding place (Marshall, 1938) and perhaps also as a plastron.

Among the aedine genera, other than *Aedes* itself, *Opifex* Hutton and *Psorophora* Robineau-Desvoidy are unique in breeding exclusively in ground pool habitats. The others (*Haemagogus* Williston (Bates, 1949), *Heizmannia* Ludlow (Macdonald & Traub, 1960), *Eretmapodites* Theobald (Gillett, 1957), *Armigeres* Theobald (Barr, 1964)) all utilize container habitats for oviposition.

and have eggs closely resembling those of container breeding *Aedes. Opifex* is unique, apart from *Mansonia*, in laying its eggs below the waterline but this is probably a specialized feature associated with the possession of hydrofuge hairs and associated mating behaviour adaptive to the exposed littoral habitats which it occupies (Kirk, 1923, Haeger & Provost, 1965, Mattingly, 1970 d and see below).

Throughout the otherwise quite diverse genus *Psorophora* (Fig. 8 b) the eggs show a remarkable constancy of ornamentation, suggesting that this is a truly monophyletic group. It possesses a number of features recalling the sabethine-toxorhynchitine stock to which it may be nearer than the other aedine genera, though these also possess a variety of striking sabethine characters affecting particularly the general facies of the adult. It seems therefore that adaptation to ground pool habitats may have taken place at a quite early stage in the evolution of this group of genera. It is noticeable also that the eggs of some subgenera of *Aedes* usually considered primitive and associated particularly with groundpools, notably *Mucidus* Theobald (Colledge, 1904, Mattingly, 1970 c) and some *Ochlerotatus* Lynch Arribalzaga (Horsfall & Craig, 1956, Craig & Horsfall, 1960, Myers, 1967, Kalpage & Brust, 1968) have an unwieldy appearance suggestive of a derivation of

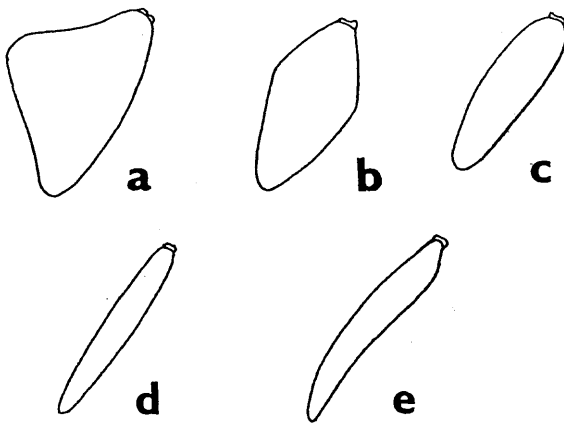


Fig. 9. - Eggs of *Aedes* spp. a. *Ae. (Mucidus) aurantius* (Theobald), b. *Ae. (Ochlerotatus) flavescens* (Muller); c. *Ae. (Stegomyia) aegypti*, d. *Ae. (Stegomyia) woodi* Edwards, e. *Ae. (Neomacleaya)* sp. Original.

the eggs of more advanced subgenera by a process of streamlining (Fig. 9). This may, however, be an oversimplification and it is interesting that some, at least, of the container breeding *Aedes* retain traces of the primitive mode

of oviposition on the water surface. *Eretmapodites* spp. (Haddow, 1942) and *Ae. aegypti* (Linnaeus) (Mattingly, 1969c) commonly lay a proportion of eggs on the water surface and this is the normal mode in the *Ae. (Coquimbatus) mariae* (Sergent & Sergent) complex (Coluzzi, personal communication) while *Ae. aegypti*, at least, normally, alights on the water even when depositing its eggs above the water line (Kennedy, 1942, Wallis, 1954). The various forms of behaviour involved in oviposition in depressions in the soil (Wesenberg-Lund, 1921, Bodman & Gannon, 1950, Husbands & Haddow, 1952, Corbet, 1965) are readily derivable from those characteristic of co-breeders. Rock pools share features of both types of habitat (Garnham, 1946). The major advance on the Sabethinae has been the development of varying degrees in the aedine genera of eggs resistant to desiccation under other adverse circumstances. This has made available to the genus *Ae.* in particular a wider geographical extension than in any other mosquito and has had important consequences for medical ecology (Mattingly, 1969c).

#### *Evolution of the larva and pupa*

Our knowledge of larval biology is less than sometimes supposed. In the field much more attention has been paid to the larval environment than to the larvae themselves. The resultant data are largely meaningless and remain so until they can be interpreted in ecological and ethological terms. The descriptive literature similarly relates largely to morphological structures of unknown functional or morphogenetic significance.

The chief functions of the larva are to remain alive long enough to become a pupa and to absorb during this time enough nourishment to meet its own requirements and for those of the pupa and newly emergent adult. The activities mainly involved are feeding, respiration and locomotion. None of these has been adequately studied.

#### FEEDING

Certain New World Sabethinae have greatly enlarged mandibles of unknown function (Fig. 10a). Other species of the same genus and species of *Wyeomyia* Theobald have enlarged maxillae and these are also present in some species of the Old World sabethine genera *Tripterooides* Gill and *Topomyia* Leicester (Fig. 10b). Their exact function is again uncertain but one section of *Tripterooides*, at least, with larvae inhabiting plant pitches, are probably used for tearing up the corpses of trapped insects.

Structures of this kind are unknown in the Toxorhynchitinae and

icinae. Their counterpart in these subfamilies is the modification of the mouthbrushes for capturing living prey, including other mosquito larvae. The particular type of modification is different in the two subfamilies though

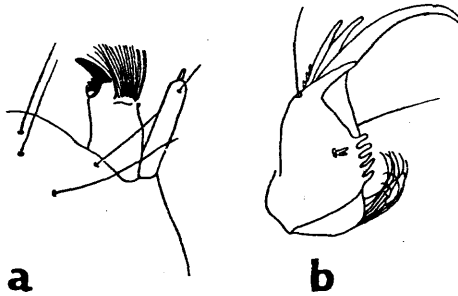


Fig. 10. - Modified mandibles and maxillae of sabethine larvae. a. *Trichoprosopon compressum* Lutz, after Lane (1953). b. *Tripteroides mathesoni* Belkin, after Belkin (1962).

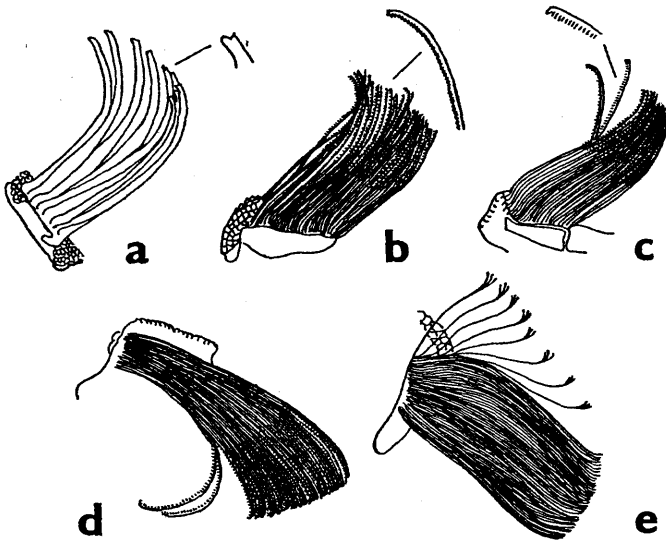


Fig. 11. Modifications of larval mouthbrushes. a. *Toxorhynchites brevipalpis* Theobald, b. *Aedes (Mucidus) grahamii* (Theobald), c. *Culex (Lutzia) halifaxii* Theobald, d. *Ps. (Psorophora) ciliata* (Fabricius), e. *Anopheles turkhudi* Liston. Original.

very similar in the three subgenera of Culicinae in which it occurs (Fig. 11). In Anophelinae the only comparable modification is the specialization of the mouthbrushes in *Paramyzomyia* for feeding on filamentous algae (Puri, 1931) which was mentioned above. (Fig. 11 e).

The aberrant *Mimomyia plumosa* (Theobald) has the mouthbrushes and the mentum entirely suppressed, apparently as an adaptation to soft bottom deposits (Hopkins, 1952). Apart from this, and comparatively few species in the other categories mentioned, the brushes of all mosquito larvae conform to two general types, respectively with browsing, by scraping food particles from a solid surface using for the purpose the pectinate inner mouthbrush setae, and filter feeding, employing long, non-pectinate mouthbrush setae to sweep suspended particles into the mouth (Fig. 12).

As can be seen from Fig. 12 both types of mouthbrush may be found in the same species. First detected in *Opifex fuscus* (Hutton, 1957), and still studied experimentally only in that species (McGregor, 1969) it is known also to occur in various *Aedes* and *Heizmannia* spp. (McGregor, 1969 b).

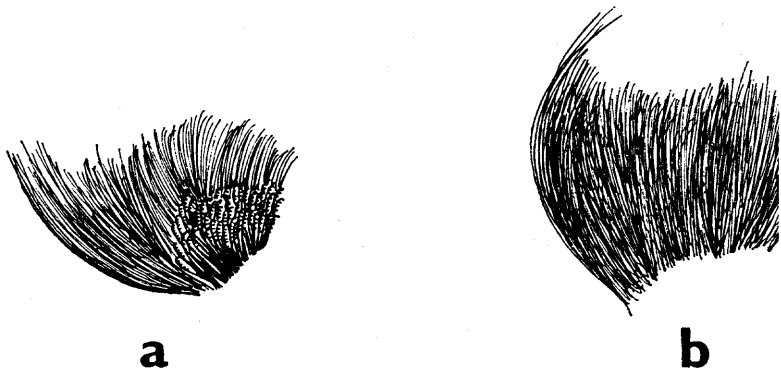


Fig. 12. - Mouthbrush dimorphism in *Opifex fuscus* Hutton. a. Browsing type, b. Filter feeding type. Original

1969 b). Although at first thought to be a genetic polymorphism it has been shown to be, surprisingly, an environmental effect. Larvae supplied with large food particles develop browsing mouthbrushes in the next instar, while larvae supplied with fine food particles develop filter feeding ones. The same larva can be persuaded to change from one to the other and back again during a single ontogeny.

The physiological basis of this remarkable phenomenon is quite unknown. It furnishes a good example of our ignorance of larval biology in general. The only comparable phenomenon at present known concerns the factor in *Stegomyia* larvae (Colless, 1956, Rosen & Rozeboom, 1954) in which hypertrophy of larval thoracic and abdominal setae has been

depend on the presence in the water of non-living suspended organic particles. Hairiness of this kind is found in an extreme form in many sabethines (Fig. 13) and in a few species of certain culicine genera (*Culex*, *Uranotaenia*, *Mimomyia*, *Aedes*). It is confined to container breeding species and may be protective against browsing by other larvae, which would associate the two phenomena ecologically (Mattingly, 1969 b).

The two types of mouthbrush are variously distributed within the different culicine genera. The browsing type is predominant in the aedine genera, very rare in *Culex* (Mattingly & Marks, 1955, Colless, 1965, Bram, 1967), a fact of some interest when it is recalled that the predatory type of mouthbrush shown in Fig. 11 occurs in both. An association of the browsing type with container habitats seems indicated and it is interesting that the



Fig. 13. - *Mimomyia (Ravenalites) deguzmanae* Mattingly. Larva. Original.

classic case of mouthbrush dimorphism comes from a rock pool species (*O. fuscus*) while the same condition appears to be shown by several species of *Aedes* subgenus *Finlaya*, a group widely associated with tree holes but containing also an important rock pool element. The intermediate nature of this type of habitat has already been noted.

#### RESPIRATION

Although employed primarily for feeding, the mouthbrushes also play a part in respiration in certain species having tracheal «gills» in the head over which they direct a current of water (Lewis, 1949, Hopkins, 1952). Dependence on additional supplies of oxygen, other than those derived

though the general body surface, also implies modifications of behaviour. Larvae of subfamilies other than the Anophelinae mostly obtain their additional oxygen by piercing the surface film with a respiratory siphon at the tip of the abdomen. Anopheline larvae, lacking a respiratory siphon, lie parallel with the surface film to which they are attached by long palmate hairs. The head can be rotated through  $180^\circ$  permitting feeding on the flora and fauna of the surface film. Larvae of tree hole breeders achieve the same effect by arching the body in a U-shape and pivoting on a short respiratory siphon. Container breeding species usually have a long siphon. Exceptions e.g. some *Culex* (*Neoculex*) and *Culex* (*Culicomyia*) might be thought to be secondarily adapted. It may be significant that many of these species tend to breed more particularly in large horizontal containers near the ground.

The genus *Mimomyia* is interesting in this connection since it has two subgenera specialized for breeding among dense aquatic vegetation in swamp habitats and a third (*Ravenalites* Doucet) which, while exhibiting many of the more striking features of the first two, breeds exclusively in container habitats (Mattingly, 1957, Mattingly & Grjebine, 1958). One such feature is the jointed antenna, unique to this genus though probably the functional equivalent of the flagelliform extension of the antenna found in the specialized swamp breeding genus *Mansonia* (Fig. 14 a, b). Other features found in *Ravenalites* though more commonly associated with swamp habitats than container breeders are the fine haired mouthbrushes of the male species and the long siphon, particularly of the species occurring in eastern Asia. Features suggestive of the container, rather than the swamp habitat, such as reduction of head setae and shortening of antenna and siphon are found, by contrast, in the species occurring in Madagascar where the genus has undergone an extensive evolutionary radiation (Doucet, 1950, 1951). The pupa of *Ravenalites* shown in an exaggerated degree various characters associated with the swamp habitat (long, slender trumpets and pads) is a reduction, amounting to virtual suppression, of the float hair on the first antennal segment as in *Mimomyia* subgenus *Etorleptiomyia* and *Mansonia* (Fig. 14 c).

Among other resemblances between *Mimomyia* and *Mansonia* is the occurrence in *Mimomyia* s. str. of several species with larval siphons modified for obtaining air from subaqueous plant tissues (Fig. 14 d and see Mattingly, 1957, Hopkins, 1952, Belkin, 1962). The siphon is much more elaborately modified in *Mansonia* (Fig. 14 e).

Various considerations suggest that if the two are, in fact, phylogenetically related then they may have evolved independently from the

little modified siphon of *Etorleptomyia* (Fig. 14 f) and this in turn from *Ravenalites*, an interesting speculation as involving the derivation of a swamp breeding from a container breeding group which will be further discussed in the following section.

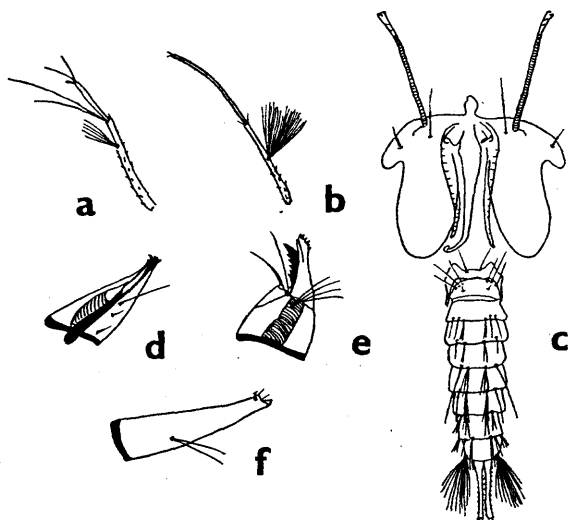


Fig. 14. - Details of early stages. Genera *Mimomyia* and *Mansonia*. a, b. Larval antenna. a. *Mim. pallida* Edwards, after Hopkins (1952), b. *Mans. metallica* (Theobald), after Gillett (1946), c. Pupa. *Mim. deguzmanae*, original, d-f. Larval siphon. d. *Mim. hybrida* (Leicester), after Mattingly (1957), e. *Mans. africana* (Theobald), based on Ingram & Macfie (1917), f. *Mim. luzonensis* (Ludlow), after Mattingly (1957).

#### LOCOMOTION

Besides their function of obtaining food, and their role in respiration, the mouthbrushes are used extensively in locomotion, most noticeably in species such as that shown in Fig. 13 in which flexion of the abdomen is almost impossible and the larvae glide through the water in a ghost-like fashion employing the mouthbrushes as propellers. In certain aedine genera (*Eretmapodites*, *Armigeres*) the normal swimming behaviour is varied by a fluttering motion adaptive, perhaps, to the thick organic sludges in which such larvae are often found. Aside from this and from a few specialized movements associated, e.g., with predation or with attachment to vegetation locomotion is mainly by abrupt side to side movements of the abdomen aided by the ventral brush. Very little is on record however, concerning the Sabethinae in which the ventral brush is virtually absent.

Bates (1949) notes an apparent ability on the part of Neosabethine larvae to crawl from one breeding place to another. A similar behaviour in *Anopheles* and in a leaf axil breeding *Aedes* are recorded in Old World Sabethinae though larvae of *Malaya* can crawl with remarkable rapidity over a wet glass plate (personal observation). There is also very suggestive evidence in the occurrence of deformation of the segments of the abdomen of larvae of one species of *Topomyia* having the character of « pro-legs » (Fig. 15 a).

Even more striking are the limb-like outgrowths on the thorax of *Tripteroides* and, very interestingly, of *Ravenalites* (Fig. 15 b), suggesting

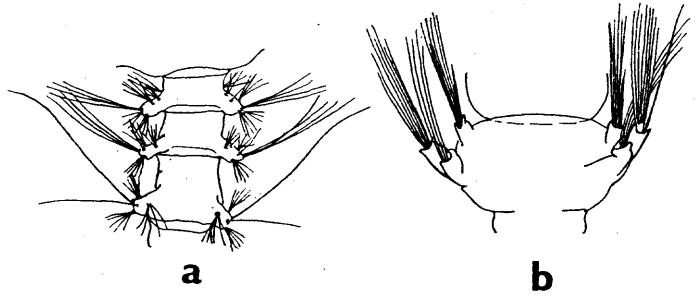


Fig. 15. - Larval structures possibly associated with crawling. a. *Topomyia papuensis* Nixon, posterior abdominal segments, b. *Mimomyia jeansottei* (Doucet). Ventral view of thorax.

association between *Mimomyia* and the Sabethinae. We are here faced again with the possible derivation of a swamp breeding genus from a container breeding one or the converse. However the choice is difficult. It would seem that the ecological conditions promoting such an evolutionary development are most probably to be sought in the tropical swamps where tree holes are constantly flooded and reexposed by changing level of the swamp water.

#### *Evolution of the adult*

The intimate association between the ecology of the egg and the mother has already been stressed. The role of the female is the accumulation of sufficient reserves for the maturation of the eggs, collaboration

male to ensure their fertility and, finally, their deposition in an environment suited to their survival and to the needs of the larvae of the next generation. The last function has already been discussed.

#### EVOLUTION OF BLOODFEEDING

Downes (1958 a), in a discussion of the evolution of bloodfeeding in the Diptera, challenges the commonly held opinion that this is a secondary mode of nutrition developed independently in a number of groups and suggests that, on the contrary, the biting Nematocera may be « the closest existing

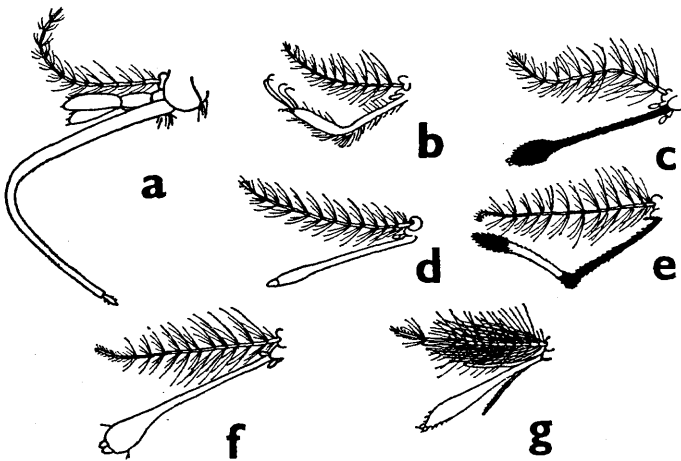


Fig. 16. - Modifications of the proboscis. a. *Toxorhynchites brevipalpis* Theobald, ♀, b. *Malaya genurostris* Leicester, ♀, c. *Topomyia spathulirostris* Edwards, ♀, d. *Limatus flavisetosus* Castro, ♀, e. *Limatus durhamii* Theobald, ♂, f. *Wyeomyia shannoni* Lane Cerqueira, ♂, g. *Ficalbia circumtestacea* (Theobald), ♂. Original.

representatives of the original Diptera ». As evidence for this he instances, inter alia, the fact that « The non-biting species or groups are irregularly scattered within normal, biting taxa, and may reasonably be regarded as secondary ». So far as the mosquitos are concerned the last statement is, however, an oversimplification.

Corresponding to Downes' « non-biting . . . groups » are *Toxorhynchites*, with the mouthparts and proboscis modified for feeding on nectar (Fig. 16 a) and the sabethine genus *Malaya* similarly restricted to feeding on the regurgitations of ants (Jacobson, 1909, Macdonald, 1962). (Fig. 16 b). Less well

known is the occurrence in the genus *Topomyia*, closely related to *Limatus*, one species with a conspicuously modified proboscis (Fig. 16 c). In the Neotropical genus *Topomyia* the proboscis is more or less normal. In the Neotropical genus *Limatus* the females have the proboscis swollen at the tip (Fig. 16 d) while the males have it swollen at the tip and curiously flexed, in two ways recalling the situation in both sexes of *Malaya* (Fig. 16 e).

The feeding habits of *Topomyia* and *Limatus* are unfortunately unknown. Macdonald & Traub (1960) note that no species of *Topomyia* is known to take blood and Macdonald (1960) suggests that they feed on nectar. In the absence of direct observations in the field an examination of the mouthparts would be informative. In females of *Toxorhynchites* the mandibles and maxillae are

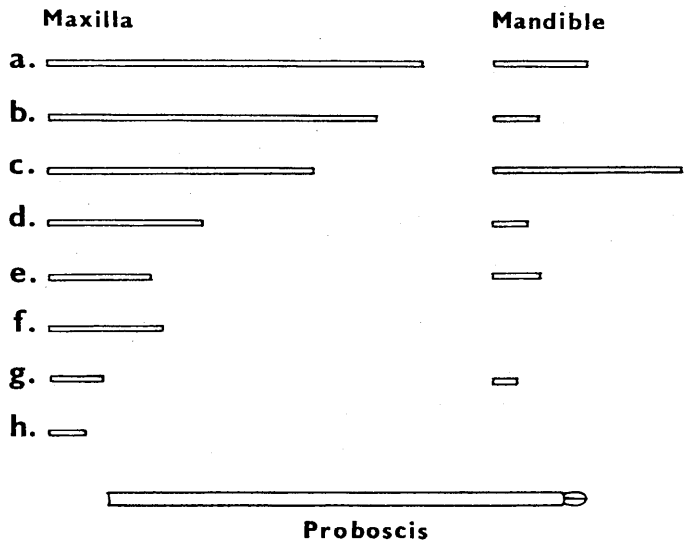


Fig. 17. - Mean length of maxillae and mandibles in males of British mosquitos, a & Staley (1935). a. *Culiseta* s. str., b. *Culiseta* (*Culicella*), c. *Anopheles* s. str., d. *Ochlerotatus* (*Finlaya*), e. *Aedes* (*Finlaya*), f. *Aedes* (*Ochlerotatus*), g. *Culex* s. str., h. *Aedes* (*Aedes*).

reduced and in those of *Malaya* they are absent (Edwards, 1932). In some species (e.g. *Culiseta* s. str.) degrees of reduction are found in males of all species though in some (e.g. *Culiseta* s. str.) the maxillae may be almost as long as the proboscis. A comparative study might well be of phylogenetic interest.

It will be seen from the foregoing that non-biting genera certainly occur in the Toxorhynchitinae and Sabethinae while the occurrence in the non-biting species in otherwise bloodfeeding genera remains pro-

In the Anophelinae and Culicinae the situation is quite different. No non-biting genera are known and the phenomenon of autogeny (the ability to produce mature eggs without a bloodmeal) is known only as a genetic polymorphism affecting a proportion of the species population rather than the species as a whole. The existence of such a polymorphism is clearly of great ecological interest though it has so far been studied mainly from a physiological point of view (Clements, 1963). Our current knowledge of its seasonal and geographical distribution is extremely limited (Moore, 1963, Corbet, 1964 b, Harwood, 1966, Spielman, 1967, Mattingly, 1967), while its distribution in the various groups of mosquitos can only be guessed at. It has been demonstrated in at least ten different genera belonging to all four subfamilies and it must be presumed to occur in many more than the few dozen species in which it has so far been detected. One factor tending to disguise its presence is the habit of some species of taking their first bloodmeal only after laying an autogenous egg batch (Tate & Vincent, 1936, Haeger & Provost, 1965).

Feeding on sugars and other plant substances was at one time thought to be characteristic mainly of male mosquitos. It is now known to occur frequently, also, among females (Downes, 1958 a, McCrae et al., 1968). Despite its advantages as a source of energy (Clements, 1955) it is suggested that in *An. gambiae*, and perhaps other anophelines, sugar meals are of minor importance (Thomson, 1951, Gillies & De Meillon, 1968). However, some *Anopheles* certainly take them (Hocking, 1953, Haeger, 1955, Downes, 1958 a). In *Culex pipiens* Linnaeus some sugars have an inhibitory effect on oviposition (De Meillon et al., 1967). No such effect has been noted in *Aedes* where regular sugar feeding occurs both in the laboratory (Gillett et al., 1962) and in the field (Nielsen & Greve, 1950, Hocking, 1953, Haeger, 1955, Downes, 1958 a). Some degree of ecological and physiological diversity evidently exists in which comparative studies may eventually reveal a phylogenetic pattern.

#### MATING BEHAVIOUR

Extensive mating sometimes takes place in male swarms (Downes, 1969, Quraishi, 1965) but, as noted by Nielsen & Haeger (1960), this does not prove that their principle function is epigamic. These authors discount the hypothesis that the epigamic element in swarming was formerly more important and that its importance has diminished in the course of evolution. The idea of mating in close proximity to the breeding place as the primitive mode with extensive male swarms and wide dispersal as later evolutionary

developments affords a useful framework for discussion (Mattingly, but on present evidence it is difficult to justify in detail. The evic reviewed below.

#### *Subfamily Toxorhynchitinae*

Very little is known. Paine (1934) notes that in *T. splendens* dispa very restricted. Copulation takes place at rest in both this species a *vipalpis* but in the latter at least it is initiated in flight (Muspratt, 19 resting males seizing the females when these approach.

#### *Subfamily Sabethinae*

Our knowledge is again very limited. Galindo (1958) notes *Sabethes chloropterus* coupling takes place at rest and is preceded by of courtship behaviour during which both sexes rest on the substrate. ation in *Wyeomyia smithii* also takes place at rest (Price, 1958) but e behaviour has not been described.

#### *Subfamily Anophelinae*

Swarming, generally accompanied by mating, has been observed in subgenera of *Anopheles* except *Kerteszia* Theobald. Some African *A* form small swarms at heights above the ground which are apparently specific (2). Swarming has been observed in nature even in some which mate readily in small cages in the laboratory (e.g. *An. atroparv* Thiel, *An. sundaicus* (Rodenwaldt), though its apparent absence in othe *quadrifasciatus* Say, *An. albimanus* Wiedemann) has been noted (& Haeger, *loc. cit.*). Mating has been said to take place in the vici the oviposition sites, after the bloodmeal (Zatek, 1915), in daytime places (Cambournac & Hill, 1940) and at the time of exodus fr emergence sites (Beyer et al., quoted by Niolsen and Haeger). It ha found to take place both before and after the first bloodmeal i *gambiae* Giles.

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(2) These were shown to me in Kenya by Mrs Van Someren and her husband who is d them in detail.

## Subfamily Culicinae

Mating with emerging females on the water surface, in *Opifex* (Kirk, 1923, Marks, 1958, Haeger & Provost, 1965) is probably an adaptation to the exposed littoral habitat. The antenna is greatly modified in both sexes (Fig. 18 a, b). Comparable behaviour in *Deinocerites* Theobald (Downes, 1966, Galindo, 1967, Provost & Haeger, 1967) may also have originated in relation to the littoral habitat but the stimuli involved differ, apparently, in being non-visual and the antennae are otherwise modified, probably in relation to mating in the dark crab holes which are the usual breeding and resting

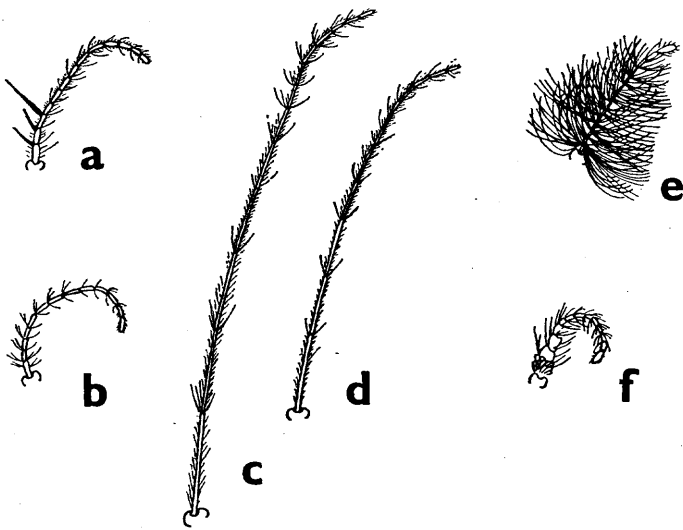


Fig. 18. - Culicine antennae. a, b. *Opifex fuscus*, a. ♂, b. ♀. c, d. *Deinocerites epitedeus* (Knab), c. ♂, d. ♀. e, f. *Aedeomyia africana* Neveu-Lemaire, e. ♂, f. ♀.

places. Despite the reduction of the antennal fibrillae (Fig. 18 c) small male swarms have been reported (Howard et al., 1912, 1915).

Berner (1947) observed *Mimomyia splendens* Theobald mating in flight immediately above the water lettuce plants among which they were breeding. This may be adaptive to the rigorous macroclimate which the species is able to tolerate (e.g. in Kano, N. Nigeria during the dry season (Mattingly, 1947)). Similar behaviour might be found, e.g., in *Uranotaenia anbydor* Dyar living in dense marginal vegetation at the head of Death Valley (Belkin

& McDonald, 1956) and some *Ficalbia* spp. ranging into relatively arid by virtue of their association with riverain vegetation (Mattingly & Ha 1955). On the above hypothesis such cases would presumably have to be interpreted as a retention of primitive behaviour patterns as an adaptation to special circumstances. Other species both of *Ficalbia* and of *Urano* have been seen swarming over open grass (Corbet, 1964 a).

Among other genera associated with dense aquatic vegetation *Lymnobia* Theobald has greatly modified antennae (Fig. 18 e, f) but nothing is known of its mating behaviour. In *Mansonia* Jayewickreme (1953) observed mating of *M. (Mansonioides) uniformis* Theobald after dark in the immediate vicinity of hosts (cattle) both on the wing and with resting blood-engorged females. The same type of behaviour almost certainly occurs in the closely related *M. africana* Theobald to judge from the simultaneous occurrence of males and females under comparable conditions (Mattingly, 1949 a, b). Corbet (1964 a) observed swarming and mating of males of *M. (Coquillettidia) fusinata* (Theobald) when the females were arriving to feed but mating apparently took place only with females in flight. Extensive swarms have been recorded in non-tropical species of this subgenus (Shute, 1933, Nielsen, 1964). Males of *M. (Coq.) xanthogaster* (Edwards) are highly aggressive sexually. I observed them in Queensland mating in a small aspirator immediately after capture. Other species observed mating in the immediate vicinity of the host include *Aedes (Diceromyia)* spp. (Hamon et al., 1955, again confirmed by my observations in Nigeria (Mattingly, 1949 b), *Ae. (Finlaya) sierrensis* (Ludlow) (Peyton, 1956), *Ae. (Stegomyia) scutellaris* (Walker) (O'Connor, 1923, Fildes & Horsfall, 1946 and my own observations in New Guinea) and *(Ochlerotatus) diantaeus* Howard, Dyar & Knab (Owen, 1937). It is difficult to find much in common between these various species other, perhaps, than a tendency to restricted dispersal. All except the *Mansonia* spp. and *diantaeus* are container breeders such as are commonly thought to be bred less widely than species with more extensive breeding grounds (though see Causey & Kumm, 1948). The association of *Mansonia* with dense aquatic vegetation and of *Ae. diantaeus* with thick forest (Carpenter & La Casse, 1956) might be significant in this connection. There seems to be no simple relationship between swarming and male aggressiveness though this needs further investigation. Some species mating readily in small cages also swarm in nature, e.g. *An. sundaicus* (Rodenwaldt) (Rao et al., 1942), *An. atroparvus* van Thiel (Bournac & Hill, 1940) and I captured mating pairs of *Culex pipiens* L. from small swarms in Burma.

The massive swarms formed, e.g., by some *Ochlerotatus* are quantitatively of a different order (Nielsen & Greve, 1950). It is tempting to associate

with the mass exodus from the breeding grounds sometimes observed in the same subgenus (Haeger, 1960) but it is not clear that such an association always exists while on the other hand mass exodus can take place under appropriate conditions even in such species as *C. p. fatigans* (Afridi & Majid, 1938) and *An. albimanus* (Le Prince & Orenstein, 1916).

Provost (1958) distinguished between species of *Psorophora* mating at any time of day and those which are thought to mate only in the evening when swarming takes place. The argument rests on the demonstration by Roth (1948) of an association between mating and the erection of the male antennal fibrillae which are permanently erect in the first type of species and erected only in the evening in the second. The situation is not, however, so simple. In *Ps. ferox* (Humboldt) seasonal variation occurs, both conditions being found (Nielsen, 1964). Nevertheless the suggestion is interesting as indicating two potentially rewarding fields for comparative study, namely the structure and function of the antenna and the significance of cyclical swarming and mating rhythms.

The form of antenna found in the common synanthropic mosquitos (Fig. 19 a, b) is commonly regarded as 'typical' but in the mosquitos as a whole there is extensive variation. The Sabethinae, in particular, show

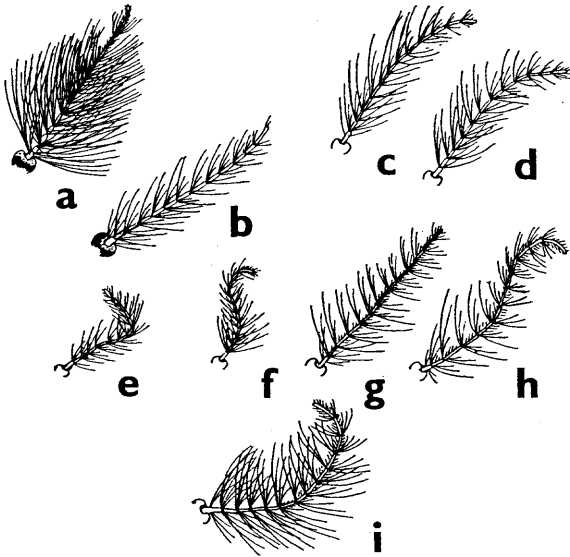


Fig. 19. Male and female antennae. a, b. *Aedes aegypti*, a. ♂, b. ♀. c, d. *Malaya genurostris* Leicester, c. ♂, d. ♀. e, f. *Bironella hollandi* Taylor, e. ♂, f. ♀. g, h. *Hodgesia malayi* Leicester, g. ♂, h. ♀. i. *Culex guiarti* Blanchard, ♀. Original.

varying degrees of reduced plumosity and reduction of terminal segments in the male amounting in some cases to virtual suppression of sexual dimorphism (Fig. 19 c, d). Sexual dimorphism is well marked in the Anopelinae with the exception of one section of *Bironella* in which the antennae are similar in the two sexes (Fig. 19 e, f). In Toxorhynchitinae it is also well developed but in some culicine genera it is almost completely suppressed (Fig. 19 g, h). Among aedine genera having at the same time some sabethine features most *Heizmannia* have the male antenna non-plumose while the female species has the terminal segments also similar in the two sexes (Mattingly 1970 e). On the other hand one subgenus has male antennae of 'narrow' type and this is true also of the whole of the related genus *Haemagogus* in which swarming has been reported (Levi Castillo, 1953) and mating takes place, in those species studied, almost entirely on the wing (Hovanitz, 1954). A few *Culex* (*Culex*) spp. have subplumose female antennae (Fig. 19 i) (Edwards, 1941) and the extreme degree of elaboration of the male antenna is found in subgenus *Lophoceraomyia* of this genus, many species of which have them ornamented with conspicuous tufts of modified scales (see, Bram, 1967, Sirivanakarn, 1968). The functional significance of these various modifications is quite unknown.

Downes (1958 b) finds the male antennae of *Ae. aegypti* to be more plumose than in other *Stegomyia* and associates this with the absence of recorded swarming, suggesting that mating in this species probably takes place near the breeding places. However, observations by MacGilchrist (1951) on *Ae. aegypti* and *Ae. albopictus* (Skuse) suggest that in both cases mating takes place in proximity to the host while in *Ae. aegypti* McClelland (1911) records small swarms of both sexes.

In *Eretmapodites*, another aedine genus with sabethine features, the antennae are plumose but shorter than usual as in some sabethines. Copulation in *E. chrysogaster* Graham is described as violent and prolonged, lasting in some cases, for more than an hour. Haddow (1946) associates this with the great complexity of the male terminalia (Fig. 20 a) but prolonged copulation has also been described in *Sabethes chloropterus* (Galindo, 1958) and *Wyeomyia smithii* (Price, 1958) in both of which the terminalia, apart from the dististyle, are relatively simple while performances of this order are entirely excluded by *Culiseta inornata* (Williston) in which copulation has been observed to last a copy from 3 hours 27 minutes to 6 hours 40 minutes (with a break of 10 minutes, in some cases, at half time!) (Rees & Onishi, 1951). The terminalia of this species are notably simple (Fig. 20 b). These prolonged periods of copulation compare with an average of 16 seconds in *Ae. aegypti* (Roth, 1942) and it is hard to believe that they are other than primitive. Antennectomized

of *C. inornata* are capable of mating and pheromones are thought to be involved (Kliewer et al., 1966). Chemical stimuli have also been thought to play a part in the mating of *Deinocerites* (Downes, 1966) and two species of *Culex* (Gjullin et al., 1967). It is possible that an evolutionary pattern may eventually be discerned in the context of chemical versus auditory stimulus and attraction.

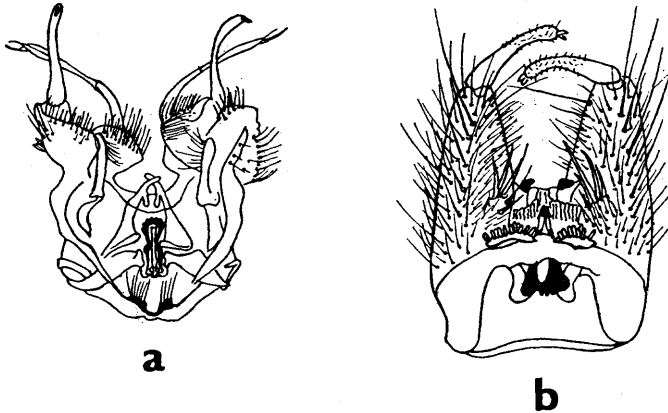


Fig. 20. - Male terminalia. a. *Eretmapodites chrysogaster*, b. *Culiseta inornata*. Original.

#### CYCLICAL BEHAVIOUR

Diel rhythms having an approximate 24 hour periodicity and affecting various activities of the adult mosquito have been described in some 200 species. The oviposition cycle is an example of such a rhythm which is particularly easy to study experimentally and it is to this that we owe most of our knowledge of the fundamentals. In the nature of things an individual mosquito cannot be expected to perform such an activity every 24 hours. The 24 hour oviposition rhythm in a population of mosquitos results from the presence of an endogenous 'clock' which determines the period during the 24 hours when those mosquitos which are ready to oviposit may do so (Gillett, 1962). The 'clock' is thus, in a sense, permissive rather than prescriptive and the various activity cycles observed in nature differ widely as between different species reflecting their different responses to the internal and external conditions by which their activity is mediated. Some ecological consequences have been discussed elsewhere (Mattingly, in press and see Corbet, 1966). The literature on the subject has yet to be comprehensively reviewed on a comparative basis and until this is done little can be said in the present context.

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It is reasonable to hope, however, from such general facts of observation as the wholly or mainly diurnal activity of sabethine and some quasi-sabethine genera, contrasted with the mainly nocturnal activity of Anophelinae, that phylogenetic patterns will eventually emerge.

The internal 'clock' was originally thought to be set solely by the transition from light to darkness (Gillett et al., 1961). More recently evidence has been adduced for an additional phase setting effect of the transition from dark to light (Taylor & Jones, 1969). It is now suggested that the two rhythms reinforce one another and that, in consequence, the geographic range as defined in terms of latitude should be derivable in principle from the diel rhythms exhibited by the species concerned (Taylor, 1969). If this should be confirmed new life may well be brought to the rather moribund subject of mosquito zoogeography which has suffered in the past from neglect of its ecological aspects but may yet contribute usefully to the study of phylogeny (Mattingly, 1962).

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## DISCUSSIONE

SACCÀ G.

Vorrei esprimere il mio apprezzamento e la gratitudine di tutti i colleghi, particolarmente di quelli che non comprendono l'inglese, all'amico Mattingly, per avere egli messo alla portata di tutti la sua interessantissima relazione, parlando in italiano.

Non avrei preso la parola se non vi fossi stato spinto da qualcosa che vorrei dire e sulla quale gradirei un commento di Mattingly e del Prof. Sadun. Ho appreso dall'agenzia « American Express », e non dagli organizzatori del Congresso, che il 2° Congresso Internazionale di Parassitologia si terrà a Washington ai primi di settembre. Quando, a termini quasi ormai scaduti, ho potuto leggere il programma, sono rimasto dolorosamente sorpreso nel constatare che in esso l'entomologia era stata praticamente dimenticata. Ora, poichè non credo vi siano dubbi sul fatto che l'Entomologia medica faccia parte della Parassitologia, come Entomologo medico, libero docente in Parassitologia, mi rivolgo al Dott. Mattingly, autorità mondiale nel campo dell'Entomologia, che tanta parte ha avuto nella

buona riuscita del 1° Congresso Internazionale di Parassitologia (Roma, 1964) per sapere quali siano le sue impressioni in merito, e al Prof. Sadun, organizzatore del Congresso di Washington, per un commento appropriato.

MATTINGLY P. F.

Sono in accordo con il Dott. Saccà perchè mi ricordo con piacere speciale il Primo Congresso Internazionale di Parassitologia in Roma. In quell'occasione mi sembrava che, grazie, credo, particolarmente al Prof. Biocca, si era raggiunto un equilibrio ammirevole fra l'Entomologia e la Parassitologia.

Questa per me, è cosa di primaria importanza perchè la nostra comprensione delle malattie trasmesse dagli antropodi riposa, sopra tutto, su una comprensione delle relazioni tra i vettori, i parassiti e l'ambiente. Senza questa e senza la collaborazione la più intima tra gli entomologi ed i parassitologi nè il controllo nè l'analisi epidemiologica sono possibili.