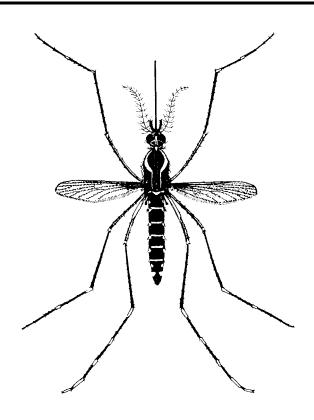
3Culicine mosquitoes (Culicinae)



Conservatively the subfamily Culicinae contains 40 genera, but as already mentioned (see Chapter 1) some taxonomists recognize many more genera, two of which are *Stegomyia* and *Ochlerotatus*, resulting in two medically important species being named *Stegomyia aegypti* and *Ochlerotatus albopictus*. However, in this book all species attributed to these two new genera are retained in the genus *Aedes*, such as *Aedes aegypti* and *Aedes albopictus*, with *Stegomyia* and *Ochlerotatus* recognized as subgenera.

The medically most important genera are <u>Culex</u>, <u>Aedes</u>, <u>Haemagogus</u>, <u>Sabethes</u> and <u>Mansonia</u>, while <u>Coquillettidia</u> and <u>Psorophora</u> are of lesser importance. Species of <u>Culex</u>, <u>Aedes</u> and <u>Coquillettidia</u> are found in both temperate and tropical regions, whereas <u>Psorophora</u> species occur only in <u>North</u>, <u>Central and South America</u>. <u>Haemagogus</u> and <u>Sabethes</u> mosquitoes are restricted to <u>Central and South America</u>. <u>Mansonia</u> occurs mainly in the tropics.

Certain *Aedes* mosquitoes are vectors of yellow fever in <u>Africa</u>, and *Aedes*, *Haemagogus* and *Sabethes* are yellow fever vectors in <u>Central</u> and <u>South America</u>. *Aedes* species are also vectors of the classical and haemorrhagic forms of dengue. All seven genera of culicine mosquitoes mentioned here, as well as some others, can transmit a variety of other arboviruses. Some *Culex*, *Aedes* and *Mansonia* species are important vectors of filariasis (*Wuchereria bancrofti* or *Brugia malayi*). *Psorophora* species are mainly pest mosquitoes but a few transmit arboviruses, while *Coquillettidia crassipes* can also be a vector of brugian filariasis.

Characters separating the subfamily Culicinae from the Anophelinae have been outlined in Chapter 1 and are summarized in Table 1.1 (page 18).

It is not easy to give a reliable and non-technical guide to the identification of the most important culicine genera. Nevertheless, characters that will usually separate these genera are given below, together with notes on their biology.

3.1 Culex mosquitoes

3.1.1 Distribution

Culex mosquitoes are found more or less worldwide, but they are absent from the extreme northern parts of the temperate zones.

3.1.2 Eggs

Eggs are usually brown, long and cylindrical, laid upright on the water surface and placed together to form an *egg raft* which can comprise up to about 300 eggs (Fig. 1.15). No glue or cement-like substance binds the eggs to each other; adhesion is due to surface forces holding the eggs together. A few other mosquitoes, including those of the genus *Coquillettidia*, also deposit their eggs in rafts.

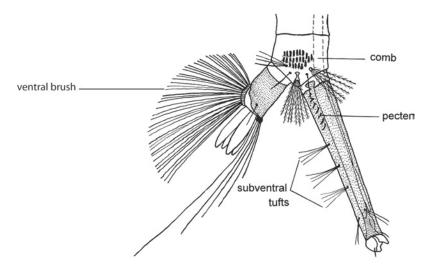


Figure 3.1 Terminal abdominal segments of a *Culex* larva, showing the long siphon with more than one (three shown here) subventral tufts of hair.

3.1.3 Larvae

The larval siphon is often long and narrow (Fig. 3.1), but it may be short and fat. There is always *more than one pair* of *subventral tufts* of hairs on the siphon, none of which is near the base. These hair tufts may consist of very few short and simple hairs, which can be missed unless larvae are carefully examined under a microscope.

3.1.4 Adults

Frequently, but not always, the thorax, legs and wing veins of the adult are covered with *dull-coloured*, often brown, scales (Plate 2). The abdomen is often covered with brown or blackish scales, but some whitish scales may occur on most segments. Adults are recognized more by their lack of ornamentation than by any striking diagnostic characters. The tip of the female abdomen is not pointed but *blunt*. Claws on all tarsi are simple and those on the hind tarsi are very small. Examination under a microscope shows that all tarsi have a pair of small fleshy *pulvilli* (Fig. 1.2).

3.1.5 Biology

Eggs are laid in a great variety of aquatic habitats. Larval habitats of most *Culex* species are *ground collections* of water such as pools, puddles, ditches, borrow pits and ricefields. Some species lay their eggs in manmade container-habitats such as tin cans, water receptacles, bottles and water-storage tanks. Only a few species are found in tree-holes and even fewer in leaf axils. Larvae of the medically most important species, *Culex*

quinquefasciatus, which is a vector of bancroftian filariasis, occur in waters polluted with organic debris such as rotting vegetation, household refuse and excreta. Larvae are also commonly found in partially blocked drains and ditches, soakaway pits and septic tanks, and in village pots, especially abandoned ones in which water is polluted and unfit for drinking. It is a mosquito that is associated with urbanization, especially towns with poor and inadequate drainage and sanitation. Under these conditions its population increases rapidly. Adults mainly bite at night.

Culex quinquefasciatus, and many other Culex species, bite humans and other hosts at night. Some species, such as Cx. quinquefasciatus, commonly rest indoors both before and after feeding, but they also shelter in outdoor resting places.

Culex tritaeniorhynchus is an important vector of Japanese encephalitis and breeds in ricefields and grassy pools. In southern Asia larvae are sometimes found in fish ponds which have had manure added to them.

3.2 Aedes mosquitoes

3.2.1 Distribution

Worldwide, the geographical range of *Aedes* mosquitoes extends well into northern and arctic areas, where they can be vicious biters and serious pests to both people and livestock.

3.2.2 Eggs

Eggs are usually black, more or less ovoid in shape, and are always laid *singly* (Fig. 1.15). Careful examination shows that the eggshell has a distinctive mosaic pattern. Eggs are laid on damp substrates just beyond the water line, such as on damp mud and leaf litter of pools, on the damp surfaces of clay pots, rock-pools and tree-holes.

Eggs can withstand *desiccation*, the intensity and duration of which varies, but in many species they can remain dry but viable for many months or occasionally a year or more. When flooded, some eggs may hatch within a few minutes, while others of the same batch may require longer immersion in water before they hatch, and consequently hatching may be spread over several days or weeks. Even when eggs are soaked for long periods some may fail to hatch because they require several soakings followed by short periods of desiccation before hatching can be induced. Even if environmental conditions are favourable, eggs may be in a state of *diapause* and will not hatch until this resting period is terminated. Various stimuli, including reduction in the oxygen content of water, changes in day length, and temperature, may be required to break diapause in *Aedes* eggs.

Larvae of many *Aedes* species occur in small *container-habitats* (tree-holes, plant axils, etc.) which are susceptible to drying out; thus the ability

of eggs to withstand *desiccation* is clearly advantageous. Desiccation and the ability of eggs to hatch in instalments can create problems with controlling the immature stages (see page 79).

3.2.3 Larvae

Aedes species usually have a short barrel-shaped siphon, and there is only one pair of subventral tufts, which arises about one-quarter or more from the base of the siphon (Fig. 3.2). There are at least three pairs of setae in the ventral brush. The antennae are not greatly flattened and there are no very large setae on the thorax. These characters should separate Aedes larvae from most of the culicine genera, but not unfortunately from larvae of South American Haemagogus. In Central and South America Aedes larvae can usually be distinguished from those of Haemagogus by possessing either larger or more strongly spiculate antennae and the comb (Fig. 3.2) not being on a sclerotized plate as in some Haemagogus.

3.2.4 Adults

Many, but not all, *Aedes* adults have conspicuous *patterns* on the thorax formed by black, white or silvery scales (Fig. 3.3, Plate 3), and in some species yellow and/or brownish scales are present. The legs often have dark and white rings (Fig. 3.4b). *Aedes aegypti*, often called the yellow fever mosquito, is readily recognized by the lyre-shaped silver markings on the lateral edges of the scutum (Fig. 3.3b). Scales on the wing veins of

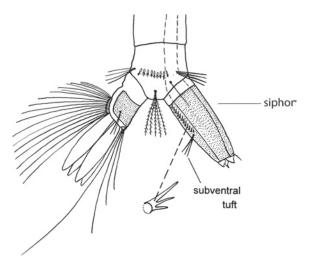


Figure 3.2 Terminal abdominal segments of an *Aedes* larva, showing the short siphon with a single subventral hair tuft.

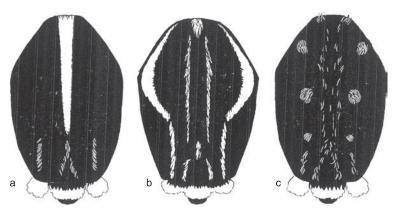


Figure 3.3 Dorsal surfaces of the thoraces of adult *Aedes* mosquitoes, showing examples of thoracic patterns of dark and pale scales: (a) *Ae. albopictus*, with a diagnostic median white stripe; (b) *Ae. aegypti*, with black scales and typical lyre-shaped silvery markings; (c) *Ae. vittatus*, with six rather indistinct lateral white spots.

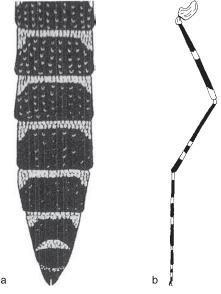


Figure 3.4 (a) Abdomen and (b) leg of an *Aedes* adult, showing typical arrangement of black and white scales.

Aedes mosquitoes are narrow and usually mainly black. In Aedes the abdomen is often covered with black and white scales forming distinctive patterns, and in the female the abdomen is pointed at its tip (Fig. 3.4a).

3.2.5 Biology

Although the larval habitats of some *Aedes* species are marshes and ground pools, including snow-melt pools in arctic and subarctic areas, many, especially tropical species, are found in natural *container-habitats* such as tree-holes, bamboo stumps, leaf axils and rock-pools, or in man-made ones such as water-storage pots, tin cans and tyres. For example, *Ae. aegypti* larvae commonly occur in water-storage pots or jars that are either inside or outside houses. Larvae occur mainly in pots having clean water intended for drinking. In some areas *Ae. aegypti* larvae are also found in rock-pools and tree-holes. *Aedes africanus*, an African species involved in the sylvatic transmission of yellow fever, breeds mainly in tree-holes and bamboo stumps, whereas *Ae. bromeliae*, another African yellow fever vector, breeds almost exclusively in leaf axils, especially those of banana plants, pineapples and coco-yams (*Colocasia* species).

Aedes albopictus (Fig. 3.3a), a vector of dengue in Southeast Asia, breeds in both natural and man-made container-habitats such as tree-holes, water-storage pots and vehicle tyres. This species was introduced into the continental USA in 1985 as dry, but viable, eggs that had been oviposited in tyres in Asia which were then exported. It can also be introduced into countries by eggs in lucky bamboo (*Dracaena* species), in which there is an increasing trade. By 2010 *Ae. albopictus* had spread to more than 29 states in the USA. It is found in many Latin American countries, in some sub-Saharan African countries, in 15 European countries, in Israel and in both Australia and New Zealand. In summary, it has been reported from more than 27 countries outside Asia. However, *Ae. albopictus* has often failed to become established in many countries having a more temperate climate or where efficient control has rapidly eliminated invasions.

Larvae of *Ae. polynesiensis* occur in both man-made and natural container-habitats, especially split coconut shells in Polynesia, whereas larvae of *Ae. pseudoscutellaris* are found in tree-holes and bamboo stumps in Fiji. Both species are important vectors of diurnally subperiodic bancroftian filariasis. *Aedes togoi*, which is a minor vector of nocturnally periodic bancroftian and brugian filariasis in China, breeds principally in rock-pools containing fresh or brackish water.

The life cycle of *Aedes* mosquitoes from eggs to adults can be rapid, taking as little as seven days, but is usually 10–12 days; in temperate species the life cycle may last several weeks to many months, and some species overwinter as eggs or larvae.

Adults of most *Aedes* species bite mainly during the *day* or early evening. Most biting occurs out of doors and adults usually rest out of doors before and after feeding.

3.3 Haemagogus mosquitoes

3.3.1 Distribution

Haemagogus mosquitoes are found only in Central and South America.

3.3.2 Eggs

Eggs are usually black and ovoid and laid singly in tree-holes and other natural container-habitats, and occasionally in man-made ones. There is no simple method of distinguishing eggs of *Haemagogus* from those of *Aedes* or *Psorophora* mosquitoes.

3.3.3 Larvae

Larvae have only one pair of subventral tufts arising, as in *Aedes* species, one-quarter or more from the base of the siphon. They resemble *Aedes* larvae but can usually be distinguished by the antennae being short and either lacking spicules or having only a very few, and by the ventral brush arising from a sclerotized *boss* (Fig. 3.5). In some species the comb teeth are arranged at the edge of a sclerotized *plate*; in *Aedes* this plate is absent.

3.3.4 Adults

Adults are very *colourful* and can easily be recognized by having broad, flat and bright metallic blue, red, green or golden scales covering the dorsal

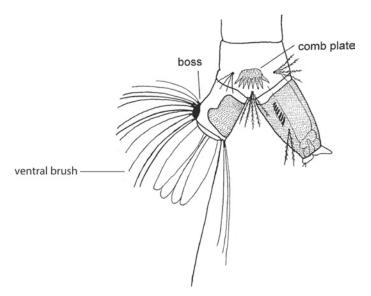


Figure 3.5 Terminal abdominal segments of a *Haemagogus* larva, showing a ventral brush arising from a dark sclerotized boss, and comb scales arranged on a small 'plate'.

part of the thorax. Like *Sabethes* mosquitoes (Fig. 3.7a), they have exceptionally large *antepronotal thoracic lobes* behind the head. *Haemagogus* adults are rather similar to those of *Sabethes*, and it may be difficult for the novice to separate these two genera. However, no *Haemagogus* mosquito has paddles on the legs, which is a conspicuous feature of many, but not all, *Sabethes* species (Fig. 3.7c).

3.3.5 Biology

Eggs can withstand *desiccation*. Larvae occur mostly in tree-holes and bamboo stumps, but also in rock-pools, split coconut shells and sometimes in assorted domestic containers. They are basically *forest mosquitoes*. Adults bite during the day and mostly in the tree-tops, where they feed on monkeys. However, under certain environmental conditions such as experienced at the edges of forests during tree-felling operations or during the dry season, adults may descend to the forest floor to bite humans and other hosts. Species such as *Haemagogus spegazzinii*, *Hg. leucocelaenus* and *Hg. janthinomys* are all involved in yellow fever transmission in forests.

3.4 Sabethes mosquitoes

3.4.1 Distribution

Sabethes mosquitoes are found only in Central and South America.

3.4.2 Eggs

Little is known about the eggs of *Sabethes* species, but they are laid singly, have no prominent surface features such as bosses or sculpturing and are incapable of withstanding desiccation. Eggs of *Sabethes chloropterus*, a species sometimes involved in the sylvatic cycle of yellow fever, are rhomboid in shape and can thus be readily distinguished from most other culicine eggs (Fig. 3.7b).

3.4.3 Larvae

The larval siphon is relatively slender and moderately long (Fig. 3.6) and has many *single* hairs placed ventrally, laterally or dorsally. *Sabethes* larvae can usually be distinguished from other mosquito larvae by having only *one pair* of setae in the ventral brush, the comb teeth arranged in a single row, or at most with three or four detached teeth, and by the absence of a pecten.

3.4.4 Adults

The dorsal surface of the thorax is covered with appressed *iridescent* blue, green and red scales (Plate 4). The *antepronotal lobes*, like those in

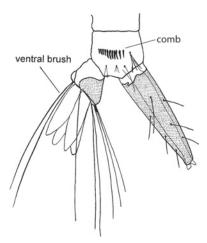


Figure 3.6 Terminal abdominal segments of a *Sabethes* larva, showing a single pair of hairs in the ventral brush, the comb, numerous single hairs on the siphon, and absence of a pecten on the siphon.

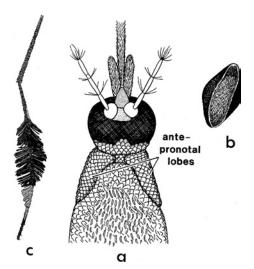


Figure 3.7 Sabethes mosquitoes: (a) head and thorax, showing antepronotal lobes forming a 'collar' behind the head; (b) an egg; (c) hindleg, showing long narrow scales forming a 'paddle'.

Haemagogus, are very large (Fig. 3.7a). Adults of many species have one or more pairs of tarsi with conspicuous *paddles* composed of narrow scales (Fig. 3.7c). Their presence immediately distinguishes *Sabethes* from all other mosquitoes. Species which lack these paddles resemble those of *Haemagogus*, and a specialist is required to identify them.

3.4.5 Biology

Larvae occur in tree-holes and bamboo stumps, but a few species are found in leaf axils of bromeliads and other plants. They are *forest mosquitoes*. Adults bite during the day and mainly in the tree canopy, but like *Haemagogus* adults may descend to ground level at certain times to bite humans and other hosts. *Sabethes chloropterus* has been incriminated as a sylvan vector of yellow fever.

3.5 Mansonia mosquitoes

3.5.1 Distribution

Mansonia is principally a genus of wet tropical areas, but a very few species occur in temperate regions.

3.5.2 Eggs

Eggs are dark brown or blackish and cylindrical, but have a tube-like extension apically which is usually darker than the rest of the egg (Fig. 3.8). Eggs are laid in sticky compact *masses*, often arranged as a rosette, which are glued to the undersurface of floating vegetation (Figs. 1.15, 3.8).

3.5.3 Larvae

Mansonia larvae are easily recognized because they have a *specialized siphon* adapted for piercing aquatic plants to obtain air (Fig. 3.9b,c). The siphon tends to be conical, with the apical part darker and heavily sclerotized, and it has teeth and curved hairs which assist a larva to attach itself to plants and insert its siphon. The pupal respiratory trumpets are also inserted into plants for respiration (Fig. 3.9a).

3.5.4 Adults

Typically adults have the legs (Fig. 3.10c), palps, wings and body covered with a *mixture* of dark (usually brown) and pale (usually white or creamy) scales, giving the mosquito a rather dusty appearance. The scattering of dark and pale scales on the wing veins gives the wings the appearance of having

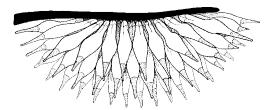


Figure 3.8 *Mansonia* eggs glued to the underside of floating aquatic vegetation.

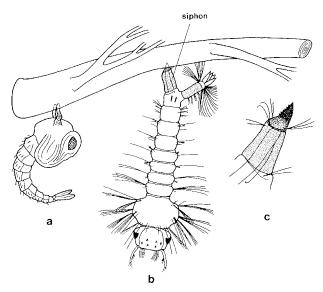


Figure 3.9 Immature stages of *Mansonia* mosquitoes: (a) pupa with respiratory trumpets inserted into an aquatic plant; (b) larva with siphon inserted into an aquatic plant for respiration; (c) larval siphon, showing serrated structures used to pierce aquatic plants.

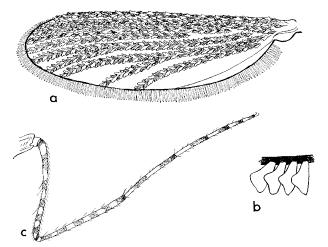


Figure 3.10 *Mansonia* mosquitoes: (a) wing, showing speckled distribution of dark and pale scales; (b) a few scales on a wing vein, showing their broad, almost heart shape; (c) leg, showing distribution of dark and pale scales giving a banded pattern.

been sprinkled with salt and pepper (Fig. 3.10a), and provides a useful character for identification. Closer examination shows that the scales on the wings are very broad and often asymmetrical and almost *heart-shaped* (Fig. 3.10b). In other mosquitoes these scales are longer and narrower.

3.5.5 Biology

Eggs are glued to the undersurface of plants and hatch within a few days; they are unable to withstand desiccation. All larval habitats have aquatic vegetation, either rooted (such as grasses, rushes and reeds) or floating (such as *Pistia stratiotes, Salvinia* or *Eichhornia* species). Larvae consequently occur in permanent collections of water such as swamps, marshes, ponds, borrow pits, grassy ditches, irrigation canals and even in the middle of rivers if they have floating plants.

Larvae and pupae only detach themselves from plants and rise to the water surface if they are disturbed. Because they are more or less permanently attached to plants the immature stages are frequently missed in larval surveys. It is therefore not easy to identify breeding places unless special collecting procedures are undertaken, such as removing plants and examining them for attached *Mansonia* larvae and pupae. Because it is difficult to get insecticides to the larvae, which may be some distance below the water surface, it is often difficult to control *Mansonia* mosquitoes with conventional insecticidal applications. However, herbicides can be used to kill the plants on which larvae are attached (see page 81).

Adults usually bite at night, but a few species are day-biters. After feeding, most *Mansonia* rest out of doors, but a few species rest indoors. The main medical importance of *Mansonia* mosquitoes is as vectors of filariasis, such as the nocturnally periodic and nocturnally subperiodic forms of *Brugia malayi* in Asia. In Africa filariasis (*W. bancrofti*) is not transmitted by *Mansonia* species, although they can be vectors of a few, but not very important, arboviruses.

3.6 Coquillettidia mosquitoes

The genus *Coquillettidia* is of lesser medical importance and is therefore described only briefly. It is mainly tropical, but a few species occur in temperate regions. *Coquillettidia* is related to *Mansonia* and has sometimes been treated as a subgenus of *Mansonia*, but species of *Coquillettidia* differ in several respects. For example, as in *Culex* species, eggs are formed into *egg rafts* that float on the water, but they are narrower and longer than *Culex* rafts. Larvae have rather conical siphons, which like those of *Mansonia* are inserted into plants for respiratory purposes, but the larval antennae are much longer than those in *Mansonia*. Adults have narrow scales on the wings, not broad or heart-shaped ones as found in *Mansonia*, and several *Coquillettidia* species are a bright *yellow*. *Coquillettidia crassipes* can be a vector of nocturnally subperiodic *B. malayi* in Southeast Asia.

3.7 *Psorophora* mosquitoes

Psorophora mosquitoes are of little medical importance and so are described briefly. They are found from Canada to South America. They are similar in

many respects to *Aedes* species: for example, their eggs look like *Aedes* eggs and like them they can withstand *desiccation*. Adults of some pest species are large mosquitoes. A specialist is required to distinguish the larvae from those of *Aedes* species. Larval habitats are mainly flooded pastures and sometimes ricefields; larvae of several species are predators. Although adults can be vectors of a few arboviruses, such as Venezuelan equine encephalitis, their main importance is as vicious biting pests.

3.8 Medical importance

3.8.1 Biting nuisance

In some cases, a considerable amount of money is spent on mosquito control not because they are vectors of disease but because they are troublesome biters. For example, some of the best-organized mosquito control operations are in North America, where large amounts of money may be spent on mosquito control, often more than in some tropical countries where mosquitoes are important vectors of diseases such as malaria. However, in northern temperate and subarctic areas of America, Europe and Asia much greater numbers of mosquitoes can be encountered biting people than in tropical countries. Although they may not be transmitting diseases to humans in these areas they can, nevertheless, make life outdoors intolerable.

3.8.2 Arboviruses

Numerous arboviruses are transmitted by culicine mosquitoes, including important ones such as those causing yellow fever and dengue. *Aedes* and *Culex* species are the most important vectors of arboviruses.

The intrinsic incubation period of a virus in humans is usually just a few days, often 3–4 days, after which virus appears in the peripheral blood and the host is viraemic. *Viraemia* lasts only a few days, typically 3 days, after which the virus disappears from the peripheral blood. A vector must bite a viraemic host if it is to become infected and transmit an infection.

A relatively high titre of arbovirus is usually required before a virus can pass across the gut wall of the mosquito into the haemolymph. From the haemolymph the virus invades many tissues and organs, including the *salivary glands*, where virus multiplication occurs. This is the *extrinsic incubation period* of development and can take 5–30 days, depending on temperature, the type of virus and the mosquito species. In most mosquitoborne viral infections the extrinsic cycle is typically 8–15 days.

3.8.3 Yellow fever (*Flavivirus*)

The arbovirus causing yellow fever occurs in Africa and tropical areas of the Americas. It does not occur in Asia or elsewhere, although mosquitoes capable of transmitting the disease occur in many countries. Yellow fever is a *zoonosis*, being essentially an infection of forest monkeys which under certain conditions can be transmitted to humans. The World Health Organization (WHO) estimates that there are 200 000 cases and 30 000 deaths a year caused by yellow fever.

Africa

About 90% of yellow fever cases occur in Africa, where it is endemic in 33 countries. Outbreaks of yellow fever occurred in 2010 in the Ivory Coast, Guinea, Cameroon, the Democratic Republic of the Congo and Senegal; in 2009 in the Central African Republic, Cameroon, Liberia, the Republic of the Congo, Guinea and Sierra Leone. In 2008 yellow fever was recorded in five West African countries, in 2007 just in Togo, but in 2006 it occurred in six West African countries. Other outbreaks had occurred prior to 2006, showing that yellow fever in West Africa is a perpetual problem.

In Africa the yellow fever virus occurs in certain cercopithecid monkeys (e.g Colobus and Cercopithecus species) inhabiting the forests. Other primates also act as reservoir hosts, and in East Africa the lesser bushbaby (Galago senegalensis) is an important host. The virus is transmitted amongst these primates by tree-hole-breeding mosquitoes, mainly Aedes africanus. This forest-dwelling mosquito bites mainly in the forest canopy soon after sunset – just in the right place and at the right time to bite monkeys going to sleep in the tree-tops. This *sylvatic cycle*, or savanna, forest or monkey cycle as it is sometimes called, maintains a virus reservoir in the monkey population (Fig. 3.11). In Africa, monkeys are little affected by yellow fever, dying only occasionally, although in East Africa infected bushbabies (Galago species) usually die. Some of the monkeys involved in the forest cycle descend from the trees to steal bananas from farms at the edge of the forest. In this habitat the monkeys get bitten by different mosquitoes, for example by Aedes bromeliae (formerly called Ae. simpsoni), a species that breeds in leaf axils of bananas, plantains, coco-yams (Colocasia species) and pineapples, and in West Africa also by other species such as tree-holebreeding Aedes furcifer, Ae. opok and Ae. luteocephalus. These species bite during the day at the edges of forests, and if the monkeys have viraemia, that is yellow fever virus circulating in their peripheral blood, the mosquitoes become infected. If these mosquitoes live sufficiently long they can transmit yellow fever to other monkeys, or more importantly to people. This transmission cycle, occurring in clearings at the edge of forests involving both monkeys and humans, is sometimes referred to as the rural cycle (Fig. 3.11). When people return to their villages, or travel to towns, they get bitten by different mosquitoes, including Ae. aegypti, a domestic species breeding mainly in man-made containers such as water-storage pots, abandoned tin cans and vehicle tyres. If people have viraemia then Ae. aegypti

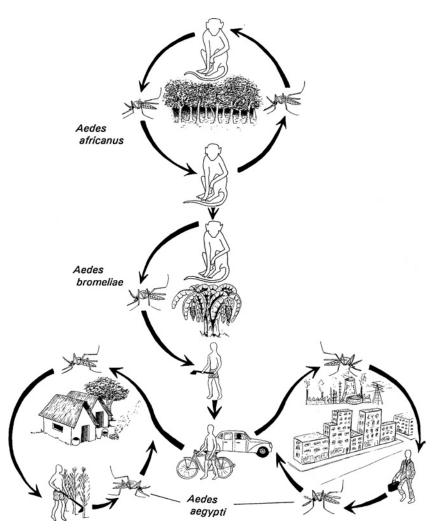


Figure 3.11 Diagrammatic representation of the sylvatic, rural and urban cycles of yellow fever transmission in Africa (only major vectors included).

becomes infected and yellow fever is transmitted among the human population by this species. This is the *urban cycle* of yellow fever transmission (Fig. 3.11).

The epidemiology of yellow fever is complicated and variable. In some areas, for example, yellow fever may be circulating among the monkey population yet rarely gets transmitted to humans because local vector mosquitoes are predominantly zoophagic. Compared to West Africa, outbreaks of yellow fever in East Africa are, for some reason, much less common.

Yellow fever virus may be *transovarially* transmitted in *Aedes* species. That is, eggs and subsequent generations arising from infected adults are born already infected with the virus. (Transovarial transmission is more usually associated with tick-borne diseases than with mosquitoes.) The virus can also be passed from congenitally infected males to females during mating, which in effect is venereal transmission. How important these routes of infection are remains unclear, but such mechanisms, especially transovarial transmission, would provide a means of virus survival during long dry seasons.

Americas

In Central and South Americas yellow fever is endemic in 11 countries. Outbreaks of yellow fever occurred in 2008 in Paraguay and Brazil, in 2007–2008 in Argentina, in 2004 in Venezuela, in 2003 in Brazil, in 2001 in Peru and Brazil and in 2000 again in Brazil. It is clear that yellow fever is not as great a problem in the Americas as in West Africa (see page 68).

In Central and South America the yellow fever cycle, although similar to that in Africa, differs in certain aspects (Fig. 3.12). As in Africa, it is an infection of forest monkeys, mainly cebid ones (e.g. howler monkeys (Alouatta species), squirrel monkeys (Saimiri species) and spider monkeys (Ateles species)), and it is transmitted among them by forest-dwelling mosquitoes. In the *sylvatic* or *jungle cycle* the vectors are *Haemagogus* species including Hg. spegazzinii, Hg. leucocelaenus and Hg. janthinomys and to a lesser extent Sabethes chloropterus, and sometimes also Aedes species. These are all arboreal mosquitoes which bite in the forest canopy and breed in tree-holes or bamboo. New World monkeys are more susceptible to yellow fever than African monkeys and frequently become sick and die. When people enter the jungle to cut down trees for timber, mosquitoes which normally bite monkeys at canopy heights may descend and bite them; if these mosquitoes are infected, people will develop yellow fever. The disease is then spread from person to person in villages and towns, as in Africa, by *Ae. aegypti* (Fig. 3.12), and this constitutes the *urban cycle*. However, no urban cases had been recorded in South America since 1942 - that is, until the outbreak in Paraguay in 2008.

Transovarial transmission has been reported in *Haemagogus* species.

3.8.4 Dengue (Flavivirus)

Dengue is the most rapidly spreading mosquito-borne viral infection in the world. An estimated 50 million dengue infections occur annually, and some 2.5 billion people live in more than 100 countries in which it is endemic. Dengue is now endemic in all WHO regions except the European Region.

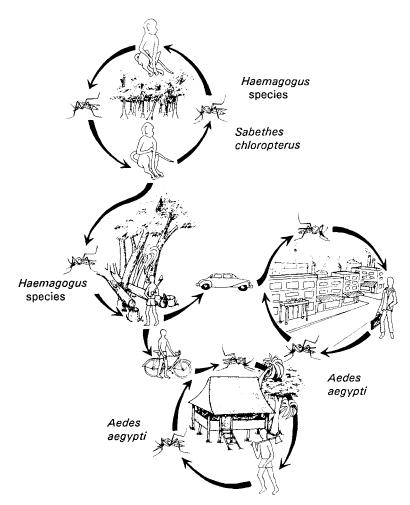


Figure 3.12 Diagrammatic representation of the jungle, rural and urban cycles of yellow fever transmission in Central and South America.

Dengue is caused by four similar viruses (DENV-1, -2, -3 and -4) and is endemic throughout most of Southeast Asia, the Pacific Region, the Indian subcontinent, sub-Saharan Africa, Central and South America and the Caribbean. In September 2009 dengue was transmitted in Key West, Florida, USA, and this was the first time dengue occurred in Florida since 1934

Dengue haemorrhagic fever is a potentially lethal complication causing infant mortality, and it has appeared in many parts of Southeast Asia and India. In 1981 haemorrhagic dengue and dengue type 4 were first noticed in Cuba. In 2007 Venezuela had over 80 000 cases, of which 6000 were haemorrhagic dengue, while in Brazil there were over 77 000 cases and at

least 70 deaths in Rio de Janeiro in the first 6 months of 2011, which is more than the combined total of cases in 2009 and 2010. Both dengue and haemorrhagic dengue are transmitted by *Ae. aegypti* and to a lesser extent by *Ae. albopictus*; both species breed in natural and man-made containerhabitats such as water-storage pots and tyres. Transovarial transmission has been reported in *Ae. aegypti* and *Ae. albopictus*. Mosquitoes of the *Ae. scutellaris* group, which also breed in natural and man-made containers, can also be vectors in some parts of the Western Pacific area. Although transmission of dengue virus amongst monkeys in forests of Sri Lanka, Malaysia, Vietnam and West Africa has been reported, there is little evidence that enzootic strains are involved in epidemics. Transmission is among the human population, and humans are the reservoir hosts. As yet there is no vaccine.

3.8.5 West Nile virus (WNV) (*Flavivirus*)

West Nile virus is a member of the Japanese encephalitis group. The virus was first isolated in 1937 from a febrile patient in Uganda. The virus has now spread to the Middle East, many African countries and about 24 European countries where there are usually only a few cases of WNV a year. However, in 2010 there were at least 173 cases and 15 deaths in Greece. In 1999 the virus was recorded for the first time from the Americas, in New York State. How the virus entered North America is unresolved, but it seems likely due to infective migrant birds. West Nile virus has been recorded from 48 states in the continental USA and in six Canadian provinces. The virus has also spread to Mexico and several countries in Central America, South America and the Caribbean.

The virus is principally an infection of birds. Crows (Corvus species) are the commonest birds in the USA to be found dead and infected with WNV, but many other bird species are infected, and laboratory experiments show some to be potentially more efficient hosts than crows. Virus has been isolated from more than 75 mosquito species, although Culex mosquitoes, such as Cx. pipiens, Cx. quinquefasciatus and Cx. tarsalis in the USA, and Cx. pipiens, Cx. torrentium and Cx. modestus in Europe, are among the most important vectors. (It has been shown that there can be co-feeding transmission: that is when an uninfected mosquito is feeding on a host very near an infected mosquito the virus from the infected mosquito can pass to the uninfected mosquito, thus making it a potential vector.) Occasionally a mosquito species that feeds on both birds and mammals, a so-called bridge vector, transfers the infection to humans, horses and other mammals. Mammals are incidental hosts and are termed dead-end hosts because mosquitoes feeding on infected mammals cannot pick up sufficient virus to infect further mammals when they bite them (Fig. 3.13).

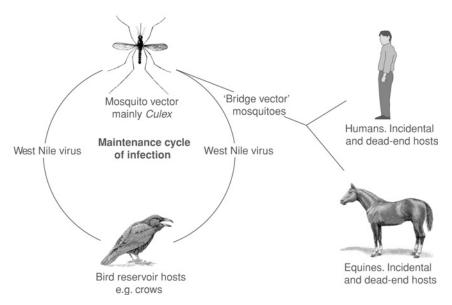


Figure 3.13 Diagrammatic representation of the transmission cycle of West Nile virus.

3.8.6 Japanese encephalitis (JE) (Flavivirus)

This virus is endemic in parts of China, eastern, southern and Southeast Asia and Papua New Guinea. Worldwide there are about 50 000 cases of JE annually, with 25-35% case fatality rates. Although there is a vaccine, presently mainly used in Korea, Japan, China, Thailand and Taiwan, there is a need for a cheaper, better and more widely available vaccine. The basic transmission cycle involves mosquitoes biting water birds, mainly herons, egrets and ibises, which are the principal reservoir hosts. Some infected mosquitoes bite pigs, which develop high viraemia and are termed amplifying hosts. If infected mosquitoes, having bitten birds or pigs, then bite humans they transmit the virus to them. Humans, however, are dead-end hosts and consequently there is no human-to-human transmission (Fig. 3.14). Transmission to birds, humans and pigs is mainly by Culex tritaeniorhynchus, Cx. vishnui and Cx. pseudovishnui, all of which are ricefield-breeding mosquitoes. Culex gelidus, breeding in streams and ricefields, is another vector and probably maintains the virus in pig-to-pig transmissions. In southern India Mansonia indiana is a secondary vector.

3.8.7 Other arboviruses

There are many other mosquito-borne arboviruses infecting humans in various parts of the world, for example Ross River virus (*Alphavirus*: Australasia), Sindbis (*Alphavirus*: Africa, Asia, Australia, Europe), Murray

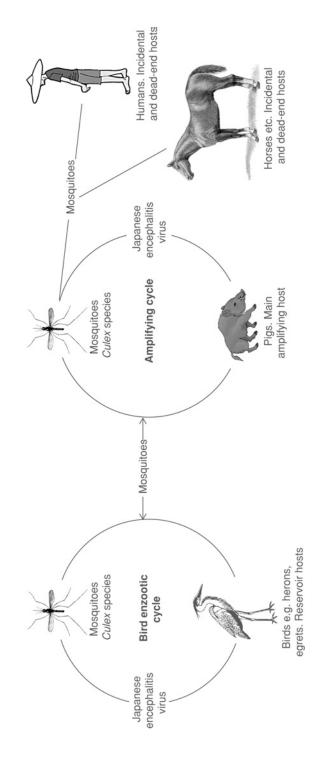


Figure 3.14 Diagrammatic representation of the transmission cycle of Japanese encephalitis virus.

Valley encephalitis (*Alphavirus*: Australia, Papua New Guinea) and Rift Valley fever (*Bunyavirus*: Africa, Saudi Arabia, Yemen). These and the more important arboviral diseases very briefly discussed below are *zoonoses*, as of course is yellow fever.

Chikungunya (CHIK) (Alphavirus)

Chikungunya virus occurs in sub-Saharan Africa, the Indian subcontinent and throughout much of Southeast Asia. In 2006 large outbreaks occurred in several islands in the Indian Ocean such as Mayotte, Mauritius, Madagascar and the Seychelles and there were 244 000 cases on Réunion with more than 200 deaths. The vectors were *Ae. aegypti* and *Ae. albopictus*. As a result of these outbreaks many infected tourists returned home to North America and Europe. In 2007 there was transmission of chikungunya virus for the first time in Europe, namely in northern Italy where there were 204 confirmed cases transmitted by *Ae. albopictus*. The outbreak was contained and there was no transmission in 2008. However, the virus has since been found in Europe in 2009, 2010 and 2011.

In sub-Saharan Africa there are about five principal vectors, all *Aedes* species, such as *Ae. africanus* and *Ae. luteocephalus*, but *Ae. aegypti* is not usually an important vector, whereas in Asia it is the main vector. In 2010 in a forested area in southeastern Gabon, *Ae. albopictus* was found to be the main vector. In Africa it appears that in sylvan areas the virus can be maintained in non-human primates such as vervet monkeys (*Cercopithecus aethiops*) and baboons (*Papio ursinus*), but whether there are cases of transmission between non-human primates and humans remains speculative.

In 2010 the virus was found in non-human primates in Malaysia, but as yet the importance of this to human cases is unclear.

St Louis encephalitis (SLE) (Flavivirus)

In southern Canada and widely distributed in the USA, extending into Mexico, Central America, the Caribbean and South America as far south as Argentina. In eastern USA it is mainly an urban disease spread by *Cx. quinquefasciatus* or *Cx. pipiens. Amplifying hosts* are chickens and peridomestic wild birds. In western USA SLE occurs mainly in rural areas with the ricefield-breeding *Cx. tarsalis* as a vector.

Eastern equine encephalitis (EEE) (Alphavirus)

In Canada, but mainly in the eastern USA, and extending from Mexico through Central America as far south as Argentina, and also in the Caribbean. It is probably the most severe encephalitis virus in humans and horses. EEE is principally an infection of birds, and in North America it is spread among them mainly by *Culiseta melanura* (the genus *Culiseta* is

not discussed in this book). It is transmitted to people and horses by various species of *Aedes*, *Culex* and *Coquillettidia*.

Western equine encephalitis (WEE) (Alphavirus)

In Canada and the USA west of the Mississippi River, and extending into South America. This is basically an arboviral infection of birds, which are *amplifying* and *maintenance* hosts. Transmission is by *Cx. tarsalis*, a ricefield-breeding mosquito, as well as by other *Culex* and *Aedes* species. *Aedes* mosquitoes also transmit the virus to mammals, including humans and horses.

Venezuelan equine encephalitis (VEE) (Alphavirus)

This is a complex of six viruses found in the southern USA through Central America to the Caribbean islands and South America as far south as Argentina. The infection is often fatal in horses and other equids but usually very mild in humans. Rodents are important *amplifying hosts* involved in enzootic transmission cycles, while birds and bats are involved in dispersing the virus. Vectors are mainly *Culex* species. Epizootic/epidemic transmission involves equines, which are the principal amplifying hosts. *Aedes taeniorhynchus*, *Culex taeniopus* and other *Culex* species in the subgenus *Melaniconion*, as well as *Psorophora confinnis*, are important vectors.

Viraemic titres produced in humans by JE, EEE, SLE, VEE and sometimes also by WEE are so low that the infection cannot be transmitted by mosquitoes from humans to humans, or from humans to other susceptible hosts. Humans are thus *dead-end hosts* for these viruses, as are horses for the encephalitis viruses infecting them.

3.8.8 Filariasis

The development in mosquitoes of filarial worms causing lymphatic filariasis is briefly described in Chapter 2 in connection with the role of anopheline vectors. Both bancroftian and brugian filariasis occur in two distinct forms. The *nocturnally periodic* form, in which the microfilariae are in the peripheral blood only at night, is transmitted by night-biting mosquitoes such as Anopheles, Mansonia and Culex quinquefasciatus. During the day the microfilariae are in the blood vessels supplying the lungs, and are not available to be taken up by mosquitoes. In *subperiodic* forms of *Wuchereria* bancrofti and Brugia malayi the microfilariae exhibit a reduced periodicity and are present in the peripheral blood during the day as well as at night, but there nevertheless remains a degree of periodicity. For example, subperiodic W. bancrofti, such as found in Polynesia, has a small peak in microfilarial density during the daytime and can therefore be called diurnally subperiodic, whereas subperiodic B. malayi in West Malaysia, Sumatra, Sabah, Thailand, etc. has a slight peak of microfilariae at night, and so can be called nocturnally subperiodic.

There are over 100 mosquito species transmitting lymphatic filariasis, but only some of the more important species can be dealt with in the following account and in Table 3.1. For a more detailed account of the vectors see Zagaria and Savioli (2002) and Foster and Walker (2009).

Bancroftian filariasis

Wuchereria bancrofti occurs throughout much of the tropics and subtropics including South America, sub-Saharan Africa, Asia and the South Pacific. It is the most widely distributed filarial infection of humans. Bancroftian filariasis is mainly an urban disease. There are no animal reservoir hosts and the parasites develop only in mosquitoes and humans.

The *nocturnally periodic* form is transmitted in Asia, South America and East Africa by *Culex quinquefasciatus*. This mosquito is widespread in the tropics and its larval habitats are waters polluted with human or animal faeces or rotting vegetation and other filth; larvae are found in septic tanks, cesspits, pit latrines, drains and ditches, and in water-storage jars if they contain organically polluted water. This mosquito has increased in numbers in many towns due to increasing urbanization and the proliferation of insanitary collections of water. Adults bite at night, and after feeding they often rest in houses. Although *Cx. quinquefasciatus* is an efficient vector in much of Africa, it is a poor vector in West Africa, where most transmission of bancroftian filariasis is by *Anopheles gambiae* and *An. funestus* and the disease is principally rural. *Anopheles* species are also vectors in parts of Asia, while in Papua New Guinea *Anopheles* are the main vectors although *Culex annulirostris, Mansonia uniformis* and *Ae. samoana* are also important in rural areas.

In the Philippines *Aedes poicilius* is the most important vector. Adults bite in the early hours of the night, mainly indoors but also sometimes outdoors. After feeding, adults rest outdoors. Larvae occur in leaf axils of bananas, plantains and coco-yams (*Colocasia*).

The *diurnally subperiodic* form occurs in the Polynesian region, from where the nocturnally periodic form is absent. The most important vector is *Aedes polynesiensis*, a day-biting mosquito which feeds mostly outdoors but may enter houses to feed; adults rest almost exclusively out of doors. Larvae occur in natural containers such as split coconut shells, leaf bracts and crab-holes, and also in man-made containers such as discarded tins, pots, vehicle tyres and canoes. *Aedes pseudoscutellaris* is another outdoor day-biting mosquito that is a vector of diurnally subperiodic *W. bancrofti*, especially in Fiji. It breeds mainly in tree-holes and bamboo stumps but larvae are also found in crab-holes. *Aedes polynesiensis* is absent from New Caledonia, and here the most important vector is *Ae. vigilax*, adults of which feed outdoors mainly during the day. Larvae are found in brackish or fresh water in rock-pools and ground pools.

Table 3.1 Summary of principal mosquito vectors of filariasis

Species and forms of filariasis	Geographical distribution	Vectors	Zoonotic reservoir hosts
<i>Wuchereria bancrofti</i> Nocturnally periodic	Throughout tropics (except Polynesia) Papua New Guinea	Anopheles, Culex quinquefasciatus Aedes samoana, Anopheles, Culex annulirostris, Mansonia uniformis	None
Diurnally subperiodic	Philippines Polynesia in general Fiji New Caledonia	Aedes poicilius, Anopheles Aedes polynesiensis Aedes pseudoscutellaris Aedes viqilax	None
Nocturnally subperiodic <i>Brugia malayi</i>	Thailand	Aedes niveus	None
Nocturnally periodic (principally open swamps)	South Asia, from India eastwards China	Anopheles, Mansonia annulata, Ma. annulifera, Ma. uniformis Aedes togoi	Not important, possibly some exist
Nocturnally subperiodic (mainly in swampy forests)	Malaysia, Indonesia, Thailand, Philippines	Mansonia bonneae, Ma. dives, Coquillettidia crassipes	Monkeys, especially leaf-monkeys (<i>Presbytis</i> species), wild and domestic cats, pappolins
<i>Brugia timori</i> Nocturnally periodic	Alor, Timor, Flores, other <i>Anopheles barbirostris</i> Indonesian islands	Anopheles barbirostris	None

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The *nocturnally subperiodic* form is found in Thailand and is transmitted by the *Aedes niveus* group of mosquitoes. Adults bite and rest outdoors; larvae are found mainly in bamboo stumps.

It should be noted that although several *Aedes* mosquitoes are vectors of filariasis, especially the bancroftian form, *Ae. aegypti* is not a vector of lymphatic filariasis. Infection rates of mosquitoes with infective larvae of *W. bancrofti* range usually from about 0.1% to 5%, depending greatly on vector species and local conditions. But in Singapore infection rates of 20% have been recorded, and in East Africa 30%.

Brugian filariasis

The *nocturnally periodic* form is principally a rural disease. It occurs throughout most of Asia, from southern India to Malaysia, Vietnam, Cambodia, Thailand and Indonesia. It is transmitted by night-biting mosquitoes, such as *Anopheles* species (Chapter 2) and *Mansonia* species such as *Ma. uniformis*, and in parts of India also by *Ma. annulifera. Mansonia* species breed in more or less permanent waters such as swamps and ponds having floating or rooted aquatic vegetation; in Kerala, India, *Ma. annulifera* also breeds in coconut soakage pits. Adults bite mainly outdoors and rest out of doors after feeding, but they may bite and rest indoors in some areas. There are no known important animal reservoirs of the nocturnally periodic form.

The *nocturnally subperiodic* form of *B. malayi* occurs in west Malaysia, Indonesia, Thailand and the Philippines, and is transmitted by *Mansonia* mosquitoes such as *Ma. dives*, *Ma. bonneae* and *Ma. annulifera*, and in Thailand and the Philippines also by *Coquillettidia crassipes*. Larvae of all these species occur in habitats with much vegetation, such as swampy forests. Adults bite mainly at night, although *Ma. dives* and *Ma. bonneae* may also bite during the day. This subperiodic form of *B. malayi* is a *zoonosis* and essentially a parasite of swamp monkeys, especially the leaf monkeys (*Presbytis* species). Humans become infected when they live at the edges of habitats harbouring these monkeys. Other reservoir hosts include *Macaca* monkeys, domestic and also wild cats, such as civets (family Viverridae) and also pangolins (i.e. scaly anteaters, genus *Manis*).

Infection rates of mosquitoes with infective larvae of *B. malayi* range from about 0.1% to 2–3%, which is slightly lower than for *W. bancrofti*, but infection rates vary according to mosquitoes and local conditions.

As mentioned in Chapter 2, the discovery of filarial worms in mosquitoes does not necessarily imply they are vectors of either *W. bancrofti* or *B. malayi*, because mosquitoes are also vectors of several other filarial parasites of animals.

3.9 Control

Repellents, mosquito nets and mosquito screening of houses and other personal protection measures (discussed in Chapters 1 and 2) can give

some relief from culicine mosquitoes. It is, however, more difficult to obtain protection from culicines than from anophelines, because many of them bite outdoors during the daytime. Spraying the interior surfaces of houses with residual insecticides, as practised for *Anopheles* control, is not usually effective for culicines, because most species do not rest in houses. Control is aimed mainly at the larvae, although aerial ultra-low-volume (ULV) insecticidal applications are sometimes used to kill adult culicine mosquitoes.

3.9.1 Aedes and Psorophora

Control of mosquitoes such as *Ae. aegypti, Ae. polynesiensis* and *Ae. albopictus*, species which breed mainly in man-made containers in both rural and urban areas, is often aimed at reducing the numbers of larval habitats, that is, control by *source reduction*. Consequently people are encouraged not to store water in pots or allow water to accumulate in discarded tin cans, bottles, vehicle tyres etc. However, persuading people to cooperate in reducing peridomestic larval habitats of mosquitoes is often difficult unless local legislation is strictly enforced. A reliable piped water supply to houses can do much to reduce *Ae. aegypti* breeding.

When source reduction is not feasible, insecticides can be used on larval habitats. Suitable products include organophosphates such as fenthion, temephos and pirimphos-methyl, insect growth regulators (IGRs) such as methoprene, pyriproxyfen or diflubenzuron, or Bacillus thurigiensis var. israelensis (Bti). Although insecticidal spraying can kill Aedes and Psorophora larvae it usually has no effect on their eggs which have been deposited at the edges of larval habitats. However, if there are ground-based or aerial applications of granular organophosphate insecticides or IGRs these will kill the young larvae when they hatch from eggs. Such applications can be made either before or after habitats have become flooded, that is *pre-* or *post-flood treatments*. Insecticidal granules landing on dry or muddy grounds remain more or less inactive until the habitats become flooded. When this occurs previously dry eggs hatch, but at the same time flooding causes the release of insecticide from the granules and this kills the newly hatched larvae. This technique helps overcome problems of controlling Aedes and Psorophora mosquitoes, whose eggs may hatch in instalments over extended periods after flooding.

Ground-based or aerial ULV application of organophosphates such as malathion, fenitrothion, pirimiphos-methyl or pyrethroids, aimed at killing adult mosquitoes, is often the most appropriate control strategy in epidemic situations.

Insecticides used to kill mosquito larvae in water intended for drinking must have extremely low mammalian toxicity; they should also impart no taste to the water. The insecticide usually recommended is temephos, in the form of 1% in briquettes or sand granules that will give a concentration of 1 mg

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active ingredient per litre of water. However, some communities refuse to have their potable water dosed with any insecticide (see Chapter 1, page 28).

Yellow fever and dengue

Africa has over 90% of the world's yellow fever cases. The best defence against yellow fever is to use the attenuated 17D vaccine. Vector control, through sustained reduction of mosquito larval habitats, nevertheless still has a role in reducing the risks of yellow fever outbreaks; it also remains the main approach for dengue control, because there are presently no vaccines available for widespread use. Epidemics of dengue, and sometimes also yellow fever, can be curtailed by killing the adult vectors with aerial ULV insecticidal spraying, where the main objective is to kill infected adult mosquitoes as rapidly as possible.

To see whether *Ae. aegypti*, a vector of dengue, could be controlled by genetic modification 3.3 million sterile transgenic male *Ae. aegypti* were released in inhabited areas on the Cayman Islands in 2009. About an 80% reduction in the *Ae. aegypti* population was achieved. Then, in trials carried out in Malaysia the following year, 6000 transgenic male *Ae. aegypti* were released in uninhabited forest sites to study their dispersal and survival, after which they were killed by insecticidal spraying. Results suggested that such an approach could be used for dengue control. See *Nature* (2011) for a discussion of these trials.

3.9.2 Culex

Culex quinquefasciatus, an important filariasis vector, is best controlled by improving sanitation and installing modern sewage systems, but often this is not feasible and insecticides have to be used. In most areas Cx. quinquefasciatus is resistant to a wide range of insecticides, and this limits the choices of chemicals that can be used. Larval habitats should be sprayed every 7–10 days, and usually relatively large dosage rates are needed because most insecticides are less effective in the presence of organic pollution, which is characteristic of Cx. quinquefasciatus larval habitats. Chlorpyrifos and temephos are two of the more effective insecticides in polluted waters. IGRs such as methoprene, diflubenzuron and pyriproxyfen have also been used against Cx. quinquefasciatus.

Tipping non-toxic expanded *polystyrene beads* (2–3 mm) into pit latrines and cesspits to completely cover the water surface with a 2–3 cm layer suffocates larvae and pupae as well as preventing female *Cx. quinquefasciatus* from ovipositing. A single application can persist for several years and give excellent control. This is a control method that is readily accepted by most communities.

Insecticidal house-spraying, as practised against malaria vectors, and insecticide-impregnated bed-nets can be effective against *Cx. quinquefasciatus* and other *Culex* species if they are both endophilic and night-biters.

In North America ULV spraying has frequently been used against vectors of the encephalitis viruses.

Lymphatic filariasis

An estimated 1 billion people in more than 83 countries are at risk of getting lymphatic filariasis, and presently more than 120 million are infected. In 2000 the Global Programme to Eliminate Lymphatic Filariasis (GPELF) was initiated, with the aim of achieving this goal by 2020. China had one of the highest incidences of lymphatic filariasis, but by 2008 China, and also Korea and Egypt, had eliminated lymphatic filariasis as a public health problem.

Control strategies involve mass distribution of microfilarial drugs administered annually, using albendazole and ivermectin in sub-Saharan Africa, and elsewhere albendazole plus diethylcarbamazine. In addition, vector populations can be reduced by using suitable chemical larvicides and the microbial agents *Bacillus thuringiensis* var. *israelensis* (*Bti*) and *B. sphaericus*, tipping expanded polystyrene beads into pit latrines and septic tanks to prevent mosquito breeding, use of insecticide-impregnated bed-nets, and possibly residual house-spraying. All of these should reduce densities of *Cx. quinquefasciatus*, a very important filariasis vector. In contrast, it is very difficult to reduce populations of *Mansonia* mosquitoes, important filariasis vectors in Asia, because adults rarely rest or bite indoors and larval habitats are often large and relatively inaccessible: see below.

3.9.3 Mansonia

Mansonia mosquitoes are usually controlled either by removing aquatic weeds upon which the larvae and pupae depend for their oxygen requirements, or by using herbicides to kill the weeds. Removing weeds, however, may result in ecological changes that allow aquatic habitats to become colonized by mosquito species that were previously excluded by the dense covering of weeds.

Insecticidal granules or pellets are more suitable than liquid formulations for killing *Mansonia* larvae, because they penetrate vegetation, sink to the bottom of larval habitats and release their insecticidal contents through the water. However, species such as *Ma. dives* and *Ma. bonneae*, which are important vectors of brugian filariasis, breed in extensive swampy inaccessible forests where control is impractical.

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- See also references at the ends of Chapters 1 and 2.