Nematocera (Ceratopogonidae, Psychodidae, Simuliidae and Culicidae) and control methods

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Summary: The biology, veterinary importance and control of certain Nematocera are described and discussed.

Culicoides spp. (family Ceratopogonidae) transmit the arboviruses of bluetongue (BT), African horse sickness (AHS), bovine ephemeral fever (BEF) and Akabane. Some other arboviruses have been isolated from these species, while fowl pox has been transmitted experimentally by Culicoides. These insects are vectors of the parasitic protozoans Leucocytozoon caulleryi and Haemoproteus nettionis, and the parasitic nematodes Onchocerca gutturosa, O. gibsoni and O. cervicalis. They also cause recurrent summer hypersensitivity in horses, ponies, donkeys, cattle and sheep.

Farm animals can die as a result of mass attack by Simulium spp., which are also vectors of Leucocytozoon simondi, L. smithi and the filariae O. gutturosa, O. linealis and O. ochengi. Venezuelan equine encephalomyelitis (VEE) and Rift Valley fever (RVF) have been isolated from simuliids, and vesicular stomatitis virus New Jersey strain has been replicated in Simulium vittatum. Simuliids are well known as vectors of O. volvulus, the cause of human onchocercosis (river blindness).

The family Psychodidae includes the genera Phlebotomus and Lutzomyia (subfamily Phlebotominae), vectors of Leishmania spp. in humans, dogs and other mammals. Vesicular stomatitis virus Indiana strain has been regularly isolated from phlebotomine sandflies.

Mass attack by mosquitoes can also prove fatal to farm animals. Mosquitoes are vectors of the viruses of Akabane, BEF, RVF, Japanese encephalitis, VEE, western equine encephalomyelitis, eastern equine encephalomyelitis and west Nile meningoecephalitis, secondary vectors of AHS and suspected vectors of Israel turkey meningoecephalitis. The viruses of hog cholera, fowl pox and reticuloendotheliosis, the rickettsiae Eperythrozoon ovis and E. suis, and the bacterium Borrelia anserina are mechanically transmitted by mosquitoes. These insects also induce allergic dermatitis in horses. They transmit several filarial worms of both animals and humans, and are of great medical importance as vectors of major human diseases, including malaria, yellow fever, dengue fever and many more diseases caused by arboviruses.


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INTRODUCTION

The family Ceratopogonidae includes 78 genera and subgenera, comprising approximately 3,900 species, but in only four genera are females known to feed on warm-blooded animals (46, 96, 116). The largest and best known genus is Culicoides, the only genus of real veterinary importance, which includes vectors of important pathogens to mammals (including humans) and birds. Some of the other blood-sucking genera, which will not be discussed here, are troublesome pests for humans. Culicoides comprises approximately 1,000 species, distributed from the tropics to the subarctic and from sea level to 4,200 m (in Tibet). Culicoides are most commonly known as ‘biting midges’ or ‘midges’. In the Americas they are known as ‘no see-ums’ or ‘punkies’, and in Australia and other countries as ‘sandflies’.

BIOLOGY

Adults (47, 96) (Fig. 1d) measure 1.5-5 mm long, with a small head bearing a pair of prominent eyes and a pair of relatively long antennae with fifteen segments. The plumose antennae of the males are auditory organs, sensitive to the female wing-beat tone, while the females have non-plumose antennae. The proboscis hangs down vertically from the head. In many species, the thorax is dorsally covered with black markings. The small elongated depressions, termed humeral pits, on the front dorsal part of the thorax, are typical only of the genus Culicoides. The short and relatively broad wings lack scales, but in many species are covered with microscopic hairs. Typical of Culicoides and other Ceratopogonids is the ‘r-m cross-vein’. In most species, the wings have contrasting dark and milky white spots, and when at rest the wings are placed over the abdomen like the blades of a closed pair of scissors. The legs are relatively short. The abdomen of the female has a rounded tip, while that of the male bears a small pair of claspers. Male adults generally emerge from pupae before the females. Emerging adults usually fly only a few hundred metres from their larval habitats, but a flight range of 4.0 km has been reported for C. variipennis (55). Culicoides, especially the high-flying species (20), could be carried by air streams for hundreds of kilometres (19). The first major function of the adult after emergence is mating, for which (in many species) the males form a swarm; individuals then leave the swarm to copulate in flight with individual approaching females. Swarming is induced by various landmarks such as a bush or the margin of a pond, or even the head of an animal (27). Only females suck blood, from a variety of mammalian (including human) and avian hosts. The blood meal volume is of the order of 0.139 µl and 0.410 µl for C. imicola and C. zuluensis, respectively (16). Some species have strong host preferences, while others will feed on a wider range of hosts. Autogenous species exist, which do not need a blood meal to mature their first batch of eggs (58), but all require a blood meal to mature subsequent batches. Both sexes feed on naturally-occurring sugar solutions. The biting activity of most Culicoides spp. is crepuscular (14) and/or nocturnal, but a few species are diurnal. The length and number of ovarian cycles vary between species, and depend on the ambient conditions. In C. grisescens, four ovarian cycles (i.e. blood feeding and oviposition) have been recorded (36), whereas three cycles have been observed for C. variipennis variipennis (68). Such a life span is long enough for any Culicoides-borne pathogen to reach the infective stage. The adult life
span of some individuals may extend to 70 days (93), while the number of generations per year depends on climate and species. In Israel, *C. imicola* has been reported to produce eight generations between July and December, with each generation lasting approximately 23 days (18). *Culicoides* lay 30-450 eggs depending on species, source of blood (host) and season (9, 47). Each egg is 350-500 µm long and is dark in colour (Fig. 1a). Eggs of most species hatch after two to nine days at favourable temperatures; for example, *C. imicola* in summer takes three days (18). Northern species (e.g. *C. grisescens*) overwinter and hatch after seven to nine months (79). Evasion of dryness by aestivation has also been recorded (47). Eggs are laid in wet soil or any sort of semi-aquatic habitat, e.g. decaying plant material (15). There are four larval instars and the fully-grown larva (Fig. 1b) is cylindrical, whitish in colour and approximately 5-6 mm long. This larval stage lasts longer than any other stage in the *Culicoides* development cycle. The larva has a conical head which bears a pair of small eyes, a pair of minute antennae, and mandibles. There are three thoracic and nine abdominal

**Fig. 1**

*Life cycle of Culicoides*

(96)
segments; these lack any appendages, except that the last segment terminates in gill-like structures which have an osmoregulatory function (respiration being cutaneous) (47, 96). Larvae move in a serpentine fashion and feed on a wide range of micro-organisms and decaying vegetable material. Many species have a narrow range of breeding-site types which can be identified, enabling control measures to be targeted for particular species. In warm countries, development of larvae may take 14-25 days; for *C. imicola* in summer, larval development takes 13-14 days (18, 96). In temperate regions, larvae of many species overwinter and therefore remain as larvae for seven months. The fourth larval instar pupates. The pupa (Fig. 1c) is 2-4 mm long, the cephalothorax bears a pair of breathing trumpets, the abdominal segments are equipped with tubercules ending in a fine hair, and the last segment bears a pair of horn-like processes. The pupal stage lasts two to ten days; two days for *C. imicola* in summer (18, 96).

**VETERINARY IMPORTANCE**

*Culicoides* are biological vectors of several economically-important arboviruses. Bluetongue virus (BTV), which mainly causes disease in sheep (BTV does infect cattle, but most infections are subclinical), originated in Africa and is now present in all zoogeographical regions. The disease can cause very high rates of morbidity (75%) and mortality (20-50%) in susceptible sheep (11, 47). Mellor (61) lists seventeen species worldwide which could be infected in the laboratory or from which virus was isolated when they were collected from the field; however, only six species were able to transmit the virus. The most important confirmed vectors are *C. variipennis* (in North America) and *C. imicola* (Africa, the Middle East and southern Europe). Circumstantial evidence suggests that the disease could be spread over long distances by wind-borne infected vectors (19).

African horse sickness (AHS) (4, 47) is an acute or sub-acute, highly fatal disease of equines, which is enzootic in Africa. Since the turn of the century, the disease has spread to the Indian subcontinent, the Middle East and southern Europe. In these new areas, outbreaks of the disease have been less frequent than in Africa. There are four clinical forms of the disease, of which the pulmonary form is the most severe. Mortality in susceptible horses may reach 90%; mules are less affected and donkeys are the least susceptible. It is assumed that the disease can exist permanently in any area of the world where winter conditions favour survival of the *Culicoides* vectors, while the existence of non-equine reservoir hosts has also been suggested as an explanation for the persistence of the virus through the winter. In addition to the role of animals in the introduction of the disease, AHS can be introduced into new areas by wind or infested airplanes. The most established field vector of AHS is the Ethiopian species *C. imicola*, but recently the virus has also been isolated from *C. pulicaris* and *C. obsoletus* in Spain (62).

Bovine ephemeral fever (BEF) (47) is an arboviral disease of cattle, which is enzootic in Africa and the oriental region and has caused epizootics in Australia. Outbreaks have also been recorded in the Middle East (99). The disease is usually not fatal or has a very low mortality rate, but morbidity among susceptible cattle in an epizootic area may reach 100%. The principal damage caused by BEF is due to the reduction of milk yield in dairy herds, delayed conception and abortion. The vectors are *Culicoides* and mosquito species. In Africa, BEF virus has been isolated from *C. coarctatus, C. imicola* (10) and a mixed pool of *C. kingi* and *C. oxystoma* (25), in Australia from *C. brevitaris* (88) and in Japan from *C. punctatus* (45). Retrospective analysis of the spread of the disease in several cases indicated that BEF was introduced by wind-borne infected vectors (69, 74).
Akabane disease is an epizootic arboviral disease which causes abortion, premature birth, still birth, and congenital arthrogryposis and hydraencephaly in cattle, sheep and goats. Epizootics have been described in Japan, Australia and Israel (98). Akabane has also been reported in several African, Middle Eastern and South-East Asian countries and in Argentina (3). The vectors are Culicoides spp. and mosquitoes. The virus has been isolated from the African species C. milnei and C. imicola (10), from the Australian C. brevitarsis and C. wadai (3, 89) and from C. oxystoma in Japan (3, 51). Evidence for long-distance, wind-borne dispersal of infected vectors has been presented in Australia (70).

Other arboviruses causing the following diseases of veterinary importance have been isolated from Culicoides spp., although Culicoides are not considered as vectors: Crimean-Congo haemorrhagic fever (22), Rift Valley fever (54), Israel turkey meningoencephalitis (17), Venezuelan equine encephalomyelitis (115) and vesicular stomatitis New Jersey (50). Other arboviruses have also been isolated from Culicoides spp., but are apparently without importance in animal health.

Fowl pox virus, which is not an arbovirus, has been experimentally transmitted by C. arakawai from infected to susceptible chickens seven days post-infection (34).

Leucocytozoon caulleryi, a protozoan parasitic disease of birds which affects blood and tissue cells of internal organs, is frequently found in chicks in South-East Asia. Infections occur frequently in Japan and have also been reported from southern California (63, 72). The vectors are C. arakawai, C. circumspectus and C. odibilis; the parasite can also develop in bovine feeders of the C. schultzei group (65, 66).

Haemoproteus nettionis is a parasite of ducks. Infections are characterised by schizogony in visceral endothelial cells, gametocyte development in circulatory erythrocytes, and presence of granules of pigment in infected erythrocytes. This parasite has been reported in tropical and temperate areas (103). The vector in Canada is C. donnesi (31).

Culicoides spp. transmit several other protozoan parasites of wild birds and mammals.

Nine species in the filarial genus Onchocerca have been recorded in cattle and water buffalo. Losses to the beef industry occur because free worms cause ugly blemishes to the carcass, and encapsulated adult worms in nodules have to be trimmed from the carcass (47, 78). The vectors of O. gutturosa are C. nubeculosus and C. kingi, while those of O. gibsoni are C. pungens, C. shortii, C. orientalis, C. oxystoma and the ceratopogonid Lasiohelea townsvillensis (56).

Four Onchocerca spp. have been recorded in equines: three in horses and one in donkeys. Onchocerca cervicalis, which causes several pathological symptoms in horses, is transmitted by C. nubeculosus and C. variipennis, and can also develop in C. obsoletus and C. parroti (47, 56). Culicoides arubae is a suspected biological vector of Onchocerca sp. in horses in the United States of America (USA) (115).

Recurrent summer hypersensitivity (29, 120), the most widely-recognised form of insect hypersensitivity in farm animals, has been reported in various places, including Australia, Canada, Israel, Japan and the USA. Skin lesions in horses and ponies caused by Culicoides bites have been reported in Australia, where the infection rate was 32-60% (85). Recently, Culicoides hypersensitivity has been reported in cattle, sheep and donkeys (120).
CONTROL

Control against nuisance species is regularly applied in tourist-frequented coasts, e.g. the Caribbean islands, Florida and Australia (1, 57), but not for the protection of farm animals. There is no practical experience of insecticidal control of adults in the field by whole-body sprays or any other method. In Australia, it has been suggested that ivermectin be used as a systemic insecticide in cattle; 99% mortality of C. brevitarsis was achieved within 10 days following treatment. Such treatment could reduce the local population and retard the spread of bluetongue viruses. An additional advantage of this treatment is that the dung of ivermectin-treated cattle is larvicidal for Culicoides spp. for up to 28 days (113). A range of recommended methods for control of adults was published in 1989 (13). The killing of larvae is practicable mainly in areas where there is a limited number of larval development sites, but it is also useful to protect special installations such as insemination centres by controlling the breeding sites within 2-4 km of the installation. Effective killing of C. varitennis larvae has been achieved with a 5% granular formulation of temphos (41; R.F. Holbrook, personal communication). For controlling C. imicola and other species breeding in heavy organic matter sites, the use of a 2% granulated preparation of the insect growth regulator cyromazine has been suggested (13).

SIMULIIDAE

INTRODUCTION

The family Simuliidae includes more than 1,270 species in twelve genera, of which the genus Simulium (comprising more than 1,000 species) is the most important. Flies of this family are commonly named blackflies. In addition to Simulium, three other genera (namely Prosimulium, Austrosimulium and Cnephia) also contain biting species. Simulium species occur worldwide except in New Zealand, Hawaii and a number of other small islands. The greatest number of species (366) occurs in the Palearctic region. There are many species complexes (46, 96).

BIOLOGY

The adult blackfly (46, 96) (Fig. 2d) is 1.5-4 mm long, with a stout body (usually black in colour) and a humped thorax. The head has a pair of large compound eyes (separated in females and joined in males), short, stout antennae with eleven distinct segments and no long hairs, and palps with five segments which are longer than the short proboscis. Mouthparts do not penetrate deeply into the host tissue and blackflies cannot bite through clothes. The colourless wings are short and broad, without scales or long hairs; at rest, the wings lay over the body like a closed pair of scissors. The abdomen is short and squat, with inconspicuous genitalia. The life cycle includes the egg stage, between six and nine larval instars, pupa and adult. Mating involves the attraction of females to male swarms, which form over visual markers near the breeding site. Blackflies of both sexes feed on plant juices and naturally-occurring sugary substances; only the females take blood meals, of a volume of approximately 1.08-3.26 µl (37). Blackflies are pool feeders and blood feeding takes approximately 4-5 min (114). Most species seem to be ornithophilic (117). Biting is restricted to daylight hours and many species seem particularly active on cloudy and overcast days. Blackflies seldom attack indoors or even in vehicles. Host detection is by chemical cues and visual orientation. Brown or
FIG. 2

Life cycle of Simuliidae
(44, 96)
black eggs are laid in batches of 150-600 on objects which are in or near running water, or directly into the water. The egg is 100-400 µm long and is triangular ovoid in shape (Fig. 2a). All preimaginal stages of the life cycle occur in running water. Some species produce dormant eggs to avoid the adverse conditions of summer or winter; in the tropics, the egg stage takes one to four days. The mature larva of the last instar is 5-13 mm long; this usually has a black head with a prominent pair of feeding brushes (Fig. 2b). Larvae of most species are filter-feeders and consume algae and detritus. They cannot easily discriminate between types of particles and swallow everything within a certain size range, which renders them vulnerable to insecticides in the form of tiny pellets (117). The body of the larva is slightly swollen behind the head and distinctly swollen towards the rear end. The rectum bears finger-like gills dorsally. The proleg – a small ventral pseudopod below the head, armed with a small circle of hooklets – co-operates with a posterior hook circlet in larval movement. The hook circlet and the proleg alternately grip a small silken pad, which is adhesively deposited on the substrate by the salivary gland. The development of whole larval instars may take one to two weeks, depending on species and temperature, but in species with overwintering larvae, larval development may take several months. Mature larvae use the silk produced by the salivary glands to spin a protective brownish cocoon (Fig. 2c), which is stuck to submerged vegetation, rocks or other objects. The larva pupates inside the cocoon and breathes through a pair of gills which extend outside. In tropical and sub-tropical areas, the pupal stage lasts for two to six days and appears to be independent of temperature. In many species, mass emergence of thousands of adults occurs. Adults of most species live for two to three weeks, but individuals may live for up to three months. The entire life cycle from egg to adult can take less than two weeks, depending on species and temperature. Adults can fly up to 200 km (109) and with wind assistance can travel many hundreds of kilometres (23, 46, 80).

VETERINARY IMPORTANCE

In northern and temperate areas, blackflies are severe pests of farm animals. Cattle killed by these insects in the Vosges in France have been estimated to have suffered an average of 25,000 bites, and in one case 55,000 bites (73). Death and illness in cattle and swine, and illness in horses, have been recorded in Germany and elsewhere (38, 52). In addition to blood sucking, blackflies inject a vasoactive histamine which stimulates an acute toxic reaction, causing pathological effects in farm animals (8). Animals are at high risk when first moved to pasture, as immunity at that time is at the lowest level. The milk yield of dairy cattle subjected to heavy blackfly attack may fall by 20-40% (114). Blackflies are the vectors of most species of *Leucocytozoon*, which are haemoparasitic protozoa. Of noted economic importance are *L. simondi* (a parasite of wild and domestic ducks and geese in Europe, North America and South-East Asia) and *L. smithi* (a turkey parasite in Europe and North America) (47). *Leucocytozoon* infections appear to be more severe in domestic species than in wild species, and deaths are most common in young birds. Simuliids are important vectors of filaroid parasites of domestic animals in many parts of the world. These flies transmit several *Onchocerca* species (e.g. *O. gutturosa*, *O. linealis* and *O. ochengi*) to cattle and also *O. volvulus* (the cause of human onchocercosis or ‘river blindness’) to humans. Although simuliids are not known to be involved in the transmission of arboviruses, infection and replication of vesicular stomatitis virus New Jersey strain has been reported from *Simulium vittatum* (5), and four isolations of Venezuelan equine encephalomyelitis virus have been reported in Colombia (90). In South Africa, Rift Valley fever virus has been isolated from simuliids (111).
CONTROL

An efficient way to reduce blackfly populations is by application of insecticides to breeding places of the insects to kill the larvae. The insecticides are applied to a few selected sites on watercourses for 15-30 min and are carried downstream, killing the simulid larvae over long stretches of water. In large river systems, insecticide is applied using airplanes or helicopters (96). Repeated treatments are necessary, as gravid females from untreated areas recolonise the treated area. Large-scale control programmes are very expensive and are seldom conducted to protect animals alone (115). Manipulative ecological methods, such as the building of dams in streams and rivers, can prevent the breeding of certain pest species (52). The organochlorines dichlorodiphenyltrichloroethane (DDT) and methoxychlor have given good results in controlling simulid larvae (30, 106). In West Africa, the organophosphate insecticide temphos has been satisfactorily used. More recently, the bacterium Bacillus thuringiensis var. israelensis (BTI) was introduced for larval control (21, 64, 115). BTI has the advantage of having little effect on other aquatic insects. As blackfly attacks are often concentrated at the ears or belly midline, repellent or insecticidal sprays are most effective when applied to these sites (115). Animal protection for six to eleven days has been achieved by applying permethrin (97). Pouring phosmet on grazing cattle provided satisfactory protection for five to six weeks (48, 49).

PSYCHODIDAE

INTRODUCTION

Blood-sucking sandflies belong to three of the five genera of the subfamily Phlebotominae in the family Psychodidae, namely: Phlebotomus, Lutzomyia and Sergentomyia. Only the first two genera are known to have medical and veterinary importance. Phlebotomus and Sergentomyia spp. are the sandflies of the Old World, while Lutzomyia spp. are present in the New World (96). Altogether, more than 600 species of Phlebotominae exist, inhabiting mainly desert, semi-arid and savanna areas – i.e. the warm tropical, sub-tropical and temperate zones of the world – although some species extend to latitude 50°N (46, 96).

BIOLOGY

Sandflies (23, 46, 95, 96, 102) (Fig. 3d) are 1.5-4 mm long, with long antennae and legs. Body colour ranges from yellow to grey, and wings and body are hairy. The wings are characterised by tapering ends and an erect resting position. The life cycle includes the egg stage, four larval instars, pupa and adult. Phlebotomines mate without forming swarms. Sandflies are pool feeders, mainly nocturnal and crepuscular. Both sexes feed on juices and sugary plant secretions (23). Only the female sucks blood, taking approximately 0.1 mg per meal and using blood proteins for egg production. Some species of sandflies are autogenous and do not suck blood to produce the first clutch of eggs. Phlebotomus spp. have been reported to bite a wide range of domestic and wild mammals and birds. Five to seven days after sucking blood from a vertebrate, the female lays 15-100 shiny brown ovoid eggs (Fig. 3a) each measuring 300-400 μm long, and deposits them in small cracks and holes in the ground or in floors, among leaf litter, between buttress roots, or wherever the temperature is mild and relative humidity is approximately 100%. Under optimum conditions, eggs hatch after 6-17 days. Larvae
Life cycle of *Phlebotomus* and transmission of *Leishmania donovani* (91, 96)
sandflies (Fig. 3b) feed on organic matter, fungi, decaying forest leaves, animal faeces and the decomposing bodies of arthropods. The greyish or yellowish-coloured mature fourth instar larva is 4-6 mm long, with a well-defined black head carrying a pair of small mandibles. This stage is characterised by thick bristles, termed 'matchstick hairs', on the head and body segments. Most species have two pairs of long hairs, called the caudal bristles, on the last abdominal segment. Larval development takes 21-60 days, depending on species, temperature and food. In the Mediterranean and in temperate areas, overwintering is by diapausing of fully-grown larvae. The fourth larval stadium pupates for 7-14 days. In *P. papatasi*, the pupal length is 2-2.5 mm (Fig. 3c). Attached remains of larval skin at the end and two pairs of caudal bristles characterise the pupa. The entire life cycle takes 30-100 days, depending on species and temperature. Flight is short-ranged, as sandflies are weak fliers, with a forward speed of the order of 0.5 m/s in still air (80), rendering these species very sensitive to wind speed. The hopping flight distance is approximately 100-200 m, but sandflies may disperse up to 1.5 km (91), which indicates the range within which control measures should be implemented to protect animals from sandfly-borne diseases. Many species in an open area tend to fly close to the ground to avoid disturbing winds. Species with a tendency to vertical flight are important, as flight above the boundary layer in an open area exposes them to long-distance wind-borne transport. Sellers (92) hypothesised that vesicular stomatitis in the USA was spread by wind-borne infected phlebotomine sandflies.

VETERINARY IMPORTANCE

The population density of sandflies in most areas is below the pest-category threshold (46); the importance of these insects lies in their role as vectors. The most important zoonosis transmitted by sandflies is leishmaniosis, a notifiable disease in animals and humans, caused by several species of the protozoan genus *Leishmania* (42, 121). Apart from infections in equines in South America, and in small ruminants in East and South Africa, and the occasional report of leishmaniosis in cats, the veterinary importance is limited to the infection in dogs (Figs 3e and 3f). For instance, *L. infantum* is among the main species causing disease in dogs, which usually occurs in a combined visceral and cutaneous form. Dogs constitute the main reservoir of infection for animals in the Mediterranean area. The incubation period is between three and seven months, or even longer, and the disease usually becomes chronic (6). The taxonomy of *Leishmania* and the epidemiology of the disease are complicated, and will not be discussed further in the context of this paper. Vesicular stomatitis is induced by a rhabdovirus which primarily affects horses, but also cattle and pigs, and is enzootic in the Nearctic and neotropical regions (39, 47). The virus induces vesicular lesions in the mouth and feet. It has been established that vesicular stomatitis virus Indiana strain can be regularly isolated from sandflies, and that these flies support viral replication and transovarial transmission (39, 107, 108). Several types of vesicular stomatitis virus have been isolated from mosquitoes and *Culicoides* species (50).

CONTROL

Prevention of diseases transmitted by sandflies can be achieved by controlling the flies, or by controlling or destroying the reservoir rodents together with their nests, habitats and food sources. Alternatively, the animals can be protected by repellents such as diethyltoluamide (91, 96). DDT and lindane residual sprays in dosages of 1 or 2 g/m² in houses have been found to be efficient (101). However, for environmental reasons,
alternative insecticides have been studied (81) and methoxychlor has been recommended due to its residual activity (119). Dichlorvos has also been used. Sandflies are very susceptible to most insecticides and no cases of resistance have been reported. Reinfestation of controlled areas is slow (46, 96).

CULICIDAE

INTRODUCTION

The family Culicidae contains three subfamilies, of which the Anophelinae and Culicinae are of medical importance. Overall, the Culicidae comprise 3,100 species in 34 genera (46). Culicinae are distributed from the tropics to the Arctic Circle, but are absent from Antarctica. Mosquitoes exist even at elevations of 5,500 m and in mines at depths of 1,250 m below sea level. Some genera have a very wide distribution, while others are restricted. In the northern temperate regions and throughout all tropical areas, the genera Culex, Aedes and Mansonia are found. Psorophora is an American genus, found from southern Canada to Argentina and in the Caribbean islands. The genera Haemagogus and Sabethes are found only in Central and South America (96).

BIOLOGY

Adult mosquitoes (Fig. 4d) (23, 46, 77, 96) can be distinguished from other dipterous insects by the characteristic venation and scaling on the wings. Scales are often also present on the thorax, abdomen, head and legs. The colour varies between species. Mosquitoes have a conspicuous forward-projecting proboscis, which penetrates the capillaries of the host (i.e. they are 'vessel feeders'). Only the females suck blood; males have reduced mouthparts and cannot pierce the skin. The mosquito body is slender and measures 4-6 mm in length, and is distinctly divided into head, thorax and abdomen. The head bears a pair of compound eyes and a pair of filamentous segmented antennae, which are feathery in males, and have short hairs in females. The palpal length differs with sex and between anopheline and culicine adults. In Anophelinae females, the palps are as long and straight as the proboscis. The thorax is slightly humped and the scales on the dorsal surface give many species distinctive patterns. Wings at rest are placed over the abdomen like a closed pair of scissors. Legs are long and slender. Only eight of the ten abdomen segments are visible and well differentiated. The last abdominal segment terminates in a pair of cerci in the female and a pair of claspers in the male. Living adult Anophelinae can be distinguished from Culicinae by the typical resting stance. The proboscis, head, thorax and abdomen of Anophelinae form a straight line at an acute angle to the surface. Most species of mosquitoes mate shortly after emergence from the pupa, and each female mates and is inseminated only once. In many species, mating is preceded by male swarming over a marker, which may be any prominent object, e.g. tree top or ground object contrasting with the background (26). Virgin females orientate towards these markers and encounter the male swarm, from which males depart to copulate on detecting the female. Mosquitoes of both sexes feed on sugary substances to provide energy for flight and dispersal, but the females of most species require a blood meal from a host to obtain the nutrients necessary for egg development. Host detection and location are accomplished by both visual and chemical (host odours) means and occur at up to 20 m. Most mosquito species are nocturnal or crepuscular, and only species of Aedes are diurnal biters. A very wide host range is exploited by the various mosquito species, including one species which feeds on mudskipper fish and
other species which feed on reptiles, amphibians, birds and mammals. The volume of a blood meal is approximately 4.0-4.5 µl (12) and is consumed in only a few minutes. Autogenous species exist, which can develop the first and subsequent batches of eggs without taking a blood meal. Digestion of a blood meal is dependent on temperature
and takes two to three days in tropical species. The ovaries develop eggs in parallel with
the digestion process. This process of blood feeding, egg maturation and oviposition
is called the gonotrophic cycle. Female *Anopheles gambiae* in Africa can undergo up to
13-14 gonotrophic cycles over a 5-6 week period. In the temperate zone, adults diapause
(hibernate) and can live for up to nine months. Only the older female sector of the
population is important in pathogen transmission, as the pathogen undergoes an
incubation period of one to three weeks in the mosquito before the female becomes
infective. The active flight of mosquitoes is short and ranges from 1-5 km, but wind
carriage may disperse the insects over 280 km or more (35, 92).

Gravid females have species-specific chemical and visual attractants to breeding
sites. They lay 30-300 eggs per oviposition, depending on species and source of blood. In
many Culiciniae, eggs are elongated or almost ovoid, while in Anophelineae they are
boat-shaped and equipped with air-filled floats (Fig. 4a). In *Anopheles, Culex* and some
*Mansonia* spp., eggs are laid on the water surface. Those of *Anopheles* are laid singly,
whereas those of *Culex* and some *Mansonia* are laid in ‘egg rafts’. Eggs of the above
genera cannot withstand dessication. *Aedes, Psorophora* and *Haemagogus* lay their eggs
just beyond the water line on mud, leaf litter or other damp substances. Eggs of these
mosquitoes can withstand varying degrees of dessication for periods ranging from
several weeks to several years, depending on the species. This feature is important for
pathogens such as Rift Valley fever virus, which are transmitted transovarially and for
which the eggs serve as a reservoir (60). Eggs hatch after 2-3 days in the tropics and after
7-14 days in temperate areas. Larvae (46, 96, 117) can live in every type of standing
water, except lake surfaces exposed to water action. The larvae (Fig. 4b) are legless,
with a bulbous thorax which is wider than either the head or the abdomen. The head has
a pair of antennae, a pair of compound eyes and a pair of mouth brushes, which are used
to sweep water-borne food particles into the mouth. Food consists of yeast, bacteria,
protozoa and many other plant and animal microorganisms. The thorax bears various
types of hairs. The abdomen has nine distinct segments, usually bearing hairs; the last
segment bears a rather complicated arrangement of hairs, a sclerotised plate and two
pairs of gills, which function in osmoregulation. The eighth segment carries a pair of
dorsal spiracles which enable the larva to breathe atmospheric air. Minute larvae may
breathe through the skin. This feature of surface breathing makes the larvae vulnerable
to control by oil spraying. In Culiciniae (Fig. 4b), these spiracles are situated at the end
of a single dark-coloured tube, termed the siphon. Anophelineae (Fig. 4b) do not have
siphons and bring their spiracles into contact with the air by positioning themselves
parallel to and below the water surface. *Anopheles* spp. are surface feeders; many other
species are bottom feeders. There are four larval instars, which take
7-14 days to develop. In temperate areas, several species overwinter as larvae, the larval
stage therefore lasting for several months.

Pupae (96) are aquatic and comma-shaped (Fig. 4c). The head and thorax are
combined in the cephalothorax which bears a pair of dorsal respiratory trumpets. Only
eight of the ten abdomen segments are visible; the last segment terminates in flat
paddles. Pupae are capable of active movement but do not feed, and spend most of their
time breathing at the water surface. The pupal period lasts for 2-3 days in the tropics and
9-12 days in temperate regions.

**VETERINARY IMPORTANCE**

Severe mosquito attack can kill livestock by exsanguination; smaller burdens cause
annoyance and blood loss, resulting in reduced weight gains and milk production
Massive mosquito attack can cause a loss in egg production by domestic fowl (28). However, the principal economic importance of mosquitoes is in the role of transmitting animal pathogens, especially arboviruses. African horse sickness occurs (in addition to Africa) in Spain, Portugal and eastern Mediterranean countries. Mosquitoes are thought to play a secondary role in the transmission of the virus, while the primary role in the field is played by *Culicoides* spp. (59, 84).

A more important role is played by mosquitoes in the transmission of Akabane virus, the aetiological agent of congenital arthrogryposis-hydraencephaly syndrome in cattle, sheep and goats (52). The disease has been reported from Japan, Australia and Israel, but antibodies have been reported from much wider areas and the virus has been isolated from *Anopheles funestus* in Kenya, and *Aedes vexans* and *Culex tritaeniorhynchus* in Japan.

Bovine ephemeral fever (47, 88) is an acute viral disease of cattle and buffalo, which occurs in sub-tropical and temperate regions of Africa, Asia and Australia. The virus has been isolated from various species of *Culicoides* and the Australian mosquito, *Anopheles bancrofti*. To date, no species has been proved to be a vector by the criteria of the Food and Agriculture Organisation of the United Nations, but *Culicoides* spp. are generally considered to be the most likely vectors.

Rift Valley fever (47, 52, 100) is one of the most important viral diseases transmitted by mosquitoes. The disease occurs only in Africa as an acute febrile disease of cattle, sheep and humans, which is characterised by high mortality in lambs and calves, and abortion in adult sheep and cattle. The virus has been isolated from nine mosquito species and experimentally transmitted by fourteen species. The important vectors in South Africa are *Culex theileri* and *Aedes caballus*; in Egypt, *Cx. pipiens* is the vector. Epizootics have been associated with heavy rains, irrigation in dry countries and winds. Long-distance wind carriage of infected insects from northern Sudan to Egypt has been suggested as the source of the Rift Valley fever outbreak in Egypt in 1977 (94).

Japanese encephalitis (52) occurs in the western Pacific islands from Japan to the Philippines, and in many eastern areas of Asia from Korea to Singapore and India. Serological evidence indicates widespread infections of swine, possibly including reproductive disorders, particularly still birth. The majority of infections are probably inapparent. The virus causes occasional epizootics of encephalitis in horses. The major vector is *Cx. tritaeniorhynchus*.

Venezuelan equine encephalomyelitis (52) is a potentially fatal virus disease of horses. The most frequent symptoms are depression, stupor, high temperature, impaired vision and impaired coordination. The virus also infects humans, in whom it produces influenza-like symptoms. The disease is known only from the western hemisphere, i.e. in Texas and further south in Central American countries. Epizootics occur at intervals of six to ten years. The virus has multiple mosquito vectors and various species have been reported from several countries, e.g. four *Psorophora* spp. were identified as vectors in an epizootic in Texas, the principal species being *Ps. columbiue* (75, 76). Isolations were also made from five *Aedes* spp., four *Culex* spp. and species from four other mosquito genera.

Western equine encephalomyelitis (52) is a febrile neurological virus disease which can kill horses, but is not usually fatal in humans. The most obvious symptoms are motor disturbances, high fever and anorexia. The disease is present in the western and central northern USA and in Canada. The virus has multiple mosquito vector species of which the most important is *Culex tarsalis*. Isolations have also been made from other
species, e.g. five *Aedes* spp., four *Culex* spp., two *Psorophora* spp., *Culiseta inornata*, *Mansonia perturbans* and *Anopheles earlei*.

Eastern equine encephalomyelitis (52, 112) is a potentially fatal virus disease of birds and horses, which may also infect humans. Infected horses show a biphasic febrile response in severe cases: clinical signs in the first febrile phase are anorexia and depression; those in the second phase include profound depression, in which the horse has a wide stance with the head hanging low until the nose almost touches the ground, drooping ears and flaccid lips. The main disease areas are along the eastern seaboard of North and South America (40). Birds are the reservoir of the virus, which is transmitted among birds primarily by *Culiseta melanura*. The vectors which are thought to transmit the virus from birds to mammals are *Aedes solicitans*, *A. vexans* and *A. canadensis*.

West Nile meningoencephalitis virus (47) is known in Africa, India, Borneo and the Mediterranean area. In France, the virus affects humans and horses, causing encephalitis (118). Birds are considered to be the reservoir from which the virus is transmitted to mammals by *Culex univittatus* and *Cx. theileri* in South Africa, and *Cx. antennatus* in Egypt. Isolations have been made from other *Culex* spp., some *Anopheles* spp., one *Mansonia* sp. and also from ticks (40).

Turkey meningoencephalitis is a neuroparalytic disease of adult turkeys which, under field conditions, affects birds older than ten weeks (43). The disease was reported in Israel in 1960, and on one occasion in South Africa (7). The virus was isolated once from an unsorted pool of mosquitoes, once from a pool of engorged *Cx. pipiens* and twice from unsorted pools of *Culicoides* (17). Laboratory infection and transmission experiments with *Cx. pipiens* were successful (71). This bird-biting species and *Aedes caspius* were found to be dominant in turkey runs in Israel (17).

Hog cholera is a highly contagious disease which causes fever, depression and degeneration of small blood vessels, and may result in death (110). Pigs exposed to mosquitoes collected during an epizootic contracted the disease. Experiments with *Aedes aegypti* proved that mechanical transmission is feasible and that the virus could be retained in the mosquitoes for three days (52, 105).

Additional arboviruses have been isolated from mosquitoes, but the possible role of these viruses in causing animal diseases is not known.

Equine infectious anaemia was thought to be mechanically transmitted by mosquitoes and other biting flies (115), but recent evidence points primarily to species in the family Tabanidae (33).

Fowl pox virus can be transmitted mechanically by chicken-biting mosquitoes. In the Sydney area in Australia, the principal vector was found to be *Cx. fatigans*; the virus was recovered from ten pools of this species (53).

Reticuloendotheliosis virus in chickens is another virus which is not arthropod-borne, but evidence from Australia suggests that the virus can be mechanically transmitted by mosquitoes. The virus was isolated on seven occasions when the dominant species was *Cx. quinquefasciatus*. Experimental transmission from donors to recipient chickens was achieved using *Cx. annulirostris* (67).

There is evidence that *Eperythrozoon ovis*, a rickettsial blood parasite of sheep, has been mechanically transmitted by *Cx. annulirostris* which could remain infective for at least fourteen hours (24, 52). Similarly, *Eperythrozoon suis* in pigs has been
experimentally transmitted by *A. aegypti*. Mosquito species are therefore likely to be mechanical vectors under natural conditions (82).

Mosquitoes were suspected as possible mechanical secondary vectors of the bacterium *Borrelia anserina* in chickens and geese, when the primary vectors, *Argas persicus* and *Dermanyssus gallinae* were absent (86, 87, 122).

Allergic dermatitis in horses, caused by allergens in the saliva of biting insects, has been reported principally as associated with *Culicoides* spp. However, some reports have associated mosquitoes with this allergy (32, 83).

**CONTROL**

Mosquitoes are most important as vectors of human pathogens, such as those causing malaria, yellow fever and dengue fever, and therefore the health and/or environmental authorities are in charge of the control of these insects in inhabited areas. The protection of animals and the control of mosquito breeding sites within farms are generally the responsibility of farm owners. The arsenal of pesticides and other means of control is too large and diverse to be detailed here. Current control policy uses the principles of integrated pest management. These principles include environmental control, e.g. draining of swamps and preventing seepages of water and sewage from animal houses, and biological control using larvivorous fish, nematodes, fungi, etc. The most efficient means of reducing mosquito populations is by controlling insect breeding sites. Selected pesticides recommended for larval control include malathion, temephos, chloropyrifos, other organophosphorous compounds, *Bacillus thuringiensis israelensis* (H-14), bacterial preparation and methoprene, an insect growth regulator. Selected recommended products for killing adult mosquitoes include the organophosphorous compounds malathion, naled, chloropyrifos and diazinon, the organochlorine methoxychlor, the carbamates carbaryl and propoxur, the botanical pyrethrin, and synthetic pyrethroids such as resmethrin, allethrin, deltamethrin and permethrin. Spraying of housed animals with commercial insecticide/insect-repellent mixtures provides short-term protection (2, 52); however, pyrethroids have demonstrated an ability to protect animals from biting flies for seven to twelve days (115).

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**NÉMATOCÈRES (CÉRATOPOGONIDÉS, PSYCHODIDÉS, SIMULIDÉS ET CULICIDÉS) ET MÉTHODES DE LUTTE. – Y. Braverman.**

**Résumé :** L’auteur décrit et discute l’importance biologique et vétérinaire de certains nématocères, ainsi que la lutte contre ces insectes.

*Les Culicoides* spp. (famille des Cératopogonidés) transmettent les arbovirus de la fièvre catarrhale du mouton, de la peste équine, de la fièvre éphémère bovine et d’Akabane. D’autres arbovirus ont été isolés chez ces
espèces ; la variole aviaire est également transmise par des Culicoides, comme cela a été démontré expérimentalement. Ces insectes sont aussi les vecteurs des protozoaires parasites, Leucocytozoon caulleryi et Haemoproteus nettionis, ainsi que des nématodes parasites, Onchocerca gutturosa, O. gibsoni et O. cervicalis. Ils provoquent, par ailleurs, une hypersensibilité estivale récurrente chez les chevaux, les poneys, les ânes, les bovins et les ovin.

Le bétail peut succomber à une attaque massive de Simulium spp., vecteurs des Leucocytozoon simondi et L. smithi ainsi que des filaires O. gutturosa, O. linealis et O. ochengi. Les virus de l’encéphalomyélite équine vénézuélienne (EEV) et de la fièvre de la Vallée du Rift (FVR) ont été isolés chez des Simulidés et on a observé la réplication du virus de la stomatite vésiculeuse (souche New Jersey) chez Simulium vittatum. Les Simulidés sont reconnus comme étant les vecteurs de O. volvulus, responsable de l’onchocercose (ou cécité des rivières).

La famille des Psychodidés comprend les genres Phlebotomus et Lutzomyia (sous-famille des Phlébotominés), vecteurs de Leishmania spp. chez l’homme ainsi que chez les chiens et autres mammifères. La souche Indiana du virus de la stomatite vésiculeuse a régulièrement été isolée chez les phlébotomes ou sandflies.

Une attaque massive de moustiques peut également s’avérer fatale pour les animaux d’élevage. Les moustiques sont, en outre, des vecteurs des virus d’Akabane, de la fièvre éphémère bovine, de la FVR, de l’encéphalite japonaise, de l’EEV, de l’encéphalomyélite équine de l’Ouest, de l’encéphalomyélite équine de l’Est et de la fièvre du Nil occidental, ainsi que des vecteurs secondaires de la peste équine et des vecteurs présumés de la ménigo-encéphalite de la dinde en Israël. Les moustiques sont des vecteurs passifs des virus de la peste porcine classique, de la variole aviaire, de la réticulendothélïose, des rickettsies Eperythrozoon ovis et E. suis, et de la bactérie Borrelia anserina. Ces insectes provoquent également une dermatite allergique chez les équidés. Ils transmettent plusieurs filaires de l’homme ou des animaux et jouent un rôle très important en médecine humaine en tant que vecteurs de maladies telles que le paludisme, la fièvre jaune, la dengue et beaucoup d’autres affections dues à des arbovirus.


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NEMATÓCEROS (CERATOPOGONIDAE, PSYCHODIDAE, SIMULIIDAE Y CULICIDAE) Y MÉTODOS DE LUCHA. – Y. Braverman.

Resumen: El autor se refiere a la importancia biológica y veterinaria de ciertos nematóceros y a la lucha contra estos insectos.

Culicoides spp. (de la familia de los Ceratopogonidae) transmiten los arbovirus de la lengua azul, la peste equina, la fiebre efímera bovina y Akabane. Otros arbovirus fueron aislados en estas especies; la viruela aviar también es transmitida por Culicoides, según se demostró experimentalmente. Estos insectos son asimismo vectores de protozarios parásitos como Leucocytozoon caulleryi y Haemoproteus nettionis, así como de nematodos parásitos como Onchocerca gutturosa, O. gibsoni y O. cervicalis. Provocan,
por otra parte, una hipersensibilidad estival recurrente en caballos, ponis, asnos, bovinos y ovinos.

El ganado puede succumbir debido a un ataque masivo de Simulium spp., vectores de Leucocytozoon simondi y L. smithii y de las filarias O. gutturosa, O. linealis y O. ochengi. Los virus de la encefalomieliitis equina venezolana y de la fiebre del Valle del Rift fueron aislados en Simuliidae y se observó la replicación del virus de la estomatitis vesicular (cepa de New Jersey) en Simulium vittatum. Los Simuliidae han sido reconocidos como vectores de O. volvulus, responsable de la oncocercosis humana (o ceguera de los arroyos).

La familia Psychodidae incluye los géneros Phlebotomus y Lutzomyia (subfamilia Phlebotominae), vectores de Leishmania spp. en el hombre tanto como en los perros y otros mamíferos. La cepa Indiana del virus de la estomatitis vesicular se ha aislado regularmente en los flebótomos (también llamados moscas de arena o beatillas).

Un ataque masivo de mosquitos puede también llegar a ser fatal para el ganado. Los mosquitos son, además, vectores de los virus de Akabane, la fiebre efímera bovina, la fiebre del Valle del Rift, la encefalitis japonesa, la encefalomieliitis equina venezolana, la encefalomieliitis equina del Oeste, la encefalomieliitis equina del Este y la fiebre del Nilo occidental, así como también vectores secundarios de la peste equina, vectores presuntos de la meningoencefalitis del pavo de Israel y vectores pasivos de los virus de la peste porcina clásica, la viruela aviar, la reticuloendoteliosis, las rickettsias Eperythrozoon ovis y E. suis, y la bacteria Borrelia anserina. Estos insectos provocan también una dermatitis alérgica en los equinos. Transmiten varias filarias del hombre o de los animales y son muy importantes para la medicina humana en la medida en que son vectores de enfermedades tales como el paludismo, la fiebre amarilla y el dengue, entre muchas otras provocadas por arbovirus.


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