

Stomoxys
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Muscid flies include many non-biting and biting genera, the former being nuisances and the latter being blood-feeders. Most species are synanthropic (closely associated with humans) and they breed in all types of organic waste. Two subfamilies are recognized: muscines (house flies, bush flies, face flies) with sucking mouthparts adapted to feeding on decaying organic matter; and stomoxines (stable flies, horn/buffalo flies) with elongate biting mouthparts adapted to blood feeding. Stable flies (*Stomoxys* spp.) attack humans and domestic animals, having serious impacts on tourism, cattle productivity and horse performance. They may also transmit a range of viral, bacterial, protozoal and helminth infections.

Classification:

Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder: Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder: Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division: Schizophora (head with frontal suture (lunule))
Section: Calyptratae (calypters cover halteres)
Family: Muscidae (house/bush/stable/buffalo flies, nuisance flies, synanthropic (associated with human activity))
Subfamily: Stomoxinae (with elongate biting mouthparts adapted to blood feeding)
Genus: *Stomoxys* (parasitic on skin of mammals)
Species: various species cause annoyance, allergy

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipteroidea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with arista, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiasis) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like arista), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinal suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calyptratae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalyptratae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or

biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Muscoidea contains 4 families: Muscidae (house flies), Fanniidae (latrine flies), Scathophagidae (dung flies) and Anthomyiidae (anthomyiid flies). The family Muscidae contains robust flies with plumose arista and wings where vein A2 is not strongly curved (unlike latrine flies). The family contains both free-living flies, some of which are nuisance pests of livestock and humans, as well as blood-sucking flies feeding on vertebrates. Over 4,200 species have been described in some 190 genera classified into 9-10 subfamilies: Achantipterinae, Azeliinae, Coenosinae, Cyrtoneurinae, Dichaetomyiinae, Muscinae, Mydaeinae, Phaoniinae, and Reinwardtiinae; with another 58 unplaced genera and several fossil genera. Alternatively, some authorities recognize 2 tribes (Muscini and Stomoxyni) in the subfamily Muscinae, while others have elevated the tribe Stomoxyni to subfamily status (Stomoxinae).

Subfamily	Genera	Hosts	Site	Transmission
Muscinae (with sponging mouthparts)	<i>Musca</i>	mammals	nonparasitic	nonparasitic
Stomoxinae (with biting mouthparts)	<i>Stomoxys</i>	mammals	skin	direct
	<i>Haematobia</i>	bovines	skin	direct

The subfamily Stomoxinae contains 4 genera (*Haematobia*, *Haematobosca*, *Stygeromyia* and *Stomoxys*) although some authorities have merged the genus *Haematobosca* (and the former genus *Lyperosia*) with *Haematobia*. These flies have elongate biting mouthparts adapted to blood feeding on domestic animals and wildlife. The genus *Stomoxys* (syn. *Stomoxis*) contains 18 species of stable flies that feed mainly on the legs and ears of horses, cattle and some companion animals (dogs). Adult flies inflict irritating bites resulting in significant annoyance to their hosts, and allergic individuals may develop papular skin lesions. Various species have been implicated as vectors in the transmission of infectious diseases, including anthrax, viral anaemia, surra (trypanosomiasis) and nematode granulomas (summer sores).

<i>Stomoxys</i> species	Hosts	Clinical signs	Distribution
<i>S. bengalensis</i> (syn. <i>S. oblongopunctatus</i>)	Artiodactyla: bovid (cattle), traps*	annoyance	Asia
<i>S. boueti</i>	Artiodactyla: bovid (buffalo); traps		Africa
<i>S. calcitrans</i> (syn. <i>S. aculeata</i> , <i>aurifacies</i> , <i>bouffardi</i> , <i>chrysocephala</i> , <i>claripennis</i> , <i>cunctans</i> , <i>cybira</i> , <i>dira</i> , <i>flavescens</i> , <i>geniculata</i> , <i>griseiceps</i> , <i>hovas</i> , <i>infesta</i> , <i>inimica</i> , <i>korogwensis</i> , <i>libatrix</i> , <i>minuta</i> , <i>nebulosa</i> , <i>occidentis</i> , <i>parasita</i> , <i>plurinota</i> , <i>praecox</i> , <i>pungens</i> , <i>rubifrons</i> , <i>soudanense</i> , <i>sugillatrix</i> , <i>tessellata</i> , <i>vulnerans</i>) (stable fly)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (deer), suid (pig); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (rabbit); Carnivora: canid (dog), felid (cat); Rodentia; Murid (rats); Primates: hominid (human), cercopithecid (monkeys); traps	annoyance, allergy (vector for trypanosomiasis, anthrax, fungi, nematodes (<i>Habronema</i> , <i>Draschia</i>))	worldwide
<i>S. indica</i> (syn. <i>S. discalis</i> , <i>hastata</i> , <i>latipennis</i> , <i>limbata</i> , <i>pratti</i> , <i>pusilla</i> , <i>triangulais</i>)	Artiodactyla: bovid (cattle), traps	annoyance	Asia
<i>S. inornata</i> (syn. <i>S. rodhainica</i>)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance	Africa
<i>S. luteola</i> (syn. <i>S. ochrosoma</i>)	traps		Africa
<i>S. nigra</i> (incl. subspp. <i>nigra</i> , <i>bilineatus</i>) (syn. <i>S. bouvieri</i> , <i>clara</i> , <i>doryphora</i> , <i>glauca</i> , <i>griseola</i> , <i>halophila</i> , <i>lafonti</i> , <i>schoutedeni</i> , <i>sexvittata</i>)	Artiodactyla: bovid (cattle, buffalo, sheep, goat); Perissodactyla: equid (horse, donkey); Primates: hominid (human); traps	annoyance (mechanical vector for trypanosomiasis (nagana, surra))	Africa
<i>S. ochrosoma</i> (syn. <i>S. flavida</i>)	Artiodactyla: bovid (cattle, buffalo), traps	annoyance	Africa

<i>S. omega</i> (incl. subsp. <i>omega</i> , <i>wigglesworthi</i>)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance	Africa
<i>S. pallida</i> (syn. <i>S. neavi</i>)	Artiodactyla: bovid (antelope); traps		Africa
<i>S. pulla</i>	traps		Asia
<i>S. sitiens</i> (syn. <i>S. dubitalis</i> , <i>separabilis</i>)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey); Primates: hominid (human); traps, dung	annoyance	Asia, Africa
<i>S. stigma</i>	traps		Africa
<i>S. taeniata</i> (syn. <i>S. brunnipes</i> , <i>intermedia</i> , <i>sellata</i>)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance (mechanical vector for trypanosomiasis (surra))	Africa
<i>S. transvittata</i>	dung		Africa
<i>S. uruma</i>	Artiodactyla: bovid (cattle, water buffalo); traps		Asia
<i>S. varipes</i>	traps		Africa
<i>S. xanthomelas</i>	Artiodactyla: bovid (cattle), traps, dung	annoyance	Africa

*Many studies report the collection of adult flies using odour-baited traps (in villages, farms and forests); or the emergence of adult flies from organic waste or animal dung collected from the environment.

Several other species have been reassigned to other genera: including *S. asiliformis* (now *Syneches muscarius*); *S. flava* (now *Fischeria bicolor*); *S. humeralis* (now *Toxotarsus humeralis*); *S. morio* (now *Hyperalonia morio morio*); and *S. stimulans* (now *Haematobia (Haematobosca) stimulans*).

Parasite morphology: Stable flies (*Stomoxys* spp.) form 4 types of morphological developmental stages: eggs, larvae, pupae and adults. The eggs are white and have an elongate sausage shape measuring around 1 mm in length with one curved side and the other straight and bearing a longitudinal groove (hatching pleat). Larvae (known as maggots) have soft cream-coloured bodies that taper from the pointed anterior end to the blunted posterior end (oestroid larvae are more cylindrical). They develop through 3 instars (L1-3) growing from 1mm up to 11-12 mm in length. The body is segmented and lacks a sclerotized head capsule but has an internal cephalopharyngeal skeleton. The anterior mouth bears mouthhooks which are small in L1-2, but large and bill-shaped in L3. The segments lack bristles and legs but have ventral patches of small spines forming creeping welts. The larvae breathe using 2 pairs of respiratory spiracles: a small pair of anterior tubercle-like spiracles (absent in L1); and a larger pair of dark caudal spiracles, each appearing as a simple hole in L1, as 2 short stout non-sinuuous slits on a weakly-pigment plate in L2, and as 3 longer sinuous slits on a heavily-pigmented sclerotized plate (peritreme) in L3. The caudal spiracles of *Stomoxys* spp. are further characterized by being subtriangular in shape and widely separated (compared to those in other muscid larvae). Mature L3 form barrel-like puparia 4-6 mm long by contraction and hardening of the tegument which gradually darkens to reddish-brown in colour. A pupa is formed inside which undergoes metamorphosis to form a winged adult which ecloses through a circular cap (like all Cyclorrhapha) rather than a longitudinal slit (like Nematocera and other Brachycera). Adult stable flies have small grey bodies 4-10 mm long, with 4 dark longitudinal stripes on the thorax and 3-7 circular black spots on the abdomen. Adults often have a thin or dense covering of fine setae (sometimes referred to as 'pollinosity'). They have 3 conspicuous body tagma: a globular head; pyriform thorax; and ovate abdomen. The large mobile head bears both a ptilinal suture and facial lunule (like other Muscoidea and Oestroidea, but unlike other calyprate flies) and 2 large brown well-developed compound eyes located laterally and separated by a frontal frons with 3 small ocelli. Adults have a pair of unique antennae that lie in an anterior groove in the head. The antennae are composed of 3 dissimilar segments, comprising a short basal scape, a longer pendulous pedicel, and a single plumose dorsal arista (bristle-like flagellum with short setae on the dorsal surface only). *Stomoxys* spp. are blood-feeders and have piercing-sucking mouthparts that are conspicuous as a stout proboscis projecting forwards when not in use. The proboscis is flanked by 2 short strap-like palps whose inner surfaces are not grooved (palps longer and grooved internally in *Haematobia*). The mouthparts comprise a small basal rostrum supporting a rigid haustellum that contains a hardened labium as a piercing structure, with the terminal labella reduced but armed with large sharp sclerotized teeth (replacing the pseudotracheae in sponging muscine flies). Once the host skin is cut, the labium is inserted into the wound and the contained labrum and hypopharynx come together to form a food canal. Blood is sucked up by the muscular pharynx (acting as a cibarial pump) and delivered to the tubular oesophagus and proventriculus (with associated storage diverticula) before being digested in the midgut with waste passed through the hindgut (with excretory Malpighian tubules) to the terminal anus. The thorax is covered by a rigid scutum which is grey with 4 prominent dark stripes (called vittae). Thoracic plates vary in their patterns of setation with stout bristles lacking on the anterior sternopleuron, hypopleuron, notopleuron (setulose in *Haematobosca*) and propleuron (sometimes setulose in *Haematobosca*). The mesothorax sports a pair of stout wings with wing membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with vein A1 vanishing before the wing margin, vein M1 curving evenly towards the margin, and the discal cell having a symmetrical trapezoidal shape. Like all Diptera, the hindwings are highly reduced to a pair of knob-like halteres used to stabilize flight. The halteres are covered by posterobasal wing lobes (calypters) that distinguish all calyprate flies. The ventral thorax gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus), and all ending in a pair of claws flanking 2 pads (pulvilli) and

several central bristles (empodium). The short broad abdomen is darker dorsally than ventrally and the first few segments have several (3-7) dark grey-black circular spots giving them a mottled pattern. The number of visible segments is generally reduced to 5 (from 10-12) because the posterior segments are modified by terminalia (anal cerci in both sexes, retractable copulatory aedeagus and claspers in males, cylindrical telescoping ovipositor in females). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) and a tubular ejaculatory duct leading to the aedeagus in the genital pouch. Females have 2 ovaries joined to oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and ovipositor.

Site of infection: Flies belonging to the genus *Stomoxys* are commonly called stable flies, but they are also known variously as beach flies, dog flies, lawn-mower flies and even biting house flies. The adults feed on blood from a small range of vertebrate hosts, mostly feeding on ungulates (horses, cattle, buffalo) but they will readily attack companion animals (dogs, cats), wildlife (deer, rabbits, rats) and even humans. Large animals are usually attacked on the legs, flanks, back and belly, while smaller animals are bitten around the face, ears, neck and legs. Stable flies now have a cosmopolitan distribution and are found on all continents except Antarctica, their dispersal aided by frequent livestock translocations.

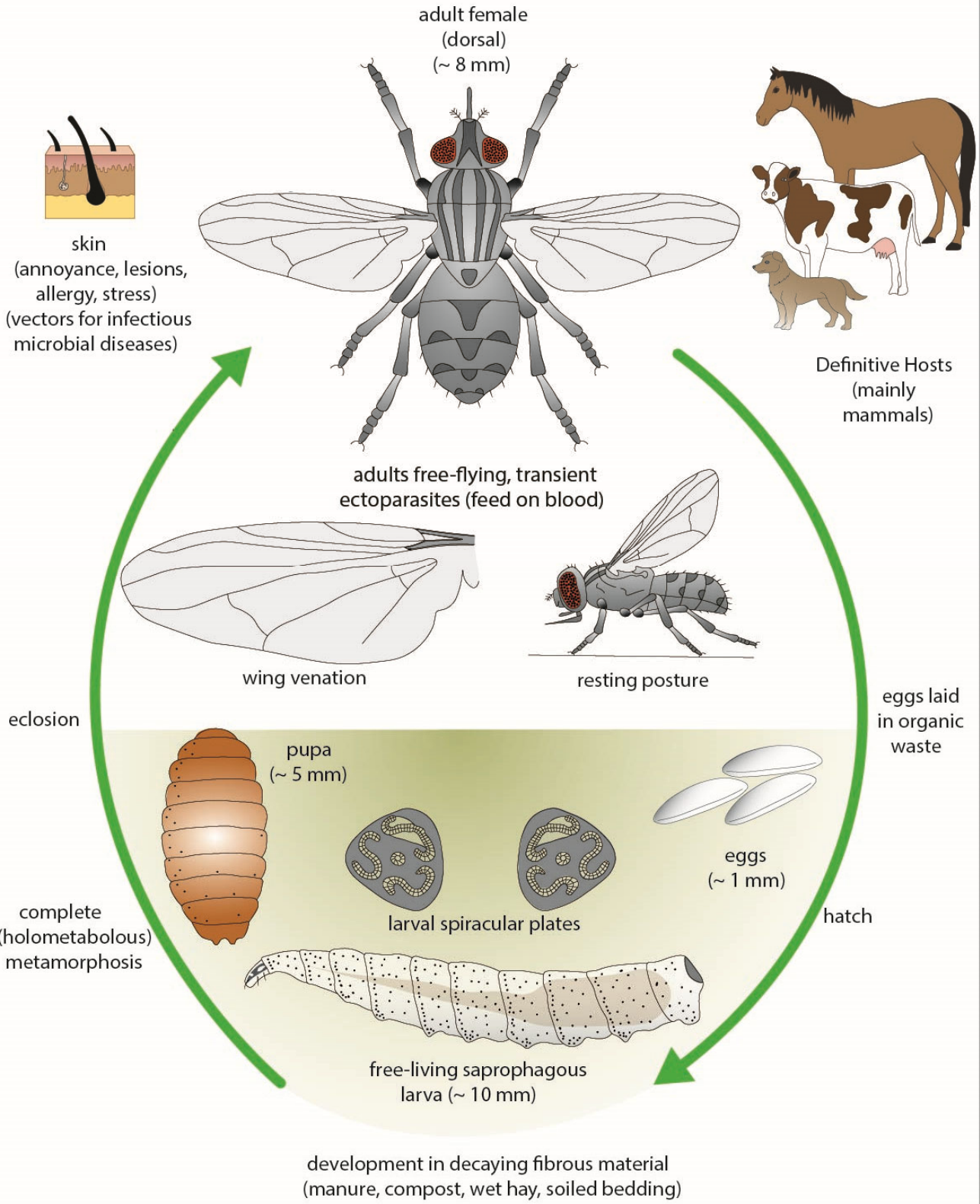
Pathogenesis: Stable flies are haematophagous and both sexes feed on vertebrate blood taking small blood meals once or several times a day (feeding lasting for a few minutes if undisturbed). They feed by cutting the skin with toothed mouthparts and then inserting stylets that couple together to form a tube to suck blood from dermal capillaries as well as deliver fly saliva. Fly bites are very painful and distressing to the host, resulting in intense irritation and disturbance (fly worry, biting stress) with livestock adopting aversive behaviours (swatting, stamping, kicking, bunching) that make them difficult to handle (muster, groom, milk). Hosts are disturbed from feeding which leads to decreased performance and productivity losses (poor weight gain, reduced milk yield). The bites cause traumatic skin damage with small punctate lesions evident as papules 5-10 mm in diameter with a small central scab. Host inflammatory responses result in welts with swelling that may cause hair covering the lesion to become raised. Hosts may attempt to relieve accompanying pruritus by biting, scratching or rubbing affected areas which can lead to self-trauma exacerbating wounds and opening them to secondary infections. Fly bites around the face and ears can lead to erythema, exudation and crust formation, including ear-edge dermatoses in dogs. While stable flies may engorge on blood up to 3 times their own body weight, most species do not attack in swarms dense enough to cause blood loss severe enough to manifest as anaemia. Stable flies are not renowned as vectors for the transmission of infectious diseases, although studies have shown they may transmit some trypanosomiasis (sleeping sickness in humans, nagana in horses, cattle, sheep and goats, surra in horses and dogs, and mal de caderas in horses, cattle, sheep and goats), possibly equine infectious anaemia (retrovirus), and act as intermediate hosts for spirurid nematodes (*Habronema* and *Draschia*) producing summer sores in horses. Recent studies have also shown that several species of stable flies may act as hosts for a diverse array of acarine mites (5 families of Mesostigmata, 2 families of Prostigmata, and 4 families of Astigmata) which attach to external body surfaces. The significance of infestations is unknown, even though one genus (*Trichotrombidium*) is known to be an obligate parasitic mite of Muscidae, while most other mites were apparently opportunistic passengers engaged in phoretic transfer (paratenic transport) between vertebrate hosts.

Developmental cycle and mode of transmission: Muscid flies exhibit holometabolous development where eggs hatch grub-like larvae which undergo pupation to transform into winged adults. Female flies are oviparous and may lay up to 500-1,000 eggs in batches of 25-30 deposited in dung or decaying organic matter. The eggs hatch in 4-5 days releasing larvae which feed, grow and moult through 3 developmental instars (L1-3) over 12-13 days depending on the temperature (longer in colder conditions, with some over-wintering as larvae in temperate regions). The larvae develop best in decaying fibrous substrates such as manure, soiled straw bedding, wet hay, silage, compost, algal mats, moist grass clippings, and mounds of decaying vegetation (including sugarcane bagasse, beet pulp and peanut hulls from processing plants). The larvae are saprophagous and feed on vegetable matter and micro-organisms including bacteria, yeasts and algae (in comparison, the larvae of some other muscid genera may also be facultative predators). Pupation then occurs in the same habitat, but often at the periphery where the soil is drier. Mature L3 cease feeding and form puparia by contraction and hardening of the tegument. A pupa forms inside and undergoes metamorphosis to an adult over a period of 6-26 days depending on temperature (longer in colder conditions). Teneral adults eclose from pupae and after a short period for their cuticle and wings to harden, they fly in search of hosts on which to feed. They are strong fliers and persistent in their efforts to feed on vertebrates. Both males and females feed exclusively on host blood, and females are anautogenous and require bloodmeals to complete gonotrophic (ovarian) cycles. Mating occurs shortly after eclosion when males perch on substrates to intercept passing females. After mating, females store enough sperm to remain fertile for life and they may produce 50-100 eggs in each ovarian cycle. Adults generally live for 1-2 months in cooler weather, but only 3-4 weeks in hotter weather. Most species are multivoltine and form multiple generations each year, the number being dependent on the prevailing climatic conditions in different geographic locations. Breeding may occur continuously in tropical and subtropical regions, but may be confined to warm seasons in colder temperate regions. Stable flies are generally most abundant in summer and autumn, and can often be observed resting in sunny locations (on trees, fences, barns, houses) seeking hosts or mates, or digesting bloodmeals. Adult flies are active during the day and prefer direct sunlight but will follow animals into the shade, including entering buildings.

Differential diagnosis: Most attacks by stable flies are indicated by the searing pain accompanying their persistent attempts to bite and feed. However, the resultant skin lesions are not pathognomonic and may be attributable to other ectoparasites. Diagnosis is usually confirmed by capturing feeding flies (by hand, nets or baits) and identifying them by close examination (aided by magnifying glasses). Stable flies are superficially similar in appearance to house flies but are slightly smaller and have a distinctive stiletto-like proboscis (for biting) while house flies have smaller stouter mouthparts (for sponging). Modern molecular biological studies have been conducted to characterize species and determine their phylogenetic relationships, mostly following polymerase chain reaction (PCR) amplification of nuclear and mitochondrial gene sequences, although the whole genome of *S. calcitrans* has been completed.

Treatment and control: If required, stable fly bites may be treated topically with anti-inflammatory, analgesic and antiseptic preparations, or systemically with corticosteroids and antihistamines, to alleviate irritation and pruritus. Agitated or distressed animals (mostly horses) may require tranquilisers. Animals may be protected from stable flies to some degree by the topical application (sprays, dusts, some pour-ons, impregnated ear-tags) of chemical insecticides, such as organochlorines, organophosphates and pyrethroids. Many preparations do not last long on hosts and need to be regularly re-applied to achieve protection. Some preparations have longer residual activities and may be used to treat animals or to spray resting sites where flies congregate, such as barnyard fences, stalls, and walls. Insecticides should not be used indiscriminately to lessen the chances of the development of insecticidal resistance and to mitigate their detrimental effects as they accumulate in the environment. Aerosol space-sprays have been used to kill adult flies in intensive-husbandry situations (stables, dairies, feedlots) but they are not effective in windy conditions, and droplet sizes need to be small enough for adequate dispersal. Chemical fly repellents (such as DEET) have also been used directly on hosts on sparsely-haired sites or in closed quarters to deter stable flies. The use of fly traps, electric grids and baits have not proven particularly effective against blood-feeding stable flies. Animal and farm management practices may be modified to protect stock from fly bites as well as to control fly populations by reducing available larval habitats. The use of fly barriers (doors, screens, curtains, nets) may protect indoor spaces, and animals may be housed during periods of peak fly activity. Every effort should be made to eliminate potential breeding sites for larvae by managing organic waste through improved hygiene and better sanitation (including dung removal, disposal of soiled bedding, periodically turning compost piles, avoiding accumulations of grass cuttings and other vegetation, storing feedstuffs high and dry, and cleaning up spilled feed). Several studies have begun to investigate methods for biological control, particularly using dung beetles to reduce larval habitats, and parasitoids (wasps and beetles) which reproduce in stable fly larvae and/or pupae.

Stomoxys





Stomoxys adult



Stomoxys eggs



Stomoxys larva



Stomoxys larval spiracles



Stomoxys pupa