

Haematobia

(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. Horn flies (*Haematobia* spp.) are significant pests of cattle throughout the world and they may also transmit bovine mastitis and filarial nematodes.

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: *Haematobia* (parasitic on skin of bovines)
Species: various species cause annoyance

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 myiasis).

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: Achanthipterinae, Azeliinae, Coenosinae, Cyrtoneurinae, Dichaetomyiinae, Muscinae, Mydaeinae, Phaoniinae, and Reinwardtiinae [some authorities recognize 2 tribes (Muscini and Stomoxyni) in the subfamily Muscinae, while others have elevated the latter tribe 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* with *Haematobia*. These flies have elongate biting mouthparts adapted to blood feeding on a wide variety of mammalian hosts, especially cattle and buffalo in both tropical and temperate regions. In particular, the buffalo fly (*H. exigua*) and the horn fly (*H. irritans*) cause significant fly worry in their hosts, papular skin lesion in allergic individuals, and act as vectors for the transmission of filarial nematodes and possibly protozoal theileriosis.

Fly species	Hosts	Clinical signs	Distribution
<i>Haematobia</i> (syn. <i>Glossinella</i>, <i>Haemathobia</i>, <i>Haphospatha</i>, <i>Hoematobia</i>, <i>Lyparosia</i>, <i>Lyperosia</i>, <i>Priophora</i>, <i>Siphona</i>)			
<i>H. exigua</i> (syn. <i>H. irritans exigua</i> , <i>australis</i> , <i>flavohirta</i>) (buffalo fly)	Artiodactyla: bovid (cattle, water buffalo, bison), camelid (camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	irritation, blood loss (vector for <i>Stephanofilaria</i>)	Asia, Australia
<i>H. irritans</i> (syn. <i>H. cornicula</i> , <i>pungens</i> , <i>serrata</i> , <i>tibialis</i> , <i>Lyperosia irritans</i> , <i>meridionalis</i> , <i>ruffrons</i> , <i>weissi</i> , <i>Conops irritans</i>) (horn fly)	Artiodactyla: bovid (cattle, water buffalo, bison, sheep, goat), camelid (camel), suid (pig); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog); Primates: hominid (human)	irritation, blood loss (vector for <i>Stephanofilaria</i> , <i>Parabronema</i> , <i>Habronema</i>)	Eurasia, North Africa, North America, Australia
<i>H. meridiana</i>	Artiodactyla: giraffid (giraffe), suid (warthog)	irritation	Africa
<i>H. minuta</i> (syn. <i>H. longipalpis</i> , <i>potrix</i> , <i>Lyperosia</i>)	Artiodactyla: bovid (cattle, buffalo, water buffalo, tiang); Perissodactyla: equid (horse); Primates: hominid (human)	irritation, blood loss (vector for <i>Stephanofilaria</i>)	Africa
<i>H. shillingsi</i>	Perissodactyla: rhinocerotid (black rhinoceros)	irritation	Africa
<i>H. spinigera</i>	Artiodactyla: bovid (cattle, buffalo), giraffid (giraffe); Perissodactyla: equid (zebra)	irritation	Africa
<i>H. thirouxi</i> (incl. subsp. <i>potans</i> , <i>thirouxi</i>) (syn. <i>H. hirudo</i>)	Artiodactyla: bovid (cattle, buffalo, sheep, impala, korrugum); Perissodactyla: equid (horse, Burchell's zebra,), rhinocerotid (black rhinoceros); Carnivora: canid (dog); Primates: hominid (human)	irritation	Africa
<i>H. titillans</i> (syn. <i>H. thirouxi titillans</i> , <i>bovina</i> , <i>equina</i> , <i>latirostris</i> , <i>scolopax</i>)	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel); Perissodactyla: equid (horse)	irritation (vector for <i>Stephanofilaria</i> , <i>Parabronema</i>)	Asia
<i>Haematobosca</i> (syn. <i>Bdellia</i>, <i>Bdellolarynx</i>, <i>Haematobina</i>, <i>Lyperosiops</i>, more recently synonymized with <i>Haematobia</i> by various authorities)			
<i>Hb. aberrans</i>	traps*, buffalo farm		Asia

<i>Hb. alcis</i> (= <i>crassipalpis</i>)	Artiodactyla: cervid (moose)	irritation	Holarctic
<i>Hb. atripalpis</i> (syn. <i>Hb. perturbans</i>)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey)	(vector for <i>Parafilaria</i>)	Palaearctic
<i>Hb. augustifrons</i>	traps		Africa
<i>Hb. aurata</i>	traps		Africa
<i>Hb. croceicornis</i>	traps		West Africa
<i>Hb. decipiens</i>	traps		Europe
<i>Hb. evecta</i>	traps		Europe
<i>Hb. hirtifrons</i>	traps		Africa
<i>Hb. kangwagyei</i>	traps		Africa
<i>Hb. latifrons</i> (syn. <i>Hb. mallochi</i>)	Artiodactyla: bovid (cattle, buffalo)		Africa
<i>Hb. praedatrix</i>	traps		Africa
<i>Hb. sanguinolenta</i> (syn. <i>Bdellolarynx</i> , <i>Haematobia aculeata</i> , <i>caraboa</i> , <i>chinensis</i> , <i>nudinervis</i> , <i>rufipes</i> , <i>Siphona carabao</i> , <i>Stomoxys chinensis</i>)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey)	irritation	Asia, Africa
<i>Hb. squalida</i> (syn. <i>Hb. lutosa</i>)	Artiodactyla: bovid (cattle, buffalo), traps		Africa
<i>Hb. stimulans</i> (syn. <i>Hb. melanogaster</i> , <i>ferox</i> , <i>geniculata</i> , <i>vernalis</i> , <i>ryszardi</i> , <i>Siphona</i>) (large horn fly, large meadow bite fly)	Artiodactyla: bovid (cattle, water buffalo), cervid (elk); Perissodactyla: equid (horse); Primates: hominid (human)	irritation, blood loss (vector for <i>Stephanofilaria</i> , <i>Setaria</i>)	Palaearctic, Central Asia
<i>Hb. trivittata</i>	traps		Eurasia
<i>Hb. uniseriata</i>	traps; Artiodactyla: suid (warthog)		South Africa
<i>Hb. wooffi</i>	Artiodactyla: bovid (cattle, buffalo)		Africa
<i>Hb. zuluensis</i>	traps		South Africa

*Collections made from environment using traps or nets for adult flies.

Parasite morphology: *Haematobia* and *Haematobosca* spp. form 4 different types of morphological stages: eggs; larvae; pupae; and adults. Eggs are ovoid, but concave on one side and convex on the other, measuring around 1mm long and appear white, yellow or tan when laid but darken to a reddish brown. Larvae (known as maggots) have white elongate tapered bodies, with an anterior pointed end bearing the head and a posterior blunted end bearing dark dorsal spiracular plates (oestroid larvae are more cylindrical). They develop through 3 instars (L1-3) growing from 1.5 mm up to 7 mm in length. Larvae lack a sclerotized head capsule but they have an internal cephalopharyngeal skeleton bearing mouthhooks (small and rounded in L1-2 and large and bill-shaped in L3). They have 12 body segments and are legless, but they have patches of tiny spines on ventral abdominal segments forming creeping welts. They breathe using 2 pairs of respiratory spiracles: a small anterior pair (absent in L1) apparent as branched tubercles; and larger posterior pair evident as simple holes in L1 and as 3 sinuous slits with an ecdysal scar on a pigmented plate (peritreme) in L2-3. In muscid larvae, the spiracular slits slant towards the midline, while those in sarcophagid larvae slant away from midline (in contrast, oestrid larvae have porous spiracular plates). Mature L3 form barrel-shaped puparia 3-4 mm long by contraction and hardening of the tegument which gradually darkens from white to reddish-brown. Inside, a pupa is formed 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 flies range in size from 3-6 mm long and have brown-grey to black shiny bodies with a dense covering of fine setae (sometimes referred to as pollinosity) which is grey-olive in *Haematobia* spp. and yellow-black in *Haematobosca* spp. They have 3 conspicuous body tagma: a rounded head; stout pyriform thorax; and ovate abdomen. The head has both a ptilinal suture and facial lunule (like other Muscoidea and Oestroidea, but unlike other calyprate flies) and 2 large red-brown compound eyes located laterally and separated by a frontal frons with 3 small ocelli. A pair of unique reddish-brown antennae lie in an anterior groove on the frons, each antenna 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 for *Haematobia* but on the dorsal and ventral surfaces for *Haematobosca*. Adult flies are biting blood-feeding species and have piercing-sucking mouthparts projecting forwards as a single proboscis when not in use. The proboscis is flanked by a pair of grey-yellow palps that are as long as the proboscis and strap-like with grooves on the internal surfaces (cf. biting *Stomoxys* flies have shorter non-grooved palps). The mouthparts consist of a small basal rostrum supporting a rigid haustellum with a hardened labium and terminal labella armed with large sharp sclerotized teeth (replacing the pseudotracheae in sponging muscine flies). Once the host skin is cut by the labella, the labium is inserted into the wound and the contained labrum and hypopharynx come together to form a food canal. Blood is ingested

using strong pharyngeal muscles and routed through 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 hard brown scutum with 2 parallel dark stripes running dorsally just behind the head. The thoracic plates vary in their patterns of setation, the hypopleuron lacking a row of stout setae, and the notopleuron and propleuron bare in *Haematobia* (like *Stomoxys*) or setulose in *Haematobosca*. The mesothorax sports a pair of stout shiny wings that are held flat over the abdomen at rest, but held at an angle to the body when feeding to form a reflective angular shape. Wing membranes are 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 calypterate 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 abdomen does not have marked dorsal patterns of pigmentation (like *Stomoxys*) and 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: Adult flies are obligatory ectoparasites that must feed on vertebrate blood to complete their life-cycles. Buffalo and horn flies feed primarily on blood from bovid hosts (especially cattle and buffalo), but they may feed opportunistically on other hosts, notably larger ungulates, and sometimes humans. Adult flies prefer short-haired dark-coloured hosts, apparently for ease of access to the skin as well as for camouflage against predators. Horn flies (*H. irritans*) were originally given their common name because they cluster around the horns, but both horn flies and buffalo flies (*H. exigua*) often congregate on areas least likely to be disturbed (neck, belly, thighs, shoulders, flanks and back). Horn flies remain in contact with their hosts both day and night, resting with their heads down (cf. stable flies rest with their heads up), while *Haematobosca stimulans* spend less time resident on their hosts. Adult flies have been observed to be most abundant on short-haired bulls, followed by steers, cows and then calves. Females flies leave their hosts usually only as long as it takes to deposit eggs in manure where the larvae develop.

Pathogenesis: These biting flies are haematophagous and both sexes use their piercing-sucking mouthparts to feed on vertebrate blood, males feed up to 20 times a day while females feed up to 40 times daily. Adult flies tend to associate with individual hosts or a small numbers of hosts within a herd, and populations of several thousand flies may occur on individual hosts. Flies move around the body of the host apparently to regulate temperature and avoid wind and rain, often relocating to the belly during the hottest parts of the day. An individual fly may consume 10-21 μ l of blood per day, so heavy infestations can cause significant blood loss resulting in anaemia, particularly in young animals. Adult flies use their labellar teeth to cut the skin and then insert their labium into the wound. The labrum and hypopharynx come together to form a food canal through which the flies suck blood from dermal capillaries as well as to inject saliva containing anticoagulant properties. Flies repeatedly insert, withdraw and re-insert their mouthparts several times during feeding, which causes considerable trauma, pain and irritation. Bites are evident as inflamed erythematous papules with a central puncture wound. These lesions can persist for several days and become scabs covered with dried exudates. The wounds are intensely pruritic, and hosts seek to relieve the itch by biting, scratching or rubbing affected regions, which may cause self-trauma and open ulcerative wounds susceptible to secondary infections, even attracting other flies. Persistent attack often leads to ventral, and sometimes periorbital, dermatitis in horses and cattle. Dermal lesions may be severe enough to cause cosmetic defects in tanned and dyed leather. Some individual hosts become allergic to fly saliva and develop hypersensitivity reactions with severe dermatitis, oedema, thickened scaly skin, alopecia and wet eczema around bites (such individuals are often culled from herds to improve herd resistance). Animals subject to sustained fly-worry exhibit many aversive behaviours (licking backs, twitching flanks, swishing tails, stamping feet, kicking at belly, standing in water) which sometimes makes them difficult to handle (muster, groom, treat). They become distracted from feeding and exhibited production losses due to decreased weight gain, reduced milk production, poor reproductive performance and damaged hides. It has been estimated that as few as 30 buffalo flies or 12 horn flies may reduce weight gain in cattle, and producers consider infestations in excess of 100-200 flies sufficient grounds to commence treatment. These biting flies are not major vectors for the transmission of infectious microbial diseases because they spend so much of their lives on individual, or only a few, hosts. Horn flies have been shown to act as intermediate hosts for the spirurid nematode *Stephanofilaria stilesi* which can cause granular dermatitis in cattle. They may act as mechanical vectors for summer mastitis caused by bacteria (*Staphylococcus aureus* and others) and possibly several other bacterial infections (*Salmonella enterica*, *Staphylococcus saprophyticus*, *Morganella morganii*, *Serratia marcescens*). Buffalo flies have been found to act as intermediate hosts for various nematodes (*Stephanofilaria*, *Setaria*, *Parafilaria*, *Habronema*) causing crusted skin lesions in cattle. Molecular screening studies have returned positive results for *Theileria orientalis* in buffalo flies, but their involvement in transmission is unknown.

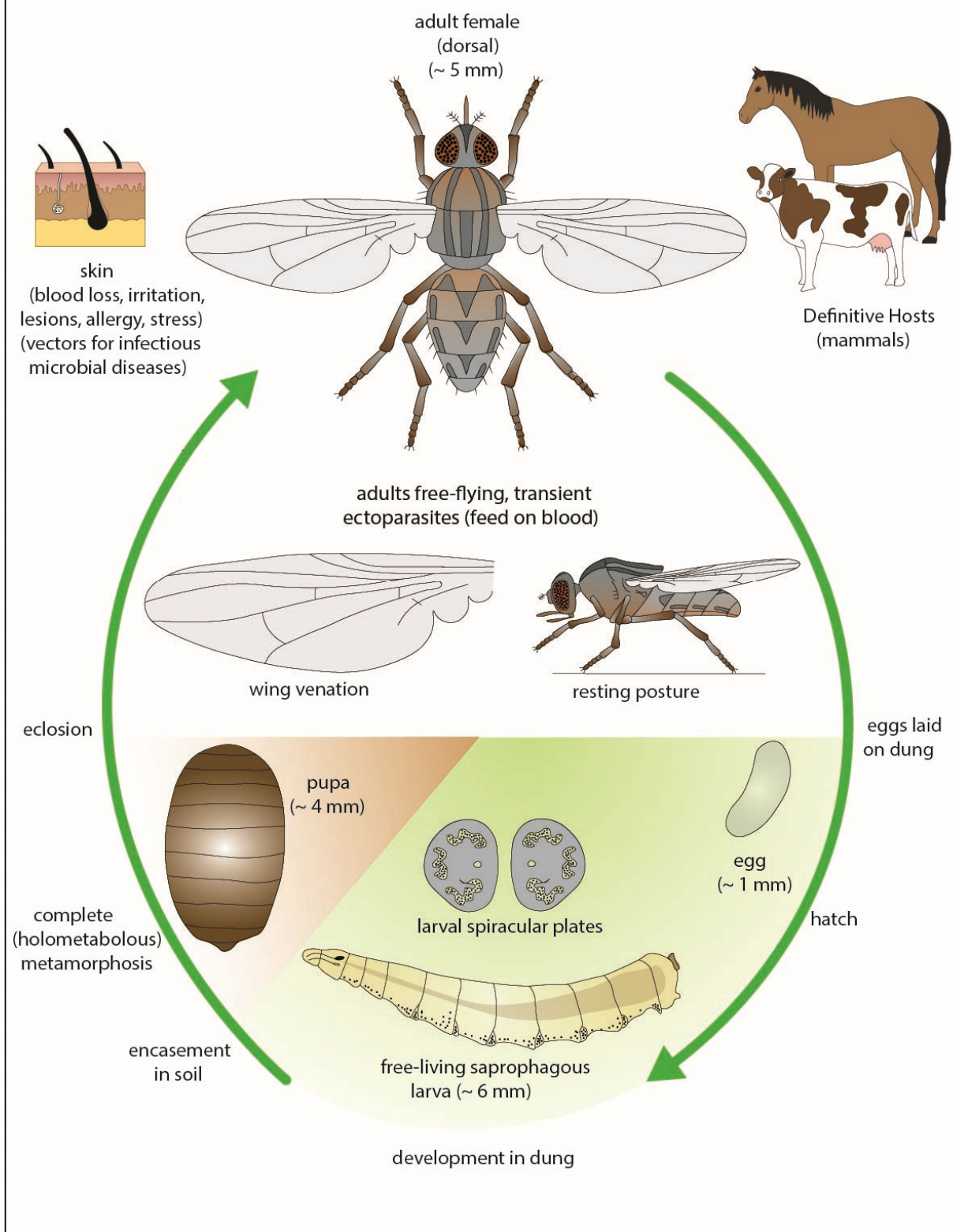
Developmental cycle and mode of transmission: Like all dipterans, these flies undergo holometabolous (complete) metamorphosis as their grub-like larval stages transform in pupae into winged adult flies. They are commonly known as dung biting flies as they breed in dung and feed by biting hosts to suck blood. Gravid female flies leave their hosts temporarily to oviposit 12-30

eggs almost exclusively in crevices or under edges (away from light) of undisturbed dung pats, sometimes on adjacent blades of grass. The dung is usually fresh (within minutes of host defaecation) and invariably from cattle or buffalo (dung from horses, sheep and other large mammals is not suitable). The eggs hatch in 12-24 hours releasing first stage larvae (L1) which burrow into nutrient-rich areas in the faeces and feed on bacteria. They develop through 2 more larval instars (L2-3) over 4-8 days before burrowing downwards away from the crust towards the soil. Mature L3 form puparia by hardening of the tegument and the enclosed pupae transform into winged adult flies over 5-8 days, although pupation may be delayed for several days or weeks depending on environmental conditions (horn fly pupae may over-winter in some temperate regions leading to synchronized emergence and fly swarms). Adult flies eclose from pupae and fly free in the environment during the day seeking hosts on which to feed (they do not survive more than a few days without a host). Once a suitable host is located, adult flies rarely leave the host unless to mate or lay eggs (although *Haematobosca* spp. spend less time on hosts than *Haematobia* spp.). Their reproductive organs mature over several days and mating commences. Both male and female flies feed on blood but females are anautogenous and require bloodmeals to complete their gonotrophic (ovarian) cycles. Females produce eggs 3-4 days after feeding and they may lay 80-100 eggs (sometimes up to 400) in their life-times. Adult flies only live for 1-3 weeks and their whole life-cycle may be completed in 10-14 days in optimal environmental conditions, but the cycle may be extended for several weeks in cooler weather (larvae do not hatch at temperatures below 11°C). Transmission from host-to-host occurs when newly-hatched adults search for hosts (sometimes flying up to 10 km), when female flies return to different hosts after laying eggs, and when flies transfer between hosts in close contact (at herding, mustering, mating, milking, etc.). Fly reproduction is continuous and most populations are multivoltine with multiple generations occurring each year (fewer in colder regions). Infestations appear seasonal and flies are more abundant in summer and autumn. *Haematobia* spp. occur in most cattle-producing regions around the world and their geographic distribution in temperate regions is often restricted to those with warmer winters (frosts kill over-wintering pupae).

Differential diagnosis: Infestations in livestock may be suspected on the basis of clinical signs (behavioural changes, skin lesions) and history (seasonal occurrence), but are readily confirmed by direct observation and identification of biting flies (small grey-black flies with thoracic stripes, overlapping wings and prominent proboscis with long palps). Other fly species associated with cattle may need to be discounted, such as stable flies, face flies and even house flies. Adult flies can be collected for examination by swatting, spraying, netting or trapping. A range of molecular biological techniques have been used to characterize species and populations following polymerase chain reaction (PCR) amplification of fly DNA (random amplified polymorphic DNA (RAPD), nuclear genes (ribosomal DNA), mitochondrial genes (cytochrome c oxidase) and even the whole genome for the horn fly). Other molecular characterization studies are investigating the diversity of bacteria associated with flies, including endosymbionts.

Treatment and control: Skin severely affected by fly bites may be treated on individual animals with topical or systemic glucocorticoids, antihistamines, antiseptics and antibiotics to relieve clinical signs (inflammation, pruritus) and combat secondary infections. Many producers resort to culling allergic cattle to improve herd resistance, but taking care not to confuse diagnoses (similar sores may be caused by other unrelated pathogens). Infestations on livestock may be combated using conventional and modern insecticides, applied as sprays, dips, dusts, pour-ons, impregnated tags, injectable or oral medications. Successful treatments have included a range of organochlorines, organophosphates, pyrethroids, carbamates, and macrocyclic lactones, but resistance to some insecticides in the first 3 categories have emerged in fly populations. Insecticides with longer residual activities have proven efficacious against persistent fly populations and the use of fly repellents (such as DEET) assists treatment. Treatment of the environment with residual insecticides has limited effect as flies reside on the hosts rather than on nearby substrates, and the treatment of dung pats is discouraged as insecticides may kill natural predators, parasitoids and parasites of flies. Several studies have shown that cattle given methoprene (topical, injectable or sustained-release boluses) produce dung pats that partially inhibit egg hatching and/or pupal eclosion, thus reducing fly populations. Alternatively, potential breeding sites may be reduced by improving pasture hygiene through dung removal, dung spreading, or introducing dung beetles. Fly traps may also be used around mustering or watering points where stock are trained to walk through darkened veiled tunnels which dislodges flies near sticky, insecticidal or electric baits. Recent studies on biological control have shown some promise with the identification of some predatory beetles, ants, wasps and other muscid larvae that kill larval and/or pupal stages, and observations that the bacterial insecticide *Bacillus thuringiensis* was highly toxic against larvae.

Haematobia





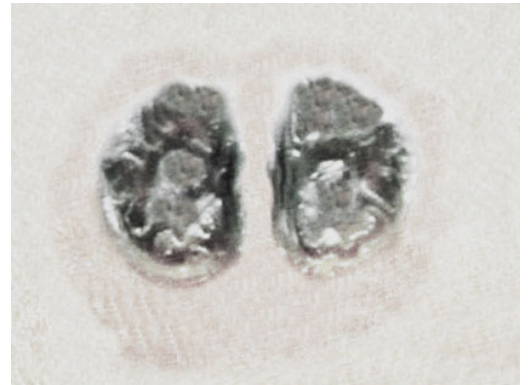
Haematobia adults



Haematobia adult



Haematobia larva



Haematobia adult