Gasterophilus
(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). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Gasterophiline larvae of *Gasterophilus* spp. develop from ingested eggs and attach to the mucosal surface of the gastrointestinal tract of horses where they may overwinter.

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:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Gasterophilinae (stomach bots)
Genus:	*Gasterophilus* (parasitic in stomach of equines)
Species:	various species cause stomatitis, ulceration

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 Hemipterodea (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 aristae, 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 myiases) (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 aristae), 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 ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (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). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	**Genera**	**Hosts**	**Strike**	**Myiasis***
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Gasterophilinae contains 5 genera classified in 4 tribes: Cobboldiini (genus *Cobboldia*), Gasterophilini (*Gasterophilus*, *Gyrostigma*), Neocuterebrini (*Neocuterebra*), and Rutteniini (*Ruttenia*). These large flies lay eggs which hatch larvae that invade the gastro-intestinal tracts of herbivores (wild and domestic ungulates). The genus *Gasterophilus* (syn. *Enteromyia, Enteromyza, Gastrophilus, Gastrus, Haemorrhoestrus, Rhinogastrophilus, Stomachobia, Progastrophilus*) contains 9 species whose larvae infect stomach and duodenum particularly of equids (horses, donkeys, mules, zebras), but also some large African wildlife (elephants, rhinoceroses) and occasionally other smaller domestic animals (e.g. deer, dogs, rabbits) and sometimes humans. These stomach bot flies are endemic in Palaearctic and Afrotropical regions, but those infecting horses have been spread around the world by numerous equine translocations. Humans become infected accidentally by ovipositing flies or by larval transfer when nuzzling pet or work horses.

***Gasterophilus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
G. flavipes (syn. *Oestrus*)	Perissodactyla: equid (donkey)	stomach	obligate myiasis	Eurasia
G. haemorrhoidalis (syn. *G. duodenalis, pallens, pseudohaemorrhoidalis, salutiferus, Oestrus*) (throat horse bot, lip bot, rectal horse bot)	Perissodactyla: equid (horse, Przewalski's horse, ass, donkey, mule, Burchell's zebra, mountain zebra); dubious record in Artiodactyla: cervid (reindeer)	buccal mucosa, tongue, stomach, duodenum, rectum	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. inermis (syn. *Gastrus*) (unarmed horse bot)	Perissodactyla: equid (horse, Przewalski's horse, ass, Burchell's zebra)	buccal mucosa, rectum	obligate myiasis (stomatitis, ulceration, anorexia)	Eurasia, Africa

G. intestinalis (syn. *G. equi, magnicornis, Oestrus bengalensis, equi p.p., gastricus p.p., gastrophilus, schwabianus*) (common horse bot, armed horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, mule)	buccal mucosa, tongue, stomach	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. meridionalis (syn. *Oestrus*) (non-spotted zebra bot)	Perissodactyla: equid (Burchell's zebra)	stomach	obligate myiasis	Africa
G. nasalis (syn. *G. albescens, clarkii, crossi, jumentarum, Gastrus subjacens, Oestrus equi p.p., fasciculosus, gastricus p.p., nasalis, salutaris, stomachinus, veterinus*) (nose horse bot, Linnaeus' horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, Burchell's zebra); dubious records in Artiodactyla: bovid (cattle, sheep, goat)	buccal mucosa, tongue, stomach, duodenum	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. nigricornis (syn. *G. viridis, Gastrus*) (broad-bellied horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass)	buccal mucosa, tongue, stomach, duodenum	obligate myiasis (stomatitis, ulceration, anorexia)	Asia, Middle-East
G. pecorum (syn. *G. gammeli, hammeli, selysi, vulpecula, Gastrus ferruginatus, jubarum, lativentris, Oestrus vituli*) (dark-winged horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, Burchell's zebra, Persian onager)	buccal mucosa, oesophagus, stomach	obligate myiasis (stomatitis, ulceration, anorexia)	Eurasia, Africa
G. ternicinctus (syn. *G. gedoelsti*)	Perissodactyla: equid (Burchell's zebra)	stomach	obligate myiasis	Africa

Parasite morphology: *Gasterophilus* spp. form 4 different types of morphological developmental stages: eggs, larvae, pupae and adults. The eggs are elongate and ellipsoidal measuring 1-2 mm long and are either white-yellow (e.g. G. intestinalis) or brown-black (e.g. *G. nasalis, G. haemorrhoidalis*). They are attached to host hairs by an attachment organ (either short and caudal, or elongate and ventral) and have a subterminal operculum (anterodorsal cap). Larvae (commonly called bots, or sometimes grubs) are initially fusiform but become cylindrical, with a narrow anterior head and a robust body tapering gradually to a truncated posterior. They are also initially white but turn red-orange (e.g. *G. intestinalis*) to yellow-green (e.g. *G. nasalis*) in color. They develop through 3 larval instars (L1-3) growing in size from 1-2 mm to 14-20 mm when mature. Larvae do not have any fleshy projections but they bear numerous body spines with blunt or sharp tips (muscoid larvae lack spines). The spines are pointed backwards and are arranged in 1-3 rows (one row in *G. nasalis*, and 2 rows in *G. intestinalis* and *G. haemorrhoidalis*) concentrated in bands at the edges of segments. The head is small (usually retracted) and lacks a sclerotized head capsule but has an internal cephalopharyngeal skeleton with prominent rasping mouthparts (mouth hooks). Larvae breathe using 2 pairs of respiratory spiracles: an small anterior pair that are often obscure (sometimes visible as small bunches of protruding tissue); and a larger posterior pair apparent as flat oval plates located within deep depressions in the caudal segment, Each plate with 3 elongate openings (2 on L1) that are characteristically curved (with a mid-elbow) in gasterophilines (other oestrid larvae form porous spiracular plates, while calliphorid larvae form plates with 3 slits surrounded by a peritreme). Mature larvae form puparia that are similar in size, shape and ornamentation to mature L3, but are somewhat shrivelled in appearance and dark brown-black in colour. The enclosed pupae transform into winged adults which eclose through a circular cap (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adult flies are large (11-15 mm long) with yellow to dark-brown bodies (resembling bumble-bees) covered dorsally with dense yellow-brown hairs and laterally with creamy-white hairs (but lacking stout bristles). Their bodies have 3 conspicuous tagma: a broad head; globular thorax; and ellipsoidal abdomen. The heads are bulbous (broad but flattened front-to-back), covered with smooth velvety hairs, and possess both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calyptrates). They have a pair of large brown compound eyes located laterally and separated by a large frons. They possess a pair of short anterior antennae, each composed of 3 dissimilar segments: a short basal scape; a short club-like pedicel; and an anterior flagellum composed of long slender tapered bristle (arista) which is bare (without setae but with small sparse microtrichia). The ventral mouthparts are small and non-functional (adults do not feed) with vestigial palps and proboscis evident as small yellow-brown knobs. The alimentary tract is rudimentary and may possibly be used for water regulation. The thorax is covered by a scutum with posterior lobe-like scutellum, both covered with fine dense setae forming transverse dark bands. A single vertical row of bristles is located on the thoracic meron (like other oestroids, but lacking on muscoid flies). The mesothorax bears one pair of wings with dark patches. The wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with Sc veins running parallel to the C vein, dm-cu cross-veins absent, and the M vein

extending to the outer trailing edge of the wing. Like all Diptera, a second pair of wings have been highly reduced to small club-like halteres thought to be used to stabilize flight. Like all calyptrate flies, the halteres are covered by hindlobes of the forewings (known as squammae or calypters), which in this case are small (other oestrids have large calypters). Similar to other oestrids, gasterophilines have bulbous swellings (greater ampulla) located beneath their wing bases. The ventral thorax gives rise to 3 pairs of long hairy legs, each comprised of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen is covered with fine dense setae arranged in light-dark patches, often appearing tricoloured with white hairs located on anterior segments, black hairs on middle segments and dark yellow hairs on posterior segments. Male flies have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct and retractable copulatory aedeagus and claspers. Female flies have 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva. Females have a strong protuberant ovipositor that is often held curved beneath the abdomen and mistaken for a sting.

Site of infection: Adult flies are not parasitic but free-living and free-flying. Females flies do seek vertebrate hosts, not to feed upon, but rather to deposit eggs on hair shafts. The emergent larvae are obligate endoparasites and can only complete their development after invading the gastro-intestinal tracts of equids (horses, donkeys, mules and even some zebra). First-stage larvae (L1) invade the oral mucosa and tongue and then migrate down the alimentary tract where L2 and L3 attach to the lining of the stomach (*G. intestinalis*), the anterior duodenum (*G. nasalis*) or the rectum (*G. haemorrhoidalis*). Some accidental infestations have been reported in humans in close contact with horses when L1 burrow into the skin causing sinuous tracks before dying.

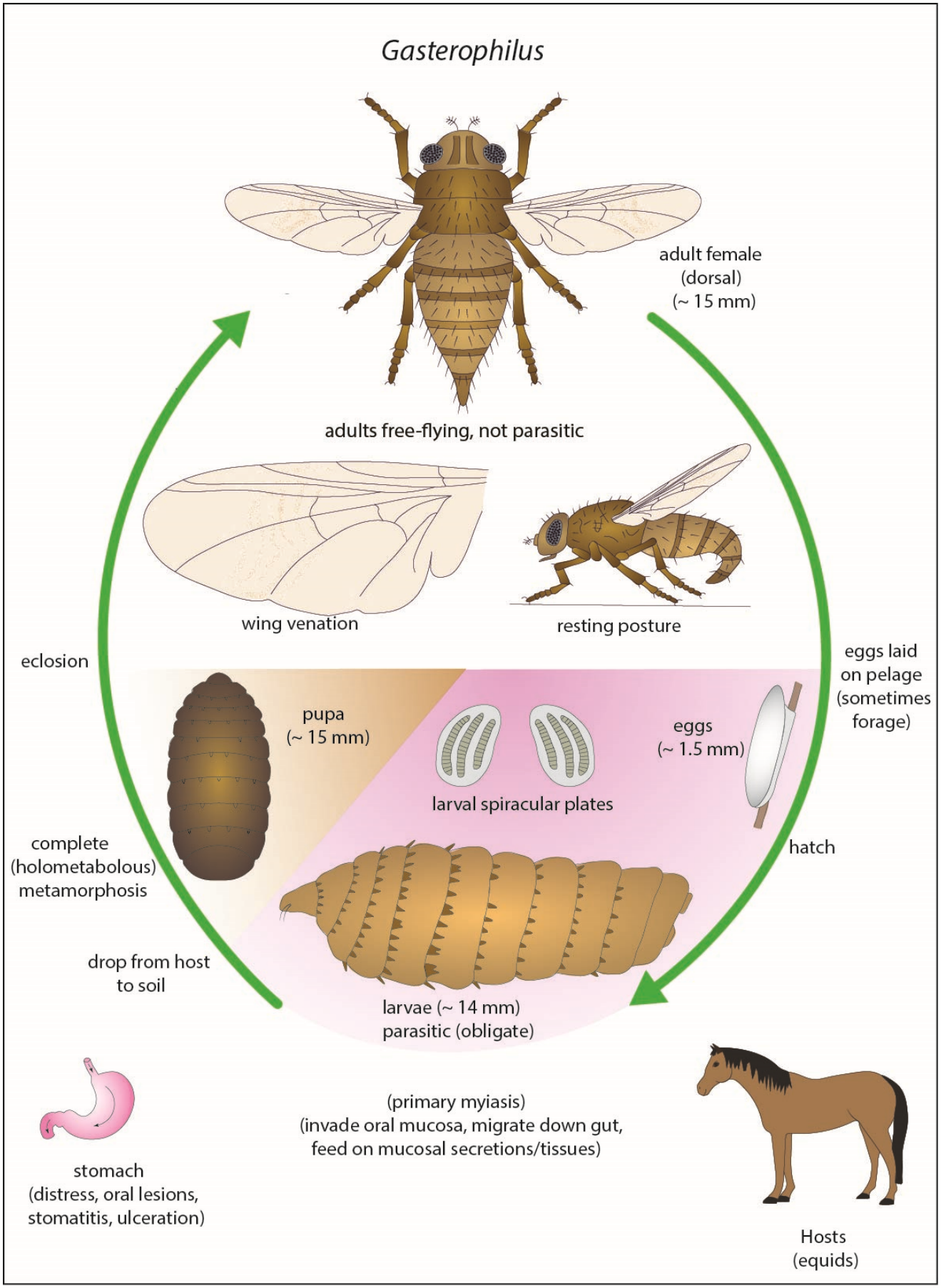
Pathogenesis: Despite the macabre spectre of having fly larvae residing within the gut, most infestations are well tolerated by hosts and clinical signs are rarely seen. Most equids appear to tolerate burdens of around 100 bots without apparent ill effects. Nonetheless, some pathology may be observed in 3 successive phases: firstly when ovipositing flies cause fly worry, secondly when invading L1 penetrate oral tissues; and thirdly when maturing larvae attach to the gut mucosa. Gravid female flies hover near their intended hosts and dart in to deposit eggs on hairs around the face, forelegs and belly. This hovering and dive-bombing behaviour may disturb some animals and cause aversive behaviours including panicky headlong flight (gadding) sometimes resulting in self-wounding. Female flies may also chase galloping horses and deposit eggs when they halt. The degree of fly worry varies for different fly species, with nearly all horse breeds reacting to *G. nasalis*, while usually only thoroughbreds and not draft breeds react to *G. intestinalis.* Eggs adhering to hairs may also irritate horses which then attempt to groom by licking (which in many instances stimulates the eggs to hatch). Larvae entering the mouth bury themselves in the buccal mucosa, gums and tongue where they may wander for around 28 days causing irritation, inflammation, excessive salivation and sometimes ulceration. Those penetrating the gums near molar teeth can cause pain upon mastication with chewing problems leading to loss of appetite and poor growth. Lesions are also prone to secondary bacterial infection, with the development of necrotic and pustular pockets and loosened teeth. Larvae then migrate down the gastro-intestinal tract taking up residence in specific locations, feeding on host tissues and secretions and developing through another 2 larval instars (L2-3). These stages typically attach to the mucosal lining of the stomach, duodenum and/or rectum, and remain immobile for 9-12 months (over-wintering inside their equid hosts). Their presence often does not cause any clinical signs, although a non-specific syndrome of unthriftiness, poor coat, mild colic and poor appetite has been ascribed to bot infestations. Large numbers of developing larvae have been associated with local inflammation, chronic gastritis, colic, epithelial sloughing, nodular mucosal proliferation, squamous cell tumours, obstructions, ulcerative erosions and abscesses, sometimes with stomach perforation, peritonitis and anaemia. Infestations with *G. pecorum* have also been associated with swallowing difficulties and obstructions (due to oesophageal inflammation, constriction and muscular hypertrophy), and those by *G. haemorrhoidalis* may occasionally cause rectal prolapse. Humans in close contact with horses may become accidentally infected when L1 invade the skin or eyes causing cutaneous myiasis (sinuous inflamed tracks, termed creeping myiasis) and ocular myiasis (irritation, conjunctivitis, corneal abrasions). Such infections are generally transient as the L1 cannot develop further in humans and usually die.

Developmental cycle and mode of transmission: Like all Diptera, these bot flies exhibit holometabolous development where eggs hatch grub-like larvae that undergo complete metamorphosis in pupae to form winged adults. Female flies are oviparous and attach eggs to hair shafts on equids, mostly around the face (*G. nasalis* under the chin, *G. haemorrhoidalis* on the nose, lips and mouth) but also on the forelegs, belly, shoulders, flanks and mane (*G. intestinalis*). Alternatively, a few species (e.g. *G. pecorum*) do not deposit eggs on hosts but attach them to plant leaves and stems liable to be consumed as forage. The eggs embryonate over 5-10 days and then hatch spontaneously (e.g. *G. nasalis* and *G. haemorrhoidalis*) or when licked (e.g. *G. intestinalis*) or when ingested with forage (e.g. *G. pecorum*). In moist conditions, eggs on forage may stay dormant for months until ingested. Hatching releases L1 that either crawl to the mouth or are ingested (crawling appears to stimulate host licking). They then penetrate the anterior end of the tongue, the buccal mucosa or the gums at interdental spaces. L1 wander in these tissues for approximately 28 days before moving to the stomach (nonglandular portion) and intestines (anterior duodenum or rectum) to mature. They moult to L2 just before or after arrival in the gut and then moult to L3 after approximately 5 weeks. Altogether, larvae may reside in hosts for up to 9-12 months, typically over-wintering in the host like other oestrid species (except the cuterebrines which overwinter as diapausing pupae). In late winter or early spring, mature L3 detach from the mucosa, pass through the intestines and exit the host with faeces. They burrow into the ground and form puparia by contraction and hardening of the integument. The enclosed pupae then transform into adults with pupation taking 3-10 weeks depending on the temperature (longer in colder conditions). Adult flies emerge from pupae and fly

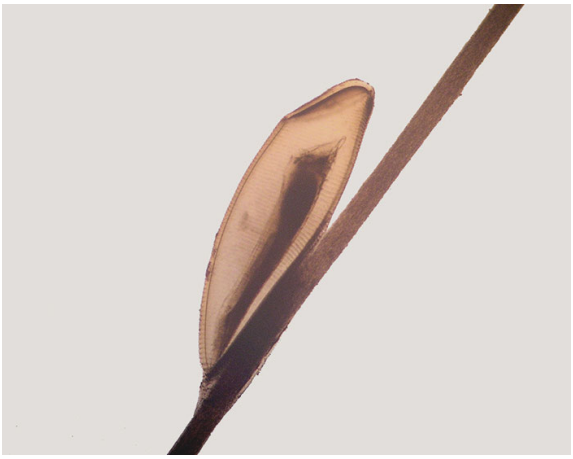
about searching for mates and hosts for their larvae (adult do not feed). Males fly to aggregation points (high ground) and wait to intercept passing females. Fertilized females are strong fliers and may fly long distances seeking hosts for oviposition using olfactory and visual senses. They have short lifespans and only live for 10-14 days, but can lay 150-1,000 eggs in that period (up to 2,500 for *G. pecorum* which deposits eggs on forage). Adult flies are active in summer during the daytime (usually early afternoon in warm sunny weather) and they are univoltine producing only one generation each year. They have a very broad distribution around the world, having been translocated to many countries with their equine hosts. Humans become infected accidentally either by ovipositing flies or by larval transfer when grooming or nuzzling pet or work horses.

Differential diagnosis: Most infestations are asymptomatic or remain subclinical and go undiagnosed. Even when clinical signs occur (unthriftiness, poor coat, mild colic, poor appetite), they are very non-specific and may be attributed to other aetiological agents or disease conditions. Infestations may be suspected when adult bot flies are observed bothering animals, or when fly eggs are detected on hairs around the face and legs. Diagnosis is made by the direct detection of larvae and their identification on the basis of their structural characteristics. However, the only stages accessible antemortem are L1 in mouth lesions and mature L3 freshly excreted in faeces. The detection of larvae developing in the oesophagus, stomach or intestines is generally made incidentally at postmortem. Clinicians have often resorted to using endoscopic techniques on particularly valuable horses to detect larvae attached to mucosal surfaces, but biopsies are not recommended as foreign material may leak into the circulation provoking allergic responses. Immunoserological tests (enzyme-linked immunosorbent assays) have been developed to detect specific host antibodies against larval extracts, with the advantage that cryptic infestations may be detected as larvae over-winter in hosts. A variety of molecular biological techniques have been used to characterize bot fly species, usually after polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA, haemoglobin-1) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Chemical insecticides are routinely used for chemotherapy and chemoprophylaxis, with a wide variety of formulations available as liquids, gels, pastes, boluses, feed additives, pour-ons, or injectables. Topical insecticides may be used regularly during fly season to discourage oviposition or kill emergent L1, but they are less effective against larvae already residing with the gastro-intestinal tract. Systemic insecticides may be used to kill bots in the buccal cavity as well as in the gastro-intestinal tract, with treatments usually conducted during autumn or early winter (after the first frost has killed the adult flies). Good efficacy has been reported for organochlorines (lindane, dichlorodiphenyltrichloroethane (DDT)), organophosphates (trichlorfon, chlorpyrifos, chlorfenvinphos, coumaphos, diazinon) but particularly for macrocyclic lactones (avermectins) which are highly effective against all larval stages. It is recommended that drugs be used selectively and judiciously to forestall the development of drug resistance (particularly to the avermectins which are also used to control helminthiases in horses). It has been noted that routine grooming during fly season can greatly reduce the incidence of myiasis, as fly eggs can be trimmed off hairs or dislodged using fine-toothed combs, and washing with warm water containing an insecticide can induce eggs to hatch and kill emergent larvae. Animal handlers should also practice good hygiene and adopt personal protective measures; including wearing insect repellents on skin and clothing, wearing rubber gloves when grooming animals, and refraining from nuzzling or kissing horses. It is also important to adopt good sanitation practices to remove and dispose of faeces which may contain mature L3 and prepupae. Horse faeces should be transported off-site so the mature larvae do not burrow into the surrounding soil to pupate.


Gasterophilus
adult female
(dorsal)
(~ 15 mm)
adults free-flying, not parasitic
wing venation
resting posture
eclosion
eggs laid
on pelage
(sometimes
forage)
pupa
(~ 15 mm)
eggs
(~ 1.5 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae (~ 14 mm)
parasitic (obligate)
(primary myiasis)
(invade oral mucosa, migrate down gut,
feed on mucosal secretions/tissues)
stomach
(distress, oral lesions,
stomatitis, ulceration)
Hosts
(equids)

Gasterophilus adult



Gasterophilus egg

Gasterophilus larvae

Gasterophilus adult