Glossina
(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). Glossinids (tsetse flies) have biting mouthparts and the base of the proboscis is bulbous. Both sexes are daytime blood-feeders on a variety of animals. Females are larviparous and pupiparous, depositing developed larvae in loose dry soil to undergo pupation. The sole genus *Glossina* only occurs in sub-Saharan Africa, and most species have been shown to transmit trypanosomes to animals (nagana) and humans (sleeping sickness).

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)
Superfamily:	Hippoboscoidea (pupa-bearers)
Family:	Glossinidae (tsetse flies, biting mouthparts, characteristic proboscis bulb, both sexes blood-feeders)
Genus:	*Glossina* (parasitic on skin of mammals)
Species:	various species cause irritation, pruritus, hypersensitivity

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). The superfamily Hippoboscoidea contains 4 families: Glossinidae (tsetse flies); Hippoboscidae (louse flies); Nycteribiidae (bat flies); and Streblidae (bat flies).

The family Glossinidae comprises the tsetse flies which are not dorso-ventrally flattened and have prominent biting mouthparts with a long bulbous proboscis embraced by long palps, antennal arista with short feathery hairs on the dorsal side only, and wings with uncrowded veins and a hatchet-shaped discal medial cell. Adult flies of both sexes feed on blood from a range of wild and domestic mammals (including humans), birds, and reptiles throughout sub-Saharan Africa. The single genus *Glossina* contains 23 species that have been allocated to 3 species-groups (now considered subgenera): the '*mortisans* group' (subgenus *G.* (*Glossina*)) occurring throughout East Africa and feeding mainly on savannah-dwelling mammals; the '*fusca* group' (subgenus *G.* (*Austenia*)) occurring throughout West and Central Africa feeding mainly on forest-dwelling animals; and the '*palpalis* group' (subgenus *G.* (*Nemorhina*)) being widespread throughout Africa in riverine and lacustrine environments and feeding mainly on local reptiles and mammals. A range of species are notorious for the transmission of haemoprotozoal trypanosomes causing serious diseases in domestic animals (nagana in cattle) and humans (sleeping sickness).

***Glossina* species**	**Hosts***	**Clinical signs [vectorial capacity]**	**Distribution**
Subgenus*: G.* (*Austenina*) ['*fusca* group'] (forest habitats)			
G. brevipalpis	Primates: hominid (human); Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, roan antelope, waterbuck, bushbuck, duiker), giraffid (giraffe), hippopotamid (hippopotamus), suid (warthog, bushpig); Proboscidea: elephantid (elephant); Perissodactyla: rhinocerotid (rhinoceros); Carnivora: hyaenid (hyena); Rodentia: hystricid (porcupine); Sauria: varanid (monitor); Aves (unspecified birds)	irritation [trypanosomiasis]	Central, East and South Africa
G. frezili	Artiodactyla: bovid (cattle)	irritation	Central Africa
G. fusca (incl. subspp. *congolensis, fusca*)	Artiodactyla: bovid (cattle, buffalo, waterbuck, bushbuck, duiker), suid (bushpig, red river hog); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	West, Central and East Africa
G. fuscipleuris	Primates: hominid (human), cercopithecid (baboon), Artiodactyla: bovid (cattle, buffalo, bushbuck), hippopotamid (hippopotamus), suid (warthog, bushpig, giant forest hog)	irritation [trypanosomiasis]	Central and East Africa
G. haningtoni	Artiodactyla: bovid (cattle)	irritation	West and Central Africa
G. longipennis	Primates: hominid (human); Artiodactyla: bovid (buffalo), giraffid (giraffe), suid (warthog); Perissodactyla: rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Struthioniformes: struthionid (ostrich)	irritation [trypanosomiasis]	East Africa
G. medicorum	Artiodactyla: bovid (cattle, bushbuck)	irritation	West, Central and East Africa
G. nashi	Artiodactyla: bovid (cattle)	irritation	Central and South Africa
G. nigrofusca (incl. subspp. *nigrofusca, hopkinsi*)	Primates: hominid (human); Artiodactyla: bovid (cattle, bushbuck), suid (pig); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	West, Central and East Africa
G. schwetzi	Artiodactyla: bovid (cattle)	irritation	Central and South Africa
G. severini	Artiodactyla: bovid (cattle)	irritation	Central Africa

G. tabaniformis	Primates: hominid (human); Artiodactyla: bovid (cattle, buffalo, sheep, goat, bushbuck, duiker), suid (pig, warthog, bushpig, red river hog); Perissodactyla: equid (donkey); Rodentia: hystricid (porcupine); Sauria: varanid (monitor)	irritation [trypanosomiasis]	West, Central and South Africa
G. vanhoofi	Artiodactyla: bovid (cattle)	irritation	Central Africa
Subgenus*: G.* (*Glossina*) ['*morsitans* group'] (savannah habitats)			
G. austeni	Primates: hominid (human); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, kudu, bushbuck, duiker, suni), hippopotamid (hippopotamus); Proboscidea: elephantid (elephant); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	East and South Africa
G. longipalpis	Primates: hominid (human, chimpanzee); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, bushbuck, duiker); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine); Aves (unspecified birds)	irritation [trypanosomiasis]	West and Central Africa
G. morsitans (incl. subspp. *centralis, morsitans, submorsitans*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, sable antelope, kudu, waterbuck, hartebeest, impala, bushbuck, reedbuck, gazelle, duiker, oribi, puku), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: equid (donkey, zebra), rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. pallidipes	Primates: hominid (human, chimpanzee); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, oryx, kudu, waterbuck, wildebeest, hartebeest, impala, bushbuck, reedbuck, gazelle, duiker), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: equid (donkey), rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: felid (cat), hyaenid (hyena); Rodentia: hystricid (porcupine); Sauria: varanid (monitor); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. swynnertoni	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, kudu, waterbuck, hartebeest, topi, impala, bushbuck, reedbuck, gazelle, duiker, steenbok), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Tubulidentata: orycteropodid (aardvark); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	East Africa
Subgenus*: G.* (*Nemorhina*) ['*palpalis* group'] (riverine habitats)			
G. caliginea	Primates: hominid (human)	irritation [trypanosomiasis]	West and Central Africa
G. fuscipes (incl. subspp. *fuscipes, martinii, quanzensis*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, waterbuck, bushbuck), hippopotamid (hippopotamus); Carnivora: canid (dog); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Serpentes (unspecified snake); Testudines (unspecified tortoise)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. pallicera (incl. subspp. *pallicera, newsteadi*)	Primates: hominid (human); Artiodactyla: suid (pig), bovid (sheep, goat, bushbuck); Rodentia: hystricid (porcupine); Anura (unspecified amphibians)	irritation [trypanosomiasis]	West and Central Africa
G. palpalis (incl. subspp. *gambiensis, palpalis*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, roan antelope, wildebeest, hartebeest, bushbuck, duiker, oribi), hippopotamid	irritation [trypanosomiasis]	West, Central and South Africa

	(hippopotamus); Perissodactyla: equid (donkey); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Crocodilia: crocodylid (crocodile)		
G. tachinoides	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog), bovid (cattle, buffalo, sheep, goat, roan antelope, waterbuck, bushbuck, duiker), hippopotamid (hippopotamus); Carnivora: canid (dog), felid (cat); Rodentia: hystricid (porcupine); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Crocodilia: crocodylid (crocodile); Serpentes (unspecified snake); Aves (unspecified birds)	irritation [trypanosomiasis]	West, Central and East Africa

*Host records include observations of tsetse flies feeding on natural, experimental and bait hosts, as well as host groups identified by molecular analyses of tsetse bloodmeals.

Parasite morphology: Tsetse flies form 4 different types of developmental stages (eggs, larvae, pupae and adults) but the eggs and larvae develop within the uterus of adult female flies. Eggs develop one at a time in the uterus and are ovoid in shape and around 1.6 mm long. A first stage larva (L1) emerges using an anterior labral tooth to break the egg chorion. The larva is supported against the ridged uterine wall by a membranous choriothete and secretions from the milk glands pool around the larval mouth to be ingested. Larvae are ellipsoidal cream-yellow segmented stages with a pair of respiratory lobes developing at the posterior end and gradually darkening to black. Larvae develop through 3 instars (L1-3), initially measuring around 1.8 mm but growing up to 7-8 mm in length. Mature L3 deposited on soil by gravid females burrow into the substrate and form a puparium by hardening of the tegument before moulting to form a pupa. These stages measure 5-7 mm long and are ovoid with distinctive posterior lobes. Following metamorphosis, winged adult flies emerge from pupae. Adult tsetse flies have narrow bodies that are not dorso-ventrally flattened and vary in colour from yellow-brown to brown-black. Adults range in size from 5-15 mm in length, depending on species, although those belonging to different groups often overlap: e.g. 8-11 mm long for *palpalis* group (generally recognized by dark brown hindtarsi), 7-10 mm for *morsitans* group (with striped dorsal abdomen); 9-12 mm for *fusca* group (with dark wings and long narrow palpi); the latter often including a *brevipalpis* subgroup measuring 10-14 mm (with pale wings and short palpi). The body of the adult fly has 3 conspicuous tagma: a small head, ovoid thorax, and conical abdomen. Both sexes have broad triangular heads with frontal ptilinal sutures (like all muscoids), 2 large brown-red compound eyes well separated laterally, short feathery antennae and prominent forward-projecting mouthparts. Each antenna is composed of 3 dissimilar segments: a short basal scape; a square middle pedicel; and a longer rectangular and curved apical flagellum characteristically with a large dorsal bristle (arista) with 17-29 short dorsal feathery (branched) setae (hairs). The mouthparts are evident as a long rigid proboscis embraced by pair of long palps. The proboscis has a unique swollen bulbous base and is composed of 2 elongate stylets (labrum and hypopharynx) protected ventrally by a rigid labium which has apical labella armed with teeth. When feeding, the labrum and hypopharynx form a food canal and the hypopharynx also contains a hollowed groove to deliver saliva into the bite site. Blood is sucked up by the strong muscular pharynx into the tubular oesophagus leading to a globular proventriculus with associated crop. The proventriculus secretes a peritrophic membrane that lines and protects the digestive midgut which contains endosymbiotic enterobacteria which are essential for vitamin B metabolism (flies without bacterial symbiotes cannot complete reproduction). Digestive waste is passed to the hindgut (connected to Malpighian excretory tubules), rectum and terminal anus. The large thorax is covered by a dorsal scutum that is usually dull light brown-grey with dark mottled patterns. The thorax has distinctive patterns of setation: all species having a hypopleuron without rows of stout setae, whereas the pteropleuron bears a few strong bristles in the *fusca* group, but only contains setulose hairs in the *palpalis* and *morsitans* groups. Additionally, the hairs fringing the thoracic squamae in the *fusca* group are numerous and curly (imparting a woolly appearance), while those in the *palpalis* and *morsitans* groups are not curly but have a neat fringe-like appearance. The mesothorax bears a pair of membranous wings that are hyaline to dusky depending on the species. Wing membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] characteristically with the M vein curving anteriorly to form a distinctive hatchet-shaped discal cell. At rest, the wings are folded flat and scissor like over the abdomen. Like all Diptera, tsetse flies have a second pair of wings that are highly reduced to knob-like halteres used to stabilize flight. Tsetse flies are also identified as calyptrate flies in that they have posterobasal wing lobes (calypters) that cover the halteres. The ventral thorax gives rise to 3 pairs of legs, each with 5 segments (coxa, trochanter, femur, tibia, and tarsus), with the latter having 5 tarsomeres terminating in 2 claws and 2 small pads (pulvilli). The legs vary considerably in colouration, but all segments of the hind-tarsi are dark brown-black in the *palpis* group, whereas only the distal segments are dark in the *morsitans* group. The abdomen is globular, often wider than long, and the membranous segments are highly expandable being able to accommodate large bloodmeals. The abdomen is often dull light brown-grey and usually marked by conspicuous dark stripes or patches imparting a mottled appearance. The terminal abdominal segments bear external genitalia that differentiates males (with a prominent dorsal button-like hypopygium) and females (without hypopygium, but with larvipositor). Males have 2 testes connected by vas deferens to a seminal vesicle leading to a tubular ejaculatory duct. The hypopygium contains an extendable phallosome and 2 pairs of copulatory claspers (superior claspers long in *fusca* group, medium in *palpis* group, and short in *morsitans* group). Females have 2 ovaries (but each with only 2 ovarioles) that are joined to oviducts forming a common duct that expands to form a uterus that accommodates one embryo at a time. The uterus, with associated spermatheca (for sperm storage) and branched accessory (milk) glands, leads to the vulva and the tip of the abdomen is elongated to form a larvipositor.

Site of infection: Adult tsetse flies are ectoparasitic and both female and male flies feed on host blood, usually biting areas where the skin is soft (neck, ears, face, feet, ankles, legs, wrists, arms). Different tsetse species have preferred hosts (particularly suids and bovids), but may feed on other hosts in the vicinity (such as elephants, hippopotamuses, porcupines, aardvarks, primates (including humans), some reptiles and birds), yet steadfastly avoiding others (e.g. zebras and wildebeest). Biological and ecological differences have been used to assign all *Glossina* spp. to 3 species-groups (now considered subgenera): the '*mortisans* group' (subgenus *G.* (*Glossina*)) feeding mainly on savannah-dwelling mammals (especially artiodactyls such as buffalo, bushbuck, kudu, duiker, springbok, giraffe, warthogs, bushpigs, rhinoceros); the '*fusca* group' (subgenus *G.* (*Austenia*)) feeding mainly on forest-dwelling animals (bushbuck, buffalo, cattle, giraffe, rhinoceros, elephant, hippopotamus, bushpig, river hog, porcupine, aardvark and even ostrich); and the '*palpalis* group' (subgenus *G.* (*Nemorhina*)) feeding mainly on reptiles (crocodiles, water monitors) and mammals (bushbuck, oxen, smaller mammals, humans) visiting watering sources.

Pathogenesis: Feeding tsetse flies first probe host skin with their stout proboscis, and then use labellar teeth on the end of the labium to penetrate the skin and lacerate dermal tissues with strong back-and-forth movements of the head. Ruptured capillaries haemorrhage into the wound and flies suck up pooled blood through a food canal formed by the labrum and hypopharynx. Feeding is aided by the injection of saliva containing anticoagulants via a hypopharyngeal groove. Both sexes feed every 4-5 days and they engorge in 1-10 minutes unless disturbed and imbibe up to 0.03 ml of blood (which doubles or triples their unfed body weight). Heavy infestations may cause blood loss severe enough to manifest as anaemia, but most attacks are not so severe. Tsetse bites are painful due to the traumatic structural damage and ensuing inflammation with bite sites becoming red, swollen and itchy. This causes significant discomfort to the host which may resort to licking, scratching or rubbing behaviours to seek relief, sometimes resulting in self-trauma exacerbating wounds and making them susceptible to secondary bacterial infections. Inflammatory lesions slowly dissipate over days but can remain tender for several weeks. Livestock subject to intermittent and constant attack may exhibit considerable fly-worry and biting-stress leading to reduced feeding efficiency, decreased performance and loss of productivity in terms of meat and milk production. Individual hosts may also develop allergic reactions to fly saliva components, with both immediate and delayed hypersensitivity reactions, and sometimes anaphylaxis, occurring after repeated bites. In Africa, tsetse flies are notorious as biological vectors for haemoprotozoan parasites, notably *Trypanosoma* spp. that cause nagana in cattle and sleeping-sickness in humans. Tsetse flies have been instrumental in limiting the establishment and development of livestock industries on the African continent, as most introduced ungulates are highly susceptible to trypanosomiasis while native wildlife are largely trypanotolerant and act as reservoirs of infection for domestic animals.

Trypanosomiasis	**Hosts**	**Main *Glossina* vectors**
Trypanosoma brucei gambesiense (West African sleeping sickness)	humans	*G. fuscipes, palpalis, tachinoides*
Trypanosoma brucei rhodesiense (East African sleeping sickness)	humans, cattle, antelopes	*G. morsitans, pallidipes, swynnertoni*
Trypanosoma brucei (nagana)	domestic animals, antelopes, warthog, lion, hyena	*G. fuscipes, longipalpis, morsitans, palpalis, pallidipes, tachinoides*
Trypanosoma vivax (nagana, souma)	domestic animals, antelopes, giraffe, warthog, zebra, lion	*G. morsitans* group*, fuscipes, palpalis, tachinoides, vanhoofi*
Trypanosoma suis	pigs, warthog	*G. brevipalpis, vanhoofi*
Trypanosoma congolense	domestic animals, antelopes, giraffe, bushpig, elephant, zebra, lion, hyena	*G. morsitans* group*, brevipalpis, fuscipes, palpalis, tachinoides, vanhoofi*
Trypanosoma simiae	pig, warthog, camel, cattle, horse	*G. austeni, brevipalpis, fusca, fuscipleuris, longipalpis, morsitans, pallidipes, palpalis, tabaniformis, tachinoides, vanhoofi*
Trypanosoma uniforme	domestic animals, antelopes, giraffe	*G. fuscipes, palpalis*

Developmental cycle and mode of transmission: Tsetse flies undergo holometabolous (complete) metamorphosis, whereby grub-like larvae transform in pupae into winged adults. Their cycle, however, differs from many flies in that females retain single eggs in the uterus where they hatch and moult through 3 larval stages (L1-3) before being laid. Larvae are sequestered in pouches against the uterine wall and nourished by milk gland secretions. This reproductive behaviour is described as adenotrophic viviparity (= "gland-fed, live-birth") with female flies being larviparous and birthing mature L3 (although a few texts state that females are pupiparous as they only release larva they are ready to pupate). During a gonotrophic cycle, eggs are released one at a time from the ovary (from alternate ovaries in subsequent cycles) and fertilized in the oviduct with sperm stored from previous matings. The egg is retained in the common oviduct which is expanded posteriorly to form the uterus. Embryogenesis occurs over 1-4 days and the resultant L1 then hatches using an egg tooth to rupture the egg wall. The larva is retained in the uterus in a membranous pouch where it respires through unique posterior polypneustic lobes and fed on secretions from specialized maternal accessory (milk) glands. The larvae grow and moult to L2 in 1-2 days and then to L3 in 2-5 days. Mature L3 grow so large that they occupy and grossly distend the abdomen. Some 7-12 days after fertilization, female flies deposit (larviposit) the solitary mature L3 on loose

sandy soil shaded by trees or other vegetation. Larvae are negatively phototactic and positively thigmotactic and immediately burrow 15-25 mm below the soil surface to form an immobile puparium by hardening of the integument. Several hours to days later, moulting occurs within the puparial case to form a true pupa. Pupation generally takes 30 days but may be extended for another 3-7 weeks in adverse environmental conditions. Adult flies eclose from pupae through a circular puparial cap using an eversible inflatable head pouch (ptilium). Teneral adults push their way to the surface of the ground to rest before taking flight. Both male and female flies feed exclusively on vertebrate blood, and it generally takes several days and a few bloodmeals before the fly cuticle hardens and the thoracic flight muscles fully develop. Obtaining nutrition from bloodmeals is assisted by enterobacterial symbionts in the midgut (*Wigglesworthia* in bacteriocytes), the symbiosis being mutualistic (obligatory for fly nutrition and fecundity). [Note that other bacterial endosymbionts also occur (*Sodalis* in various tissues, and *Wolbachia* mainly in reproductive tissues) but are not essential for fly survival]. Female flies are sexually receptive soon after emergence, but males require several bloodmeals before they become fertile. During mating, sperm is transferred in a spermatophore and stored in female spermathecae (females are fertile for life after a single mating, but they often mate more than once). Males mate once or twice and only live for 2-3 weeks. Females are anautogenous and require bloodmeals in order to complete their gonotrophic (ovarian) cycles. While females usually live for 20-40 days, sometimes up to 3-4 months, they generally only produce 2-3 offspring during their life-times. Adult tsetse flies search for hosts for only a few hours during the day flying up to 1 km, and spend the remaining time sheltering in shaded places such as trees or bushes. They are attracted to their hosts mainly by chemical (esp. expired carbon dioxide) then visual (shapes, contrasting colours, movement) cues, and are able to follow odour plumes upwind for 100-200 m before zeroing in on hosts. Flies vary in their seasonal abundance, often coinciding with the availability of hosts, but may not be present throughout the whole year. Their geographic distribution in so-called fly belts differs according to species; with those in the *fusca* group inhabiting forest ecosystems along coastal West Africa and Central Africa; those of the *mortisans* group distributed throughout inland savannah regions adjacent to coastal forests (often in close association with herds of herbivores migrating over African plains), and those of the *palpalis* group found along rivers, lakes and streams throughout East, Central and West Africa.

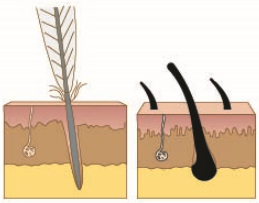
Differential diagnosis: Clinical signs exhibited by humans and animals bitten by tsetse flies are nonspecific (painful pruritic lesions) and may be attributable to other ectoparasites (including stable flies, horse flies, and clegs). Diagnosis is generally made by direct observation of feeding tsetse flies, and confirmed by capturing specimens for microscopic examination and identification. At rest, tsetse flies fold their wings flat one over the other over the abdomen, while other flies hold their wings in different attitudes. Under magnifying lenses, the wings of tsetse flies possess a distinctive hatchet-shaped discal cell not found in any other flies. Tsetse flies also have a prominent forward-projecting proboscis and feathery drooping antennae. The differentiation of tsetse species is based on a range of small morphological differences, particularly involving patterns of setation and colouration of various body parts. Various biochemical and genetic techniques have been used to characterize tsetse fly species, including matrix-assisted laser desorption/ionisation (MALDI) spectroscopy and isoenzyme electrophoresis. More recently, molecular biological techniques have been applied not only to the identification of tsetse bloodmeals but also to the characterization and phylogeny of tsetse fly species, particularly those acting as vectors for trypanosomes, or those hosting enterobacterial symbionts. Polymerase chain reaction (PCR) protocols have been used to amplify nuclear and mitochondrial gene sequences, with genomic databases being established from hybridization and fingerprinting studies.

Treatment and control: Fly bites may be treated using topical or systemic anti-inflammatory and anti-pruritic preparations to alleviate symptoms, antihistamines to moderate allergic reactions, and even antiseptics and antibiotics to prevent or curtail secondary infections. Most treatment and control programmes target adult tsetse flies as they are the only parasitic stages (even carrying eggs and larvae to term), whereas free-living pupae are encysted in soil. Insecticides have basically been used in 4 different ways: as topical or systemic preparations to treat livestock at risk; as aerial preparations to kill flying adults in the environment; as residual sprays to treat fly resting sites on vegetation; and as killing agents in traps and baits. Studies have reported variable successes with most insecticide groups: including inorganic metal-based formulations (sulphur, arsenate and copper compounds), organochlorines (dichlorodiphenyltrichloroethane (DDT), lindane, dieldrin, endosulfan), organophosphates (fenitrothion, iodofenphos, tetrachlovinphos, naled, crotoxyphos, chlorfenvinphos, fenthion, pirimetaphos, azamethiphos), carbamates (carbaryl, methylcarbamate, bendiocarb, propoxur), pyrethroids (deltamethrin, resmethrin, bioresmethrin, cismethrin, permethrin, cypermethrin, dimethylcyclopropanecarboxylates) and macrocyclic lactones (spinosad); with endosulfan, dieldrin and deltamethrin proving particularly effective. No appreciable insecticide resistance has been reported in tsetse fly populations, but treatment programmes have changed over decades due to environmental concerns about some compounds (particularly DDT which has now largely been discontinued). Many insecticides used to treat livestock do not have long-lasting activity, so they need to be reapplied at regular intervals, although some pyrethroids have good residual activity and need only be used once (effectively transforming animals into live baits). It is to be remembered that these insecticides are not deterrents or repellents and do not prevent fly bites, but flies coming into contact with therapeutic doses on the skin or in the blood have reduced vigour and survival, thus depleting local populations. Unfortunately, attempts to treat wild animals, acting as reservoir hosts for both tsetse flies and trypanosomes, have largely proven ineffective due to the sheer numbers involved, their wide dispersed distributions and their relative inaccessibility. Various aerial-based programmes have been developed to disperse insecticides into the environment as aerosols in space sprays, using thermal exhaust or rotary atomiser equipment in helicopters or fixed-wing aircraft. Spraying may only be carried out in suitable meterological conditions (avoiding wind and rain) and is generally ineffective in forested terrains. Other problems have been encountered with spray composition (many need to be emulsified in oil), incorrect droplet sizes (dissipate when too small, fall to ground or only on top of vegetation when too big), variable residual activity (many need to be regularly reapplied) and

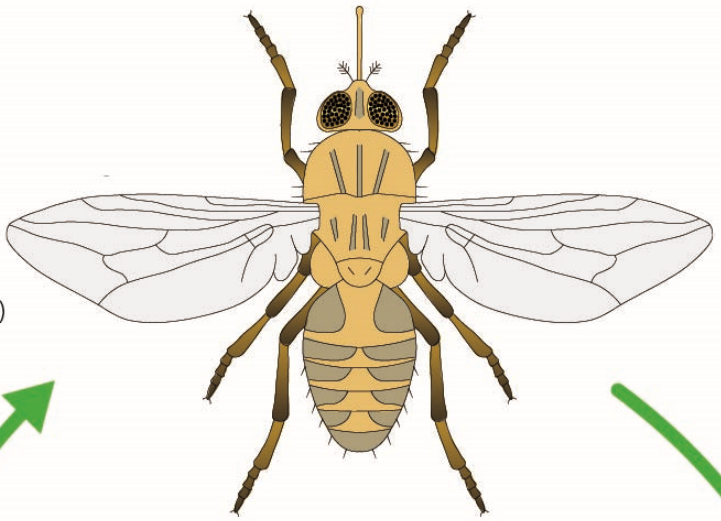
environmental concerns (untoward impacts on local ecosystems, particularly involving water, thus caution is required when targeting riverine tsetse species). Many African countries have adopted ground-based spraying programmes where insecticides with good residual activity are applied to sites where flies rest (teneral adults rest on shady soil, mature adults rest underneath leaves, twigs and branches of trees, bushes and other vegetation). Hand-spraying may be done on foot using knap-sacks or from vehicles using mechanized broadcasters. Comparative studies demonstrated that the selective application of sprays to soil and vegetation in hot-spots around villages, pens and water sources often had greater effect that indiscriminate spraying. Various ingenious traps and baits have been developed that use chemical and visual attractants (carbon dioxide, shapes and colours imitating ungulates) to lure tsetse flies onto surfaces treated with residual insecticides. Good success has been reported in small areas using blue-black cloth soaked in pyrethroids and mounted on box frames, but they generally require costly maintenance particularly during rainy/stormy seasons. Other efforts to control fly populations near villages and farms involved habitat destruction (by clearing land) and excluding reservoir hosts (by fencing or culling), but despite initial benefits these strategies have been discontinued due to increasing concerns regarding the conservation of wildlife and ecosystems. Promising results have been achieved by releasing cultured male flies that have been sterilized by irradiation or chemical means, but they were sometimes not competitive enough for mates to markedly reduce fly populations. Humans may enhance their personal protection by wearing thicker clothing (neutral-coloured long-sleeved shirts and pants), applying insect repellents to bare skin and clothing (although most have proven poorly effective against tsetse), installing fly screens and bed nets in households, and changing work patterns to avoid flies during the hottest part of the day when they seek shelter in forests, bushlands and riverine vegetation (exposure to flies is directly linked to certain activities like forestry and fishing). Future studies may also explore methods for the biological control of tsetse flies using natural predators or pests, which include wasps, ants, bombyliids and beetles that kill pupae, as well as spiders, dragonflies, assassin flies and wasps that prey on adult flies. Many countries across Africa utilize multiple integrated approaches to control tsetse flies to curb the ravages of human and animal trypanosomiases, with education programmes helping to raise public awareness and participation.

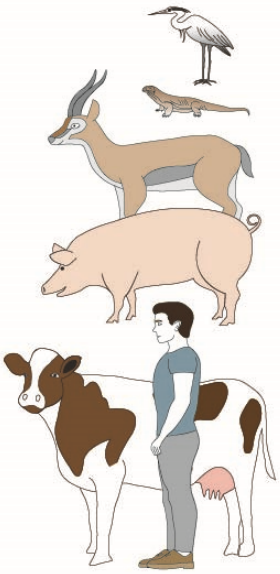
Glossina

adult female
(dorsal)
(~ 10 mm)



skin
(blood loss, irritation,
lesions, pruritus, allergy)
(vectors for infectious
microbial diseases)

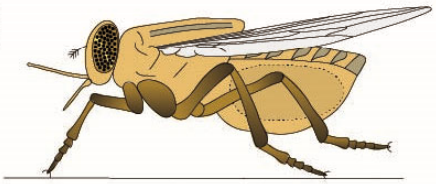




Definitive Hosts
(mammals, birds,
reptiles)

adults free-flying and transient ectoparasites
(females require bloodmeal for reproduction)

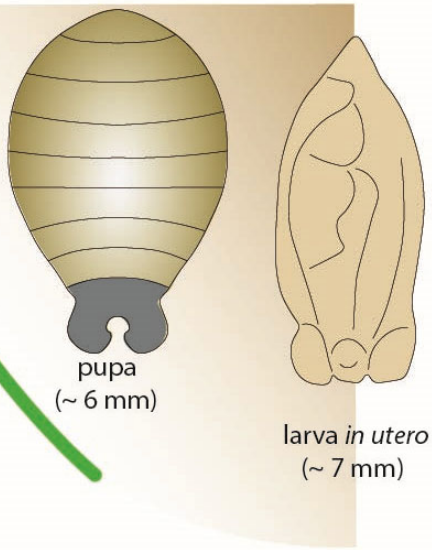
wing venation



resting posture

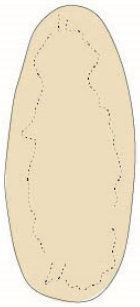
eclosion

eggs
in utero
larvate



pupa
(~ 6 mm)

larva *in utero*
(~ 7 mm)



egg *in utero*
(~ 5 mm)

complete
(holometabolous)
metamorphosis

adult females larviparous, deposit
larvae in loose dry shaded soil

Glossina adults

Glossina adult

Glossina adult

Glossina adult