Cochliomyia*, *Chrysomya
(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). Calliphorids (blow flies) are not parasitic as adults but their larvae help destroy carcasses and may cause traumatic cutaneous myiases (flystrike, screwworm infestation) in live mammals. Adult flies are large and often metallic in colour. Eggs laid on hosts release larvae which may penetrate the skin to feed on subcutaneous tissues. Most species are facultative invaders causing primary, secondary or tertiary strike, although several (notably screwworms) are obligate parasites. Larvae of *Cochliomyia* (primary screwworm) and *Chrysomya* (Old World screwworm) enter through mucous membranes and wounds in a range of mammals and cause serious life-threatening lesions.

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:	Calliphoridae (blow flies, often metallic, larvae cause myiases (flystrike/screwworm infestation))
Genus:	*Cochliomyia* (primary screwworm) (parasitic on skin/subcutaneous tissues of mammals)
Genus:	*Chrysomya* (Old World screwworm) (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause myiases in animals

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 contains 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, written as two words to distinguish them from other fly-like insects with compound names such as dragonflies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Calliphoridae is characterized by blow flies with metallic iridescent bodies (blue-black, violet-blue, green), strong bristles, well-developed mouthparts and antennae, and weak post-scutellum. The family contains over 1,100 species of blow flies, carrion flies, bluebottles, greenbottles and cluster flies which help destroy carcases, although many species have been implicated in larval myiasis ('flystrike') in living animals. Most invasions are facultative (opportunistic) causing primary, secondary or tertiary flystrike (categorized according to whether they initiate strike or occur later), although several species (notably screwworms) are obligate parasites whose larvae must develop in flesh. The larvae of most blow fly species are not selective feeders and they exhibit broad host specificity, usually for mammals, occasionally birds and less commonly amphibians and reptiles. Myiasis-causing flies have been found worldwide, particularly in temperate and tropical regions with large domestic livestock populations, but also in cooler regions where wildlife abound. Some 75 genera have been described in 11 subfamilies: Ameniinae, Aphyssurinae, Auchmeromyiinae, Calliphorinae, Chrysomyinae, Helicoboscinae, Melanomyinae, Mesembrinellinae, Phumosinae, Rhiniinae and Toxotarsinae, with another 14 unplaced genera and several fossil genera. The subfamily Chrysomyinae comprises blow flies distinguished by setose stem veins, and 2 tribes are recognized : Chrysomyini with 8 genera (including *Chrysomya* and *Cochliomyia*); and Phormiini with 6 genera.

Family	Genera	Hosts	Strike	Myiasis*
Calliphoridae	*Lucilia*	mammals	primary	Facultative (AU, CU, GI, NP, TR, UG)
	Calliphora	mammals	secondary	Facultative (AU, CU, GI, NP, TR, UG)
	Cochliomyia	mammals	primary, secondary	Facultative or obligate (TR)
	Chrysomya	mammals	primary, secondary	Facultative or obligate (TR)
	Cordylobia	mammals	primary	Obligate (CU, TR)

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

Several genera in the subfamily Chrysomyinae have medical and veterinary significance as larval stages cause debilitating myiases (notably *Chrysomya, Cochliomyia, Compsomyiops, Phormia, Protophormia, Protocalliphora*). The genus *Chrysomya* (syn. *Achoetandrus, Ceylonomyia, Chrysomja, Crysomya, Pycnosoma, Pycnosomops*) contains 38 species recorded as carrion-feeders or as obligate or facultative invaders of domestic animals and humans, including the notorious screwworms and the bird-nest blow flies. Several species commonly cause facultative fly strike in sheep around the world (e.g. *Ch. rufifacies, Ch. micropogon* (*mallochi*) and *Ch. varipes* renowned as secondary strike flies), while one species (the Old World screwworm *Ch. bezziana*) causes obligate myiasis in animals and humans, usually invading through wounds. Several species have proven to be important in forensic science as their proclivities for corpses and their regular life cycles allow investigators to retrospectively predict time of death. The genus *Cochliomyia* contains 4 species, with their screwworm larvae infesting numerous animal species, including humans, throughout the American tropics. Different species feed either on living tissue (e.g. the primary or New World screwworm *Co. hominivorax*) or necrotic tissue (e.g. the secondary screwworm *Co. macellaria*).

Parasite species	Hosts	Location	Clinical signs (vectorial capacity)	Distribution
Cochliomyia				
Co. aldrichi	Mammalia (various domestic and wild animals, plus carrion)	skin (wounds)	necrophagous, secondary facultative myiasis	Americas
Co. hominivorax (syn. *Callitroga americana*) (New World screwworm, American screwworm, primary screwworm)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other wild and domestic animals)	skin (orifices, wounds)	obligate myiasis [cavernous lesion, liquefaction, necrosis, haemorrhage]	Americas
Co. macellaria (syn. *Co. violacea*) (secondary screwworm)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other domestic animals and wildlife, plus carrion)	skin (wounds)	secondary facultative myiasis [forensic applications] (mechanical vectors for botulism in birds, salmonellosis, poliomyelitis and swine influenza)	Americas
Co. minima	Mammalia (various domestic and wild animals, plus carrion)	skin (wounds)	necrophagous, primary or secondary facultative myiasis	Americas
Chrysomya				
Ch. albiceps (syn. *Ch. indica, Compsomyia flaviceps*) (hairy-maggot blow fly)	Mammalia (various domestic and wild animals); carrion (pig, rat)	skin	necrophagous, secondary facultative myiasis [forensic applications]	Africa, Mediterranean, Americas
Ch. bezziana (Old World screwworm)	Artiodactyla: bovid (cattle, sheep); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other domestic and wild animals)	skin (orifices, wounds)	obligate myiases [cavernous lesions, liquefaction, necrosis, haemorrhage]	tropical Africa, Asia, India
Ch. cabrerai	traps			South-East Asia
Ch. chani	carrion (monkey, pig, rabbit, incl. human cadavers)		necrophagous	South-East Asia
Ch. chloropyga (syn. *Ch. costata, dejeanii, epanalepsis, lalandii, sensua, soror, trygaea*)	Artiodactyla: bovid (sheep); carrion (pig, impala), dung		necrophagous, secondary facultative myiasis	Africa
Ch. defixa	Mammalia (native animals)			Southeast Asia
Ch. flavifrons (syn. *Ch. fulvipes)*	traps			Australia
Ch. fulvicruris	traps			Europe
Ch. greenbergi	traps			Indonesia
Ch. incisuralis	traps			Australia
Ch. inclinata (syn. *Ch. grienieri, roubaudi, tellinii*)	Primates: hominid (human); Rodentia: murid (cane rat); carrion		necrophagous, secondary facultative myiasis	Africa
Ch. latifrons	traps			Australia
Ch. laxifrons	traps			Africa
Ch. marginalis (syn. *Ch. regalis*)	Artiodactyla: bovid (cattle) impala); carrion (pig); dung	skin (wounds)	necrophagous, secondary facultative myiasis	Africa, Central Asia
Ch. megacephala (syn. *Ch. duvaucelii, gratiosa*) (Oriental latrine fly)	Mammalia (various domestic and wild animals); carrion (pig)	skin	necrophagous, secondary facultative myiasis [forensic applications] (mechanical vector for enteric pathogens)	worldwide

Ch. micropogon (syn. *Ch. mallochi p.p.*) (steel blue blow fly)	Mammalia (various domestic and wild animals); carrion	skin	necrophagous, secondary facultative myiasis	Australia
Ch. nigripes	carrion (incl. human cadavers), traps			Australasia
Ch. norrisi	traps			New Guinea
Ch. oumeensis	traps			Africa
Ch. pachymera	traps			Madagascar
Ch. pacifica	traps			Pacific
Ch. phaonis	carrion		necrophagous [forensic applications]	Central Asia
Ch. pinguis (syn. *Ch. nigriceps*)	carrion (incl. human cadavers)		necrophagous	Eurasia
Ch. polymita (syn. *Ch. atrifrons*)	traps			Africa
Ch. putoria	carrion (pig); dung		necrophagous (mechanical vector for enteric bacteria)	Americas, Africa
Ch. rufifacies (syn. *Ch. pingi*) (secondary green blow fly, green hairy-maggot blow fly)	Artiodactyla: bovid (cattle, sheep); Carnivora: canid (fox), mustelid (badger); Mammalia (various domestic and wild animals); carrion	skin	necrophagous, secondary facultative myiasis [forensic applications]	Australasia, Orient, Americas
Ch. sabroskyi	traps			New Guinea
Ch. saffranea (syn. *Ch. mallochi p.p.*)	traps			Australasia
Ch. samarensis	traps			Philippines
Ch. schoenigi	traps			Philippines
Ch. semimetallica	dung, carrion		necrophagous	Australasia
Ch. sulcifrons (syn. *Ch. noonadan*)	traps			Australasia
Ch. tagulai	traps			New Guinea
Ch. thanomthini	traps			South-East Asia
Ch. vanemdeni	traps			Africa
Ch. varipes (syn. *Ch. annulipes*) (small hairy-maggot blow fly)	Mammalia (various domestic and wild animals); carrion, dung	skin	necrophagous, secondary facultative myiasis	Australia, Pacific
Ch. villeneuvi	Primates: hominid (human cadaver)		necrophagous [forensic applications]	Asia
Ch. yayukae	traps			Indonesia

*Adult flies collected from environment using traps or nets.

Parasite morphology: These blow flies form 4 different types of morphological stages during their development: eggs; larvae (3 instars); pupae; and adults (males and females). Eggs are white-cream in colour and elongate measuring 1.0-1.5 mm long with a tapered end at one side. They are oviposited in loose or overlapping clusters on the edges of wounds or body orifices. Larvae (commonly called maggots) are cream in colour and have cylindrical bodies narrowing anteriorly (cf. muscoid larvae are more tapering). They develop through 3 larval instars (L1-3) and grow up to 15-17 mm in length. They have 12 segments, most with a band of small dark spines encircling the body giving the larva a threaded screw-like appearance (hence the common name of screwworm). Some species have smooth bodies between the bands of spines, while others may have fleshy tubercles projecting from segments (e.g. *Ch. bezziana* has 10 or more spines around the spiracular area, while *Co. macellaria* with spines in V-shape at the anal protuberance). The larvae lack sclerotized head capsules, but they have an internal cephalopharyngeal skeleton bearing rasping mouthhooks. All larvae breathe using 2 sets of respiratory spiracles: a small anterior pair which are brown to orange in colour (pigmentation extending to tracheal trunks in *Co. hominivorax* but not *Co. macellaria*) and have 7-10 openings (*Cochliomya*) or 4-13 openings (*Chrysomya*); and a larger posterior pair evident as caudal plates, each with an incomplete sclerotized periphery (peritreme) and 3 large oval slits (in contrast, oestrid larvae have porous spiracular plates). Mature L3 form puparia which are light to dark brown in colour, ellipsoidal measuring 9-11 x 3-4 mm and have a few circular body segments. The appendages of the enclosed pupae are visible externally and are held closely appressed to body. Adult flies eclose through a circular cap (like all Cyclorrhapha) and not through a longitudinal slit (like Nematocera and Brachycera). Calliphorid flies are large measuring up to 8-12 mm long and have stout setate bodies characteristically metallic green to bluish-green (like polished metal). *Cochliomyia* spp. are usually blue-green to violet-green with 3 prominent black longitudinal stripes on the thorax, while *Chrysomya* spp. have shiny blue-black to blue-green bodies with 2 faint dark stripes on the thorax and narrow dark bands along the posterior margins of the abdominal segments. Different species may be distinguished by variations in their colouring and ornamentation, e.g. *Ch. rufifacies*

has a black band on each abdominal segment, while *Ch. varipes* has black and yellow banded legs. Adult flies have 3 conspicuous tagma: a large rounded head; a stout shield-like thorax; and a pyriform abdomen. The head often bears a pale face (yellow for *Chrysomya*, yellow-orange to red for *Cochliomyia*) with both a ptilinal suture and a facial lunule (like all Muscoidea and Oestroidea but unlike other calypterate flies). The head also has 2 large well-developed compound eyes that are usually red-brown to orange in colour (closer together in males than females) and 2 short pendulous antennae, each composed of 3 dissimilar segments: a short basal scape, a club-like pedicel with a complete dorsal seam, and a single large dorsal bristle (arista) that is bilaterally plumose (setae on both sides). Adult calliphorids have well-developed sponging mouthparts to feed on liquids, but they do not bite hosts and do not feed on blood. The ventral proboscis comprises a basal rostrum flanked by short palps, a cylindrical haustellum with a sheath-like labium housing an anterior labrum and a slender hypopharynx; and a terminal sponging labellum. Ingested liquids pass through the tubular oesophagus to the globular proventriculus (with saccular diverticulum) then into the digestive midgut, hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a shield-like scutum with a small posterior lobe (scutellum). The dorsal scutum contains either long dense setae (*Cochliomyia*) or short sparse setae (*Chrysomya*) as well as stout bristles, including a vertical row on the meron (lacking on muscoid flies), and a stout row on the hypopleuron. The mesothorax gives rise to 2 lateral narrow wings which are usually clear (glassy in the case of *Ch. bezziana*) and sometimes with coloured basicosta (e.g. brown for *Co. hominivorax* and yellow for *Co. macellaria*). Wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with chrysomine flies having setate stem veins (not bare like calliphorine) and M veins that angle sharply upwards near the wing margin. The wings have prominent hind lobes (calypters, squamae) with setae on their dorsal surfaces. Like other dipterans, the hindwings have been highly reduced to small club-like halteres used to stabilize flight. Like all calyptrates, the halteres are covered by the calypters. Oestroid and muscoid flies are further distinguished from other calyptrates by the presence of bulbous swellings (greater ampulla) below the wing base. The ventral thorax is the point of attachment for 3 pairs of long thin dark legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus), all terminating in 2 claws with pad-like pulvilli surrounding a central bristle (empodium). The abdomen is segmented and tapered posteriorly, ending in pointed terminalia (male aedeagus, female ovipositor). Males have 2 testes with vas deferens connecting to a seminal vesicle (with lateral accessory glands) leading to the tubular ejaculatory duct and retractable copulatory aedeagus and claspers. Females have 2 ovaries linked by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and a cylindrical telescoping ovipositor.

Site of infection: Adult flies are not parasitic on animals, but female flies lay their eggs near damaged skin or body orifices and the emergent larvae invade host tissues. Many species are necrophagous in carrion, while some may invade the tissues of living animals causing primary or secondary myiases (fly strike). Several *Chrysomya* spp. cause facultative (secondary) fly strike in ruminants around the world, and one species (*Ch. bezziana,* the Old World screwworm) is notorious for causing obligate myiasis in animals and humans in Africa, India and Asia. *Cochliomyia* spp. are primary or secondary invaders in the tissues of numerous animal species, including humans, throughout the American tropics. One species (the New World (American) screwworm *Co. hominivorax*) causes obligate (primary) myiasis in living tissues, while other species (e.g. *Co. macellaria*) cause facultative (secondary) myiasis in necrotic tissue. Screwworm flies are not highly host specific and the adult flies lay their eggs at the edges of wounds (cuts, scratches, bites, shearing, dehorning, castration, umbilicus) or orifices (nostrils, mouth, eyes, ears, anus, vagina) of many animal species, including domestic animals, wildlife and sometimes humans.

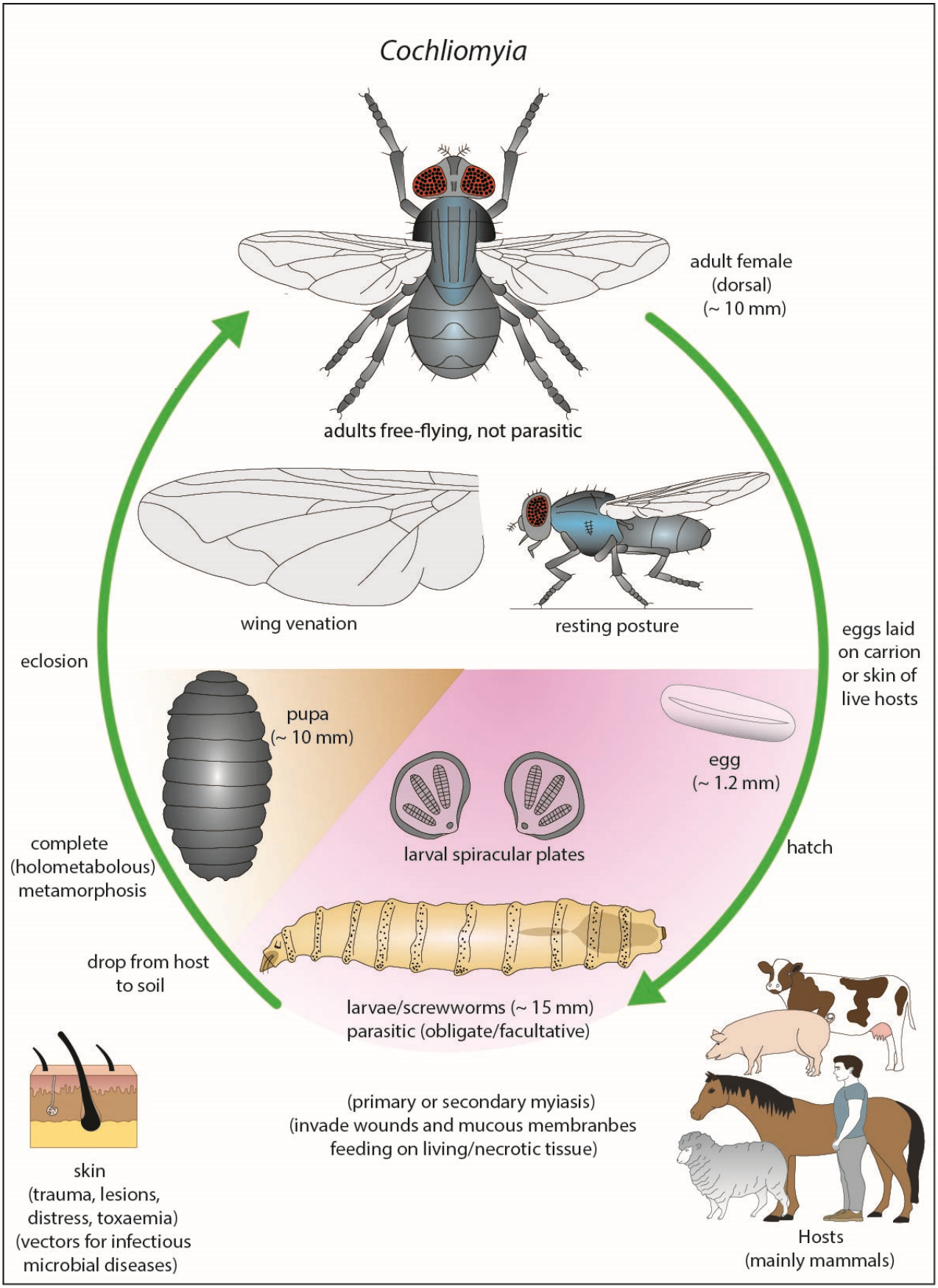
Pathogenesis: Larvae of these blow flies are commonly called screwworms as they burrow headfirst into host flesh and resemble woodwork screws. The larvae require protein-rich foods from animal tissues to complete their development, but they cannot penetrate intact skin. Instead, they invade through wounds or orifices causing cutaneous myiasis. Larvae hatching from one batch of eggs laid by a female fly near a minor skin wound may lead to an expanding lesion packed with several hundred maggots. The larvae feed using their hook-like mouthparts to scrape at host tissues dislodging fragments that are bathed in larval salivary enzymes and sucked up as a nutrient soup. The extent of tissue damage is dependent on the duration and intensity of infestation. Larvae often feed gregariously burrowing into the flesh causing pocket-like lesions that are not solely confined to superficial cutaneous regions, but may become cavernous and involve internal organs. Feeding maggots cause severe pain and distress to the host, eliciting a range of aversive and defensive behaviours (biting, scratching, rubbing, swatting, twitching, galloping, etc.) which are not only energy expensive but may also further open wounds to secondary infections. Untreated, lesions often worsen with progressive necrosis, ulceration, haemorrhage and liquefaction resulting in fluid leakage and purulent pungent odours (often attracting other myiasis-producing flies). Although mature and replete larvae leave host wounds to pupate, infestations are usually not synchronous but involve continuous or successive waves of developing larvae and the cumulative tissue damage is often irreversible. Animals become depressed, anorexic, lose condition, and may die (from dehydration, toxaemia/septicaemia, and various organ failures). In endemic regions, it is essential that any traumatic wounds in livestock due to natural causes (fighting, thorns, bites and disease) or husbandry practices (shearing, tagging, branding, dehorning, tail-docking, crutching, mulseing, castration) be treated as soon as practicable to reduce the incidence of life-threatening myiasis. Female flies are attracted to wounds not only to oviposit eggs but also to feed on exudates and liquids. Several screwworm species have been implicated as mechanical vectors for various microbial diseases, including botulism in birds, salmonellosis, poliomyelitis and swine influenza.

Developmental cycle and mode of transmission: Blow flies undergo holometabolous development where grub-like larvae metamorphose in pupae into winged adults. Female flies are oviparous and may lay 50-400 eggs every 2-4 days on the edges of wounds or body orifices, either in single masses (e.g. *Co. macellaria*) or in overlapping rows (e.g. *Co. hominivorax*). The eggs hatch within 12-24 hours releasing larvae which invade moist host tissues and commence feeding. Larvae develop through 3 instars (L1-3) over 4-12 days, burrowing deeper into host tissues. When L3 become mature and replete with food, they cease feeding and migrate out of the wound dropping to the ground as prepupal stages. They burrow into the topsoil (often beneath leaves and organic debris) and form puparia by contraction and hardening of their teguments. Pupae form within and undergo metamorphosis to adult stages over several weeks. Pupation may take anywhere from 7-60 days depending on prevailing environmental conditions (longer in colder weather, some species over-wintering as pupae in temperate regions). Teneral adult flies eclose through circular caps and after a short resting period to dry and harden their cuticles, they fly in search of mates and hosts. Adult flies are generally strong fliers and may travel more than 20 km seeking food and mates. Males become sexually mature within 1 day while females mature over 3-4 days. Males feed on plant liquids (such as flower nectar) and they often linger near flowering shrubs to intercept females. Males mate aggressively and frequently, while females usually only mate once but store enough sperm to remain fertile for life. Females are attracted by moisture and odours from wounds on vertebrate hosts and they feed on exudates and fluids near wounds. Most species (including *Co. hominivorax* and most *Ch. bezziana* strains) are autogenous and do not require protein meals to complete gonotrophic (ovarian) cycles and produce eggs. However, others (such as *Co. macellaria* and a few *Ch. bezziana* strains) may be anautogenous and do require additional nutrients in order to produce their first eggs. Female flies live for 1-3 weeks and may produce over 1,000 eggs in their life-times. The whole life-cycle may be completed in warm tropical regions in as little as 3 weeks, but may be extended for several months in cooler temperate regions (when pupae over-winter).

Differential diagnosis: Infestations are provisionally diagnosed by the direct observation of penetrating cutaneous lesions containing fly larvae feeding head-down on host tissues. Diagnoses are confirmed by the collection and identification of larvae on the basis of their morphological characteristics, especially spiracle and tracheal morphology, pigmentation, and armature (setation). It is advisable to collect larvae from deep within the wound to increase the chances of collecting mature stages, and to kill larvae in boiling water prior to fixation for ease of observation. In case of doubt, larvae can be cultured in the laboratory on meat or synthetic medium until they mature, pupate and transform to adult flies. Immunodiagnostic studies have also been conducted to detect host immune responses to larval excretory-secretory (ES) antigens, and monoclonal antibodies have been developed to differentiate screwworm species in enzyme-linked immunosorbent assays (ELISA). Modern molecular biological studies have now been developed to characterize species and examine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (28S ribosomal DNA, internal transcribed spacers, elongation factor-1 alpha) and mitochondrial (cytochrome c oxidase I) gene sequences.

Treatment and control: Screwworm infestations require urgent medical intervention as they will often progressively worsen and become life-threatening. Wounds should be thoroughly cleansed with antiseptics, necrotic tissue debrided (under local anaesthesia for penetrating wounds) and larvae extracted by surgical removal, suffocation or insecticide treatment. Patients may require supportive therapy, including analgesics, anti-inflammatories, antibiotics and rehydration. Larvae can be smothered by covering their spiracles with occlusive dressings (oily creams or salves, such as petroleum jelly, lanolin, paraffin or mineral oil, beeswax, and sometimes nail polish, adhesive tape, chewing gum, butter) and they can sometimes be coaxed from wounds using stringent antiseptics (hydrogen peroxide, chloroform in vegetable oil). It is now more usual practice to treat wounds with larvicidal insecticides, which have been variously applied as impregnated dressings, smears, tars, pour-ons, sprays, dips, suspensions, gels, powders and dusts, as well as oral or injectable systemic preparations. Early formulations containing creosote, eucalyptus oil, paraffin, phenol and others were painted directly onto wounds mixed with resinous tar, while next generation formulations incorporated a wide range of insecticidal organochlorides (such as dichloro-diphenyl-trichloroethane (DDT), lindane) and organophosphates (such as coumaphos, diazinon) into topical powders, pastes and sprays. However, significant problems were encountered with drug toxicity and flies developing resistance to organochlorides (especially DDT) and organophosphates (many are now banned as dips although some are still available as dressings). More recently, topical formulations of pyrethroids (permethrin, cypermethrin, deltamethrin) and spinosyns (spinosad) as well as systemic applications of salicylanilides (closantel) and macrocyclic lactones (notably ivermectin, doramectin) have been used to treat myiases with great effect. Domestic livestock may be protected for up to 10 weeks using insecticides with good residual activity (organophosphates and pyrethroids applied topically or via impregnated eartags), and some insect growth regulators (cyromazine, dicyclanil) have given protection for up to 8 weeks. Macrocyclic lactones are available as injectable, pour-on or oral medications or in the form of a controlled-release intra-ruminal bolus. In addition to chemotherapy and chemoprophylaxis, other strategies can be used to prevent and control myiases, mainly by minimizing predisposing conditions (stock husbandry and management); and reducing fly populations (environmental management). Livestock should be subject to regular health surveillance and quarantine so that wounds can be quickly detected and treated promptly. Various husbandry practices may be adopted to prevent screwworm infestation, including regular dagging and crutching (clipping soiled wool/hair around the perineum), tail docking (amputation) and Mules' operation (removal of skin folds around breech). Attention should also be paid to wounds associated with ear-tagging, dehorning, branding, castration and even the umbilical cord stump of newborns. Many blow fly species have been shown to multiply in carrion so every effort should be made to remove and destroy carcases in the field. Several studies have used carcases treated with chemo-attractants and insecticides as baited traps for fly control, but large-scale programmes pose many logistic problems. Good results have been obtained in controlling (and even eradicating) screwworm populations in several Central American regions by releasing sterile (irradiated) males bred in the

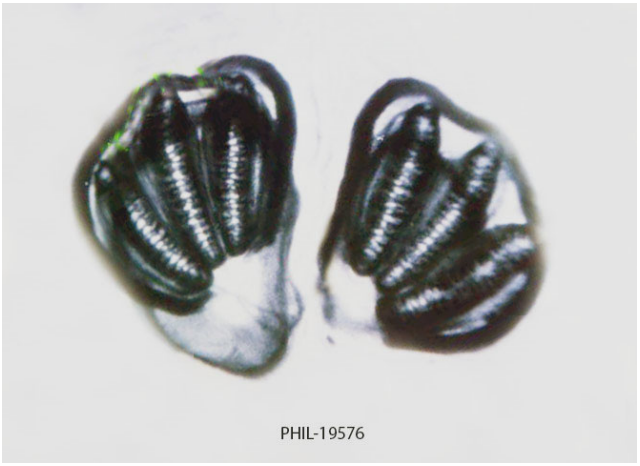
laboratory to compete for mates. Many interventions can be used to great effect in intensive agricultural systems, but are less appropriate for extensive systems and for wildlife management. Reservoirs of natural infestations may persist in wild animal populations in pockets of inaccessible areas, so further land clearance and utilization needs to account for sporadic encounters. Several recent studies have also examined the possibility of developing a vaccine for screwworm infestations. Animals vaccinated with larval extracts (esp. peritrophic membranes) showed reduced larval growth and increased larval mortality upon challenge, but the underlying mechanisms of protection remain to be determined.


Cochliomyia
adult female
(dorsal)
(~ 10 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrion
or skin of
live hosts
egg
(~ 1.2 mm)
hatch
larval spiracular plates
larvae/screwworms (~ 15 mm)
parasitic (obligate/facultative)
drop from host
to soil
pupa
(~ 10 mm)
eclosion
complete
(holometabolous)
metamorphosis
(primary or secondary myiasis)
(invade wounds and mucous membranbes
feeding on living/necrotic tissue)
skin
(trauma, lesions,
distress, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mainly mammals)

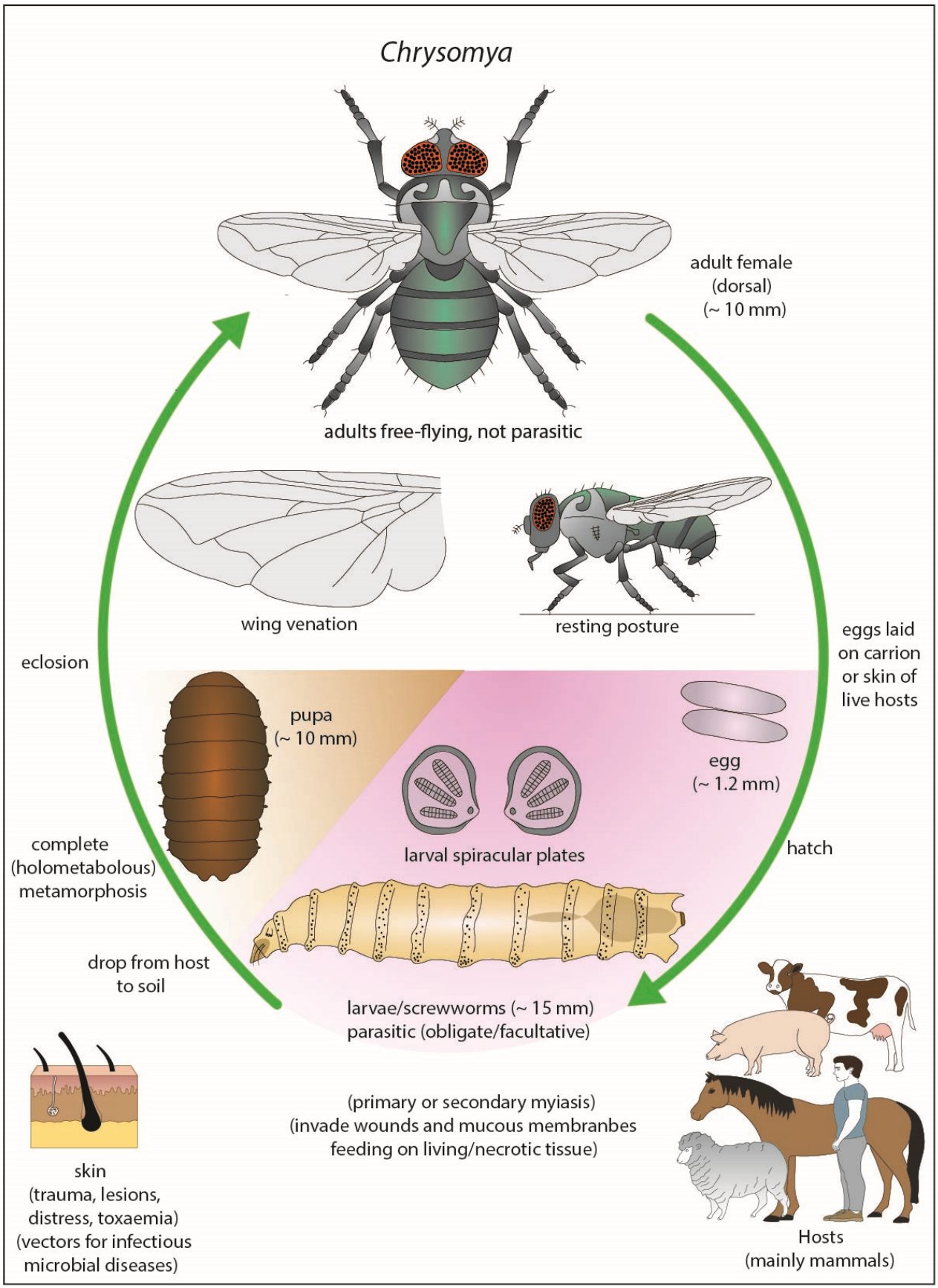
Cochliomyia adult

Cochliomyia eggs

Cochliomyia larva



Cochliomyia larval spiracles


Chrysomya
adult female
(dorsal)
(~ 10 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrion
or skin of
live hosts
egg
(~ 1.2 mm)
eclosion
pupa
(~ 10 mm)
larval spiracular plates
hatch
complete
(holometabolous)
metamorphosis
drop from host
to soil
larvae/screwworms (~ 15 mm)
parasitic (obligate/facultative)
(primary or secondary myiasis)
(invade wounds and mucous membranbes
feeding on living/necrotic tissue)
skin
(trauma, lesions,
distress, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mainly mammals)

Chrysomya adult

Chrysomya eggs

Chrysomya larvae

Chrysomya pupa