

Tunga

(insect: flea)

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. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Tungids (sand fleas, chiggers) are unusual in that female fleas are permanently attached to their mammalian hosts, residing in excavated sinuses in the skin and releasing eggs from their protruding abdominal segments. Infestations by *Tunga penetrans* have been associated with nodular and ulcerated skin lesions in humans and pigs.

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: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Tungidae (chigoes/jiggers/chiggers/chique/sand fleas, females burrow under skin, enclosed in sinus)
Genus: *Tunga* (parasitic on skin of mammals)
Species: *T. penetrans* (causes nodular/ulcerated lesions in humans and pigs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipteroidea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensillum with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic
Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaeartic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensillum with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaeartic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Although thought to be closely related to the Pulicidae, recent molecular studies have placed the Tungidae at the base of flea phylogeny in association with basal mammalian hosts. Members of the family Tungidae (= Dermatophilidae, Hectopsyllidae, Rhynchoprionidae, Echidnophagidae p.p., Sarcopsyllidae p.p.) are characterized by small simple bodies (small triangular heads and compressed thoracic segments) and reduced chaetotaxy (including the absence of both genal and pronotal ctenidial combs). Four tungid genera are recognized from a range of warm-blooded hosts: namely, *Hectopsylla* from nonvolant mammals, bats and birds, *Rhynchopsyllus* from bats, *Neotunga* from pangolins, and *Tunga* from small mammals. The latter two genera also exhibit a unique process known as neosomy whereby female fleas burrow into the host skin and undergo accelerated development (tachygenesis) with abdominal hypertrophy and encystment. In contrast, females of most other flea genera detach from their hosts after feeding, although pulicid stick-fast fleas, *Echidnophaga*, do undergo partial neosomy and remain attached. Neosomy (previously called teleomorphosis) has been defined as the pronounced interstadial growth of unsclerotized parts of the abdomen without moulting. It allows females to take maximum advantage of food resources and greatly increases their reproductive potential (readily producing over 1,000 eggs each).

Genera	No. spp.	Hosts	Ctenidia (combs)		Disease	Vector
			Genal (head)	Pronotal (thorax)		
Tungidae						
<i>Tunga</i>	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	<i>Staphylococcus</i> , <i>Wolbachia</i> , tetanus
Pulicidae						
<i>Pulex</i>	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
<i>Echidnophaga</i>	23	birds, rodents, carnivores, marsupials	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis
<i>Xenopsylla</i>	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
<i>Ctenocephalides</i>	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonellosis, typhus, plague, dog tapeworm, filarial nematode
<i>Spilopsyllus</i>	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Ceratophyllidae						
<i>Ceratophyllus</i>	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
<i>Nosopsyllus</i>	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

A total of 13 *Tunga* spp. have been described from wild and domestic mammals in tropical and subtropical regions, notably South and Central America, sub-Saharan Africa and parts of Indo-China. These species have been divided into two groups: the 'penetrans' group (referable to the subgenus *T. (Tunga)*) containing 6 species (fusion of pronotum and mesonotum dorsally complete, spiracles of terga II-IV absent), and the 'caecata' group (referable to the subgenus *T. (Brevidigitata)*) containing 7 species (fusion incomplete, spiracles present). Most *Tunga* spp. show little host specificity and infest multiple host species living in sympatry, particularly in areas with sandy soils in which immature fleas lay in wait of passing/resting hosts. Two species (*T. penetrans* and *T. trimamillata*) may infest humans causing ulcerative dermal lesions (tungiasis) mainly on the feet (around margins, toes and toenails), particularly in people who go barefoot. The lesions may become ulcerative and are highly prone to secondary bacterial infections, including tetanus which may prove fatal.

<i>Tunga</i> species	Hosts	Location	Clinical signs	Distribution
<i>penetrans</i> group (rodents, armadillos, anteaters, ungulates, carnivores and primates)				
<i>T. bondari</i>	Pilosa: myrmecophagid (southern tamandua); Cariamiformes: cariamid (red-legged seriema)	abdomen, legs	cysts	Brazil
<i>T. hexalobulata</i>	Artiodactyla: bovid (zebu)	foot	cysts	Brazil
<i>T. penetrans</i> (syn. <i>Pulex</i> , <i>Acarus</i> , <i>Rhynchoprion</i> , <i>Dermatophilus</i> , <i>Sarcopsylla</i>) (sand fleas, chiggers, jiggers, chigoes)	Primates: hominid (human, gorilla), atelid (southern brown howler monkey), cercopithecoid (baboon, guenon); Artiodactyla: bovid (cattle, sheep, goat), camelid (llama, vicuna), suid (pig, bushpig), tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (South American tapir); Proboscidea: elephantid (African bush elephant); Carnivora: canid (dog), felid (cat, jaguar); Rodentia: caviid (guinea pig, Brazilian guinea pig), cuniculid (lowland paca), dasyproctid (Central American agouti, red acouchi), hystricid (porcupine), murid (black rat, brown rat, house mouse); Cingulata: chlamydophorid (big hairy armadillo, six-banded armadillo), dasypodid (nine-banded armadillo, southern long-nosed armadillo); Pilosa: myrmecophagid (collared anteater, giant anteater)	feet, toes, scrotum, muzzle	cysts, pruritus, pain, ulceration	Latin America, Africa, Asia

<i>T. terasma</i>	Cingulata: chlamyphorid (giant armadillo, six-banded armadillo, southern naked-tail armadillo), dasypodid (nine-banded armadillo)	abdomen, toes	cysts	Brazil
<i>T. travassosi</i>	Cingulata: dasypodid (nine-banded armadillo)	abdomen	cysts	Brazil
<i>T. trimamillata</i>	Primates: hominid (human); Artiodactyla: suid (pig), bovid (cattle, sheep, goat); Rodentia: caviid (capybara)	feet, perianal	cysts	Ecuador, Peru
<i>caecata</i> group (primarily rodent hosts)				
<i>T. bonneti</i>	Rodentia: cricetid (yellow-rumped leaf-eared mouse, Darwin's leaf-eared mouse)	tail	cysts	Chile
<i>T. bossi</i>	Rodentia: cricetid (striped Atlantic forest rat)	tail	cysts	Brazil
<i>T. caecata</i>	Rodentia: murid (black rat, brown rat, house mouse), cricetid (Cursor grass mouse, bolo mouse, Atlantic forest climbing mouse, scaly-footed water rat, black-footed pygmy rice rat, hociúdo)	ears	cysts	Brazil
<i>T. caecigena</i>	Rodentia: murid (black rat, brown rat, house mouse, southwestern Asian house mouse); Eulipotyphla: soricid (Asian house shrew)	ears	cysts	China, Japan
<i>T. callida</i>	Rodentia: murid (black rat, brown rat, southwestern Asian house mouse, Chevrier's field mouse), cricetid (southwest China vole)	perianal	cysts	China
<i>T. libis</i>	Rodentia: cricetid (soft grass mouse, Andean leaf-eared mouse, Darwin's leaf-eared mouse)	ears	cysts	Ecuador, Chile
<i>T. monositus</i>	Rodentia: cricetid (pack rat, desert wood rat, deer mouse, cactus mouse, canyon mouse)	ears	cysts	North America

Parasite morphology: *Tunga* spp. form 4 different and unique types of morphological stages during their developmental cycles: namely, eggs; larvae (2-3 instars); pupae (in cocoons); and adults (small laterally-flattened fleas but gravid females become large and swollen). The eggs are shiny white-yellow ovoid stages measuring approximately 0.6 x 0.3 mm. The larvae are yellow-brown vermiform (worm-like) stages with segmented bodies. Each of the 13 segments has an uneven circle of backwards-facing bristles and the last segment bears 2 lobes carrying an anal brace. The larvae have darker sclerotized heads with strong mandibles and mandibular teeth well-adapted for biting and chewing, and rudimentary maxillary palps and a labrum can be observed. The heads do not have eyes but have a pair of bar-like antennae that extend forwards. The larvae moult through several instars (2 for *T. penetrans*, 3 for other *Tunga* spp.) growing from 1-3 mm in length. Mature larvae void their guts of food and bend in a U-shape shortly before forming pupal cocoons. The cocoons are sticky and become covered with adherent sand grains and detritus. The enclosed pupae are exarate with free appendages (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Adult fleas are reddish brown in colour with bilaterally symmetrical but laterally compressed bodies measuring 0.5-1.5 mm long (except for gravid females which become swollen and globular measuring up to 4-10 mm in diameter. Adults have hard chitinized plates (sclerites) and are sparsely setate (with few setae and entirely lacking genal and pronotal combs). They have 3 conspicuous body parts: a large angular double-curved head; a short narrow thorax; and an expandable abdomen. The head is flattened and angular, forming a triangular shape with a well pronounced frontal tubercle. Some species have a more rounded head while others have a slight depression on the top. The cheeks (gena) in *T. penetrans* have deep grooves which are absent in *T. trimamillata*. All species have a pair of short compact club-like antennae (3-segmented) flattened against the head and not within antennal grooves (fossae). They vary in their possession of eyes which, when present, may be small or large noncompound eyes (clusters of ocelli), sometimes pigmented. Adults have long ventral piercing-sucking mouthparts (lacking mandibles and teeth) that project conspicuously from the head. The mouthparts are located between 2 pairs of sensory palps: a pair of long 4-segmented maxillary palps (first segment longer in *T. trimamillata*, second segment longer for *T. penetrans*) arising from short lobes (stipes), and a pair of long 5-segmented labial palps arising from a short basal labium. The feeding mouthparts consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated, and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). *Tunga* adults differ from other fleas in that they have well-developed laciniae and an epipharynx which facilitate burrowing. All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of a tubular foregut (anterior pharynx, elongate oesophagus, globular proventriculus armed with spines), a large expandable midgut (simple undivided digestive organ, unlike the more elaborate divided midguts (with diverticula and caeca) of most other haematophagous arthropods), a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 distinct dorsal sclerites (pronotum, mesonotum, metanotum) that are surrounded by 3 humps in female *T. trimamillata* but absent in *T. penetrans*. The fusion of the pronotum and mesonotum is complete in the *T. penetrans* group, but incomplete in the *T. caecata* group. The ventral thorax is the point of attachment for 3 pairs of legs: each with 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all ending in 2 claws. The legs are setate, with more spines on the first tarsal segment and hindleg tibia of *T. trimamillata* than *T. penetrans*. The hindlegs are enlarged which enables them to jump, but they are poor jumpers as the legs are very slender. Like all fleas, they jump using unique elastic resilin pads to store energy under compression, rather than muscular contraction. The expandable abdomen is segmented, with rows of hair-like structures on each segment. The *T. caecata* group has small lateral spiracles located laterally on dorsal abdominal sclerites (tergites II-IV) which are absent in the *T. penetrans* group. In non-gravid females, the last abdominal tergite in *T. trimamillata* protrudes

outwards forming a small tail, but not in *T. penetrans*. The size and shape of the abdomen can be readily used to distinguish sexes, as marked sexual dimorphism occurs after maturation with females exhibiting considerable hypertrophic growth (up to 80-100 times) between abdominal segments II and III. This unique process is known as neosomy (previously called teleomorphosis) and has been defined as the pronounced interstadial growth of unsclerotized parts of the abdomen without moulting. This results in gravid females having dramatic size increase (up to 10 mm in diameter) accompanied by extensive morphological degeneration, major integumental chitin synthesis, and protracted and extensive egg development (200-1,000 eggs). Female fleas expose their posterior respiratory spiracles as well as their anal and vaginal apertures at the surface of the host skin, all contained within a caudal disc (varying in shape from flattened, conical to cylindrical, and in size from as wide as long, longer than wide, or wider than long). Different *Tunga* spp. can be distinguished by their hypertrophic forms, ranging from globular without lobes (*T. penetrans*, *caecata*, *travassoi*, *libis*, *bossii*, *bonneti*) or with 3 lobes (*T. trimamillata*), 4 lobes (*T. callida*, *terasmam*, *caecigena*), 6 lobes (*T. hexalobulata*), 8 lobes (*T. monositus*) or mushroom-shaped (*T. bondari*). Mature females have 2 ovaries with oviducts leading to the uterus which is connected to the vagina located in a bursa copulatrix (grooved depression to receive male organ) with an associated spermatheca (sperm storage organ with a globular-elongate body (bulga) and a short-long thin-thick tail (hilla)). Male fleas remain small and do not undergo neosomy. However, they have distinctive and highly elaborate genitals (probably the most complex in the animal kingdom). They have 2 testes with tubular vas deferens leading to a seminal vesicle with an ejaculatory duct connected to a long thin delicate intromittent organ (penis). The penis is attached to an aedeagal apodeme (penis plate) and has extendable penis rods coiled and retracted within an endophallic sac. The phallosome has proximal and distal arms articulated in the middle just before the ejaculatory duct and almost as long as the penis plate. Copulation is aided by posterior claspers which have immovable processes (basimeres) and movable processes (telomereres) connected to a manubrium.

Site of infection: Adult *Tunga* fleas are obligate haematophagous ectoparasites of terrestrial vertebrates, whereas pre-adult stages (eggs, larvae and pupae) are free-living stages, usually in sandy soil. *Tunga* spp. exhibit variable host specificity, but most infest only a few host species living in sympatry. Collectively, members of the *T. penetrans* group have been found in 20 mammalian families (comprising rodents, armadillos, anteaters, ungulates, carnivores, and primates) and one avian family (a predatory terrestrial bird), while members of the *T. caecata* group are confined to 3 mammalian families (cricetid and murid rodents and Asian shrews). Only 3 species have been found on domestic animals (*T. penetrans*, *trimamillata*, and *hexalobulata*), the former 2 also being found on humans. While most other fleas leave their hosts after feeding, female *Tunga* fleas penetrate the epidermis forming furuncular nodules as they continue feeding and become grossly hypertrophied and filled with eggs. In humans, lesions are usually found in regions of body that regularly contact soil, notably periungual and subungual regions (around or under nails), the soles of the feet, and interdigital spaces, but other sites may also be involved, including the neck, upper limbs, buttocks and genital regions. In animals, female fleas usually burrow into the skin of the feet and legs but they can also invade ventral body surfaces and sometimes the neck and face.

Pathogenesis: Both male and female fleas feed on blood from vertebrate hosts, but males are transient feeders detaching after meals, whereas females burrow head-first into the skin and stay attached to feed, expand and produce eggs. Adults have well-developed mouthparts with cutting laciniae used to penetrate skin and a stabbing epipharynx used to suck blood from dermal blood vessels. Bite sites are evident as erythematous (reddened) papules surrounded by inflamed tissues, with inflammation heightened by allergic/hypersensitivity reactions to flea saliva. Inflammation may last for several days to weeks, and become encrusted with dried exudates. Female fleas burrow deeply into the skin causing lesions that appear as blisters or furuncular nodules. They undergo massive abdominal hypertrophy in a process known as neosomy (intrastadial development with new cuticle formation) and produce large numbers of eggs (200-1,000) as they stay *in situ* until death. The lesions appear as black-brown dots at the centre of swollen red tissues surrounded by white halos of thin skin. The central dots are where the female flea extends her spiracles, anus and vagina to breathe, defaecate and release eggs. The expanding lesions exert pressure on local tissues (including nerves and blood vessels) resulting in sensations ranging from mild irritation with pruritus to serious discomfort with great pain (sometimes crippling the host). Researchers have recognized 5 different stages in the development of lesions (Fortaleza classification). Stage 1 involves penetration of the female flea into the epidermis over 3-7 hours causing a focal red spot (~1 mm in diameter). This stage is initially asymptomatic but may produce some irritation, inflammation, erythema and pruritus. Stage 2 involves growth of the flea as it feeds over several days resulting in dark spots surrounded by erythema (~5 mm in diameter). The lesions are pruritic and host scratching may facilitate secondary bacterial infections, sometimes resulting in with nail deformation or loss. Stage 3 involves hypertrophy of the flea as it encysts over 1-2 weeks into a spherical nodule 7-10 mm in diameter which is evident as a white-gray-yellow papule with a brown-black center and surrounded by a halo of pale thin stretched hyperkeratotic skin. As the fleas engorge and lay eggs, hosts often experience pulsating pain that may limit their mobility and feeding efficiency. The lesions become covered by black scabs after the fleas expel their eggs. Stage 4 involves involution of the lesion after the majority of eggs are expelled and the hypertrophic zone crumples. Host reactions over several weeks cause the lesions to shrink and the surrounding skin becomes wrinkled and crusted. Stage 5 is the final repair period which lasts for several weeks as the host expels the flea carcass and repairs the skin, leaving a characteristic circular indurated scar. Two species (*T. trimamillata* and *T. penetrans*) cause tungiasis in humans (most commonly in children 5-9 years old and in males), with infestations by the former species being the most painful as the fleas are larger. In animals, infestations of the feet/hoooves may compromise motility leading to feeding difficulties with reduced weight gain or weight loss, and decreased milk production. Infestations of the teats may lead to mastitis, agalactia and neonatal mortalities (young unable to suckle). Multiple lesions have been associated with the formation of pustules and suppuration, with lymphadenopathy and lymphoedema. Open or ulcerated lesions are highly susceptible to secondary bacterial infections, mostly by

Staphylococcus aureus and Gram-negative bacteria, but also including Enterobacteriaceae, *Enterococcus faecalis*, *Streptococcus pyogenes*, *Bacillus* spp., *Pseudomonas* spp. and other anaerobic bacteria. Infected lesions become further enlarged leading to the formation of abscesses, cellulitis, phagedenic ulcers, hyperkeratosis, fissures, phlegmons, septicaemia, thrombophlebitis, lymphangitis, osteomyelitis, onycholysis (loss of nails), and gangrene with spontaneous amputation of toes. Lesions may also act as portals of entry for *Clostridium tetani* causing tetanus, which may be fatal. Molecular screening studies on sand fleas have also isolated *Yersinia pestis* (the cause of plague) as well as enigmatic *Wolbachia* spp. (Gram-negative bacteria that have been found as intracellular symbiotes (mutualists or parasites) in a range of insects and nematodes).

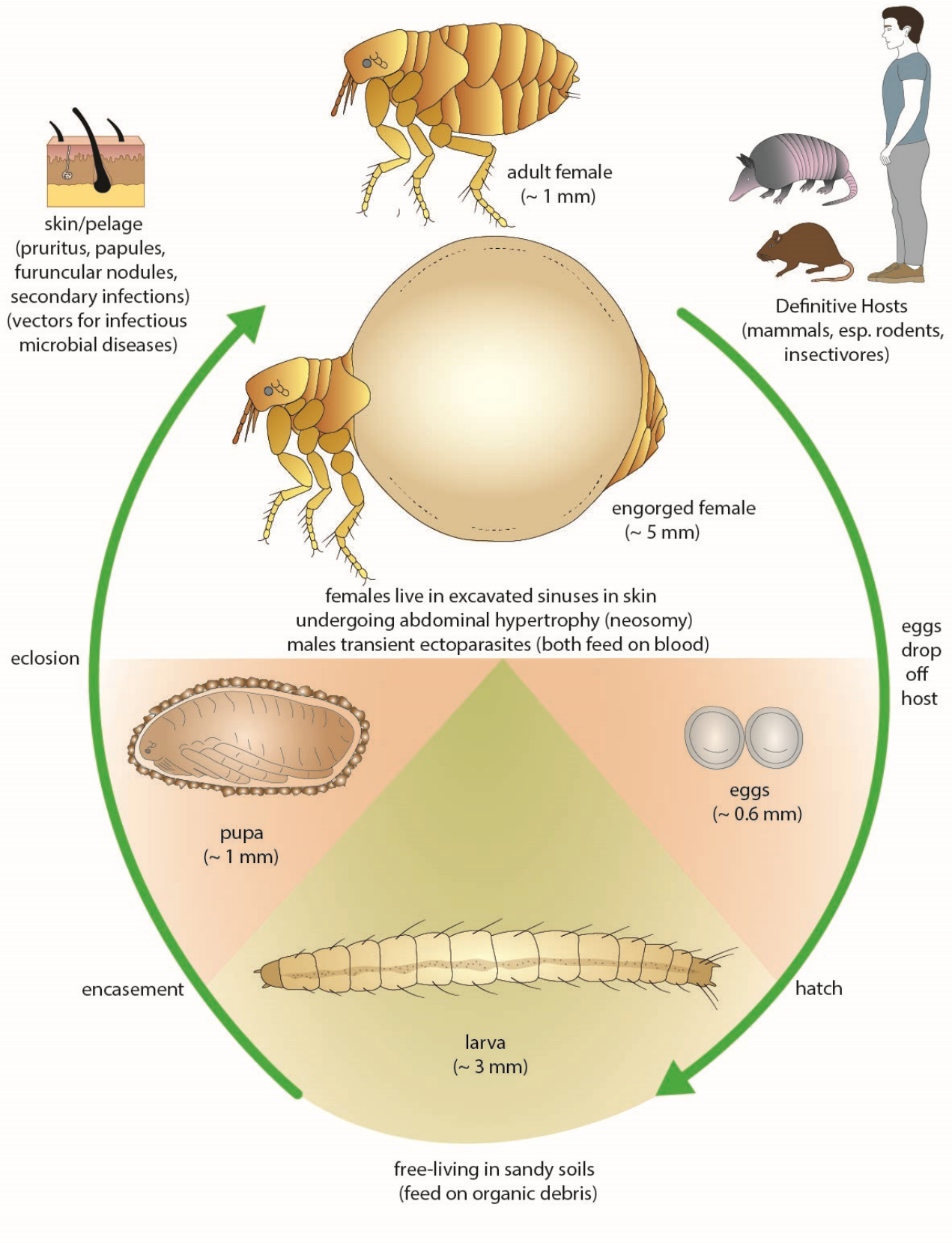
Developmental cycle and mode of transmission: Like other fleas, *Tunga* spp. exhibit holometabolous development where vermiform larvae undergo complete metamorphosis in pupae to form adult fleas. Unlike other fleas, however, the female fleas attach permanently to their hosts, even burrowing into the skin and undergoing massive hypertrophy of their abdomens as they produce numerous eggs. Females lay eggs through their posterior genital aperture which protrude from the centre of the skin lesions. The eggs may become entangled in exudative material but most drop off the hosts into the surrounding environment. Hosts scratching at lesions also assist the release of eggs from lesions. Eggs landing in suitable substrates (fine-grained sandy soils that are warm and dry) hatch after 1-6 days releasing vermiform larvae. Larvae are usually found at depths of 2-5 cm as surface layers are too hot and deeper layers are too poor in oxygen for survival and growth. The larvae feed on organic debris in the environment and develop through 2 or 3 instars over 6-18 days. Mature larvae form thin-walled cocoons that become covered in particulate material. The enclosed stages undergo pupation to form adult fleas which emerge from the puparia after 5-15 days. Adult fleas may reside in the soil for several weeks to months while waiting for hosts. When they sense the presence of hosts (by vibration and odours), adults jump onto the skin to feed, sometimes making prodigious leaps of up to 35 cm. Both sexes require bloodmeals to become sexually mature (unfed free-living stages do not mate). Mature males search for receptive females feeding on hosts and mate before dropping off and dying. Unfertilized females also drop off hosts and die, whereas fertilized females burrow into the skin and continue feeding as they undergo considerable hypertrophy (by the process of neosomy) and produce eggs. Females may increase in size up to 80-100 times over 4-6 weeks and they may produce over 200-1,000 eggs when patent for the last 2-3 weeks before they die. Most *Tunga* spp. are univoltine and only breed once each year, with fleas being most abundant during the dry season (high soil humidity associated with rainy seasons impairs larval development and adult flea survival). Hosts that are most susceptible to infection are those that utilize habitual resting/sleeping places under trees, poor people that reside in huts/buildings with sandy earthen floors, and people who go barefoot or wear open sandals.

Differential diagnosis: Infestations are strongly indicated by the detection of characteristic skin lesions, even though they vary in appearance over time (initially small red spots but progressing to large pale papules with dark centres surrounded by halos of thin skin and then crusted nodules). Careful attention should be paid to patient history, symptoms and signs, as a range of other conditions may cause similar enigmatic lesions, including other arthropods (ticks, myiasis, mite bites, fire ant bites), bacteria (abscesses, pustular dermatitis, acute paronychia, interdigital and pododermatitis, foot rot, mastitis), viruses (warts, vesicular diseases in swine and ruminants), fungi (mycotic granulomas), inflammatory conditions (foreign body granulomas, vasculitis), neoplasms (tumours, early melanoma) and developmental abnormalities (ingrown toenails, subungueal exostosis). Patent infestations are often diagnosed by the macroscopic or microscopic detection of shiny white flea eggs on or near skin lesions, sometimes associated with crusted blood and flea excreta (the spiracles, anus and vagina of resident fleas protrude from the central punctum). Careful examination may even reveal periodic pulsation of the central dark spot as the flea defaecates or lays eggs. The identification of *Tunga* spp. often relies on the examination of non-neosomic stages, as intact specimens of neosomic females are difficult to obtain (their hypertrophic status also obscures many morphological features). When hypertrophic forms are available, different species clusters may be recognized on the basis of their overall globular (e.g. *T. penetrans*) or multilobular structure (e.g. *T. trimamillata* with 3 lobes, *T. callida* with 4 lobes, *T. hexalobulata* with 6 lobes, and *T. monositus* with 8 lobes). Molecular biological techniques have been applied to the characterization of species and phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (internal transcribed spacer regions I and II of ribosomal RNA) and mitochondrial (cytochrome oxidase II, large subunit (16S) ribosomal RNA) gene sequences.

Treatment and control: Most infestations are self-limiting and may resolve without treatment after 5 or more weeks. However, various treatment options may be sought depending on the number, size, location, age and severity of lesions. Various poultices have been used to some effect, most providing symptomatic relief, including mercury ointment, rocou tincture, turpentine, castor oil, palm oils, cassava and tobacco infusions. In the case of swollen painful lesions, recourse is usually made to the surgical removal of fleas. Folklore remedies practiced for centuries have involved flea extraction using heat-treated sharpened thorns or clean needles (auguring), but surrogate efforts using unsterilized safety pins, scissors, knives or wood splinters may aid the transmission of blood-borne infections (e.g. hepatitis, human papilloma virus, human immunodeficiency virus) as fleas cannot be removed without causing bleeding. Modern techniques involve local excision or sterile curettage by enlarging the wound around the posterior end of the flea and removing it using sterile tweezers, forceps or needles. It is important that fleas be removed in their entirety as any residual fragments may provoke inflammatory and hyperkeratotic reactions. Alternative but uncommon treatment options have included local cryotherapy and electro-desiccation of nodules. Every effort should be made to clean wounds to prevent secondary bacterial infections, using sterile saline or disinfectant washes, sterile dressings, anti-pruritic and anti-inflammatory ointments and topical or systemic antibiotics (notably to prevent pyoderma and tetanus). Attempts to suffocate fleas by occlusive coverings of oily

compounds such as vaseline or petroleum jelly (as used against fly larvae causing myiasis) are not recommended because they do not remove the flea or its remnants from the skin and do not give quick relief from painful lesions. There are no completely effective drug treatments for flea lesions, although several topical and a few systemic preparations do kill fleas, but their carcasses remain within the lesions which complicates healing processes. Variable results have been reported in the treatment of infestations in humans and animals (particularly pigs and dogs) using volatile fixatives (formaldehyde, chloroform), some natural oils (coco oil, jojoba oil, *Aloe vera* extracts) and insecticidal chemicals, including organochlorides (lindane, dichloro-diphenyl-trichloroethane (DDT)), organophosphates (metrifonate, coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), pyrethroids (permethrin, cyfluthrin, cypermethrin), arylpyrazoles (fipronil), macrocyclic lactones (ivermectin) and even some anthelmintics, including benzimidazoles (thiabendazole) and nitrothiazoles (niridazole). Many of the insecticidal chemicals had greater effect when used therapeutically to treat early infestations (before neosomic lesions were present) or when used prophylactically to prevent infections. It is advised that domestic animals (including pets) be regularly treated with anti-flea compounds, such as pyrethrin sprays or malathion powder. Flea control programmes must also include attempts to prevent infestations or re-infestations by new fleas arising from free-living stages, as flea eggs, larvae and pupae can persist in sandy soils for extended periods. Some success has been reported when treating the immediate environment (especially soil in houses and animal pens) with insecticides that have long residual activities, including organophosphates (malathion), pyrethrum and synthetic pyrethroids (cypermethrin, deltamethrin), polycyclic aromatic hydrocarbon (naphthalene) and juvenile hormone mimetics (methoprene). The floors of animal pens and houses should be kept clean by regular sweeping or watering earthen floors, or by paving or cementing them. Domestic animals and humans should be housed separately, and domiciles should undertake vermin control using barriers, traps or baits. Humans living in endemic regions should adopt personal protection measures such as regularly washing hands and feet, wearing gloves when handling soil, wearing closed shoes and using insect repellent lotions, such as diethyltoluamide (DEET). Communities should also be made aware of tungiasis through public health education campaigns.

Tunga





Tunga adult



Tunga eggs



Tunga lesions