Spilopsyllus
(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. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Spilopsyllus* spp. have genal (oral) and vertical pronotal (thoracic) combs and infestations have been associated with irritation and tissue damage in rabbits. The fleas also act as vectors for the transmission of myxomatosis.

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:	Pulicidae (parasites of mammals)
Genus:	*Spilopsyllus* (parasitic on skin of rabbits)
Species:	various species cause irritation, skin lesions

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). 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	sensilium 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 Palaearctic
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	sensilium 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	Palaearctic, 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. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

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

Spilopsyllus is a monotypic genus with a single species (*S. cuniculi*) originally described from rabbits in Europe but now distributed throughout the world due to the numerous translocations of hosts during colonization and more recently attempts using fleas as vectors for the spread of viral myxomatosis for the biological control of rabbits. Infestations may also be found on small mammals and some birds living in sympatry with rabbit populations, including companion animals.

***Spilopsyllus* species**	**Hosts**	**Clinical signs**	**Distribution**
S. cuniculi (rabbit flea)	Lagomorpha: leporid (European rabbit, European hare, mountain hare); Carnivora: felid (cat, wildcat), canid (dog, red fox), mustelid (Eurasian otter, stoat, least weasel, European polecat); Rodentia: cricetid (bank vole), sciurid (eastern gray squirrel); Eulipotyphla: soricid (common shrew); Artiodactyla: cervid (European fallow deer); Anseriformes: anatid (mallard); Charadriiformes: alcid (Atlantic puffin); Galliformes: phasianid (grey partridge); Passeriformes: parid (Eurasian blue tit); Procellariiformes: procellariid (Manx shearwater); Strigiformes: strigid (little owl); Suliformes: phalacrocoracid (great cormorant)	irritation, tissue damage (+ vector for myxoma virus causing myxomatosis; *Francisella tularensis* causing tularemia, nonpathogenic *Trypanosoma nabiasi*)	worldwide

Parasite morphology: Like all fleas, the rabbit flea *Spilopsyllus cuniculi* forms 4 different types of morphological stages during its development: namely, eggs; larvae; pupae; and adults. The eggs are pearly white and ovoid measuring around 0.5 mm in length. They hatch to release elongate vermiform (worm-like) larvae which develop through 3 instars growing in length from 1-5 mm. The larvae are eruciform having cylindrical segmented bristly bodies with darker sclerotized heads possessing powerful mandibles and mandibular teeth. Mature third-stage larvae form silken ellipsoidal cocoons around 2 mm long and transform through pupae into adults. The larval head and some abdominal segments are lost and the body becomes compressed (shorter and wider) during pupation. Pupae are exarate with free appendages (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Following pupation, adult fleas eclose (emerge) from their pupal cocoons. Adults range from 1-2 mm in length and have laterally-compressed dark-brown bodies which are heavily chitinized with hard plates (called sclerites). They exhibit unique chaetotaxy (patterns of setation) with most spines, setae and bristles facing backwards so they do not impede forward movement of the flea through the pelage or plumage, but resist host grooming by catching on hairs or feathers when dragged backwards. In particular, *Spilopsyllus* has a unique combination of spines in comb-like rows (ctenidia) on the cheeks (genal) and thorax (pronotal). The pronotal ctenidia have a horizontal axis and contain 6-7 blunt spines on each side, while the genal ctenidia are

oblique (almost vertical, and not horizontal like *Ctenocephalides* spp.) with 4-6 straight blunt spines on each side. The body has 3 conspicuous tagma: an angular head; a compact thorax; and a bulbous abdomen. The head has a rounded frons (forehead) with small frontal tubercle (brow) and the genal process (cheek) lacks a spine. There are 2 lateral simple noncompound eyes (clusters of ocelli) located high on the head, followed by a pair of short compact club-like antennae (3-segmented) held in protective grooves (fossae) and then 2 stout spines located behind them. Adult fleas have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between 2 pairs of sensory palps: one pair consisting of long 4-segmented maxillary palps arising from short maxillary lobes (stipes); and the other pair consisting of long 5-segmented labial palps arising from a short basal labium. The mouthparts (fascicle) 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). 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 canal consists of a tubular foregut (anterior pharynx, salivary glands inserted apically, elongate oesophagus, small globular proventriculus), a large expandable digestive midgut (simple undivided gut, unlike the more elaborate divided midguts (with diverticula and caeca) in most other haematophagous arthropods), and a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 distinct segments (pronotum, mesonotum and metanotum), the former being more than half as long as the pronotal ctenidial spines. The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in a pair of curved claws. The hindmost pair of legs are much longer and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The ovate abdomen has 10 segments but the last 3 are highly modified by sensory and genital structures. The dorsal sclerotized plates (tergites) of segments 2-7 have a single row of setae and respiratory spiracles are located laterally. Both male and female fleas have a flat dorsal plate-like organ (sensilium or pygidium) with several dome-like structures with small bristles. Male fleas are smaller than females, and have highly elaborate genitals (arguably the most complex in the animal kingdom) consisting of an aedeagal apodeme (penis plate) with extendable penis rods which are coiled and retracted within an endophallic sac. The penis is thin and delicate and cannot enter the female without the support of the rods and posterior claspers. Males have 2 testes connected by tubular vas deferens to a seminal vesicle opening into the ejaculatory duct. Female fleas have 2 ovaries joined by tubular oviducts to the globular uterus opening to the vagina with a bursa copulatrix (depression to receive male organ) and associated saccular spermatheca (for sperm storage).

Site of infection: The adult stages of *S. cuniculi* are obligate ectoparasites of terrestrial mammals (mostly lagomorphs and a few small carnivores, rodents and shrews). On occasion, infestations have also been detected on several ground and water birds, often those close to or associated with burrows. Adults are often found clustered around the bases of the ears, along the ear margins, and sometimes the nose and eyelids of mammals, and around the neck and heads of birds. All other stages (eggs, larvae and pupae) occur in the external environment, particularly in burrows.

Pathogenesis: Adult rabbit fleas are relatively sedentary and remain attached to their hosts for long periods with their piercing-sucking mouthparts embedded in the skin while they periodically feed on host blood. Flea attachment and feeding causes traumatic structural damage to the skin with irritation, inflammation and pruritus. Light infestations often remain subclinical, but fleas tend to congregate on the ears of rabbits and their presence in large numbers may cause crusty lesions. Animals may attempt to groom infested regions by scratching or biting which may lead to self-trauma and wound exacerbation. Heavy infestations may cause blood loss sufficient enough to manifest as anaemia. When feeding, adult fleas inject saliva containing vaso-active compounds (anticoagulant, vasodilatory and anti-inflammatory chemicals) and some individual hosts exhibit allergic/hypersensitive reactions with expansive lesions but rarely with systemic effects. Lesions on other animals appear to be more subdued as fewer fleas appear to be involved in infestations (presumably due to the unique reproductive life cycle of the flea coinciding with that of the host (outlined below). Adult fleas have also been shown to act as vectors for infectious micro-organisms, including the bacterium *Francisella tularensis* causing tularemia (rabbit fever), the nonpathogenic protozoan parasite *Trypanosoma nabiasi,* and the myxoma virus causing myxomatosis. Indeed, rabbit fleas have been deliberately introduced into certain rabbit-infested regions to spread myxomatosis in attempts at biological control of pest populations (with good success due to the narrow host specificity of the fleas, their nidicolous burrow-inhabiting behaviour, their 'vertical' transmission between rabbit generations, and their ability to maintain viraemia for prolonged periods). Molecular screening studies have also detected the bacterium *Bartonella alsatica* in wild rabbits, but their involvement in the transmission of disease to humans (endocarditis and lymphadenitis) remains speculative.

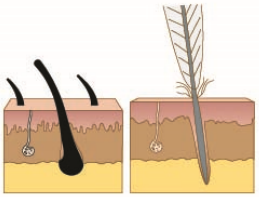
Developmental cycle and mode of transmission: Rabbit fleas exhibit holometabolous development where grub-like larvae undergo complete metamorphosis in pupae to become adult fleas. Their life-cycle is quite unique, however, as flea reproduction is coincident and contingent on host reproduction. While fleas may parasitize rabbits of any age and gender, they only complete reproduction when in contact with female rabbits (does) in late pregnancy or with newborn rabbits (kits). Female fleas only mature and complete egg development when they feed on blood from pregnant does containing high levels of oestrogens and corticosteroids (the presence of progesterones in non-pregnant rabbits inhibits or delays flea maturation). The presence of the pregnancy-related hormones also enhances flea defaecation rates (up to 5-fold) thus facilitating greater contamination of the burrow with flea dirt (flea faeces containing partially digested blood). When young rabbits are born, fleas move onto them within hours to feed and lay eggs, as well as to mate. Newborn rabbits (1-10 days old) emit airborne and urinary kairomones (pheromone-like chemicals that only benefit the receiver rather than the emitter) which attract fleas and stimulates copulation. Gravid female fleas lay non-sticky eggs which drop off hosts into the surrounding environment, particularly in burrows where humidity levels are high

enough (>50%) for their development. The eggs hatch after several days releasing larvae which feed on organic debris and detritus, especially flea dirt. The larvae develop through 3 instars over 15-45 days depending on environmental conditions (longer in colder conditions). Mature third-stage larvae form pupal cases (cocoons) in which they transform into adult fleas over 8-10 days. Adult fleas then emerge from cocoons, notably in response to vibrations caused by nearby hosts. They locate and feed on hosts within several days, but may survive without further feeding for several weeks (with some reporting periods up to 9 months in cold conditions). Sexual maturation of both male and female fleas occurs when they feed on pregnant does, and gravid females may lay up to 50 eggs per day for a few weeks around newborn kits. The whole life-cycle may be completed in as little as 14-21 days under ideal (warm humid) conditions, but may take as long as 6 months in adverse (dry cold) conditions. In many temperate and subtropical regions, infestations in wild lagomorphs appear to be seasonal, with peaks observed over summer.

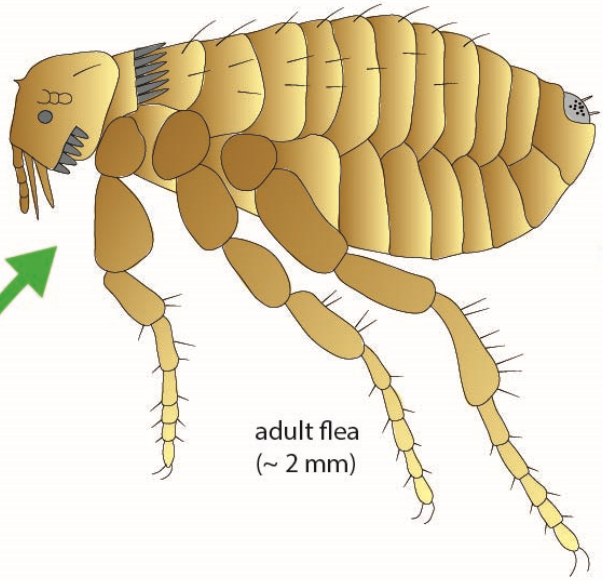
Differential diagnosis: Infestations are generally detected by finding fleas, flea dirt or eggs when parting the pelage or using a fine-toothed flea comb, particularly near crusted lesions along the ear margins. Adult fleas are best recovered and examined microscopically for their distinctive morphological features (esp. rounded head with small tubercle, oblique genal comb, and horizontal pronotal comb). Molecular biological techniques have been used to examine flea phylogenetic relationships by polymerase chain reaction (PCR) amplification of several gene sequences (18S ribosomal DNA, 28S ribosomal DNA, elongation factor 1-alpha, and cytochrome oxidase II).

Treatment and control: Laboratory animals and pets may be treated with various conventional and modern insecticides, including organophosphates (chlorfenvinphos, diazinon, malathion, trichlorfon), pyrethroids (permethrin, cypermethrin), chloronictinyles (imidacloprid), carbamates (carbaryl), arylpyrazoles (fipronil), macrocyclic lactones (selamectin) and some insect growth regulators (lufenuron). Treatments are available as sprays/mousses, shampoos/washes, powders or spot-ons, but attention should be paid to any contra-indications as several products may have toxic side-effects on rabbits (e.g. impregnated anti-flea collars should never be used on rabbits as they cause severe irritation and burning of the skin). Symptomatic relief may be sought using glucocorticoids to alleviate dermatitis and pruritus, and systemic antibiotics may be required to combat any secondary bacterial infections associated with flea bites and skin lesions. It is advised that any animals being translocated be quarantined and screened for infestations and that all in-contact animals be treated at the same time. Animal holding facilities should also be decontaminated using environmental insecticides with good residual activity against free-living stages (eggs, larvae and/or pupae); such as organophosphates and pyrethroids in flea bombs or sprays. Facilities should be kept clean, with regular disinfection (washing, shampooing, vacuuming, or steam-cleaning but ensuring substrates dry thoroughly) and frequent changes of bedding materials (particularly during rabbit breeding seasons).

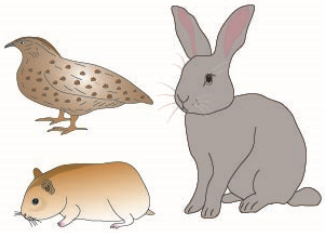
Spilopsyllus



skin, pelage/plumage
(irritation, dermatitis,
crusty lesions, anaemia)
(vector for infectious
microbial diseases)



adult flea
(~ 2 mm)

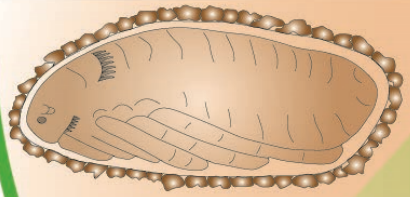


Definitive Hosts
(mammals,
esp. rabbits,
some birds)

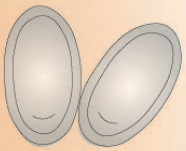
adult ectoparasitic on host
(feed on blood)

eggs
drop
off
host

eclosion

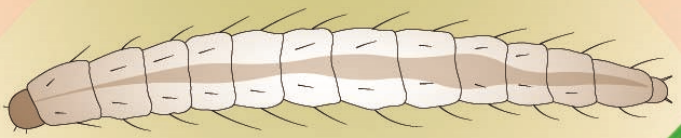


pupa
(~ 1 mm)



eggs
(~ 0.5 mm)

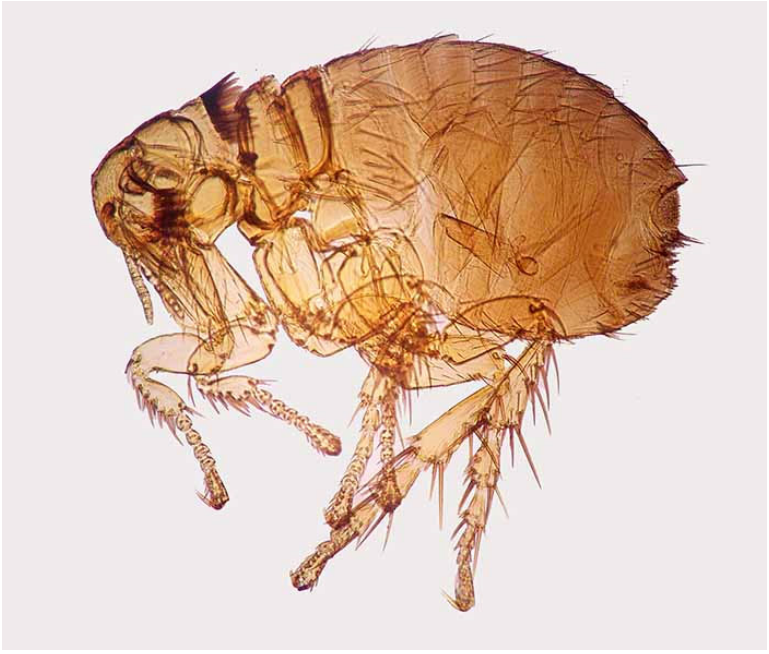
encasement



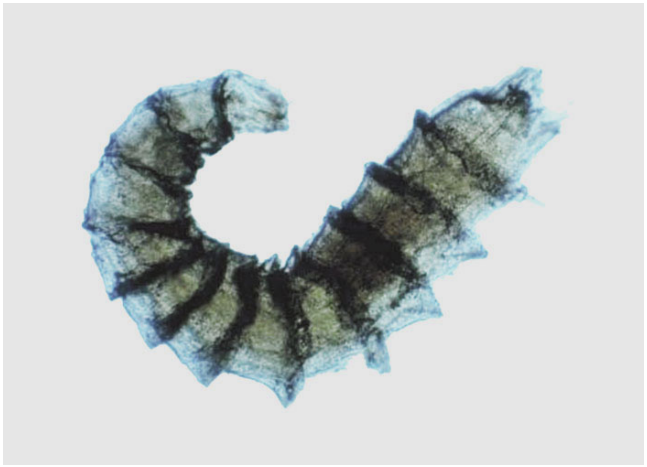
larva
(~ 4 mm)

hatch

free-living in external environment
(esp. bedding, warrens, hides, nests)



Spilopsyllus adult



Spilopsyllus larva