

Echidnophaga

(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 *Echidnophaga* spp. have short thoracic segments and infestations by these stick-tight (stick-fast) fleas have been associated with irritation and dermatitis in domestic and companion animals.

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: *Echidnophaga* (parasitic on skin of mammals/birds, sticktight/stickfast fleas)
Species: various species cause dermal lesions on wild and some domestic 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 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. 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						
<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
Tungidae						
<i>Tunga</i>	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	<i>Staphylococcus</i> , <i>Wolbachia</i> , tetanus
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

Echidnophaga spp. are characterized by the presence of angular pentagonal heads (rather than smooth rounded heads like other pulicids) and the absence of genal and pronotal ctenidia (combs). Females of most flea genera detach from their hosts after feeding, but those of *Echidnophaga* spp. undergo partial neosomy (abdominal development) and remain attached to the skin for most of their lives (hence their common name as stick-fast or stick-tight fleas). [Note that tungid fleas undergo complete neosomy whereby adult females burrow into the skin and undergo accelerated development (tachygenesis) with marked abdominal distention and encystment.] Some 23 *Echidnophaga* spp. have been described from a range of avian and mammalian hosts, most species having a broad host specificity and occurring on sympatric hosts. These fleas are widespread throughout the world, particularly in tropical and subtropical regions where warm moist environmental conditions are more conducive to flea development. They are often prevalent in areas where domestic poultry are kept, and some species are responsible for significant economical losses on commercial chicken farms. Some species have also been implicated in the transmission of bacterial and viral diseases, including bubonic plague, rickettsial fevers, and myxomatosis.

<i>Echidnophaga</i> species	Hosts	Clinical signs	Distribution
<i>E. aethiops</i>	Chiroptera: nycterid (Egyptian slit-faced bat, large slit-faced bat), rhinolophid (Darling's horseshoe bat, bushveld horseshoe bat), megadermatid (yellow-winged bat)		Africa
<i>E. ambulans</i>	Monotremata: tachyglossid (short-beaked echidna); Lagomorpha: leporid (rabbit)		Australia
<i>E. aranka</i>	Diprotodontia: potoroid (boodie)		Australia
<i>E. bradyta</i>	Carnivora: herpestid (meerkat, yellow mongoose, common slender mongoose); Rodentia: murid (bushveld gerbil), mustelid (striped polecat), petedid (South Africa springhare), sciurid (Cape ground squirrel)		Africa
<i>E. calabyi</i>	Diprotodontia: vombatid (common wombat, hairy nosed wombat)		Australia
<i>E. cornuta</i>	Diprotodontia: vombatid (common wombat, southern hairy nosed wombat)		Australia
<i>E. eyrei</i>	Diprotodontia: vombatid (wombat); Rodentia: murid (roof rat)		Australia
<i>E. gallinacea</i> (sticktight flea)	Galliformes: phasianid (chicken, red-winged francolin, turkey), numidid (guineafowl); Accipitriformes: accipitrid (black sparrowhawk); Anseriformes: anatid (duck); Columbiformes: columbid (crested pigeon, rock dove, Namaqua dove); Passeriformes: corvid	irritation, ulceration, pruritus, allergic	worldwide

	(Australian magpie), estrilidid (quailfinch), fringillid (yellow canary), hirundinid (white-backed swallow, brown-throated martin), malaconotid (southern boubo), meliphagid (noisy miner), meropid (little bee-eater, white-fronted bee-eater), motacillid (Cape wagtail, African pied wagtail, long-legged pipit), muscicapid (Arnot's chat), ploceid (red-billed quelea); Strigiformes: strigid (marsh owl); Suliformes: phalacrocoracid (reed cormorant), sulid (Cape gannet); Carnivora: canid (dog, golden jackal, black-backed jackal, Cape fox, kit fox), felid (cat, African wildcat, black-footed cat, caracal, serval), herpestid (meerkat, yellow mongoose, common slender mongoose, marsh mongoose, Cape gray mongoose, white-tailed mongoose, Selous's mongoose, banded mongoose), hyaenid (aardwolf, striped hyena, brown hyena), mustelid (striped polecat), viverrid (common genet, rusty-spotted genet, African civet, small Indian civet); Lagomorpha: leporid (European rabbit, black-tailed jackrabbit, scrub hare, Jameson's red rock hare); Dasyuromorphia: dasyurid (brush-tailed phascogale), myrmecobiid (numbat); Diprotodontia: potoroid (boodie), phalangerid (common brushtail possum); Peramelemorphia: thylacomyid (greater bilby); Monotremata: tachyglossid (short-beaked echidna); Rodentia: hystricid (Cape porcupine), murid (brown rat, black rat, red rock rat, Namaqua rock rat, African grass rat, South African vlei rat, bush vlei rat, Brandt's whistling rat, creek groove-toothed swamp rat, greater sticknest rat, acacia rat, multimammate mouse, Griselda's striped grass mouse, four-striped grass mouse, Cape gerbil, Cape short-eared gerbil, hairy-footed gerbil, highveld gerbil), nesomyid (South African pouched mouse), pedetid (South African springhare), petromurid (dassie rat), sciurid (Cape ground squirrel); Macroscelidea: macroscelidid (rufous elephant shrew, western rock elephant shrew, round-eared elephant shrew, four-toed elephant shrew); Eulipotyphla: erinaceid (four-toed hedgehog, South African hedgehog), soricid (musk shrew); Artiodactyla: bovid (goat, cattle); Perissodactyla: equid (horse); Primates: cercopithecid (grivet, king colobus, Chacma baboon), hominid (humans)	dermatitis	
<i>E. iberica</i>	Lagomorpha: leporid (rabbit)		Europe
<i>E. inexpectata</i>	Artiodactyla: suid (desert warthog)		Africa
<i>E. larina</i>	Artiodactyla: suid (pig, desert warthog, red river hog), bovid (cattle, common duiker, red-flanked duiker harnessed bushbuck); Carnivora: canid (dog, African wild dog, black-backed jackal, Cape fox), felid (cat, black-footed cat, African wildcat, lion, leopard, serval), herpestid (meerkat, white-tailed mongoose), hyaenid (aardwolf, spotted hyena, striped hyena, brown hyena), viverrid (common genet); Lagomorpha: leporid (rabbit); Perissodactyla: equid (horse); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (crested porcupine, Cape porcupine), murid (red rock rat); Anseriformes: anatid (white-faced whistling duck); Coliformes: coliid (red-faced mousebird)		Eurasia, Africa
<i>E. liopus</i>	Monotremata: tachyglossid (short-beaked echidna); Rodentia: murid (rat)		Australia, India
<i>E. macronychia</i>	Diprotodontia: potoroid (boodie)		Australia
<i>E. murina</i>	Rodentia: murid (Sundevall's jird, black rat), dipodid (greater Egyptian jerboa)		Middle-East
<i>E. myrmecobii</i>	Diprotodontia: macropodid (eastern grey kangaroo), phalangerid (common brushtail possum), potoroid (boodie), pseudocheirid (common ringtail possum), vombatid (common wombat); Peramelemorphia: thylacomyid (bilby); Dasyuromorphia: dasyurid (tiger quoll, eastern quoll, red-tailed phascogale, fat-tailed dunnart, kultarr), myrmecobiid (numbat); Rodentia: murid (long-haired rat, black rat, brown rat, greater sticknest rat, rakali, house mouse, Mitchell's hopping mouse); Lagomorpha: leporid (European rabbit); Carnivora: felid (cat), Canid (dog, red fox); Primates: hominid (human); Serpentes: elapid (eastern brown snake)		Australia
<i>E. ochotona</i>	Lagomorpha: ochotonid (pika)		China
<i>E. octotricha</i>	Diprotodontia: vombatid (hairy-nosed wombat)		Australia
<i>E. oschanini</i>	Rodentia: murid (great gerbil); Passeriformes: muscicapid (isabelline)		Asia

	wheatear)		
<i>E. perilis</i>	Diprotodontia: potoroid (boodie), vombatid (hairy-nosed wombat); Peramelemorphia: thylacomyid (bilby); Dasyuromorphia: myrmecobiid (numbat); Rodentia: murid (black rat); Lagomorpha: leporid (European rabbit); Carnivora: felid (cat), Canid (dog, red fox); Primates: hominid (human); Monotremata: tachyglossid (short-beaked echidna)		Australia
<i>E. popovi</i>	Carnivora: mustelid (European badger)		Europe
<i>E. suricatta</i>	Carnivora: herpestid (meerkat)		Africa
<i>E. tarda</i>	Carnivora: felid (African wildcat), hyaenid (striped hyaena)		Africa
<i>E. tenerifensis</i>	Rodentia: murid (rat)		Canary Islands
<i>E. tiscadaea</i>	Rodentia: dipodid (Gobi jerboa)		Mongolia

Parasite morphology: *Echidnophaga* spp. form 4 different types of morphological stages during their development: namely, eggs; larvae (3 instars); pupae; and adults. The eggs are shiny white ovoid stages approximately 0.5 mm long. They hatch to release elongate vermiform (worm-like) larvae which moult twice growing up to 6 mm long. The larvae have soft white-yellow segmented bodies (3 thoracic and 10 abdominal segments) with numerous stout bristles protruding from each segment. They have darker sclerotized heads possessing powerful dentate mandibles well adapted for biting and chewing. Mature third-stage larvae produce silk from mandibular glands and create loosely-woven pupal cocoons which are sticky and become covered with debris from the surrounding environment. Pupae are roughly ovoid measuring around 4 mm long and they are initially white-yellow in colour but become brown with adherent debris. The larval head and last 3 segments are lost during pupation and the pupal body becomes compressed (shorter and wider). They are exarate pupae with legs free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). The pupae have begun to develop elongated mouthparts, short antennae, inconspicuous eyes, and setae and bristles. Adult fleas are wingless dark brown insects, with laterally compressed bodies ranging from 1.0-2.5 mm long. They are covered by a heavily chitinized exoskeleton with hard plates (sclerites) but with reduced chaetotaxy; i.e. their covering of bristles and spines is sparse and limited to a few rows on thoracic and abdominal segments and legs. Unlike many other flea genera, *Echidnophaga* spp. do not have comb-like rows (ctenidia) of bristles on their cheeks (genal) or thorax (pronotal). Adult fleas have 3 conspicuous body parts: an angular head; small thorax; and ovoid abdomen. The head is highly distinctive and has a sharply angular dorsal profile forming a squarish-pentagonal shape. The frons (forehead) is heavily sclerotized and integricipit (without an interantennal suture). The antennae are composed of 3 short club-like segments held in protective grooves (fossae) with 2 setae posteriorly. The head bears 2 well-developed simple (non-compound) eyes (clusters of ocelli) located laterally, and has large mouthparts projecting conspicuously from the antero-ventral surface. The piercing-sucking mouthparts are located between sensory palps consisting of a pair of long 4-segmented maxillary palps as well as a pair of long unsegmented labial palps. The actual mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being broad with serrated edges used to puncture skin; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas) and used to enter a capillary. 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 an anterior pharynx (with salivary glands inserted apically), elongate oesophagus, small globular proventriculus (armed with spines to prevent regurgitation), large expandable midgut (simple undivided organ lacking diverticula and caeca, unlike the more elaborate divided midguts of most other haematophagous arthropods), tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax is short and narrowed dorsally, with 3 small segments (pronotum, mesonotum, and metanotum) lacking a meral rod (vertical thickening). The ventral thorax gives rise to 3 pairs of long muscular legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) with the hind-coxae having an inner patch of spiniform setae, and all legs terminating in 2 claws. The hindmost pair of legs are much larger than the others, and are well adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The abdomen is ovate and has 10 segments, but the last 3 segments are highly modified by genital and sensory structures. Both sexes have a flat dorsal plate-like organ (sensillum or pygidium) with several (8-14) dome-like structures with central bristles. Males are smaller than females (1.0-2.0 v. 2.0-2.5 mm long) and have highly elaborate genitals (possibly the most complex in the animal kingdom). Males have 2 testes connected by vas deferens to a seminal vesicle and ejaculatory ducts leading to an aedeagal apodeme (penis plate) and extendable penis rods coiled and retracted within an endophallic sac. The penis is thin and pliable and cannot enter the female without the support of the rods and posterior claspers. Females have 2 ovaries connected by oviducts to the uterus leading to the vagina. The uterus has an associated bursa copulatrix (depression to receive male organ) and a subglobular spermatheca (for sperm storage) connected to the bursa by a sclerotized tube.

Site of infection: Adult fleas are obligate ectoparasites that live on the skin and feed on blood from warm-blooded vertebrate hosts. The fleas exhibit variable host specificity and usually infest small numbers of mammalian hosts (particularly rodents, carnivores, marsupials and ungulates) as well as some avian hosts (including passerines, fowl, and water birds). The fleas are photophobic and preferentially attach to dermal surfaces shielded from sunlight, and they also attach for long periods of time to bare skin or skin sparsely covered with hair/fur or feathers (hence their common names of sticktight or stickfast fleas). Adults usually attach to the ventral abdomen, ear canals, pinnae, periorbital skin, scrotum and interdigital webs of mammals, while they preferentially attach to the head, wattle, comb and anus of birds. Eggs, larvae and pupae are free-living stages in the environment and are strongly associated with animal resting sites (such as burrows, dens, hides and nests).

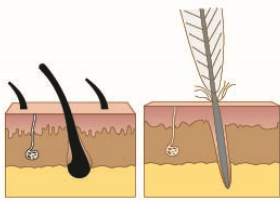
Pathogenesis: Infestations by adult fleas vary considerably in their pathogenic impacts on their hosts, ranging from transient irritating pests to persistent aetiological agents of mild-severe clinical disease (skin lesions, anaemia) contributing to poor health and production losses (reduced meat and egg production) with occasional mortalities. The severity of infestation depends on both host and parasite variables, including parasite virulence, site of infestation, host susceptibility (age and nutritional status) and host resistance (immunological status). Light infestations are generally subclinical, mild infestations may cause intermittent dermatitis and production losses, while heavy infestations may cause severe disease characterized by ulcerative lesions. Adult fleas feed on host blood using their mouthparts to pierce the skin and suck blood. Their mouthparts also have barbed edges that allow the fleas to attach and hold fast to their hosts. During feeding, the fleas inject saliva containing vaso-active compounds (anticoagulants, vasodilators and anti-inflammatories) to assist blood flow. Heavy infestations have been associated with blood loss severe enough to manifest as iron-deficiency anaemia. Female fleas also tend to burrow into the skin and remain attached using their mouthparts even when not feeding. Flea bites cause tissue trauma with localized dermatitis, oedema and pruritus. Animals become restless and seek relief by vigorous grooming (biting/pecking, scratching, rubbing), often resulting in further trauma and opening wounds to secondary bacterial infections. Birds often show feather loss due to excessive preening. Attachment and bite sites may become ulcerated with serous discharges and small haemorrhages. Gravid female fleas may lay eggs in ulcerative subcutaneous wounds, which is thought to contribute to further inflammation due to the presence of foreign material. Infestations around the eyes and ears can lead to swelling and lesions which compromise sight and hearing in smaller animals, sometimes progressing to blindness and deafness. Infested animals have a reduced ability to forage or hunt and their general health declines with subsequent wasting due to starvation, and sometimes death. There are miscellaneous reports of these fleas harbouring potentially pathogenic microbes but their role in disease transmission is unclear due to the characteristic stick-tight behaviour of adult fleas on individual hosts. Molecular screening studies have detected various *Rickettsia* spp. (potentially involved in rickettsioses) and even *Yersinia pestis* (aetiological agent of bubonic plague). One species (*E. myrmecobii*) has been shown to transmit myxoma virus (causing myxomatosis) to rabbits, with virus particles residing in flea gut and mouthparts for several weeks.

Developmental cycle and mode of transmission: Like all fleas, *Echidnophaga* spp. exhibit holometabolous development whereby vermiform larval stages undergo complete metamorphosis in pupae to form adult stages. Gravid female fleas lay 1-4 eggs each day on their hosts, even in ulcerations. The eggs usually drop from the hosts into the external environment, often being found in bedding or nesting materials. They hatch in 4-16 days depending on prevailing environmental conditions, taking longer in colder conditions. Vermiform (worm- or maggot-like) larval stages emerge and feed on organic debris using their biting/chewing mandibles. Food sources include manure, eggshells, flea dirt (adult flea faeces consisting of pellets of dried blood that have dropped from the host into the environment), and even other larvae. They are negatively phototactic (move away from light) and positively geotactic (move towards the earth) and are able to burrow into soil, leaf litter, nests and even carpets. There are 3 larval instars with 2 moults occurring over several weeks. Mature larvae burrow deeper into the soil and form cocoons in which they pupate to adult stages over 9-31 days, although they may remain as pupae for several months in harsh dry or cold environmental conditions. Adult fleas eclose (emerge) from pupae when environmental conditions (particularly temperature) are favourable, when disturbed by vibrations or mechanical pressure, and when stimulated by the presence of host body heat and increased carbon dioxide concentrations. They search for suitable hosts and are able to jump to heights of 20-40 cm. They need to find a host within 5-8 days as both male and female fleas are obligate haematophagous ectoparasites and require bloodmeals to survive and mature sexually. After mating, female fleas remain attached to their hosts for 2-6 weeks. Some authorities consider that stick-tight fleas exhibit partial neosomy (enlargement or formation of new external structures by secretion of new cuticle) during their attachment phase. Sticktight behaviour and prolonged feeding causes the formation of ulcers, in which the female lays her eggs. Most eggs drop out of wounds onto the ground, but some may remain caught up in secretions until they hatch whereupon the larvae drop out to the ground. The whole life-cycle may be completed in 30-60 days, but may take longer when environmental conditions fluctuate. Transmission between hosts generally occurs when newly emergent adult fleas quest for hosts, although adults (particularly males) may also move between hosts in close contact or proximity. Because *Echinophaga* spp. require organic material for their developmental cycles, infestations are most common in rural areas where domestic animals are free-ranging and may intermingle with other reservoir hosts. Infestations have been reported to spread into wildlife in adjacent areas such as woodlands, marshlands and nature reserves.

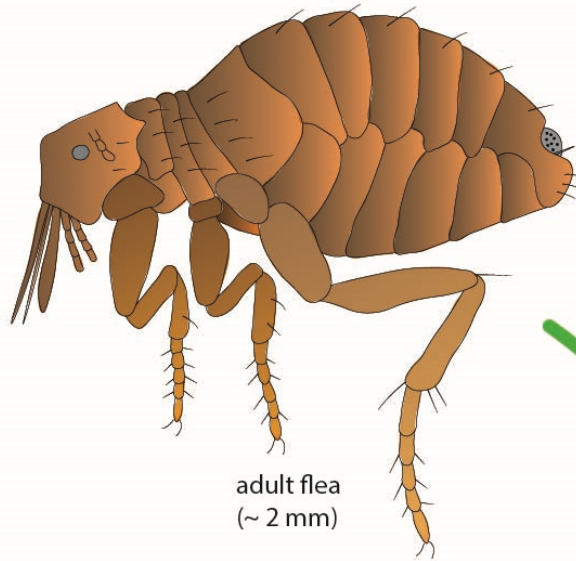
Differential diagnosis: Infestations can be suspected on clinical grounds (flea bites, ulcerated lesions) and the detection of flea dirt (faeces) in the pelage or plumage (which turns red when moistened). Provisional diagnoses are confirmed by the direct detection of adult fleas, usually clustered together in lesions particularly in areas of bare skin and around the head. However, fleas can sometimes be difficult to detect because of their small size and their habit of partially burrowing into the skin (stick-tight attachments). Because they are similar in size, shape and coloration to other ectoparasites (other fleas and ticks), specimens should be collected for microscopic examination. Most other fleas are readily detached or quickly move away from light, whereas stick-tight fleas are difficult to pull off and often tear. *Echidnophaga* spp. are easily identified under magnification due to the angular shape of the head, the sparse covering of setae and bristles and the absence of genal and pronotal combs. Molecular biological techniques have been applied to the characterization of species following the amplification of nuclear (ribosomal RNA) gene sequences by polymerase chain reaction (PCR).

Treatment and control: Clinical infestations are usually treated with chemical insecticides, as the physical removal of fleas using tweezers or forceps is laborious and very difficult as the adult stick-tight fleas are firmly embedded in host skin. A range of commercial insecticides are available as topical preparations (sprays, shampoos, washes, pastes, mousse, powders) or as systemic preparations (oral, injectable, or spot-ons). Effective control has been reported following treatment with organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), pyrethrin and synthetic pyrethroids (permethrin, cyfluthrin, cypermethrin), carbamates (carbaryl), arylpyrazoles (fipronil), natural products (rotenone) and some insect growth regulators (IGRs, such as lufenuron). It is recommended that animals with ulcerated lesions also be treated with antibiotics to prevent secondary bacterial infection. Single treatments with insecticides that have long-lasting residual activity may be sufficient to prevent reinfestation, while multiple treatments several weeks apart are required for products that have poor residual activity. It is further recommended that the immediate environment (particularly bedding, nests, burrows and hides) be treated with environmental insecticides (such as flea bombs and sprays containing organophosphates or pyrethroids) or desiccants (such as sodium polyborate). Various preventive strategies may be adopted to disrupt transmission cycles, particularly those involving improved sanitation (regular removal of manure/litter, frequent changing of bedding/nesting materials), good hygiene (grooming, water/dust baths), isolating livestock (vermin-proof enclosures, pasture/pen rotation, quarantine), and regular health surveillance (screening and treatment).

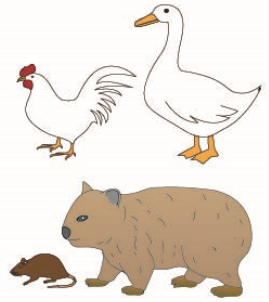
Echidnophaga



skin, pelage/plumage
(irritation, dermatitis,
ulceration, anaemia)
(possible vectors for
infectious diseases)



adult flea
(~ 2 mm)

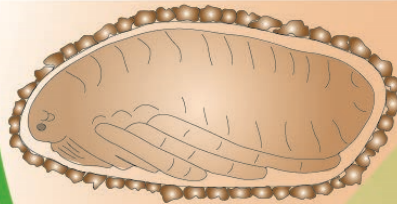


Definitive Hosts
(mammals, birds)

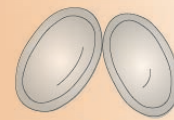
adult ectoparasitic on host
(stick tight and feed on blood)

eclosion

eggs drop
off host



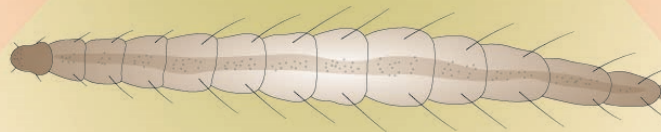
pupa
(~ 3 mm)



eggs
(~ 0.5 mm)

encasement

hatch

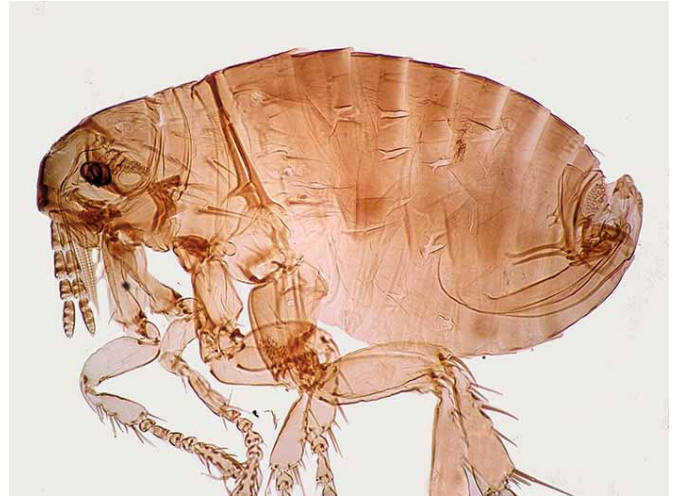


larva
(~ 5 mm)

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



Echidnophaga adult female



Echidnophaga adult male



Echidnophaga eggs



Echidnophaga larva