Ceratophyllus
(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. Ceratophyllid fleas occur as ectoparasites on small rodents and birds, many being associated with nest habitats so adult fleas are transient parasites. Infestations by *Ceratophyllus* spp. have been associated with irritation, pruritus and allergic dermatitis in domestic birds and animals, including humans.

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:	Ceratophyllidae (parasites of small rodents and birds)
Genus:	*Ceratophyllus* (parasitic on skin of rodents and birds)
Species:	various species cause dermatitis

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. Ceratophyllid fleas are characterized by their elongate laterally-compressed bodies, the absence of genal combs but the presence of pronotal combs. Some 45 genera have been identified in 2 subfamilies: Ceratophyllinae (*Aenigmopsylla, Aetheca, Amalaraeus, Amaradix, Amphalius, Baculomeris, Brevictenidia, Callopsylla, Ceratophyllus, Citellophilus, Dasypsyllus, Eumolpianus, Glaciopsyllus, Hollandipsylla, Igioffius, Jellisonia, Kohlsia, Libyastus, Macrostylophora, Malaraeus, Margopsylla, Megabothris, Megathoracipsylla, Mioctenopsylla, Myoxopsylla, Nosopsyllus, Opisodasys, Orchopeas, Oropsylla, Paraceras, Paramonopsyllus, Pleochaetis, Plusaetis, Rostropsylla, Rowleyella, Smitipsylla, Spuropsylla, Syngenopsyllus, Tarsopsylla, Thrassis, Traubella, Psittopsylla*) and Dactylopsyllinae (*Dactylopsylla, Foxella, Spicata*). Species from several genera are considered to be serious pests of domestic poultry and companion animals, while the remainder infest a wide range of wild animals.

Genera	No. spp.	Hosts	Ctenidia (combs)		Disease	Vector
			Genal (head)	Pronotal (thorax)		
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
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

The genus *Ceratophyllus* contains some 64 species allocated to 6 subgenera: namely, *C.* (*Ceratophyllus*) with 37 spp., *C.* (*Celeophilus*) with 2 spp., *C.* (*Emmareus*) with 11 spp., *C.* (*Amonopsyllus*) with one sp., *C.* (*Monopsyllus*) with 10 spp., and *C.* (*Rosickyiana*) with a single species. The former 3 subgenera are found mainly on birds, and the latter 3 subgenera mainly on squirrels. The fleas are found mostly in temperate Holarctic regions, with some 38 spp. confined to the Palaearctic (Eurasia), 14 spp. to the Nearctic (North America), 4 spp. to the Neotropics (Central and South America), and the remainder occurring several other subregions. The species *C. gallinae* (hen flea or European chicken flea) is regarded to be a pest species in domestic poultry but is not considered to be an important vector of disease. Adult fleas, however, are highly agile and exhibit broad host specificity being able to infest a wide range of birds (particularly nesting birds) and some small mammals.

***Ceratophyllus* species**	**Hosts**	**Clinical signs**	**Distribution**
C. adustus	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed wood swallow); Piciformes: picid (woodpecker); Rodentia: erethizontid (North American porcupine)		North America
C. affinis	Passeriformes: hirundinid (barn swallow)		Holarctic
C. altus	Falconiformes: falconid (American kestrel); Strigiformes: strigid (Andean pygmy owl)		Americas
C. (*M.*) *anisus*	Rodentia: murid (black rat, brown rat)		Eurasia
C. arcuegens	Passeriformes: hirundinid (cliff swallow)		North America
C. avicitelli	Passeriformes: muscicapid (isabelline wheatear, stonechat)		Eurasia
C. balati	Passeriformes: motacillid (rock pipit)		Europe
C. (*E.*) *borealis* (cliff/rock birds-nest flea)	Charadriiformes: alcid (Atlantic puffin), larid (European herring gull, Arctic tern); Passeriformes: alaudid (Eurasian skylark), cinclid (white-throated dipper), corvid (red-billed chough), motacillid (European rock pipit, grey wagtail, white-browed wagtail), muscicapid (northern wheatear, common redstart, African stonechat), passerid (snowfinch), prunellid (dunnock), sylviid (common whitethroat), troglodytid (Eurasian wren), turdid (thrush); Suliformes: sulid (northern gannet)		Holarctic
C. breviprojectus	Passeriformes: hirundinid (red-rumped swallow)		Tibet
C. calderwoodi	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed wood swallow); Piciformes: picid (woodpecker)		Eurasia, Australia

C. caliotes	Passeriformes: hirundinid (common house martin, sand martin, cave swallow)		Holarctic
C. celsus	Passeriformes: hirundinid (sand martin, cliff swallow)		North and Central America
C. (*E.*) *chasteli*	Suliformes: phalacrocoracid (European shag)		Europe
C. chutsaensis	Passeriformes: muscicapid (isabelline wheatear); Lagomorpha: ochotonid (pika)		Asia
C. ciliatus	Rodentia: sciurid (chipmunk)		North America
C. coahuilensis	Passeriformes: hirundinid (cave swallow)		North America
C. (*E.*) *columbae* (pigeon flea, pigeon nest flea)	Columbiformes: columbid (rock dove, blue rock pigeon, common wood pigeon); Carnivora: felid (cat); Primates: hominid (human)	irritation, anaemia, allergic dermatitis	Holarctic
C. delichoni	Passeriformes: hirundinid (common house martin)		Europe
C. diffinis	Podicipediformes: podicipedid (red-necked grebe)		North America
C. enefdeae	Passeriformes: tyrannid (Say's phoebe), muscicapid (wheatear), corvid (Eurasian magpie)		Holarctic
C. (*C.*) *farreni*	Columbiformes: columbid (common wood pigeon); Passeriformes: hirundinid (common house martin, barn swallow), passerid (house sparrow); Carnivora: felid (cat)		Palearctic, Asia
C. (E.) fionnus	Procellariiformes: procellariid (Manx shearwater)		Europe
C. frigoris	Passeriformes: motacillid (gray wagtail)		Russia
C. (*C.*) *fringillae* (house sparrow/starling flea)	Passeriformes: alaudid (Eurasian skylark), corvid (carrion crow), fringillid (common chaffinch), hirundinid (common house martin, sand martin, barn swallow), motacillid (European rock pipit, white-browed wagtail), muscicapid (spotted flycatcher), parid (Eurasian blue tit, great tit), passerid (house sparrow), prunellid (dunnock), sturnid (common starling), sylviid (common whitethroat); Strigiformes: strigid (tawny owl); Apodiformes: apodid (common swift); Carnivora: felid (cat); Primates: hominid (human)		Eurasia
C. (*C.*) *gallinae* (hen flea, European chicken flea)	Galliformes: phasianid (chicken, grey partridge, ring-necked pheasant, willow ptarmigan); Accipitriformes: accipitrid (Eurasian sparrowhawk, red kite); Anseriformes: anatid (kelp goose); Charadriiformes: larid (black-legged kittiwake), stercorariid (parasitic jaeger); Falconiformes: falconid (merlin); Gruiformes: rallid (corn crake, common moorhen); Passeriformes: acrocephalid (sedge warbler), aegothelid (long-tailed tit), alaudid (Eurasian skylark), apodid (common swift), calcariid (snow bunting), certhiid (Eurasian treecreeper), cinclid (white-throated dipper), corvid (common raven, carrion crow, rook, western jackdaw, Eurasian jay, red-billed chough), emberizid (yellowhammer, common reed bunting), fringillid (common linnet, European goldfinch, European greenfinch, common chaffinch, twite, Eurasian siskin, red crossbill), hirundinid (common house martin, sand martin, barn swallow), motacillid (European rock pipit, meadow pipit, tree pipit, white wagtail, grey wagtail, white-browed wagtail), muscicapid (European robin, common nightingale, northern wheatear, bluethroat, pied flycatcher, spotted flycatcher, black redstart, common redstart, African stonechat), parid (coal tit, Eurasian blue tit, great tit, marsh tit), passerid (house sparrow, Eurasian tree sparrow), phylloscopid (wood warbler, willow warbler), prunellid (dunnock), regulid (goldcrest), sittid (Eurasian nuthatch), sturnid (common starling), sylviid (Eurasian blackcap, garden warbler, common whitethroat, lesser whitethroat, barred warbler), troglodytid (Eurasian wren), turdid (redwing, common blackbird, song thrush, mistle thrush); Columbiformes: columbid (rock dove, stock dove, Eurasian collared dove, common wood pigeon); Piciformes: picid (great spotted woodpecker, Eurasian wryneck); Procellariiformes: procellariid (northern fulmar); Strigiformes: strigid (little owl, tawny owl);		Eurasia

	Suliformes: phalacrocoracid (European shag); Rodentia: cricetid (common vole, short-tailed field vole), echimyid (coypu), murid (brown rat, wood mouse), sciurid (eastern grey squirrel); Lagomorpha: leporid (European rabbit); Artiodactyla: bovid (cattle), cervid (Indian muntjac); Carnivora: canid (dog, red fox), felid (cat), mustelid (European pine marten, stoat, ferret, least weasel); Chiroptera: vespertilionid (common noctule); Primates: hominid (human)		
C. (*E.*) *garei* (ground-nesting bird flea)	Anseriformes: anatid (northern shoveler, Eurasian teal, mallard, tufted duck, northern pintail, common scoter, common eider, red-breasted merganser); Charadriiformes: alcid (Atlantic puffin), charadriid (common ringed plover, northern lapwing), larid (European herring gull, common gull, lesser black-backed gull, great black-backed gull, black-headed gull, Arctic tern), scolopacid (dunlin, common snipe, Eurasian woodcock, common redshank); Columbiformes: columbid (rock dove); Galliformes: phasianid (red-legged partridge, willow ptarmigan, grey partridge, ring-necked pheasant); Gruiformes: rallid (common moorhen); Passeriformes: corvid (Eurasian skylark, hooded crow, carrion crow, western jackdaw, red-billed chough), emberizid (yellowhammer, common reed bunting, corn bunting), fringillid (common linnet, European greenfinch, common chaffinch), hirundinid (barn swallow), motacillid (European rock pipit, meadow pipit, white wagtail, grey wagtail, white-browed wagtail), muscicapid (European robin, northern wheatear, whinchat, African stonechat), panicrid (bearded reedling), passerid (house sparrow), prunellid (dunnock), regulid (goldcrest), sturnid (common starling), troglodytid (Eurasian wren), turdid (common blackbird, ring ouzel); Piciformes: picid (Eurasian wryneck, green woodpecker); Strigiformes: strigid (long-eared owl); Suliformes: phalacrocoracid (European shag); Rodentia: cricetid (bank vole), murid (wood mouse, Eurasian harvest mouse); Lagomorpha: leporid (European rabbit, European hare); Carnivora: mustelid (stoat)		Holarctic
C. gilvus	Passeriformes: hirundinid (cliff swallow)		North America
C. glaphyrus	Passeriformes: parid (coal tit)		
C. hagoromo	Procellariiformes: procellariid (streaked shearwater); Charadriiformes: alcid (tufted puffin)		Japan
C. (*C.*) *hirundinis* (house martin flea	Passeriformes: hirundinid (common house martin, sand martin, barn swallow); Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken)		Europe
C. idius	Passeriformes: hirundinid (barn swallow, tree swallow, purple martin)		North America
C. igii	Anseriformes: anatid (shelduck)		Russia
C. lari	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow); Piciformes: picid (woodpecker)		North America
C. (*Rosickyiana*) *lunatus*	Carnivora: mustelid (ermine, marten)		Holarctic
C. maculatus	Passeriformes: hirundinid (common house martin)		Russia
C. nanshanensis	Passeriformes: hirundinid (red-rumped swallow, Eurasian crag martin)		China
C. niger (western chicken flea, black hen flea)	Galliformes: phasianid (chicken); Strigiformes: strigid (northern saw-whet owl, long-eared owl); Piciformes: picid (green woodpecker, wryneck)		North America
C. olsufjevi	Passeriformes: hirundinid (common house martin)		Russia
C. orites	Passeriformes: hirundinid (common house martin); Rodentia: murid (Mongolian gerbil)		Asia
C. pelecani	Charadriiformes: larid (western gull); Pelecaniformes: pelecanid (pelican)		North America
C. petrochelidoni	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow), hirundinid (American cliff swallow); Piciformes: picid (woodpecker)		North America
C. phrillinae	Rodentia: murid (Himalayan field mouse)		Nepal

C. pullatus	Passeriformes: passerid (house sparrow, tree sparrow)		Europe
C. qinghaiensis	birds nest		China
C. rauschi	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow); Piciformes: picid (woodpecker, northern flicker)		North America
C. (C.) rossittensis	Passeriformes: corvid (carrion crow); Strigiformes: strigid (owl)		Holarctic
C. (*C.*) *rusticus* (house martin flea)	Passeriformes: hirundinid (common house martin, barn swallow); Columbiformes: columbid (common wood pigeon)		Europe
C. (*M.*) *sciurorum*	Rodentia: sciurid (eastern grey squirrel), cricetid (European water vole, bank vole), glirid (hazel dormouse, European edible dormouse), murid (wood mouse); Lagomorpha: leporid (European rabbit); Eulipotyphla: soricid (common shrew); Carnivora: canid (red fox), mustelid (pine marten, stoat, least weasel); Primates: hominid (human); Columbiformes: columbid (stock dove, common wood pigeon); Passeriformes: corvid (western jackdaw, Eurasian magpie), motacillid (white-browed wagtail), turdid (mistle thrush); Strigiformes: strigid (tawny owl)		Eurasia
C. sclerapicalis	Passeriformes: hirundinid (common house martin, red-rumped swallow)		China
C. scopulorum	Passeriformes: hirundinid (cliff swallow)		North America
C. sinicus	Lagomorpha: ochotonid (pika)		China
C. spinosus	Falconiformes: falconid (lesser kestrel)		Eurasia
C. sternacuminatus	Passeriformes: hirundinid (tree swallow)		North America
C. (*C.*) *styx* (sand martin flea)	Passeriformes: hirundinid (sand martin, common house martin), cinchlid (white-breasted dipper), corvid (western jackdaw), parid (Eurasian blue tit), sturnid (common starling); Rodentia: cricetid (bank vole)		Holarctic
C. titicacensis	Suliformes: phalacrocoracid (Neotropic cormorant)		South America
C. tribulis (syn. *C. passerinus*)	Passeriformes: passerid (Eurasian tree sparrow)		Russia
C. (*C.*) *vagabundus* (corvid/heron nest flea)	Passeriformes: corvid (common raven, carrion crow, western jackdaw, Eurasian magpie, red-billed chough), motacillid (Eurasian rock pipit), muscicapid (spotted flycatcher, northern wheatear); Charadriiformes: alcid (Atlantic puffin, crested auklet, parakeet auklet), larid (European herring gull, black-legged kittiwake), scolopacid (ruddy turnstone); Columbiformes: columbid (rock dove); Falconiformes: falconid (peregrine falcon); Accipitriformes: accipitrid (European honey buzzard); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (grey heron); Procellariiformes: procellariid (northern fulmar, manx shearwater); Strigiformes: strigid (tawny owl); Suliformes: phalacrocoracid (European shag, great cormorant, neotropical cormorant)		Holarctic
C. vison	Rodentia: sciurid (red squirrel)		Eurasia
C. wui	Apodiformes: apodid (Himalayan swiftlet)		Asia
C. yamane	Rodentia: glirid (Japanese dormouse)		Japan
C. zhovtyi	Strigiformes: strigid (Eurasian pygmy owl)		Russia

Parasite morphology: *Ceratophyllus* spp. form 4 different morphological types of developmental stages: eggs; larvae (3 instars); pupae (in cocoons); and adults (male and female fleas). The eggs are pearly white ovoid stages measuring 0.5-0.6 mm in length. Larvae are elongate grey-white vermiform (worm-like) stages with segmented bodies (13 segments) and brown sclerotized heads with powerful mandibles and mandibular teeth adapted for biting and chewing. The larvae are essentially cylindrical although the middle segments are somewhat flattened dorsoventrally and the caudal segment bears a pair of anal struts. Each segment is adorned with small backward-facing bristles that increase in length posteriad. Larvae develop though 3 instars growing in length from 1.6-4.0 mm. Mature larvae form silken cocoons that are roughly ovoid measuring 2-3 mm. The cocoons are sticky and become covered with small particulate matter from the environment. The enclosed pupae are considered to be exarate as their appendages appear free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Adult fleas have shiny brown laterally-flatted bodies 2 to 4 mm in length that are covered with hard chitinized plates (sclerites). They have unique patterns of setation (chaetotaxy) with most setae, spines and bristles facing backwards so they do not hinder forward movement through the plumage or pelage, but will catch on feathers or hairs if dragged backwards by host grooming. In particular,

Ceratophyllus spp. have a distinctive comb-like row of 12-14 horizontal spines on each side of the first thoracic segment (known as the pronotal comb or ctenidium). They lack genal (cheek) ctenidia like some other fleas (e.g. *Ctenocephalides* and *Spilopsyllus*). Adults have 3 conspicuous body parts (tagma): a small anterior head, a short thorax, and an elongate abdomen. The head is integricipit (without an interantennal suture) and has a smoothly-rounded frons (forehead) with a small downward-facing frontal tubercle. There are a pair of compact club-like lateral antennae (3-segmented) held flattened against the head but not within grooves (no antennal fossae). Large noncompound eyes (clusters of ocelli) are located below the antennae, and there are 3 strong setae located below each eye. Adult fleas have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between 2 sets of sensory palps (a pair of 4-segmented palps arising from short maxillary lobes, and a pair of 5-segmented palps arising from a short basal labium). The functional 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). These 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, small 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 rectangular dorsal sclerites: an anterior pronotum (with pronotal comb), a middle mesonotum, and a posterior metanotum (with marginal spinelets). The thoracic mesopleuron (ventral sclerite) has a vertical thickening of the wall (known as a pleural ridge or meral rod). The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all ending in a pair of strong claws. The legs are setate and characteristically have 4-6 bristles on inner surface of the hind-femur bit no spines on basal sections. The hindmost legs are considerably enlarged and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The abdomen is elongated and consists of 10 segments, although the last 3 segments are highly modified by sensory and genital structures. The dorsal sclerites (tergites) have more than one row of setae as well as lateral respiratory spiracles. Both males and females have a flat dorsal plate-like organ (sensilium or pygidium) with antesensillial setae. Male fleas are smaller than females, and have highly elaborate genitals (possibly the most complex in the animal kingdom). Males have 2 testes joined by tubular vas deferens to a seminal vesicle and an ejaculatory duct connected to an aedeagal apodeme (penis plate) with extendable penis rods held coiled and retracted within an endophallic sac. The penis is thin and delicate and must be supported during copulation by the penis rods and posterior claspers. Female fleas have 2 ovaries connected by tubular oviducts to a globular uterus opening to the vagina located within a bursa copulatrix (depression to receive male organ) with associated subglobular spermatheca (organ for sperm storage after mating).

Site of infection: Adult fleas are obligate blood-sucking ectoparasites of vertebrate hosts, while all pre-adult developmental stages are free-living in the external environment. *Ceratophyllus* spp. exhibit variable host specificity, with around half infesting mammals (belonging to 16 mammalian families, including carnivores, bats, shrews, rabbits, rodents, and humans), and half infesting birds (belonging to 25 passerine and 20 non-passerine families, including poultry, waterfowl, seabirds, shorebirds, several forest-dwellers and a few birds of prey). Only 9 species are found on both mammals and birds, particularly those infesting poultry and aviary birds that opportunistically feed on pets and humans in the immediate vicinity. Adult fleas often feed on hosts in sites that are difficult to groom: such as the head, neck, back and limbs of mammals; and the head (including the comb and wattles when present), breast, belly and around the vent of birds.

Pathogenesis: Adult fleas jump onto hosts to feed on blood by inserting their mouthparts into the skin and sucking blood from the dermal vasculature. The fleas are highly mobile on hosts and feed repeatedly until replete before dropping off to rest in the environment. Flea bites cause traumatic skin damage with variable inflammation depending on the sensitivity of the host animal (some animals become hypersensitive to flea saliva). Bite sites are often visible as small lesions on the skin surrounded by red inflamed tissues that are pruritic. Hosts often peck/bite, scratch or rub affected areas exacerbating wounds sometimes resulting in crusted papules with alopecia or feather damage. Animals may become agitated or restless and appear dishevelled. Open wounds are also prone to secondary bacterial infections. Sensitized animals may develop allergic dermatitis with severe itching and rashes. Humans that have been subjected to repeated attacks sometimes develop allergic urticarial reactions. While the volume of blood ingested by individual fleas may be small, repetitive feeding and heavy infestations may lead to anaemia with consequential iron deficiency, sometimes proving fatal especially in young fowl. Chronic infestations in domestic animals have been associated with production losses, manifest as decreased egg production, reduced weight gains (sometimes weight loss) and poor growth contributing to host emaciation and weakness. Experimental studies on nestling birds have shown infestations reduce host fitness as evidenced by reduced body mass and poorer bone development. The impact of the fleas on the growth performance of host nestlings was more noticeable in years with lower temperatures and higher precipitation. *Ceratophyllus* spp. are not considered to be important vectors for the transmission of infectious diseases, although recent molecular screening studies have shown they may carry various bacterial pathogens, including the Mountain Altai strain of plague, *Rickettsia africae* and several *Bartonella* spp.

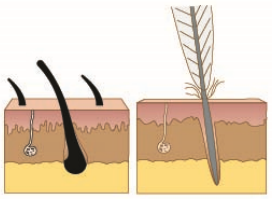
Developmental cycle and mode of transmission: *Ceratophyllus* spp. exhibit holometabolous development in that grub-like larvae undergo complete metamorphosis in pupae to form adult fleas which are ectoparasitic on vertebrate hosts. Adult fleas of most species do not attach permanently to hosts but detach after feeding and rest in the environment to digest their bloodmeals (although a few species apparently reside longer on hosts). The adults and larvae of several species may be found in bird droppings, but most

species are nidicolous and strongly associated with nests, dens or other resting sites; ranging from cavity nests in bushes and trees (passerines), nest holes and cliff crevices (seabirds), wet ground nests (water birds), and subterranean burrows (rodents). Fleas are known to infest other animals that come into contact with, or take over, nests and burrows, particularly pet animals. Humans may become infested when handling poultry or injured birds, and fleas may also invade houses from nests under the eaves. Gravid female fleas lay eggs singly or in small batches on firm substrates in the environment, particularly woody or leafy vegetation forming nests or particulate material forming burrows. The eggs hatch in 6-10 days releasing first-stage larvae which use their cutting/chewing mandibles to feed on organic debris, particularly flea dirt (pellets of dried blood excreted by adult fleas). The larvae develop through 3 instars over several weeks (15-37 days). Mature larvae form sticky cocoons which become covered in detritus from the environment. The encased larvae transform into pupae and then adult fleas over 10-23 days, but the adults generally do not eclose (emerge) until conditions are favourable. Fleas often overwinter in their cocoons and only emerge when temperatures rise is spring and when they sense that hosts may be present (combination of tactile stimuli such as vibration, body heat, and increased carbon dioxide concentrations). Emergent fleas are negatively geotactic and disperse upwards in vegetation taking up ready-postures oriented towards light. They jump onto hosts when triggered by reductions in light intensity (e.g. caused by shadows of passing hosts). Adults are transient blood-feeders and attach to hosts only for short periods to feed while spending most of their time in nests or burrows. They may fast for long periods of time (months) and resume feeding when nests are re-occupied. They apparently do not require bloodmeals in order to copulate, but females only produce eggs after feeding. In wild bird populations in temperate regions, flea reproduction is often synchronized with the breeding season of the host. In warmer regions, some flea species may complete 2-3 generations each year, while infestations in domestic birds may occur year-round.

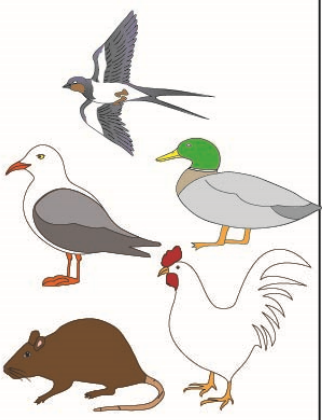
Differential diagnosis: Light infestations may remain asymptomatic or subclinical, while heavier infestations may be suspected on clinical grounds (irritated hosts with focal lesions, dermatitis and anaemia). Diagnosis is usually afforded by the direct detection of fleas on hosts upon macroscopic examination, even though their presence may be irregular and transient. Specimens are best collected for microscopic examination and identification by their unique morphological characteristics (particularly head shape, presence of pronotal comb and absence of genal comb, and chaetotaxy (patterns of setation)). Various molecular biological techniques have recently been used to characterize species and infer phylogenetic relationships, including polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA and internal transcribed spacer regions) and mitochondrial (cytochrome oxidase) gene sequences, analyses of nucleotide microsatellite loci, and determining the complete mitochondrial genome.

Treatment and control: It is important to isolate infested animals both to facilitate treatment and also prevent the spread of infestations. Individual fleas can be carefully removed from host pelage or plumage using fine-toothed combs, tweezers or forceps, but most fleas quickly detach and even leave their hosts when disturbed. A range of cleaning products have been used to moderate infestations and alleviate clinical signs in individual birds or mammals, including shampoos, sprays, balms and ointments with either flea repellent activity or soothing anti-inflammatory and anti-pruritic activity. Topical antibiotics may be applied to bite lesions to minimize the risk of secondary bacterial infections. Heavy or widespread infestations in domestic animals are usually treated with insecticidal chemicals, including boric acid powder, organophosphates (coumaphos, diazinon, malathion), pyrethroids (permethrin, cypermethrin), carbamates (carbaryl), chloronictinyles (imidacloprid), arylpyrazoles (fipronil), macrocyclic lactones (selamectin) and some natural products (rotenone, and even apple cider vinegar). However, careful attention should be paid to any contra-indications, as some flea products for pets may be highly toxic to birds (such permethrin, carbaryl or boric acid powder). Most of these flea species are nidicolous so every effort should be made to decontaminate the immediate environment to prevent rapid re-infestation. This can be done by improved sanitation (removing manure/litter), increased hygiene (regular change of nesting/bedding materials), applying environmental insecticides with long-lasting residual activity (sprays or powders with sulphur, carbaryl, coumaphos, malathion, permethrin, spinosad or insect growth regulators such as methoprene), or providing flea desiccants (such as diatomaceous earth which act to dehydrate fleas). Domestic animals may also be protected by regular health inspections, preventing roaming behaviours, excluding wild animals from holding facilities (improving barriers, and vermin control) and using quarantine procedures (for new or translocated animals).

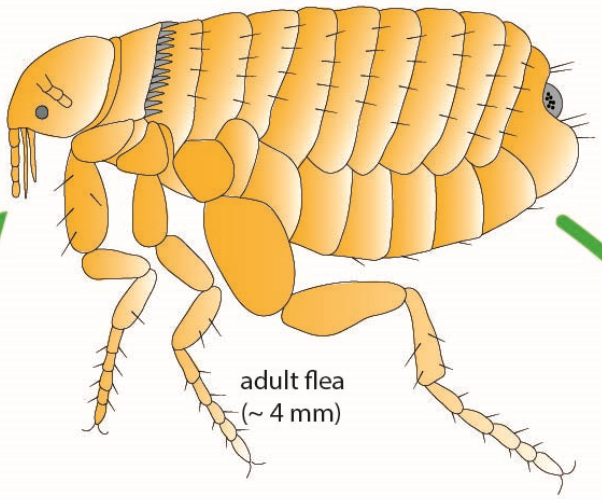
Ceratophyllus



skin/pelage
(irritation, pruritus, allergic dermatitis)
(possible vectors for infectious diseases)



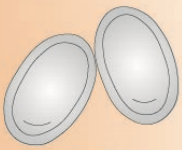
Definitive Hosts
(birds, mammals, esp. rodents)



adult flea
(~ 4 mm)

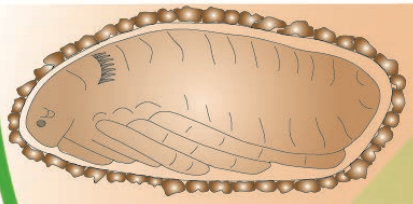
adults are often nidiculous and transient ectoparasites (feeding on host blood)

eggs laid on soil, plants

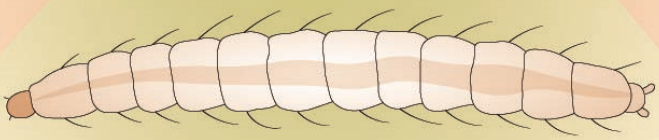


eggs
(~ 0.5 mm)

eclosion



pupa
(~ 1 mm)



larva
(~ 3 mm)

encasement

hatch

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

Ceratophyllus adult