Heterodoxus
(insect: louse)

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. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Amblycera lice have maxillary palps and four-segmented antennae located in grooves. Boopiids occur on mammals and marsupials, and infestations by *Heterodoxus* spp. have been associated with pruritus and dermatitis in dogs and macropods.

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:	Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order:	Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder:	Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily:	Amblycera (with maxillary palps, large rounded heads, 4-segmented antennae in antennal grooves)
Family:	Boopiidae (parasitize mammals/marsupials)
Genus:	*Heterodoxus* (parasitic on skin/hair of dogs/macropods)
Species:	*H. spiniger* (causes pruritus in dogs)

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). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Members of the family Boopiidae are parasitic on mammals and have 6 pairs of abdominal spiracles but only one segment between the thorax and the first abdominal segment bearing spiracles (whereas members of the family Menoponidae are parasitic on birds and also have 6 pairs of abdominal spiracles but have 2 segments between the thorax and first abdominal segment bearing spiracles). Some 57 boopiid species have been described from 8 genera (*Boopia*, *Heterodoxus*, *Latumcephalum*, *Macropophila*, *Paraboopia*, *Paraheterodoxus*, *Phacogalia*, *Therodoxus*). The genus *Heterodoxus* contains 24 species, one of which (*H. spiniger*) occurs on various canid and viverrid carnivores around the world, while the remaining 23 species are only found on particular macropodid marsupials in Australasia.

***Heterodoxus* species**	Hosts	Location	Clinical signs	Distribution
H. alatus	Diprotodontia: macropodid (pademelon)	skin		Australia
H. ampullatus	Diprotodontia: macropodid (brush-tailed rock wallaby)	skin		Australia
H. ancoratus	Diprotodontia: macropodid (whiptail wallaby)	skin		Australia
H. briscoei	Diprotodontia: macropodid (brush-tailed rock wallaby)	skin		Australia
H. calabyi	Diprotodontia: macropodid (tammar wallaby, black-striped wallaby)	skin		Australia
H. closei	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. harrisoni	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. hughendensis	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. insularis	Diprotodontia: macropodid (allied rock	skin		Australia

	wallaby, unadorned rock wallaby)			
H. insulatus	Diprotodontia: macropodid (allied rock wallaby, unadorned rock wallaby)	skin		Australia
H. keleri	Diprotodontia: macropodid (brown dorcopsis)	skin		New Guinea
H. lesoueefi	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. longitarsus	Diprotodontia: macropodid (red-necked wallaby)	skin		Australia
H. maai	Diprotodontia: macropodid (brown dorcopsis)	skin		New Guinea
H. macropus	Diprotodontia: macropodid (agile wallaby)	skin		Australia
H. maynesi	Diprotodontia: macropodid (brush-tailed rock wallaby, unadorned rock wallaby)	skin		Australia
H. mitratus	Diprotodontia: macropodid (lesser forest wallaby)	skin		New Guinea
H. murrayi	Diprotodontia: macropodid (Godman's rock wallaby)	skin		Australia
H. octoseriatus	Diprotodontia: macropodid (brush-tailed rock wallaby, unadorned rock wallaby)	skin		Australia
H. orarius	Diprotodontia: macropodid (Godman's rock wallaby)	skin		Australia
H. pygidialis	Diprotodontia: macropodid (Lumholtz's tree kangaroo)	skin		Australia
H. quadriseriatus	Diprotodontia: macropodid (quokka)	skin		Australia
H. spiniger (syn. *H. armiferus*)	Carnivora: canid (dog, red wolf, gray wolf, coyote, side-striped jackal, golden jackal, gray fox), viverrid (African civet, giant forest genet), rarely felid (cat); Diprotodontia: macropodid (agile wallaby)	skin (head, dorsum)	unkempt coat, pruritus	cosmopolitan in tropical and subtropical zones (except Europe)
H. ualabati	Diprotodontia: macropodid (swamp wallaby)	skin		Australia

Parasite morphology: Boopiid chewing lice form 3 different types of morphological stages: eggs (nits); nymphs (3 instars); and adult lice. The eggs are oval-elliptical measuring 0.8-0.9 mm in length and are often white-yellow in colour. They are glued (cemented) to host hairs along one side and surface of the eggs bears numerous small scales (pentagonal-rectangular scutes) arranged obliquely. The eggs are operculate and have an anterior disc-like ridged lid with a short central polar rod. Mature eggs hatch to release first-stage nymphs which moult through another 2 nymphal stages before forming adults. The nymphs are similar in morphology to adults but are smaller, less sclerotized, have fewer body setae, and lack genitalia. Adult lice are pale-tan to dark-brown in colour and have elongate dorsoventrally-flattened bodies measuring up to 2.5 mm in length. They have 3 distinct body parts (head, thorax, abdomen) usually covered in short setae. Their heads are broad (almost as wide as the body), hemispherical (with a smooth rounded anterior section) and sparsely setate (but with conspicuous posteriorly-directed lateral spines). They have small vestigial eyes positioned laterally in front of short clavate antennae (each composed of 4 segments) which are not conspicuous as they are concealed in deep grooves or fossae (like all other amblyceran lice, but grooves absent in ischnoceran lice). The biting/chewing mouthparts are ventrally located and consist of large opposing mandibles (lying parallel to the ventral surface such that the condyles are ventral and the ginglymus is dorsal), a posterior plate-like labrum (often with an anterior hyaline pad (pulvinus)), lateral maxillae, and an anterior labium. In chewing lice, the maxillae and labium are reduced in size (compared to sucking lice) and the maxillae are single lobed and attached to the lateral margins of the tripartite labium. Amblyceran chewing lice also have a pair of small maxillary palps, each composed of 4 segments (palps absent in ischnoceran lice). The oral cavity opens to the foregut (with pharynx, oesophagus and small crop (merely an enlargement of the oesophagus in amblyceran lice), a large midgut (with ventriculus and anterior caeca), and a hindgut (with pylorus, papillae and rectum). Amblyceran lice apparently lack a mycetome (bacteriome or stomach disc) harbouring bacterial/fungal endosymbionts, although proteobacteria are often present in the gut (in contrast, anopluran sucking lice have a well-developed mycetome and ischnoceran chewing lice have a weakly developed mycetome). The thorax is small, oval and bipartite with an anterior prothorax while the central and posterior segments are fused together. The ventral surface gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus) and terminating in paired tarsal claws. The abdomen in elliptical and composed of 8 segments, each with transverse rows of dense setae, lateral spines and spiracles (openings to the tracheal (breathing) system). Adult lice exhibit moderate sexual dimorphism, with male lice being slightly smaller than female lice. Mature males have 3 pairs of testes (cf. 2 pairs in ischnoceran lice), tubular vas deferens coalescing into a seminal vesicle opening into the genital sac equipped with a sclerotized aedeagus (tubular copulatory or intromittent organ with dorsal gonopore and terminal endophallus (pseudopenis)) supported by a basal apodeme (plate-like sclerite) and lateral parameres (rod-like sclerites). Mature females have ovaries with polytrophic ovarioles connected via tubular oviducts to a globular uterus fitted with accessory glands (for glue production) and spermatheca (for sperm storage after mating) opening into the vagina equipped with a genital plate and valvula. Females do not possess ovipositors but their terminal abdominal segment is bifurcated with apical sickle-shaped lobes (gonopods) with bluntly or sharply pointed appendages and setae to aid in egg deposition.

Site of infection: These chewing lice are obligate ectoparasites on the skin of their mammalian hosts, motile stages (nymphs, adults) living amongst the hair/fur close to the skin, and eggs (nits) attached to hair shafts. Most species are oioxenous (specific for individual host species) although *Heterodoxus spiniger* exhibits broader host specificity (described from a macropodid marsupial but more commonly found on canids and viverrids (rarely felids)). These ambylceran lice are less specialized and more mobile than ischnoceran lice and are often found widespread over their hosts, particularly over dorsal surfaces.

Pathogenesis: Many infestations are light and remain asymptomatic or subclinical, but heavier infestations may cause mild-severe clinical disease, characterized by inflammation, pruritus and unkempt coats. *H. spiniger* has been associated with clinical disease on canines on all continents except Antarctica and Europe. Nymphs and adult lice use their mandibles to chew or scrape host epidermal tissues feeding on sloughed skin and blood seeping from epidermal wounds. Feeding lice cause skin inflammation (dermatitis) with hyperkeratosis and variable levels of pruritus. Infested animals become restless, distressed and attempt to relieve the itching by frantic grooming (licking, biting, scratching and rubbing afflicted body parts) resulting in unsightly unkempt coats, alopecia (hair loss), skin lesions due to self-trauma and secondary infections, impaired thermoregulation, poor growth and even weight loss. Infestations are generally worse on young, old, sick or stressed animals due to their compromised physiological and/or immunological states.

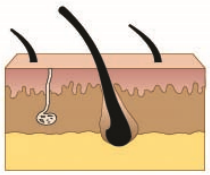
Heterodoxus spiniger has been shown to act as an intermediate host for the double-pored tapeworm *Dipylidium caninum* of dogs whereby the cysticercoid stage develops in the louse and may be ingested during grooming. *H. spiniger* has also been found to harbour larval stages of the filarial nematode *Dipetalonema reconditum* which infects dogs. Recent molecular screening studies have also detected bacterial gene sequences (β subunit of RNA polymerase) from *Acinetobacter* spp. in *Heterodoxus spiniger* from dogs.

Developmental cycle and mode of transmission: Boopiid lice may complete their entire life-cycles in the pelage of individual hosts within 3-4 weeks, and there are no free-living transmissive stages. Female lice attach eggs to host hairs where they develop and hatch releasing first-stage nymphs. These stages undergo hemimetabolous development with gradual (incomplete) metamorphosis occurring through another 2 nymphal stages before moulting to adult lice. Nymphs and adult lice that become dislodged from hosts cannot survive for long periods off the host, usually dying within hours or a few days in the external environment. Transmission between hosts therefore occurs when dislodged lice crawl onto new hosts in direct or close contact or via infested bedding or grooming equipment. The transmission of infestations is greatest when hosts have prolonged contact as occurs in over-crowded groups, nursing groups, shared dens and resting places, and during cooler months of the year (autumn and winter) when animals may congregate for shared thermoregulation.

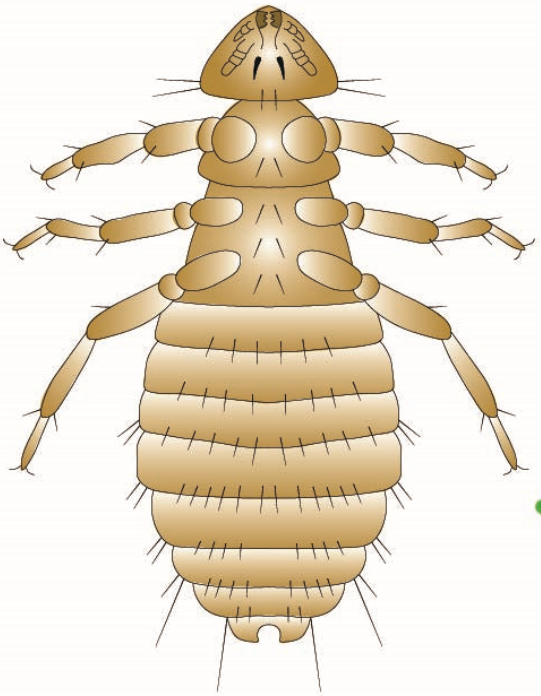
Differential diagnosis: Infestations may be suspected on clinical grounds when hosts exhibit restlessness, pruritus, repetitive grooming, skin lesions, and alopecia. Definitive diagnosis is made by the direct detection of lice and/or their eggs by visual examination when parting the coat. Detection may be assisted by using magnifying glasses and sticky tape impressions to retrieve eggs or lice for microscopic examination and identification (*Heterodoxus spiniger* should be distinguished from *Trichodectes canis* in regions where both species occur). Lice may also be collected from the skins of deceased hosts by combing or brushing the hair, scrubbing in detergent washes, performing alkaline skin digests, or by placing hides in plastic bags as lice rapidly abandon dead hosts (post-mortem examinations conducted after 24 hours are often negative for lice). Molecular biological techniques have been used to characterize species and examine phylogenetic relationships by polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S ribosomal RNA).

Treatment and control: A wide range of insecticides have been used to effectively treat louse infestations, including organophosphates (diazinon), carbamates (propoxur, carbaryl), pyrethrin, pyrethroids (phenothrin, cyphenothrin, etofenprox, permethrin, cypermethrin, deltamethrin), formamidines (amitraz), macrocyclic lactones (ivermectin, moxidectin, selamectin), phenylpyrazole (fipronil), chloronicotinyl (imidacloprid), and several insect development inhibitors (methoprene or pyriproxifen but in combination with other insecticides). Most chemicals were not effective against eggs so repeat treatments were required 7-14 days later to avoid re-infestation. Care should also be given to guidelines and regulations governing chemical usage as some chemicals are quite toxic or may elicit adverse side-effects. Chemicals are available as topical applications (shampoos, sprays, powders/dusts, neck collars) or as systemic formulations (injectable, oral, spot-ons). Treatment may be aided by clipping matted fur and by using grooming devices (brushes and fine-toothed combs) to help remove lice, although adherent nits are difficult to dislodge without using conditioners to lubricate coats and ease tangles. It is advised to treat all animals in contact or confinement, and symptomatic relief may be provided using topical anti-inflammatory creams and antibiotics for damaged skin and secondary infections. Common-sense management practices may also be used for preventive control by minimizing contact with infested individuals (through quarantine, isolation or exclusion), maintaining clean housing and bedding (through washing or chemical treatment), decontaminating equipment (regular cleaning of food and water bowls, and grooming equipment), avoiding over-crowded unsanitary conditions, and keeping hosts healthy, well-nourished and well-groomed.

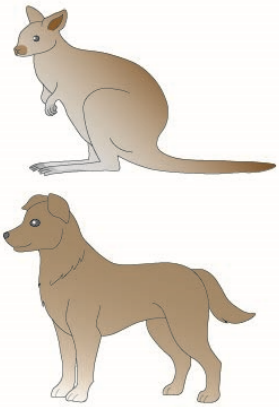
Heterodoxus



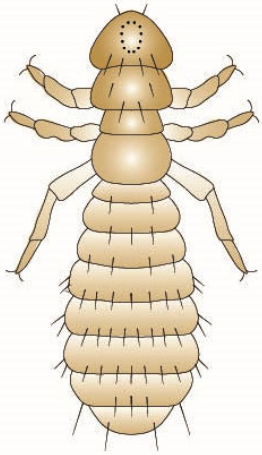
skin/pelage
(irritation, pruritus,
dermatitis)



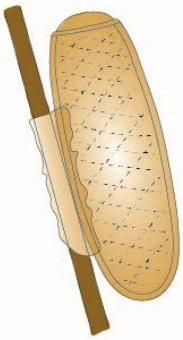
adult (ventral)
(~ 2.5 mm)



Definitive Hosts
(carnivores, marsupials)



nymph (dorsal)
(~ 1.5 mm)



egg
(~ 0.9 mm)

all stages ectozoic on host
(motile stages feed on skin/scurf)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

Heterodoxus adult female

Heterodoxus adult male