

Rhabditis, Pelodera
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes rhabditid species which are small slender cylindrical worms with a rhabditiform oesophagus (swollen posteriorly and anteriorly). Adult worms have a small buccal capsule and the males are non-bursate (lack a copulatory bursa). Most rhabditoids are free-living saprophytic nematodes living in warm moist soil/detritus. They have typical life-cycles progressing through eggs, four larval stages and reproductive adults (males being non-bursate). The larvae of some species, however, may opportunistically invade mammalian hosts through hair follicles, orifices or wounds. Several *Rhabditis* and *Pelodera* species have been associated with pruritus, erythema and pustule formation in dogs, cattle and horses.

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: Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class: Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Family: Rhabditidae (protandrous hermaphrodite (male becomes female), parasitic and free-living generations)
Genus: *Rhabditis/Pelodera* (opportunistic invaders of skin/orifices of animals)
Species: various species cause skin or udder lesions

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of

most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
<i>Incertae sedis</i> Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IH)
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Rhabditoidea contains worms with phasmids, amphids, an open rod-shaped buccal cavity (stoma), a bulbous oesophagus and an excretory system with lateral canals. Some 12 families are recognised: Agfidae, Alirhabditidae, Angiostomatidae, Brevibuccidae, Carabonematidae, Chambersiellidae, Diploscapteridae, Rhabdiasidae, Rhabditidae, Rhabditonematidae, Steinernematidae, and Syrphonematidae [some authorities include the family Strongyloididae in this superfamily, although recent molecular studies now place it separately in the superfamily Strongyloidoidea]. Rhabditid worms are protandrous hermaphrodites (where male worms becomes female). They are mostly free-living terrestrial nematodes, often living in decaying organic material as bacterivores or saprophytes. Several species have been shown to form phoretic relationships with other organisms to aid their dispersal: e.g. dauer larvae may attach themselves to the external surfaces of invertebrates (esp. insects) or invade the tissues of soft-bodied invertebrates (such as earthworms). A few species have also been found to be opportunistically parasitic when special third-stage larvae penetrate the skin of vertebrates (mostly rodents) which are used as paratenic (transport) hosts. These transient infections sometimes cause dermatitis. The family Rhabditidae contains up to 50 genera, including *Rhabditis* and *Pelodera*. Most cases of rhabditic dermatitis in mammals involve some 16 of the 170 described *Rhabditis* spp. and only 2 of the 30 *Pelodera* spp. (note that some authorities regard these 2 genera to be separate, some consider them to be synonymous, and others consider *Pelodera* to be a subgenus of *Rhabditis*). Adult worms have a small buccal capsule, a rhabditiform oesophagus, the integument possesses longitudinal and transverse striae and lateral caudal alae, the males are abursate with medium spicules and the females are oviparous or viviparous.

Rhabditid species	Hosts	Location [Clinical signs]	Distribution
Genus <i>Pelodera</i>			
<i>P. strongyloides</i> (incl. subsp. <i>dermatitica</i>) (syn. <i>Rhabditis</i>)	free-living (often in manure); opportunistic infections by L3 in Rodentia: murid (mouse, striped field mouse, yellow-necked mouse, large Japanese field mouse, wood mouse), cricetid (bank vole, field vole, meadow vole, greater long-tailed hamster, northern collared lemming, North American brown lemming, North American deer mouse); Carnivora: canid (dog); Primates: hominid (human)	skin [pruritus, alopecia, dermatitis]	Europe, North America
<i>P. teres</i>	free-living (in soil); opportunistic infections in Primates: hominid (human)	skin [pruritus]	Europe
Free-living species: <i>P. arnbomi</i> , <i>chitwoodi</i> , <i>coarctata</i> , <i>comandorica</i> , <i>conica</i> , <i>cutanea</i> , <i>cylindrica</i> , <i>cystilarva</i> , <i>icosiensis</i> , <i>kolbi</i> , <i>lambdiensis</i> , <i>litoralis</i> , <i>melisi</i> , <i>merionis</i> , <i>monohysteroides</i> , <i>nidicolis</i> , <i>operosa</i> , <i>orbitalis</i> , <i>par</i> , <i>parateres</i> , <i>pellio</i> , <i>plicata</i> , <i>pseudoterres</i> , <i>punctata</i> , <i>serrata</i> , <i>stammeri</i> , <i>tretzeli</i> , <i>typica</i> , <i>voelki</i>			
Genus <i>Rhabditis</i> (syn. <i>Pelodytes</i> , <i>Cuticularia</i>)			
<i>R. adenobia</i>	Coleoptera: scarabaeid (rhinoceros beetles)		Africa
<i>R. axei</i> (syn. <i>Pelodera</i> , <i>R. usei</i> , <i>R. gracilis</i> , <i>R. tenuicaudata</i> , <i>R. pseudoelongata</i> , <i>R. elongata</i>)	free-living (in soil); opportunistic infections by L3 in Gastropoda: achatinid (giant African snail, banana rasp snail); Galliformes: phasianid (chicken); Primates: hominid (human)	skin [pruritus]	Africa
<i>R. chabaudi</i>	Gymnophiona: ichthyophiid (common yellow-banded caecilian, brown caecilian)		Sri Lanka
<i>R. cutanea</i>	free-living (often around rodent nests); opportunistic infections by L3 in Rodentia: murid (wood mouse, yellow-necked mouse)	hair follicles	Europe
<i>R. donbass</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. elongatus</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. esperancensis</i>	Coleoptera: curculionid (white-fringed weevil)		South America
<i>R. gracilis</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. inermis</i> (syn. <i>R. faecalis</i> , <i>R. hominis</i> , <i>R. schachtietla</i> , <i>R. inermoides</i>)	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. macrocerca</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. niellyi</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. orbitalis</i>	free-living (often around rodent nests); opportunistic infections by L3 in Rodentia: murid (brown rat, mouse, striped field mouse, small Japanese field mouse, large Japanese field mouse, yellow-necked mouse, European wood mouse, Eurasian harvest mouse), cricetid (common mole, field vole, long-tailed vole, European water vole, European snow vole, European pine vole, Tatra pine vole, southern red-backed vole, northern red-backed vole, Hokkaido red-backed vole, grey red-backed vole, Japanese grass vole, bank vole, California vole, northern collared lemming, steppe lemming, Siberian brown lemming), glirid (hazel dormouse)	orbit, conjunctival sac, skin	Eurasia, North America
<i>R. pellio</i> (syn. <i>Choriorhabditis</i> , <i>R. genitalis</i>)	opportunistic infections by L3 in Primates: hominid (human); Oligochaeta: lumbricid (earthworm)		
<i>R. taurica</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	

<i>R. terricola</i> (syn. <i>R. aspera</i>)	free-living (in soil); opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
<i>R. usuii</i>	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
Free-living species: <i>R. aberrans, acarta, allgeni, anchispora, anomala, arizonae, armata, australis, bengalensis, berolina, blumi, bonaerensis, borealis, bovis, brassicae, brevispina, buetschlii, cacti, caulleryi, ciliata, coffeae, colombiana, cornwalli, costai, craspedocerca, cristata, cucumeris, curvicaudata, dacchensis, dentata, dimorpha, drosophilae, dubia, dudichi, duthiersi, ehrebaumi, elongata, entzi, erschowi, fertilior, filiformis, flagellicauda, fluviatilis, formosana, freitasi, friderici, fungicola, fruticicola, gongyloides, gracilicauda, guenini, guignardi, gurneyi, hartmanni, hermaphrodita, heteruroides, heterurus, impar, insectivora, insolita, insulana, intermedia, jagdishii, johnstoni, karachiensis, kherai, koernerii, krylovi, lacustris, lepida, leptodera, longicaudata</i> (syn. <i>crenatus</i>), <i>longipapillata, luciani, lumbriculi, macrospiculata, macrourea, maculosus, mairei, marina, marionis, maupasi, maxima, membranosa, mucronata, musicola, myriophila, necromena, neopapillosa, nidrosiensis, obesa, octopleura</i> (syn. <i>leptura</i>), <i>oculi, ocyppodis, olitorius, oxycerca</i> (syn. <i>parapillosa</i>), <i>papillosa</i> (syn. <i>ikedai</i>), <i>paraciliata, paraelongata, parateres, pellioides, pheropsophi, producta, pseudoelongata, pseudolichura, pseudoxyerca, rainai, reciproca, regenfussi, regina, resistens, rhabditiformis, riemanni, rovinjensis, rupaekraeae, scarabaeum, sechellensis, sergenti, seurati, silvatica, simplex, sonora, stasileonovi, stalbergi, stercorarius, sylvatica, succaris, suecica, synpapillata, terrestris, tripartita, typhae, typica, uliginosa, uncinata, valida, varsaviensis, velata, verneti, viguieri, voigti, wohlgemuthi, zarinae</i>			

Parasite morphology: Rhabditid nematode species form 3 different stages in their developmental cycles: eggs, larvae (4 stages designated L1-L4) and adult worms. All stages are free-living, but in some instances, third-stage larvae (L3) may invade invertebrate or vertebrate hosts. Several worm species have been shown to form 3 different types of L3 (process known as triphenism): regular L3 (free-living); arrested (dauer) L3 (sometimes on or in invertebrate transport hosts); and special parasitic L3 (invade superficial tissues of vertebrate transport hosts). The parasitic L3 are long and thin, measuring from 600-750 µm in length by 30-65 µm in diameter. The larvae do not develop further within their hosts but may undergo modest growth (up to 940 µm in length). They are surrounded by a flexible cuticle with transverse striations, lateral alae and a short-pointed tail (65-100 µm long). The mouth bears lips and opens into a short buccal cavity (20-30 µm long) connected to a rhabditiform oesophagus (with 2 characteristic bulbs) and tubular intestines (cells often become packed with lipid droplets giving the body an opaque appearance). When parasitic L3 are excised from host tissues and cultured, they may establish a free-living generation of adults which mate and produce small round eggs which larvate after oviposition. Adult worms are cylindrical (0.5-2.0 mm long by 35-100 µm wide) and surrounded by a weakly annulated cuticle (with longitudinal and transverse striae). The head is tapered and bears lips which are closed and do not form an open cup. The oesophagus is rhabditiform with 2 swellings, an elongate one near the middle and a rounded terminal one with a simple valvular apparatus. The tail is often pointed (leptoderan), sometimes bluntly rounded (peloderan), and bears membranous caudal alae supported by sets of rays. Adult worms are sexually dimorphic, with males being shorter than females (0.5-1.5 mm cf. 1.0 -2.0 mm). Males have a small posterior accessory piece (no gubernaculum) and 2 curved spicules which may protrude from the cloaca. Females have 2 ovaries, opposed and reflexed, a bifid uterus and median vulva. Most species are oviparous and lay small round-ellipsoidal eggs (55-72 x 25-40 µm) although some species may be viviparous and release first-stage larvae.

Site of infection: These nematodes are free-living in soil or water, but some species may produce special L3 that opportunistically infect the skin (especially hair follicles), and sometimes the conjunctival sacs, of various vertebrate hosts (mostly rodents, but sometimes domestic and companion animals and humans).

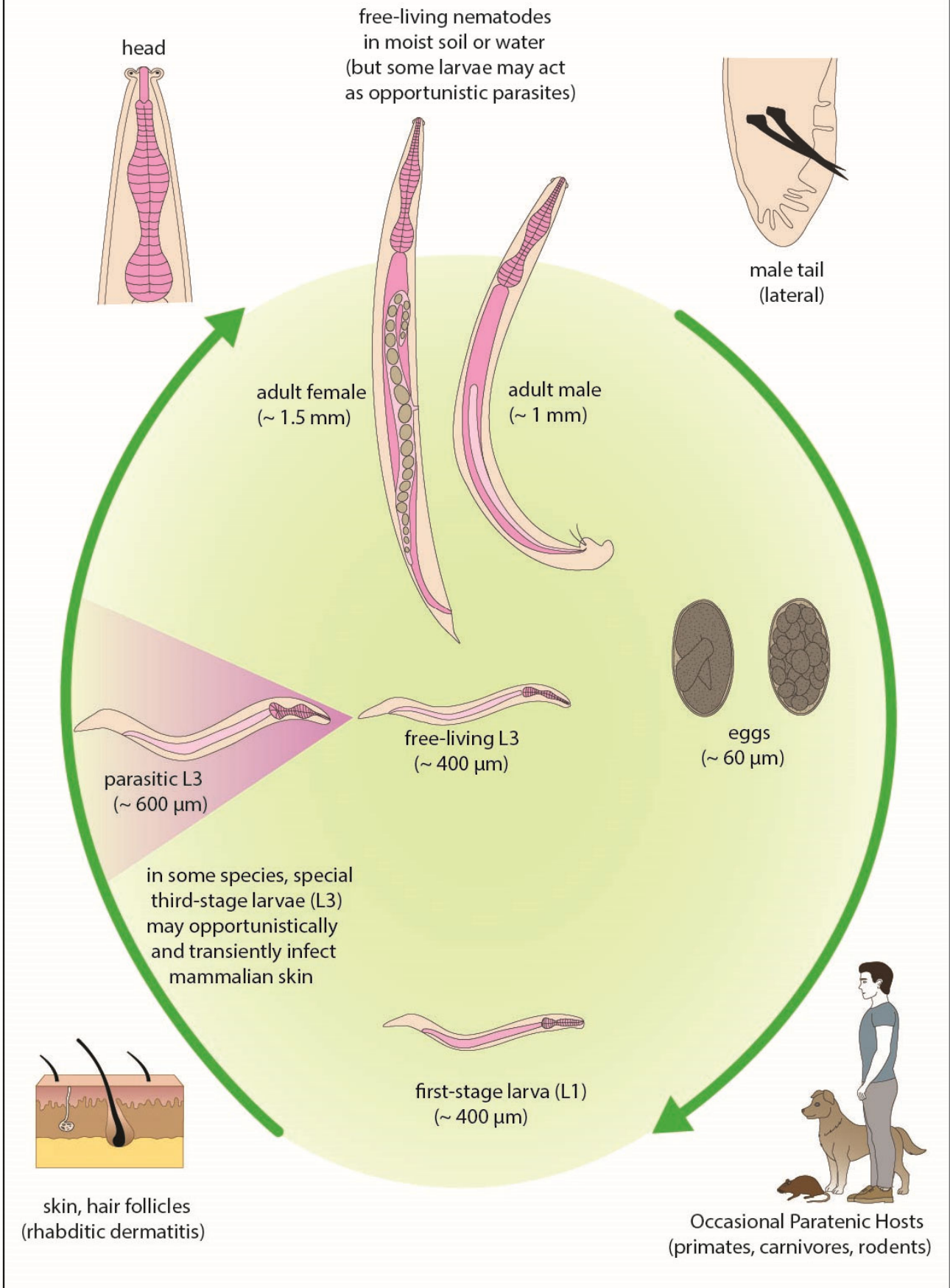
Pathogenesis: Infections by parasitic L3 may cause mild to severe dermatitis in mammals whose skin has come into contact with the ground, notably limb extremities, ventral abdomen and thorax, and perineum. While larvae are ubiquitous as free-living organisms in decaying organic matter especially in moist soil, only some larvae are opportunistically parasitic and may penetrate mammalian skin. Invasion may be facilitated by pre-existing dermatoses, wounds, sores, or when the integrity of the skin is compromised by adverse environmental conditions (e.g. by prolonged exposure to mud or damp bedding). Rhabditic dermatitis has been reported as a rare nonseasonal acute disease in dogs, cows, horses, sheep, guinea pigs and people. Clinical signs include erythema and alopecia with papules, pustules, crusts, erosions or ulcerations. Most individuals experience intense pruritus, although it may be moderate or episodic in others. Histopathological examination frequently reveals acanthotic epidermis, follicular hyperkeratosis, folliculitis with perifollicular infiltrates of eosinophils, mast cells and lymphocytes, furunculosis and sometimes pyogranuloma formation. Infections in dogs in Europe and North America have been associated with severe ulcerative dermatitis and deep pyoderma, notably in animals housed outdoors on damp straw bedding. Infections in cattle in tropical Africa and South America have been associated with otitis externa, media and interna, otorrhea, and occasionally meningitis with depression, abnormal behaviours (circling), recumbency and death. Transient ocular infections in some rodent species in Europe have involved up to 100 larvae per eye without producing any noticeable clinical signs.

Developmental cycle and mode of transmission: These nematodes are normally free-living with life-cycles involving eggs hatching to release larvae which undergo 4 moults to form adult worms. Most species live in moist soil or water where they feed on bacteria and decaying organic material. In addition to forming transient free-living L3, some species have been shown to form dauer L3 which undergo developmental arrest, retaining their L2 cuticle and surviving in low moisture conditions. Dauer larvae of several species have been found attached to the exoskeletons of invertebrates (notably insects) and sometimes within the tissues of soft-bodied invertebrates (notably earthworms), utilizing them simply as paratenic (transport) hosts for dispersal. However, a few species may also form larger special L3 which can opportunistically parasitize the superficial tissues of mammalian hosts. These larvae are longer and thinner than their free-living counterparts, and are highly active without requiring a film of moisture to move. They are sensitive to heat and vibration and can invade mammalian tissues where they reside apparently deriving nourishment by endosmosis. They may undergo some modest growth but otherwise do not develop further in host tissues, thus effectively utilizing them as paratenic (transport) hosts. When the larvae leave host tissues, under suitable environmental conditions they resume free-living development and moult to form adult worms, thus completing their cycle.

Differential diagnosis: Rhabditic dermatitis is frequently indicated on the basis of clinical symptomatology (characteristic skin lesions) and history of exposure (esp. contact with damp bedding). However, many other parasitoses may cause similar signs, such as demodicosis, scabies, dermatophytosis, pyoderma, and cutaneous larval migrations involved in hookworm dermatitis, dirofilariasis, dipetalonemiasis and strongyloidiasis. Infections may be confirmed by the microscopic detection of characteristic larvae in skin scrapings or biopsies (motile intact larvae from fresh tissues or cross-sections of larvae from fixed tissues). Larvae are readily cultured on ordinary blood agar plates, forming adults a few days after the initial bacterial bloom. One strain has been kept in culture for over 3 decades, with routine weekly subculturing.

Treatment and control: Most infections resolve spontaneously as the larvae are only transient residents in host tissues. Short-term corticosteroids have been used primarily to relieve intense pruritus. Some relief has also been afforded to affected animals by the regular application of insecticidal preparations (dips or sprays), although this may have been protective against secondary infections. Infection control should include improving hygiene by removing and destroying infested bedding materials (esp. moist straw) and moving animals to clean dry surroundings.

Pelodera, Rhabditis





Rhabditis adult worm



Rhabditis egg



Rhabditis larva