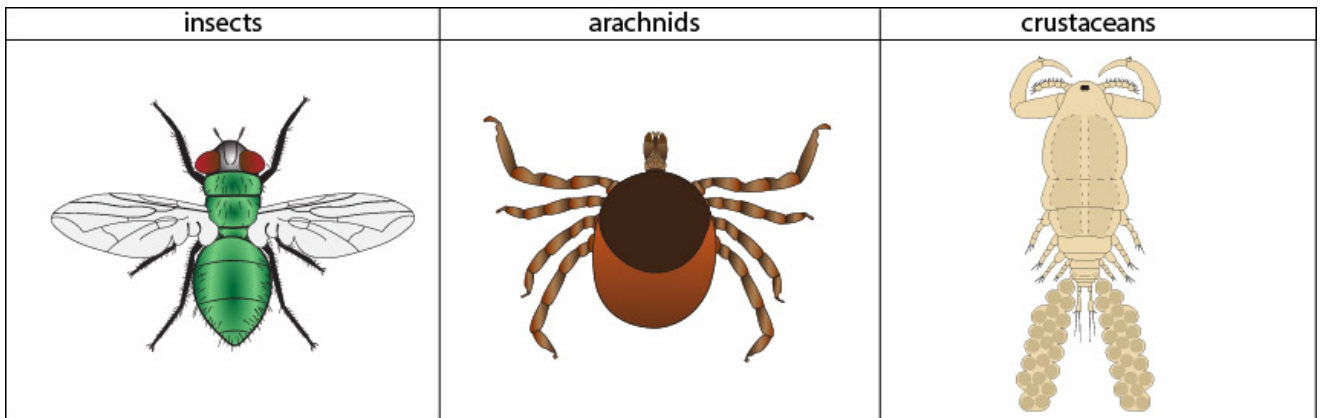


ARTHROPOD PARASITES

Arthropods form a huge assemblage of small coelomate animals with “jointed limbs” (hence the name arthro-pods). They exhibit segmentation of their bodies (metamerism) which is often masked in adults because their 10-25 body segments are combined into 2-3 functional groups (called tagmata). They exhibit varying degrees of cephalization whereby neural elements, sensory receptors and feeding structures are concentrated in the head region. Arthropods possess a rigid cuticular exoskeleton consisting mainly of tanned proteins and chitin. The exoskeleton is usually hard, insoluble, virtually indigestible and impregnated with calcium salts or covered with wax. The exoskeleton provides physical and physiological protection and serves as a place for muscle attachment. Skeletal plates are joined by flexible articular membranes and the joints are hinges or pivots made from chondyles and sockets.

The main arthropod assemblages include crustaceans (crabs, lobsters, crayfish, shrimp), arachnids (spiders, scorpions, ticks, mites) and insects (beetles, bugs, earwigs, ants, bees, termites, butterflies, moths, crickets, roaches, fleas, flies, mosquitoes, lice). Most parasitic arthropods belong to 2 main groups: the 6-legged insects; the 8-legged arachnids; and the multi-legged crustaceans.

- Insects have 3 distinct body parts, commonly called the head, thorax and abdomen. The head has 2 antennae and the thorax has 6 legs arranged in 3 bilateral pairs. Many insect species also have 2 pairs of wings attached to the thorax. Parasitic insect species include fleas, flies and lice which actively feed on host tissues and fluids at some stage in their life-cycles.
- Arachnids have 2 body parts known as the prosoma (or cephalothorax) and opisthosoma (or abdomen). The cephalothorax has 8 legs arranged in 4 bilateral pairs and arachnids do not have wings or antennae. Important parasitic assemblages include the ticks and mites which bite into tissues and feed off host fluids.
- Crustaceans have 16-20 segments (sometimes more) with one or more thoracic segments fused with the head to form a cephalothorax. They have 2 pairs of antennae, 2 pairs of maxillae and a pair of mandibles on the head, followed by a pair of biramous appendages on most body segments. Several assemblages contain parasitic groups; notably copepods and branchiurans on fish and pentastomes in reptiles and mammals.



Taxonomic classification

Traditionally, arthropod assemblages were classified together on the basis of their shared morphological characteristics; notably the possession of hardened exoskeletons and articulated joints. Various groups were recognized apparently representing variations on these unifying themes. However, phylogenetic studies conducted using extended character sets, particularly developmental biology and molecular gene sequences, revealed many new clades not previously recognized using traditional characters. While the integrity (monophyly) of many lower taxa (families and genera) were frequently validated, alternative hypotheses regarding their kinship (higher taxonomic relationships) were warranted.

Metazoa are multicellular eukaryotes with differentiated tissues that form a major division in the animal kingdom, exclusive of the sponges. They are triploblastic (with three body germ layers), most have a coelom (body cavity) and they exhibit bilateral symmetry (except the cnidaria (jellyfish) which exhibit radial symmetry). Their embryonic development includes a blastula stage, and two major lineages are recognized depending on the type of cleavage at the 8-cell embryonic stage and the fate of the blastopore: the protostomes (exhibiting determinate cleavage, mostly spiral, the blastopore becoming the mouth) and the deuterostomes (indeterminate radial cleavage, the blastopore becoming the anus). The deuterostomes comprise the echinoderms (starfish) and the chordates (including all vertebrates) while the protostomes contain most of the invertebrate animals. Molecular studies found that two major protostome lineages were well supported: the enigmatic Lophotrochozoa containing the platyhelminth parasites and the unique Ecdysozoa containing the nematode and arthropod parasites.

The Ecdysozoa are typified by organisms which have hard cuticles and can only grow by periodic moulting (ecdysis). They comprise the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (with jointed limbs). The latter three groups were grouped together in the Panarthropoda as they possessed coelomate bodies (in contrast to the pseudocoelomate nematodes), but their coelomic compartments were reduced to open circulatory systems (haemocoels). The arthropods are considered to have undergone 'arthropodization' by having hardened cuticles, segmented bodies with flexible jointed appendages and moulting cycles controlled by hormones. The development of hard exoskeletons that provide protection (against predators and desiccation) and facilitate movement (anchoring muscles and appendages) are considered to have allowed aquatic arthropods to have colonized terrestrial environments and even facilitated flight. Arthropods are both numerous and speciose, with representatives inhabiting all available habitats on Earth, both free-living (aquatic and terrestrial) and symbiotic (commensals, mutualists, parasites).

Morphotypic studies had previously identified two types of arthropods: those with uniramous appendages (single branches) and those with biramous appendages (two branches). The centipedes, millipedes, pauropods, symphylans and insects were classified together in the group Uniramia, but subsequent molecular phylogenetic studies did not support this classification. More recently, the myriapods, hexapods and crustaceans were classified in the group Mandibulata, based on their possession of mouthparts comprising mandibles rather than chelicerae. However, the mandibles of the cognate assemblages are quite different and do not appear to have evolved from a common ancestor. Those of crustaceans are multi-jointed and gnathobasic (biting/chewing surfaces on mandible bases) while those of myriapods and hexapods are single-jointed and 'entire-limb' (biting surface on distal edge). On the basis of all available evidence, five arthropod subphyla are currently recognized: Trilobita ('three-lobed' trilobites, extinct), Myriapoda ('many-footed' centipedes, millipedes, pauropods, symphylans), Chelicerata ('claw-horned' spiders, horseshoe crabs, ticks, mites), Crustacea ('shelled' crabs, lobsters, barnacles, tongue worms) and Hexapoda ('six-footed' insects). The latter two subphyla (Crustacea and Hexapoda) are regarded to be sister assemblages and have been placed in the clade Pancrustacea on the basis of shared gene sequences, tripartite brains, appendages of the third post-acronal segment forming the mandibles, and all head appendages (except the first antennae) being used for feeding sometime in their life-cycles.

Chelicerates have two tagmata (cephalothorax (prosoma) and abdomen (opisthosoma)) and six pairs of cephalo-thoracic appendages that include a pair of chelicerae (mouthparts), a pair of pedipalps (but no antennae) and four pairs of legs. Three classes are recognized: Pycnogonida ('compact-kneed' sea spiders), Merostomata ('thigh-mouthed' horseshoe crabs and extinct eurypterids) and Arachnida ('spiders' and allies). The cephalothorax of arachnids forms a carapace-like shield, their abdominal appendages are reduced, lost or modified, and the first or second abdominal somite is modified as a genital somite. Four arachnid groups are recognized: Araneae (spiders), Scorpiones (scorpions), Opiliones (harvestmen = daddy longlegs) and Acari (ticks and mites). The cephalothorax and abdomen of acarines is completely fused and their mouthparts (comprising central chelicerae with lateral pedipalps fusing ventrally to form a hypostome) are carried on a small anterior projection (capitulum) often covered by a dorsal rostrum or tectum. Ticks are macroscopic haematophagous ectoparasites with respiratory spiracles (stigmata) posterior to their legs (order Metastigmata). Mites are microscopic acarines that may be free-living, particularly in leaf litter, or parasitic in the epidermal tissues of vertebrate hosts. Gamasid mites have spiracles between the second and fourth pair of legs (order Mesostigmata), trombidiform mites have spiracles on the capitulum (order Trombidiformes, suborder Prostigmata), while sarcoptiform mites do not have spiracles but respire through the body surface (order Sarcoptiformes, suborder Astigmata).

Crustaceans are shelled arthropods with gnathobasic mandibles, biramous appendages, second antennae, unique nauplius larvae and most have stalked compound eyes. Six classes are recognized: including the rare Remipedia ('oar-footed' remipeds in caves) and Cephalocarida ('shrimp-headed' cephalocarids in marine sediments); the prevalent Brachiopoda ('gill-footed' fairy-, brine-, tadpole-, clam-shrimp and water fleas in aquatic environments) and Ostracoda ('shelled' mussel- and seed-shrimp in aquatic environments); and the highly speciose Maxillopoda ('jawbone-footed' shrimp, barnacles, copepods, brachiurans, pentastomes) and Malacostraca ('soft-shelled' crabs, lobsters, shrimp, isopods, amphipods and allies). Maxillopod subclasses include Mystacocarida ('moustache-shrimp' on beaches), Tantulocarida ('tiny shrimp' in marine benthos), Cirripedia ('curly hair-footed' free-living or parasitic barnacles), Copepoda ('oar-footed' copepods free-living in aquatic environments or parasitic on aquatic hosts), Brachiura ('gill-tailed' parasitic fish lice), and Pentastomida ('five-mouthed' tongue worms parasitic in lungs of reptiles). Of the 14 malacostracan orders, four prevalent groups include the Isopoda ('equal-footed' isopods in terrestrial and aquatic environments and some ectoparasites of fish and other crustaceans), Amphipoda ('both-sided' amphipods in aquatic environments, some being parasitic on aquatic hosts), Euphausiacea ('shining-bright' planktonic krill) and the speciose Decapoda ('ten-footed' crabs, shrimps, lobsters).

Hexapods are better known as insects. They have three tagmata (head, thorax and abdomen), an exoskeleton composed of plates (sclerites), whole-limb mandibles, one pair of antennae, six uniramous legs, Malpighian tubules and usually two pairs of wings. Two classes are recognized: the Entognatha whose mouthparts have their bases within the head capsule and mandibles with one articulation; and the speciose Insecta with ectognathous mouthparts (bases lie outside the head capsule) and mandibles usually with two regions of articulation. The entognathan orders Protura ('first-tailed' proturans), Diplura ('double-tailed' japygids and campodeids) and Collembola ('glue-wedged' springtails, jumping bristletails and snow fleas) are represented by small insects living mostly in soil or humus. The ectognathous insects are divided into two subclasses: the Apterygota without wings and the Pterygota with wings (usually two pairs, sometimes reduced to one pair or none). The wingless apterygotes are represented by the order Thysanura ('tassel-tailed' silverfish and bristletails). The winged pterygotes have been classified into two infraclasses: Paleoptera with outspread wings and Neoptera with wings that fold back over the body. The paleopterans are divided into two orders which undergo hemimetabolous (incomplete) development: Odonata ('toothed' dragonflies and damselflies) and Ephemeroptera ('day-winged' mayflies) with massive or vestigial mouthparts respectively. The neopterans are divided into 3 superorders; Orthopteroidea with straight wings and biting/chewing mouthparts, Hemipteroidea (Exopterygota) with piercing/sucking mouthparts and hemimetabolous (incomplete) development where the young resemble adults but have externally developing wings, and Holometabola (Endopterygota) with holometabolous (complete) development) where the young do not resemble adults and develop wings inside the body.

Orthopteroidea comprise nine orders: Orthoptera ('straight-winged' grasshoppers, locusts, crickets, katydids); Blattodea ('roach-formed' cockroaches); Phasmatodea ('apparition-formed' stick and leaf insects); Mantodea ('soothsayer-formed' mantids); Mantophasmatodea ('soothsayer-apparition-formed' gladiators); Isoptera ('equal-winged' termites); Plecoptera ('twisted-winged' stoneflies); Embiidina ('lively-formed' webspinners); and Dermaptera ('skin-winged' earwigs). Hemipteroidea are divided into 15 orders, including the Zoraptera ('pure-wingless' zorapterans); Psocoptera ('rub-away-winged' psocids, book lice, bark lice); Hemiptera ('half-winged' true bugs, hoppers, cicadas, whiteflies, aphids, scale insects); Thysanoptera ('tassel-winged' thrips); and Phthiraptera ('wingless lice'). Holometabolans are classified into several broad groups: neuropteroids containing the orders Neuroptera ('net-veined' dobsonflies, ant lions, lacewings), Megaloptera (alderflies) and Raphidioptera (snakeflies); coleopteroids containing the orders Coleoptera (sheath-winged' beetles, fireflies, weevils) and Strepsiptera ('twisted-winged' stylops, twisted wing parasites); hymenopteroids comprising the Hymenoptera ('membrane-winged' ants, bees, wasps) with highly developed social systems; and the panorpoid complex of orders Mecoptera ('long-winged' scorpion-flies), Trichoptera ('hair-winged' caddisflies), Lepidoptera ('scale-winged' butterflies, moths), Siphonaptera ('siphon-bearing wingless' fleas) and Diptera ('two-winged' true flies, midges and mosquitoes).

Supergroup: Amorphea	(unikonts, with single flagellum, or nonflagellated amoebae)
Opisthokonta	(stages with single posterior flagellum)
Holozoa	(metazoans, filasterans, ichthyosporeans, choanomonads)
Metazoa	(multicellular eukaryotes)
Protostomia	(triploblastic, spiral cleavage)
▪ Group: Ecdysozoa	(cuticle moulted = ecdysis)
Nematoidea	(collagenous cuticle without microvilli)
Phylum: Nematoda (= Nemata)	(pseudocoelomate roundworms, tubular digestive tract, dioecious)
Phylum: Nematomorpha	(horsehair worms, aquatic)
Phylum: Kinorhyncha	(spine-necked worms, marine sediments)
Phylum: Priapulida	(priapulids, marine sediments)
Phylum: Loricifera	(loriciferans, marine sediments)
Panarthropoda	(haemocoel, ventrolateral appendages)
Phylum: Onychophora	(velvet worms, litter)
Phylum: Tardigrada	(water bears, mosses, lichen, moist soil)
Phylum: Arthropoda	(calcification of chitinous cuticle, jointed limbs, segmental sclerites, cephalic ecdysial glands, setae, lateral compound eyes)
♦ Subphylum: Chelicerata	(2 tagmata (cephalothorax + abdomen), chelicera, no antennae)
• Class: Pycnogonida	(sea spiders)
• Class: Merostomata	(horseshoe crabs)
• Class: Arachnida	(spiders and allies, 4 pairs legs, carapace, slit sensilla)
•• Order: Araneae	(spiders)
•• Order: Scorpiones	(scorpions)
•• Order: Opiliones	(harvestmen = daddy longlegs)
• Subclass: Acari	(ticks and mites, segmentation inconspicuous, with capitulum)
•• Superorder: Parasitiformes	(ticks and some mites)
••• Order: Metastigmata	(Ixodida) (ticks, macroscopic, spiracles/stigmata posterior to legs)
••• Order: Mesostigmata	(gamesid mites, spiracles/stigmata between second and fourth legs)
•• Superorder: Acariformes	(diverse mites)
••• Order: Trombidiformes	(trombidiform mites)
••• Suborder: Prostigmata	(spiracles/stigmata on capitulum)
••• Order: Sarcoptiformes	(sarcoptiform mites)
••• Suborder: Astigmata	(without spiracles, respire through body surface)
♦ Subphylum: Crustacea	(shells, biramous, 2 pairs antennae, 2 pairs maxillae, nauplius larva)
• Class: Remipedia	(remipeds)
• Class: Cephalocarida	(cephalocarids)
• Class: Brachiopoda	(fairy-, brine-, tadpole, clam-shrimp, water fleas)
• Class: Ostracoda	(mussel- and seed-shrimp, some fish parasites)
• Class: Malacostraca	(crabs, lobsters, shrimp)
•• Order: Euphausiacea	(krill)
•• Order: Isopoda	(dorsoventrally flattened, lack carapace, some fish parasites)
•• Order: Amphipoda	(laterally compressed, thoracic gills, mostly free-living)
•• Order: Decapoda	(crabs, crayfish, lobster, shrimp, 5 pairs walking legs)
• Class: Maxillipoda	(nauplius with maxillipodan eye, 5 cephalic, 6 thoracic and usually 4 abdominal segments plus telson)
• Subclass: Mystacocarida	(marine beaches)
• Subclass: Tantulocarida	(parasitic on deep-sea crustaceans)
• Subclass: Cirripedia	(barnacles, some crustacean parasites)
• Subclass: Copepoda	(elongate body, naupliar then copepodid instars, some fish parasites)
• Subclass: Branchiura	(fish lice, flattened bilobed head, carapace expands laterally)
• Subclass: Pentastomatida	(tongue worms, anterior end with mouth and two pairs tiny claws)
•• Order: Cephalobaenida	(obliquely-paired hooks, medial genital opening, single oviduct)
•• Order: Porocephalida	(horizontally-aligned hooks, posterior genital opening, two oviducts)

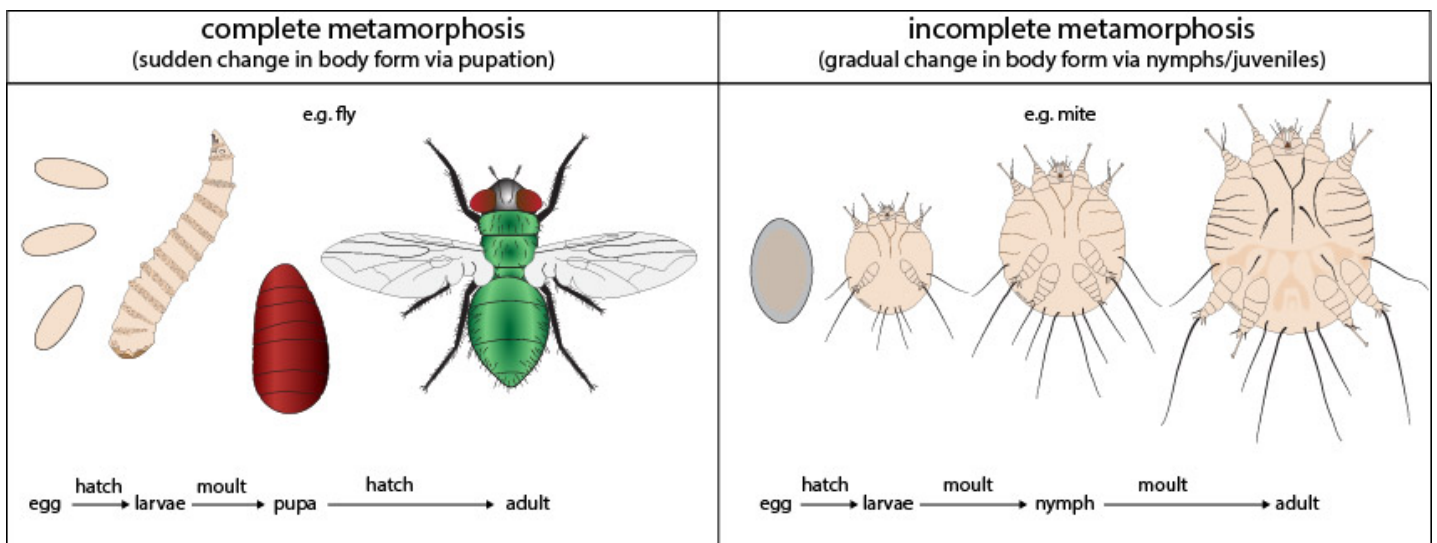
- ♦ Subphylum: Hexapoda (3 tagmata (head+thorax+abdomen), 3 pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
 - Class: Entognatha (entognathous mouthparts (bases inside head capsule))
 - Order: Protura (proturans)
 - Order: Diplura (diplurans)
 - Order: Collembola (springtails)
 - Class: Insecta (ectognathous mouthparts (bases lie outside head capsule))
 - Subclass: Apterygota (wingless)
 - Order: Thysanura (silverfish, bristletails)
 - Subclass: Pterygota (winged)
 - Infraclass: Paleoptera (outspread wings)
 - Order: Odonta (dragonflies, damselflies)
 - Order: Ephemeroptera (mayflies)
 - Infraclass: Neoptera (wings fold back over body)
 - Superorder: Orthopteroidea (biting/chewing mouthparts)
 - Order: Orthoptera (grasshoppers, locusts, crickets, katydids)
 - Order: Blattodea (cockroaches)
 - Order: Phasmatodea (walking-sticks, leaf insects)
 - Order: Mantodea (mantids)
 - Order: Mantophasmatodea (gladiators)
 - Order: Isoptera (termites)
 - Order: Ptecoptera (stoneflies)
 - Order: Embiidina (webspinners)
 - Order: Dermaptera (earwigs)
 - Superorder: Hemipteroidea (= Exopterygota) (young resemble adults, have externally developing wings, piercing/sucking mouthparts)
 - Order: Zoraptera (zorapterans)
 - Order: Psocoptera (psocids, book lice, bark lice)
 - Order: Hemiptera (true bugs, hoppers, cicadas, whiteflies, aphids, scale insects)
 - Order: Thysanoptera (thrips)
 - Order: Phthiraptera (lice, wingless, sucking (anoplura), chewing (mallophaga))
 - Superorder: Holometabola (= Endopterygota) (young do not resemble adults, holometabolous (complete) development, with internally developing wings)
 - Neuropteroid groups (net-veined flies)
 - Order: Neuroptera (dobsonflies, ant lions, lacewings)
 - Order: Megaloptera (alderflies)
 - Order: Raphidioptera (snakeflies)
 - Coleopteroid groups (beetle-shaped)
 - Order: Coleoptera (beetles, fireflies, weevils)
 - Order: Strepsiptera (stylops, twisted wing parasites)
 - Hymenopteroid group (highly developed social systems)
 - Order: Hymenoptera (ants, bees, wasps)
 - Panorpoid groups (complex of orders)
 - Order: Mecoptera (scorpionflies)
 - Order: Lepidoptera (butterflies, moths)
 - Order: Trichoptera (caddisflies)
 - Order: Siphonaptera (fleas, laterally compressed, pupation)
 - Order: Diptera (true flies, nematocera with long filamentous antennae (midges, mosquitoes), brachycera with short stout antennae (flies))

Biodiversity

Collectively, arthropods account for a substantial share of global biodiversity, both in terms of species richness and relative abundance. There are over 1,000,000 species of insects, 50,000 species of arachnids and 67,000 species of crustaceans. They are very successful and adaptable organisms and are capable of forming large populations due to their rapid and fertile reproduction rates. Many species are also able to withstand adverse environmental conditions by undergoing periods of developmental arrest (diapause). The protection afforded by their exoskeletons allows them to colonize many habitats and they overcome the problem of growing larger in a non-expandable exoskeleton by undergoing periodic moulting (or ecdysis) which is mediated by hormones. Developmental stages between moults are referred to as instars. Moulting is a complex process and its timing is mediated by many environmental and physiological cues. It involves detachment of the hypodermis from the procuticle, partial resorption of the old cuticle, production of a new epicuticle, dehiscence (splitting) of the old cuticle, emergence of the animal, stretching and expansion of the new cuticle by air and/or water intake, and then sclerotization of the new cuticle.

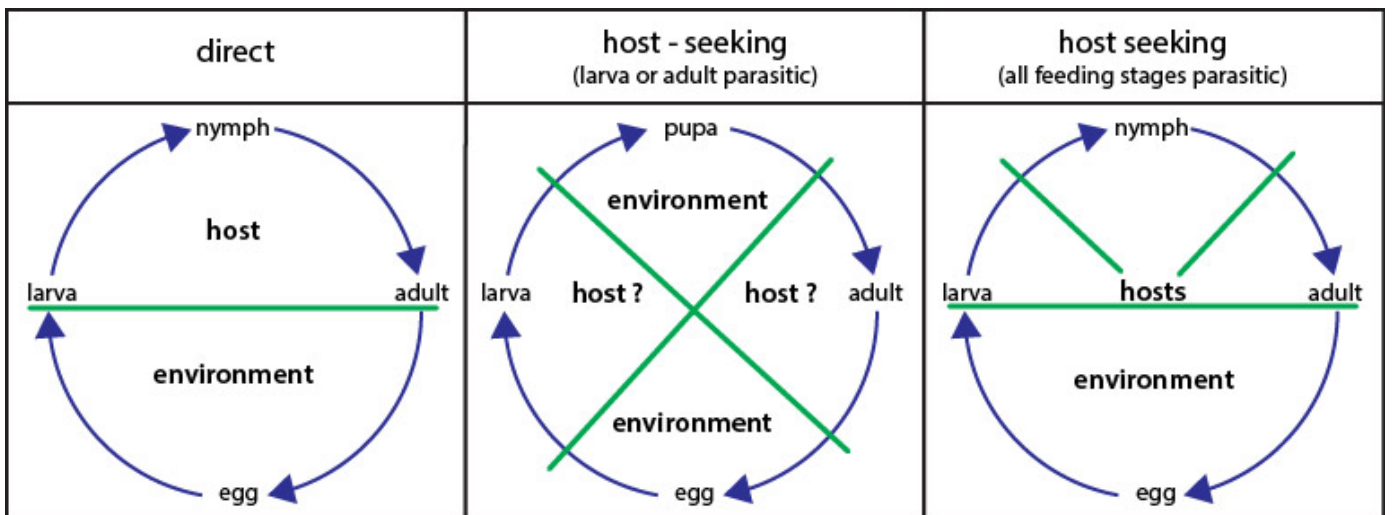
Life-cycles

Adult arthropods are generally small in size, most are visible but some remain microscopic. Arthropod sexes are separate and fertilization is internal. A wide range of mating behaviours, insemination and egg production strategies are involved. In most species, the egg develops into a larva: i.e. a life-cycle stage that is structurally distinct from the adult and must undergo metamorphosis (structural reorganization) before becoming an adult. This metamorphosis may be complete (involving major changes during a pupation stage) or incomplete (involving gradual changes in nymph stages). For example, the grub-like larval stages of flies and fleas form cocoon-like pupae where they undergo complete metamorphosis and emerge as radically different adult insects. In contrast, the larval instars (or nymphs) of lice, ticks and mites undergo incomplete metamorphosis through a series of moults gradually becoming more adult-like in appearance, as do the nauplii, copepodid and juvenile stages of crustaceans.



Arthropods are involved in nearly every kind of parasitic relationship, either as parasites themselves or as hosts/vectors for other micro-organisms (including viruses, bacteria, protozoa and helminths). They are generally ectoparasitic on, or in, the skin of vertebrate hosts. Many species are haematophagous (suck blood) while others are histophagous (tissue-feeders) and bite or burrow in dermal tissues causing trauma, inflammation and hypersensitivity reactions. Infestations are transmitted from host-to-host either by direct contact or by free-living larvae or adults actively seeking hosts.

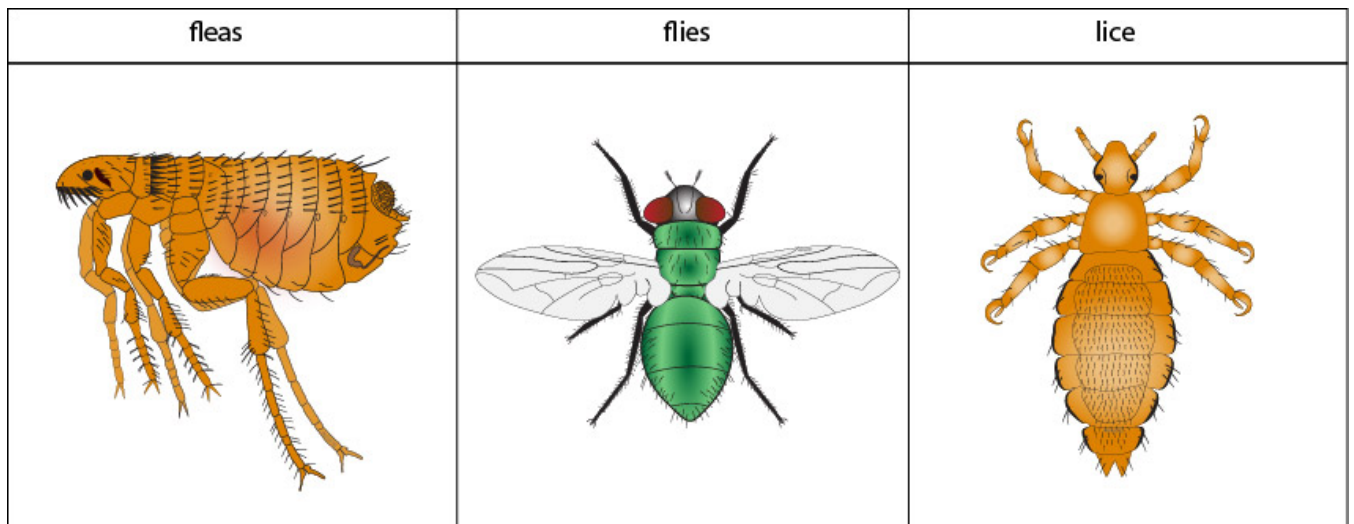
- Direct transmission of infective stages occurs when hosts come into close contact with each other in terrestrial or aquatic environments. Larvae, nymphs or adults may cross from one host to another, while eggs may contaminate shared holding facilities, bedding, clothing or equipment. Insects (fleas and lice) and arachnids (mites) rely on close contact between hosts..
- Many adult insects actively seek hosts in order to feed or lay eggs. Winged insects (mosquitoes, flies) fly to new hosts to feed while fleas jump onto passing hosts. Some adult flies (bot flies) do not feed on their hosts but deposit eggs from which larvae emerge and feed on host tissues and exudates. When replete, larvae leave their hosts to pupate in the external environment.
- Tick larvae actively seek hosts by climbing vegetation and questing for passing hosts. Some species complete their life-cycle on the same host (one-host ticks) while others detach after feeding and drop to the ground to moult before seeking new hosts as nymphs or adults (two-host or three-host ticks). Larval and juvenile stages of crustaceans actively swim about in aquatic environments actively seeking hosts.



Overview of major arthropod groups parasitizing animals

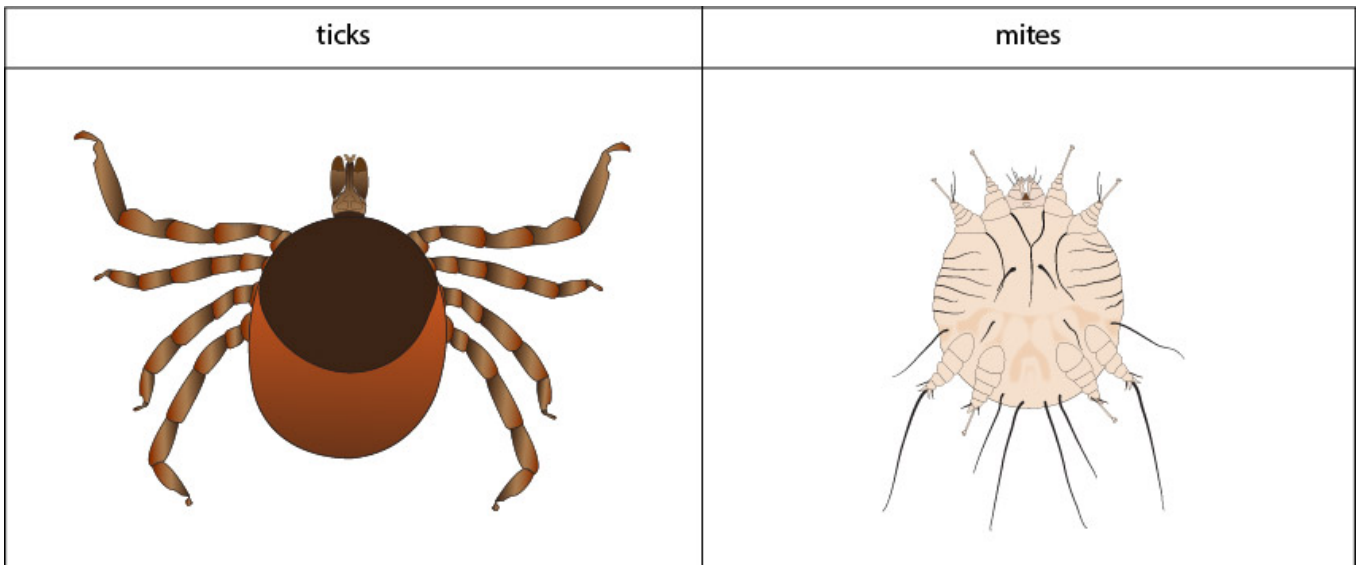
Insects are incredibly biodiversity forming numerous species and large populations in aquatic and terrestrial habitats as well as in association with other organisms acting as hosts. Most parasitic insect species belong to three main groups: the jumping fleas (Siphonaptera); the winged flies (Diptera); and the wingless lice (Phthiraptera).

- Fleas are bilaterally-flattened wingless insects with enlarged hindlimbs specially adapted for jumping (up to 100 times their body length). Jumping fleas are accomplished using elastic resilin pads which expand explosively when uncocked from the compressed state. Fleas 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. There are some 2,500 flea species, most parasitic on mammals (especially rodents) and some on birds. They vary in the time spent on their hosts ranging from transient feeders (rodent fleas) to permanent attachment (sticktight fleas and burrowing chigoes).
- Flies and mosquitoes are winged insects with two pairs of wings attached to the thorax and a well-developed head with sensory and feeding organs. They undergo complete metamorphosis involving a pupation stage. Different species vary in their feeding habits, both as adults (parasitic or free-living) and larvae (parasitic or free-living). There are over 120,000 species belonging to 140 families. Two main suborders are recognized on the basis of structural differences, Nematocera (adult stages parasitic, larval stages often free-swimming) and Brachycera (adult stages parasitic or free-living, larval stages often predaceous).
- Lice are small wingless insects, dorsoventrally flattened, with reduced or no eyes and enlarged tarsal claws for clinging. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to hair/feathers whereas nymphs and adults cling to hair/feathers. Two orders of lice are recognized on the basis of their mouthparts: the Mallophaga (chewing/biting lice) with some 3,000 species infesting birds and mammals; and the Anoplura (sucking lice) with 500 species found on mammals



Many non-spider arachnids (subclass Acari) are found as parasites on animal or plant hosts. They belong to two main groups: the macroscopic ticks and the microscopic mites. Many species are important in human and animal medicine as causes of disease or as transmission vectors for other pathogens.

- Ticks are epidermal parasites of terrestrial vertebrates that may cause anaemia, dermatosis, paralysis, otoacariasis and other infections (transmit viral, bacterial, rickettsial, spirochaete, protozoal and helminth pathogens). They feed mainly on blood and their mouthparts are armed with small backward-facing teeth to aid in attachment. All ticks undergo gradual/incomplete metamorphosis whereby larval and nymphal instars resemble adults. The integument is relatively thick and respiration occurs via spiracles (usually only one pair) and trachea. Two major families of ticks are recognized on the basis of many morphological features: the Ixodidae (hard ticks with a tough cuticle and a large anterodorsal scutum) with some 650 species that infest mammals, birds and reptiles; and the Argasidae (soft ticks with a leathery integument and no scutum) with 160 species that infest mainly birds and some mammals.
- Mites are microscopic arachnids which undergo gradual or incomplete metamorphosis. Adults and nymphs have 4 pairs of legs whereas larvae have 3 pairs. Over 30,000 species of mites have been described, many are free-living species, some are plant parasites while others are parasitic on terrestrial and aquatic hosts. Most parasitic species feed on skin debris or suck lymph, some burrow into the skin, some live in hair follicles, and some in the ear canals. Their mouthparts are variable in form but the hypostome is never armed with teeth. The integument is usually thin and three orders are recognized on the basis of their respiratory systems: the Mesostigmata with respiratory spiracles (stigmata) near the third coxae; the Prostigmata (Trombidiformes) with spiracles between the chelicerae or on the dorsal hysterosoma; and the Astigmata (Sarcoptiformes) without tracheal systems as they respire through the tegument.



Most crustaceans are free-living in aquatic or terrestrial environments, but some have become parasitic on or in other animals residing in the same habitats. Parasitic representatives belong to 3 main maxillipodan assemblages: Copepoda and Branchiura which are ectoparasitic on fish, and Pentastomida which are endoparasitic in reptiles and mammals.

- Copepods have elongate segmented bodies and they undergo gradual metamorphosis involving nauplii and copepodid developmental stages prior to adult formation. Some species are ectoparasitic on the skin and gills of freshwater fish and have been associated with lesions, respiratory difficulties and mortalities, with *Lernaea* and *Ergasilus* spp. causing problems in aquaculture facilities.
- Branchiurans (commonly known as fish lice) have round flat bodies with mouthparts modified for sucking blood from fish hosts. They have direct cycles with eggs releasing larvae (metanauplii) that gradually develop to juveniles then adults. Many *Argulus* spp. have been reported as ectoparasites on the skin and gills of marine and freshwater fish causing painful bites and haemorrhagic lesions.
- Pentastomes have elongate worm-like bodies with few appendages, apart from 2 pairs of tiny claws near the mouth contributing to their 'penta-stome' appearance. They are alternatively known as tongue worms as the adults are parasitic in the respiratory passages of snakes or carnivorous mammals, with heteroxenous life-cycles involving larval and nymphal stages in rodent intermediate hosts.

