Macrofauna – Coleoptera

Morphology

The defining feature of beetles (Coleoptera) is the hardened forewings (elytra) that cover their body. The largest known beetles are more than 160 mm long (e.g. *Dynastes hercules*), but most beetles are less than 5 mm long. Their colours are variable, although most soil-dwelling beetle species are brown or black. Their body shape is also variable: some have long horns or sharp tusks, some can curl up like myriapods (see page 57), some are flat and some are slim. A number of soil beetles, such as the genus *Carabus*, are wingless. [68, 69]

Taxonomy

Beetles are hexapods belonging to the order Coleoptera. This includes four suborders: Archostemata, Adephaga, Myxophaga and Polyphaga. Of these, Adephaga and Polyphaga have more species than other suborders, including most soil species.

Microhabitat

In terrestrial environments, many beetles can be found in soil, humus and leaf litter, under logs or in decomposing wood, under stones, in dung, carrion and in the fruiting bodies of many types of fungi (see pages 38-41). Numerous beetles (families Carabidae, Leiodidae, Staphylinidae and Scarabaeidae) are well adapted to the soil environment. Some carrion beetles (family Silphidae) and some dung beetles (family Scarabaeidae) build nests in the soil, in which they take care of their brood. Some species, such as some members of the family Staphylinidae, live solely in caves while others are myrmecophiles (ant lovers) or termitophiles (termite lovers) as they strikingly resemble ants or termites (see pages 54-55) and live in their hives.

Diversity, abundance and biomass

There are more than 370 000 described species of Coleoptera – it is the largest and most diverse order of organisms on the planet, making up about 40 % of all described insect species, and about 30 % of all described animal species. The abundance and biomass of beetles on ephemeral and nutrient-rich resources, such as carrion and dung, are very high. Beetles significantly contribute to decomposition processes. Besides being abundant and varied, soil beetles are able to exploit the wide diversity of food sources that are available in their habitat. Many species are predators of small soil animals such as earthworms, collembolans and nematodes (see pages 46-47, 50, 58). Others feed on fungi or dead wood.

A recent study has shown that the dung beetle *Scarabaeus satyrus* uses the Milky Way to navigate during night time. This is the first known species to do so in the animal kingdom. (KKE)

The caring gravediggers

- Burying beetles bury carcasses of small vertebrates, such as birds and rodents, as a food source for their larvae.
- They are unusual among insects in that both the male and female parents take care of the brood.
- Although parental responsibilities are usually carried out by a couple of beetles, a male or a female may also care for the brood alone, when the other partner is lost or the carcass is small.
- Sometimes more than two unrelated individuals can raise a brood together, when the carcass is large or many potential competitors are present.

The carcass of a mouse which was rolled into a ball by a burying beetle in Japan. Burying beetles belong to the genus *Nicrophorus* and are the best-known members of the family Silphidae. (MN)

Diversity of Coleoptera: (**a**) a male of the dung beetle *Liatongus minutus* has a long horn used for defense; (**b**) the tiger beetle *Cicindela japonica* with its sharp tusks; (**c**) the rove beetle *Ecitophya* sp. from Peru resembles its ant hosts (neotropical army ants) in overall body shape and colouration; (**d**) the beetle *Madrasostes* sp. from Ecuador can curl up when in danger; (**e**) the ground beetle *Trechiama lavicola* has degenerated eyes and hindwings to adapt to cave and underground life; (**f**) a rove beetle *Aleocharinae* sp. (the upper one) living in a termite (lower one) nest; (**g**) the stag beetle *Aesalus asiaticus* from Japan feeds on decaying wood and fungi; (**h**) the beetle *Aspidiphorus* sp. covered by spores of a slime mould feeding on it; (**i**) the burying beetle *Nicrophorus concolour* feeding their larvae. (YA, TK, MN)

Macrofauna – Soil insect larvae

The vast majority of insects, up to 95 % in fact, are linked to the soil during their life cycle. Some lay eggs in the soil or use it as a substrate for overwintering. Due to very specific features of the soil as a habitat, insect larvae have made numerous adaptations to live in this particular environment. According to their life cycle, insects can be classified as holometabolous, hemimetabolous or ametabolous, depending on whether they undergo complete, incomplete or no metamorphosis, respectively (see box below). Larvae of hemimetabolous insects do not undergo substantial changes in their body form; they are often called nymphs and look very similar to adult insects lacking well developed wings and the ability to reproduce. The holometabolous larvae differ greatly from the adult and often occupy different ecological niches. The change to adulthood occurs during pupation. Morphologically, holometabolous insects are very diverse and cover a wide range of trophic levels, from detritivores to herbivores and predators. Among different species, they may vary from less than 1 mm to 12 cm. [70, 71]

Hemiptera larvae

Cicada nymphs (Hemiptera) may be among the most well-known, most likely due to their long life in the soil and huge biomass. They feed by sucking sap from roots and can live in the soil for up to 17 years. Emergence of over 300 nymphs of periodical cicadas per square metre represents the highest recorded biomass (up to 4 000 kilos per hectare) for any terrestrial animal.

A nymph of cicada. Cicadas live underground in this form for most of their lives, at depths ranging from about 30 centimetres down to 2.5 metres. Eventually, they construct an exit tunnel to the surface and emerge. (GW)

Metamorphosis

- The word 'metamorphosis' derives from Greek *meta* (change) and *morphe* (form).
- Metamorphosis refers to a major change in form or structure, usually associated with the development of the wings. One of the most dramatic forms of metamorphosis is the change from the immature insect into the adult form.
- Metamorphosis is sometimes accompanied by a change of habitat or behaviour.
- In insects there are different types of metamorphosis. The principle is that metamorphosis is closely linked to wing development; therefore:
  - ametabolous are wingless insects (apterygota), so they do not develop wings (no metamorphosis);
  - hemimetabolous insects have wings that develop gradually (incomplete metamorphosis);
  - holometabolous insects have wings that develop during the pupation period (inactive) where the insect undergoes dramatic physiological and morphological changes to acquire the wings and to feed on different things (complete metamorphosis).
- In hemimetabolous insects, immature stages are called nymphs. Development proceeds in repeated stages of growth and moult (ecdysis); these stages are called instars. The juvenile forms closely resemble adults but are smaller and lack adult features, such as well developed wings and genitals. The differences between nymphs in different instars are small, often just differences in body proportions. Examples of the hemimetabolous insects are: aphids, cicadas and leafhoppers.
- In holometabolous insects, immature stages are called larvae, and differ markedly from adults. Insects that undergo holometabolism pass through a larval stage, then enter an inactive state called pupa, or chrysalis, and finally emerge as adults. Examples of the holometabolous insects are: beetles, flies, ants and bees.

Diptera larvae

Diptera larvae in general look like small worms as they are all legless. However, their ecological functions are very diverse. Some of them mine taproots (see page 43) and feed on the internal cortex. Others live in litter or dung, which they decompose.

Dipteral larvae show diverse feeding habits. (**a**) Larvae of *Delia radicum* (the cabbage fly) feed on the cabbage plant taproot. (**b**) Dipteral larvae (family Bibionidae) living in litter. (TT)

Lepidoptera larvae

Lepidoptera larvae show diverse feeding strategies. The majority feed on green plants. Ghost-moth larvae in Tibet dig soil and feed on live roots. They are often infected by a caterpillar fungus (*Ophiocordyceps sinensis*, Ascomycota) valued in herbal medicine. Some others live in ant colonies, and are fed mouth-to-mouth by ants, or feed on residuals of ant food.

Some Lepidoptera larvae in the soil have interesting relationships with other organisms. (**a**) *Ippa conspersa* larvae in their figure-eight-shaped shell. They are scavenging around an ant nest. (**b**) A mushroom-like structure with a bright orange head of the parasitic fungus *Cordyceps militaris* growing from a Lepidoptera pupa. (TT)

Coleoptera larvae

Coleoptera larvae are represented by hundreds of families with different feeding habits. Some longhorn beetle larvae (Cerambycidae) bore into roots or rhizomes. Click beetles and scarabaeid larvae chew fine roots or decaying plants. Some scarabaeid larvae are parasitised by Hymenoptera. Tiger beetle larvae (Cicindelidae) live in cylindrical burrows, and wait for their prey to pass by on the soil surface.

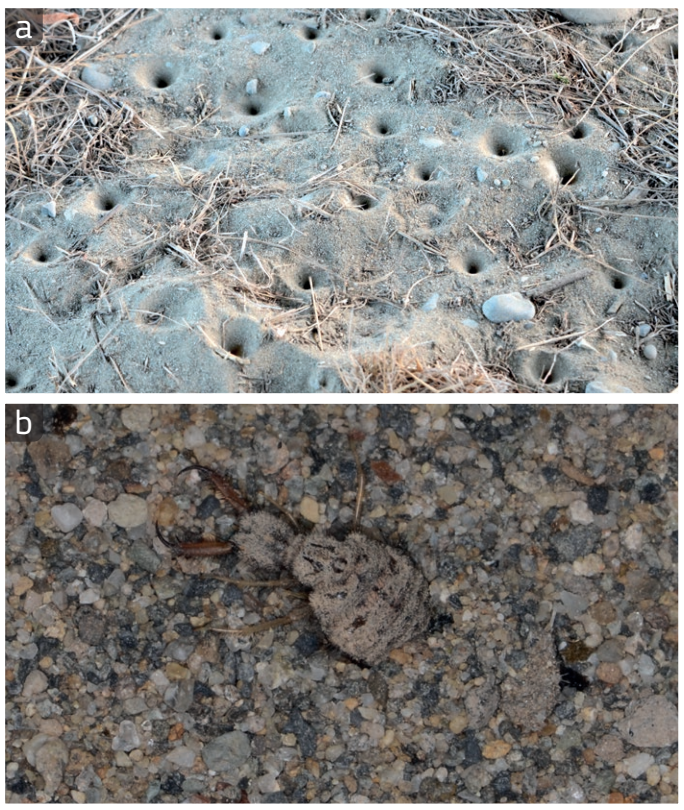
The Coleoptera species *Anoplophora malasiaca*. (**a**) Larva, which undergoes complete metamorphosis, and lives in plant roots, is very different from (**b**) the adult. (TT)

One works, the others feast

- Some parasitic species undergo hypermetamorphosis, which refers to a class of variants of holometabolism. In hypermetamorphosis some larval instars (usually the first one) are functionally and morphologically distinct from each other.
- In the beetle family Meloidae, the first instar is called triungulin (as it has three claws on each foot) and actively seeks out prey on which subsequent instars feed.
- Triungulin is elongated and flattened and in this form it does not feed. When it finds its prey it moults, transforming into a scarabaeiform or vermiform larva that does not hunt, but feeds.

Neuroptera larvae

Most Neuroptera larvae are predators, with elongated mandibles. By using the mandibles, they catch and pierce prey, and inject digestive juices. Ant lions (family Myrmeleontidae) create pitfall traps, and eat small arthropods that fall in.



Ant lions (Neuroptera) build their (**a**) traps in sand, and (**b**) wait for prey to pass. Ant lion is a name applied to a group of about 2 000 species of the family Myrmeleontidae. (TT)

Macrofauna – Ground- and litter-dwelling macrofauna

Introduction

The soil surface and leaf litter are important components of soil and may represent a perfect habitat. In particular, leaf litter, made up of dead plant material, such as leaves, bark, needles and twigs, that has fallen to the ground, is very rich in nutrients and keeps the soil moist. It also offers the perfect conditions in which to build nests: hiding places and protected spots. Many of the organisms inhabiting the ground and the litter fall within the group of soil macrofauna (animals that are at least one centimetre long). Macrofauna include myriapods, beetles, insect larvae, slugs, snails, spiders and scorpions (see pages 57, 59-60). Some of these organisms spend their entire lives on the soil surface and in leaf litter, while others are found only there at certain points in their lives. These organisms may have a high ecological importance (e.g. as decomposers of litter). In these pages, we focus on the Arachnida (e.g. spiders and scorpions), Gastropoda (e.g. snails and slugs) and some Hymenoptera (e.g. mining bees). [72, 73]

Arachnida

The class Arachnida are arthropods. Their eight legs that distinguish them from insects, which have six legs. The most well-known groups of arachnids are spiders (order Araneae) and scorpions (order Scorpiones). Spiders come in a large range of sizes, from less than 1 mm up to 30 cm, such as the Goliath birdeater (*Theraphosa blondi*), a spider belonging to the tarantula family. Scorpions range in size from 9 mm up to specimens such as the Mexican cave-dwelling *Typhlochactas mitchelli* that can reach up to 20 cm. Spiders' bodies consist of two sections (tagmata): the cephalothorax or prosoma at the front, and the abdomen or opisthosoma at the back. Spiders have a pair of cephalic appendages in front of the mouth (chelicerae), which they use to inject venom into prey from venom glands. Scorpions' bodies are also divided into two regions: the head (cephalothorax), the abdomen (opisthosoma), which is subdivided into mesosoma (seven segments) and the metasoma or tail (five segments plus a sixth, the telson, bearing the sting). The sting consists of the vesicle, which holds a pair of venom glands, and the aculeus, the venom-injecting barb. Spiders make up a very large group of organisms comprising more than 40 000 species. About 1 700 species of scorpion have been recordered to date. Spiders and scorpions are found on all major land masses, except Antarctica. Both groups are predators. They mostly prey on insects, although a few large species can also take lizards, birds and small mammals. An exception is represented by the herbivorous spider species *Bagheera kiplingi*. Soil is often used as their hunting ground, in which they use different methods of capturing prey. One of the most clever strategies is adopted by the ambush 'trapdoor spiders' (family Ctenizidae); they burrow holes into the soil, often closed by trapdoors and surrounded by networks of silk threads that alert these spiders to the presence of prey. Scorpions are nocturnal hunters, remaining in underground holes or under rocks during the day. Scorpions can survive long periods of food deprivation thanks to a specific food-storage organ and slow digestion process; some are able to survive 6-12 months of starvation.

(**a**) The Goliath birdeater, *Theraphosa blondi*, the world's largest spider. (**b**) A specimen of *Habronattus amicus* feeding on a bristletail. (**c**) A trapdoor spider, *Bothriocyrtum californicum*. (**d**) *Homalonychus theologus* has bristles that serve to gather sand/soil particles, thus providing a natural camouflage. (SM, MH)

(**a**) The scorpion *Vaejovis carolinensis* showing its sting and chelate pedipalps. (**b**) A scorpion feeding on its prey using its chelicerae. (**c**) Before the first moult, a scorpion's brood cannot survive without the mother, since they depend on her for protection and to regulate their moisture levels. (MH, TIW, FK)

Gastropoda

Snails and slugs are the two most relevant groups of gastropods related to soil. Taxonomically, they are both included in the order Pulmonata. The clear difference between them is the presence of a conspicuous shell in snails, which is very reduced, totally absent or internal in slugs. A snail's shell is made of calcium carbonate and has the typical spiral shape. Both snails and slugs range greatly in size; the largest species can reach 30 cm. Around 25 000 snail species are present worldwide, whereas only approximately 5 000 slug species exist. Terrestrial snails are usually herbivorous; however, some species are carnivores. Most slugs feed on a broad spectrum of organic materials, including leaves from living plants, lichens (see page 42), fungi (see pages 38-41) and even carrion. Some slugs are predators and eat other slugs and snails or earthworms (see page 58). Some snail and slug species can cause damage to agricultural crops and garden plants and are, therefore, often considered as pests.

(**a**) A banana (*Ariolimax californicus*) slug. This nickname is due to the colouration. (**c**) Two snails (*Helix* spp.) feeding on a mushroom. The spiral shell is their distinctive feature. (BLO, SJE)

Burrowing or mining bees

- Not all bees (Arthropoda, Ectognatha, Hymenoptera) live in hives like honey bees do and, in fact, five of the seven recognised families of bees are ground-nesting bees (approximately 70 % of the 20 000 known bee species). Their burrows can reach 60 cm in depth and the entrance is often marked by a small mound of excavated soil. Depending on the species, the female fills the brood cells at the end of the branched burrow with pollen, honey or a mixture of nectar and pollen and, once the clump reaches the right size (sometimes after a good number of trips to flowers), she lays an egg on each one. The larva hatches within a few days, grows quickly and pupates within a few weeks. The adults emerge the following spring after hibernation.
- Unlike social bees and wasps, ground-nesting bees do not live in colonies, although some species could nest in large groups ('gregarious nesters') and become so visible, especially in lawns and paths, that gardeners consider them as pests. However, in reasonable numbers they will not harm your garden. They are not aggressive insects even though the females do have stings.
- These solitary bees (specifically *Colletes* and *Andrena*, two common widespread genera) are good pollinators of economically important plants. They are often 'oligolectic', meaning that they collect pollen from only a select few plant species, and if that plant becomes rare or extinct, so does its pollinator.

A bee emerging from its nest in the soil. (JB)