The Biology of the Collembola (Springtails): The Most Abundant Insects in the World

Editor's Introduction | The Collembola, or springtails, are amongst the smallest but most successful animals. These tiny creatures are the most abundant insects in the world, found in vast numbers in almost all habitats from the seashore to the tops of mountains. Steve Hopkin, senior lecturer in Zoology at the University of Reading, takes us on a tour of the miniature world of the Collembola.

Most people come across Collembola when they lift a stone in their garden, or turn over the compost heap. Their frantic attempts to escape by leaping in a series of jumps may catch the eye for a few seconds but they soon manage to hide from view and are forgotten. Collembola are only really noticed by humans as occasional pests of crops, or when they mass in huge swarms on snow where they are known as 'snow fleas'. Although Collembola share the character of absence of wings with true fleas, the two groups differ in that the fleas (Siphonaptera) lost their wings as a secondary adaptation to their parasitic lifestyle whereas the common ancestor of Collembola never possessed the power of flight.

The body of Collembola can be divided into three main regions. The head bears a pair of antennae, a pair of eyes with a maximum of eight individual lenses (ocelli) in each (some species are blind) and the mouthparts, which are entognathic--held inside the head capsule. The thorax consists of three segments, each bearing a pair of legs. The abdomen is comprised of six segments although in several species, some of the abdominal segments may fuse making the intersegmental boundaries difficult to resolve.

All researchers agree that the Collembola form a monophyletic group i.e. they evolved from a single common ancestor. Members of the Collembola are defined by a particular characteristic that they all share--a special tube on the ventral side of the first abdominal segment (the abdominal segment nearest the head). This ventral tube is a thin-walled structure that has evolved for fluid exchange. The name, Collembola, derives from the Greek words 'cole', meaning glue, and 'embolon', meaning piston, and was first used by Lubbock (1873). The tube is a 'glue piston' because some Collembola use it for adhering to smooth surfaces. Some also use their tubes for grooming. They extrude the tubes right over the head to the back of the body. They then move their front legs across the ventral tube and then start grooming themselves rather like a rabbit or a gerbil.

Steve Hopkin

Dicyrtomina ornata (2 mm) 'grooming' using fluid extruded from the ventral tube.

Steve Hopkin

A preserved specimen of *Orchesella villosa* (4 mm) showing the spring, or furca (on the left), which is usually held under the body.

The feature that gives the Collembola their common name of springtails is the springing organ or furca. It arose during evolution from a pair of appendages that fused at their bases. It is located on the ventral side of the fourth abdominal segment and is usually folded under the body, held in place by a catch, or tenaculum, on the third abdominal segment. The furca consists of a fused area called the manubrium and a pair of structures called dentes (singular dens). On the end of each of these is a hook-like structure called a mucro. The springtails use their mucros to push or hook against the ground, providing the leverage to enable them to jump. Some species of Collembola are able to propel themselves many

times their own length in a fraction of a second. The fastest jumping species are able to respond to stimuli in about 18 milliseconds. But there are many other species of Collembola that have lost the furca; it has become a vestigial structure or is completely absent in some soil- and cave-living species.

The diet of most Collembola consists of fungal hyphae and general organic detritus in soil. They are not as important as earthworms in fuelling decomposition but are responsible for between 1 per cent and 30 per cent of total soil invertebrate respiration depending on the habitat (a typical figure for temperate woodland is 6 per cent). Collembola that live in trees graze on algae and lichens from the surface of bark and there are several species that prey on other Collembola and their eggs.

Collembola are small animals. Most are only a few millimetres long or less although the Central European Tetrodontophora bielanensis (Family Onychiuridae) can reach 9 mm in length, and some members of the tropical Subfamily Uchidanurinae (Family Neanuridae) grow to 10 mm or more. The largest species found in the UK is Tomocerus longicornis, which measures about 6 mm, excluding antennae. One of the smallest is Megalothorax minimus, less than half a millimetre in length.

Steve Hopkin

One of the smallest springtails, *Megalothorax minimus* (0.25 mm) under the head of one of the largest, *Tomocerus longicornis* (6 mm).

Louis Deharveng and Paul Cassagnau

Paralobella orousetti (1.5 mm) from the Philippines.

Some Collembola are multi-coloured. In Paralobella orousetii from the Philippines, the head and first two thoracic segments are yellow, the third thorax segment and the first three abdominal segments are red, and the remaining abdominal segments are white.

Collembola are found all over the world and in a great variety of habitats, from the seashore to the highest peaks of the Himalayas. *Cryptopygus antarcticus* is common in the Antarctic and is the only Collembola to have appeared on a postage stamp.

As well as being widespread, Collembola are unquestionably the most abundant insects in the world. An average square metre of soil in a temperate grassland or woodland yields at least 40,000 individual Collembola and figures as high as 200,000 per square metre have been recorded. Most habitats are home to at least 20 to 30 different species; populations are usually comprised of two or three hyper-abundant species along with a number of rarer taxa. In the tropics, up to 150 species have been found per square metre when the numerous individuals living in epiphytes in the trees are taken into account.

New species are being discovered all the time, in relatively well-known localities as well as others that are not so well-known. A member of the genus *Megalothorax* was discovered in the catacombs of St Stephen's cathedral in Vienna in 1996 by Erhard Christian who gave it the species name *sanctistephani.*

The Collembola are an extremely ancient group that branched off along their own evolutionary

path very early on during the evolution of the line that led to the higher insects. However, their exact position within the Arthropoda is not yet resolved. Some authors believe that Collembola have quite close affinities with the Crustacea (the group that includes crabs, shrimps and woodlice). This conjecture is supported by recent molecular phylogenies. The oldest fossil Collembola (which is the oldest fossil insect known) is a species called *Rhyniella praecursor* from the Rhynie Chert in Scotland of 400 million years in age. The specimens have entognathous mouthparts (inside the head capsule), which is a characteristic feature of Collembola.

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Sminthurid springtail (1 mm) preserved in Baltic amber dating to 40 million years.

A large number of Collembola specimens have been found preserved in amber dating to about 40 million years. These specimens do not differ much from their modern descendants. Amber from the Cretaceous period, about 100 million years ago, has also preserved a range of Collembola specimens, some of which are extremely unusual and have features not found in present-day species. It has been suggested that, as with the dinosaurs, there were many diverse evolutionary lines of Collembola that died out at the end of the Cretaceous during the major extinction event that took place 65 million years ago.

The Collembola are classified into three Orders, the Arthropleona, Neelipleona and Symphypleona (see Table 1), the latter being the commonest. Arthropleona comprises species that are more or less elongate (i.e. longer than they are wide) and in which the boundaries of the thoracic and abdominal segments are fairly easy to see. In contrast, the Neelipleona and Symphypleona are spherical in shape with poorly defined inter-segmental boundaries on the body.

The order Arthropleona is subdivided into the Superfamily Poduroidea, more commonly known as Poduromorpha, and the Superfamily Entomobryoidea, more commonly known as Entomobryomorpha. Most species of Poduromorpha live in the soil or leaf litter, are generally slow-moving, and have a well-developed first thoracic segment, which is clearly visible in animals viewed from above. The Entomobryomorpha tend to live among low vegetation and in trees, are quite active and have a reduced first thoracic segment not visible from above. However, it should be borne in mind that there are exceptions to these broad generalisations.

The Poduromorpha is divided into six Families, all of which are represented in Britain and Ireland. Hypogastruridae, Onychiuridae, and Poduridae have mandibles with a molar plate which probably serves to grind the food. Brachystomellidae, Neanuridae and Odontellidae have reduced mouthparts (mandible without a molar plate, or mandible completely absent). Members of these latter three families feed mainly on food in suspension, or pierce their food to release the contents (e.g. Frieseinae which feed on the eggs of other Collembola).

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Podura aquatica (2 mm). This species is common on the surfaces of puddles and streams.

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Neanura muscorum (3 mm), a common species under logs and in leaf litter.

Neanura muscorum (Neanuridae), is extremely common in Britain and Ireland. It has extremely large salivary glands making up as much as 15 per cent of the body weight. The nuclei of the cells within the glands contain giant chromosomes with very clear banding. It was an unfortunate accident (from the springtail worker' s point of view!) that giant chromosomes were discovered in Drosophila (fruit fly) before those of Collembola.

On 26 May 1996 in Austria, firemen were called to what they were told was a chemical spill. On arrival they discovered a patch on the road comprising several million specimens of Ceratophysella sigillata (Hypogastruridae). Species of Ceratophysella often form enormous swarms on roads, glaciers, snow and on the surfaces of puddles. The members of these swarms all leap together in the same direction using the orientation of the sun to navigate. They have small expandable sticky sacs on their antennae that help them to adhere to the substrate when they land after a jump to prevent them from tumbling too far.

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Ceratophysella bengtssoni (1.5 mm) stuck to the ground, after a jump, by the sticky sacs on the antennae.

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Kalaphorura burmeisteri (2.5 mm), a blind species with a vestigial furca.

The Onychiuridae have defensive glands on the surface of the body that secretes a nasty-tasting chemical to repel potential predators like ants. They include the species Kalaphorura burmeisteri which, like its close relatives, is blind and has a very reduced furca. Onychiurus, another genus of Onychiuridae has, like many species of Collembola, a structure behind each antenna called the post-antennal organ. It is not clear what the function of this organ is although it is most probably chemosensory. The post-antennal organ is important in taxonomy for separating genera and some species.

Members of the second Arthropleona Superfamily, the Entomobryomorpha, have a reduced first thoracic segment. There are nine Families, only five of which have representatives in Britain and Ireland (Cyphoderidae, Entomobryidae, Isotomidae, Oncopoduridae and Tomoceridae). Two species of Cyphoderidae occur in the nests of ants in Britain (*Cyphoderus albinos* and the recently-discovered *Cyphoderus bidenticulatus*). Oncopoduridae is represented by the very rare *Oncopodura crassicornis*, which is known from only a handful of sites.

Folsomia candida (Isotomidae) is used widely in ecotoxicological experiments because it is parthenogenetic (males absent) and is very easy to breed in the laboratory. This species has fused abdominal segments 4, 5 and 6, a characteristic feature of the genus Folsomia.

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A laboratory colony of *Folsomia candida*. The largest adult is 2 mm in length.

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Orchesella cincta (2.5 mm) is commonly found under logs and stones in gardens.

Some Entomobryidae are covered in finely-striated scales rather like those of butterflies, that give them an iridescent colour. Lepidocyrtus cyaneus is such a species and is extremely common under stones and in leaf litter. Other common entomobryids include Orchesella cincta and Entomobrya nivalis. The latter species is particularly tolerant of dryness and is a common inhabitant of epiphytic lichens on trees.

Tomocerus longicornis (Tomoceridae) is a very common species that has extremely long antennae. The insect will roll its antennae into a spiral when irritated. This habit is a useful field character for scientists in the field wishing to identify live specimens.

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Tomocerus longicornis (5 mm) with rolled antennae.

Neelipleona is a small order of only about 25 species worldwide. All species are tiny (most less than 0.5 mm in length) and live in soil and leaf litter. *Neelus minutus* and *Megalothorax minimus* are common. They have a globular appearance and bear a superficial resemblance to Symphypleona. However, Neelipleona differ in that the body is formed largely by expansion of the thoracic rather than abdominal segments.

The third Order of Collembola is the Symphypleona. These have a rounded body shape and are frequently seen on the surfaces of leaves and ponds demonstrating their considerable jumping abilities. Indeed the first springtail to be illustrated in a scientific book was the symphypleonid Allacma fusca in 1743. A common (and quite large) species in gardens is Dicyrtomina ornata.

Steve Hopkin

Dicyrtomina ornata (3 mm), commonly regarded as one of the most attractive species.

The males of some symphypleonids are among the smallest of insects, as little as 0.18 millimetres in length. Deuterosminthurus pallipes, which is very common on vegetation on gardens in the south of England, is only about a millimetre in length but along with many other symphypleonids, has an elaborate courtship behaviour. This involves 'head butting' and dancing by the male in order to entice the female to take up a spermatophore that he has deposited on the substrate.

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A pair of *Deuterosminthurus pallipes* (1.0 mm) 'head butting' during courtship.

Collembola are not as economically important as certain species of moths or aphids but one species, *Sminthurus viridis* the 'Lucerne flea', can cause substantial economic damage. It is very common in Europe, where it is controlled by its natural enemies. However, *Sminthurus viridis* has been introduced to several countries where it apparently has few natural predators. In Australia the Lucerne flea is quite a serious economic pest and there are certain parts of Tasmania where at least 10 per cent of the crops are sprayed annually to control its activities.

In common with many other areas of science, the dissemination of knowledge on Collembola has been revolutionised by the Internet. There are at least 50 scientists throughout the world studying the taxonomy, ecology and biology of springtails and an average of 200 scientific publications on the group appear each year. Although Collembola are not as familiar as high profile groups of invertebrates such as butterflies and dragonflies, they provide almost endless opportunities for scientific discovery.

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