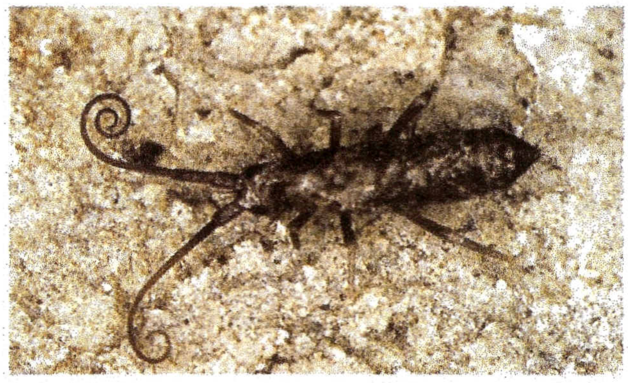
Springtails – in search of Britain's most abundant insects

Orchesella villosa on a liverwort. Steve Hopkin

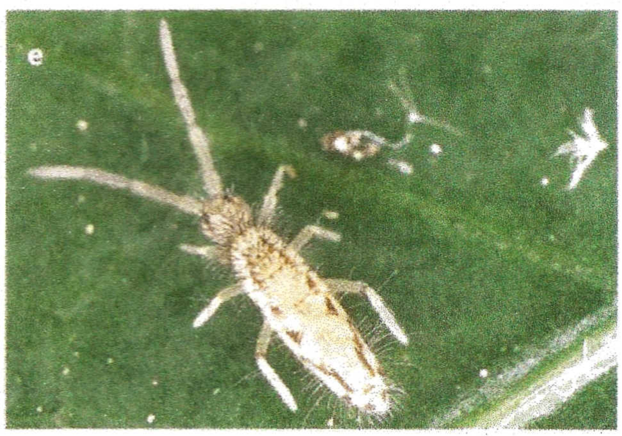
Geoff Frampton and Steve Hopkin

Springtails (Collembola) may be found in almost any habitat, from the littoral zone to the Scottish and Welsh mountains, in fields, woodlands, on the surfaces of ponds and lakes, and in our offices, houses and greenhouses. They are the oldest known group of insects, having inhabited Earth for at least 400 million years. Collembola are also the most abundant of our British insects, with numbers in excess of 40,000 per m^2 not unusual in soil and leaf litter. Yet springtails are given only scant mention in most entomological textbooks and insect field guides. Because of their small size (the largest UK species is 6mm in length), people have, understandably, been discouraged from studying them. Even Charles Darwin appears to have been unimpressed by these 'wingless, dull-coloured minute insects' (Darwin 1871).

Darwin's view was not shared by everyone, and certainly not by his close friend Sir John Lubbock, who, in 1873, published *Monograph of the Collembola and Thysanura*. It was Lubbock who first used the name 'Collembola' for springtails, and his monograph was an important zoological landmark in that it critically appraised the disorganised state of springtail taxonomy, drawing attention to the problem of synonymy caused by the inconsistent naming of species by different workers. The monograph also served to highlight the diversity and beauty of springtails, in a series of colour plates (painted by the deaf and dumb artist A T Hollick) which, to this day, remain unrivalled in their detail and quality. During the 20th century, interest in springtail taxonomy increased: many new species have been described and the world list now numbers nearly 6,500 species,



a *Lepidocyrtus cyaneus*, one of the commonest springtails in fields and gardens.
b *Folsomia candida*, a subterranean species, used as the 'standard' springtail in many laboratory studies.
c *Tomocerus longicornis*, our largest springtail.
d Species of *Deuterosminthurus* are common on foliage, where they appear as slow-moving tiny yellow specks.
e *Entomobrya nivalis*.
All photographs: Steve Hopkin



compared with 130 listed by Lubbock (1873). However, until recently, no comprehensive taxonomic key to the British species had been published since Lubbock's monograph, a situation which, together with the small size of springtails, has undoubtedly hindered our understanding of their ecology in comparison with that of other insects.

As we begin the 21st century, the relatively low profile of springtails as members of the British fauna and in ecological studies could be set to change. In 1997, *Biology of the Springtails* was published (Hopkin 1997), the most comprehensive account of springtail biology in more than 40 years. In addition, the preliminary version of *A Key to the Springtails of Britain and Ireland* is currently being tested (Hopkin 2000). This will be the first identification guide to the British springtail fauna (of which there are at least 250 species) since Lubbock's monograph. The springtail key will be followed by the launch of a recording scheme, to ascertain for the first time the regional distributions of British species. Concurrently with these developments, research studies are starting to unravel the complex ecological interactions of springtails, revealing the potential importance of these tiny animals, for example as promoters of decomposition and soil fertility, as prey for beneficial farmland arthropods, and as sensitive indicators of the effects of farming practices, including those of pesticide use, on 'non-target' fauna.

Evolution and classification of springtails

Springtails, along with proturans (Protura) and bristletails (Diplura and Thysanura), have traditionally been placed in the insect Sub-class Apterygota, the so-called 'primitive wingless insects' that have never evolved wings. This higher taxonomy is to be found in many entomological textbooks and field guides (e.g. Chinery 1993). However, it

***Megalothorax minimus*, one of our smallest springtails, is dwarfed by *Tomocerus longicornis*.** Steve Hopkin

is now widely recognised that Apterygota is not a monophyletic group and that the springtails and proturans are related only distantly to the true insects, although the phylogenetic position of springtails is still uncertain (Giribet & Ribera 2000). Current opinion (Hopkin 1997), based on a strictly cladistic classification, retains Collembola as insects in the broad sense, as a Class within the Hexapoda, but together with the proturans they form a separate group (Parainsecta) from the other 'true' insects (Euinsecta).

The fossil springtail *Rhyniella praecursor*, discovered together with Devonian plant fragments in Lower Devonian chert in Aberdeenshire, Scotland, is direct evidence that Collembola existed at least 400 million years ago. But springtails are soft-bodied, so their remains are rarely fossilised. The discovery of Silurian coprolites (fossilised faeces) that could be of springtail origin raises the possibility that springtails existed on Earth even earlier (Sherwood-Pike & Gray 1985). Molecular evidence suggests that the ancestor of springtails was a multi-segmented crustacean-like aquatic animal that became progressively adapted to a terrestrial environment. As land plants evolved and increased in complexity, so springtails radiated to exploit the available niches and today they occupy a wider global distribution than any other arthropod group. An indication of springtails' resilience can be seen among specimens preserved in 40-million-year-old amber (fossilised plant resin), which bear a remarkable resemblance to extant species (Hopkin 1997).

***Orchesella cincta*, a common species of woodlands, hedgerows and gardens.** Steve Hopkin

Springtail biology basics

Springtails are often referred to both as members of the mesofauna (they are intermediate in size between micro-organisms and the largest invertebrate soil animals, such as beetles) and as microarthropods (they rank among the smallest members of the Arthropoda). Morphologically, most springtails fall into two distinct groups: the elongate Arthropleona, which have clearly separate thoracic and abdominal segments, and the Symphypleona, in which part of the thorax is fused with the abdomen to give the body an overall globular appearance. A notable feature that distinguishes springtails from all other insects is that the abdomen has, at most, only six segments. It is also unique to springtails that growth and moulting continue after the animals have reproduced.

There are usually three types of ventral appendages on the abdomen: a 'ventral tube' on the first segment, a 'retinaculum' on the third segment, and the jumping organ or 'furcula' on the fourth segment. The ventral tube acts as an adhesive organ on slippery surfaces and is important in regulating the animal's water balance. Elongate thin-walled sacs contained within the ventral tube may be extruded under haemostatic pressure and in some species reach forward and over the head to groom the antennae, before being retracted again. When viewing springtails under a microscope, the sudden and momentary appearance of these sacs from underneath the body is certainly a peculiar sight. The ventral-tube sacs have also been observed to aid in righting the animal when it lands upside-down after a jump. The ventral tube is clearly an important organ of springtails and gave rise to Lubbock's name 'Collembola', from the Greek *colle* (glue) and *embolon* (piston).

The common name of 'springtail', on the other hand, clearly relates to the posterior jumping organ. When at rest, this is held against the underside of the body by the retinaculum, which acts rather like a catch. When the 'catch' is released, the furcula springs downwards and backwards under haemostatic pressure, propelling the insect upwards and forwards into a 'jump'. This method of locomotion is used mainly as an escape response from predators or unfavourable chemical or microclimate conditions. Time-lapse video recordings have shown that springtails somersault during a jump and can travel several centimetres in a fraction of a second. The pattern of jumping varies among species and with the structural complexity of the habitat they occupy. Species which can retract the furcula while in flight are able to jump again as soon as they land, whereas other species need a brief period of rest between jumps.

The morphology of springtails varies markedly with their vertical distribution. Species living above ground are often brightly pigmented, with eyes (comprising up to eight ocelli on each side of the head), long antennae and a well-developed furcula. Among them is our largest British springtail, *Tomocerus longicornis*, which reaches up to 6mm in length (excluding antennae). On the other hand, species that live entirely below ground are typically small, unpigmented (white), blind species with short antennae and a furcula that is reduced to a small stub, or lacking altogether.

Ecological importance of springtails

An important prey resource

Almost all polyphagous (generalist) predatory arthropods feed to some extent on springtails, with money spiders (Linyphiidae), predatory mites (Acari) and ground beetles (Carabidae) being particularly important consumers. Many of these predators are also natural enemies of crop pests such as cereal aphids, and the presence of springtails as an alternative prey could be important in supporting predator populations at times of low pest abundance (Sunderland *et al.* 1997). Several predatory ground beetles and rove beetles have evolved morphological adaptations that enable them to feed as stenophagous (specialist) predators almost entirely upon springtails. Ground beetles of the genus *Notiophilus* and rove beetles of the genus *Stenus* have enlarged eyes to enable them to hunt springtails by daylight, while the ground beetles *Leistus* spp. and *Loricera pilicornis* use stout setae around the mouthparts and on the basal antennal segments respectively to pin down springtails where the beetle's mandibles can reach them. Not all attacks on springtails succeed, and springtails are often seen with antennae of unequal lengths, where one or more antennal segments have been lost to a predator; regeneration of the last segment can occur, which makes the antenna look normal but with fewer than the usual number of segments. All predators of springtails may in turn be eaten by vertebrate wildlife, including insectivorous birds and small mammals. Indeed, springtails themselves may be eaten directly by vertebrates, sometimes in large numbers (Hopkin 1997).

Springtails as consumers

The diet of springtails is varied. Most species are fungivorous, with fungal hyphae being preferred over most other food types; but springtails also eat pollen grains and partially decomposed leaf litter, while some species are herbivorous and others carnivorous. They have been observed feeding on plant-pathogenic nematodes and may assist in their control, but, conversely, they could have an undesirable effect if they eat entomopathogenic nematodes or fungi that control insect pests. Springtails which feed upon plant-pathogenic fungi are inherently beneficial, and a number of studies (see Hopkin 1997) have proposed the use of these species as a means of biologically controlling fungal plant diseases, for example by introducing springtails into plant pots in glasshouses.

The feeding behaviour of springtails can influence the decomposition process and nutrient-cycling in a number of complex ways. Springtail faeces derived from the ingestion of dead vegetation increase the surface area of partially decomposed material that can be colonised by primary decomposers such as bacteria and fungi. The faeces are also an important source of nitrates in forest soils and may aid dispersal of the spores or cysts of fungi, bacteria and other soil organisms. Springtail grazing tends to stimulate bacterial and fungal growth and, in legumes, can improve nitrogen fixation by increasing the number of root nodules (Lussenhop 1996). Selective grazing on the other hand may reduce fungal biomass of some species and affect the species composition of primary decomposers. The overall impact of springtails on decomposition is difficult to quantify in the field given the complexity of interactions, and depends on the abundance of springtails in relation to that of other soil fauna. They are probably most important where earthworms are rare or absent, as in acidic or polluted sites.

One way of investigating the role of soil animals in decomposition and nutrient-cycling is to construct miniature ecosystems – known as microcosms, mesocosms or terrestrial model ecosystems – that permit controlled manipulation of individual ecosystem components. A number of studies have compared model ecosystems with and without springtails, or with different numbers and abundance of springtail species, to investigate their effects on ecosystem processes. Probably the most famous example of such an experimental approach is the 'Ecotron' (Lawton 1994), but even this relatively complex model ecosystem contains only seven springtail species, compared with the 40 or so that may be present in temperate arable fields or woodlands. Microcosm experiments have shown clearly that the presence or absence of individual springtail species can strongly affect nutrient-cycling, such as nitrogen mobilisation (Mebes & Filser 1998), but such single-species manipulations are difficult to relate to real ecosystems, as not all species have equal ecological weight (Lawton 1994), and because the combined effects of several species can differ considerably from the effects of the same species individually (Mebes & Filser 1998). Notwithstanding these interpretational difficulties, springtails in temperate ecosystems probably have, on balance, a beneficial impact on decomposition and nutrient-cycling as their selective feeding indirectly increases nutrient availability to plants (Hopkin 1997).

Springtails in multi-trophic interactions

The soils of most ecosystems contain a rich abundance and diversity of arbuscular-mycorrhizal (AM) fungi. The roots of around 80% of all terrestrial plants have symbiotic relationships with these fungi, whose hyphae act like an extended root network and facilitate increased nutrient uptake, as well as conferring other benefits on the plant, such as increased drought tolerance. Some plants are entirely dependent upon AM fungi for normal growth, and there is evidence that AM fungi make a major contribution to the maintenance of plant biodiversity and to ecosystem functioning (van der Heijden *et al.* 1998). If the feeding activities of springtails affect AM fungi, then clearly these animals could have an important impact upon biodiversity and ecosystem functioning.

It was initially supposed that springtails, being predominantly fungivorous, reduce the functioning of the mycorrhiza and are thus detrimental to plant growth. But recent choice experiments have shown that springtails in fact prefer to eat non-AM fungi, a behaviour that might actually favour plant growth by reducing competition between mycorrhizal and non-mycorrhizal fungal species, or by increasing nitrogen mineralisation (Gange 2000).

There are also other ways in which springtails could potentially have a beneficial impact on plant growth, including the intriguing possibility that feeding upon mycorrhizal fungi would cause changes in the performance of herbivorous insects on the same plant, by altering the plant's nutrient status. There is, indeed, evidence from a non-mycorrhizal study that the presence of springtails in soil can lead to a decrease in the reproduction of aphids feeding upon the leaves of clover (Scheu *et al.* 1999). It is easy to see that this trophic cascade could extend even further, as predatory mites in the soil, by preying upon the soil springtails, could also contribute to the effects on above-ground herbivore performance. These are certainly exciting, if rather complex, times for studying springtails in food-web ecology!

Pest status

Theobald (1910) listed 23 springtail species as injurious to various crops, but early records of these insects causing crop damage are rather shaky, as the mere presence of insects on a damaged plant was often enough for farmers to brand them as the culprits. There is no doubt that certain herbivorous springtails can damage field crops, mainly by chewing away at stems or roots, but attacks are usually localised and brief. A range of plant species is injured, for instance, when the surface-dwelling 'garden springtail' *Bourletiella hortensis* bites into the stems of seedlings (Hopkin 1997), while subterranean species of *Onychiurus* can injure sugar-beet plants by feeding upon the roots. However, springtails are pests of sugar beet only when alternative food sources are unavailable, as occurs when weeds are completely removed by herbicide use (Larink 1997).

The sporadic nature of springtail damage means that springtails are not economically significant as crop pests in northern Europe. It is worth remarking, however, that *Sminthurus viridis*, a species that occurs in Britain (and which was formerly restricted to the Northern Hemisphere before becoming more widely distributed with anthropogenic assistance), is one of the most serious insect pests of field crops in Australasia. This springtail has earned the name 'Lucerne-flea' on account of its devastation of lucerne and clover crops, principally in semi-arid regions, where numbers in excess of 50,000 per m^2 can arise when rainfall triggers the synchronised mass-hatching of drought-resistant eggs. Our laboratory studies have shown that synchronised mass-hatching of springtails would also occur in Britain under certain scenarios of drought followed by rain (Alvarez *et al.* 1999), but a field investigation of the effects of southern England's 1997 spring drought did not show a favourable effect of the drought on any of 14 springtail species monitored (Frampton *et al.* 2000). This may be due in part to a larger controlling influence of natural enemies on springtail populations in northern Europe. Money spiders, for instance, which are important predators of springtails, have been found to be twice as species-rich and five times more abundant in England than in parts of New Zealand (Topping & Lövei 1997).

The Lucerne-flea *Sminthurus viridis*. Barry Lockyer

Side-effects of pesticides

Agricultural fields are one of the major habitat types in Britain (arable crops occupy one fifth of the land surface), and within these springtails are often our most abundant arthropods. Though not pests, they are likely to be exposed to a range of farming practices, including pesticide use. However, side-effects of pesticides on springtails, in comparison with other arthropods, have been very poorly studied. Most laboratory tests of pesticide effects have used easily cultured species, particularly the parthogenetic, soil-inhabiting *Folsomia candida*, but, as Hopkin (1997) remarks, this is 'about as ecologically sound as choosing a mole as a "typical" mammal'. Indeed, *F. candida* has recently been found to be toxic to some predators (Toft & Wise 1999), so it is hardly suitable as a model springtail where predator-prey interactions are concerned.

The most realistic way to determine effects of pesticides is to monitor communities of organisms in the field, but very few studies have attempted this with springtails. In general, the pesticides most harmful to springtails are the organophosphate and some carbamate insecticides, particularly if they are applied in consecutive seasons, which prevents population recovery in the long term (Frampton 2000). Synthetic pyrethroids, which are the most frequently used insecticides in Britain, appear in general to be more harmful to predatory arthropods than to springtails, which can result in an increased abundance of springtails following spraying (Frampton 1999). Such an indirect effect of pesticide use cannot be detected in laboratory tests that exclude predators, underlining the limitations of standardised laboratory test methods.

Fungicides can be harmful to springtails both directly and by removing their fungal food supply (Frampton & Wratten 2000), and may also influence plant-mycorrhiza associations. Such indirect effects of pesticides have the potential to complicate further the already intricate multi-trophic interactions in which springtails participate. An important finding from the field studies is that even closely related springtail species may respond differently to pesticide use. In a long-term monitoring study, for example, repeated use of organophosphate insecticides in five consecutive years led to the virtual disappearance of the springtail *Entomobrya nicoleti* from a sprayed area, whereas the related species *E. multifasciata* was able to recover much more quickly and was not adversely affected in the long term (Frampton 2000).

It is a mystery why these species respond so differently. Perhaps they differ in their dispersal powers, and hence their ability to repopulate the sprayed area. In fact, surprisingly little is known about springtail dispersal behaviour in temperate ecosystems, perhaps because these animals, in which moulting occurs throughout the life cycle, are not very amenable to mark-recapture studies. Another possible explanation could be that, if *E. nicoleti* has a more fragmented distribution pattern, the springtails would be less able to reach the treated area from source populations. It was discovered in the mid 1980s that many predatory arthropods colonise fields from source populations in hedgerows, but only recently has evidence emerged that this may also be true for some springtail species (Alvarez *et al.* 2000). There is obviously much we need to learn about the ecology of our most abundant insects.

Springtails of fields, woods and gardens

Field and woodland habitats can each harbour as many as 40 different species of springtail, though many are tiny, subterranean animals that are rarely noticed. One of the most widespread springtails seen on the ground surface in agricultural fields throughout Europe, and also in gardens, is *Lepidocyrtus cyaneus* (1.5mm long when fully grown). Viewed through a hand lens, this springtail has the appearance of a tiny steel-blue bullet scurrying around on the soil surface. Also common on the soil surface in fields and gardens, particularly in damp areas, are larger, dull green springtails of the genera *Isotoma* and *Isotomurus*. Many of these are plain, but some, such as *Isotomurus maculatus* (2.5mm), have distinctive patterns. Several species are characteristic of woodland and tend to be absent from cultivated fields, although they are often present in hedgerows. These include the large *Tomocerus longicornis* and *Orchesella cincta* (3mm), both of which are very common in gardens and easily identified with the aid of a hand lens. Freshly moulted *T. longicornis* are dark grey but become yellow in colour as their scales wear off, while *O. cincta* has a distinctive lateral stripe on its abdomen. Another common species, which is sometimes seen dropping from trees and tall plants, is the distinctively patterned *Entomobrya nivalis* (2mm).

The aforementioned species are elongate in appearance, being members of the Order Arthropleona. Globular-shaped springtails of the Order Symphypleona are also widespread and abundant in fields, woodlands and gardens, but most, such as springtails of the genus *Deuterosminthurus* (1mm), which are often seen as tiny slow-moving yellow specks on leaves, are too small to identify without a microscope. An exception is the Lucerne-flea (3mm), which can be abundant on clover and legumes. Its bright green, rounded body is unmistakable when viewed through a hand lens, although at a distance these animals are sometimes mistaken for aphids.

Collecting springtails

Some of our larger springtails are relatively easy to find by looking closely at the soil surface, under stones and logs, in leaf litter and on paths and walls. They sometimes occur indoors, particularly where temperature and humidity are high, and they can be abundant in greenhouses. The most productive places to look are those where vegetable matter is decomposing (compost heaps, leaf litter, or rotting wood), or where there are patches of algae or moss.

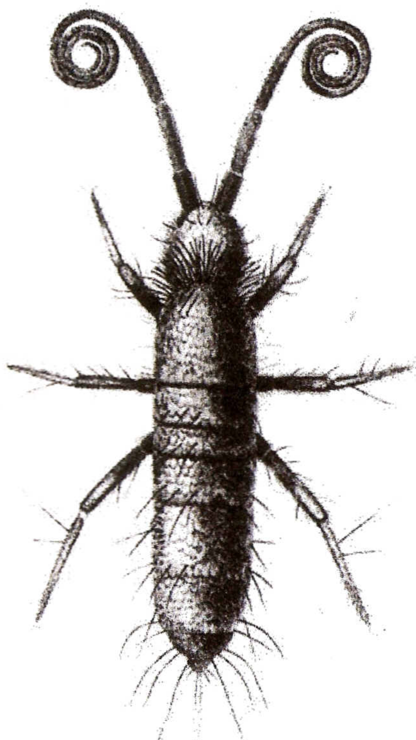
The insects can be collected from the surface of soil by using a pitfall trap made from an empty jam jar or yoghurt pot sunk into the ground, flush with the ground surface, so that insects walking across the ground fall into it. Traps can be left for several hours, but the longer the trapping period, the higher the risk that the captured springtails will become dehydrated or be attacked by predators such as mites, beetles or spiders that fall into the trap. 'Suction'-sampling with a garden vac is another way of obtaining these insects from the ground surface, while insects present on vegetation can be collected by shaking the vegetation over a collecting tray (a white plastic ice-cream or margarine tub is ideal for this purpose). Springtails are very susceptible to dehydration, so it is prudent to place a piece of damp tissue paper at the bottom of each pitfall trap or collecting tray.

A more permanent collecting tub or 'culture box' can be made by filling an ice-cream or margarine tub to a depth of 1-2cm with plaster of Paris, which, when moistened, will provide a more reliable source of humidity. Crevices in the surface make ideal places for springtails to lay their eggs. When provided with a lid (perforated to permit air circulation), such a culture box can be used to keep springtails alive for weeks or even months, if suitable food is present (dried baker's yeast is adequate as a food for some species). The longevity of springtails kept in culture boxes depends on getting the right combination of temperature, humidity and food, which differs among the species. It is also important to ensure that cultures do not become infested with fungal hyphae. The easiest way of dealing with this is periodically to tip the springtails into a clean culture box.

If a low magnification (10-40 times) binocular microscope is available, a fascinating exercise is to examine a fresh sample of soil or leaf litter microscopically, to see the variety of active soil invertebrates, including springtails, that is present.

Identifying springtails

Identification of most springtail species requires the use of a good-quality compound microscope. However, some of our larger species are distinctive enough to be identifiable with the naked eye or with the aid of a hand lens. Unfortunately, few insect textbooks and field guides can be relied upon for accurate springtail identification, but comparison of insects with those pictured here should be sufficient to identify adults of the large, common species *Orchesella cincta*, *Orchesella villosa*, *Sminthurus viridis* and *Tomocerus longicornis*.



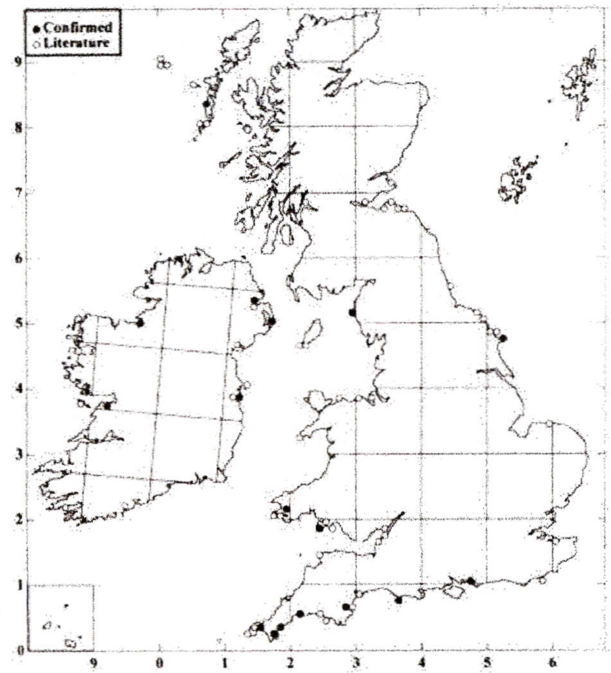
Tomocerus longicornis. From Lubbock (1873). Drawing by A T Hollick, a deaf and dumb artist.

For the more determined 'collembologist' with a suitable microscope, *A Key to the Springtails of Britain and Ireland* will enable identification of all British springtail species when the final version is published, following a period of evaluation (Hopkin 2000). This will be the most authoritative identification key to British springtails since the monograph of Lubbock (1873) and should benefit studies of springtail ecology, which have undoubtedly been hindered in the past by the difficulty of species identification.

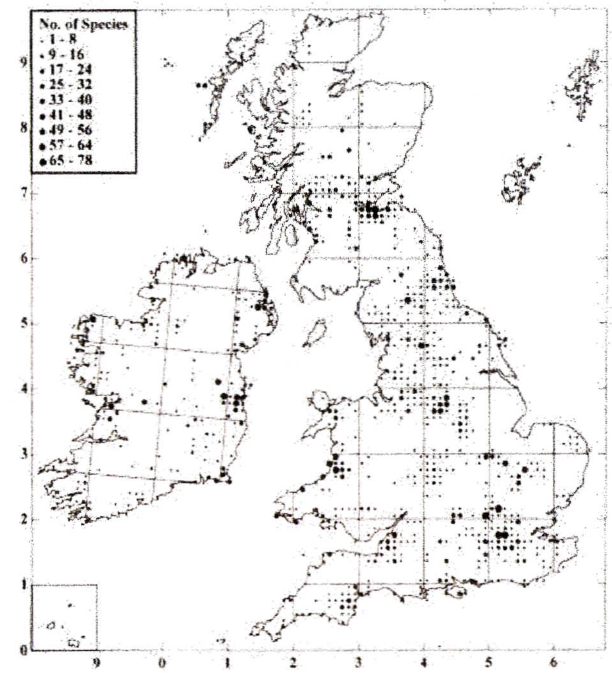
Conservation

There are many reasons for ensuring the survival of individual species, in particular the need to protect or enhance biodiversity and ecosystem function. To ensure the survival of a species, it is essential to know its geographical distribution and dispersal ability in relation to the availability of suitable habitat. For springtails, however, hardly any information exists on the distributions of species in Britain – we literally have no idea how rare, or endangered, many of our springtail species are. Even for the species mentioned above, which are common in fields and gardens, it is not possible to picture their distribution patterns on a regional scale. There is clearly a compelling case for the distributions of springtails to be mapped, and this task has been started at the University of Reading.

Preliminary distribution maps for several species, based on a limited number of literature records as well as recent observations, are already showing that certain springtails have a restricted occurrence in Great Britain and Ireland (http://www.ams.rdg.ac.uk/zoology/collembola/maps/). *Anurida maritima*, for example, is a coastal species, while the highly distinctive *Lathriopyga longiseta* appears to be confined to the south-west of England. However, there are large parts of Britain where, so far, the presence of springtails has not been investigated, particularly in North Wales, eastern England, the Lake District and much of Scotland. The mapping scheme will be launched as a formal Collembola recording scheme in 2003 in order to improve the coverage of the distribution maps. Ultimately, this



Map showing 10km square records of *Anurida maritima*.



Map showing 10km square records of all springtail species.

should allow the true distribution of species to be determined, as well as changes in patterns of species' distributions over time. Only then shall we have a clear picture of the state of health of our springtail communities.

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