COLLEMBOLA

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INTRODUCTION

Collembola (commonly known as "springtails") are currently considered to be a monophyletic Class of the Phylum Arthropoda (1) although their exact taxonomic position is still the subject of some debate. Many authors treat Collembola as insects. However, many of the old ideas on arthropod evolution are being reassessed in the light of modern evolutionary theory and molecular phylogeny so their placement may change.

There are three main Orders of Collembola. Members of the **Arthropleona** (about 5500 species) have a more or less elongated body shape and range from highly active surface-dwelling species to those that live out all their lives in the depths of the soil. An example of this Order is *Folsomia candida* (Fig. 1), which belongs to the Family Isotomidae. It is familiar to ecotoxicologists as one of a suite of "standard test soil organisms," which are used to assess the toxicity of new chemicals before they are released into the environment. The **Symphypleona** (about 1000 species) have a much more rounded body shape and are mostly attractively patterned, surface-living species. A typical example is *Dicyrtomina ornata* (Fig. 2) (Subfamily Dicyrtominae). The **Neelipleona** are very small soil inhabiting springtails (typically 0.5 mm in length) with only about 25 species known in the world. They have a rounded body shape and bear a superficial resemblance to Symphypleona.

MORPHOLOGY

The oldest fossil Collembola (indeed the oldest fossil insects) are specimens preserved in Rhynie Chert of more than 400 million years in age. Collembola are present in amber in which remarkable detail is preserved (Fig. 3). The most obvious feature of Collembola is the jumping organ or furca, which is clearly visible in the specimen shown in Fig. 1 projecting behind the animal in its "sprung" state. The furca evolved through the basal fusion of a pair of appendages on the fourth abdominal segment and is capable of propelling some springtails many times their own body length in a fraction of a second. The spring developed as an escape mechanism to avoid predators. Species of Collembola confined to the soil have a reduced furca to ease their movement between soil particles and tightly packed leaf litter. Some have lost the jumping organ altogether. The maximum number of ocelli in each eye is eight, but these are often reduced and many soil-dwelling and cave species are blind.

All Collembola have a *ventral tube* that consists of eversible sacs derived from a pair of appendages on the first abdominal segment. This organ is extremely important in fluid balance but can also function as a sticky appendage to enable springtails to adhere to slippery surfaces. In some species, the vesicles of the ventral tube may extend more than twice the length of the body and be used for self-righting after a jump. Lubbock introduced the scientific name for springtails in 1873 (2). He rightly considered the ventral tube to be the most characteristic feature of the group and gave them the name Collembola based on the Greek *Colle* (= glue) and *embolon* (= piston).

Collembola are small animals. Most are only a few millimeters long although the Central European species *Tetrodontophora bielanensis* can reach 9 mm in length, and some members of the Subfamily Uchidanurinae grow to 10 mm and bear brightly colored "spines." The tiniest and least-pigmented species tend to be those that live permanently in the spaces between particles of soil or sand. The blood of some Collembola possesses chemicals that act as powerful feeding deterrents to predators (3).

ECONOMIC IMPORTANCE

The majority of springtails feed on fungal hyphae or decaying plant material. In the soil, they may influence the growth of mycorrhizae (4) and control fungal diseases of some plants (5). In general, these effects are beneficial; however, there are a few species, including *Sminthurus viridis* the "Lucerne flea," which feed directly on plant material. In Australia, a country to which *S. viridis* has been introduced, the species can cause significant

Fig. 1 Adults and juveniles of *Folsomia candida*. The largest specimen is 2 mm in length. (Photograph by Steve Hopkin.)

Fig. 2 *Dicyrtomina ornata* (1.5 mm in length). (Photograph by Steve Hopkin.)

Fig. 3 Symphypleonid springtail (1 mm in length) preserved in Baltic amber of 40 million years in age. (Photograph by Steve Hopkin. Specimen supplied by Andrew Ross, Natural History Museum, London.)

economic damage (6). Some springtails are carnivorous and eat nematodes, rotifers, and even other Collembola.

LONGEVITY

Springtails are generally short-lived. Few survive as adults for more than a year or two. The documented longevity record is held by *Pseudosinella decipiens*, which survived for up to 67 months in the laboratory, although some cave species, or those in very cold climates, may live longer. Most Collembola continue to moult after reaching reproductive maturity and may alternate reproductive and "sexually dormant" instars through several cycles. Several species are parthenogenetic (males absent) including *Folsomia candida* (Fig. 1).

HOW MANY SPECIES?

Approximately 6500 species of Collembola have been described although it is difficult to give an exact figure as there are many species yet to be discovered, especially in countries such as Australia and New Zealand where there is a high level of endemism. The most recent estimate of the total number of species of all insects on the earth quotes a figure of between 5 and 10 million, less than 20% of which have been described (7). In view of their cryptic behavior and relative lack of scientific study, it is likely that at least 50,000 species of springtail exist on our planet.

DISTRIBUTION

Collembola have a very wide global distribution. They are abundant on every continent, including Antarctica, where *Biscoia sudpolaris* and *Antarctophorus sudpolaris* have been found crawling among lichen at a latitude of 84° 47′S, the most southerly location for any invertebrate (8). *Aackia karakoramensis* occurs on newly fallen snow in the Himalayas at an altitude of 7742 meters (9). *Folsomides arnoldi* is abundant in Australian deserts (10).

Collembola are common on the seashore. *Anurida maritima* is a marine species and is one of the most familiar invertebrates of the littoral zone in Europe (11). Several species live almost permanently on the surface of freshwater, including the common and widespread *Podura aquatica*, a frequent sight on puddles after rain, sometimes in huge numbers. Species of *Hypogastrura* are abundant and are important in clearing growths from the percolation filters of sewage beds.

Many species live all their lives in the soil, where they penetrate more than 150 cm below the surface. Others live on trees and are abundant in rain forest canopies. In one study, about one million Collembola of 16 species were collected from 100 m^2 of dry forest in Mexico by insecticide fogging (12). Some Collembola are specialized for living in sand (13).

DIVERSITY

Habitats with extreme climates such as deserts and polar regions support few species of Collembola, but sites with many niches have a diverse springtail fauna. Collembola seem to follow the general rule that diversity is inversely related to latitude; that is, there are more species in tropical than in temperate zones. In tropical rain forests, more than 130 species m^{-2} have been found in soil, leaf litter, and aboveground vegetation (14). In more temperate forests, diversity is lower, but it is not unusual to find more than 40 species in deciduous woodland (15). Collembola exhibit dominance patterns typical of most groups of terrestrial arthropods. The majority of individuals are usually represented by a small number of common species. In most populations, a large fraction of the species (usually $>50\%$) is rare with dominance values of $<1\%$.

"SWARMING"

Collembola are most obvious when they swarm. Most reports are of species in the family Hypogastruridae. They occur following synchronized reproduction in conditions of ideal humidity and temperature and abundant food supply. There are numerous references in the literature to swarming, particularly on snow and glaciers (e.g., 16). Swarms certainly can be huge, often comprising several millions of individuals. The reasons for this behavior are not completely understood although in most cases the Collembola are probably searching for a more favorable habitat after becoming overcrowded.

ABUNDANCE

Collembola are extremely abundant in soil and leaf litter. In most terrestrial ecosystems they occur in high numbers, typically between 10^4 and $10^5\,m^{-2}$. Densities of springtails of more than $10^5\,m^{-2}$ have been found in pine forests in India and Japan, moorland in England, and dry meadows in Norway. Collembola are particularly abundant in agricultural soils that are farmed "organically" (17). In the rain forests of Seram, Indonesia, Collembola comprise about 20% of the total number of arthropods on tree trunks and 50% and 60% of the total from soil and leaf litter, respectively (18). However, because of their small size the contribution of Collembola to total soil animal biomass and respiration is low, typically between 1% and 5% in temperate ecosystems, but up to about 10% in some arctic sites and as much as 33% of total soil fauna respiration in ecosystems in early stages of succession. Typical values for the dry weight of springtails in temperate ecosystems are $0.15\,g\,m^{-2}$ in deciduous woodland and $0.3\,g\,m^{-2}$ in limestone grassland.

EFFECTS ON SOIL STRUCTURE

Despite their relatively low biomass, springtails are extremely important in influencing the structure of some soils. For example, "alpine pitch rendzinas" on limestone are composed mainly of a deep black humus layer of 15 to 20 cm in depth that is formed almost entirely of Collembola feces (19). Most soils contain millions of collembolan fecal pellets m^{-2}, and these must be beneficial in slowly releasing essential nutrients to plant roots as the pellets are broken down by microbes.

ROLE IN DECOMPOSITION

The main effect of Collembola on decomposition and "soil respiration" is through feeding on fungal hyphae. At certain densities of Collembola, grazing of mycorrhizae on roots can stimulate growth of the symbiont and improve plant growth (4). In other situations, Collembola may reduce disease by consuming pest fungi (5).

Selective grazing by springtails may be an important factor limiting the distribution of certain species of basidiomycete fungi in the field. However, many of these effects are density-dependent, and too little information is available for quantifying accurately the specific contribution of Collembola to "indirect" or "catalytic" decomposition. Nevertheless, the influence of springtails on decomposition and nutrient availability must be significant in many ecosystems.

FURTHER READING

Further information can be found in the review by Hopkin (20), which contains a list of the most important references on Collembola published before 1996. An up-to-date list of Collembola publications from 1995 onward is available at http://www.ams.rdg.ac.uk/zoology/collembola/. A very detailed Collembola site is maintained by Frans Janssens at http://www.geocities.com/CapeCanaveral/Lab/1300/. This includes a world checklist of species together with identification keys to genus level for most families. Since the publication of Hopkin (20) a number of important monographs have been published that should be consulted for recent developments in taxonomy and biology. These are

- a major revision of the Iberian Collembola by Jordana et al. (21)
- a second edition of the key to North American Collembola by Christiansen and Bellinger (22)
- the first volume of a key to the Nordic Collembola by Fjellberg (23)
- an identification guide to South American Collembola by Heckman (24)
- a review of Collembola found associated with streams and lakes in Europe by Palissa (25).

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