STUDIES OF SOIL FAUNA WITH SPECIAL REFERENCE TO THE COLLEMBOLA

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BY PETER F. BELLINGER[2]

This investigation was carried out with the following objectives in view: (1) to gather information about the composition of the soil fauna in certain local habitats; (2) to compare the fauna in these habitats and draw any conclusions possible about their similarities or differences and about the ecological limitations of the individual species; and (3) to study those phases of the biology of the species on which information could be gained from the analysis of periodic samples taken in the same areas. Particular attention was paid to the Collembola because of their abundance and the relative simplicity of determining specimens.

A considerable number of ecological studies of the fauna of soil and humus have been carried out in Europe in recent years.[3] In this country, however, the subject has received little attention — perhaps because the fundamental taxonomic work has hardly been begun. It must be emphasized that the survey discussed here, which was confined to a very few discrete and distinctive localities, goes only a little way toward remedying this deficiency. We have reason to believe that the animal life of the soil plays a role in its economy which has hardly been appreciated on this side of the Atlantic; the activity of the microfauna is evidently of great importance in the determination of the character and fertility of the organic constituents of the soil. A great amount of work must still be done if we are to reach a satisfactory understanding of the nature of this activity. It is hoped that the results and ideas presented here, however tentative, may stimulate a renewed attack on this neglected aspect of soil biology.

HABITATS STUDIED

An intensive study was made of certain groups of the soil fauna in the following habitats: (1) a pure stand of red pines (*Pinus resinosa* Ait.); (2) a pure stand of white pines (*Pinus strobus* L.); (3) a stand of young white pines in an old field area; (4) an unplanted old field area; and (5) a mixed stand of mature white pines and hemlocks (*Tsuga canadensis* L.). The first four areas are all immediately adjacent on the east shore of Mt. Higby Reservoir in Middlefield, Middlesex County, Connecticut; the last is part of the Cathedral Pines, a grove in Cornwall, Litchfield County, Connecticut.

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[1] This bulletin was taken from a dissertation presented to the Faculty of the Graduate School of Yale University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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[3] No attempt has been made to summarize the literature on soil fauna and ecology of the Collembola; the interested reader is referred to the works of Franz (1950), Maynard (1951), and Salmon (1951) for extensive bibliographies.

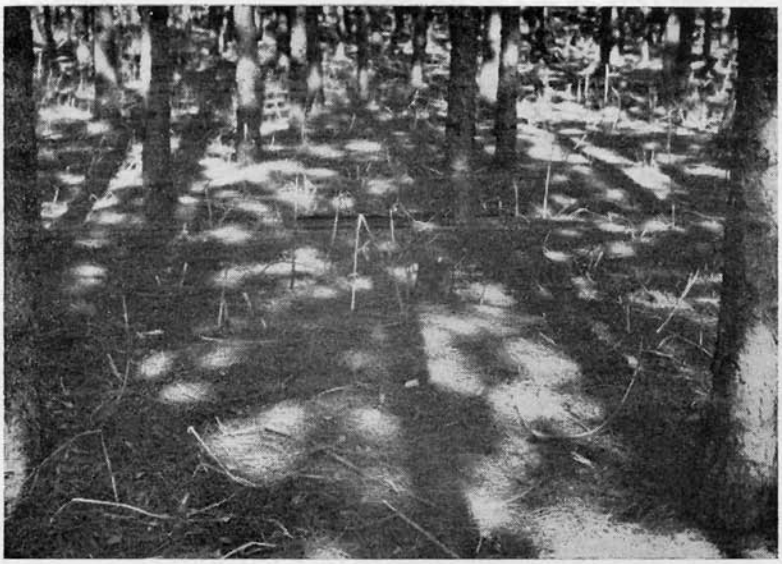

Figure 1. Ground cover in the red pine stand, Area 1. The litter layer consists mainly of the needles of red pine. The upright stalks of the previous summer's growth of pokeweed are conspicuous. Samples were taken in the vicinity of the stump in the center of the picture.
The ground cover in Area 2, white pine stand, was very similar in appearance.

Figure 2. The plantation of young white pines, Area 3. The thin humus under these trees forms islands in the old field area; the vegetation surrounding these islands is similar to that in Area 4 except for the presence of a few young hardwoods. Area 1 is seen in the background.

The areas in Middlefield are on land from which the original vegetation has been completely cleared and, for the most part, replaced with pine plantations. All four have a brown podzolic soil, a loam of the Cheshire series grading toward the Wethersfield series in the lower areas (3 and 4). (These series are defined in Lunt (1948).)

The red pine stand, Area 1, is a planted stand about 35 years old (Figure 1). The trees are in regular rows at intervals of about six feet. A considerable number of trees have been removed and their places in the rows are represented by their decaying stumps. The surface litter is of variable thickness, but averages from one to two inches deep; it consists almost entirely of leaves, twigs, and cones of red pine. There is a heavy growth of poison ivy (*Rhus radicans* L.) in part of the stand. Samples were taken at a point about 20 yards from the nearest edge of the stand (Figure 2). Aside from the pines, the only plant in the immediate collecting area is pokeweed (*Phytolacca americana* L.), which is common but scattered.

Area 2 was just north of Area 1 (Figure 1). It is a pure, planted stand of white pines, also about 35 years old and similarly laid out. Except for the absence of poison ivy and the appearance of the litter, which consists of needles and other fragments of white pine, the two stands are very similar. Samples were taken at points about 20 yards from the nearest edge of the stand.

To the west of the pine stands there is a cleared area extending down to the shore of the reservoir. This area was formerly planted with red pine, but these were all removed when about six feet high in 1935. In 1945 a large part was replanted with young white pines (Figure 2). Aside from these pines, this Area (3) differs from Area 4 in having heavier undergrowth and a number of young deciduous trees, principally *Cornus racemosa* L. Samples were taken in the sparse litter under the young pines.

Area 4 is one of the unplanted parts of this cleared area (Figure 3). It is covered with a heavy growth of grasses, principally red top (*Agrostis alba* L.), bunchgrass (*Andropogon scoparius* Michx.), and Indian grass (*Sorghastrum nutans* (L.)), mixed with low herbs. Samples were taken at various points in this area.

Area 5, in the Cathedral Pines, is situated on a steep hillside facing toward the south and west, at an altitude of 800 to 900 feet in the southeastern part of the Berkshire Hills. It is uncertain whether or not this is a virgin stand, but some of the pines are known to be over 200 years old and the area has probably remained untouched for that length of time at least. The grove consists of very large white pines and hemlocks, the latter being more numerous and a few young, scattered hardwoods (Figure 4). The brown podzolic soil is a bouldery, loamy sand of an undeveloped profile. The bedrock (a metamorphic schistose) is only two or three feet below the surface, with frequent outcroppings. Some physical and chemical characteristics of the soil and humus are given in Table 1. The litter layer here also averages one to two inches in depth, but is somewhat more compact than in the Middlefield stands because of the presence of hemlock needles; the pine needles are the most conspicuous element (Figure 5). The

Figure 3. Ground cover in Area 4. Grasses make up the greater part of the vegetation. An old furrow may be seen at the left of the picture.

Figure 4. The main collecting site in the white pine and hemlock stand, Area 5. Most samples were taken in the hollows to the right of the tree in the left foreground. The outcropping mentioned in the text is out of the picture to the left.

Figure 5. Ground cover in Area 5. Partridgeberry plants, ferns and scattered hardwood leaves may be seen on the surface. Needles of white pine are conspicuous in the litter. Hemlock needles are too small to be seen individually, but a few small twigs bearing needles are visible.

TABLE 1. CHARACTERISTICS OF LITTER, SOIL, AND HUMUS FROM THE SAMPLING AREAS[1]

Layer	Mineral soil				Litter & humus			Upper
Area	1	2	4	5	1	2	5	4
Hygroscopic moisture[2]	3.06	2.17	2.74	2.97	7.56	8.16	8.80	2.69
	2.97	2.27	2.58	2.60	8.81	8.61	9.42	2.36
Organic carbon[2]	8.67	9.24	7.7	12.64	....	....	....	....
	9.96	5.77	6.6	12.80				
Total nitrogen[2]	.36	.23	.36	.39	1.03	1.50	1.31	.35
	.30	.24	.24	.23	1.33	1.31	1.18	.48
Available phosphorus[3]	73	95	13	84	57	72	63	44
	68	101	15	86	51	61	60	54
Layer	Litter	Humus	Mineral Soil	0-1" depth	1-2" depth	2-4" depth		
Area	5	5	5	4	4	4		
pH	3.98	4.06	4.29	4.73	4.52	5.00		
Base capacity[4]	45.4	72.2	25.1	16.9	17.8	16.3		
Water holding capacity[5]	....	....	69.0	58.9	57.3	48.7		

[1] First four determinations run in duplicate, in Soils Laboratory, Yale School of Forestry. Last three carried out by Soils Department, The Connecticut Agricultural Experiment Station.

[2] Given as per cent of oven-dried weight of sample.

[3] Given as parts per million.

[4] Given as milliequivalents per 100 grams air-dry material.

[5] Given as per cent of water-free weight.

only low plants in the main collecting area are small herbs and creepers, of which partridgeberry (*Mitchella repens* L.) is the most conspicuous. Most samples were taken in a hollow behind a large outcropping. This hollow is poorly drained, and in the spring a pool forms in the lowest part (covering several winter sampling sites). One sample (October, 1950) was taken at a point about 20 yards uphill from the others.

PROCEDURE

The areas were sampled periodically from October, 1950, to September, 1951, inclusive. Areas 1 and 2 were sampled every month, the others somewhat less regularly. Normally, two adjacent samples were taken at the same time. Samples from areas 1 and 2 were always taken on the same date, as were those from areas 3 and 4.

Samples were taken by hammering into the ground a metal ring with an area of about 64 square inches and removing the soil and humus within this ring. With the exception of the October samples and a few from later months, each sample was divided into two parts. In the pine stand samples the plane of separation was the dividing line between unincorporated organic matter and true soil. In areas 3 and 4, where no such clear-cut separation is present, the division was more arbitrary but roughly followed the lower limit of the compact masses of grass roots. Soil was collected to a depth of one to several inches below the level of the plane of division; since by far the greater part of the fauna occurs in the uppermost layer, the variation in depth probably had an insignificant effect on the number of organisms collected. The separation served two purposes: it reduced the amount of material to be put in each funnel, and it permitted some analysis of the vertical distribution of individual species.

On most occasions, temperature readings were taken at depths of one and two inches (measured from the surface of the litter layer) and on the surface, using dial soil thermometers. The readings obtained, together with the collection data for each sample, are given in Table 2.

On several occasions the humidity between the litter and soil layers was measured with a soil hygrometer; because of the size of the pick-up unit, it was not possible to take measurements within the thin litter layer. In all cases the atmosphere was found to be saturated, within the limits of accuracy of the instrument. This is probably the normal condition except in the most superficial layer of loose litter, or during periods of extreme drought.

Samples were transported in containers of heavy waxed cardboard. In the laboratory they were weighed, if this could be done immediately, and placed in a separating funnel (Tullgren, 1917). Separation was allowed to proceed for from five to eight days; the fauna was collected in 80 per cent alcohol.

TABLE 2. COLLECTION RECORDS

Date	Centigrade temp. Air	1"	2"	Subdivided	Weight-grams upper	lower	Remarks
Area* 1 — *Red Pine							
Oct. 24, 1950	......	......	......	No	......	......	
				No	......	......	
Nov. 23, 1950	......	......	......	Yes	1140	1520	
				Yes	790	1450	
Dec. 12, 1950	1.2	3.3	4.8	Yes	700	1360	
				Yes	840	1800	
Jan. 30, 1951	-7.8	0	0.5	No	......	......	
				No	......	......	
Feb. 27, 1951	8.3	5.5	4.4	Yes	1450	2420	Count dubious:
				Yes	2040	2270	humus fauna poor
Mar. 27, 1951	9.4	0.5	1.3	Yes	1400	2600	
				Yes	1840	2640	
Apr. 18, 1951	10.0	6.2	5.3	Yes	1090	3120	
May 23, 1951	21.1	17.6	14.8	Yes	470	1400	
				Yes	700	1750	
June 22, 1951	23.3	18.0	15.8	Yes	......	......	
July 20, 1951	20.0	17.0	16.5	Yes	640	2230	
				Yes	640	1740	
Aug 24, 1951	19.0	19.0	18.5	Yes	770	1680	
				Yes	......	......	
Sept. 21, 1951	24.2	19.0	16.8	Yes	620	1430	
				Yes	540	1590	
Area* 2 — *White Pine							
Oct. 24, 1950	......	......	......	No	......	......	
				No	......	......	
Nov. 23, 1950	......	......	......	Yes	910	1740	
				Yes	830	1430	
Dec. 12, 1950	1.2	3.9	5.0	Yes	960	1780	
				Yes	1080	1980	
Jan. 30, 1951	-7.8	0	1.1	No	......	......	
				No	......	......	

TABLE 2. COLLECTION RECORDS (CONT.)

Date	Centigrade temp. Air	1"	2"	Subdivided	Weight-grams upper	lower	Remarks
Feb. 27, 1951	7.8	4.0	2.8	Yes	1390	2520	
				Yes	1800	2400	
Mar. 27, 1951	6.1	1.5	1.3	Yes	1590	1880	Count dubious: humus fauna poor
				Yes	1700	1880	
Apr. 18, 1951	10.0	5.8	5.4	Yes	1220	2400	
				Yes	1500	2120	
May 23, 1951	20.6	15.2	13.0	Yes	560	2580	
				Yes	780	1200	
June 22, 1951	23.9	16.6	15.0	Yes	910	3100	
				Yes	940	2440	
July 10, 1951	19.6	16.2	16.0	Yes	500	1760	Lower layer not counted: mold
				Yes	880	2490	
Aug. 24, 1951	......	......	......	Yes	......	......	
				Yes	......	......	
Sept. 21, 1951	24.5	18.8	16.3	Yes	560	1750	
				Yes	480	1620	
Area 3 — Young White Pines							
Oct. 24, 1950	......	......	......	No	......	......	
	......	......	......	No	......	......	
Dec. 16, 1950	1.0	3.0	3.3	Yes	1200	1440	
				Yes	1380	980	
Feb. 7, 1951	6.5	0	0	No	1810		
				No	2220		
Mar. 7, 1951	11.1	3.2	1.3	Yes	1380	2680	
				Yes	1440	2410	
Apr. 10, 1951	16.1	7.9	7.7	Yes	1030	1750	
				Yes	1250	2280	
June 5, 1951	18.3	15.5	15.0	Yes	1840	1400	Lower layer not counted: mold
				Yes	880	1380	
July 13, 1951	23.5	18.4	18.1	Yes	380	1720	
				Yes	440	1340	
Aug. 3, 1951	21.1	18.8	17.8	Yes	620	1190	
Sept. 15, 1951	28.5	21.0	19.2	Yes	240	1180	

TABLE 2. COLLECTION RECORDS (CONT.)

Date	Centigrade temp. Air	1"	2"	Subdivided	Weight-grams upper	lower	Remarks
Area 4 — Old Field							
Oct. 24, 1950	......	......	......	No	......	......	
				No	......	......	
Dec. 16, 1950	0.5	2.7	2.8	No	2180		
				Yes	2020	1340	
Feb. 7, 1951	......	......	......	No	1680		Sample not counted: mold
Mar. 7, 1951	11.1	2.0	......	Yes	1470	2380	
				Yes	1980	3080	
Apr. 10, 1951	16.6	12.4	10.5	Yes	1980	2220	
				Yes	1850	1910	
June 5, 1951	19.2	17.0	16.5	Yes	1440	2480	
				Yes	1240	2340	
July 13, 1951	23.5	25.0	24.1	Yes	800	1360	Lower layer not
				Yes	600	1900	counted: mold
Aug. 3, 1951	21.1	21.0	22.0	Yes	1040	2060	
				Yes	1220	1860	
Sept. 15, 1951	28.0	23.6	21.2	Yes	800	2260	Lower layer not
				Yes	1390	1520	counted: mold
Area 5 — White Pine and Hemlock							
Oct. 31, 1950	......	......	......	No	......	......	
Dec. 19, 1950	-6.1	0	1.5	Yes	1000	1900	
	-6.1	0.8	2.2	Yes	960	900	
Jan. 30, 1951	-9.6	0	1.5	Yes	......	......	Count dubious:
				Yes	......	......	humus fauna poor.
Feb. 13, 1951	5.6	0	0.2	Yes	1160	1890	
Apr. 3, 1951	2.0	3.0	3.5	Yes	1200	3300	Count incom-
				Yes	1120	1980	plete: too much soil
May 16, 1951	25.6	12.9	9.4	Yes	840	2020	
				Yes	790	1630	
June 13, 1951	13.9	12.4	10.1	Yes	655	1650	
				Yes	850	2100	
July 27, 1951	23.9	18.3	16.0	Yes	590	1580	
Aug. 31, 1951	24.4	18.8	17.0	Yes	580	1840	
				Yes	710	1200	
Sept. 28, 1951	13.3	12.0	12.3	Yes	......	......	

Not all the samples collected could be counted. A few containers with loosely fitting lids lost alcohol by evaporation and developed a growth of mold which obscured the animals. In other cases so much debris came through the funnel that the animals could not be sorted out. Finally, several samples appear to be deficient for unknown causes; the number of animals collected was so small either in comparison to the other sample of the pair or in relation to the number in the other part of the same sample that some artificial obstruction to the operation of the funnel is suspected.

Counting was done under a binocular dissecting microscope. The animals were picked up with forceps or a fine pipette and sorted into one-dram vials. Collembola were counted, so far as possible, by species. Insects were sorted to the smallest readily recognizable group, usually to order or family. Other arthropods were sorted to class only.

For the determination of species of Collembola, specimens were mounted in Salmon's (1949) polyvinyl alcohol-lactophenol medium or were cleared and expanded in warm lactic acid, and were then studied under a compound microscope. These procedures were followed with the majority of specimens at the beginning of the study; thereafter, increasing familiarity with the fauna permitted determination of most specimens under the dissecting microscope.

THE FAUNA[1]

The distribution and some phases of the biology of the Collembola, particularly, and of some other groups will be discussed in the following sections. Certain of the determinations, however, need qualification, and the occurrence of some groups which could not be determined should be mentioned.

The Collembola were determined by the author; the assistance of Dr. H. B. Mills and Dr. K. A. Christiansen has been invaluable, but it has not been possible to refer to them more than a very small part of the collections, and the responsibility for any errors committed cannot lie with them. The classification employed here follows that given by Salmon (1951) to the generic level, with a few exceptions (e. g. the use of *Onychiurus* and *Anurida* in the broad sense).

The names used for some of the species are tentative; exact determinations will not be possible until the American fauna is better understood. These include *Anurida granaria, Pseudachorutes subcrassoides, Folsomia fimetaria, F. multiseta,*

[1] The original tables giving the distribution of the Collembola and other Arthropods by months, and sub-samples have been bound and filed at The Connecticut Agricultural Experiment Station, and in Sterling and Osborne Zoological libraries of Yale University. The Connecticut Agricultural Experiment Station copy is available on a library loan basis to anyone desiring to study the detailed data.

Lepidocyrtus cyaneus, L. pusillus, L. curvicollis, Sminthurinus aureus, S. brunneus, S. similitortus. The Neelidae, for the most part, and young specimens of such genera as *Entomobrya* and *Sminthurinus* were not determined beyond genus. In a few cases (*Mesaphorura, Xenylla,* small white isotomids) the possibility of error in the identification of some young specimens exists.

In other cases in which identification has been made only to genus, the individuals concerned almost certainly represent undescribed species. This is true of the specimens so listed in *Friesea, Odontella, Spinisotoma, Sminthurus,* and perhaps *Neosminthurus,* as well as of the two additional types of Isotomidae with anal spines. Sufficient material of these species was not available to permit their description.

An attempt is made, in the following pages, to present a key suitable for the determination of Collembola from situations similar to those studied here. Since samples from other localities would almost certainly include some additional species, the key has been expanded, so far as possible, to include all genera known from eastern North America, except a few which are purely aquatic or littoral. On the other hand, it has not seemed advisable to include species other than those taken, unless it has been possible to study material and unless the species is one which is likely to occur. However, the key is set up, so far as possible, so that species not mentioned will clearly not fit and will be recognized as something different. Couplets in parentheses run to species or genera not certainly found in the present study. For reasons mentioned above, the species of *Entomobrya* and *Sminthurinus,* and the genera of Neelidae, are not run out.

The key is, to a certain extent, a compilation from the works of Stach, Folsom, Gisin, Maynard, Mills, and Salmon. Every effort has been made, however, to simplify determinations by selecting the most clear-cut characters, and as far as the species actually collected are concerned, personal study of the specimens is the foundation.

The terms used in the key may be found in any general work on the Collembola; in a few cases obscure terms have been defined. Examination of the figures in any of the works listed at the beginning of this section will assist materially in running down specimens. Maynard's (1951) extensive and well illustrated work should be particularly useful.

It should be noted that, while the key is adequate for the determination of genera in almost every case, many young individuals will not run to species even if the species is included here. If the specimen possesses a distinct genital plate (to be seen on the posterior border of the fifth abdominal sternite in adult specimens), and still will not run, it is probably not included. In a very few cases young individuals will not run even to genus. The most notable cases are in the Isotomidae; the ventral setae on the manubrium are never numerous in first instar specimens, so very young *Isotoma* are likely to be misplaced in *Proisotoma. I. eunotabilis* is particularly likely to be misidentified, since very young specimens may appear to have only one or two eyes; fortunately this is a very common species, and mature specimens should always be found with the immatures.

For the identification of the specimens on which this key is based, the following papers were employed: Folsom (1913, 1916, 1917, 1937); Gisin (1944); Handschin (1929); Maynard (1951); Mills (1934); Salmon (1951); Stach (1947, 1949a, 1949b, 1951).

Key to the Collembola

1 Body elongate and cylindrical or depressed; at least six body segments distinctly separate; head prognathous, antennae attached anteriorly (in these species); suborder ARTHROPLEONA 2

Body globular; segmental boundaries for the most part obscure; head hypognathous, antennae attached dorsally; suborder SYMPHYPLEONA 57

2 First thoracic tergite well developed, bearing setae; tergites not imbricate; furca, when present, clearly arising from fourth abdominal segment; family HYPOGASTRURIDAE 3

First thoracic tergite reduced, without setae, partly fused with second; tergites usually imbricate; furca, when present, usually appearing to arise from fifth abdominal segment; superfamily ENTOMOBRYOIDEA 22

3 Pseudocelli present; sense organ of third antennal segment complex; postantennal organ usually elongate, with many papillae; mandibles with molar plate;[1] furca absent or rudimentary (in American species); eyes absent, color white; subfamily ONYCHIURINAE 4

Pseudocelli absent; sense organ of third antennal segment with only two small sense clubs and no protective papillae; post-antennal organ usually round or oval, sometimes absent; mandibles with or without molar plate; furca and eyes present or absent; usually pigmented 5

4 Unguiculus absent; sense organ of third antennal segment with two sense clubs bending towards each other.............. genus *Mesaphorura* Boerner (1901)

[1] The mouth parts can usually be seen in specimens cleared in warm lactic acid or mounted in Salmon's fluid.

a Fifth abdominal segment with two dorso-lateral spines overhanging the posterior edge .... *M. iowensis* Mills (1934)

No such spines present .... b

b Tubercles of postantennal organ in four rows .... *M. collis* Bacon (1914)

Tubercles of postantennal organ in two rows c

c Sixth abdominal segment with coarse tubercles .... *M. granulata* Mills (1934)

This segment finely tuberculate .... *M. clavata* Mills (1934)

Unguiculus present; sense clubs in sense organ of third antennal segment parallel .... genus *Onychiurus* Gervais (1891)

a Tubercles of postantennal organ irregularly lobed; anal spines absent; unguiculus without lamella .... *O. fimetarius* L. (1707)

Tubercles of postantennal organ smooth .... b

b Tubercles of postantennal organ parallel to its long axis c

Tubercles perpendicular to long axis .... d

c One pseudocellus on antennal base .... *O. sibiricus* Tullberg (1876)

Two-three pseudocelli on antennal base .... *O. subtenuis* Folsom (1917)

d Unguiculus 2/3 length of claw or more; three-four pairs of pseudocelli on posterior border of head, none on first thoracic segment .... *O. armatus* Tullberg (1869)

Unguiculus 1/3-2/3 length of claw; two pairs of pseudocelli on posterior border of head, two pairs on first thoracic segment .... *O. parvicornis* Mills (1934)

5 Mandibles present, with well-developed, ridged molar plate; subfamily HYPOGASTRURINAE 6

Mandibles without ridged molar plate, sometimes absent 10

6 Furca, eyes, and pigment present 7

Furca, eyes, and pigment absent; postantennal organ with four or five tubercles in a circle; fourth antennal segment with two cylindrical sense hairs .... *Willemia intermedia* Mills (1934)

7 Postantennal organ absent; five eyes on each side .... genus *Xenylla* Tullberg (1869)

a Dens and mucro confluent .... b

Dens and mucro distinctly separate; mucro straight with narrow lamella .... *X. humiçola* Fabricius (1790) b Mucro hooked, with short lamella .... *X. grisea* Axelson (1900)

Postantennal organ present; eight eyes on each side 8

8 Postantennal organ a single four-lobed tubercle; unguiculus minute or absent .... genus *Schoettella* Schaeffer (1896)

a Unguiculus absent; four dorsal clavate hairs on tibiotarsus .... *S. ununguiculata* Tullberg (1869)

Unguiculus present, minute; two dorsal clavate hairs on tibiotarsus .... *S. glasgowi* Folsom (1916)

Postantennal organ with four-five separate tubercles; unguiculus distinct 9

9 An eversible sac present between third and fourth antennal segments (not always visible) .... *Ceratophysella armata* Nicolet (1841)

Eversible sac absent .... genus *Hypogastrura* Bourlet (1839)

a Dentes dorsally with conical spines; anal spines much shorter than claw .... *H. nivicola* Fitch (1846)

Dentes without spines .... b

b Three clavate tenent hairs in a transverse line on tibiotarsus; mucro with ventral edge straight and not upturned apically; anal spines less than 1/2 as long as claw, curved .... *H. humi* Folsom (1916)

At most one clavate tenent hair on tibiotarsus c

c Unguiculus without lamella; dentes more coarsely granulate than manubrium; anal spines less than 1/2 length of hind claw; color blue .... *H. manubrialis* Tullberg (1869)

Unguiculus with distinct basal lamella .... d

d Tenent hair not clavate .... e

Tenent hair clavate; body setae normally serrate and capitate; anal spines as long as claw .... *H. packardi* Folsom (1902)

e Anal spines 1/2 length of hind claw; pale with scattered dark mottling .... *H. montana* Maynard (1951)

Anal spines relatively longer .... *Ceratophysella armata* Nicolet (1841)

10 Furca present, unless mandible is sickle-shaped 11

Furca absent, mandible without molar area, toothed 17

11 Mandible with smooth molar area, or sickle-shaped without teeth or molar area, or absent; anal spines and unguiculus present or absent; subfamily BRACHYSTOMELLINAE 12

Mandibles present, apically toothed, without molar area; anal spines absent (in our species); unguiculus absent; subfamily PSEUDACHORUTINAE .... genus *Pseudachorutes* Tullberg (1871)

a Tibiotarsus with one tenent hair; 5-10 tubercles in postantennal organ .... *P. corticicolus* Schaeffer (1846)

Tenent hair absent; 9-12 tubercles in postantennal organ .... *P. subcrassoides* Mills (1934)

12 Mandibles present 13

Mandibles absent 14

13 Mandibles with basal, smooth molar area and apical teeth; anal spines absent; unguiculus present; six eyes on each side .... *Microgastrura minutissima* Mills (1934)

Mandibles without molar area, sickle-shaped without apical teeth; three or more anal spines present (in our species); unguiculus absent .... genus *Friesea* Dalla Torre (1895)

a Eight eyes on each side; furca present, somewhat reduced; three anal spines; blue .... *F. mirabilis* Tullberg (1871)

Eyes absent; furca absent; 5-7 anal spines; white .... *F.* sp. undet.

14 Mucro not lobed 15

Mucro with two diagonal pocket-like lobes 16

15 Anal spines absent; eight eyes on each side; unguiculus absent; pigmented; postantennal organ with four lobes .... *Brachystomella stachi* Mills (1934)

Anal spines present; eyes reduced in number; unguiculus bristle-like; unpigmented .... genus *Xenyllodes* Axelson (1903)

16 Head, legs, and dentes with strong spines .... genus *Superodontella* Stach (1949)

Without such spines .... genus *Odontella* Schaeffer (1897)

17 Sixth abdominal segment bilobed; subfamily NEANURINAE 18

Sixth abdominal segment rounded; subfamily ANURIDINAE 20

18 Sixth abdominal segment clearly visible in dorsal view; three eyes on each side; color blue .... *Neanura muscorum* Templeton (1835)

Sixth abdominal segment hidden under fifth 19

19 Fifth abdominal segment with two tubercles .... genus *Bilobella* Stach (1950)

Fifth abdominal segment with three tubercles .... genus *Lathriopyga* Caroli (1910)

20 Postantennal organ present 21

Postantennal organ absent .... genus *Paranura* Axelson (1902)

21 Head of maxilla toothed, with lateral lamellae; eyes absent; white; postantennal organ with 9-25 tubercles .... *Anurida granaria* Nicolet (1847)

Head of maxilla needle-like, without lamella; postantennal organ with 5-11 tubercles (in our species) .... genus *Micranurida* Boerner (1901)

a Two eyes on each side; white or blue .... *M. pygmaea* Boerner (1901)

Eyes absent; white; rudiment of furca present as a single lobe .... *M. furcifera* Mills (1934)

22 Setae simple, serrate, or feathered, not brush-like (except *Metisotoma*); scales absent; the last two or three abdominal segments sometimes fused; abdominal segments not strikingly different in length; furca sometimes reduced; antennae with four simple segments; postantennal organ usually present; family ISOTOMIDAE 23

Scales and/or brush-like setae present; abdominal segments always distinct, the third or fourth sometimes elongate; furca always well developed; antennae sometimes ringed or with extra segments; postantennal organ absent 47

23 With spines dorsally on the last abdominal segments 24

Without such spines 26

24 Furca very short; mucro bidentate or absent; anus ventral; four long anal spines on papillae .... genus *Tetracanthella* Schoett (1891)

Furca longer, well developed; mucro at least tridentate; anus terminal 25

25 Anal spines short, on low papillae which are confluent and form a yellow wrinkled area on the posterior dorsal part of the abdomen (males only; females will run out in couplet 42) .... *Spinisotoma* sp.

Anal spines elongate, on high papillae which are separate and not distinct in color .... (probably two undescribed genera)

26 Furca absent 27

Furca present, distinct 28

27 Eight eyes on each side; well pigmented .... *Anurophorus laricis* Nicolet (1841)

Only one eye on each side; white with scattered dark granules .... *Pseudanurophorus binoculatus* Kseneman (1934)

28 Fourth abdominal segment fused with fifth and sixth 29

Fourth abdominal segment not fused with fifth 30

29 Postantennal organ absent; mucro falcate .... *Folsomina onychiurina* Denis (1931)

Postantennal organ present; mucro with at least two teeth (two only in these species) .... genus *Folsomia* Willem (1902)

a Eyes and pigment absent; dens longer than manubrium; manubrium ventrally on each side with a row of three setae, followed by two more in line with the middle one .... *F. fimetaria* L. (1758)

Two eyes on each side, body weakly pigmented; manubrium ventrally with numerous setae .... *F. multiseta* Stach (1947)

30 Fourth abdominal segment a simple ring like the preceding ones, the furca clearly attached to it; body elongate; prothorax well developed for the family; eyes and pigment reduced 31

Fourth abdominal segment not a simple ring; furca appears to arise from the fifth segment 32

31 Fifth and sixth abdominal segments fused and shortened; eyes absent; mucro clearly separate from dens; (in this species) manubrium ventrally with two pairs of setae, body weakly pigmented .... *Isotomodes tenuis* Folsom (1934)

Fifth and sixth abdominal segments not fused; mucro not distinctly separate from dens; two widely separated eyes on each side (in this species) .... *Folsomides parvus* Folsom (1937)

32 Tergites imbricate (in unexpanded specimens); segments not bulging; prothorax reduced 33

Tergites not imbricate; intersegmental constrictions deep; prothorax well developed for the family .... genus *Guthriella* Boerner (1906)

33 Eyes and pigment entirely absent 34

Eyes present (in our species), sometimes reduced in number; pigment usually present 35

Postantennal organ absent; mucro tridentate .... *Isotomiella minor* Schaeffer (1896)

Postantennal organ present, with thick walls divided into quadrants; mucro bidentate .... *Micrisotoma achromata* Bellinger (1952)

35 Dentes without spines 37

Dentes dorsally with two rows of spines 36

36 One spine on manubrium (in our species); mucro quadridentate .... genus *Tomocerura* Wahlgren (1900)

Manubrium without spines; mucro tridentate (synonym of last?) .... genus *Semicerura* Maynard (1951)

37 Two pairs of bothriotricha (long, very fine setae) on the second, third, and fourth abdominal tergites; (in our species) mucro without ventral lamella, common body setae not serrate .... *Isotomurus palustris* Mueller (1776)

Bothriotricha absent 38

38 Dens without bladder-like appendage 39

Dens with a transparent bladder-like appendage overlapping mucro .... genus *Appendisotoma* Stach (1947)

39 Postantennal organ normal, thin-walled 40

Postantennal organ with thick, irregularly divided margin .... genus *Heteroisotoma* Stach (1947)

40 Claw without a tunica 41

Claw with a tunica (dorsal membrane connecting the lateral teeth) .... genus *Agrenia* Boerner (1906)

41 Manubrium ventrally with many setae 42

Manubrium ventrally with at most two pairs of setae 44

42 Tibiotarsus with one to three clavate tenent hairs 43

Tibiotarsus without tenent hairs .... genus *Isotoma* Bourlet (1839)

a Four eyes on each side; mucro tridentate .... *I. eunotabilis* Folsom (1937)

Eight eyes on each side; mucro quadridentate, without lamellae, with apical tooth much smaller than anteapical; head shorter than thorax .... b

b Apical tooth of mucro bent up; gray-blue (females only; males will run out in couplet 25) .... *Spinisotoma* sp.

Apical tooth of mucro straight; purple or black (variety without tenent hairs) .... *Vertagopus arborea* L. (1758)

43 Fifth and sixth abdominal segments ankylosed .... *Pseudisotoma sensibilis* Tullberg (1876)

Fifth and sixth abdominal segments not ankylosed .... genus *Vertagopus* Boerner (1906)

a Furca longer than antennae; apical tooth of mucro straight .... *V. arborea* L. (1758)

Furca shorter than antennae; apical tooth of mucro bent up; mainly corticicole .... *V. cinerea* Nicolet (1841)

44 Head not unusually large 45

Head unusually large, broader than body .... genus *Metisotoma* Maynard (1951)

45 Dentes dorsally lobed or crenulate, or shorter than manubrium; mucro of various forms, not boat-shaped 46

Dentes longer than manubrium, dorsally smooth; mucro boat-shaped, lamellate, bidentate........ genus *Ballistura* Boerner (1906)

46 Dentes crenulate or not, variable in length; fifth and sixth abdominal segments separate; (in this species) dentes short, dorsally weakly lobed; five eyes on each side, pigment absent except for eye patches .... *Proisotoma minima* Absolon (1900)

Dentes longer than manubrium, dorsally crenulate; fifth and sixth abdominal segments fused........ genus *Isotomina* Boerner (1903)

47 Mucro hairy; dentes two-segmented; third abdominal segment longer than fourth; family TOMOCERIDAE........ genus *Tomocerus* Nicolet (1841)

a Two large dental spines at posterior end of series, and intermediate spines all smaller; antennae shorter than body; body color (without scales) pale .... *T. flavescens* Tullberg (1871)

One large dental spine at end of series, and one large spine in middle; mucro without lamella between apical and proximal teeth; anal spines not tridentate .... b

b Unguis with two inner teeth; maxilla with tuft of hairs .... *T. bidentatus* Folsom (1913)

Unguis with four-six inner teeth; maxilla without tuft of hairs .... *T. vulgaris* Tullberg (1871)

Mucro without hair; dentes one-segmented; fourth abdominal segment at least as long as third; family ENTOMOBRYIDAE 48

48 Dentes dorsally smooth; mucro bidentate, with elongate shaft; pigment and eyes absent; apparently found only with ants; subfamily CYPHODERINAE........ *Cyphoderus assimilis* Boerner (1906)

Dentes dorsally crenulate; mucro short, falcate or bidentate with basal spine; subfamily ENTOMOBRYINAE 49

49 Body scaled 50

Body without scales 53

50 Eight eyes on each side, or claw with large winglike paramedian teeth 51

One eye on each side; teeth of claw small; antennae five-segmented in adult; tribe ORCHESELLINI, part .... *Ptenura nitida* Templeton (1835)

51 Body scales pointed, ribbed; dentes not scaled .... genus *Willowsia* Shoebotham (1917)

a Body banded and laterally striped with purple .... *W. platani* Nicolet (1841)

Body solid purple, or yellow with purple bands only; head yellow .... *W. buski* Lubbock (1869)

Body scales rounded, striate; dentes ventrally scaled (fresh specimens) 52

52 Claw with large winglike paramedian teeth; eyes usually reduced in number; pigment usually absent .... genus *Pseudosinella* Schaeffer (1897)

a Eyes (normally) two on each side of head; unguiculus untoothed; antennae 1¼ length of head .... *P. alba* Packard (1873)

Eyes absent; unguiculus with outer winglike tooth; antennae 1½ length of head; claw with median tooth .... *P. petterseni* Boerner (1901)

Teeth of claw small; eight eyes on each side; sometimes well pigmented .... genus *Lepidocyrtus* Bourlet (1839)

a Ground color white, with or without small amounts of purple pigment .... b

Ground color dark, or banded with gray or blue c

b Second thoracic tergite projects beyond the head .... *L. curvicollis* Bourlet (1839)

Second thoracic tergite not so developed .... *L. cyaneus* (pale form) Tullberg (1871)

c Second thoracic tergite projects beyond the head .... *L. christianseni* Goto (1953)

Second thoracic tergite not so developed .... d

d Color solid purple, not in fine flecks .... *L. pusillus* L. (1767)

Color blue or gray, solid or in bands .... *L. cyaneus* Tullberg (1871)

53 Claw with winglike paramedian teeth; eyes absent (in this species) .... *Sinella coeca* Schoett (1896)

Teeth of claw small 54

54 Mucro falcate .... genus *Drepanura* Schoett (1891)

Mucro bidentate 55

55 Antennae four-segmented; fourth abdominal segment more than twice as long as third 56

Antennae, in adults, five or six-segmented; fourth abdominal segment about twice as long as third; tribe ORCHESELLINI, part .... genus *Orchesella* Templeton (1835)

a Body with six transverse purple bands on a pale ground .... *O. hexfasciata* Harvey (1895)

Body dark, or light with a heavy transverse band on the third abdominal segment; head dark .... *O. cincta* L. (1758)

56 Eyes on dark eye patches .... genus *Entomobrya* Rondani (1861)

No dark eye patches; body completely pale .... genus *Isotobryoides* Maynard (1951)

57 Thorax larger than abdomen; dentes two-segmented; antennae shorter than head; eyes absent; minute species .... family NEELIDAE

Thorax reduced; dentes one-segmented; antennae longer than head; eyes always present, sometimes (*Arrhopalites*) unpigmented; usually larger species; family SMINTHURIDAE 58

58 Third antennal segment longer than fourth; subfamily DICYRTOMINAE 59

Fourth antennal segment the longest 61

59 Claw without a tunica 60

Claw with a tunica; antennae not subsegmented .... genus *Dicyrtomina* Boerner (1903)

60 Antennae subsegmented; tibiotarsus of third leg with serrate setae; this species evenly colored .... *Ptenothrix unicolor* Harvey (1893)

Antennae not subsegmented; tibiotarsus without serrate setae .... genus *Dicyrtoma* Bourlet (1842)

61 Sacs of ventral tube smooth (except *Neosminthurus*); integument granulate; segmentation of thorax usually indicated; fourth antennal segment with no more than five subsegments (except *Katiannina* and some *Sminthurides*); subfamily SMINTHURIDINAE 62

Sacs of ventral tube tuberculate or wrinkled (in adults); integument smooth; segmentation of thorax obsolete; fourth antennal segment with at least six subsegments, sometimes with 15-20; subfamily SMINTHURINAE 68

62 Genital and anal segments separate, the former bearing one pair of bothriotricha; antennae of male not modified; female with anal appendages (ventral, curved, sometimes branched spines) tribe KATIANNINI 65

Genital and anal segments ankylosed, bearing two pairs of bothriotricha; antennae of male modified for clasping; female without anal appendages; tribe SMINTHURIDINI .... genus *Sminthurides* Boerner (1900) 63

63 Tibiotarsal organ (large bristle and two pegs) present on tibiotarsus of third leg 64

Tibiotarsal organ absent; this species with serrate setae on tibiotarsus of third leg .... S. (*Sphaeridia*) *serratus* Folsom & Mills (1938)

64 Mucro ribbed or expanded at tip .... subgenus *Sminthurides* s. str.

a Tip of mucro bulbous; ventral lamella ending in a tooth .... S. (*Sminthurides*) *lepus* Mills (1934)

b Mucro tapering, with ribbed edges, 1/3 as broad as long; fourth antennal segment of female not ringed or subdivided .... S. (*Sminthurides*) *malmgreni* Tullberg (1876)

Mucro tapering, not ribbed.................subgenus *Stenacidia* Boerner (1906)

65 Eyes not reduced; dentes without spines; tenent hairs usually present 66

Eyes reduced to one on each side; tenent hairs absent; dentes usually with spines..............................genus *Arrhopalites* Boerner (1906)

a Fourth antennal segment subsegmented .... b

Fourth antennal segment not subsegmented .... *A. diversus* Mills (1934)

b Dentes with spines; generally well pigmented, eyespot black .... *A. binoculatus* Boerner (1901)

Dentes without spines; white, eyespot not pigmented .... *A. coecus* Tullberg (1871)

66 Fourth antennal segment not subsegmented 67

Fourth antennal segment subsegmented ....genus *Katiannina* Boerner (1906)

67 Sacs of ventral tube tuberculate in adult; claw with a strong tunica .... *Neosminthurus* sp.

Sacs of ventral tube smooth; claw generally without a tunica; body setae simple .... genus *Sminthurinus* Boerner (1901)

68 With clavate tenent hairs which parallel tibiotarsus; tribe BOURLETIELLINI 69

Tenent hairs, if present, outstanding; tribe SMINTHURINI 70

69 Male with clasping organ of hooks and spines dorsally on sixth abdominal segment; this species dark brownish-blue to black .... *Bourletiella hortensis* Fitch (1863)

Clasping organ absent (or male unknown) ....genus *Deuterosminthurus* Boerner (1901)

70 Fourth antennal segment with 16 or more subsegments; (this species) claw with a tunica, tenent hairs absent, mucro with seta and inner edge only serrate, color pale yellow or greenish .... *Sminthurus fitchi* Folsom (1896)

Fourth antennal segment with less than 16 subsegments ....genus *Sphyrotheca* Boerner (1906)

Other Arthropods

The Acarina were by far the most numerous animals in almost all samples. Since they made up from 70 to more than 90 per cent of the total fauna, they probably are the most important group in the soil and humus from a biological point of view. In the present study it was not possible to do more than count (or, in the case of the richer samples, estimate) their numbers, without making any distinction between species. The material is at present being worked up, and will, we hope, be discussed in a later paper. For the present, only the total numbers are recorded (Table 3).

In most cases the numbers of other Arthropods are too small to permit an analysis of their distribution in the various areas. The exceptions will be discussed in later sections.

ANALYSIS

The present section is devoted almost entirely to the Collembola. The reason for this limitation is that, with the sample size used, most groups of arthropods are not collected in large enough numbers or with great enough regularity to permit more than the most superficial analysis of their distribution. The two main exceptions are the Collembola and Acarina, which are present in all the samples studied; as noted in the last section, it was impossible to determine the Acarina, and since even closely related species may differ conspicuously in their distribution (as the data on Collembola clearly show), it is not advisable to place any reliance on a study of the population differences of the mite fauna as a whole. Supporting information from other groups of arthropods will be given here when it seems desirable to do so.

Table 3. Numbers of Acarina

	Area 1		Area 2		Area 3		Area 4		Area 5	
Oct.	720	1430	2020	2300	1220	950	440	175	821	......
Nov.	3420[1] / 200	6170 / 260	55000 / 2130	9500 / 260	......[2]	......	......	......	......	......
Dec.	350 / 300	2210 / 90	1610 / 140	620 / 40	630 / 50	770 / 30	790	850 / 2640	10340 / 620	2530 / 470
Jan.	220	1310	220	1030	......	......	......	......	380 / 20	20[3] / 30
Feb.	110[3] / 520	740 / 230	820 / 30	7390 / 60	3390	830	......	......	1900 / 200	......
Mar.	1750 / 110	430 / 20	10[3] / 590	3930 / 180	4320 / 30	6310 / 250	3990 / 50	3560 / 160	......	......
Apr.	4100 / 120	......	725 / 100	2000 / 130	6290 / 1150	2580 / 100	2180 / 100	350 / 560	4740 / 20	385[3] / 430
May	5425 / 525	13000 / 200	6900 / 80	9700 / 50	......	......	......	......	2450 / 145	4150 / 110
June	6450 / 185	......	12100 / 50	......	5175 / 100	3400 /	3200 / 5	3125 / 15	3275 /	1530 / 80
July	9800 / 100	7200 / 100	5500 /	950	4500	5850	2175	1250	5250	......
Aug.	9200 / 100	7700 / 300	13400 / 100	11700 / 100	5975 / 200	......	7300 / 1400	4300 / 1300	8800 / 700	8000 / 500
Sept.	5800 / 500	5000 / 300	15000 / 400	17600 / 170	1710 / 200	......	......	4000 / 800	1500 / 75	......
Mean[4]	4570		8365		3540		3000		4700	

[1] Upper and lower layers.

[2] Indicates no sample taken, or mites not counted.

[3] Count open to suspicion (see Table 2).

[4] Excluding dubious counts.

Differences and Similarities Between Areas

Methods of Analysis

It was clear from a preliminary examination of the tables that some species, at least, differed in their abundance in different areas. The interpretation of this fact was, however, obscured by the irregularity of occurrence even within one area, which could be seen by comparing almost any two samples taken on the same date in the same place. It appeared that the distribution of the soil fauna was far from uniform; an observation to this effect was made by Glasgow (1939) who found that the populations of four species of Onychiuridae occurred in the soil in definite colonies whose size was characteristic of the species. The causes of this irregularity are not well understood; local differences in the composition of the substrate may account for it in part, but there also seems to be a tendency toward hyperdispersion or "clumping" of organisms even in a homogenous environment.

With the small number of samples available, the uncertainties introduced by these local variations in fauna, by the effects of seasonal differences, and by suspicions of error in operation of the funnels in some cases complicate the analysis of the results. Although no detailed statistical analysis is attempted here, certain methods have been employed to bring out the extent of the differences in the fauna of the areas. These techniques are used more for the purpose of clarification than to provide mathematical proof of the conclusions to be drawn.

The regularity of occurrence of a species in a given area may be expressed as a "frequency number" equal to the per cent of the samples from that area in which the species occurs, as has been done by Agrell (1941) and others. Frequency numbers for the species of Collembola are given in Table 4. It should be noted that these numbers are not strictly comparable from one species to another, because some species are found at certain times of the year only (see below, under seasonal variation). It seems reasonable to assume, however, that the frequency numbers give an indication of the relative regularity of occurrence of the same species in different areas.

A further method of comparison of the same species in two areas is to compare the numbers of specimens observed in two areas on corresponding collection dates. The significance can be interpreted by the $X^2 = \frac{(a-b)^2}{a+b}$,
where *a* is the number of cases in which the species occurs in greater numbers in the first area, and *b* is the number of cases in which the reverse is true. The resulting value of X^2 is significant at the .05 level if it exceeds 3.84; this implies that the numbers of the species are actually greater

TABLE 4. FREQUENCY NUMBERS OF COLLEMBOLA

Per Cent of Samples from Each Area in Which the Species Occurs	Area 1	Area 2	Area 3	Area 4	Area 5
Ceratophysella armata	....	4	6	6	94
Hypogastrura humi	....	....	....	....	6
H. montana	....	....	....	....	6
H. nivicola	....	....	....	6	....
Schoettella ununguiculata	50	83	56	19	....
Xenylla grisea	9	....	....	....	....
X. maritima	9	....	....	....	....
Willemia intermedia	14	96	6	13	81
Microgastrura minutissima	5	....	....	13	....
Friesea mirabilis	64	83	75	56	38
F. (Polyacanthella) sp.	....	....	....	....	6
Brachystomella stachi	....	....	31	63	....
Odontella spp.	....	13	....	....	6
Pseudachorutes subcrassoides	59	43	69	63	63
P. corticicolus	5	....	....	....	....
Anurida granaria	....	....	....	....	19
Micranurida pygmaea	32	48	50	13	75
M. furcifera	....	....	....	....	6
Neanura muscorum	100	61	19	13	63
Onychiurus subtenuis	....	....	....	....	63
O. sibiricus	32	57	44	44	88
O. armatus	....	....	....	....	31
O. parvicornis	86	91	19	6	88
O. fimetarius	....	....	....	....	19
Mesaphorura collis	....	....	6	25	6
M. granulata	36	52	88	81	81
M. iowensis	64	65	50	50	100
Folsomides parvus	....	....	....	13	....
Isotomodes tenuis	....	....	....	....	69
Anurophorus laricis	....	....	6	13	....
Pseudanurophorus binoculatus	....	....	....	....	19
Folsomia fimetaria	100	83	75	63	94
F. multiseta	....	....	....	....	13
Folsomina onychiurina	....	....	56	75	6
Proisotoma americana	32	4	6	12	38
Isotomiella minor	50	57	6	50	81
Micrisotoma achromata	....	....	....	....	50
Vertagopus arborea	....	....	....	....	81
Spinisotoma sp.	....	....	....	....	50

TABLE 4. FREQUENCY NUMBERS OF COLLEMBOLA (CONT.)

Per Cent of Samples from Each Area in Which the Species Occurs	Area 1	Area 2	Area 3	Area 4	Area 5
Isotoma eunotabilis	100	91	75	75	100
Isotomurus palustris	....	....	....	6	....
Isotomid with anal spines (A)	....	....	....	....	13
Isotomid with anal spines (B)	....	....	....	13	....
Tomocerus flavescens	32	9	94	13	50
Entomobrya nivalis (incl. young)	41	70	94	88	31
E. griseoolivata	9	4	6	....	13
E. atrocincta	....	....	....	....	6
Willowsia platani	....	4	....	....	6
Sinella caeca	....	....	....	....	6
Lepidocyrtus cyaneus	14	83	88	88	25
L. curvicollis	....	....	....	....	25
L. pusillus	....	....	....	....	13
Pseudosinella alba	73	65	....	....	13
P. petterseni	....	....	38	38	....
Orchesella hexfasciata	....	....	....	....	63
Sminthurides lepus	....	....	13	31	38
S. malmgreni?	5	....	....	....	6
Sphaeridia serratus	23	22	....	....	19
Arrhopalites binoculatus	....	....	....	....	38
A. spp. - young	5	4	6	....	13
Sminthurinus aureus	36	30	38	19	31
S. "brunneus"	14	57	13	....	31
S. "similitortus"	9	....	....	....	63
S. spp., undet.	41	48	19	6	63
Neosminthurus sp. undet.	....	....	....	....	31
Bourletiella hortensis	....	4	....	6	6
B. sp. - young	....	....	6	....	....
Sminthurus fitchi (incl. young)	55	43	56	63	56
S. sp. undet.	....	....	....	....	6
Ptenothrix unicolor	....	4	13	19	6
Neelidae	77	61	19	13	44
Mean frequency	39	46	38	33	39
Per cent in each frequency class					
0-25	36	32	48	58	45
26-50	33	16	18	14	22
51-75	15	29	18	19	16
76-100	15	23	15	8	17
Total species (or species groups)	33	31	33	36	58

in one area than in another. Comparisons of this sort have been made between each pair of areas for the commoner species of Collembola. The results are summarized in Table 5, in which are listed all cases in which the population of a species seems to be significantly greater in any one area. This table is the principal basis for the following discussion.

Table 5 summarizes the faunal differences between areas. In the first part, under each area are listed the other areas which have a significantly smaller population of the species in question.

TABLE 5. SIGNIFICANT DIFFERENCES BETWEEN AREAS IN THE COLLEMBOLAN FAUNA

	Area 1	Area 2	Area 3	Area 4	Area 5
Ceratophysella armata					1,2,3,4
Schoettella ununguiculata	4,5	1,4,5	4,5		
Willemia intermedia		1,3,4,5			1,3,4
Friesea mirabilis		1,4,5			
Brachystomella stachi			1,2,5	1,2,5	
Pseudachorutes subcrassoides				5	
Micranurida pygmaea					4
Neanura muscorum	3,4,5				3
Onychiurus subtenuis					1,2,3,4
O. sibiricus					1,2,4
O. armatus					1,2,3,4
O. parvicornis	3,4	3,4			1,3,4
Mesaphorura granulata			1	2	2
M. iowensis					3,4
Isotomodes tenuis					1,2,3,4
Folsomia fimetaria	2,3,4	4			4
Folsomina onychiurina			1,2,5	1,2,5	
Proisotoma americana					2
Isotomiella minor	3	3			3
Micrisotoma achromata					1,2,3,4
Vertagopus arborea					1,2,3,4
Spinisotoma sp.					1,2,3,4
Isotoma eunotabilis	3,4	4			4
Tomocerus flavescens			1,2,4,5		

TABLE 5. SIGNIFICANT DIFFERENCES BETWEEN AREAS IN THE COLLEMBOLAN FAUNA

	Area 1	Area 2	Area 3	Area 4	Area 5
Entomobrya nivalis		1	1,5	1,5	
Lepidocyrtus cyaneus		1,4,5	1,5	1,5	
Pseudosinella alba	3,4,5	3,4,5			
P. pettersoni			1,2,5	1,2,5	
Orchesella hexfasciata					1,2,3,4
Sminthurides lapus					1,2
Sphaeridia serratus	3				
Arrhopalites binoculatus					1,2,3,4
Sminthurinus "brunneus"		1,3,4			
S. *"similitortus"*					1,2,3,4
S. spp., unidentified	3	3			
Neelidae	3,4,5	3,4			

In the following section are listed the number of significant differences between each pair of areas, at each level of significance.

Areas	First exceeds second		Second exceeds first	
	5 per cent	1 per cent	5 per cent	1 per cent
1 & 2	1	0	1	5
1 & 3	4	5	3	4
1 & 4	1	7	1	4
1 & 5	3	1	7	8
2 & 3	2	5	3	1
2 & 4	2	8	1	3
2 & 5	2	3	7	6
3 & 4	1	1	0	0
3 & 5	6	1	7	8
4 & 5	4	2	9	8

Differences in Species Occurrence

It is quite possible that not all the differences listed in Table 5 are real; but some, at least, seem so clear-cut that they must represent real differences in the fauna. Some of the cases may be considered in greater detail, as examples.

Ceratophysella armata, while occurring rarely in the other areas, is common only in the Cathedral Pines (as is the case with quite a number of other species). The distribution is the more surprising with this species, since it is known to occur in a great variety of habitats. American authors record it from moss, humus, soil, under bark, and on mushrooms (where it is said to be the commonest species of collembolan); Stach (1949a) records it from about the same range of habitats in Europe. Agrell (1941) found it generally distributed in Lapland, in soil, litter, and moss, but, curiously, not in conifer stands! This species has been regarded as among the most widespread of Collembola, and the most eurytopic (which is not the same thing). Recent studies by Gisin (1949) indicate that *C. armata* auct. is really a complex of closely similar species, or races, with different ecological preferences. Knowledge of the American fauna is not sufficiently advanced to permit a similar breakdown of the group; nevertheless, it seems clear that what is called *armata* here is far from being completely eurytopic.

Schoettella ununguiculata, the second common member of the subfamily, has a nearly opposite distribution; it is completely absent from the Cathedral Pines. It is clearly more abundant in the needle layer than in the old field, and apparently commoner in the white pine litter than elsewhere, with an enormous summer population here.

The third member of the Hypogastrurinae, *Willemia intermedia*, is found in numbers only in Areas 2 and 5. This species is very small, unpigmented, lacks the spring, and (unlike the somewhat similar Onychiuridae) is lightly sclerotized. These characters suggest that it is pretty well restricted to the humus layer; surface forms are generally pigmented and have a spring, and those inhabiting the mineral soil (where, in fact, this species is seldom found) typically have a less flexible integument. This may explain its rarity in the old field areas. Furthermore, it should be particularly susceptible to desiccation, because of its relatively large surface area and thin cuticle; perhaps the coarseness of the humus in the red pine stand (because of the larger needle size) makes it less favorable on account of the possibility of temporary lowering of humidity in the uppermost layers.

Isotoma eunotabilis, unlike the above species, has a generally uniform distribution and is usually the commonest collembolan in any area. The very closely related European *I. notabilis* is an extremely eurytopic species (Gisin (1943); Agrell (1941)).

Lepidocyrtus cyaneus is notable for the fact that it is common in all the Middlefield areas except the red pine stand. This sort of difference is particularly interesting because the two pine stands are so similar in appearance and in most of the fauna. If the observed difference is a real one, the problem is further complicated by the fact that the majority of specimens in the old field areas are of a very pale form (possibly a different species) which is much less common elsewhere.

The case of *Pseudosinella alba* and *P. petterseni* is similar but more striking. The former species was found only in the conifer stands; the latter, only in the old field areas. The species are obviously distinct and easily recognizable.

A number of other species have a localized distribution; most of these are confined to Area 5 (*Onychiurus armatus* and *fimetarius*, *Isotomodes tenuis*, *Folsomia multiseta*, *Orchesella hexfasciata*, and others). Some of these (notably *O. armatus* and *O. hexfasciata*) are widespread and recorded from a considerable number of habitats. Others, such as *Pseudanurophorus binoculatus* (not previously recorded from North America), are either less widely distributed or have been entirely overlooked. It is not surprising that the Cathedral Pines has a considerable number of species not found in the other areas, since it is rather far removed from them; on the other hand, it has most of the species occurring at Middlefield, and a more varied population in general. It may be suggested that the environment here is actually more varied, permitting the occurrence of a wider range of ecological types.

It may be seen also that most of the species with a more general distribution occur in greater numbers in the conifer stands. This may be because of the generally more favorable conditions here, brought about by the thicker humus layer and consequent protection from desiccation; consequently, the greater numbers of many species here may be an expression of an effect common to the fauna as a whole and not peculiar to any one species.

As already noted, most of the arthropod groups aside from the Collembola are present in such small numbers that very little can be said about their distribution in the various areas. There are some exceptions, however, that are worth mentioning.

Among the pseudoscorpions, *Microbisium confusum* was found in small numbers and infrequently in Areas 1, 2, 3, and 4, but in larger numbers and high frequency in Area 5; while *Chthonius tetrachelatus* was found only in Areas 3 and 4.

The isopod *Porcellio rathkei* was found only in the Middlefield areas. This is an introduced species, and it is possible that it has not extended its range to the higher northwestern parts of Connecticut. The same may be true of the centipede *Sigibius puritanus,* which Crabill (*in litt.*) thinks is identical with a European species.

Polyxenus fasciculatus was quite common in the Middlefield areas, except the old field. This species is very commonly found under bark on pine stumps in the red and white pine stands, and perhaps this accounts for its abundance in these areas. Perhaps a preference for humus rather than soil explains its absence from Area 4; the same might be true of *Trichopetalum lunatum,* which, however, also occurs in the Cathedral Pines.

The root-feeding aphids of the genus *Prociphilus* were most numerous in the planted white pine stand, less so in the white pine-hemlock stand, and not common in other habitats. The material very likely includes several species, one of which almost certainly feeds on the roots of white pine, and it is suggested that the observed distribution of the genus is correlated with restriction of the common species to this food plant. The other records may represent either stray specimens or other species.

The *Phylloxera* sp., recorded only from Areas 3 and 4 with one doubtful specimen in the red pine stand, most likely feeds on surface vegetation, which is almost absent from the sampling areas in the pine stands.

The Thysanoptera provide the most remarkable example of ecological differentiation which was found. Not a single species was found, either in the pine stands or in the old field areas. All of the species found commonly in areas 3 and 4 are typical open grassland inhabitants (Stannard, in litt.) except for one species which is not well known. In the pine stands the only common thrips is, appropriately, *Eurythrips silvarum*.

Midge larvae (*Hydrobaenus*) were most frequent in the planted white pine stand, and only a single specimen was found in Area 4. These larvae, and those of the Empididae, seem to live by preference in humus.

Significant differences in the occurrence of the remaining groups might well appear if larger numbers of specimens were available. Such differences are, in fact, suggested in a number of cases (e.g., larvae of Cantharidae and Elateridae). A different collecting technique, permitting collection of these larger animals from a greater volume of soil, would probably be required to demonstrate this.

Characterization of the Areas

Since the composition of the fauna obviously varies somewhat from one area to another, it remains to be seen how far the latter can be distinguished and characterized in terms of the fauna. This can only be done on a relative basis, since the habitats studied are only a few among many in the region. It is of interest, however, to see which of these habitats are the most distinct, and what the degree of similarity is among them.

As mentioned above, Area 5 supports the most varied fauna. The number of species of Collembola recorded from here is much larger than from any of the other areas (58 species or species groups, against 36 in Area 4, the second highest). This area has two advantages, from the point of view of the soil fauna: as a conifer stand, it provides a relatively thick layer of humus with consequent protection from the elements and a large and stable food supply; and it has remained undisturbed for a long period, permitting the development of a "mature" community of animals as well as plants. While its geographical separation from the other areas may explain some of the observed differences in the fauna, these other characteristics, and particularly the maturity, are more important factors in accounting for the richness of the fauna.

In the Middlefield areas, there are few clear-cut differences between the areas. However, the pine stands certainly support a much larger population than the old field areas, probably, once again, because of the presence of a thick humus layer in the former. On the other hand, the number of species does not appear to be significantly different. The slight difference in number is the result of the presence or absence of records of the rarer species.

In this connection, it is interesting to note that the frequency distribution of the species is quite different in the different areas. At the end of Table 4 are listed the per cent of the species in each area falling in each of four frequency classes: 0-25, 25-50, 50-75, and 75-100. In all areas the first class is the largest. But in Area 2 only about a third of the species fall in this class, while in Area 4 well over half do so. In the highest class the difference is reversed; almost a quarter of the species in Area 2 fall here, but only 8 per cent in Area 4. It may be suggested that the old field, though a less favorable habitat in general conditions, and one with a smaller total fauna, is a more varied one than the white pine stand (which has an apparently uniform litter and very little surface vegetation). In other words, the fauna in the old field is reduced, but the number of species for which at least marginal niches are available is the same or even larger.

As may be seen from Table 4, the Middlefield pine stands have no species of Collembola not found elsewhere. The difference between the two stands is very slight, and consists almost entirely of slightly greater numbers of some species in Area 2; the commonness of *Lepidocyrtus cyaneus* in Area 2 and its virtual absence in Area 1 is the most conspicuous exception.

The two old field areas are also extremely similar. They share three species not found elsewhere, and lack one found in the other three areas. There is some evidence that the fauna in Area 3 is changing in the direction of that of the pine stands, but the process has not progressed far and the two areas differ very little.

Causes of Population Differences

The main end of the preceding discussion has been to establish the fact that, for the Collembola at least, superficially similar areas may support significantly different populations. This has been demonstrated both for the individual species and for the populations as a whole. It now remains to be seen what conclusions can be drawn as to the causes of these differences.

The present section, in large part, must be speculative. For a proper understanding of the relationships between an animal and its environment, both must be very thoroughly understood, and in this case vital information is lacking on both sides. The tolerance of Collembola in general for conditions of temperature and humidity is reasonably well known, and there is some information on their preferential reactions to these factors and to light; but except for the first two factors no extensive comparative work has been done. Other possible agents have not been studied at all in their effect on this group, although a number have been suggested as important in limiting distribution of particular species. On the other hand, the characteristics of the soil as they affect the fauna are poorly known, although, in view of the extensive work that has been done on the structure and chemistry of soil, this could probably be remedied easily enough if it were clear what factors had to be looked for. Nevertheless, it should be possible to make some decision as to what factors could or could not be responsible for the sort of faunal differences observed in this study, and to point out some influences which are clearly of the greatest importance.

The Collembola as a group are generally considered to be extremely eurytopic. There are certain obvious exceptions: the littoral species; those known only from the surface of fresh water; true cave forms (if there really are any absolutely confined to caves); a few species confined to snow fields; and commensals found only in association with ants or termites. But when these extreme cases are eliminated, the Collembola appear at first to have no clear-cut ecological limitations. This fact in itself accounts in large part for the poor state of our knowledge of their ecology; apart from the obvious difficulties in investigating such apparently tenuous variations in habitat preference as they show, relatively little work has been done on the problem because of its unattractive nature. Still, ecological differences among species have been found by many students of the group, and various suggestions have been made as to the causes of these differences. In the following paragraphs some of these suggestions, and some others which have not previously been advanced but may have merit, will be considered and, so far as possible, evaluated in relation to the findings reported above.

Geographical Distribution. Many species of Collembola have an extraordinarily wide distribution. Such species as *Ceratophysella armata* and *Onychiurus fimetarius* are found throughout the holarctic region, in Australia and New Zealand, and in Africa (*fimetarius*), South America (*armatus*), and Indonesia. Some of this dispersion has undoubtedly been accomplished by human agencies, but this cannot be the universal explanation (Salmon, 1949a). Many more species have probably been overlooked and have a much wider distribution than hitherto recorded. Nevertheless, many species undoubtedly have a relatively narrow range, and purely geographical factors, apart from other considerations such as climate, must account for faunal differences between similar but widely separated localities. It is, of course, unlikely that geography alone could be responsible for the differences found in this study except in the case of introduced species (as was suggested above for *Porcellio rathkei*).

Macroclimatic Factors. So far as the permanent soil fauna is concerned, the macroclimate operates only indirectly, by its effect on the microclimate and moisture content of the soil. Moisture will be dealt with later. However, it is convenient to consider here the effects of temperature, the fluctuations of which are at least parallel in soil and atmosphere, and of some other minor factors.

The temperature tolerance and preference of Collembola have been studied by a number of investigators. Falkenhan (1932) gives the extreme range for *Sminthurides aquaticus* as -7.5 degrees to 39 degrees C., with the optimum about 20 degrees. According to Ripper (1930) the limits for normal growth of *Hypogastrura manubrialis* are between 6 degrees and 24 degrees C. but the animals remain active down to 1 degree and survive gradual cooling to -8 degrees. Nordberg (1936), who studied Collembola from birds' nests, found an extreme range of 3-9 degrees to 40-48 degrees C., and an optimum of 23-27 degrees for both *Xenylla maritima* and *Entomobrya marginata*. Strebel (1932) reports for *Hypogastrura purpurascens* an extreme range of -15 degrees to 39 degrees C., and an optimum of 3-15 degrees; *Sminthurinus niger* apparently is somewhat less tolerant of low temperatures, but survives somewhat higher temperatures than *H. purpurascens*. Agrell (1941) gives the extreme range observed in twenty-four species; the lower limits range from 2-4 degrees C. for *Deuterosminthurus insignis* down to -4 to -10 degrees C. for *Folsomia microchaeta* and the upper limits from 34-35 degrees to 36-38 degrees (both for a number of species). In temperature preference experiments Agrell found little evidence of a high degree of selectivity on the part of specimens given a choice of a range of temperatures from 0-25 degrees C., but judging from his figures it appears that in general the species which commonly live on or above the soil surface (*Entomobrya, Tomocerus, Neanura,* and several sminthurids, as well as *Isotoma notabilis,* were found with greater frequency in the part of the apparatus above 15 degrees, while most true soil inhabitants were not so restricted, or were commoner in the portion at 10-15 degrees. He also established the fact that, for *Isotoma viridis* and *Lepidocyrtus lanuginosus* at least, the tolerance for low temperature was greater in adult individuals than in young, and that, in all species tested, resistance to cold increased with the decrease of mean atmospheric temperatures in the fall.

Temperatures in the soil are, in general, more stable than those in the adjacent atmosphere. From Table 2 it may be seen that the range of soil temperatures recorded in this study is considerably less than the range of air temperatures, and there is evidence of a lower day-to-day fluctuation in the occasional cases where soil temperatures exceeded air temperatures in summer or were exceeded by them in winter. The lowest soil temperature recorded was 0 degrees C. (at 1 inch and 2 inch depth), and the highest 25 degrees C. (at 1 inch depth). It is quite likely that the latter figure does not represent the actual upper limit, since daily measurements were not taken. However, a soil temperature greatly exceeding this figure is improbable.

It will be noted that these temperatures fall well within the over-all range of tolerance reported for the Collembola. The lower limits reported by Nordberg are exceeded, but Nordberg's animals were taken from an environment with a normally high temperature, which fact is reflected in their high upper limit of tolerance. It appears from Agrell's (1941) experiments on cold adaptation that Collembola can adjust themselves to low temperatures without difficulty, at least down to the lowest temperatures that might be expected to occur in soils in the temperate region. In several samples taken in winter in Area 5 it was found that the major proportion of the soil fauna was in the part of the humus layer which was frozen solid; these animals may have been immobilized, but were certainly alive since they came through the funnel.

It therefore seems likely that Collembola can endure the normal range of soil temperatures, and that the latter cannot be a factor in their distribution, at least so far as the extremes of temperature are concerned. Two exceptions to this conclusion should be noted: in regions of perma-frost, or of exceedingly cold winters without snow cover, the soil temperature may fall so low as to be lethal to some species at least, so that presumably these species could survive the winter, if at all, only in the egg state; and in warm climates the soil temperature in bare ground might exceed the thermal death point. Very low temperatures would not necessarily limit the distribution of Collembola in general; even in temperate latitudes many sminthurids are known to winter in the egg state, and the great hardiness of this stage should make survival possible under the most extreme arctic conditions; but it may be that some species cannot survive under these conditions, though this is more likely to be true for tropical species which are also limited by other requirements. Really high temperatures, on the other hand, are to be expected only in desert regions or in areas artificially cleared of vegetation, in which cases the low humidity and lack of organic matter for food would probably be more stringent limiting factors.

The possible limiting effect of temperature preference (optimum) cannot be so easily rejected. Agrell's (1941) work indicates that differences in preference certainly exist between even closely related species. On the other hand, any species of collembolan occurring in the temperate region must be able to develop and reproduce at temperatures varying within a rather wide range. The only possible exception to this would be the case of arctic and high alpine animals, living in areas where the soil is frozen for the greater part of the year and never reaches a temperature more than a few degrees above zero centigrade. A number of species apparently confined to such habitats are known; adaptation to a very low optimum temperature may account for the distribution of such species. The case may be similar for tropical species living in regions of approximately constant temperature.

Another way in which temperature may have an effect on distribution is in the varying length of the period during which the soil is not frozen. In arctic or alpine localities with a short growing season species which develop slowly may be unable to reach maturity in a single season; if such species are unable to survive the winter in the immature state, they could not exist in such areas. This may be the reason for Agrell's (1941) failure to find *Tomocerus vulgaris* in the sterile alpine region in Lapland, although it occurs commonly at lower altitudes; this large species has an annual life cycle, and the young, appearing in spring, are not fully grown until late summer. On the other hand, species adapted to a short summer may be unable to compete successfully with other species at lower altitudes or in warmer latitudes. In both these cases, however, the effect of temperature in limiting distribution is probably confined to arctic climates and does not influence temperate faunas.

The conclusion, on the basis of present information, is that the Collembola of temperate regions at least are not limited in their distribution by the effects of temperature alone.

Precipitation in general acts only indirectly through its effect on soil moisture. Occasional heavy rains might, by removing humus and top soil, destroy the habitat of the Collembola and render the area unsuitable; but this is best regarded as a catastrophic occurrence for which no defensive adaptation is possible. The amount of snowfall might be of importance in some northern areas, since a deep snow cover mitigates the effect of winter temperatures. But this again appears to be an insignificant factor in temperate regions.

Wind is probably of importance in two ways: it may aid directly in the dispersal of species of Collembola (but, normally, only of those species which are not confined to the soil and humus); and, by stripping litter from exposed areas and depositing it in sheltered locations, it may create both unfavorable and extremely favorable habitats. Its effect can hardly be more than extremely local, however.

It is possible that atmospheric pressure has a direct effect on the distribution of particular species. The only reasonable possibility would be in preventing the free exchange of fauna between lowlands and high altitudes. Very little evidence is available on this point, and none at all for the lower arthropods. Scudder (1889) reports that specimens of the White Mountain Butterfly, *Oeneis semidea,* became lethargic when brought down from the summit of the Presidential Range (their only habitat in New England) to low altitudes, and suggests that the pressure difference was responsible. According to Remington (personal communication) this is not wholly borne out by modern experience; the butterflies are fairly active in confinement at sea level. It has not been possible to get them to oviposit normally at low altitudes, which again suggests an effect of pressure; but this is in contrast to experiences with high altitude species of *Oeneis* from western North America, which oviposit freely when brought to much lower altitudes (Remington, 1952). The possible effects of pressure differences merit further consideration, but they can hardly be considered of general importance.

Microclimatic Factors — Humidity. The Collembola are known to be extremely sensitive to the humidity of the atmosphere. The classic work on this problem is that of Davies (1928), who studied the survival time of five species (*Isotoma viridis, Entomobrya multifasciata, Tomocerus vulgaris, Sminthurus viridis, Dicyrtomina minuta*) in atmospheres of various degrees of saturation. He found that *I. viridis* and *D. minuta,* which survive for eight hours and fifty hours respectively in a saturated atmosphere (under the conditions of the experiment), showed a drop in survival time to one hour and five hours respectively at 90 per cent relative humidity, and that *I. viridis* died as quickly in a saturated atmosphere as at 90 per cent saturation if not allowed to come in contact with water. These species are small, delicate, and without long setae or scales. *T. vulgaris* tolerated both these conditions about equally well, but showed a striking drop in survival time (from thirty to three hours) at 50 per cent saturation. This species is large and has a heavy clothing of scales, but normally lives in the litter layer. The other two species showed a marked decrease in survival time between 100 per cent and 50 per cent saturation, but survived for considerable periods (five and ten hours respectively) even in a completely dry atmosphere. *E. multifasciata*, a form with a dense clothing of long setae which presumably hinder evaporation by creating a dead air space around the animal, is well known to occur in dry situations (under bark, on foliage). *S. viridis* is practically naked, but has tracheae; it is obviously adapted to humidities below saturation, since its normal habitat is in vegetation above the ground.

The results of other investigators agree in general with those of Davies. Ripper (1930) found that *Hypogastrura manubrialis* could survive at humidities of 50-60 per cent, but needed an atmosphere at or near saturation for normal development. He also found that, in a dish with dry and moist filter paper, specimens remained on or under the latter. Strebel (1932) reports that *Hypogastrura purpurascens* died in one day at 55 per cent relative humidity, and *Tomocerus minor* in six hours, while *Lepidocyrtus curvicollis* and *Entomobrya marginata* were somewhat more resistant. He believes that the short survival times found by Davies even at high humidities are caused by deterioration of the atmosphere or by adhesion of the animals to water droplets. He also demonstrated a positive hydrotaxis in *H. purpurascens* and *T. minor*, which species were observed to assemble on a damp surface in preference to a dry one. Agrell (1941) gives a table of the survival times of 28 species at 55-62 per cent relative humidity; only *Neanura muscorum*, two species of *Entomobrya*, and three sminthurids survived for more than two hours, and all of these are surface-living species.

Only Ripper gives any data on the optimum humidity. The experiments of Agrell on this point relate only to the moisture content of the soil and humus, and not to the degree of saturation of the soil atmosphere, as shown by the fact that *Isotoma notabilis*, which according to his data prefers a "dry" environment, survived for only 3-4 minutes at 55-62 per cent relative humidity. It is obvious that the optimum humidity must be considerably above the lowest saturation tolerated, and it appears likely that an atmosphere at or near saturation is necessary for maintenance of the great majority of species, including the true soil inhabitants.

For this reason it might be expected that any soil or humus supporting a population of Collembola would have an atmosphere at or near saturation. There is, in addition, evidence in the present study for this suggestion. As reported on page 10, direct measurement of the humidity between litter and soil in all areas indicated that the soil atmosphere had a humidity of at least 95 per cent. Furthermore, Agrell (1941) quotes an investigation by Thamdrup (1939) into the relation between soil moisture and humidity of the soil atmosphere, in which it was demonstrated that if the water content exceeds 20 per cent by weight the atmosphere is essentially saturated. Agrell doubts this on purely theoretical grounds (because of the correlation observed by him between moisture content and distribution of species of Collembola, which he cannot explain except by the effect of humidity), but does not give any contradictory evidence. It seems likely that under normal conditions humidity in the soil is at or near saturation. This, of course, is not necessarily true for the most superficial layer, particularly the litter in conifer stands; but the fauna of this layer is relatively poor compared with that of the humus below.

If the true soil animals require an atmosphere near saturation, and the soil under normal conditions provides such an atmosphere, then obviously humidity cannot generally be a factor in producing local faunal differences. It should be noted also that in dry weather, when the uppermost layers of the soil might not provide a suitable environment, the fauna can undoubtedly survive temporarily by migrating to a lower layer; evidence for such a movement is given in the clearest possible fashion by the process by which the Berlese Funnel operates. Since such migrations are possible, only prolonged dry spells can have any important effect on the fauna, and unless such periods are so frequent and regular as to constitute a major feature of the area, their effect on the fauna will be only to reduce its numbers and not to produce a qualitative change toward a normal population of xerophile animals.

There is a possibility that conditions in the old field, Area 4, sometimes vary from the optimum state of saturation. No direct evidence is available, but the shrinkage of the population in periods of reduced rainfall suggests that such a drop in humidity is taking place. It must be admitted that the greater lability of the old field area in this respect may be a contributing factor in the difference in fauna between this habitat and the planted pine stands nearby. However, the samples taken under the young white pines reveal essentially the same fauna as that found in Area 4, and, as will be seen in a later section, the population size here seems to be *inversely* correlated with rainfall. And while it is possible that humidity difference may be responsible for the slightly different character of the fauna in Areas 3 and 4, it seems highly unlikely that any such factor can be effective in the more stable environment of the mature pine stands, with their thick litter layer and shade.

Microclimatic Factors — Composition of the Soil Atmosphere. The amount of carbon dioxide in the soil atmosphere is higher than in the free atmosphere; this amount varies in different localities and increases at greater depths, where it may reach a level as high as 8 per cent. The carbon dioxide content is dependent on the biomass of the soil, fauna and flora, and also on the ease of diffusion between soil and atmosphere (Franz, 1950).

In view of the anaesthetic effects of carbon dioxide in high concentrations, it is conceivable that local differences might have some effect on the fauna, particularly at the lower levels. However, no information on this point is available.

Soil Structure. Kuehnelt (1950) points out the importance of particle size and pore volume of soil for the occurrence of soil animals. So far as the Collembola are concerned, the latter factor may be effective in two ways: the mean diameter of the pore spaces will limit the size of the animals which can inhabit the soil, and the total pore volume will limit the size of the populations. Pore diameter, however, can only act to restrain the passage of animals in those parts of the soil which are not penetrated by the burrows of earthworms and channels left by decaying roots.

Very little work has been done on pore volume from a comparative viewpoint; some investigations are summarized by Franz (1950). Its possible effects on the distribution of the soil fauna cannot be evaluated until the existence of local differences between soils, correlated with faunal differences, have been demonstrated. It is improbable that structural factors have any limiting effect on the fauna of the loose, porous litter and humus layers.

Moisture Content of the Soil. This is a different matter from the humidity of the soil atmosphere, a fact not sufficiently appreciated by some investigators. As has been shown, differences in soil humidity probably have only a minor effect in limiting the distribution of soil organisms in temperate regions with adequate rainfall. On the other hand, there is considerable evidence indicating a correlation of species distribution with soil moisture. Hammer (1944) considers that the soil fauna of Greenland (exclusive of purely littoral species) may be divided into two communities only, one characteristic of damp and the other of dry habitats. (Hammer, however, considers humidity the important factor). Gisin (1943) has analyzed the soil fauna from the standpoint of the nature of the habitat, and lists a number of species which are characteristic of dry or damp soil. Agrell (1941) lists for the commoner species which he studied in Lapland the range of water content of the soils in which the species occurred. He also studied the distribution of animals in a soil sample with an artifically controlled range of water content and found that, in general, species occurring in nature in dry soils were more frequent in the dry part of the experimental soil, while the reverse was true for species found in nature in damp soils; the correlation between "preferred" moisture content and the moisture content of the natural soils where the species was found was rather close. The "preference" of individuals of the same species from soils with different water contents was quite different, approaching generally the conditions found in the source environment.

The difficulty in evaluating the effect of soil moisture on distribution lies in the lack of information on the manner in which moisture, aside from the factor of atmospheric humidity, can affect the animals. It is not even clear how animals are able to distinguish between differences in moisture content, though Agrell's data suggest that they can do so. Until some information on this problem is available, it must be considered probable that the differential effect of soil moisture is indirect, through its influence on some other factor such as the microflora.

Chemical Differences in Soils. A differential distribution, comparable to that correlated with moisture content, is apparently shown by some species with respect to the acidity of the soil. No such correlation was found by Agrell (1941), but Gisin (1943) has been able to identify some species of Collembola as characteristic of soils with low or high acidity. This association, even if real, is quite likely indirect also. It is noteworthy that Ripper (1930) was not able to find any difference in egg-laying or development in *Hypogastrura manubrialis* over a pH range of 5.8 to 8.0; possibly such differences might have been apparent at higher acidities. On the other hand, Maclagan (1932) was able to establish a difference in oviposition by *Sminthurus viridis* in soils of different acidity; relatively fewer eggs were laid in soils with a pH of 4.1, 5.5, or 7.8 than in those with a pH of 6.5.

The data presented in Table 1 reveal that both Area 4 and Area 5 have a rather acid soil; the pH is lower in the latter than in the former, and probably lower in areas 1 and 2 also, in view of the well-known effect of conifer stands on soil acidity. Whether the slight differences which are recorded have any part in controlling the composition of the fauna cannot be determined on the basis of the evidence at hand.

Kuehnelt (1950) mentions the possibility of an effect of the concentration of electrolytes in the soil, but states that in soil with a high salt content near a salt lake it was not possible to demonstrate a characteristic fauna. More evidence on this point is needed.

Some other chemical characteristics of soil might have an effect on the distribution of soil fauna (e.g., content of nitrates, phosphates, trace elements, etc.), but no information at all is available on this question. It is probable that the influence of such factors, if any, would be indirect.

Vegetation. The composition of the macroflora of an area obviously has a great effect on the nature of the soil and humus. The difference in the thickness of the humus layer between conifer stands and hardwood stands or meadows is particularly apparent, and in this case the macroflora certainly influences the populations of soil animals, since areas with a thick layer of decomposing vegetation characteristically support a more numerous and varied fauna than others. As far as species differences in the vegetation are concerned, there is so far very little evidence to indicate whether the correlation observed between plant species and animal communities, of the sort reported above, is direct or indirect. (An obvious exception is the case of the few soil animals, such as root aphids, which feed directly on living plant tissues.) The most natural method of characterizing an area is in terms of its macroflora, and it is quite possible that this method makes an appreciation of the causes of faunal differences more difficult, by obscuring more important factors.

Fenton (1947) reports the results of a number of investigations in which it was found that the palatability of hardwood leaves to earthworms and millipedes is closely parallel to the calcium content of the leaves. The possibility of differential preferences in organic matter as food on the part of those soil organisms which consume such matter directly should not be overlooked. As will be noted in the next section, studies on the normal food of soil organisms, in contrast to enumerations of substances eaten under laboratory conditions, are regrettably scanty. A study of the viability of cultures of species of soil organisms when supplied with decomposing organic matter from various species of plants might yield valuable information on the causes of the apparent association of animal species with plant communities.

Microflora. The soil, and particularly the humus layer, supports a large and varied flora of small fungi; bacteria must also be exceedingly abundant, and in the uppermost layers some green algae may be present. The Collembola, with their small entognathous mouthparts, are more likely to feed on this microflora than on organic debris in general, at least until the decomposition of the latter has proceeded to a considerable extent and the texture has been softened. Both the amount and the composition of the soil flora may therefore be of considerable importance in the distribution of these animals.

The difficulty here is that so little is known about the food habits of Collembola in a state of nature. As observed by various writers, in culture the group is extremely catholic in its tastes. For example, Strebel (1932) found that *Hypogastrura purpurascens*, *Onychiurus armatus*, and *Sminthurides niger* fed on any organic matter provided. The usual food may be much more limited. Handschin (1924) found nothing but conifer pollen in the gut contents of *Isotoma saltans;* this species is restricted to glaciers and snow fields, where little other food is to be expected. Collembola which occur in the vegetation above ground feed on plant tissues (some species may become serious pests by damaging crops). In an interesting review Macnamara (1924) mentions a number of species which feed on dead animal tissues (including *Anurida maritima*, the common intertidal species, and *Proisotoma sepulchralis* Folsom, which has so far been reported only from human graves), and describes the feeding habits of two species which are true carnivores, feeding on living Collembola: *Friesea sublimis* and *Isotoma macnamarai.* He suggests that in general those species with a molar plate on the mandible are normally vegetarian, while those without this structure (including only some subfamilies of the Hypogastruridae) may feed on animal matter, which requires less mastication. Some species of the latter group are clearly adapted to living on fluids only, since their needle-like mouthparts and small oral opening are evidently incapable of dealing with solid food.

For the humus and soil fauna, fungi are the most apparent source of food. An adaptation to a diet of particular species or groups of species of fungi on the part of some Collembola is a distinct possibility, Strebel's observations notwithstanding; it is unlikely that all possible diets are equally favorable for development, and such a restriction is similar to the situation found in many phytophagous insects, which are more or less closely limited to one host plant though the larvae can feed on other species which will not permit normal growth.

It is much easier to explain the limiting effect of chemical and other factors on the microflora than on the soil fauna directly. If, therefore, some relationship between species of Collembola and particular kinds of fungi could be demonstrated, the observed, and otherwise inexplicable, limited occurrence of species of Collembola might be easily explained. This is a field of investigation on which nothing, so far, has been done, and one which seems the most promising line of attack on the problem of distributional differences in the soil fauna.

Faunal Interrelationships. Aside from predation, favorable or deleterious effects of populations of one species on those of another have not so far been recorded for the soil fauna. Agrell (1941) found no evidence of a depressant effect of large numbers of one species on the numbers of another species of collembolan. A number of animals are predatory on Collembola. Agrell found that the numbers of gamasid mites varied in his samples proportionately with the numbers of young Collembola on which they probably prey. Other important predators include pseudoscorpions (Franz, 1950), and ants of the tribe Dacetini (Creighton, 1950). Brown (unpublished) reports that a colony of a species of Dacetini commensal in the nest of another ant quickly cleaned out the commensal Collembola also living in the nest. Under most conditions, however, it is doubtful that predators can entirely eliminate populations of a prey species, except perhaps in the case of species which are marginal in the area for other reasons. The presence or absence of prey species may, of course, affect the distribution of specific predators and parasites.

History of the Area. Major changes in the vegetation of an area, such as are caused by fire or by human interference or by the normal succession of flora may obviously have important effects on the soil fauna, if only through their effect in reducing or increasing the amount of organic matter forming the humus layer. There is a possibility of a "lag effect" associated with abrupt changes of this sort. If, for example, an area is suddenly changed from a conifer stand with a thick humus layer to grassland with practically none, by lumbering and plowing for instance, the species closely associated with the humus might be completely wiped out, leaving only those adapted to a wider range of environments. The rate of repopulation of an area of this sort has not been studied, but it is conceivable that the repopulation might be sufficiently delayed as to lag behind the reappearance of conditions suitable for the species originally eliminated. The greater number of species of Collembola in the Cathedral Pines stand than in the areas in Middlefield has been noted in the Subsection 3 above; perhaps some such factor is partly responsible. This cannot be the entire explanation, since a few specimens of one of the common and characteristic Cathedral Pines species (*Ceratophysella armata*) have been taken at Middlefield, and if this were the only factor causing the faunal difference that species should be common in both areas. In any case, some knowledge of the rate of horizontal dispersal of soil fauna is a prerequisite for the evaluation of this possibility. The only evidence so far available comes from the work of Baweja (1939), who found that in plots of soil nine feet square which had been thoroughly sterilized the soil fauna did not reach the level of that in the control plots for approximately six months. Dispersal time over greater distances would not necessarily be proportionately greater.

In connection with this discussion of possible limiting factors, it should be pointed out that the tolerance of an individual or even of a population, for a given set of conditions, is not necessarily typical of the tolerance of the species as a whole. Ecological races and individual differences are as likely to occur in Collembola as in other animals. This is borne out by the observations of Agrell (1941) reported above on differences in temperature and moisture preference of individuals of the same species from different localities. An interesting experiment by Willem (1901) on *Isotoma tenebricola* and *I. stagnalis* (according to Stach, 1947, these are probably synonyms of *Proisotoma minuta* (Tullberg, 1871)) provides further evidence. Willem had described these two shortly before as distinct species; the former was a pale animal found in a dark environment, the latter a well pigmented form living in a habitat exposed to sunlight. By transplanting populations between the habitats Willem was able to reverse the amount of pigmentation in the two "species."

Vertical Distribution

The separation of the samples into two parts, which was done primarily to increase the efficiency of the extraction of the fauna, permits drawing some conclusions on the occurrence of the fauna at different levels. Most samples were divided into two fractions, the upper including the litter and humus in the pine stand samples and the soil as far down as the bottom of the clumps of grass in Areas 3 and 4, and the lower fraction containing the mineral soil to a depth of several inches. From the numbers of specimens of a species found in the two subsamples, it is possible to determine the extent to which the species penetrates into the soil below the uppermost layers. Obviously no conclusions can be drawn about differences in preference between litter and humus layers.

In Table 6 are listed the total numbers of various species in the upper and lower subsamples from the various areas, based on the samples for which separate counts on the two fractions are available (and omitting some samples for which the counts are believed to be highly inaccurate). The selection of species to be included in this table has been somewhat arbitrary. In general the most abundant species are listed for each area; data on some of these are included for comparative purposes even from areas where their numbers are small. It may be said that any species not included in this list either does not penetrate into the lower layers at all, or is present in such small numbers that no estimate of the extent of such penetration can be made. The last figure in each line gives the per cent of individuals found in the lower subsample.

This method is obviously subject to considerable error, and the picture it gives of the vertical distribution of species is only a first approximation to the true distribution. The principal sources of error are: the variation in the point of separation of the subsamples (probably greater in the case of Areas 3 and 4, in which the two layers are not sharply delimited); occasional contamination

TABLE 6. VERTICAL DISTRIBUTION OF COLLEMBOLA [1]

Species	Area	Total in upper layer	Total in lower layer	Per cent in lower layer
Ceratophysella armata	5	344	19	5.2
Schoettella ununguiculata	1	364	3	.8
	2	5049	4	.1
	3	102	35	25.5
Willemia intermedia	2	775	14	1.8
	5	185	6	3.1
Friesea mirabilis	1	154	4	2.5
	2	1219	12	.1
	3	148	0	0
Pseudachorutes subcrassoides	1	35	1	2.8
	2	50	1	2.0
	3	179	7	3.8
	4	235	1	.4
Micranurida pygmaea	1	36	2	5.3
	2	53	1	1.9
	3	34	1	2.9
	5	221	16	6.8
Neanura muscorum	1	295	14	4.5
	2	115	3	2.5
	5	22	1	4.3
Onychiurus subtenuis	5	101	11	9.8
O. sibiricus	1	1	14	93.3
	2	46	15	24.6
	3	49	2	3.9
	4	12	15	55.6
	5	259	174	40.2
O. armatus	5	22	28	56.0
O. parvicornis	1	536	8	1.5
	2	783	14	1.8
	5	1220	20	1.6

[1] The figures are the total numbers of specimens in all the samples on which reliable counts were made for both upper and lower subsamples.

TABLE 6. VERTICAL DISTRIBUTION OF COLLEMBOLA (CONCL.)

Species	Area	Total in upper layer	Total in lower layer	Per cent in lower layer
Mesaphorura granulata	1	22	3	12.0
	2	47	13	21.7
	3	30	70	70.0
	4	92	370	80.1
	5	79	55	41.0
Mesaphorura iowensis	1	740	9	1.2
	2	555	105	15.9
	3	184	20	9.8
	4	196	65	24.9
	5	687	85	11.0
Isotomodes tenuis	5	615	236	27.7
Folsomia fimetaria	1	1235	61	4.7
	2	705	41	5.5
	3	127	12	8.6
	4	41	15	22.7
	5	2851	141	4.7
Folsomina onychiurina	3	21	34	61.8
	4	189	79	29.9
Isotomiella minor	1	454	21	4.4
	2	875	7	.8
	4	114	10	8.1
	5	1059	29	2.7
Vertagopus arborea	5	303	19	5.9
Isotoma eunotabilis	1	3336	67	2.0
	2	1624	20	1.2
	3	319	34	9.6
	4	158	3	1.9
	5	6350	79	1.2
Lepidocyrtus cyaneus	2	742	23	3.0
	3	276	11	3.8
	4	118	1	.8
Pseudosinella alba	1	66	18	21.4
	2	365	9	2.5
Orchesella hexfasciata	5	103	3	2.8
Neelidae	1	931	18	1.9
	2	285	1	.3
	5	48	0	0

of the lower subsample by surface material spilled in collecting the upper portion; and the possible effects of seasonal variation in the center of distribution of the species. The figures are of course more significant for those species which occur in large numbers. In spite of these objections, it seems likely that a high percentage value for a species, particularly in relation to the percentages given for the other species in the same area, indicates a greater (and, probably to some extent, a deeper) penetration into the lower layers. No attempt will be made to evaluate the smaller differences.

The fauna as a whole, and the numbers of almost every species in all areas, are much greater in the upper than in the lower subsample. This is certainly due to the much greater amount of organic matter in the upper layers of the soil and in the humus, which also supports a larger microflora and therefore provides a superior environment even for those species which are adapted to a deeper penetration into the soil. Species which do show evidence of such penetration are in the minority. It may be that these forms are more numerous in the lower part of the superficial layers, as might be suggested by their structure (which will be considered below), but no evidence on this point is available.

The species which have the greatest percentage of specimens in the lower subsample are: *Onychiurus subtenuis, sibiricus,* and *armatus; Mesaphorura granulata* and, less distinctly, *M. iowensis; Isotomodes tenuis; Folsomina onychiurina;* and, in one area each, *Pseudosinella alba, Folsomia fimetaria,* and *Schoettella ununguiculata.* The last case is quite unexpected and in strong contrast to the distribution of this species in the other two areas in which it is common. This species is most abundant in the Middlefield pine stands, and much less so in the young pine plantation for which this peculiar value is calculated; and the value obtained is dependent almost entirely on the counts for the single month of July. On theoretical grounds it is very unlikely that S. *ununguiculata* is a normal inhabitant of the lower soil layers. The case of *P. alba* is the reverse; it is a species which might well be expected to occur in relatively high numbers in the lower layers. *Folsomia fimetaria* also might be expected to favor the deeper layers; but its highest percentage in the lower subsample is in Area 4, where its numbers are small and where many species appear to have a lower center of distribution. The figures are more convincing for the other species mentioned, and the penetration of these species into the deeper layers is not surprising.

On the basis of comparative morphology, the primitive collembolan should logically be a humus form, as pointed out by Gisin (1943). The primitive types should have had well developed mouth parts, pigment, eyes, furca, and postantennal and antennal sense organs, and relatively short antennae and short, simple vestiture. Many species fitting this description inhabit humus, while most of those confined to other habitats are specialized in one or more respects.

Species inhabiting the deeper soil layers are not exposed to light and have no need of rapid movement, but must be able to move around through the minute spaces in the soil. They would be expected, therefore, to be white, blind, with particularly well developed sense organs, with the furca reduced or absent, and of small size and with very short and scanty vestiture. These specifications are fitted most nearly by representatives of the subfamily Onychiurinae, which for the most part is confined to the soil. (It is interesting to note that the most conspicuous exception, the European litter-inhabiting species *Tetrodontophora bielanensis* (Waga, 1842), has well developed pigment and a powerful spring and is very large—enormous, in fact, for a collembolan.)

Generalizations of this sort are, of course, subject to numerous exceptions. Eyes and pigment are very commonly lost in the Collembola, and this reduction is well seen in all the species found here to be characteristic of the deeper layers. None of these species are particularly large (*Folsomina* and the species of *Mesaphorura* are very small indeed). The other requirements, however, are evidently less rigid. *Folsomina*, for instance, has a very well developed furca and lacks the postantennal organ (but has well developed sense organs on the fourth antennal segment), and *Isotomodes* has not completely lost its pigment.

On the other hand, these specializations do not necessarily prevent the species from inhabiting the upper layers. *Onychiurus parvicornis*, the commonest species of the genus in the conifer stands, has a low percentage of occurrence in the lower subsample, and has been taken under bark as well as in humus. Some species which lack pigment and eyes appear definitely to be confined to the humus; these include *Willemia* and the neelids.

A little further information on the fauna of the deeper layers is available. While the soil profile in the old field area was being studied, two small samples were taken, one at about the lowest level reached in the ordinary samples, the other about a foot below the surface. These samples are certainly free from contamination from the upper layers. The first contained ten *Mesaphorura granulata*. The second, deeper sample contained two *M. granulata*, one *M. iowensis*, seven *Pseudosinella pettersoni*, and one specimen of *Arrhopalites* (sp. not determined). These forms at least are capable of survival well below the superficial layers of the soil.

The vertical distribution of the collembolan fauna as a whole shows an interesting variation between the areas. The percentage of specimens occurring in the lower subsample is low, in general, in Areas 1, 2, and 5, and higher in Areas 3 and 4. This can be seen more clearly if the species which are evidently capable of deep penetration are ignored. It is probable that this difference reflects the fact that there is a sharp line between humus and soil in the conifer stands, and not in the old field areas.

Volz (1934) has studied the vertical distribution of species of Collembola in forest soils in Europe. He divided the species studied into those with a relative

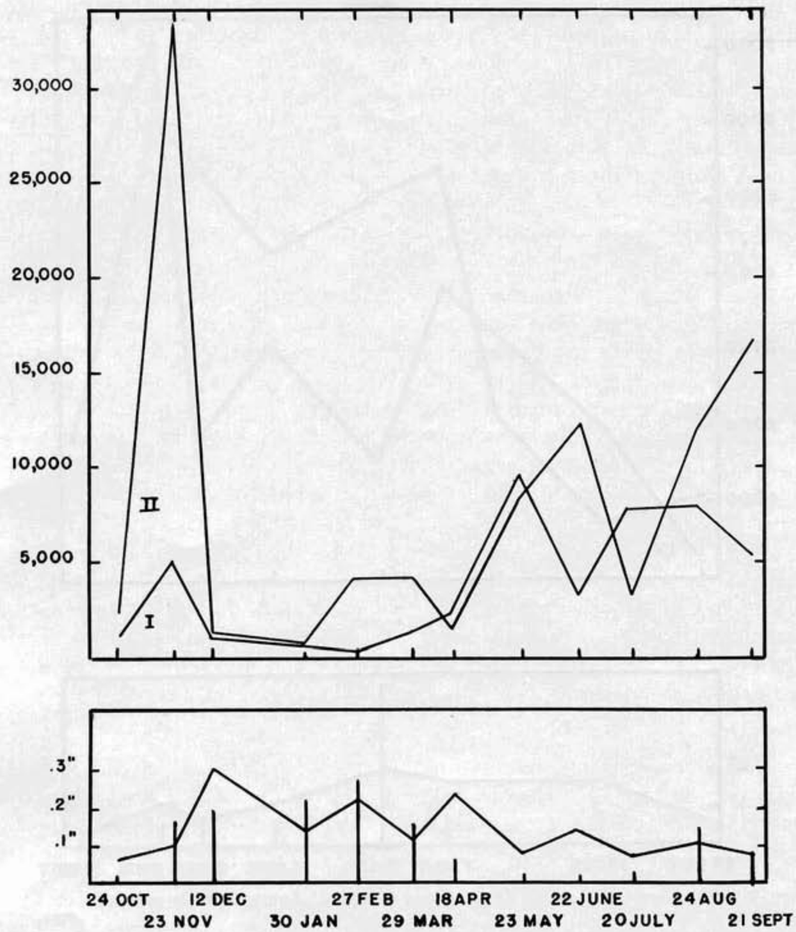

Figure 6. Numbers of Acarina collected in Areas 1 and 2. Average daily rainfall below.

maximum in the litter (*Tomocerus, Lepidocyrtus, Entomobrya*); those with a relative maximum in the humus (including *Megalothorax, Pseudachorutes, Ceratophysella*); and those with a relative maximum in the soil proper (*Onychiurus, Tullbergia, Isotomiella minor*). The order agrees well with the results of this study, although the present data suggest a relative maximum in the soil only for four species and, even for these, not in all areas. *I. minor,* however, has a relatively low percentage in the lower layers in the Connecticut areas. *Folsomina* and *Isotomodes* are not found in the area Volz studied.

Seasonal Variation

Seasonal fluctuations of the Collembola and mites are shown in the graphs. For each area the numbers of Acarina (Figures 6, 7 and 8), of total Collembola (except for the sminthurids and *Tomocerus*) (Figures 9, 10 and 11) and of selected species of Collembola are plotted for each collecting date. The values

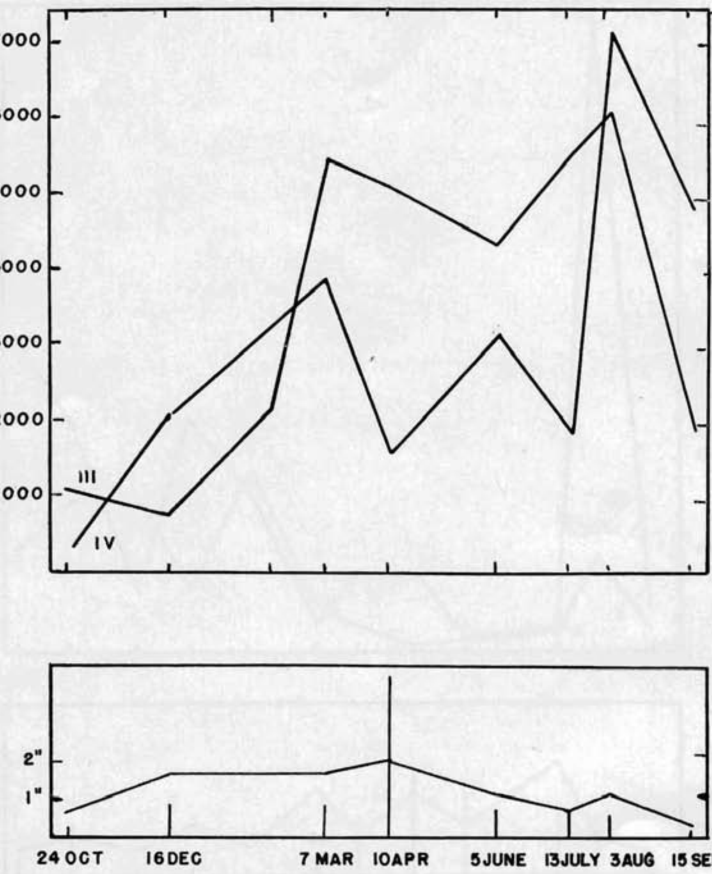

Figure 7. Numbers of Acarina from Areas 3 and 4. Average daily rainfall below.

are the mean for the date, if two samples were counted. For the sake of clarity the scale (which is indicated) is varied somewhat; it would be impossible to show clearly the variation in a species occurring in low numbers only on a scale which would also accommodate on a single page the enormous numbers of the Acarina or the peak populations of *Isotoma eunotabilis*. The choice of species plotted is somewhat arbitrary, since the small and irregular numbers of many species do not show any clear trend with time.

The majority of species of Collembola studied appear to breed continuously throughout the year, although their abundance is far from constant at different seasons. There are, however, a few exceptions, which may be considered separately.

Tomocerus flavescens evidently has a single generation a year (Figure 12) (as Agrell, 1941, reports for *T. vulgaris*). Adults (or at least specimens large

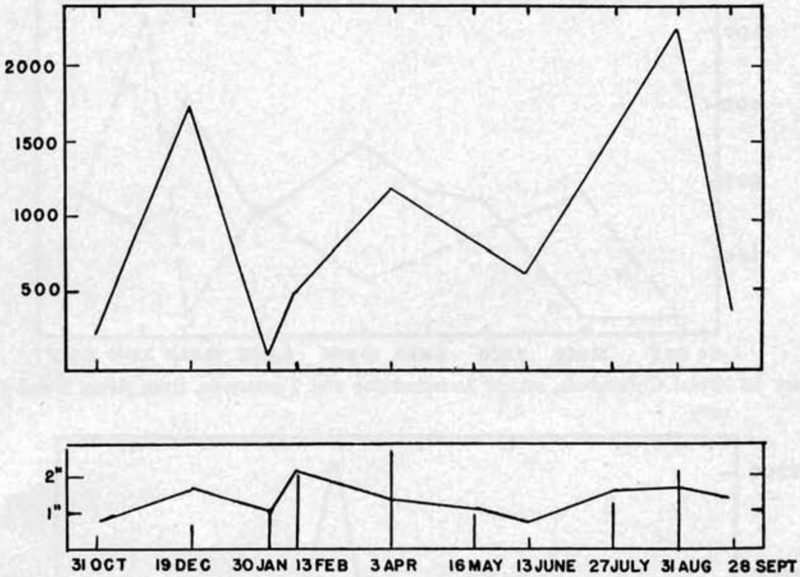

Figure 8. Numbers of Acarina from Area 5. Average daily rainfall below.

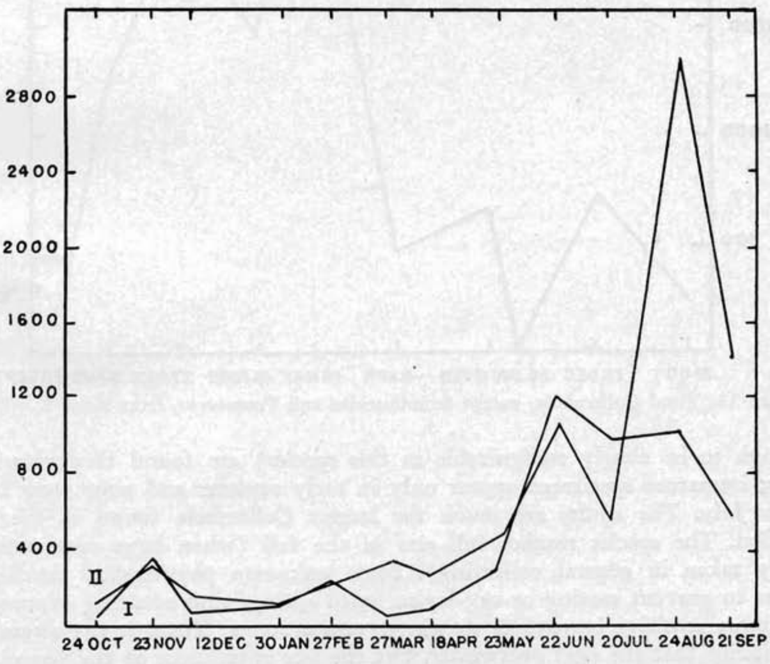

Figure 9. Total Collembola, except Sminthuridae and *Tomocerus,* from Areas 1 and 2.

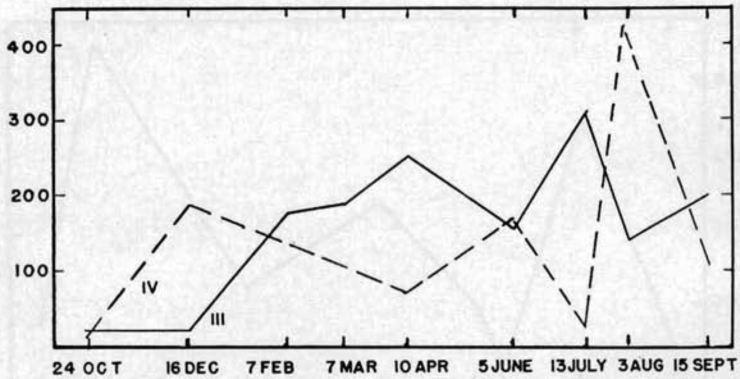

Figure 10. Total Collembola, except Sminthuridae and *Tomocerus,* from Areas 3 and 4.

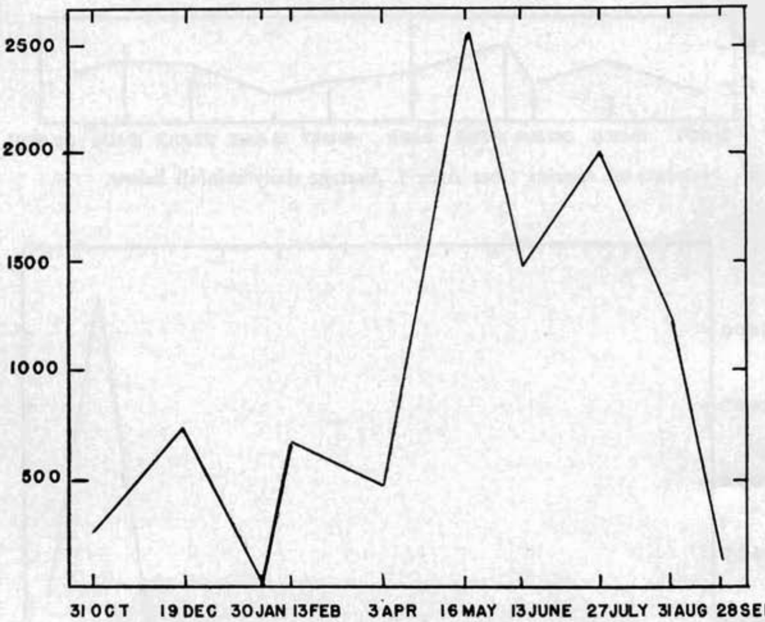

Figure 11. Total Collembola, except Sminthuridae and *Tomocerus,* from Area 5.

enough to be clearly recognizable as this species) are found throughout the year; immature specimens appear only in early summer and none were found after July. The adults are much the largest Collembola found in the areas studied. The species reaches full size in the fall (when large specimens are easily taken in general collecting). Some unknown physiological mechanism seems to prevent mating or egg-laying until spring, thus avoiding exposure of the more sensitive immatures to winter temperatures. There is the alternative possibility that the eggs overwinter, but the late appearance of the young, and

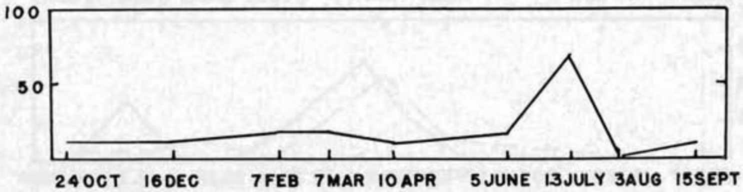

Figure 12. Number of *Tomocerus flavescens* from Area 3.

the survival of the adults until spring, make this less probable.

The sminthurids in general show an annual cycle of another sort. These species are found only during the warmer months, and apparently overwinter in the egg stage. The evidence of this is conclusive for *Sminthurus fitchi* (Figure 13) and the other species appear to follow the same pattern except for *Sminthurinus aureus* and perhaps the species of *Sminthurides* (for which the data is incomplete). It is noteworthy that many species of sminthurids are characteristically feeders on herbaceous vegetation. This is of course not available in winter, which would account for the seasonal occurrence of such forms. It is uncertain whether any of the species collected in these samples have this habit (except for *Ptenothrix unicolor* and *Bourletiella hortensis,* which are commonly seen above the surface), but possibly both the food preference and the annual cycle are general in the family, and the exceptions to the latter are secondary.

Sminthurus fitchi was not found between November (adults only) and February (young specimens). The very early appearance of some of the young may have been caused by premature hatching of the eggs in the funnel. The data suggest that there are two generations of this species during the summer, since in all areas young specimens disappeared in June but were found again in July or August.

Sminthurinus aureus, as observed in this study, practically reverses the seasonal pattern of the other sminthurids. In the Middlefield areas it was taken only from October through April. The unidentified *Sminthurinus* taken during this period were probably young of the same species, from which they differed only in their small size and lack of yellow pigment. Strebel (1932) refers to S. *aureus* as a winter species, but this clearly means only that it is present throughout the year, unlike most other sminthurids, since others have found it in summer also (Handschin, 1929; Gisin, 1943). It occurs in the Cathedral Pines in summer also, which makes the matter more puzzling.

One true winter species was taken. This is *Hypogastrura nivicola,* the "snow flea," taken only in Area 4 in December. The species is frequently abundant, sometimes astonishingly so, in winter and early spring (Folsom, 1916) but then disappears entirely. According to Stach (1949a) it "lives concealed as young individuals" during the summer. The absence of any specimens which might have belonged to this species from all other samples suggests that such

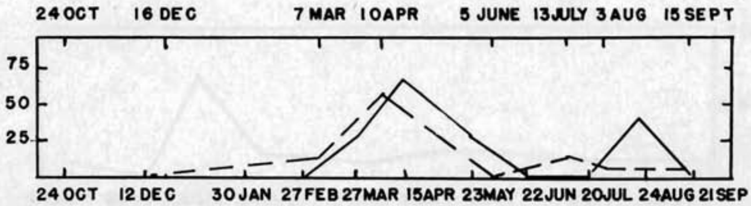

Figure 13. Numbers of *Sminthurus fitchi* from Area 1 (solid line) and Area 4 (broken line).

individuals occupy a different habitat, unless the summer is actually passed in the egg stage.

Since the species mentioned above have life cycles which are clearly limited by the seasons, they have been treated separately. It is possible that some others are similarly dependent; but all the common species occur, although generally with lower frequency, in winter as well as in summer, and adults and young are generally found together. The apparent exception in the case of *Entomobrya nivalis* (Figure 14) is due to the fact that it was possible, through the kindness of Dr. Christiansen, to determine all specimens in the fall and winter samples, whereas this could not be done for those collected later.

The relatively stable environment of the soil animals is probably subject to significant variation, over short periods, in only two factors. The effects of temperature are clearly shown in the restriction of the peak populations of most species to the spring and summer months. However, the considerable tolerance of the Collembola for gradual changes in temperature permits most of them to exist and breed throughout the range likely to be encountered in the warmer months in this region, and more detailed effects cannot be studied without continuous records of the soil temperature, which are not available.

Records of soil moisture and soil humidity are also lacking. But these must be dependent upon rainfall, for which complete data are available from both the collecting areas. To assist in studying possible correlation of the abundance of soil organisms with rainfall, the latter has been plotted for each area. For each sampling date the average daily rainfall since the previous sample (for the preceding 30 days in the case of the first samples) and the same for the preceding ten days are given.

It should be noted that an increase in soil moisture may or may not be followed by an immediate increase in the fauna; if such occurs, it is probably because of the hatching of eggs under the newly favorable conditions. The response in general is probably slower, and variable from one species to another. On the other hand, a sharp decrease in soil moisture, if sufficient to bring about a decrease in humidity, will almost certainly reduce the numbers because of the death of delicate species (unless these can withdraw to the deeper layers). Therefore, the effects of low rainfall should be more marked than those of high rainfall, which is actually the case.

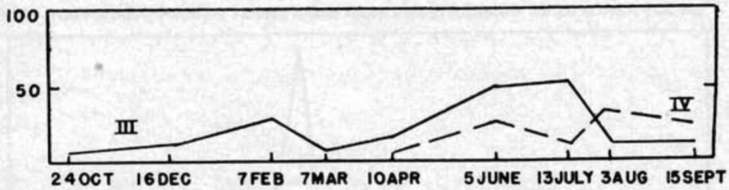

Figure 14. Numbers of *Entomobrya nivalis* from Areas 3 and 4.

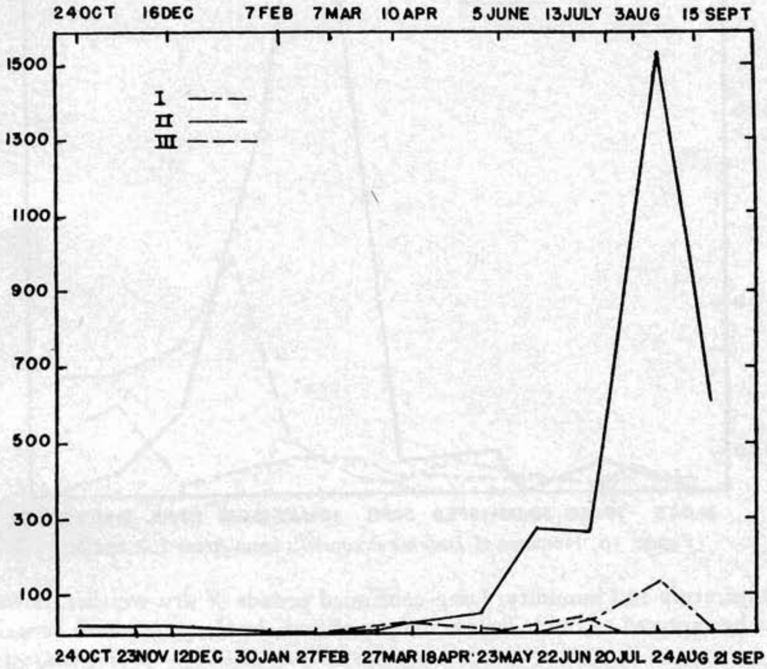

Figure 15. Numbers of *Schöttella ununguiculata* in Areas 1, 2 and 3. See Figures 6 and 7 for average rainfall.

It is very improbable that variation in precipitation has any large effect on the soil fauna during the winter months. With the low temperatures prevailing, evaporation is minimized; the humus and upper soil layers are frequently frozen; and the usual presence of a snow cover makes a drop in humidity below saturation impossible. This fact will account for the evident lack of correlation between the rainfall data and the numbers of Collembola or Acarina during this period.

In the warmer months, on the other hand, low rainfall combined with a higher evaporation rate may result in a certain amount of desiccation of the upper layers. This effect should be more pronounced in Area 4 than elsewhere, since this area is directly exposed to the sun and has no protective layer of litter to create a dead air space insulating the soil from atmospheric variations

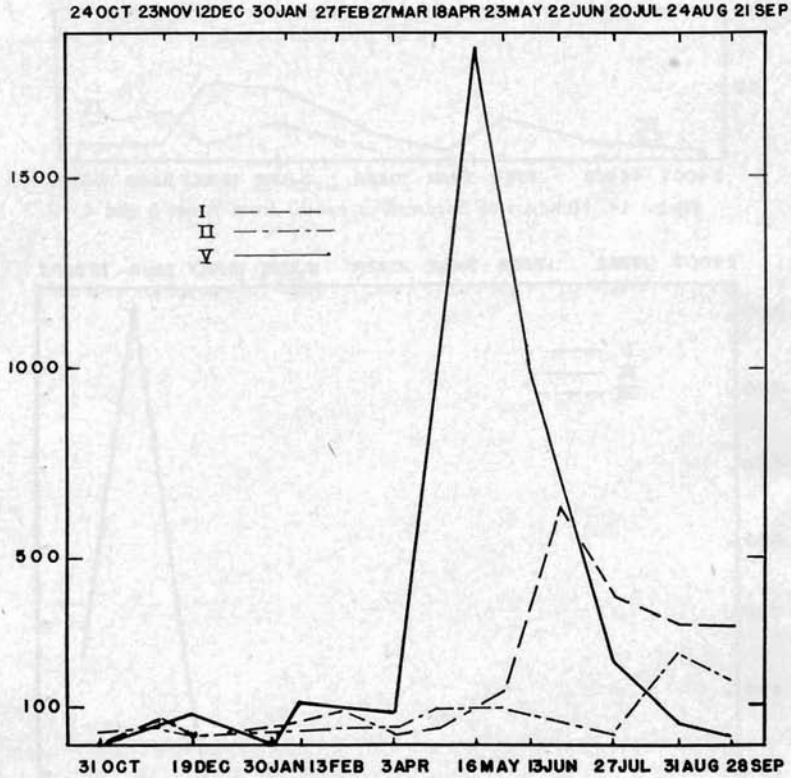

Figure 16. Numbers of *Isotoma eunotabilis* from Areas 1, 2 and 5.

in temperature and humidity. Long-continued periods of dry weather, however, might be expected to result in lowered populations in the pine stands as well.

It will be noted that the numbers recorded from all areas in the first (October) samples taken are remarkably low. The fact that these samples were not divided into upper and lower layers before being placed in the funnel is probably a contributing factor here, since the efficiency of the separation method is highest if the layer of material in the funnel is thin. However, the very low rainfall during the 10 and 30-day periods preceding the collection of the samples is perhaps more important. This is one respect in which the graphs for all areas agree.

With this exception, the correlation of rainfall with numbers of soil fauna in the pine stands is not striking. Perhaps the exceedingly high numbers of *Schoettella ununguiculata* in Area 2 (white pine) in August (Figure 15) result in part from the considerable rainfall during the preceding ten-day period. The great majority of the specimens found on this date were in their first instar, judging from their very small size and the absence of pigment except in the

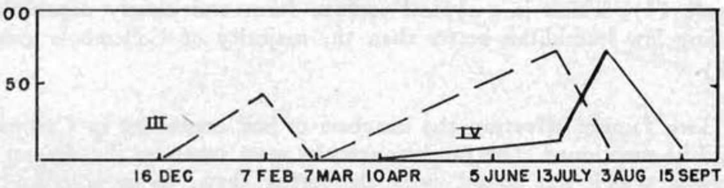

Figure 17. Numbers of *Isotoma eunotabilis* from Areas 3 and 4.

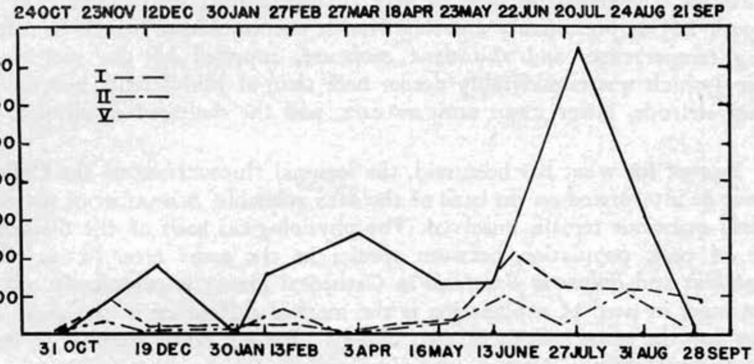

Figure 18. Numbers of *Folsomia fimentaria* from Areas 1, 2 and 5.

eyespots; among them were a number of individuals which had not yet emerged from the egg, though they were clearly on the point of doing so. It is not clear how these eggs happened to pass through the funnel. It they were in the soil waiting to hatch under favorable conditions, the rainfall might well be the direct cause of the large numbers. On the other hand, it is possible that these eggs were actually laid by females in alcohol; in this case the effect of precipitation, if any, can only have been indirect in stimulating mating or egg-laying among the adults. It is not known, unfortunately, how long the eggs of this species are normally incubated before laying.

The correlation between rainfall and soil fauna in Area 4 (old field) during the summer looks significant. This is the area in which a direct relation is most likely. The very interesting fact may be observed that the graphs of Collembola in Areas 3 and 4 from March on are practically mirror images. The actual sampling spots in Area 3 are isolated, protected habitats in terrain similar to that in Area 4. It may be suggested that the fluctuations in this area are also indirect effects of variation in rainfall (and perhaps other factors). Under unfavorable conditions a migration of individuals from the surrounding, exposed region might take place, leading to an actual increase of the population at the same time that the numbers in Area 4 were being reduced. Note that this negative correlation between the areas is not marked in the case of the Acarina; the latter are for the most part very small and probably not so mobile as the Collembola (and their dependence on a saturated atmosphere may not be so rigid). The correlation is also less evident in the case of *Entomobrya nivalis* (Figure 14), which is a typical surface form and clearly capable of withstanding low humidities better than the majority of Collembola (see Davies, 1928).

Two factors affecting the numbers of soil organisms in Cathedral Pines should be mentioned. The January samples were taken at the deepest point in a hollow, which was found, with the spring thaw, to be completely waterlogged. The very low numbers in these samples may be the result of this saturation. The enormous peak in May (caused mainly by *Isotoma eunotabilis*) (Figure 16) is presumably correlated with the combined favorable effects of rising temperatures and abundant moisture, supplied by the melting snow cover (which was considerably deeper here than at Middlefield, because of the higher altitude, lower mean temperatures, and the sheltered situation).

Except for what has been said, the seasonal fluctuations of the Collembola cannot be interpreted on the basis of the data available. A number of particularly critical questions remain unsolved. The physiological basis of the difference in time of peak population between species in the same area (e. g., *Isotoma eunotabilis* and *Folsomia fimetaria* in Cathedral Pines) is completely unknown. Even more in need of explanation is the marked difference in the shape of the curve for the same species in two closely adjacent areas, such as is seen for *Isotoma eunotabilis* in Areas 1 (red pine, peak in June) and 2 (white pine, peak in August). These problems, however, cannot be resolved until much more information on the species concerned and their ecological requirements are at hand.

SUMMARY

1. Soil and humus support a large fauna of arthropods, rich both in number of species and number of individuals. The Acarina are numerically the dominant group, followed by the Collembola. In addition, the Chilopoda, Symphyla, Homoptera (soil aphids), Coleoptera, and Diptera are well represented. Other groups of arthropods occur with relatively lower frequency. Some of the latter are true soil animals (Chelonethida, Entotrophi, Formicidae); others which may be collected in soil samples are inhabitants of the surface vegetation (many Hemiptera and Thysanoptera), or only temporarily present in the litter (Araneida, adult Diptera, and holometabolous pupae), or parasites of other species (mostly Hymenoptera).

2. Evidence has been presented which indicates that species of all groups of soil animals for which information is available exhibit decided habitat preferences, judging from the difference in frequency of occurrence and in numbers of the same species in samples from different collecting areas. Particularly complete information on this point is available in the case of the Collembola. Almost every species which was well represented in the samples collected showed decided differences in frequency and population size between the areas in which collecting was done. In most cases these differences were only quantitative, but a considerable number of species occurred commonly in one, two, or three of the five collecting areas but were not found in the others.

3. Of the areas studied, the virgin white pine and hemlock stand in Cornwall has the most varied fauna, with nearly 60 species of Collembola in comparison to 30 to 40 in the other areas. The latter do not differ conspicuously among themselves in number of species. The red and white pine stands at Mt. Higby Reservoir support a larger population than the young white pine stand or the old field. This difference is probably caused by the thick layer of humus in the pine stands, which forms an environment particularly favorable for the Acarina and Collembola.

4. The factors determining the habitat preference of species of soil animals are very poorly understood. Those which are probably of the greatest significance include the moisture content of the soil, the amount and kind of organic matter present, and the nature of the flora (particularly the microflora). The influence of these agents and some others have been considered in detail from a theoretical viewpoint. It is not possible, on the basis of present knowledge, to isolate the critical limiting factors for any species collected in this study (except for one species of soil aphid whose distribution may be tied to that of its probable food plant, white pine).

5. The various members of the soil fauna penetrate the soil to different depths, some being confined to the superficial layers while others may be found as far down as organic matter is present. Specific differences in vertical distribution have been pointed out in the Collembola. The species which

occurred with greater frequency in the lower layers of the soil have a tendency toward loss of pigment, eyes, and furca; these are obviously adaptations to their subterranean mode of existence. The same specializations may, however, be found in species which were not commonly found below the uppermost layers of soil.

6. Populations of soil animals show a marked seasonal fluctuation in number of individuals. The seasonal pattern may be strikingly different in different species of Collembola. Some correlation of the population size with rainfall is evident in the warmer months. Seasonal variation in temperature and soil moisture content (of which rainfall is a crude measure) are probably the most important factors in controlling population size. The interaction of these factors with intrinsic control of the life cycle may be expected to account for the development of peak populations of individual species at different times.

7. Nothing is more clearly brought out by the present investigation than the inadequacy of current knowledge of the soil fauna. Even from a taxonomic standpoint most groups of soil animals are very poorly known. There are many problems of great ecological interest arising from the complex nature of the community, and the considerable effect which it has on the structure and chemistry of the soil and thereby on the vegetation supported by the latter. Analysis of these problems, with emphasis on the experimental approach, is greatly to be desired.

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A study of this type would be beyond the capacity of a single individual, and I have received valuable assistance from many people. It is a pleasure to acknowledge their contributions.

My knowledge of the Collembola, a group with which I was unfamiliar when the project was begun, was materially increased by the advice of Dr. K. Christiansen, now at the American University, Beirut, who also identified representatives of the difficult genus *Entomobrya*. More recently, Dr. H. B. Mills, Chief, Illinois Natural History Survey Division, has examined representatives of many species and corrected some erroneous determinations.

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Methods used for the analysis of the data were suggested by Dr. M. H. Quenouille and Mr. D. Calhoun, Yale University. The photographs of the areas were taken by Mr. B. McFarland, The Connecticut Agricultural Experiment Station; the graphs of seasonal variation are the work of Mrs. J. A. Davenport.

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