ECOLOGY OF COLLEMBOLA

BEING A THESIS PRESENTED BY

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Contents

B./

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I. General Introduction.

The animal group with which this work is concerned is a primarily wingless order of Insecta which includes some of the most ubiquitous of animals. Collembola have been recorded as the first colonisers of embryo soils formed by weathering of rock on mountains and occur at a considerable density in most soils. They are also common in environments ranging from the leaves and flowers of higher plants to rock pools and the littoral zone of the sea shore. The present investigation is restricted to species which are typically soil dwelling.

The soil, as has been adequately shown by previous pedological studies, consists essentially of a system of inorganic and dead organic particles, the interstices of which support a wealth of plant and animal life. In this system the roots of higher plants, fungal mycelia and other plant organisms exist in association, or competion, with a vast assembly of animal forms varying in size from minute protozoa to the larger invertebrate and burrowing vertebrate species. In this soil fauna distinction can be made between two/

types; in the first of these only part of the life cycle, usually an immature stage, is spent in the soil. The second type, in which the whole life is passed in the soil, normally forms the major part of the soil fauna. This second group can be conveniently sub-divided further into those which burrow actively in soil, including the Lumbricidae or earthworms, and those which make use of pre-existing pores and cavities in the soill including most of the smaller forms, from protozoa, living in the water film on soil particles, to the arthropod groups of mites, Collembola, Myriapoda and, more rarely, Crustacea. In his review of the soil fauna, Fenton (1947) classified the members of the fauna in three groups based largely on size; those of less than 40μ were termed micro-fauna, which includes protozoa, small nematodes, rotifers and so on; those of 40μ to several centimetres were termed mesofauna and included largely nematodes and annelids, as well as soil insects and mites; while those larger than a few centimetres were termed macrofauna and consisted of the vertebrate members of the soil fauna. Murphy (1953) preferred the term meiofauna to mesofauna on the ground that this group had more affinities to the microfauna due to the inability to burrow in the soil.

The importance of Lumbricidae in top soil formation/

and in the break-down of plant debris in the soil was recognised by Darwin (1881) but only in more recent years has consideration been given to the possible effect of the soil arthropods in this connection. The potential importance of these animals in the soil has led to many investigations of the populations of soil micro-arthropods including Collembola. Among the earliest quantitative works on the soil fauna in Britain are those of Morris (1921, 22, 27) and Thompson (1924), whose pioneer work includes the first estimates of populations of grassland and arable soils. With improving technique, subsequent investigations of the fauna of different soils have been made, yielding more precise estimates of populations. Table 1 shows some of the more important quantitative works on the mesofauna, including Collembola, which are available.

Studies of the biology and life history of Collembola are less numerous than population studies although the order is of particular interest because there is no metamorphosis and all age groups in the population have similar feeding habits and biology. Previous investigation of life histories has been restricted mainly to a few species including two which have achieved/

	Biotope	Nature of Investigation	Size of Sample	Number of samples for comparison	Extraction Method
Morris (1922)	Arable	S.V.	9 inch cube	1	Hand sorting
Thompson (1924)	Arable grassland	Species distr. comparative	9 inch cube	1	Hand sorting sieving.
Agrell (1954)	Various sandy soils	Species distr. comparative	400 c.c.	1	Berlese funnel
Ford (1935)	Grassland	S.V.	6 inch square surface 3 x 3 x 9 inch soil	1	Berlese funnel sieving-hand sorting
Frensel (1936)	Meadows	Species distr. comparative	25 cm.^{2} area	1	Sieve - Berlese funnel
Ford (1937)	Grassland	Species distr. S.V.	20 x 10. cm. grass herbage	1	Berlese-Tullgren funnels
Baweja (1939)	Arable	Effect of soil sterilisation	3 x 6 x 9 inches	1	Ledell flotation
Glasgow (1939)	Meadow	S.V.	8 inch^2 area 9 inch depth	1	Ledell flotation
Hammer (1944)	Various	Comparative	1/100 m^2	1	Unheated funnel
Bels-Pogh (1947)	Pasture	Comparative S.V.	1/100 m^2 5 cm. depth	5	Berlese funnel
Agrell (1941)	Various	Species distr. comparative	400 c.c.	1	Berlese funnel
Schaller (1949)	Two calc. soil types	Comparative S.V.	1,000 c.c.	1	Tullgren funnel
Strenzke (1949)	Damp soils	Comparative S.V.	10 x 10 cm. area 10 cm. depth	10	Tullgren funnel
Van der Drift (1951)	Beechwood	Species distr. S.V.	40 cm.^{2}	10	Tullgren funnel
Macfadyen (1952)	Peatland	Comparison S.V.	10 cm.^{2} area 5 cm. depth	10	Modified funnel

Table 1: Summary of previous work on soil fauna including Collembola.

S.V. Seasonal variation.

economic importance, viz. Sminthurus viridis (L.) (MacLagan 1932) and Hypogastrura manubrialis Tullb. (Ripper 1930). Other species whose biology have been studied are H. purpurascens (Lubb.) (Strebel 1932), Orchesella spp. (Lindemann 1950) and H. armata (Nic.) (Britt 1951). The lack of information is, in part, due to the difficulty of directly observing such small and often subterranean animals in the field and also to the strict conditions necessary for successful rearing in the laboratory.

The most important physical factor influencing life in the soil is the high relative humidity present in the pore spaces. Thamdrup (1939) has shown that in temperate climatic conditions, the level of relative humidity in the air spaces of the soil is rarely less than saturation. The relative humidity in the soil is appreciably lowered only under extreme drought conditions. The almost constant high humidity of the environment is associated with a lack of resistance to desiccation in many soil arthropods. Davies (1928) showed that susceptibility to desiccation was most marked in normally soil-dwelling Collembola.

The gaseous composition in the air spaces at different levels in the soil is unknown. Where/

chemical break-down of organic material is progressing rapidly much carbon dioxide is produced. Although there will tend to be an equilibrium with the atmospheric air, at certain levels in the soil there may be a considerable concentration of carbon dioxide. In stored products infested with the mite Acarus siro (L.) such a high concentration of carbon dioxide does occur and it has been shown by Hughes (1945) that this mite shows a resistance to high concentrations of carbon dioxide in the air. A study by Ruppel (1953) of the physiology of various species of Collembola showed that typically soil-dwelling Collembola had a higher resistance to concentrations of carbon dioxide than other species.

The effect of hydrogen-ion concentration of the soil on Collembola is a matter of controversy. MacLagan (1932) has shown that in Sminthurus viridis (L.), normally an inhabitant of surface soil and leaves of plants, hydrogen-ion concentration affects egg-laying, reproduction and growth, but no evidence is available of a similar effect in soil-dwelling species. Gisin (1944) considered, on the basis of extensive qualitative soil sampling, that soil Collembola could be divided/

into acidophil and basophil groups according to the frequency of their occurrence in acid or basic soils. Other workers, including Agrell (1941), consider this factor to have little importance in the distribution of Collembola.

Of the feeding of Collembola, there is also a scarcity of published information. The report of MacNamara (1924) and records of those species injurious to crops Folsom (1933) and also the preference experiments of Strebel (1932) are our main sources of information. Schaller (1950) has worked on the quantitative effect on humus production of the feeding of various species but in both this and the other aspects of the bionomics of Collembola many questions are as yet unanswered.

In the present work an attempt has been made to determine quantitatively the population of Collembola present in soil and litter under cover of bracken Pteridium aquilinum (L.) Kuhn. This population is compared with that found in two adjacent areas of moor - and meadow grassland. The fluctuation of the population in bracken soil was observed over a period of two years. A field investigation was also made on the effect of lime and phosphate soil treatment on the populations of soil/

Collembola.

Laboratory studies of various species found under bracken were carried out in relation to the reproduction and life history of several species and their resistance or susceptibility to atmospheres with high carbon dioxide concentrations and to low humidity conditions. The food preferences of various species ~~was~~ were also studied.

The results obtained from the laboratory studies are discussed in relation to the field investigations.

II Field Studies

A. Introduction

The investigations included in this part of the work are firstly an attempt to define the quantitative distribution of Collembolan species in three biotopes*, moorland with bracken and grass-cover and adjacent meadow. Secondly, the observation, by repeated sampling over a period of two years, of seasonal fluctuations in size and distribution of the population in the soil and humus under bracken; and thirdly, to determine whether chemical 'fertiliser' applications to the soil had an appreciable effect on the Collembolan population. In order that the results should be as representative as possible, the number of samples was large enough to be consistent with theoretical requirements for estimates of soil population, although practical consideration of processing difficulties imposes some restriction. As a preliminary to field investigations of the soil fauna, a consideration of suitable methods of sampling and extraction of the fauna is essential.

* The term biotope is used as defined by Gisin (1944) in distinction from habitat which is taken to describe a particular type of micro-environment within the biotope.

The methods employed in soil micro-arthropod studies can be considered in two categories; firstly the size and number of samples taken and secondly, the means by which the fauna is separated and collected from the samples. Related to the first of those categories is the question of expression of the population observed in terms of soil surface area or volume of material.

The earliest quantitative field studies on soil micro-arthropods, including Collembola, in this country are those of Morris (1921, 1922, 1927) and Thompson (1924). These investigations were concerned with the population of grass and arable land and have set a pattern for much of the subsequent research on the soil fauna here, not only in the type of environment studied, but also in extraction methods. Both Morris (1927) and Thompson (1924) used a combination of hand sorting and wet sieving which is the predecessor of modern flotation methods of extraction. The basis of flotation-extraction methods is the system introduced by Ladell (1936) which involved flotation of the organic constituents of the soil sample in a solution of magnesium sulphate after preliminary break-down of the larger soil particles and agitation of the sample in the solution. The investigations in which this/

method or a modification has been used include Baweja (1939) on cultivated soil at Rothamsted, Glasgow (1939) on grassland at Slough, Salt et al (1948) on pasture land at Cambridge and Sheals (1956,57) on old grassland. The animals can not be readily separated out by this method when there is a high organic matter content in the soil. This may be partly the reason for the restriction of most British work to arable and grass land where the organic content of the soil is low. Modifications by Salt and Hollick (1948) include the attempted separation of plant from animal material from the flotation apparatus at a benzene/water interface. The wetting action of benzene on the insect cuticle results in the transfer of the insects to the benzene side of the interface, whence they may be removed by a variety of methods. The latest improvement (Raw 1955) is in the addition of sodium hexameta-phosphate to the broken-up soil sample in water whereby the dispersion of the particles is enhanced. Although laborious, there is little doubt that the improved flotation methods are effective for soils with low organic matter content but care and experience are required of the manipulator.

The alternative extraction method which has been widely used is the so-called automatic or funnel method which is based on the technique employed by Berlese/

(1905) in his qualitative work on soil animals. The original Berlese funnel consists of a metal funnel surrounded by a water jacket. On top of the funnel is placed a sieve with a suitable aperture size on which the sample is placed. Desiccation of the soil sample is assisted by filling the water-jacket with hot water. Migration of the animals from the sample during desiccation results in the animals falling down the funnel where they are collected in a vessel containing water or a suitable fixative. In the modification described by Tullgren (1918), for quantitative purposes, desiccation was carried out by means of an electric lamp situated above the sample; this was claimed to improve the extraction because of the gradual decrease in humidity from the surface combining with temperature and light effects to drive the animal downward. Ford (1937) further modified the apparatus so that a number of small samples could be accommodated giving a more accurate estimate of population. In her work on the micro-arthropoda of Greenland, Hammer (1944) found that extraction on funnels was more complete without heat being applied, and also suggested that it was important that samples should be as undisturbed as possible and that they/

should be turned so that the surface soil faced downwards, thus allowing the animals to use existing pores for migration from the sample. Further refinements in the funnel technique were described by Haarlov (1947) involving mainly leaving a space between the sample and the sides of the funnel to minimise condensation of moisture on the sides of the glass funnel in which small forms tend to be trapped. The latest modifications are those of Murphy (1951) and MacFadyon (1953) who have designed apparatus in which undisturbed cores are subjected to very low but continuous heating from the upper surface thus producing a sharp humidity gradient in the sample. These authors stress the importance of using as low a temperature as is consistent with such a humidity gradient in producing a gradual desiccation in the sample. These improved funnel techniques appear to be suitable for litter and raw humus samples. Their use with samples of high mineral content has been criticised by Raw (1956) and Sheals (1957) who found that samples tended to form a hard mass which prevented migration of the animals out of the sample.

Funnel sampling methods have been widely used in recent investigations on soil fauna, particularly by Continental workers, including Agrell (1934), Frenzel (1936), Weis-Fogh (1947), who used Berlese Funnels,/

and Strenzke (1949) and Schaller (1949) who used Tullgren funnels.

The importance of sample size and the number of samples required to give a reasonably accurate estimate of a field population has not been fully considered by many workers. It has been suggested for some time that soil animals tend to be aggregated in their distribution. This was shown by Glasgow (1939) in his study of Collembola and by Salt and Hollick (1946) in the case of elaterid larvae. Several other studies including that of Macfadyen (1953) support the view of a non-randomised distribution of micro-arthropods. Thompson (1929) believed that a single nine inch cube was sufficient to give a representative sample of the population in her investigations but this was shown by Glasgow (1939) to be unsuitable and that a large number of smaller samples was necessary. The investigations of Hammer (1944) also supported the argument that single large samples could lead to a misleading impression of the population present in a particular biotope. From another point of view Murphy (1953) suggests that large samples tend to favour the larger members of the/

fauna, smaller arthropods being trapped in the mass of the sample. From the evidence it appears that a number of small samples is necessary for quantitative work, particularly where the fluctuation and distribution of the more abundant species is being considered.

The expression of the population on the basis of area or volume of material has been a matter of some controversy. The main arguments for expression in terms of volume appears to be that the soil micro-arthropods are influenced by the amount of living space available. This opinion has been expressed by Van der Drift (1951) and has been accepted by many of the continental workers. However as Weis-Fogh (1948) and other workers have shown, the factor which influences the amount of sub-strate available to the individual is the volume of pore space or rather the area of the walls of the pore cavities, a measurement difficult to make; where the samples on which an estimate is based are taken from a thin, relatively homogeneous layer, then, for comparative purposes, the volume relationship is probably valuable. A most useful guide, whether the results are expressed in terms of area or of volume is given by the depth of the sample; this figure has been included by/

Van der Drift (1952) in whose work sample volume has been taken as the unit. Macfadyen (1952) summarises the claims for volume and area of the fauna and proposes that area is more logical for two reasons. Firstly, the primary energy supplied by the sun is applied over the surface area of the soil being utilised there by plant material; and secondly, the known condensation of the population into a relatively thin layer between litter and true soil is liable to lead to misleading impressions of density of population if expressed in terms of volume of material which may vary in thickness and in relative richness of fauna.

As a compromise, suggested by Murphy (1953), the expression of the fauna in terms of area with an indication of depths sampled appears to offer a satisfactory solution until pore space measurements, as given by Haarlov (1955), are more readily obtainable.

In the present field studies units of 10 cm^2 cross-sectional area and 5 cm. depth are used. The estimates of the populations have been based on as large a number of samples as practicable. For comparison of the fauna of Bracken, grass moor and meadow, twelve such samples have been taken at two depths 0 - 5 cm. and 5 - 10 cm. from each area on/

each sampling occasion. A total of 108 of the samples is used in this investigation. In the seasonal investigation of the fauna of Bracken 16 samples, also at two levels, were taken on each sampling occasion giving a total of 416 samples for the whole seasonal study. The investigation of lime and phosphate applications on the fauna was based on a 5 x 5 Graeco-latin square from each plot of which 2 random samples were taken on two occasions at the 0 - 5 cm. level. The results of this study are based on 100 samples.

In the first two investigations, extraction of the fauna from the upper layer samples was carried out by means of a battery funnel technique essentially the same as that described by Macfadyen (1953), details of the apparatus being given in an appendix and from the lower samples by a flotation technique similar to that described by Raw (1955). The samples from the lime-phosphate experiment were also treated by the flotation technique. The sample cores were taken in aluminium tubes which were held in a specially designed sampling instrument. The tubes enclosing the samples were placed in polyethylene containers for transport to the laboratory. The containers were washed out with 70% alcohol and any Collembola which had escaped from the sample were added to the final /

extraction.

After extraction, and washing in the case of animals extracted by flotation, the micro-arthropods and other soil organisms were transferred to a shallow transparent counting dish. The use of guide lines marking out the width of the field of the low power microscope, under which examination of the animals was made, facilitated sorting. The Collembola from each sample were mounted on slides in a gum-chloral hydrate mountant for subsequent identification, counting and measurement of individuals. In the comparative study, measurement of the dimensions of individuals allowed an estimate of volume of each species to be made, thus giving an approach to biomass estimation in terms of volume of animals in the sample volume.

B. Comparison of the populations of Collembola in various Biotopes.

Description of the sampling area and methods

The sampling area was at Drumclog moor, near Milngavie, Dunbartonshire, (grid ref. 26/554764) eight miles to the north west of Glasgow. The samples were taken from the north east corner of the moor and from an adjacent meadow. The plant cover of this part of the moor is predominantly Nardus stricta with localised areas of bracken. The meadow plant cover consisted of a rather poor sward with Poa pratensis and Poa spp. interspersed with Agropyron repens and other rough grasses and broad leaved weeds. The meadow had received application of ground limestone at the rate of two tons per acre in 1954, two years previous to the sampling.

The results of chemical analysis of the three soils is shown in Table 2. The Bracken and grass moorland profiles exhibit a fairly typical moorland mor structure with a distinct layering of litter and humus. The meadow soil, may be described as a grass mull type with an apparently even distribution of organic material throughout the profile. The area is shown on a geological map /

	pH		% Loss on ignition.			
	Upper	Lower	Upper	Lower	% K_2O	% P_2O_5
Bracken	4.44	4.80	33.1	11.3	0.0245	0.002
Grassmoor	4.43	4.98	29.6	11.8	0.024	0.0019
Meadow	5.46	5.40	13.5	13.0	0.0095	0.001

Table 2: Chemical analysis of soils from three sampling areas; each figure is the mean of five samples. Samples dried at 100° C.

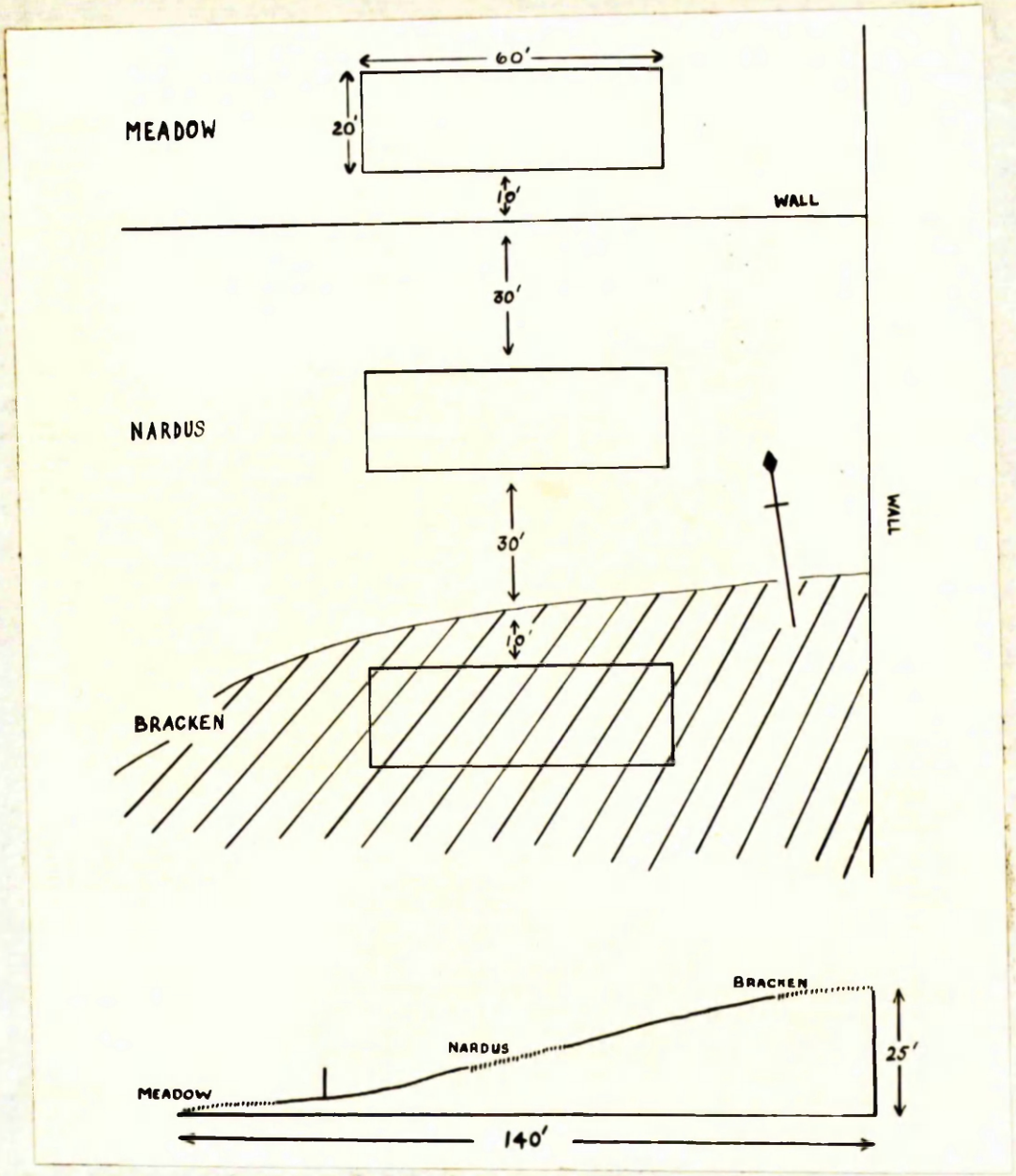


Fig. 1. Comparison of biotopes - Lay-out of sampling plots.

Plate 1. View of sampling site from north.

(Geol.Survey 1931) as lying on Calciferous Sandstone.

Three sampling plots each measuring 60 feet by 20 feet were laid out as shown in Fig. 1. Twelve samples of the surface 5 cms. and 5-10 cm. depth were taken from each plot on three occasions, 28th September, 1956, 26th January, 1957 and 23rd May, 1957. Samples were taken in the sampling tubes previously described and immediately placed in polyethylene containers for transport to the laboratory. Surface vegetation was removed before sampling. The sampling tube was inserted into the upper stratum and removed with the sample by means of a handle which locked into the upper end of the cylinder. The corresponding lower sample was then obtained by inserting another cylinder through the cavity remaining after removal of the upper sample. The Collembola were extracted from the upper samples by means of the funnel apparatus and from the lower samples by flotation. After mounting on slides for identification and counting, the Collembola were measured by means of a micrometer eyepiece. The means of measurements of length, breadth and height in Arthropleone and of diameters of Symphypleone species were used to give an estimate of volume of each species present in each sampling. The mean volume for each species at the three sampling times is shown in the table in Appendix II.

Results

The species obtained in the three areas are shown in Table 3. This includes all the species obtained in the quantitative samples and also several species from larger qualitative samples which were taken occasionally. The list includes one species Onychiurus armatus Tullberg. sensu Gisin new to Britain and a species, new to Science, subsequently described by Gisin (1957) from specimens supplied from Milngavie, as Sminthurinus flammeolus n.sp. One species of Proisotoma was not determined. This species appears to be closely related to P. minima (Absolon) but characters of the furca prevented inclusion under this species. Unfortunately insufficient well preserved material was available to describe this species adequately. Of the species obtained in quantitative samples and forming more than 5% of the population two were restricted to the meadow site, namely Onychiurus uliginatus Gisin and Folsomia fimetaria (L.). No species were restricted to either of the bracken or grass moorland sites but three species found in both were not present in the meadow, namely O. procampatus Gisin, F. candida Will. and Sminthurides schötti Axels.

In the quantitative samples T. krausbaueri and /

		Bracken	Grass Moor	Meadow
	Tullbergia callipygos Boerner	x	2.2	x
	T. krausbaueri (Boerner)	23.6	16.5	31.9
	T. quadrispina Boerner	6.5	3.9	1.0
*	Onychiurus armatus Tullberg sensu Gisin			x
	O. latus Gisin	x	x	
o	O. furcifer Boerner	x		
	O. procampatus Gisin	16.0	11.1	
	O. uliginatus Gisin			10.6
	Friesea mirabilis (Tullberg)	x	4.0	10.6
	Neanura muscorum (Templeton)	x		
	Brachystomella parvula (Schaeffer)	3.7	10.8	1.7
	Hypogastrura denticulata (Bagnall)	x	x	7.1
	Anurida comellinii Gisin		x	x
	Folsomia candida Willem	7.3	5.2	
	F. fimetaria (L.)			6.4
	F. manolachei Bagnall	6.8	7.3	2.2
	F. quadrioculata (Tullberg)	9.3	16.0	5.1
	Isotoma notabilis Schaeffer		x	
	I. viridis Bourlet	1.2	2.1	15.9
	Isotomiella minor (Schaeffer)	x	x	
o	Proisotoma sp.	x		
	Lepidocyrtus lanuginosus (Gmelin)		x	
o	Tomocerus vulgaris Tullberg	x		
o	Pseudosinella immaculata (Lie - Pettersen)			x
	Arrhopalites sericus Gisin	x	x	
	Sminthurides schötti Axelson	9.1	10.1	
	S. pumilis (Krausbauer)	x	1.6	4.1
+	Sminthurinus flammeolus Gisin	x	x	x
	S. aureus (Lubbock) v. ochropus (Reuter)		x	
	Sminthurus viridis (L.)			x
	Number of species	21	21	17

Table 3 : List of species present in three sampling areas and percentage composition of population.

* species new to Britain.
\+ species new to Science.
o in qualitative samples only.
x indicates species present but forming less than 1% of total population of Collembola.

O. procampatus were abundant in bracken and grass moorland. In the meadow site T. krausbaueri was always present in relatively large numbers. However there was some variation in the proportions of the various species on the three sampling occasions (Table 4) which necessitates separate consideration of each sampling.

First sampling - September 1956.

In this sampling the fauna of the bracken site was dominated by T. krausbaueri, O. procampatus, B. parvula and F. candida. The other species forming more than 5% of the population were F. manolachei, F. quadrioculuta and Sminthurides schötti. The grass moorland samples were dominated by T. krausbaueri, O. procampatus and B. parvula with F. manolachei and F. quadrioculata as the other species forming more than 5%. The most abundant species in the meadow site were T. krausbaueri, O. uliginatus and H. denticulata. Folsomia fimetaria, F. quadrioculata and I. viridis which each formed more than 5% of the population.

Second sampling - January 1957.

On this occasion the bracken fauna had again T. krausbaueri and O. procampatus as the most /

abundant species with F. manolachei and S.schötti next in abundance. The grass moorland site had T. krausbaueri and O. procampatus as abundant members with S. schötti, F. manolachei and F. quadrioculata also forming a large part of the population. In the meadow site T. krausbaueri and Friesea mirabilis were the most numerous with Isotoma viridis next in abundance and with O. uliginatus in smaller numbers than in the first sampling.

Third sampling - May 1957.

In this sampling the bracken samples had T. krausbaueri and O. procampatus as the most numerous species with F. quadrioculata also important numerically. Grass moorland samples had Folsomia quadrioculata as the dominant species with T. krausbaueri, B. parvula and O. procampatus forming the large part of the other species present. The meadow samples had T. krausbaueri and I. viridis as the most abundant species with Hypogastrura denticulata and O. uliginatus also present in numbers representing large proportions of the population.

The percentages of the species present expressed /

in terms of body volume (Table 4) gives differences in ranking from that given by numerical data. This is shown particularly by T. krausbaueri which is a small species and, although numerically abundant in most of the samples, is a minor constituent of the population in terms of volume of individuals or biomass.

The distribution of each species throughout the biotope, as measured by the percentage of samples in which the species occurs, is of some importance and in most continental studies of soil populations use is made of the frequency classes of Krogerus (1932). Those species occuring in 50% or more of the samples are considered constant. Those occurring in less than 50% of the samples but in 20% or more are called accessory and those occurring in less than 20% are called accidental. All the abundant species in the samplings were constant . The frequencies are shown in Table 5.

The results of statistical analysis of the square-root transformed date of the occurrence of the more abundant species common to bracken and other sampling sites, namely T. krausbaueri, O. procampatus and F. candida are given in Table 6. This shows a significantly larger/

Sampling site	Bracken				Grass moor				Meadow		
Sampling	I	II	III		I	II	III		I	II	III
O.procampatus	100	100	75	O.procampatus	66	92	75	O.uliginatus	75	66	33
T. krausbaueri	50	100	100	T.krausbaueri	66	50	75	H.denticulata	75	41	50
B.parvula	50	16	41	B.parvula	50	75	8.3	F.mirabilis	58	83	16
F.candida	50	50	66	F.mirabilis	41	0	50	T.krausbaueri	58	100	83
F.manolachei	41	41	16	F.manolachei	33	66	50	F.candida	50	75	0
S.schötti	41	83.3	25	I.viridis	33	0	41	F.quadrioculata	41	50	16
F.quadrioculata	33	66.7	75	F.candida	25	66	91	I.viridis	41	0	0
I.viridis	25	0	25	T.quadrispina	25	0	25	T.quadrispina	25	66	25
T.quadrispina	16	16	83.3	S.schötti	16	50	41	S. pumilis	0	16	0

Table 5. Comparison of population of Collembola from three sampling sites.

Frequency of occurrence of each species measured by percentage of samples in which the species is present.

Sampling date		September 1956			January 1957			May 1957		
Species	Comparison	diff.of means	s.e.	t.	diff.of means	s.e.	t.	diff.of means	s.e.	t.
	bracken grassmoor	0.2042	0.2261	0.90	0.6100	0.3795	0.26	0.7350	0.2735	2.69
T.krausbaueri	bracken meadow	0.1584	0.1998	0.79	0.5300	0.4294	1.23	0.5225	0.3089	1.69
	meadow grassmoor	0.0458	0.2263	0.20	0.5300	0.4322	1.23	0.2125	0.1088	1.95
O.procampatus	bracken grassmoor	0.2792	0.2309	1.21	0.1725	0.2580	0.67	0.2291	0.1990	1.15
F.candida	bracken grassmoor	0.4083	0.1949	2.09	0.1600	0.1752	0.91	0.0867	0.1897	0.46
	bracken grassmoor	0.3716	0.3274	1.14	0.8100	0.4780	1.69	0.1275	0.5491	0.23
Total Collembola	bracken meadow	0.2650	0.3121	0.85	0.4408	0.5711	0.77	0.6275	0.5211	1.20
	grassmoor meadow	0.6366	0.3143	2.03	0.3692	0.4442	0.83	0.7550	0.5395	1.40

Table 6. Statistical analysis of square-root transformed data of the comparison of populations from three sampling sites.

5% probability level; $t = 2.07$ for 22 degrees of freedom.

	September 1956						January 1957						May 1957					
	Bracken		Grassmoor		Meadow		Bracken		Grassmoor		Meadow		Bracken		Grassmoor		Meadow	
	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V
F.kraussbaueri	13.8	0.4	13.5	0.6	13.3	0.6	30.2	1.0	22.0	0.7	39.9	0.3	31.5	0.6	10.1	0.2	36.2	0.8
O.pracampatus	27.6	21.5	25.6	31.4	0	0	19.0	26.3	11.6	12.4	0	0	12.3	20.6	6.1	8.1	0	0
O.uliginatus	0	0	0	0	22.2	32.2	0	0	0	0	7.6	2.1	0	0	0	0	7.2	12.6
F.mirabilis	0	0	9.0	1.6	8.2	1.6	0.4	0.1	5.6	0.8	16.8	1.2	1.5	0.4	0	0	2.0	0.5
E.parvula	10.3	5.1	13.5	11.4	2.2	2.1	1.2	0.7	9.8	6.1	0	0	4.9	5.5	11.3	10.6	4.6	5.6
E.denticulata	0	0	0	0	12.6	14.9	0	0.3	0	0	3.4	0.7	0.5	0.7	0.8	1.0	9.9	15.2
F.candida	17.2	0.8	2.3	0.2	0	0	5.2	0.3	6.2	0.4	0	0	7.4	0.8	4.8	0.4	0	0
F.fimetaria	0	0	0	0	11.9	1.0	0	0	0	0	7.2	0.1	0	0	0	0	0.66	0.1
F.cancleschei	6.9	6.9	5.6	8.3	0	0	15.7	19.4	9.5	10.4	1.0	0.3	1.5	2.9	4.8	8.0	6.6	14.0
F.quadriocculata	6.9	5.4	7.9	10.5	10.4	15.8	8.9	21.3	9.5	4.3	4.8	1.2	15.3	27.0	27.8	41.2	1.3	2.5
I.viridis	2.6	2.8	4.5	8.2	9.6	19.0	0.4	16.8	1.2	38.1	9.6	93.0	2.0	2.8	2.4	2.1	30.3	35.2
S.pallis	0	0	0	0	2.2	2.2	0	0	0	0	6.2	1.4	0	0	0	0	0.66	3.4
S.schötti	8.6	6.0	4.5	5.3	0	0	18.9	21.1	16.0	14.0	0	0	2.0	3.1	3.6	3.8	0	0

Table 4: Percentage species composition of population of Collembola in three biotopes by numbers and by volume.

N = Numbers V = Volume

population of T. krausbaueri in bracken than grass moorland in May 1957 (t, 2.69; d.f.,22) and also a significantly larger population of F. candida in bracken than grass moorland in September 1956 (t, 2.09, d.f., 22). There were no significant differences in any of the other comparisons. Some of the other species common to the sampling sites were not present in sufficient abundance in all areas to merit statistical treatment of the comparisons. These species include Isotoma viridis and Hypogastrura denticulata which were found abundantly only in the meadow site and Brachystomella parvula and Tullbergia quadrispina which were present in appreciable numbers only in the bracken and grass moorland sites.

The number of total Collembola obtained in the samplings (Table 7) was largest in the second sampling in all three sites. The grass moorland samples were largest with a population equivalent to 28.1 Collembola per 10 square centimetres and the bracken site samples gave 20.7 Collembola per 10 square centimetres. The first sampling had the lowest population with populations ranging from 7.4 Collembola per 10 square centimetres for the grass moorland site to 11.3 Collembola per 10 square centimetres from meadow. The population on /

	Sept. 1956			Jan. 1957			May, 1957			Total			
	Total	No/10 cm^2	Ratio u/l	Total	No/10 cm^2	Ratio u/l	Total	No/10 cm^2	Ratio u/l	Total	No/10 cm^2	Ratio u/l	Vol(m
Bracken	116	9.7	1.9	248	20.7	2.0	203	16.9	0.6	657	15.8	1.3	20.1
Grassmoor	89	7.4	2.4	337	28.1	1.9	248	20.7	2.8	674	18.7	2.2	25.4
Meadow	135	11.3	2.4	291	24.3	0.8	156	13.0	1.4	592	16.4	1.2	57.5

Table 7: Distribution of total populations of Collembola in three sampling areas.

U - upper L - lower

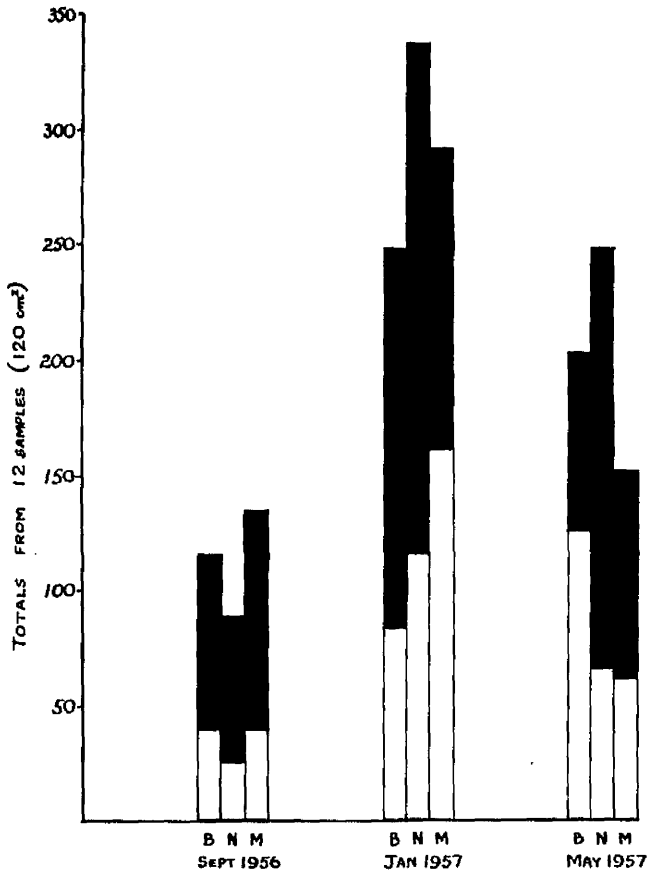


Fig. 2. Total populations of Collembola from three sampling sites on three occasions. upper samples black.

B - bracken, N - grass moorland, M - meadow.

the third sampling was intermediate in size in all three sites. Analyses of the mean differences between each site approached significance at the 5 per cent level only on the first sampling between the grass moorland population and the meadow population (t, 2.03, d.f., 22).

Vertical distribution

The distribution of the species between upper and lower samples is shown in Table 8. Statistical analysis of the differences in various species on the three sampling occasions is shown in Table 9. T. krausbaueri was significantly more abundant in the lower than upper samples in all the samplings. O. procampatus was more abundant in the upper samples from bracken and grass moorland over the three samplings but the difference was statistically significant only in the first sampling of grass moorland and the second sampling of bracken. F. mirabilis was not significantly more abundant at either depth. Significantly greater numbers of Folsomia candida were found in the upper samples from bracken in the first two samplings, in the lower samples from bracken in the third sampling and in the upper samples from grass moorland in the second sampling. F. fimetaria, which was found only in the meadow site, occurred in significantly greater numbers in the samples from the lower level in the second sampling.

	Beech		Grass Woodland		Heather	
	Upper	Lower	Upper	Lower	Upper	Lower
T. krausbaueri	13	142	7	104	15	174
T. callipygos	9	4	1	14	0	3
T. quadrispina	3	40	1	25	0	6
O. procampatus	73	32	46	29	-	-
O. uliginatus	-		-	-	65	0
F. mirabilis	2	2	20	7	26	37
I. parvula	19	5	73	0	10	0
I. denticulata	1	0	2	1	50	4
F. candida	29	19	23	12	-	-
F. fimetaria	-	-	-	-	16	22
F. manolachei	44	1	45	4	13	0
F. quadrioculata	59	2	105	3	25	4
I. viridis	8	0	12	2	87	7
S. pusillus	2	0	11	0	22	2
S. schötti	59	1	67	1	0	0

Table 8 : Vertical distribution. Totals obtained from upper (raw humus) and lower samples on three sampling occasions.

Sampling time		September 1956				January 1957				May 1957			
Species	biotope	mean	s.e.	t	d.f	mean	s.e.	t	d.f	mean	s.e.	t	d.f
T.kraussbaueri	bracken	-2.0000	0.2753	7.26 xxx	5	-4.0830	1.7052	2.40 x	11	-4.8330	0.3791	12.75 xxx	11
	grassmoor	-1.2500	0.1628	7.68 xxx	7	-5.6670	1.4477	3.91 xx	11	-2.1110	0.3124	6.75 xxx	8
	meadow	-2.0000	0.3257	6.14 xxx	6	-8.1667	2.3958	3.41 xx	11	-4.7000	1.2494	3.76 xx	9
O.procampatus	bracken	1.0000	0.6513	1.54	11	1.9167	0.5562	3.45 xx	11	0.6667	0.7178	0.93	8
	grassmoor	1.6250	0.5495	2.96 x	7	0.4545	0.6785	0.67	10	0.1111	0.4512	0.25	8
F.minabilis	grassmoor	1.6667	0.7139	2.24	4	0.5555	0.4941	1.12	8	1.5000	0.8672	1.72	3
	meadow	0.1428	0.2592	0.55	6	1.3000	1.0445	1.24	9	-	-	-	-
F.candida	bracken	1.0000	0.2768	3.61 x	5	1.5000	0.5607	2.68 x	5	-0.6250	0.2110	2.96 x	7
	grassmoor	0.3333	0.1421	2.35	2	1.3333	0.1882	7.08 xx	5	1.0000	0.4768	2.10	5
F.fimetaria	meadow	0.2500	0.2951	0.85	7	-0.3000	0.4183	7.17 xxx	9	-	-	-	-
Total Collembola	bracken	3.0000	1.3315	2.25 x	11	9.0000	3.1238	2.88 x	11	-4.2500	3.0028	1.42	11
	grassmoor	3.2500	1.2502	2.60 x	11	9.0000	3.3046	2.72 x	11	6.5833	4.1533	1.59	11
	meadow	4.5833	1.4646	3.13 xx	11	-2.5083	3.4452	0.73	11	2.5000	3.1562	0.79	11

Table 9. Statistical analysis (untransformed data) of vertical distribution of Collembola from three sampling sites. The means were obtained from differences, in number of Collembola, between upper and lower samples. Negative means indicate density greater in lower than upper sampling levels.

x significant at 5% probability level
xx significant at 1% probability level
xxx significant at 0.1% probability level

The analysis of the vertical distribution of total Collembola shows that the population was significantly greater in the upper layers in all three sampling sites at the first sampling. In the second sampling the bracken and grass moorland sites again had significantly greater population in the upper samples but differences in the population of the upper and lower meadow samples were not significant. No significant difference in the vertical distribution of Collembola from the three sites was found on the third sampling.

Discussion

Previous soil faunal research in Britain has been confined mainly to grassland. The works with which faunal comparison can be made here are those of Glasgow (1939), Salt et al (1948), MacFadyen (1953) and Sheals (1957). Qualitatively the results of the present investigation are most closely comparable with Sheal's study of old grassland at Glasgow using a flotation extraction method. Many of the species are the same as those found at Milngavie and it is worth noting that the main representative of the Onychiuridae there, as reported by Sheals (1957), was O. uliginatus, found here only in the meadow samples. The relative abundance of this species and T. krausbaueri is in close agreement /

with the present findings. Of the other two works the investigation of fenland by Macfadyen (1953) to some extent agrees with the species encountered at Milngavie, but the Collembolan fauna in his work was dominated by F. quadrioculata, with F. mirabilis as the second most abundant component. The Onychiuridae and Tullbergidae were found in relatively much smaller numbers. The investigation of pasture near Cambridge by Salt et al (1948) showed fewer species in common with the present study; though the fauna was dominated by one of the Onychiurids, O. alborufescens and T. krausbaueri. The species found there also included I. viridis, which was quite abundant and F. fimetaria. In this the faunistic composition at Cambridge was in accord with the present findings for the meadow samples.

Frenzel's (1936) quantitative work is among the most comprehensive of the continental studies on grassland. His "leit-formen" for meadows include several species found in the present work, namely F. mirabilis, O. armatus, T. krausbaueri, F. quadrioculata, I. notabilis, I. viridis and L. lanuginosus. F. fimetaria was found in his /

dry Hundesfeld meadow which had received manurial treatment. The species composition of grass moorland at Milngavie is similar to the Brachystomella parvula 'synusia' of alpine grassland described by Gisin (1943). The species associated with B. parvula in this 'mesophil hemiedaphic' synusia are I. viridis, L. cyaneus, S. schötti, I. notabilis, F. quadrioculata, Sminthurinus aureus and Sminthurides pumilis. With the exception of L. cyaneus all these species were found at Milngavie in grass moorland. Numerically B. parvula, F. quadrioculata and S. schötti formed one third of the total population of Collembola in this biotope. The occurrence of the two closely related species F. quadrioculata and F. manolachei is also of particular interest. F. manolachei has been recorded only a few times previously and never before in association with F. quadrioculata. Gisin (1958) has found a successive relation between the occurrence of F. quadrioculata and another related species F. nana Gisin in terms of height of alpine pastures. F. fimetaria was also found by Gisin (1943), in an extensive qualitative investigation of Collembola, to be characteristic of dunged meadows and is included as one of a group of /

'Anthropogenous' types together with I. viridis and B. parvula. The members of the Onychiuridae encountered in Milngavie were until recently included in the species O. armatus Tullb. The division of this species by Gisin (1952) gave rise to a number of new species of whose distribution there are still few published records. O. procampatus, however, has been recorded from high alpine pastures and in rough grassland in England, and is regarded by Gisin (1956) as a typical inhabitant of primitive soils. O. uliginatus has been found in alpine pastures and in damp soils by Gisin (1956) as well as in grassland by Sheals (1957) mentioned above. This species has also been found by the author in freshly sown grassland at Cleland, Lanarkshire.

The work of Gisin (1949) and Gisin (1951) has shown that in the maturation of compost a succession of Collembola can be followed. The results obtained in these studies suggests that differences in soil condition are indicated by the species composition of the populations of Collembola present. This has been further confirmed by Gisin (1956 a,b) from the results of investigation of the effect of addition of Krilium to the soil and in a comparison showing the effect of weathering on the compost fauna. The population of /

two types of calcareous soil has been studied by Schaller (1949), who found that, although most species were common to the two soil types studied, at least three in each soil type were not represented in the other, and quantitative differences were evident in some of the other species. Murphy (1955) has related qualitative differences in Collembola to a succession of mosses in bog.

The quantitative results obtained in the present work are somewhat smaller than those in some recent studies on Collembola. The samples however were not necessarily taken when maximum populations were expected. The density ranged from a mean of 7.4 individuals per 10 cm^2 in the September sampling of grass moorland to a mean of 28.1 individuals per 10 cm^2 in the January sampling. From the totals, the three sampling occasion means were obtained of 15.8 individuals per 10 cm^2 in bracken, 18.7 individuals per 10 cm^2 in grass moorland and 16.4 per 10 cm^2 in Meadow. Comparison with the results of other soil faunal researches is, of course, complicated by the effect of different extraction techniques, effect of seasonal and annual fluctuation and so on. The figures obtained by Macfadyen (1952), for example, using funnel technique to examine the populations under three types of gras

cover in fenland, were 25 individuals per 10 cm^2, 24 individuals per 10 cm^2 and 7.2 individuals per 10 cm^2 to a depth of 5 cm. These figures are means of 13 monthly samplings and are enhanced by very large numbers of a single species F. quadrioculata which was found as a minor constituent of the Milngavie populations. Salt et al (1948) used a flotation apparatus and in a sampling in November obtained numbers representing 43.1 Collembola per 10 cm^2 in their 6 inch deep samples; they considered that this was representative of the order of magnitude of populations in English meadows. Little evidence is available of the Collembolan population of other soil types in Britain, but Continental studies are available on the Collembola of woodland. Van der Drift's (1951) study of a beech forest floor is particularly interesting because it gives details of individual volume of species and thus allowed him to make biomass estimations. Details of the numerical results obtained and biomass estimates where available, in recent studies of various Biotopes are shown in Table 10. The results of many of the other continental studies, including those of Schaller (1949), are based on volume of sample without details of depth and cannot readily be transformed to compare with other /

Author	Biotope	Depth of Sample	Density (No./10 cm²)	Biomass (vol. mm³/50 cm³)	g./m²
(Salt et al 1948)	Pasture	6 inches	43.1	-	-
(MacFadyen 1952)	Fen (Molinia	5 cm.	25.0	1.40	14.0
	(Deschampsia	5 cm.	24.0	1.20	12.0
	(Juncus	5 cm.	7.2	0.34	3.4
(Van der Drift 1951	Beechwood	?(Humus layers) only	+41.0	2.43	-
(Sheals 1957)	Grassland	6 inches	22.8	-	-
(Milne)	(Bracken	10 cm.	15.8	*0.45	4.5
	(Grassmoor	10 cm.	18.7	0.60	6.0
	(Meadow	10 cm.	16.4	1.39	13.9

* upper 5 cms. only; + quoted by Van der Drift in MacFadyen (1952)

Table 10. Density and biomass of Collembola from various studies compared with the results of the present work.

The volume figures for fenland are transformed from mass figures, taking density as approx. as reported by MacFadyen in Murphy (1953).

results; but estimates calculated by Macfadyen give 15.9 and 25.0 Collembola per 10 sq. cm. for Schaller's (1949) investigations of calcareous soil types and 8.5 Collembola per 10 sq. cm. for Weis-Fogh's (1947) grass plain study. However, there would seem to be no conclusive evidence available at present to justify the conclusion that any particular biotope supports a much greater number of Collembola than others. In terms of biomass or volume of individuals, it is possible that differences may more easily be shown. The investigation by Weis-Fogh (1947) of the micro-arthropod fauna of seven vegetation types on permanent pasture showed a correlation between pore space and the size of micro-arthropods; this correlation he considered was dependent mainly on two factors. Smaller forms were found in soil with smaller pores in which they find protection from predators. Larger forms are unable to make use of small soil pores and are thus susceptible to desiccation in conditions of low humidity. These larger forms were found by Weis-Fogh (1947) to be largely confined to places with dense vegetation which afforded some protection from /

low humidity in dry weather. At Milngavie, the meadow appears to offer more suitable micro-environmental conditions for larger forms than the other two biotopes, which support a much smaller volume of Collembola.

The vertical distribution on Collembola in relation to morpho-ecological characters has been studied by Gisin (1943) who found that these insects could be separated into three groups on the basis mainly of morphological characters, such as development of the eyes and pigmentation. The Euedaphic or true soil dwelling types in this classification include most of the Onychiuridae and Tullbergidae. Inhabitants of the surface and upper soil layers or Hemiedaphon include most of the pigmented Arthropleone types and the third or Atmobios group is represented by Collembola largely independent of the soil and living mainly on macroscopic plant material. The vertical distribution of the species found at Milngavie are largely in agreement with this classification. T. krausbaueri, a typical euedaphic species, was found concentrated in the lower 5-10 cm. samples. The Onychiurids present were found either in the upper 0-5 cm. samples as in O. uliginatus or distributed between the two sampling levels as in O. procampatus. F. fimetaria was /

distributed evenly between the two layers but F. candida was more abundant in the upper layers. Of the supposed hemiedaphic types only F. mirabilis was not concentrated in the upper layers and showed an even vertical distribution. Investigations of the vertical distribution in the various humus and soil layers have been conducted by Schaller (1949). In his Rendzina samples Onychiurus armatus and T. krausbaueri were concentrated in the F or raw humus layer, but the brown earth soil fauna had a concentration of O. armatus and T. krausbaueri in the B or true soil horizon. Strenzke (1949) in his study of damp meadow soils found O. armatus and T. krausbaueri in the deeper layer. F. mirabilis was found at both levels studied, but upper dwelling individuals had darker pigmentation. F. fimetaria is considered a deep soil dweller by Strenzke but he found that other Folsomia spp. were more evenly distributed. Van der Drift (1951) found in the beech forest floor that O. armatus had greatest density in the Fx. humus layer. Volz (1934) in his study of forest soil found O. armatus and T. krausbaueri in deeper layers.

Glasgow's (1939) study of grassland at Slough shows a higher concentration of O. armatus and T. krausbaueri in /

the top 4½ inches of soil. O. ambulans and T. quadrispina were more abundant in deeper soil. MacFadyen (1952) reported a greater concentration of T. krausbaueri and O. armatus in 5 - 10 cm. layer in fenland, whilst Sheals' (1957) grassland figures indicate a greater abundance of Onychiurus spp. in a 3 - 9 in. stratum than in 0 - 3 in. (0 - 7.6 cm. approx.) stratum but also show greater density of T. krausbaueri in the upper layer. Weis-Fogh (1947) found a relationship between depth distribution and soil grain size. Species, commonly regarded as surface living, were found at lower levels in larger grain soils, thus minimising the distinction between euedaphic and hemiedaphic groups. There appears also to be some seasonal effect on vertical distribution. This forms a reasonable explanation for apparent inconsistency in reports of depth distribution without invalidating the fundamental morpho-ecological classification in terms of vertical distribution.

Summary

1. The Collembolan populations of three adjacent areas showing successive change in vegetation and soil type have been estimated and compared from a series of three samplings of each area.

2. Qualitative differences in the species composition were marked; several species in meadow appeared to replace species found only in bracken and grass moorland. Previous records of species distribution are discussed and also the possible indication of soil condition by Collembola.

3. The species composition of the hemi-edaphic Collembolan fauna of grass moorland was found to agree with B. parvula synusia of Gisin.

4. Numerical differences in the comparison of total Collembola from the three sampling sites were in all cases not statistically significant.

5. Biomass estimation was attempted by direct measurement and calculation of volume. The volume of Collembola from the meadow was considerably greater than from the other two biotopes.

6. The depth distribution of the various species was examined and agrees generally with previous findings.

C. Phenology of a population of soil Collembola under bracken Pteridium aquilinum (L.) Kuhn.

Description of sampling area and methods.

The results on which this investigation is based were obtained by sampling eight rectangular plots measuring 6 feet by 3 feet laid out as shown in Fig. 3. The plots are situated on an area of moor with a cover of bracken Pteridium aquilinum (L.) Kuhn near Milngavie previously described in the comparative study. Paired samples were taken at random from each plot at two-monthly intervals from December 1955 until October 1957 with the exception of the period April to June 1957 when observations were made each month. The samples of 10 $cm.^2$ surface area and 5 cm. in depth were taken in aluminium cylinders and placed in polyethylene bags for transport to the laboratory. An upper litter and raw humus sample and a lower true soil sample was obtained from each of the paired sampling sites in each plot. Extraction of Collembola from the upper samples was carried out by the funnel method and from the lower samples by flotation. Subsequent treatment for identification and counting of individuals has already been described. The size of individuals of various species was obtained by direct measurement. /

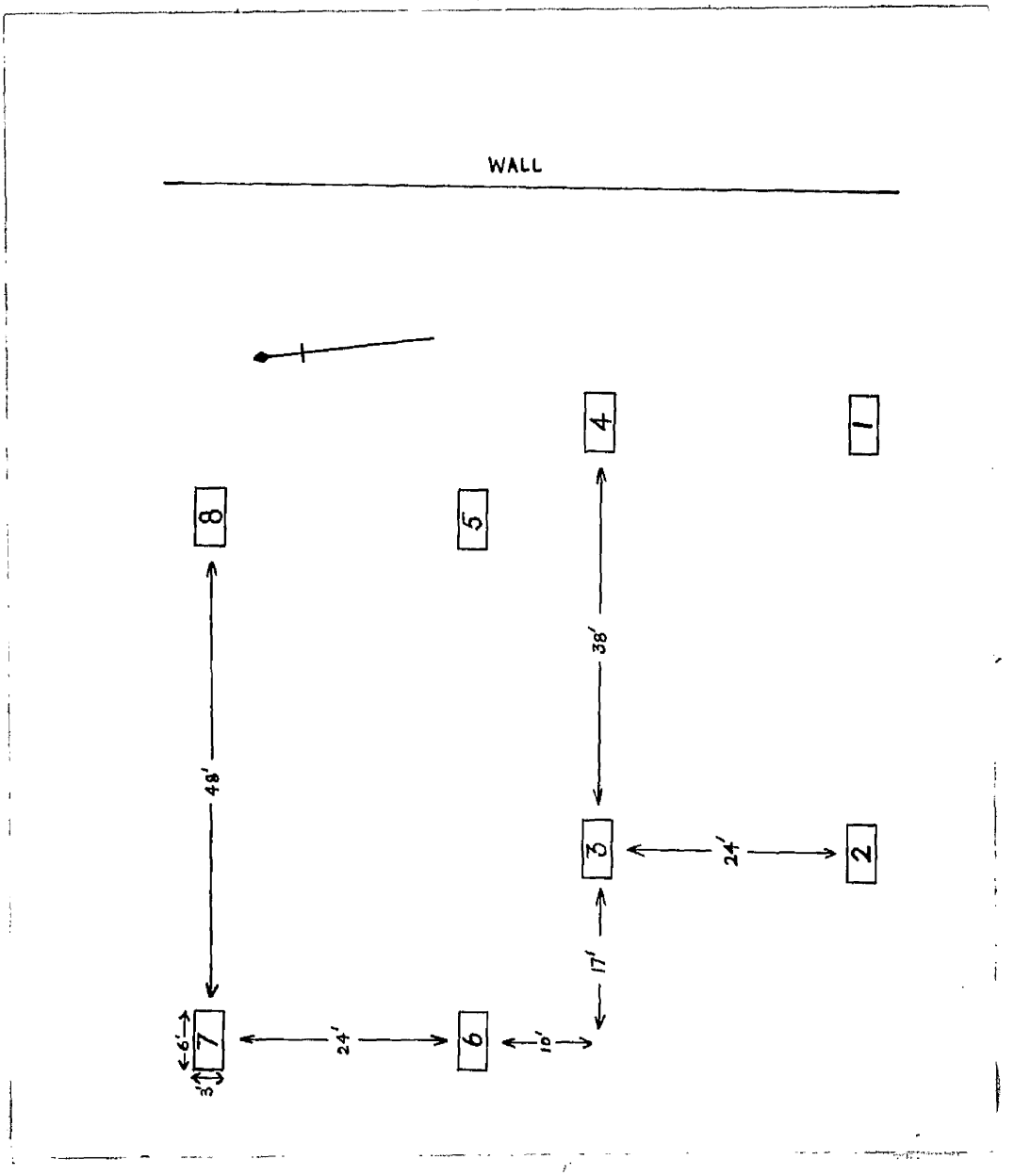


Fig. 3. Phenological study - lay-out of sampling plots.

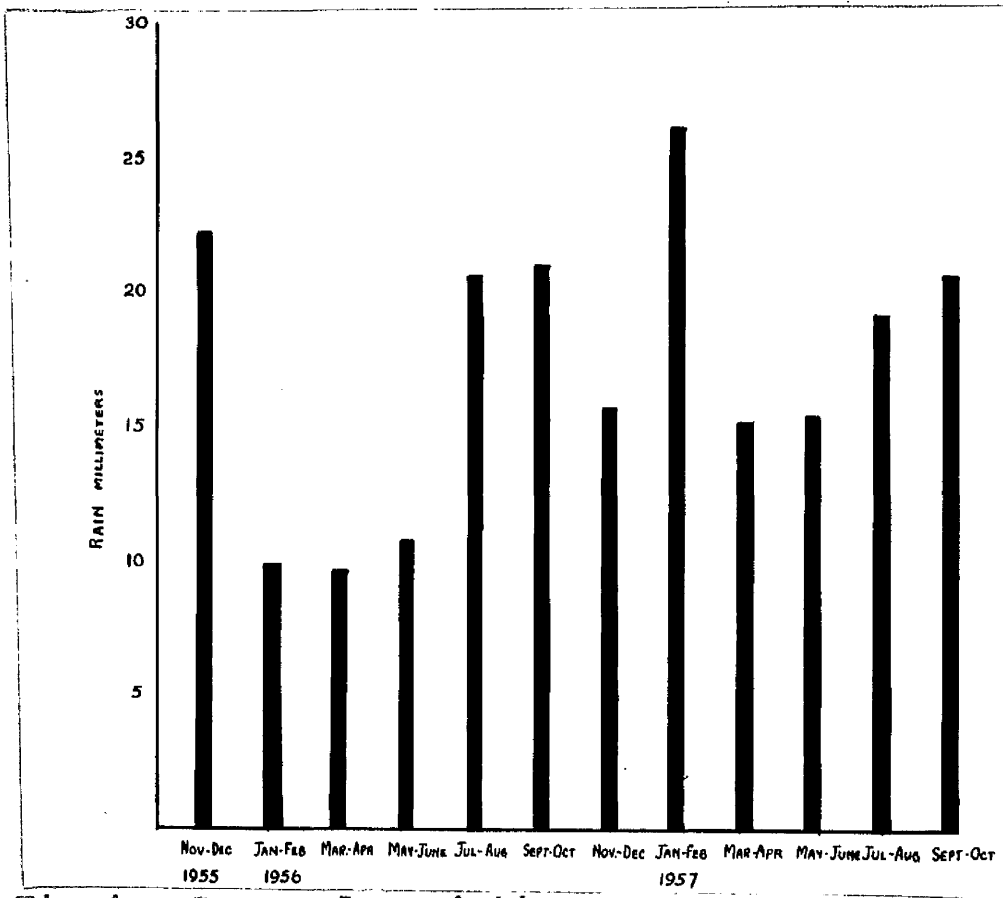


Fig.4. Seasonal variation : Average weekly rainfall during periods preceding sampling.

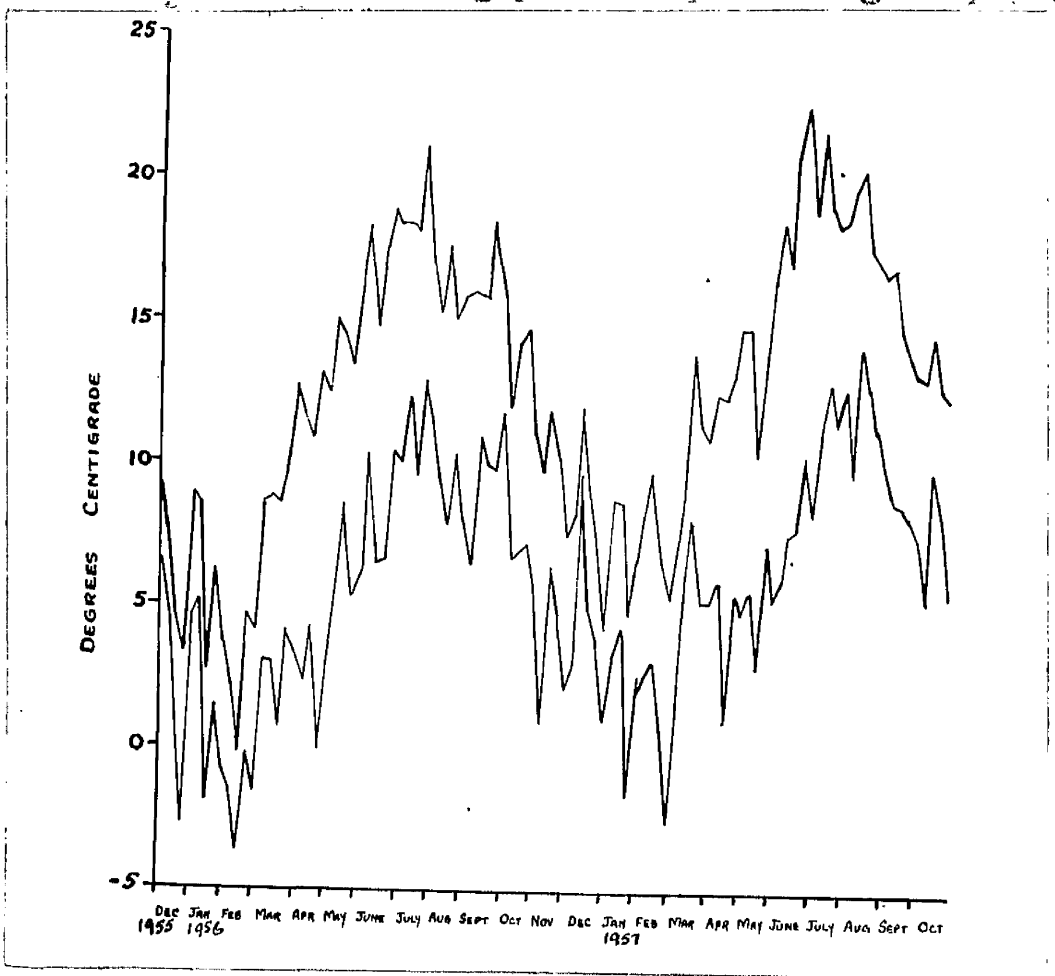


Fig.5. Seasonal variation : Mean maximum and minimum air temperature during sampling period.

Records of air temperature and rainfall during the period of the investigation were obtained from the Meteorological Office at Renfrew and are shown graphically in Fig. 4, 5. Renfrew is situated at sea-level about four miles south of the sampling site which is 350 ft. above sea-level approximately. The figures are not intended as an accurate guide to conditions prevailing at the sampling site at a particular time but as an indication of the fluctuation in weather conditions during the period of investigation. The water content of the upper samples taken from each plot during the period April - August 1957 was found by air-drying the samples at 100°C. The mean water content expressed as percentage of initial sample weight is shown in Table 13.

Statistical treatment of the results was carried out by the analysis of variance technique with initial square root transformation of the raw data. This procedure was necessary because of the non-random distribution of the population. The degrees of freedom in relation to variation in time, plots and depth were allocated as shown below.

		df.
	Times	12
	Plots	7
	Depth	1
1st order interaction	(Times/Plots	84
	(Times/Depth	12
	(Plots/Depth	7
2nd order interaction (error)		84
	Total	207

Results

The species composition of the fauna and the fluctuations in proportions of various species are shown in Tables 3 and 11. The Collembola in individual samples is shown in Appendix 2. On most occasions the fauna is dominated by the species Onychiurus procampatus Gisin and Tullbergia krausbaueri (Boern.), the combined population of which formed more than 50 per cent of the total on all but three occasions. The proportions of the minor members of the fauna varied from time to time.

The fluctuations in the total population and in various species is shown in Fig. 6-15, which are based on the numbers obtained from all 16 samples covering a total area of 160 cm.^{2} on each sampling occasion.

	1955	1956					1957						
	Dec.	Feb.	Apl.	June	Aug.	Oct.	Dec.	Feb.	Apl.	May	June	Aug.	Oct.
Tullbergia krausbaueri	19.9	28.5	28.6	24.5	19.4	12.1	27.2	30.0	31.1	22.1	20.1	14.7	21.7
Onychiurus procampatus	27.0	21.8	29.8	33.4	35.2	41.2	31.9	31.8	32.2	43.3	46.0	18.0	23.2
Folsomia candida	18.4	18.8	17.9	2.2	5.5	1.5	4.3	5.0	4.8	3.3	6.9	4.8	2.4
Folsomia quadrioculata	5.7	4.8	7.1	5.9	3.2	6.0	5.2	3.5	6.3	10.0	12.1	2.9	3.5
Folsomia manolachei	9.9	3.0	0	4.8	2.6	4.0	5.2	8.5	9.3	6.7	3.1	10.6	11.4
Isotoma viridis	3.5	2.4	3.6	7.3	1.1	6.5	0.2	.6	1.1	1.8	2.1	5.5	8.3
Friesea mirabilis	5.0	3.0	2.4	2.1	2.9	1.0	0.7	.9	2.2	0	1.4	2.6	3.2
Brachystomella parvula	0	0.6	0	1.6	0.7	1.0	2.4	3.2	1.1	2.1	.7	8.8	9.8
Sminthurides schötti	0	0.6	0	4.8	12.1	14.1	16.3	8.5	5.2	4.2	2.8	4.3	11.0

Table 11 : Percentage species composition of population in seasonal samples.

The results of statistical analyses are shown in Tables 12, 13 and 14. Individual measurements of length of the members of certain species were also obtained and the mean length and distribution of size groups is shown in Fig. 16 - 19. Of total Collembola obtained in the samples (Fig. 6) the maximum populations occurred in June and December 1956 and May 1957. The lowest populations were found in April and October of both 1956 and 1957. The numbers obtained in the sampling ranged from a minimum of 84 per 16 samples, equivalent to a population of 5.3 Collembola per 10 cm^2; in April 1956, to 423 individuals per 16 samples or 26.4 individuals per 10 cm^2 in December 1956. The very low population at the beginning of the sampling period was associated with abnormal drought conditions for some months previous to the sampling period. The variation in total Collembola was statistically significant at the 0.001 level of probability. (F-value 8.43 d.f.; n1-12,n2-84).

The populations of O. procampatus and T. krausbaueri Fig. 7 and 8 show fluctuations similar to that shown /

	1955	1956						1957							F Times	F Times/Plots	F Times/Depth
	Dec.	Feb.	Apl.	June	Aug.	Oct.	Dec.	Feb.	Apl.	May	June	Aug.	Oct.	F Times	S.E.	Plots	Depth
Total Collembola	46.8	50.1	36.2	74.2	62.2	52.1	80.4	67.4	62.6	67.1	65.6	64.2	61.7	8.43	2.88	1.45	2.72
Sellbergia krausbaueri	24.7	28.2	24.1	39.1	31.4	24.3	41.4	35.8	35.0	34.1	31.4	28.8	30.6	2.96	2.26	0.92	2.44
Onychiurus procampatus	26.2	27.2	25.0	43.4	38.4	37.1	45.8	40.7	39.1	44.1	46.1	30.1	32.2	6.24	2.15	0.14	3.67
Folsomia candida	25.3	26.6	21.7	19.1	22.9	17.2	22.5	21.2	20.3	19.6	22.3	21.0	18.4	3.23	1.02	0.85	3.00
Folsomia quadriculata	18.5	18.8	18.2	22.6	18.9	20.0	22.7	20.0	21.1	25.2	26.3	19.2	19.4	2.15	1.26	1.20	0.85

Table 12: Seasonal Totals of Square root transformed data and statistical analysis.

84 degrees of freedom $\sqrt{2}$ t : = P0.05, 2.82; P0.01, 3.72: P0.001, 4.82

Interection: Times/Plots - F values, d.f.n. = 84, n_2 = 84 P0.05, 1.35 : P0.01, 1.50.

Times/Depth - F values, d.f.n. = 12, n_2 = 84 P0.05, 1.88 : P0.01, 2.42.

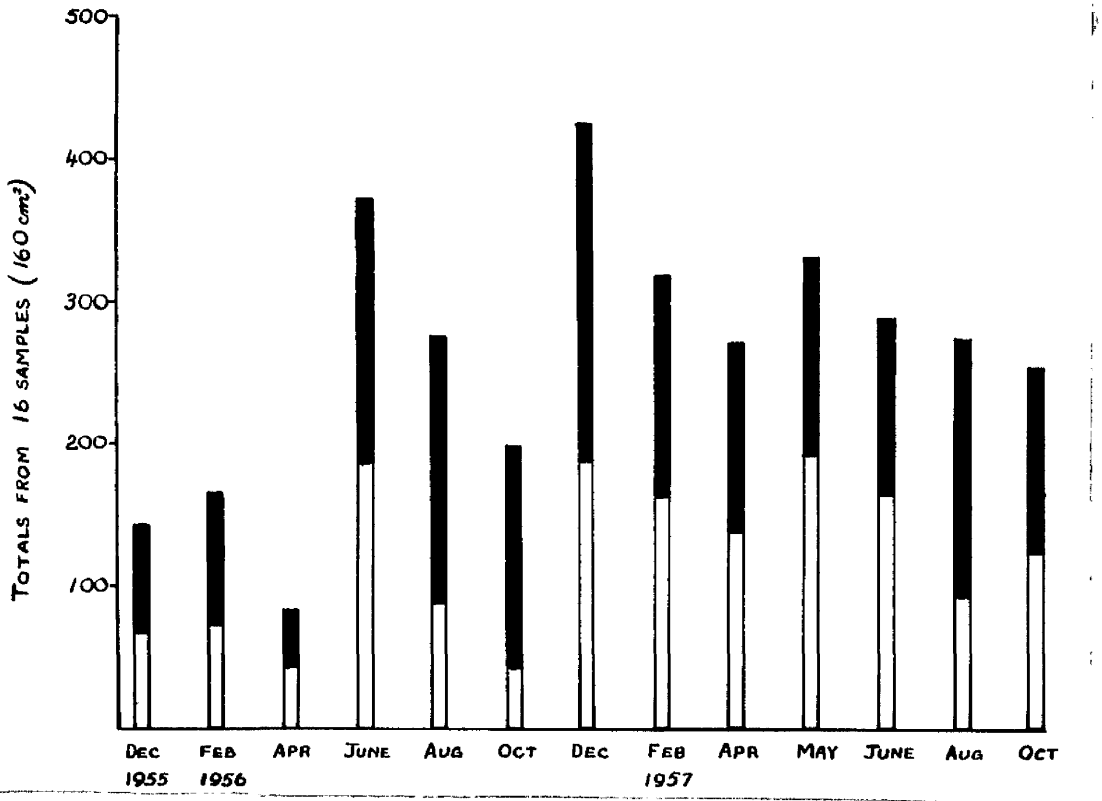


Fig.6. Seasonal variation ; Total Collembola obtained from samplings - upper samples black.

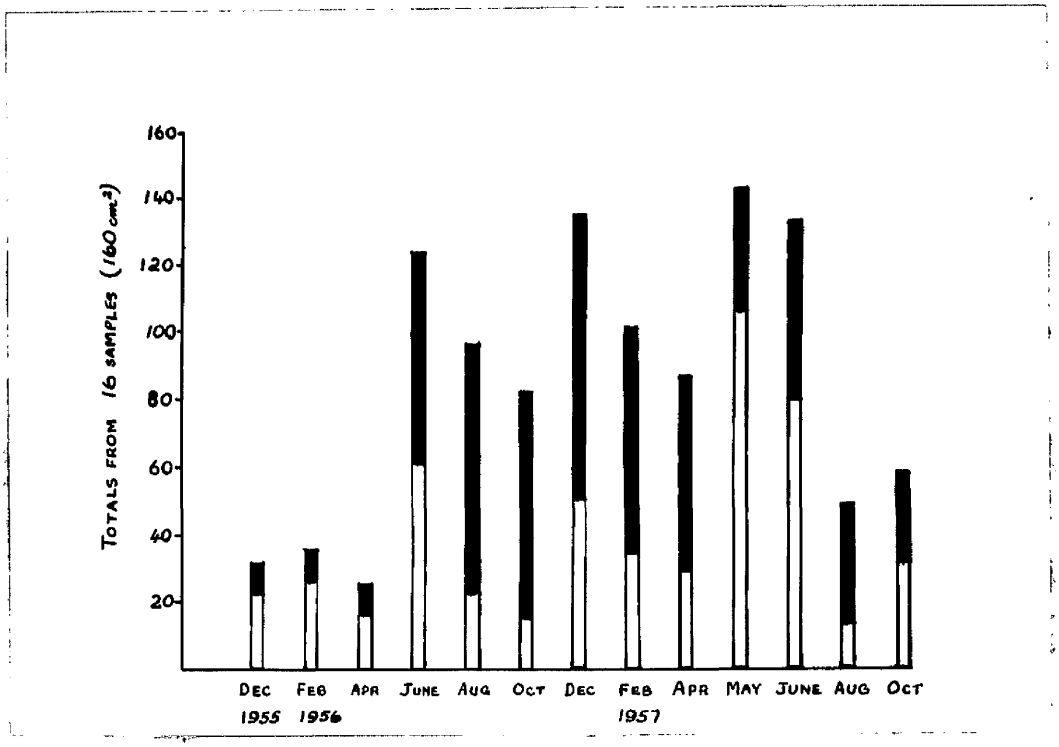


Fig.7. Seasonal variation : Number of O. procampatus obtained from samplings - upper samples black.

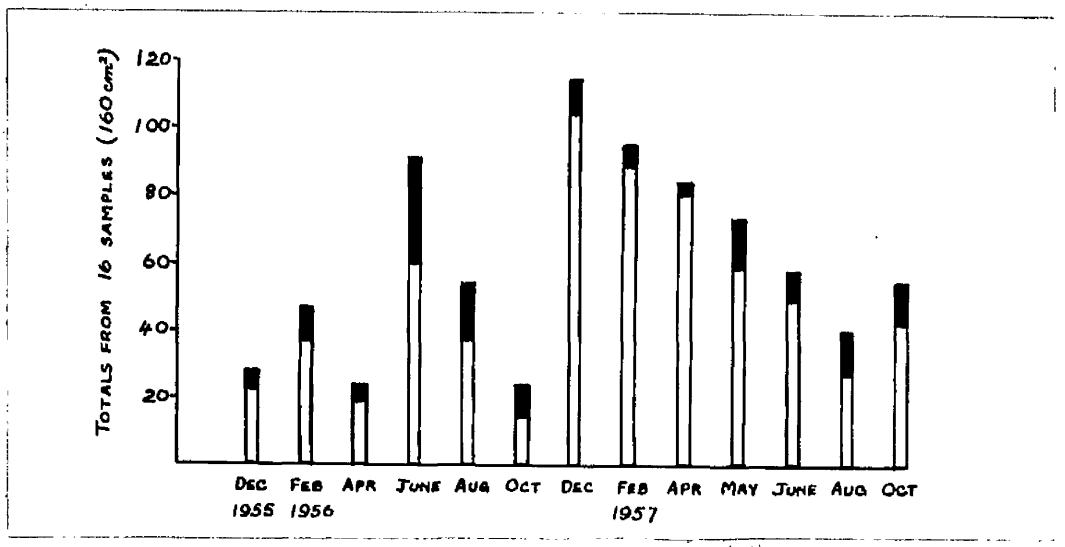


Fig.8. Seasonal variation : Numbers of T. krausbaueri obtained in samplings - upper samples black.

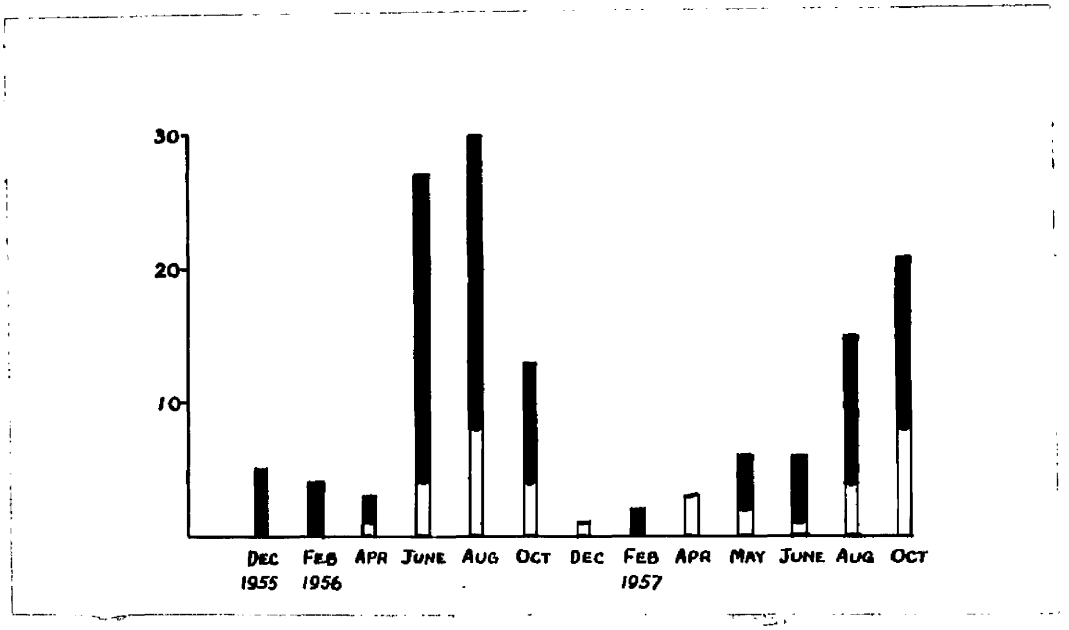


Fig.9. Seasonal variation : Numbers of I. viridis obtained in samplings - upper samples black.

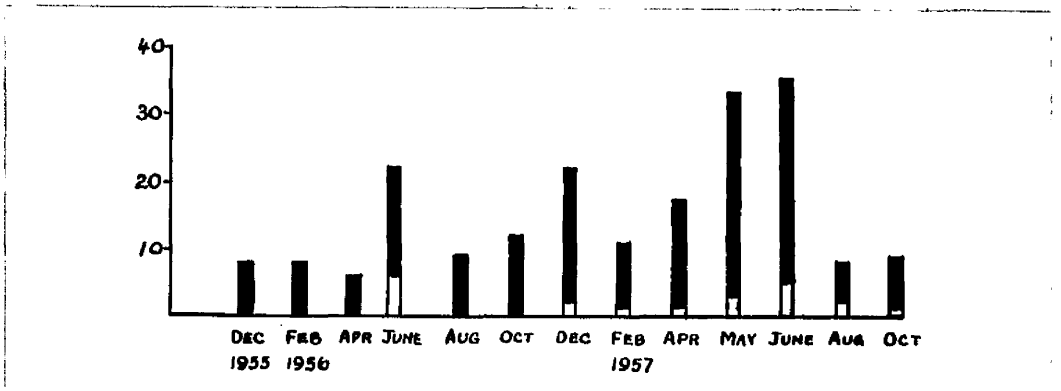


Fig.10 Seasonal variation : Numbers of F. quadrioculata obtained in samplings - upper samples black.

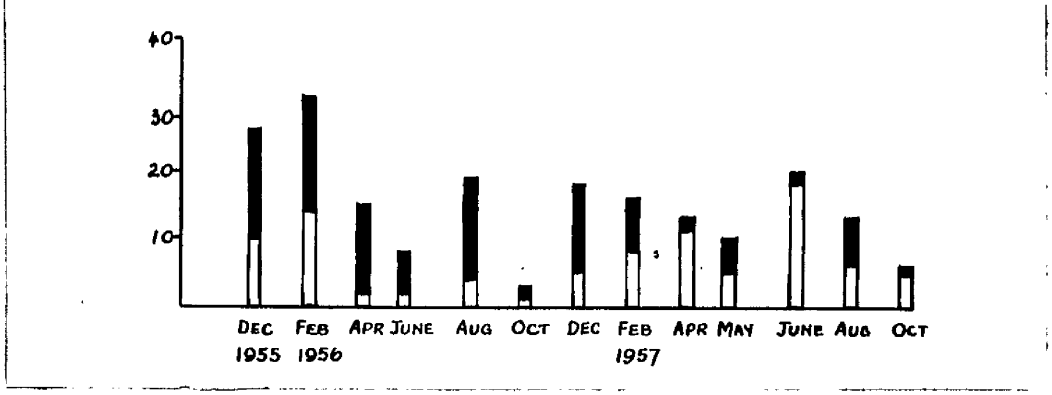


Fig. 11 Seasonal variation : numbers of F. candida obtained in samplings - upper samples black.

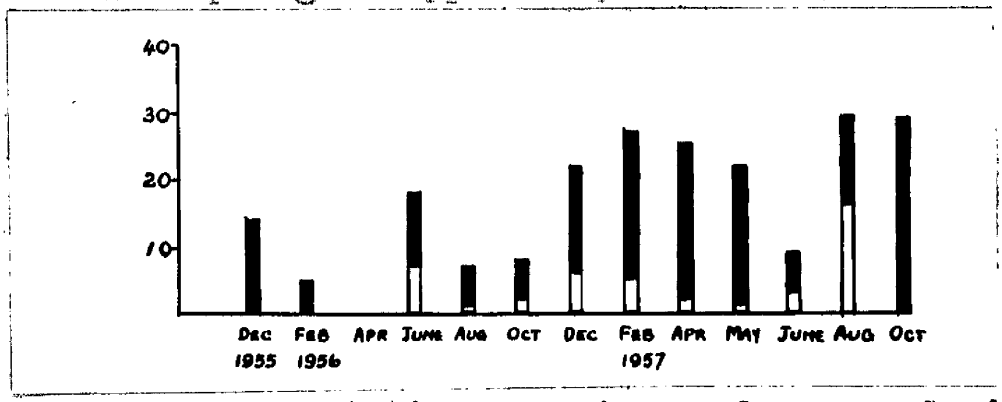


Fig. 12 Seasonal variation : Numbers of F. manolachei

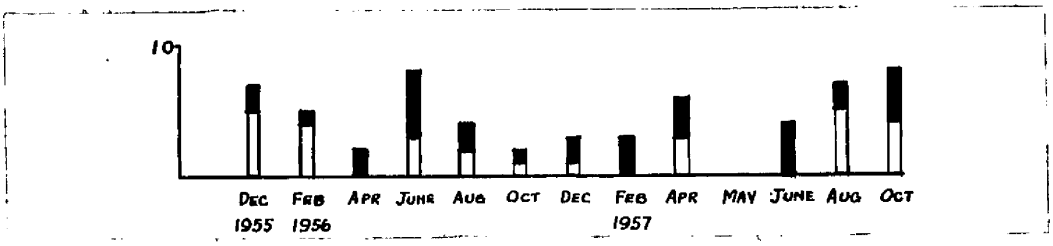


Fig. 13 Seasonal variation : Numbers of Friesea mirabilis

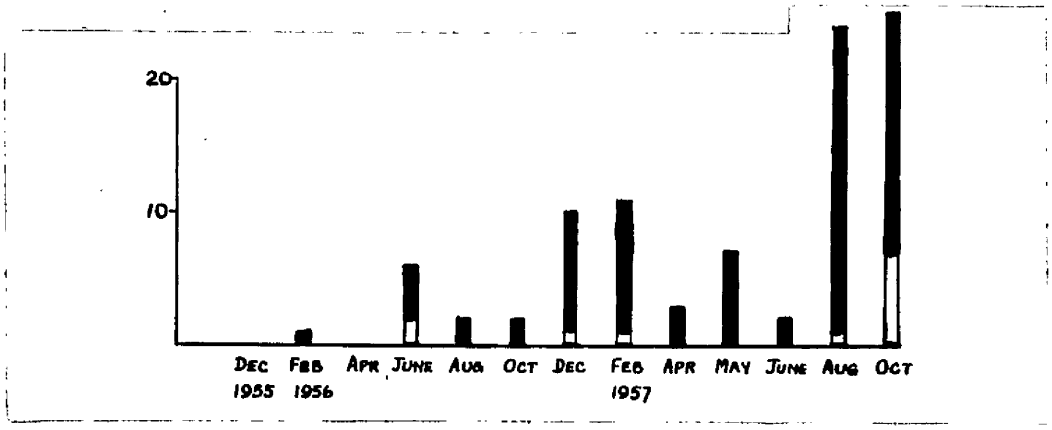


Fig. 14 Seasonal variation : Numbers of B. parvula

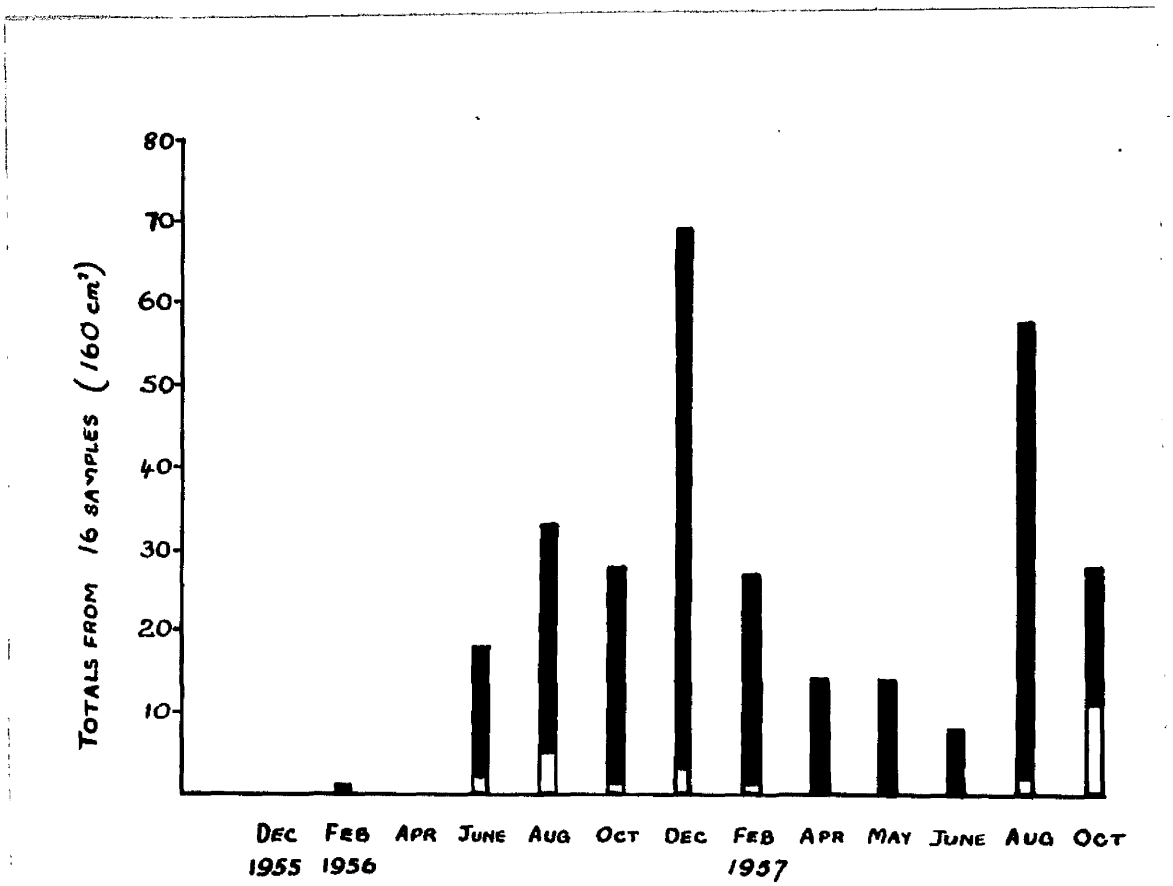


Fig.15. Seasonal variation : Numbers of S. schötti obtained in samplings - upper samples black.

by the total population and are largely responsible for the pattern shown by the total. Examination of size distribution(Fig.16, 17) confirms that the maxima coincide with abundance of young individuals. The analysis of variance of O. procampatus shows significance in time at the .001 probability level (F-value 6.24, df.; n1 - 12, n2 - 84) that of T. krausbaueri shows significance at the .01 probability level. (F-value 2.96, df.; n1 - 12, n2 - 84).

The fluctuation of Isotoma viridis shown in Fig. 9 is of a different pattern. In 1956 maximal population occurred in June and August. After August the population rapidly declined until subsequent increase in May 1957. The age distribution of this species (Fig.18) shows that over-wintering individuals are fully grown; increase in numbers in early summer is shown typically by a large number of small individuals. The population of Folsomia quadrioculata (Fig.10) had well defined maxima in June and December in 1956 and also in June 1957 but in F. candida (Fig.11) and F. manolachei (Fig.12) the trends were not as consistent. Friesia mirabilis (Fig.13) showed maxima in December 1955, June 1956 and April and October 1957. /

The variation in Brachystomella parvula (Fig.14) was exceptional in that very low populations were observed in the earlier samples with subsequent maxima in June 1956, December 1956 - February 1957 and May 1957 but exhibiting a marked increase in the last two samplings in August and October 1957.

Depth distribution and vertical migration

The total population of Collembola in the upper samples was significantly larger than in the lower(Table 14). The analysis of the results for four species T. krausbaueri, O. procampatus, F. candida and F. quadrioculata gave statistical significance for depth distribution in all except F. candida which was evenly distributed between the two sampling levels. Of the other species only T. krausbaueri was more abundant in the lower than in the upper samples.

The interaction term Times/Depth in the analysis (Table 12) gives a measure of the change in vertical distribution during the sampling period. For the total population this term was significant at the 0.01 probability level, and considering individual species O. procampatus was highly significant at the .001 probability level, T. krausbaueri and F. candida at the 0.01 level. The population of F. quadrioculata did

not show any significant change in depth distribution./

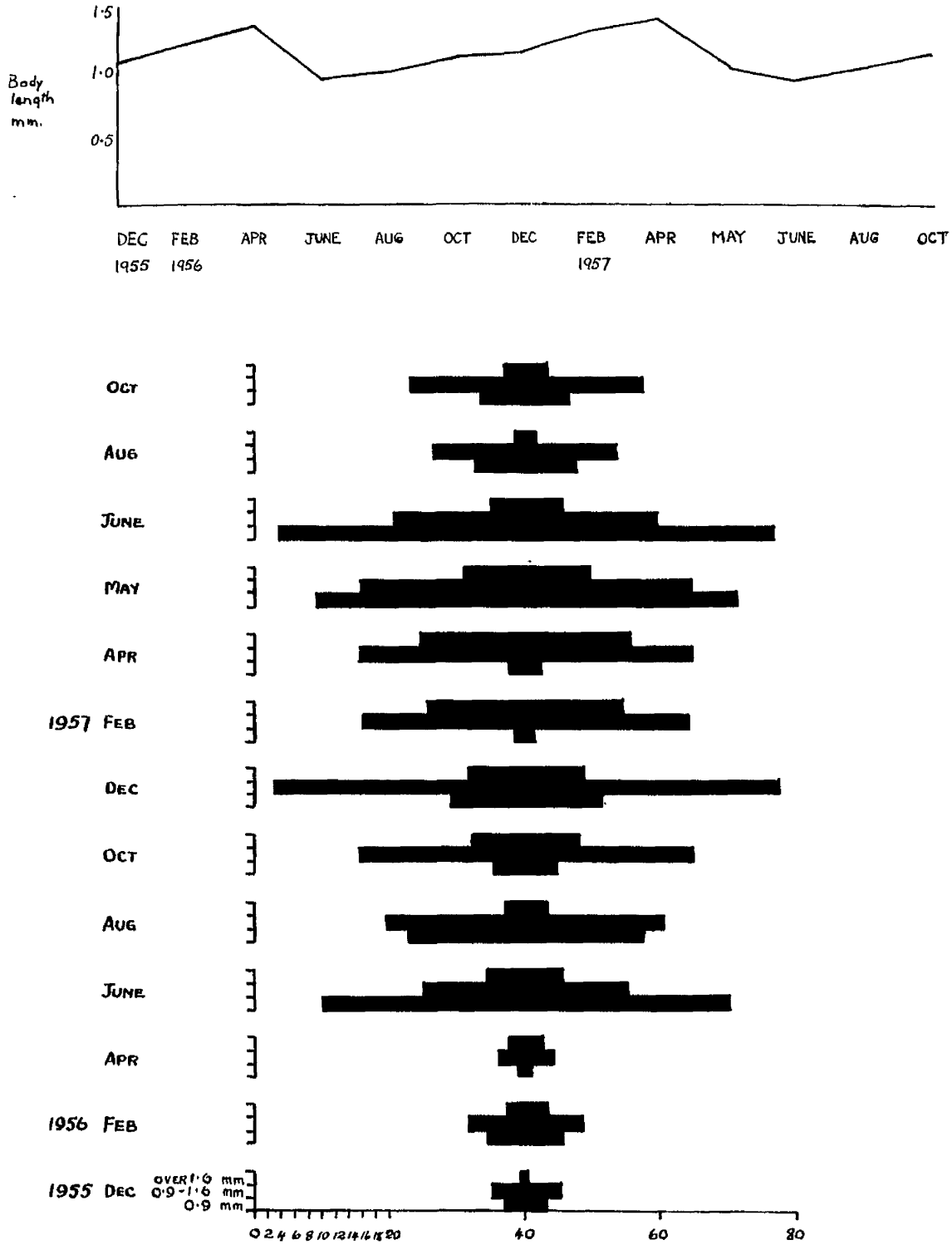


Fig. 16. Seasonal variation : O. procampatus - mean individual body length and number of individuals in arbitrary size groupings.

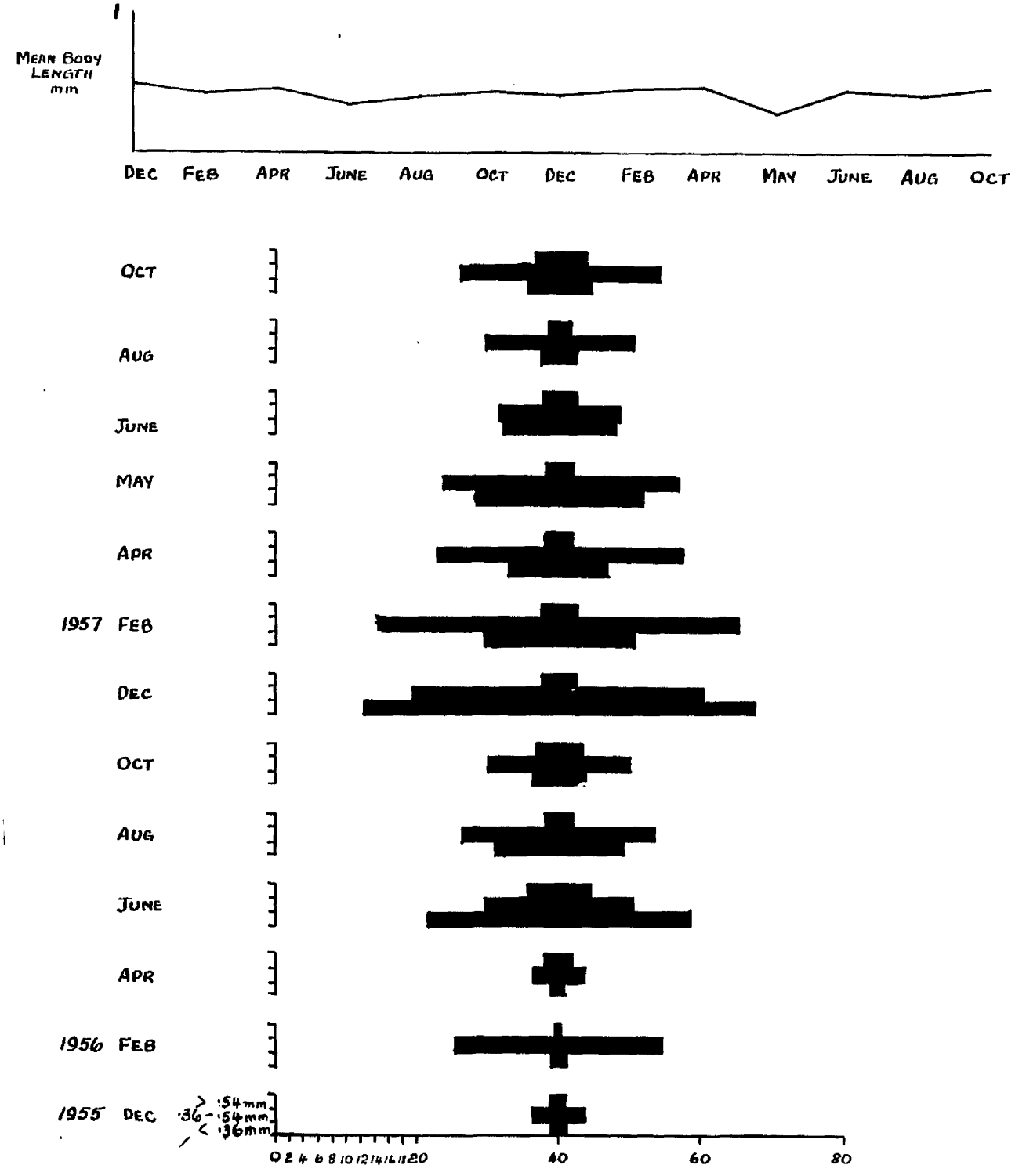


Fig. 17. Seasonal variation : T. krausbaueri - mean individual body length and number of individuals in arbitrary size groupings.

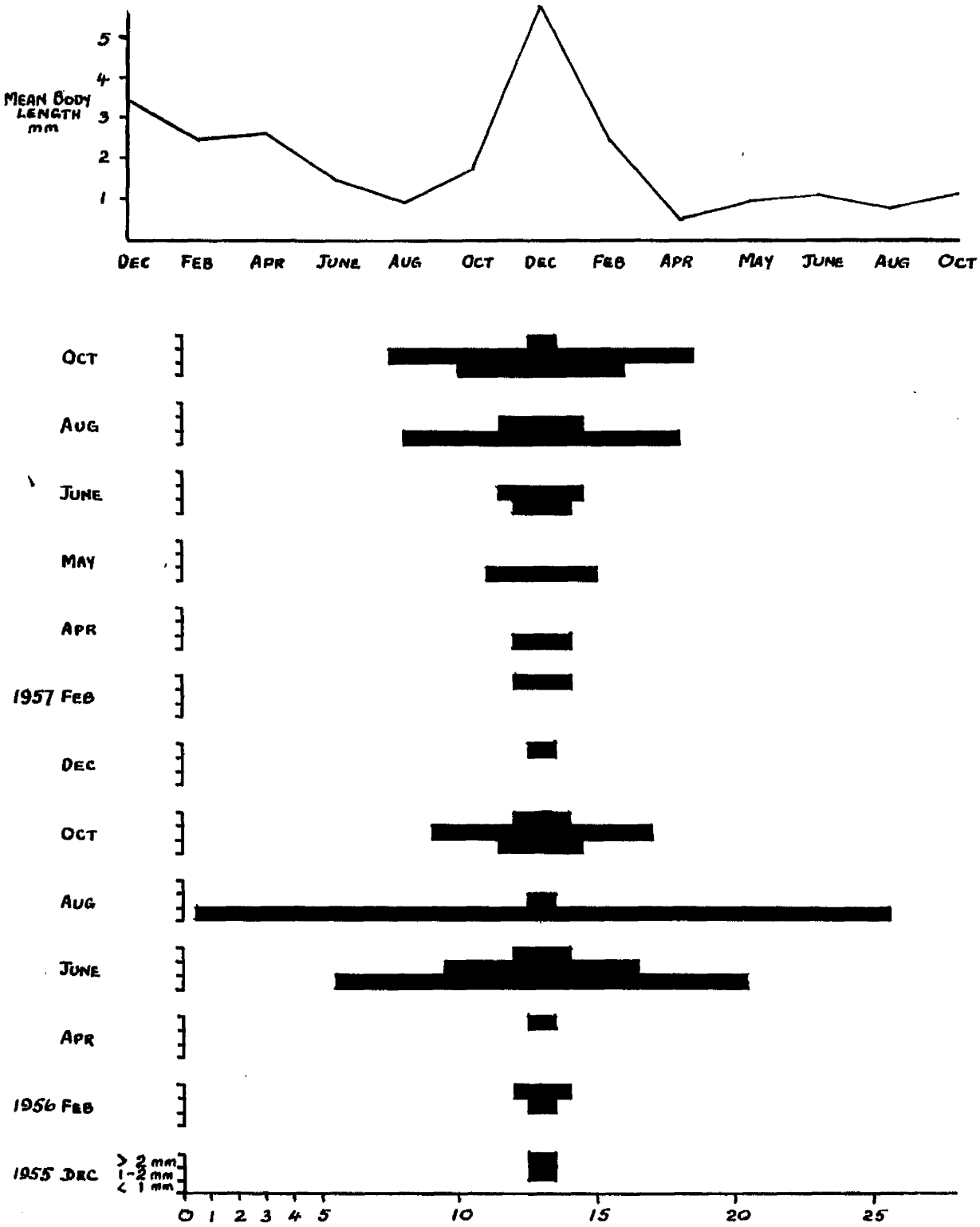


Fig. 18. Seasonal variation : I. viridis Mean individual body length and number of individuals in arbitrary size groupings.

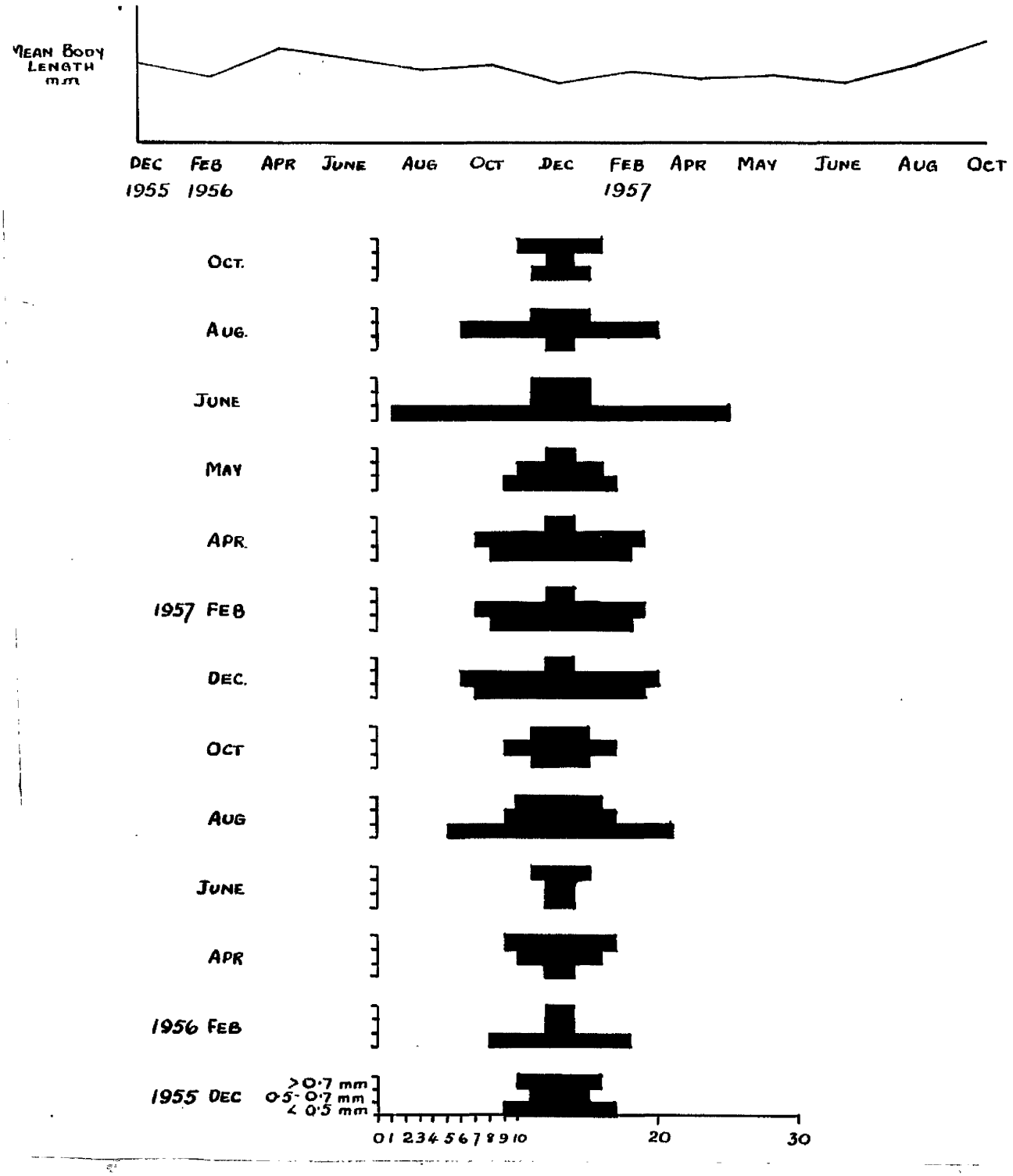


Fig. 19. Seasonal variation : F. candida - mean individual body length and number of individuals in arbitrary size groupings.

	I	II	III	IV	V	VI	VII	VIII	F plots	S.E.	F Plots/Depth
Total Collembola	95.7	89.5	96.7	97.5	107.6	88.8	104.6	110.9	2.39	3.65	1.42
Bulborgia Krausbaueri	46.2	45.5	49.7	51.5	52.8	51.1	55.5	56.6	0.94	-	0.73
Onychiurus procampatus	57.6	47.9	54.7	68.2	70.3	54.7	54.9	67.3	4.48	2.73	2.74
Folsomia candida	36.5	35.3	34.1	33.2	38.4	34.9	35.4	31.2	1.38	-	2.46
Folsoma quadrioculata	32.4	33.3	36.5	29.4	33.9	32.8	34.6	37.8	1.30	-	0.90
Mean water content of samples (% age)	42.5	56.3	47.7	43.9	43.7	49.2	48.8	52.7			

Table 13. Plot totals of square root transformed data and statistical analysis with mean water content of samples from each plot.

* 84 degrees of freedom. F2: = 20.05, 2.82: 20.01, 3.72: 20.001, 4.82

Interaction: Plots/Depth. F values d.f.= 7 n2 = 84 20.05, 2.15. 20.01, 2.86

	Relative density in upper samples (density in lower = 100)	F.
Total Collembola	109.8	6.27 *
Tullbergia krausbaueri	59.3	82.20 * * *
Onychiurus procampatus	110.5	4.67 *
Folsomia candida	105.4	1.92
Folsomia quadrioculata	142.4	53.95 * * *

Table 14: Vertical distribution over 13 sampling occasions - square root transformed data.

Degrees of freedom $n_1 = 1$ $n_2 = 84$

Levels of significance * P0.05 * * * P0.001.

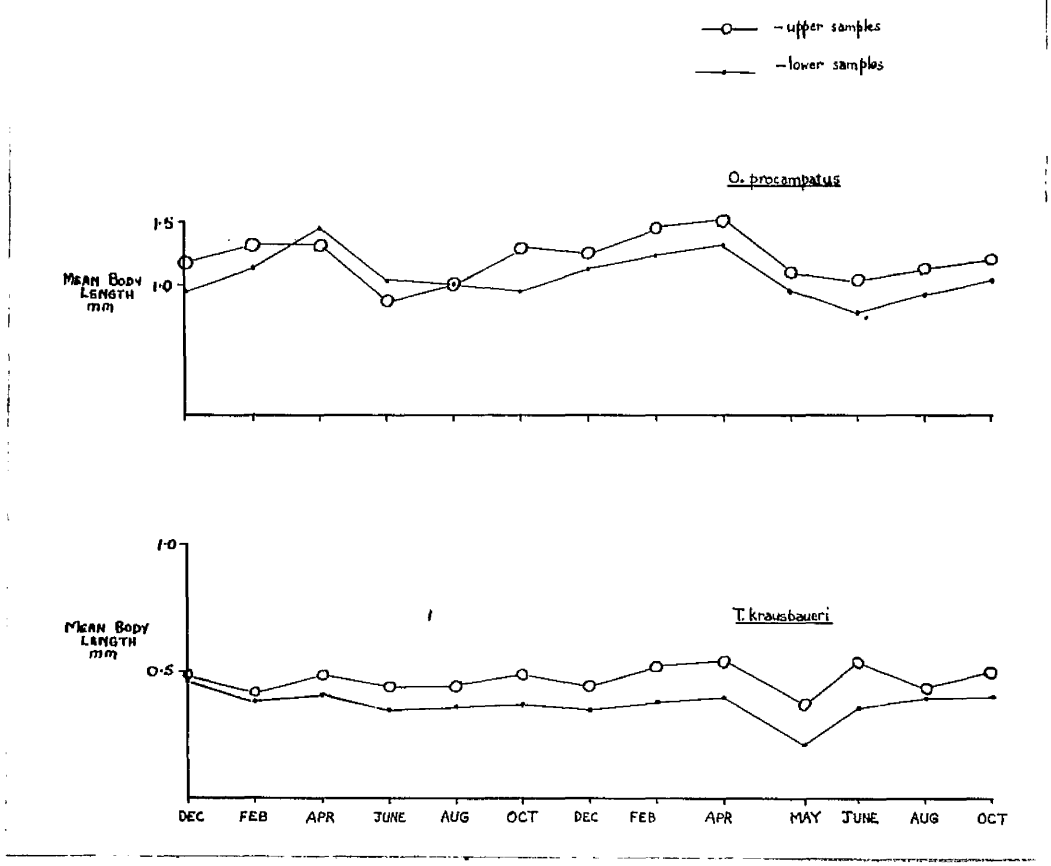


Fig. 20. Seasonal variation : Mean individual body length of two species in upper and lower sampling layers.

The main change in vertical distribution is shown as increase in the population occurring in the lower layers coinciding with increasing population. There is a tendency for concentration of smaller individuals in the lower layers. The mean lengths of individuals of O. procampatus and T. krausbaueri from upper and lower sampling layers are shown in Fig.20.

Plot Differences.

In the analysis of total numbers of Collembola obtained from each plot (Table 13) three significant differences were observed. In the analysis of individual species, however, only in the case of O. procampatus were significant differences found between plots. In plots IV, V and VII the number of individuals of O. procampatus was significantly higher than the yield from the other five plots.

In the interaction term times/plots, significance at the 5% probability level was found only in the analysis of total Collembola. No significance was found in the analysis of individual species showing that seasonal trends were consistent throughout all plots.

The results obtained from the interaction term plots/depth is interesting. This measures the extent /

to which the vertical distributions of the animals are consistent in all eight plots. Differences in both O. procampatus and F. candida were found to be significant at the .05 probability level.

The distribution of age groups shows a typical concentration of young forms coinciding with population maxima. Decrease of the base of the age-group pyramid with decreasing population can be seen. High mortality of younger forms occurs. This results in very small winter populations of I. viridis consisting of large individuals. In the species T. krausbaueri the occurrence of young forms in May 1957 is not coincident with a marked peak in population size but, nevertheless, indicates a new generation.

Other Apterygota.

Specimens identified as Campodea staphylinus (Westw.) (Diplura) and Eosentomon armatum Stach (Protura) were obtained in the samples. The populations represented were too small, however, to justify an account of their phenology.

Discussion

Seasonal fluctuation

The variation in seasonal abundance of the soil fauna, including Collembola, has been the subject of several investigations in Britain. In a series of studies, Ford (1935, 37, 38) showed that in grass-land and, particularly, in tussocks of Bromus, population maxima of Collembola tended to occur in winter. In one of these investigations (Ford 1938) is one of the few records of age or size distribution of a natural population of a Collembolan species. Ford (1938) found that the age variation of individuals of Pseudachorutes subcrassus Tullb. decreased with increasing numbers. The investigation of Glasgow (1939) was concentrated on four species Onychiurus armatus Tullb., O. ambulans (L.), Tullbergia quadrispina Boern. and T. krausbaueri (Boern). Glasgow's (1939) results showed that the populations of O. armatus and O. ambulans had distinct maxima in winter and all species were at a minimum in April of one year. This minimum was related by Glasgow to exceptionally cold climatic conditions. At Slough T. quadrispina had a maximum in May whereas T. krausbaueri had a more uneven fluctuation with peak populations every four months. Glasgow also reported a positive correlation with moisture for the population of O. armatus in the wet season and for O. ambulans in the dry season. /

Baweja's (1939) study of the effect of sterilisation of the soil on the fauna included details on seasonal fluctuation, with a tendency to maxima in late autumn and early winter. In the more recent and detailed study by Macfadyen (1952) it was found that in fen-land a maximum occurred in winter and minimum in August. A smaller increase in May was suggested as being related to relatively larger numbers of young individuals. The fluctuation in numbers of all species of Collembola coincided in Macfadyen's (1952) study. Continental studies of seasonal abundance of Collembola do not usually show the same type of fluctuation apparently common in this country and such differences are perhaps to be expected where more extreme climatic conditions are encountered. For example in Greenland as reported by Hammer (1944), the extreme low temperature for a large part of the year results in a short active breeding season in summer. Agrell (1941), in his study of Collembola of Swedish Lappland, agrees that under these conditions only one or, at most, two generations occur in one year. Both Agrell (1941) /

and Hammer (1944) found a periodicity in the occurrence of different species after winter. In a study of wet habitats in Germany, Strenzke (1949) found seasonal maxima in autumn which he considered are related to moisture conditions and abundance of organic food material in the form of plant litter; low populations in July and August he relates to dry conditions. Differences in the occurrence of increases of the populations of different species was found. T.krausbaueri had a peak population in October, F.quadrioculata in November and F.mirabilis in February. Schaller (1949) found little evidence of seasonal fluctuation in Collembolan populations but there is evidence of maximum population in late autumn and early winter. In a study of a beech forest floor Van der Drift (1951) found maximum population in summer and minimum in winter.

The results of the present study agree with the well substantiated evidence of winter maxima of population of Collembola in this country. The periodicity of population maxima shown by Glasgow (1939) agrees closely with the results from Milngavie, particularly in the case of T.krausbaueri. The study

of age distribution, as suggested by Agrell (1941), is important in showing the occurrence of new generations, particularly where numbers do not indicate this. This is shown by the age distribution of T. krausbaueri in the present study. The interaction of various climatic factors appears to result in producing suitable micro-climatic conditions for reproduction. The difference in optimal conditions required for various species of Collembola and the length of post-embryonic development before maturation are, together, responsible for differences in phenology. The results obtained in the investigation of seasonal variation in places with widely differing climatic conditions and from various biotopes in which different micro-climatic effects are experienced show not unexpected discrepancies. The evidence suggests that although many species in this country have regular half yearly maxima occurring in summer and winter this is not universal for all species or habitats.

Vertical distribution.

A vertical migration of Collembola has been recorded by several workers. Volz (1934), in a study of woodland soil, reported a downward migration in /

response to low air temperatures. This was also shown by Strenzke (1949) in his study of samp soil types and also by Schaller (1949). In the work in Britain, Glasgow (1949) found O. ambulans nearer the surface in Spring and Macfadyen (1952) found maximum concentration of Collembola in lower layers in February. The results from Milngavie are in general agreement with those of other workers. The vertical migration of individuals, however, is not necessarily a complete explanation of change of population density from layer to layer. It can be seen from the Milngavie results that smaller individuals tend to be concentrated in the lower samples and maximum density in the lower layers is generally coincident with increasing total population. This is shown particularly well in O. procampatus, T. krausbaueri and I. viridis. Other studies (Glasgow 1939, Macfadyen 1952), in which such vertical changes in density have been reported also show a similar coincidence of greater density in the lower layer with maximal populations. Weis-Fogh (1947) reported the occurrence of numerous young individuals of I. viridis in the lower soil layer in June. It appears at least possible, from this evidence that the downward vertical migration is due to the increase of younger forms which tend to be found at lower depths. /

The depth distribution of the species agrees with that found in the comparative study of bracken, grass moorland and meadow.

Horizontal Distribution.

Glasgow (1939) found that O. armatus tended to be aggregated into colonies less than 12 inches in diameter. The other species in Glasgow's (1939) study also showed aggregation but in larger patches. Other members of the soil fauna are known to be distributed in aggregations, this has been shown for example by Salt & Hollick (1946) for elaterid larvae. Salt et al (1948) also found that Collembola and other soil organisms have a non-random aggregated distribution. Macfadyen (1952) and Sheals (1957) confirm that Collembola tend to be aggregated in distribution. The factors influencing this type of distribution are not known, although Glasgow (1939) suggests that the factor measured by ignition loss in soil may have some effect. Murphy (1953) suggests that the clumping of newly laid eggs by certain species may be responsible. In the results from Milngavie the population of O. procampatus was found to be concentrated in significantly greater density in three of the plots than in the others. Soil moisture measurements do not /

appear to be related to this distribution and no apparent difference in physical factors was found.

Summary.

1. A series of samples was taken from the humus layers and true soil under cover of bracken (Pteridium aquilinum (L.) Kuhn) over a period of two years.
2. Maximum total Collembolan populations occurred in winter and early summer, though the growth of populations of different species varied from species to species.
3. Measurement of individual Collembola extracted from samples showed that the age distribution in each species varied with population growth.
4. Younger individuals of each species were found to have greater density in the lower sampling layer especially at population maxima.
5. Evidence of change of population density from upper to lower layer is shown and this is discussed in relation to the 'vertical-migration' reported in other investigations.
6. A non-random distribution is noted for O. procampatus.

D. The effect of chemical fertiliser applications to the soil on the population of Collembola.

Description of the sampling area and methods.

The sampling plots were laid out on arable field at Cleland, Lanarkshire, subject to a normal crop rotation. The lay-out was in the form of a 5 x 5 graeco-latin square with plots measuring 9 x 11 yards. Lime and phosphate materials had been added in the previous five years to bring the salt content of the plots up to five levels of lime and phosphate. The details of the plots and treatments is shown in Fig. 21 and Table 16. The soil is typically podzolic and the original soil reaction is acidic in the region of pH 5. The crop immediately preceding the first sampling on June, 1956 was hay, the field was in ley until a second sampling in July, 1957.

Paired samples were taken at random from each plot on each sampling occasion. Each sample was taken to a depth of 5 cm. in sampling tubes of 10 cm. cross sectional area giving samples volume of approximately 50 $cm.^3$ Vegetation was cut close to the soil surface. The extraction was by the flotation method described by Raw (1955) and other details of technique are as previously described in the previous two investigations. /

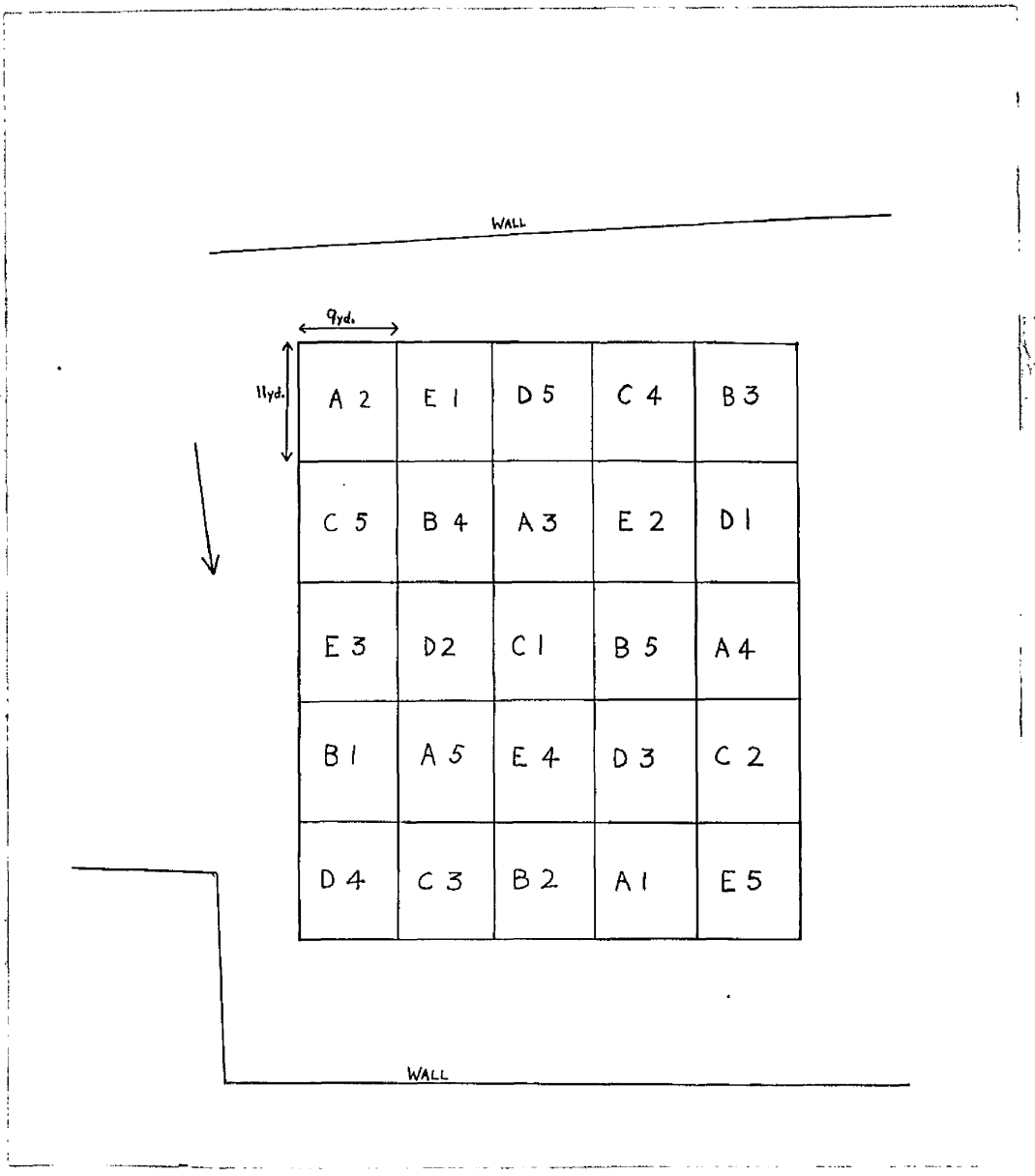


Fig. 21. Effect of chemical fertiliser treatment to the soil : Layout of sampling plots.

There was no obvious difference in the vegetation in relation to the treatments but the micro-flora was probably affected although no estimation of such changes was made.

Results

The qualitative composition of the fauna is shown in Table 15. One species has not previously been recorded for Britain. Several of the species appear to be typical of grassland conditions, but low populations, possibly due to cultivated conditions, are recorded. The means of total Collembola and of the most abundant species Onychiurus uliginatus, T. krausbaueri and I. viridis are shown in Table 16. No significant relation to treatments was found in the analysis of the data. The mean population in the first sampling was 5.3 individuals per 10 cm^2 and in the second 11.2 individuals per 10 cm^2. The relative composition of the fauna differed on the two sampling occasions, this is shown particularly in the abundance of Isotoma viridis in the second sampling.

Discussion

The composition of the fauna is similar to that found in the meadow faunal survey already described. This is particularly evident in the second /

Tullbergia krausbaueri (Boern.)

Onychiurus uliginatus Gisin

* O. sublatus Gisin

Anurida comellinii Gisin

Friesea mirabilis (Tullb.) f. reducta Stach.

Folsomia quadrioculata (Tullb.)

F. fimetaria (L.)

Isotoma notabilis Schaeff.

I. viridis Bourl.

Sminthurides pumilis (Krausb.)

Sminthurinus aureus (Lubb.)

Sminthurus viridis (L.)

Table 15 : List of species found in experimental plots at Cleland.

* species new to Britain.

Treatments	Total Collembola		I.viridis		T.krausbaueri		O.uliginatus	
Lime (to pH)	1956	1957	1956	1957	1956	1957	1956	1957
A - 7.25	6.1	9.3	-	1.7	2.1	2.6	2.3	1.5
B - 8.25	4.9	14.8	-	2.6	1.0	2.0	2.4	3.3
C - 9.25	5.9	7.8	-	1.6	1.6	2.1	1.4	1.3
D - 10.25	3.3	8.6	-	3.4	1.3	2.0	0.5	0.8
E - 11.25	6.3	14.8	-	3.0	1.7	5.6	1.6	2.8
Phosphate (lbs. P_2O_5/acre)								
1 - 25	4.3	14.0	-	2.3	1.6	1.6	1.6	1.6
2 - 50	4.7	8.7	-	2.5	0.9	2.1	1.0	0.7
3 - 100	7.5	3.7	-	0.9	1.9	0.8	2.8	0.4
4 - 200	3.5	14.0	-	2.0	1.1	4.7	1.0	3.0
5 - 400	6.5	14.9	-	3.0	2.2	4.0	1.5	2.0

Table 16 : Effect of soil chemical fertiliser treatments on the population of Collembola. Treatments of plots and mean numbers of Collembola per sample (area 10 $cm.^2$)

second sampling in which the effect of cultivation is minimised. The occurrence of the species O.uliginatus, Isotoma viridis, Folsomia fimetaria, Sminthurus viridis and Sminthurides pumilis appears to be typical of this type of grassland. Particularly striking is the increase in the hemiedaphic species I.viridis shown in the second sampling. Reduction of the soil arthropod fauna and especially hemiedaphic forms under arable conditions is well-known (Frenzel 1936, Sheals 1956) and between samplings the population appears to be recovering from this effect.

The effect of manurial application on the soil fauna was investigated by Morris (1927), who found that application of farmyard manure increased both the size of the population and the number of species present, but that the application of phosphatic fertiliser and ammonium salts had little effect on the soil faunal population. Little further published evidence is available on the direct effect of chemical fertiliser treatment of the soil on the micro-arthropod fauna, but it has been shown that changes in conditions during the maturation of compost (Gisin 1952) result in a qualitative succession of Collembola. The addition of artificial conditioning agents to the soil (Gisin 1956) result in similar changes in the population. The long term effect of lime and phosphate application to the soil will undoubtedly be a change/

change in the condition but no evidence was found that such changes are reflected by the population of Collembola.

Summary

1. The effect of various levels of lime and phosphate applications to the soil was investigated by sampling the plots on two occasions.
2. No consistent relation was found between treatments and the qualitative or quantitative distribution of the population of Collembola.
3. Qualitatively the population is similar to that already found in meadow-land at Milngavie, particularly when cultivation effects tend to be overcome.

III. Laboratory studies

A. Studies on the life-histories of various species of Collembola.

The life cycle of only a few species of Collembola have been previously investigated and no information has been hitherto available on the life of the species encountered in the field studies reported by the author. The species on which observations were made and reported here are Tullbergia krausbaueri (Boern.), Onychiurus furcifer Boern., O. latus Gisin, O. procampatus Gisin, Folsomia candida Will., Neanura muscorum Temp., and Isotoma viridis Bourl.

Methods

The primary requirement in the rearing of most soil arthropods under laboratory conditions is the maintenance of a high relative humidity in the culture vessel. This has been achieved by previous workers on Collembola by various methods. Ripper (1930) and Strebel (1932) used a substrate of soil, which, while giving a closer approach to natural conditions, renders continuous observation difficult. Moistened filter paper has been widely used, in small containers and tubes, to ensure high humidity level in studies on arthropods and was used by Britt (1951) in his study of Hypogastrura armata. The introduction /

by Searls (1928) of a technique for rearing Symphylids using plaster as a moisture source helped also to solve the problem of providing a suitable stable sub-strate for the animals. In a recent study of arthropleone Collembola, Schaller (1953) used a plaster block with glass-covered observation cells. Addition of powdered charcoal before mixing the plaster assists in observation of unpigmented animals (Wharton 1946, Edwards, 1955). Petri dishes 7 centimetres in diameter with a layer of plaster 2 - 3 mm. in depth were used as breeding dishes in the present study. Cultures of the species F. candida for observation of development, were made in small petri dishes 4 centimetres in diameter, similarly treated with plaster. Plaster blocks, with cells for individual insects, as described by Edwards (1955), were used for observation of other species. Water was added to those dishes every week, a few drops only being required. Cultures were attempted in temperature controlled conditions at 5°C. $\pm 2^{\circ}$, 12°C. $\pm 1^{\circ}$, and 24°C. $\pm 1^{\circ}$.

Food was provided in the form of bracken spores, which were found to be suitable for most species. This material has advantages over yeast, starch and other matter which have been used previously as food for Collembola in culture.

The spores are easily applied and evenly spread over the culture medium; there is little deterioration of the food and fungal contaminants are not encouraged. These properties make frequent changes of the food material unnecessary.

Difficulty was encountered due to contamination of eggs, in early stages of development, by fungi, mainly Penicillium sp. The growth of mycelia on the egg surface caused shrivelling and death of most of the affected eggs. This difficulty was overcome, to some extent, by sterilising the culture dishes before use and by brushing the eggs periodically with distilled water. Fungi pathogenic to eggs of Collembola have been previously reported by Goto (1956).

Measurements were made using reflected light by means of a micrometer eye-piece which when used in a monocular microscope with 1 inch objective gave readings in divisions of 30μ. This magnification was used for measurement of length and head width in all species except F. candida in which measurements were made with 2/3 inch objective giving eye-piece divisions of 10.4μ which was also used for measurement of eggs of all species. Owing to the /

difficulty of direct observation of individuals the measurement of growth in F. candida was made by removing ten individuals at intervals from a mass culture, in the small petri dishes previously mentioned, from eggs laid within 24 hours. Observation of development of the other species was made from specimens in individual plaster block cells 8 - 10 mm. in diameter and 5 mm. in depth. A considerable number of individuals was reared without accurate measurement for observation of maturation, number of eggs and other aspects of their biology. One outstanding difficulty in making a precise study of these species is the lack of conspicuous sexual dimorphisim so that the sexes could not be determined with any accuracy in life. Assumption of a 1:1 sex ratio has been made but this must be regarded with caution as there have been reports of a predominance of females in populations of certain species (Ripper 1930).

Specimens were obtained from soil and humus under bracken by extraction on Berlese funnels. The insects were collected in a vessel containing water from the surface of which they were removed to breeding dishes./

Results.

Tullbergia krausbaueri (Boern.)

This is a small unpigmented species with a maximum length of less than 1 mm. It has been found mainly in the deeper layers of the soil and is widely distributed. Eyes and furca are absent and movement is rather sluggish. The eggs (Plate 2) are smooth, unpigmented and globular, measuring 0.09 - 0.10 mm. before development. They were laid either singly or in pairs on the surface of the culture medium. Developing eggs become flattened and disc-like in shape, measuring 0.13 mm. in greatest diameter, immediately before hatching. Hatching takes place by splitting of the chorion across the width of the disc. Newly hatched individuals are similar to the adults in appearance except in lack of opacity and measure 0.24 mm. in length. Development of the eggs took from 15 to 20 days at 12°C. No development occurred at 5°C. or 24°C. Sexual maturity was attained from 30 to 40 days after hatching, in the third instar, at 12°C. The growth of fifteen individuals at this temperature is shown in Table 17. Ecdyses occurred at intervals of 8 to 15 days, and continued throughout life at irregular intervals, without appreciable change in length after attaining a length of 0.63 mm. Eggs were laid at 5°C, 12°C and 24°C; a mean of 10 eggs/

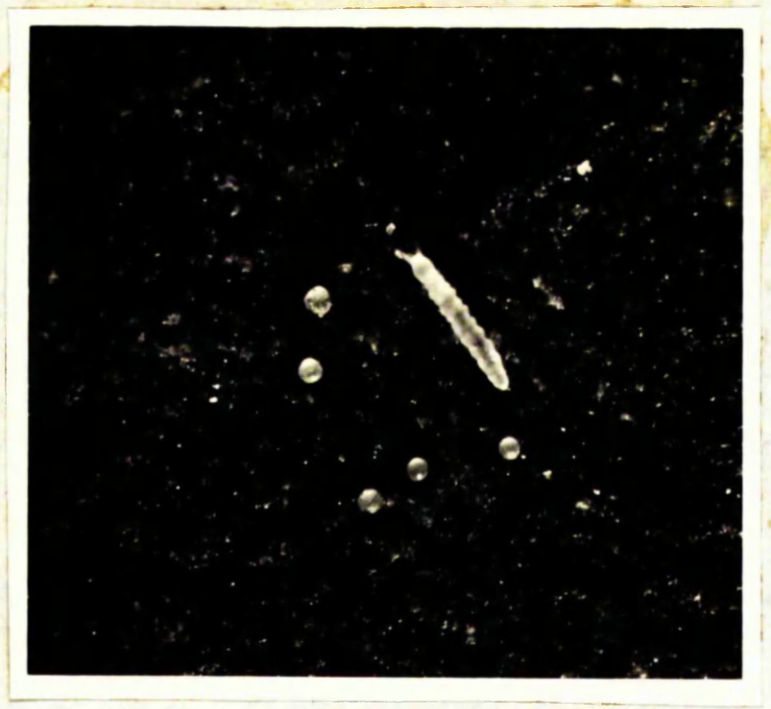


Plate 2. T. krausbaueri - adult and eggs. x 25.

Plate 3. O. procampatus - adult and eggs. x 26.

Instar	Length mm.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean
1	0.24 – 0.39	6	6	6	8	8	8	8	9	9	12	8	8	8	9	7	8.0
2	0.39 – 0.45	18	18	18	21	21	18	21	21	14	21	20	20	20	28	23	20.1
3	0.45 – 0.54	26	26	28	24	24	24	29	30	27	28	30	30	26	37	33	28.1
4	0.54 – 0.63	42	42	47	40	40	39	45	45	44	40	47	47	43	50	47	43.9

Table 17: Development of T. krausbaueri – the figures in the body of the table refer to the number of days from hatching for 15 individuals to attain each development stage at 12°C.

Instar	Length mm.	Head Width mm.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean
1	0.42 – 0.60	0.12 – 0.15	2	2	2	2	2	1	1	1	1	1	1	1	2	2	2	1.5
2	0.60 – 0.84	0.15 – 0.21	3	4	3	3	3	3	3	3	3	3	3	4	3	3	3	3.1
3	0.84 – 1.05	0.21 – 0.24	4	6	5	5	6	4	4	4	4	4	4	7	6	6	7	5.1
4	1.05 – 1.29	0.24 – 0.27	6	11	8	8	8	7	9	7	11	9	11	11	10	10	12	9.2
5	1.29 – 1.50	0.27 – 0.30	10	13	12	12	13	11	13	11	15	13	14	15	13	12	16	12.9

Table 18: Development of O.furcifer – the figures in the body of the table refer to the number of weeks from hatching for 15 individuals to attain each development stage at 12°C.

Weeks from Hatching	1		5		9		12	
	Length mm.	Head Width mm.	Length mm.	Head Width mm.	Length mm.	Head Width mm.	Length mm.	Head Width mm.
1	0.45	0.14	0.60	0.18	1.05	0.24	1.20	0.27
2	0.45	0.12	0.66	0.18	0.96	0.21	1.26	0.27

Table 19: Development of O.furcifer at 24°C - from measurements of 2 individuals.

was laid by each female at 12°C. assuming a sex ratio of 1:1.

At 12°C. in the laboratory adults survived for more than 6 months.

Onychiurus furcifer Gisin.

O.furcifer is an unpigmented species with no eyes, and a distinct but small furca, which distinguishes it from other species of the family Onychiuridae. The eggs are smooth, globular and unpigmented and measure 0.17 - 0.19 mm. before development. Development of the egg appears to be similar to that of T. krausbaueri, the diameter of the egg increasing to 0.21 mm. before hatching. Groups of up to 6 eggs were laid on the surface of the culture medium or in cavities with a small opening to the surface. Development of the egg lasted 26 - 30 days at 12°C. and 11 - 15 days at 24°C. Newly hatched specimens measured 0.42 mm. in length and 0.12 mm. in head width. The subsequent growth of 15 specimens in plaster block cells was followed and measurements made at intervals (Table 18). Four ecdyses at intervals of 2 - 4 weeks were observed and sexual maturity was attained in the fourth instar, 9 - 12 weeks from hatching at 12°C. Mortality was very high at 24°C./

and only two individuals, the measurements of which are shown in Table 19, were successfully reared under these conditions. Eggs were not laid at 24°C. At 12°C. a mean of 9 eggs was laid by each female assuming the sex ratio 1:1 in a culture of twenty specimens.

Onychiurus latus Gisin

This species is distinguished by the presence of yellow pigmentation. It is considerably larger than O. furcifer, mature specimens measuring more than 1.5 mm. and is found in the humus and upper soil layers. It is similar to the remainder of the Onychiuridae in the lack of eyes and furca. The eggs were laid singly or in small groups on the surface of the culture medium; they are smooth surfaced, globular and unpigmented, measuring 0.22 mm. in diameter before development and increasing to 0.26 mm. in greater diameter before hatching. Development time from laying to hatching was 19 - 22 days at 12°C. and 8 - 10 days at 24°C. The size of newly hatched specimens was 0.60 - 0.72 mm. in length and 0.15 mm. in head width. Individual measurements of 10 individuals were made at 12°C. Four ecdyses occurred before sexual maturity; the time for development is shown in Table 20. Pigment was developed in the second instar. Eggs were laid 16 - 23 weeks /

Instar	Length mm.	Head Width mm.	1	2	3	4	5	6	7	8	9	10	Mean
1	0.63 – 0.78	0.15 – 0.18	1	1	1	1	1	1	1	1	1	1	1.0
2	0.78 – 1.05	0.18 – 0.24	5	7	5	7	7	4	5	4	4	4	5.2
3	1.05 – 1.20	0.24 – 0.30	7	9	8	9	9	8	8	5	6	6	7.5
4	1.20 – 1.50	0.30 – 0.36	13	14	13	15	17	11	13	8	18	13	13.5
5	1.50 – 2.10	0.36 – 0.42	20	22	21	21	28	17	21	18	31	25	22.8

Table 20: Development of O.latus Gisin – the figures in the body of the table refer to the number of weeks from hatching for 10 individuals to attain each development stage at 12°C

after hatching. There was no egg laying at 24°C. and young individuals survived for only 1 - 3 weeks at this temperature. At 5°C. egg development did not take place. Eggs were laid by mature specimens after 27 weeks at this temperature. At 12°C. a mean of 6 eggs was laid by each female in a culture of 60 mature specimens if the sex ratio is assumed to be 1:1.

Under laboratory conditions at 12°C. survival for 12 months is common. At 5°C. seven individuals survived for 12 months out of 40 adults.

Onychiurus procampatus Gisin.

This is closely related species to O.latus but is slightly smaller and unpigmented. The eggs (Plate 3) are similar to those of O.latus in appearance and size and were laid singly or in pairs on the surface or in cavities of the culture medium. Embryonic development was slower than that of O.latus, the range being 31 - 33 days at 12°C. No development took place at 5°C. or 24°C. Newly hatched specimens measured 0.60 - 0.66 mm. in length and 0.15 mm in head width and were otherwise similar to mature specimens in appearance. Observations and measurement of the post - embryonic development of 15 individuals was made and the results are shown on Table 21. Egg laying commenced in the fourth/

Instar	Length mm.	Head Width mm.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean
1	0.60 – 0.78	0.15 – 0.18	1	1	2	2	2	4	3	3	3	1	3	4	2	2	2	2.3
2	0.78 – 1.11	0.18 – 0.21	6	9	12	12	9	10	7	6	7	3	6	9	4	5	11	7.7
3	1.11 – 1.29	0.21 – 0.24	12	11	14	14	12	15	9	8	8	7	14	11	8	7	14	10.9
4	1.29 – 1.65	0.24 – 0.27	14	14	17	19	16	22	20	16	19	14	16	16	17	15	19	16.9
5	1.65 – 1.95	0.27 – 0.30	16	17	28	29	22	28	27	21	21	21	22	24	25	24	28	23.5

Table 21: Development of O.procampatus Gisin – the figures in the body of the table refer to the number of weeks from hatching for 15 individuals to attain each development stage at 12°C.

Days after emergence	1		3		8		10		15		19		22		33		38	
	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.
Micrometer Divisions	30	9	33	9	39	9	48	11	57	13	65	15	56	14	65	16	72	16
	33	9	32	9	44	9	46	11	50	12	58	14	74	17	66	15	70	17
	34	9	32	9	47	10	45	11	59	13	59	14	54	14	74	17	74	17
	30	9	35	9	44	9	44	11	53	12	55	13	64	16	57	15	74	16
	32	9	37	9	41	9	49	11	52	13	48	12	58	14	65	15	55	16
	34	9	30	9	39	9	44	11	50	12	53	13	52	14	66	16	67	17
	35	9	34	9	44	9	36	10	50	12	53	13	58	14	67	16	54	16
	29	9	30	9	51	10	38	10	52	12	50	13	52	13	65	16	65	17
	31	9	31	9	43	9	34	10	50	12	60	14	61	16	66	16	70	16
	33	9	31	9	44	10	35	9	50	12	64	15	50	14	66	16	62	14
Mean	32.1	9	32.5	9	43.6	9.3	41.9	10.5	52.3	12.3	56.5	13.6	57.9	14.6	65.7	15.8	66.3	16.2
Actual Size mm.	0.33	0.09	0.34	0.09	0.45	0.10	0.66	0.11	0.54	0.13	0.59	0.14	0.60	0.15	0.68	0.16	0.69	0.17

Table 22: Development of F. candida Will.

- measurements of 10 individuals taken from a culture at 12°C.

l = length h = width of head capsule.

Days after emergence.	1		5		8		10		15		28	
	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.	l.	h.
Micrometer Divisions	34	9	41	9	53	12	55	15	71	17	86	21
	33	9	44	9	49	12	64	15	70	17	90	20
	34	9	42	10	51	12	63	15	73	17	90	20
	32	8	44	10	44	11	70	15	60	14	85	20
	34	8	39	10	46	11	68	15	60	15	87	20
	34	8	35	10	40	11	79	15	70	17	80	21
	30	8	32	9	55	12	65	15	72	17	73	20
	30	8	33	9	38	11	72	15	67	16	89	21
	30	8	42	10	50	13	66	15	65	16	87	21
	35	9	39	10	49	13	65	15	59	15	80	21
Mean	32.6	8.4	39.1	9.6	47.5	11.8	66.7	15	66.7	16.1	84.7	20.5
Actual size mm.	0.34	0.09	0.41	0.10	0.49	0.12	0.69	0.16	0.69	0.17	0.88	0.21

Table 23: Development of F. candida Will.

- measurements of 10 individuals obtained from a culture of 24°C.

l = length h = width of head capsule.

Plate 4. F. candida - adult and eggs. x 33.

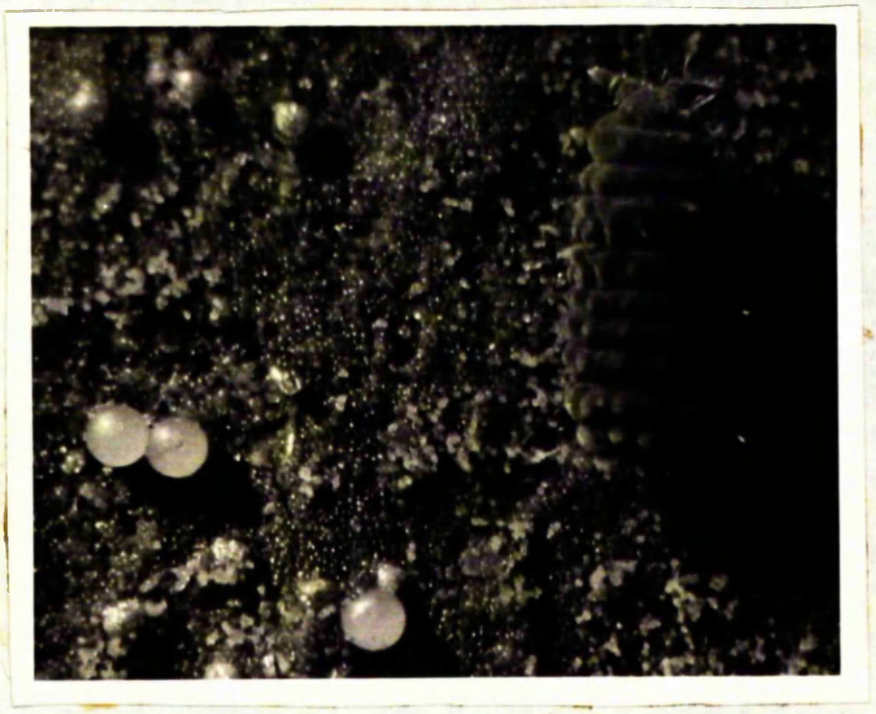


Plate 5. N. muscorum - adult and eggs. x 29.

instar, 18 - 22 weeks after hatching.

In laboratory cultures at 12°C. the original adults have been found to survive for more than 12 months. In cultures at 5°C. 27 individuals survived after 12 months from 40 originally introduced.

Folsomia candida Will.

F. candida is an unpigmented, blind species of the family Isotomidae with a well developed furca. The insect has an active running movement and springs readily if disturbed. Under bracken it has been found by the author to be evenly distributed between the humus and upper true soil layers. The eggs (Plate 4) are smaller and more transparent than those of the Onychiuridae, but are also globular and smooth surfaced. They were laid in groups of 9 - 36 with a preference for cavities in the plaster medium with an external aperture less than 0.5 mm. in diameter. There is a tendency for oviposition at the same site by a number of individuals so that large egg masses are formed. At 5°C. development of the egg took 90 days, at 12°C. 13 - 15 days and at 24°C. 7 - 9 days.

Newly /

hatched individuals were transparent and measured 0.30 - 0.35 mm. in length and 0.09 mm. in head width but were otherwise similar to the adult. Due to the very active habits of these insects and to other considerations direct observations of the growth of individuals ~~was~~ were not made. Estimates of growth by measuring 10 individuals at intervals from cultures at 12°C. and 24°C. are shown in Tables 22 and 23. At 12°C. eggs were laid 30 - 40 days after emergence from the egg, at 24°C. maturity was attained after 20 - 24 days from hatching. A mean per mature female of 29 eggs at 5°C., 22 eggs at 12°C. and 30 eggs at 24°C. was laid in the two weeks after maturation.

Isotoma viridis Bourl.

This species is a large (over 2 mm.) member of the family Isotomidae with well developed pigmentation and furca. It runs actively and has also a very strong springing movement when strong stimulus is applied. Adults were found mainly in the upper humus layers under bracken and it can be taken as typically a surface dwelling form.

The eggs are smooth surfaced, globular, measuring 0.21 mm. in diameter before development with pale red pigmentation and the mature female lays one clutch of /

36 - 54 eggs. Oviposition was always on the surface of the culture medium. Development of the eggs did not take place at 5°C.; at 12°C. development to hatching lasted 16 - 20 days and at 24°C. lasted 6 - 9 days. The newly hatched young measure 0.57 - 0.63 mm. in length and 0.15 mm. in head width. A pale red pigment is present in the body fluids of the young, possibly carotenoid in nature, giving the young its colour. Surface pigment becomes apparent only after the first ecdysis. Attempts at rearing this species to maturity were unsuccessful.

Neanura muscorum (Temp.)

This is also a large species with a maximum length of over 2 mm. and with dark blue pigmentation. The furca is developed but does not appear to function and movement of the insect tends to rather slow and ponderous. It was found under bracken in the surface humus layer. The eggs (Plate 5) are comparatively large measuring 0.28 mm. in diameter before development and 0.39 mm. in greatest diameter before hatching. They are globular with a lightly marked surface and cream coloured. Mature females were found to lay 6 to 10 eggs either singly or in pairs on the surface of the culture medium. Development of the egg at 12°C. lasted 12 - 13 days /

but no development took place at 5°C. or 24°C. The newly hatched insects measured 0.75 - 0.84 mm. in length and 0.24 mm. in head width and have a pale grey-brown "ground" pigmentation with pale purple pigment on the head and darkly pigmented eyes. At 12°C. purple surface pigment became obvious after 8 days and developed progressively; at 24°C. pigment was less well developed in the young. Growth did not take place at either temperature and maximum survival of young was 70 days at 12°C. and 30 days at 24°C. The failure was possibly due to lack of suitable food material as the mouth parts differ from those of the other species investigated in being drawn out and stylet-like, probably indicating a difference in feeding habits.

Discussion.

Comparable investigations of the life histories of arthropleone Collembola are few: the species concerned being Hypogastrura manubrialis (Tullb.) by Ripper (1930), H. purpurascens (Lubb.) by Strebel (1932), Orchesella cincta (L.) by Lindemann (1950) and H. armata Nic. by Britt (1951). A summary of some of the results of these studies is shown in Table 24.

Ripper's (1930) investigation of H. manubrialis was prompted by the economic importance of this insect in causing damage to mushroom beds. The mature female is

reported to lay eggs in groups of approximately thirty /

	Egg-laying				Development				
Species	Colour	Shape	Size mm.	Number	Embryonic Days		Post Embryonic Days	Number of ecdyses before maturity	Length of newly hatch insect. mm.
					10°C.	22°C.			
Hypogastrura manubrialis (Tullb.)	White	Globular	0.18	30	36	19	35-49	6 (every 5-7 days)	0.49
(Ripper 1930)									
H.purpurascens (Lubb.)	White	Globular	0.18	20-30	19	28	42-49	5 (every 4-15 days)	-
(Strebel 1932)									
					12°C	24°C	12°C.	23°C.	
Orchesella cincta (L.)	White	Globular	0.20-0.25	-	21	8	160-170	40-60	10-12	0.4 - 0.5
(Lindemann 1950)									
						24°C.		24°C.	
H. armata Nic.	White	Globular	0.16	28		8		15-19	3-4	0.14
(Britt 1951)									

Table 24: Comparison of results of previous studies of the life histories of Collembola.

in cavities in the soil. The young were unpigmented but otherwise similar to the adult. Ecdyses were observed every 5 - 7 days and sexual maturity was attained five to seven weeks from the eggs being laid but environmental condition for post-embryonic development is not reported. A suggestion that parthenogenesis occurs is deduced from the fact that a high proportion of females (which Ripper (1930) could distinguish from males) was found in the cultures.

Strebel (1932) in his study of H. purpurascens obtained similar results for the life of this species. In both of these investigations 'moulting societies' are reported in which groups of individuals are formed in which moulting takes place practically simultaneously. This behaviour was not observed in any of the species investigated in the present study. The work of Britt (1951) on H. armata suggests that this species is also similar in development to the other members of the genus previously investigated although development time is somewhat shorter. Females are reported to reach maturity, in the third to fourth instar, in 23 - 27 days at 24°C. In all three species the appearances and size of the eggs and number laid are in close agreement.

The investigation by Lindemann (1950) of O. cincta showed the relation of temperature to rate of development /

of the egg which ranged from 21 days at 12°C. to 6 days at 24°C. For another species O. villosa the pre-maturation period is said to last 30 - 50 days at 22 - 23°C. and 130 - 180 days at 10 - 12°C. Young individuals of O. cincta have diffuse violet 'ground colour' and surface pigmentation during the 10 - 13 instars reported before maturity. The development of pigment in this species appears to be similar to that of I. viridis and N. muscorum.

The method of sperm transfer was not observed in any of these studies and our knowledge is limited to the report by Schaller (1953) that in the species Orchesella villosa and Tomocerus vulgaris spermatophores are deposited on the surface of the sub-strate. The females are then said to place the abdomen in contact with one of the spermatophores before eggs are laid. Schaller (1953) also reports that no eggs were laid by isolated females / tending to confirm that parthenogenesis does not occur. In the present work eggs were not laid by any of the species reared in individual cells before introduction into a communal breeding dish. Investigation of the culture medium in the breeding dishes, however, did not reveal the presence of structures similar to the /

spermatophores described by Schaller (1953).

In comparison with previously reported records of development of Collembola, the embryonic development time of the species in the present study show the same order of magnitude i.e. 2 - 3 weeks at 12°C. (Table 25). Increase of temperature to 24°C. approximately halves the development time as might be expected from purely chemical ~~physical~~ considerations. The length of time for post-embryonic development of F. candida and T. krausbaueri is similar to that reported for Hypogastrura spp. (Ripper 1930, Strebel 1932, Britt 1951) but the other species studied have much longer post-embryonic development time (9 - 22 weeks at 12°C.) which is close to the results reported by Lindemann (1950) for O. villosa (18 - 26 weeks at 12°C.). The post-embryonic development times for I. viridis and N. muscorum are probably also of this order of magnitude.

The results obtained are interesting if studied in conjunction with the seasonal variation data reported in a previous section. At 12°C. the complete life cycle of T. krausbaueri lasts 7 - 9 weeks, of F. candida 6 - 8 /

	Egg-laying					Development						
Species	Colour	Shape	Size mm	Number	Mean Number per Female During Life	Embryonic 5°C.	12°C.	24°C.	Post Embryonic 12°C.	24°C. Days	Number of ecdyses before maturity	Size of young (newly hatched) mm. Length	Head Widt
F.krausbaueri	White	Globular	0.09-0.10	1-2	10	- 15-20	-		30-40	-	3	0.24	-
O.furcifer	White	Globular	0.17-0.19	1-6	8	- 26-30	11-15		63-84	-	4	0.42	0.1
O.latus	White	Globular	0.24-0.25	1-2	6	- 19-22	8-10		112-161	-	4	0.63	0.1
O.procampatus	White	Globular	0.23	1-2	7	- 31-33	-		126-154	-	4	0.60	0.1
F.candida	White	Globular	0.11-0.13	9-36	22-30	90 13-15	7-9		30-40	20-24	-	0.33	0.0
I.viridis	Palered	Globular	0.21	27-54	45	- 16-20	6-9		-	-	-	0.57	0.1
N.muscorum	Cream	Globular	0.25-0.27	1-2	6-10	- 12	-		-	-	-	0.69	0.2

Table 25: Summary of results of the present study of life histories of Collembola.

weeks, of O. furcifer 11 - 14 weeks and of the other Onychiurus species, 19 - 27 weeks. Under climatic conditions prevailing at Milngavie it might be expected that those species with longer life cycles are unlikely to produce more than two generations in one year and with low winter temperatures may be restricted to one generation. This is reflected to some extent in the field results; for example, I. viridis shows a single yearly peak in population, O. procampetus has a twice yearly peak and F. candida has an irregular variation suggestive of a short life cycle and more rapid change of population size in response to external factors. Suitable temperatures for the development of the species studied here lie between 5°C. and 24°C. The effect of the lower temperature, although slowing down and preventing reproduction in many species, nevertheless ensures a fairly stable level of population. The high temperature, although increasing the rate of development of some species, causes such a high mortality rate, except in F. candida, that reduction in the population would be expected if subjected to this temperature for more than a few days.

The large egg masses formed by the females of F. candida will tend to produce a non-random aggregated distribution in natural populations.

Summary.

1. Observations were made of the life history of seven species of Collembola.

2. Life cycles at 12°C. were found to vary from 6 - 8 weeks at 12°C. for F. candida Will. to 22 - 27 weeks at 12°C. for O. procampatus Gisin.

3. The results are compared with previous work and the relation of the present results to field studies is discussed.

B. The influence of carbon-dioxide concentration on soil Collembola.

Introduction.

The gaseous environment of soil dwelling animals is not well known. It seems probable, however, that in a soil horizon, where decomposition is active, a high concentration of carbon dioxide will be found and it is reasonable also to suppose that the inhabitants of such soil layers will have a greater resistance than other species to relatively high carbon dioxide concentration. A similarity in conditions is to be found in stored food products infested with mites or other arthropod pests , and it has been shown by Hughes (1943) that a common pest of cereal products, Acarus siro (L.), does indeed show a tolerance to high carbon dioxide concentrations. Kuhnelt (1950) suggest that subterranean Collembola show a similar tolerance, but exact information is limited to the work of Ruppel (1953), in his physiological investigation of this group. The present study is concerned with the effect of high carbon dioxide concentrations on seven species /

species of Collembola whose distribution in the humus and soil layers has also been investigated in field studies.

Methods.

The apparatus used in the experiments is similar to that described by Hughes (1943) and is shown in Fig. 22. Flasks A and B had each a volume of 700 ml. and were the reservoirs of nitrogen and carbon dioxide in the experiments. Alkaline pyrogallol was added to flask A to absorb oxygen, flask B was filled with carbon dioxide at atmospheric pressure from a cylinder of the pure gas. By adjusting the height of the levelling funnel C, which contained pure glycerol, appropriate volumes of carbon dioxide, nitrogen and air were drawn into the graduated gas mixing chamber to give the required levels of carbon dioxide concentrations, with a constant proportion of air (50 per cent.) When the appropriate mixtures were obtained the levelling funnel was raised so that a slow stream of the gas mixture passed through the observation tube, the gas chamber being emptied in approximately sixty minutes. The observation tube contained moistened charcoal/plaster medium as shown in Fig. 22. The experimental specimens were added to the observation tube some thirty minutes before each experiment and observations on their condition were made by low power /

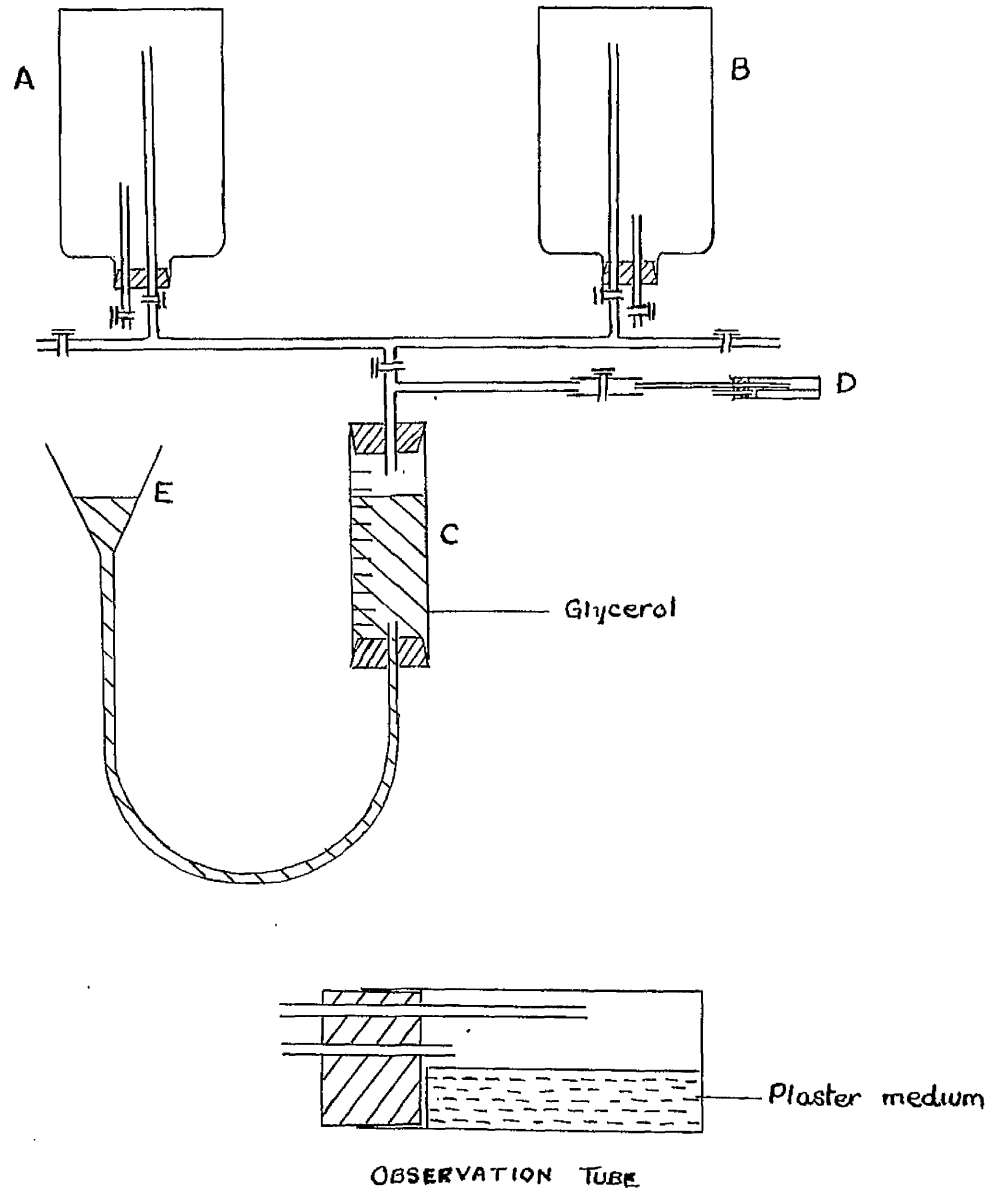


Fig. 22 Influence of carbon dioxide concentrations - apparatus.

binocular microscope. Failure of motionless animals to respond to mechanical stimuli was recorded. Ten individuals of Folsomia candida Will., Onychiurus latus Gisin, O. procampatus Gisin, Tullbergia krausbaueri (Boern. and five specimens of Friesea mirabilis (Tullb.), Neanura muscorum (Temp.) Isotoma viridis Bourl. were used in the experiments.

Results.

The introduction of the gas mixtures to the observation tube caused a slight increase in activity in all species but this may have been due to the purely mechanical disturbance of the gas. The increase in activity was not noticeable after a few minutes. Subsequent observations at five minute intervals gave the results shown in Table 26. At the 50 per cent level of carbon dioxide concentration all species were immobilised in five minutes except F. mirabilis and N. muscorum which were active for a rather longer period. At the 30 per cent level I. viridis was most rapidly affected, resistance being no greater than at the 50 per cent level, but progressive increase in survival time was shown by T. krausbaueri, O. procampatus and O. latus, all of which were immobilised within ten minutes and F. candida in twenty minutes to F. mirabilis and N. muscorum, which survived for thirty /

Concentration CO_2 / Species	5%	10%	20%	30%	50%
F. candida	No effect	60	40	20	5
I. viridis	No effect	10	10	5	5
Friesea mirabilis	No effect	No effect	No effect	30	10
N. muscorum	No effect	No effect	No effect	35	15
O. latus	No effect	30	20	10	5
O. procampatus	No effect	30	20	10	5
T. krausbaueri	No effect	20	20	10	5

Table 26 : Effect of various concentrations of carbon dioxide on 7 species of Collembola: time in minutes before total anaesthesia.

to thirty five minutes. At the 20 per cent level a similar gradation of effect was shown, with all species having longer periods of activity and N. muscorum and F. mirabilis completely unaffected. At the 5 per cent level of concentration no effect was shown by any of the experimental specimens although this atmosphere was maintained in the observation tube for twelve hours. In all cases where specimens were rendered motionless at the higher concentrations of carbon dioxide recovery was complete within a few hours of exposure to normal atmosphere.

Discussion

The potential importance of soil animals having resistance to high carbon dioxide concentrations has already been mentioned and Ruppel (1953) found in the course of an investigation, mainly on the action of the ventral tube, that Onychiurus armatus Tullb. was not affected by a concentration of 30 per cent carbon dioxide in air, whilst Orchesella villosa and Tomocerus vulgaris were affected at a 1 - 2 per cent concentration. In the present work the high resistance of O. armatus was not shown by any of the species examined. Greatest resistance was shown by F. mirabilis and N. muscorum, /

which withstood an atmosphere containing 20 per cent carbon dioxide; other species were completely resistant only to 5 per cent concentration. From the study of vertical distribution in the field sampling, results show that F. mirabilis and Folsomia candida are evenly distributed in the humus and upper soil layers, although, owing to the method of sampling, the results may also indicate a concentration at the interface of these two layers. O. latus and O. procampatus were found more abundantly in the upper humus layers and adult specimens of I. viridis were almost completely restricted to the surface. T. krausbaueri is typically an inhabitant of the lower, true soil, horizon. Relating this distribution to the susceptibility or resistance of these species to carbon dioxide concentration, there is an indication that species restricted to either the upper or the lower layer are less resistant to atmosphere of high carbon dioxide content. To some extent this agrees with the work of Ruppel (1953), who found that the surface dwellers Orchesella villosa and Tomocerus vulgaris were relatively very susceptible to carbon dioxide in comparison with Onychiurus armatus.

Summary/

Summary

1. The effect of concentrations of carbon dioxide in the atmosphere on seven species of soil dwelling Collembola is recorded.
2. A variation in resistance between species was found, five species being resistant to a 5 per cent concentration and two species to 20 per cent concentration.
3. The relation between resistance and natural depth distribution of these species is discussed with reference to previous work.

C. The influence of low relative humidities on soil Collembola.

Introduction.

It has been shown by Thamdrup (1939) among others, that only in very severe drought conditions is the relative humidity of the atmosphere in soil pores appreciably lowered from saturation level. In view of this fact, it is to be expected that in the evolution of soil dwelling arthropods there would be a reduction in the powers of resistance to desiccation. It is possible, however, that, particularly in those forms living nearest the surface, there may be exposure from time to time to abnormally dry conditions and the physiological evolution of a group of diverse habits may lead to an increase or reduction in powers of survival in low relative humidities. Information on the resistance of five species is given by Davies (1928) in whose study the only species found to have a definite resistance to desiccation was the tracheate Sminthurus viridis L. The ability to survive periods of desiccation in the egg stage of this species has been found to be well developed (Davidson 1928) and the eggs of other species appear to have a similar resistance (Strebel 1930, Ripper 1932).

Methods/

Methods.

The atmospheric conditions of various relative humidities were produced by having appropriate potassium hydroxide solution in screw-cap jars measuring 7 cm. in height and 9 cm. in diameter (Fig. 23). The densities of the solutions to produce the required relative humidity values of 20, 50, 80 and 90 per cent are according to data supplied by Buxton and Mellanby (1934) and Solomon (1951). The appropriate densities of potassium hydroxide solution required to obtain those relative humidity values at 20°C. is shown in Table 27.

The control jar contained water only, giving 100 per cent relative humidity; in this, small petri dishes 4 cm. in diameter, with a thin covering of plaster on the base, were supported by glass plates approximately 2 cm. above the surface of the solution. The experimental material was assembled several weeks before the experiments to allow an equilibrium in humidity conditions to be attained. The experimental specimens were obtained from breeding cultures in which 100 per cent relative humidity was continuously maintained. Ten specimens of each species were added to the small petri dishes and the covers were tightly closed. Continuous observation was then made through /

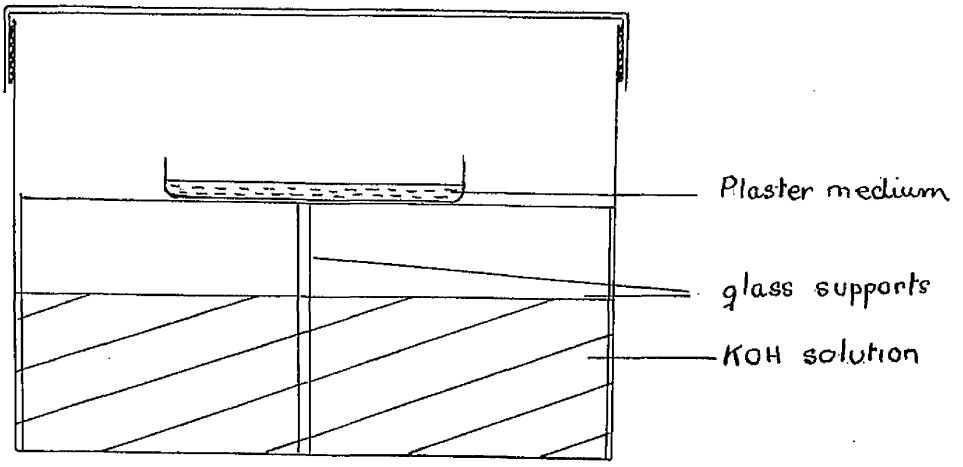


Fig. 23 Effect of low relative humidities - apparatus.

Relative humidity at 20°C	90	80	50	20
Density of KOH solution at 15°C	1.108	1.181	1.330	1.479

Table 27 : Density of potassium hydroxide solutions required to produce various relative humidities.

Species	Relative humidity 20%	50%	80%	90%	100%
I. viridis	20	20	95	295	No effect
F. candida	15	15	60	240	No effect
O. latus	15	15	60	90	No effect
O. procampatus	15	15	30	60	No effect
T. krausbaueri	15	15	15	30	No effect

Table 28: Survival times (minutes) of five species of Collembola at various relative humidities.

the side of the glass jars and the period before all specimens of each species were immobilised was noted. The species investigated were Tullbergia krausbaueri (Boern.) Onychiurus latus Gisin, O. procampatus Gisin, Folsomia candida Will. and Isotoma viridis Bourl.

Results.

The survival time for the five species in these experiments is shown in Table 28. The control specimens were unaffected during the time of observation and after a further lapse of several days continued to show no ill effects. At 90 per cent relative humidity a gradient of survival time is shown from 30 minutes for the small unpigmented species T. krausbaueri to 295 minutes for the largest species I. viridis. At the lower relative humidities a similar gradient can be seen until at 20 per cent relative humidity the survival time for all species was 15 minutes except I. viridis which survived for slightly longer. For each species there appears to be a critical level below which desiccation is very rapid. In T. krausbaueri this level lies between 80 and 90 per cent relative humidity and for the other species between 50 and 80 per cent relative humidity.

Discussion /

Discussion

The results obtained for the species I. viridis are in agreement with Davies' (1928) results, taking into consideration differences in experimental conditions. Davies' (1928) experiments were carried out at 25°C. with specimens in glass tubes covered with cheese cloth at the lower end and suspended over solutions of sulphuric acid in flasks. He found that at 90 per cent relative humidity I. viridis survived for 90 minutes, at 50 per cent relative humidity for 60 minutes, at 20 per cent relative humidity for 30 minutes. At 100 per cent relative humidity, survival of I. viridis was limited to eight hours. In the present experiments the specimens of I. viridis at 100 per cent relative humidity were healthy after several days, at 90 per cent relative humidity the species survived somewhat longer than in the previous work, namely for 295 minutes; but at the lower levels of relative humidity present records show a similar survival time or rate of desiccation. I. viridis and T. vulgaris were the most susceptible of Davies' species in comparison with E. multifasciata, D. minuta, and S. viridis. The former species are more typically soil and litter /

dwellers. The very pronounced resistance of S. viridis to low humidity conditions is related by Davies (1928) to the presence of tracheae; but it is also distinctly related to the normal environment of this species which lives mainly on macrosopic vegetation. In the present work on purely soil and litter dwelling species a relationship appears to exist between their vertical distribution in nature and their susceptibility to low relative humidities. T. krausbaueri is the most susceptible in the experiments and is characteristically an inhabitant of the lower soil layers. O. procampatus was found in field studies to be rather evenly distributed between the humus and true soil layers and shows a slightly greater resistance to desiccation. O. latus is a larger species which apart from the present record of distribution has been found only in woodland litter and is a typical litter species. It shows a slightly greater resistance than O. procampatus at 80 per cent relative humidity. The position of F. candida is not so easily explicable in this context. It is evenly distributed between humus and true soil layers and despite a complete lack of pigmentation it has a well developed furca and is very active, suggesting adaption to surface living. The survival of F. candida at 90 per cent relative /

humidity is considerably longer than that of O. latus but is similar at low humidities. The most resistant species was I. viridis, a large darkly pigmented species, the adults of which are typical of the surface layers of soil and litter. Davies (1928) suggests various mechanisms by which resistance to low humidities may be effected in Collembola. Hygroscopic hairs and scales for example are present in one of his more resistant species, E. multifasciata; but were also present in T. vulgaris, one of the most susceptible. The presence of tracheae in S. viridis has already been mentioned but another characteristic of the species is the possession of a well developed ventral tube with long protrusible vesicles. There is a relation between the development of the ventral tube, in the species investigated, and resistance to desiccation. The most susceptible species, from the experimental evidence, is T. krausbaueri which has a small ventral tube in relation to body size. Surface living arthropleone species, for example, Isotoma viridis and Entomobrya multifasciata have a larger ventral tube in relation to body size and a resistance to desiccation which is intermediate between that of the true soil dwellers and that of species, such as Sminthurus viridis, which are, more or less, independent of the soil.

Summary/

Summary

1. The resistance of five soil and litter dwelling species of Collembola on exposure to atmospheres of low relative humidity was examined.

2. All species were found to be susceptible to desiccation at relative humidities of 90 per cent and lower.

3. A range of survival time at the various levels of relative humidity is noted, from 30 minutes for T. krausbaueri and 295 minutes for I. viridis at 90 per cent relative humidity.

4. There appears to be a critical level in relative humidity below which desiccation and death are very rapid.

5. The present results and similar previous records are discussed in relation to natural environment and the mechanism of resistance to low humidities.

D. The food of soil Collembola

The feeding habits of the soil fauna are important both in relation to humus formation and possible pest status. Of the few soil animals whose feeding has been studied, Lumbricidae appear to play the most important role in incorporation of deposited organic material with the mineral soil. Darwin (1881) found that the activity of the earthworm population in England in one year was responsible for the formation of 10 tons of top soil in every acre. The effect of soil arthropods can not be so conclusively demonstrated although it has been reported by Schaller (1950) that a population of 100 thousand Collembola per square metre were capable of producing 183 c.c. of humus annually. This is equivalent to about 1 ton of humus per acre. The actual material which is ingested by soil Collembola is still controversial to some extent. It was reported by Schaller (1950) that fresh leaves were not eaten and there is a rather general opinion that living plant material is rarely attacked by Collembola. There have, nevertheless, been many reports of damage to plants by these animals (Folsom 1933, Brown 1953) and there is some reason to believe that they can cause appreciable damage to living plant tissues under certain conditions.

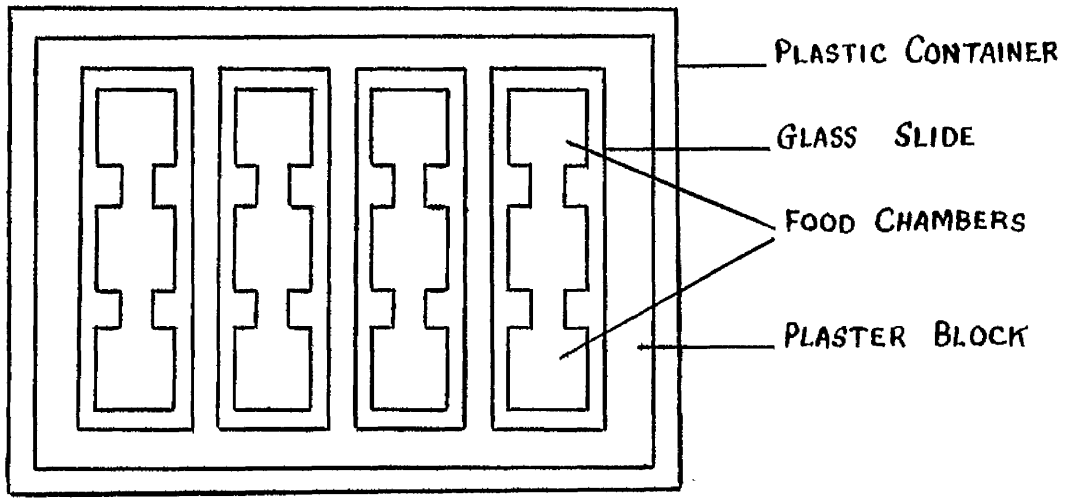
The following account is based firstly on observation of

Collembola obtained in field samplings of bracken soil and secondly on food preference experiments with various species in the laboratory. These observations were intended primarily as a means of discovering a suitable diet for Collembola in laboratory cultures but may also be a guide to further study.

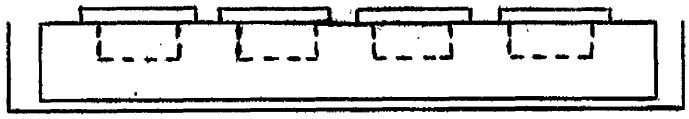
Methods

The procedure for collection and mounting of specimens has been described previously. In a number of these specimens the gut contents were retained during the extraction processes and the material was usually recognisable. The samples on which the observations were made were taken in February 1956, August 1956, December 1956 and June 1957.

In the preference experiments a plaster dish, shown in Figure 24, was used. The food material was presented in the opposing food chambers of each section of the dish. Two similar food presentations were made to each species in the experiment with the food positions exchanged to reduce the effect of position of the food. Adult specimens of Tullbergia krausbaueri, Onychiurus procampatus, Onychiurus latus, Folsomia candida and Isotoma viridis/



Top view.



Side view.

Fig. 24 Food preference experiments - Feeding dish.

were used in the experiments. Five specimens of I. viridis and ten specimens of the other species were introduced into each of the middle chambers of the dish in each experiment. The animals were observed twice during a period of 10 days after introduction of the food, after 5 and after 10 days. Direct observation of feeding by low power microscope was made in each species and in addition these observations were verified by inspection of the gut contents of the unpigmented species.

Results

The material found in the gut of specimens from field sampling could be divided into four categories namely soil, in which small mineral particles predominated; organic debris, in which larger particles showing distinct plant structure were present; fungus, including hyphae and spores; and spores of bracken (Pteridium aquilinum (L.) Kuhn). These categories account for most of the gut contents observed but in few exceptions other material was present including cuticle and setae of other species of Collembola. The numbers of individuals observed and the occurrence of the various food categories are shown in Table 29. On all four/

Species	February 1956 Number examined	Soil	Organic debris	Fungus	Bracken spores	August 1956 Number examined	Soil	Organic debris	Fungus	Bracken spores
T.krausbaueri	13	100%	-	-	-	12	100%	-	-	-
O.procampatus	12	16.7%	58.3%	8.3%	16.7%	14	43.5%	52.2%	4.3%	-
F.candida	12	100%	-	-	-	10	100%	-	-	-
I.viridis	6	-	50%	33.3%	16.7%	0	-	-	-	-
	December 1956					June 1957				
T.krausbaueri	14	100%	-	-	-	12	100%	-	-	-
O.procampatus	12	54.2%	25%	12.5%	8.3%	21	42.9%	47.6%	9.5%	-
F.candida	10	100%	-	-	-	8	100%	-	-	-
I.viridis	0	-	-	-	-	6	66.6%	-	33.3%	-

Table 29 Observation of gut contents present in four species of Collembola obtained from field sampling of bracken soil.

occasions all specimens of T. krausbaueri and F. candida had soil only in the gut. In February and December 1956 all four categories were found in the specimens of O. procampatus. Bracken spores were absent from the gut of O. procampatus on the other two occasions August 1956 and January 1957. This was associated with the deposition of spores from bracken in late autumn. The maximum number of occurrences of soil in O. procampatus was in December 1956. The results of the analysis of individual size shows that this was coincident with a maximum of young individuals which presumably feed on smaller particles.

Specimens of I. viridis were observed only in February 1956 and June 1957. In the specimens from the February samples, half had organic debris in the gut and the remainder had mainly fungus and bracken spores. In the June sampling no organic debris was found in the gut of I. viridis and soil formed two-thirds of the gut contents. This was coincident with a very large proportion of young individuals of this species in the population. /

The comparisons in the preference experiments were between a, bracken spores and granular starch (Analytical Reagent) ; b, spores and powdered charcoal ; c, spores and fine grain mineral soil ; d, spores and bracken prothalli ; e, starch and prothalli. Starch, charcoal and soil were chosen as a means of presenting material of fine grain size. The fine soil was obtained by wet sieving a sample of soil, from bracken cover, through a fine mesh sieve (B.S.100 mesh). The prothalli were grown from spores germinated on a nutrient agar medium and a single prothallus was removed to the plaster dish for each experiment. The prothalli continue to grow on the plaster surface. The results of observation of the subsequent feeding of the five species which were investigated are shown in Table 30.

The specimens of T. krausbaueri showed a choice of powdered charcoal and soil in preference to bracken spores although the spores were eaten occasionally. In the species O. latus the comparisons showed a tendency to prefer spores to starch, soil or prothalli, although all the materials presented were eaten to some extent. In the comparisons in which O. procampatus was studied, there appeared to be a choice of charcoal in preference to bracken spores but /

Comparison	a		b		c		d		e	
Species	spores	starch	spores	charcoal	spores	soil	spores	prothalli	starch	prothalli
T.krausbaueri	-	-	0	20	3	17	-	-	-	-
O.latus	20	8	-	-	10	4	29	18	-	-
O.procampatus	29	1	2	15	16	4	55	2	-	-
F.candida	2	37	14	3	1	19	-	-	25	18
I.viridis	13	0	10	0	-	-	9	4	-	-

Table 30: Observation of feeding of various species in food preference experiments.

the spores were taken more frequently compared with the other materials offered. Individuals of F. candida showed a preference for starch in the comparison with bracken spores and in the comparison with bracken prothalli. Soil was also eaten in preference to bracken spores by F. candida but the spores were more frequently eaten by this species when offered with powdered charcoal. The specimens of I. viridis showed a definite preference for spores in the three comparisons (a, b and d) in which they were observed.

Feeding on the bracken prothalli resulted in notches being made along the edges of the flat expansion of green tissue. A similar type of damage had previously been produced on fresh leaves of tomato seedlings when introduced into a dish containing a number of individuals of Onychiurus spp. In these unpigmented species the green material was clearly visible along the length of the gut and the food resulted in giving the frass conspicuous coloration due to unchanged green chlorophyll pigment. /

Discussion

MacNamara (1924) in a review of the food of Collembola considered that, with a few exceptions, softened organic material, fungus and algae were the main sources of food. He also gives records of feeding on pollen grains, either deposited, or directly from flowers.

Strebel's (1932) experiments with various species of Collembola showed that any softened organic material was eaten, except where extreme acid, salty or sweet material was involved. Similarly, Britt (1951) found that specimens of Hypogastrura armata Nic. ate a large variety of organic material including starch, butter, cheese, fungal mycelia and yeast. Specimens in breeding culture were found by Britt to exist on a diet restricted to yeast.

The feeding of Collembola on plant debris and the effect of this feeding on forest litter was investigated by Schaller (1950) who found that although leaves were not eaten when fresh, they were readily consumed when softened by primary decay organisms.

The pest status of a number of species of Collembola was summarised by Folsom (1933). Typical damage caused by soil Collembola, according to Folsom, is the eating/

of holes in leaves of seedlings, gnawing of young stems just below soil surface level and destruction of fine rootlets and root hairs. Damage to the roots of sugar cane by a number of species of Collembola including Onychiurus armatus Tullb. is reported by Spencer and Stracener (1930). More recently Brown (1953) reported that tomato seedlings are susceptible to attack when large populations of soil Collembola including Onychiurus spp. are present. The experiments of Murphy and Doncaster (1957) showed an interesting possibility of direct beneficial effect of feeding by Collembola in the destruction of cysts of plant feeding nematodes (Heterodera spp.). It is reported by these authors that the eelworm cysts are perforated by individuals of O. armatus (Tullb.) and other species and the cyst contents eaten. It is also claimed that appreciable damage to natural populations of cyst-forming eelworms may be caused in this way.

It has been suggested by Conway (1953) that feeding of the soil population of Collembola on spores and sporelings of bracken helped in the suppression of the gametophyte generation of this plant. In observation of individuals of O. procampatus from bracken soil in the present study more than 300 spores were commonly found in the gut.

However it is improbable that this would seriously affect the natural development of bracken considering the large number of spores deposited by the plant.

In the present work the results show that certain Collembola living in bracken soil feed mainly on the small particles present, which may include inorganic material. The diet of small species and young individuals of large species seems to be restricted to particles of small size. Presumably sufficient organic food material is present on the surface of the mineral soil grains ingested by these to supply their nutritional requirements. Delicate parts of living plant material form suitable food material for some species but such structures were not shown to be preferred to particulate matter where available. From an economic aspect, appreciable damage by Collembola to cultivated plants is to be expected only where large populations are i proximity to delicate plant structures, for example, parts of young seedlings in contact with or just below soil surface level. It has been noted that the diet of T. krausbaueri tends to be restricted to small particles, including mineral soil. A relation can be demonstrated between the depth distribution of this species, which is found mainly in lower soil layers, and the preferred food /

material. A similar preference is shown by the young of some species which also occur at lower depths. Also, T. krausbaueri is notably ubiquitous in distribution and this may be related to the similarity in material available at lower depths in different soils. A much greater diversity of food is available in the surface layers of the soil and this may influence the distribution of species of Collembola which are usually found in such layers. A long term investigation would be required to distinguish possibly delicate preferences for different types of organic material including micro-flora.

Summary

1. The gut contents of specimens of four species of Collembola obtained from sampling of bracken soil, are recorded.
2. The observations of specimens from field samples indicated that feeding took place on mineral soil particles, bracken spores, fungus and particles of general organic debris. Specimens of T. krausbaueri had mineral soil particles only in the gut, other species had various types of material.
3. Laboratory preference experiments on five species of Collembola showed that materials of small particle size, other than bracken spores, were eaten and in some cases were preferred to bracken spores. Living green plant material was also eaten in some cases.

E. An investigation of pigmentation in *Onychiurus latus* Gisin.

Introduction

O. latus is a relatively large species of the family Onychiuridae, mature specimens measuring 2 - 3 mm. in length. The species was found rather abundantly in litter in certain areas of bracken and moorland grass at Milngavie. The only previous record of the occurrence of the species is in forest litter in various localities in England (Gisin 1956). *O. latus* differs from most of the other species of the Onychiuridae in possessing a pigmentation of various intensities of yellow or orange. Other species with similar pigmentation include *O. alborufescens* (Voegler) and *O. flavidulus* Bagnall. The pigment is rapidly lost in specimens preserved in alcohol or in organic fixatives and is obviously fat-soluble. The nature and importance in metabolism of these pigments has not been previously investigated.

Distribution of the pigment

The distribution of the pigment in specimens of *O. latus* was observed by partially clearing in a chloral hydrate/glycerol medium. Centres of /

pigmentation were observed in the body cavity arranged segmentally along each side of the insect from the first thoracic to the sixth abdominal segment and also along the length of the mid gut and surrounding the oesophagus. This corresponds to the distribution of the fat body in these insects which remains well developed throughout life. In young individuals pigmentation is barely distinguishable until 10 - 20 days from emergence. With increasing age pigmentation is intensified progressively.

The effect of starvation and different food material was also investigated. After thirty days at 12°C. in culture with no suitable food material the survivors were almost completely unpigmented. These specimens differed from other naturally unpigmented species in a relative lack of opacity. Specimens feeding on decomposing potato and on bracken spores showed no apparent difference in pigmentation during this period.

Chemical nature of the pigment

From approximately 900 adult specimens of O. latus 4 ml. of yellow pigment solution was extracted in acetone. /

Subsequent treatment in the analysis of the pigment was according to the method described by Fox and Pantin (1941). The pigment was transferred to ether by diluting the acetone with water and all traces of acetone removed by further washing with water. On the addition of 90 per cent methanol to the solution the pigment remained in the ether layer. After hydrolysis with alcoholic potassium hydroxide and partition in 90 and 95 per cent methanol the pigment remained in the epiphasic layer. The ether solution was added to a column of magnesium oxide and ether was added to develop a chromatogram according to the technique described by Karner and Jucker (1950). A distinct yellow band was obtained near the top of the column. The pigment was then eluted from the column by addition of ether and a final volume of 20 ml. taken for spectroscopic analysis. The absorption spectrum obtained in the "Unicam" Ultra-violet absorption was spectrophotometer is shown in Fig. 25. Slight absorption is shown in the visible range from 485 to 390mμ in the blue-violet region, the absorption curve rises in the ultra-violet range to a conspicuous peak at 280 - 287 mμ. A further test with the pigment /

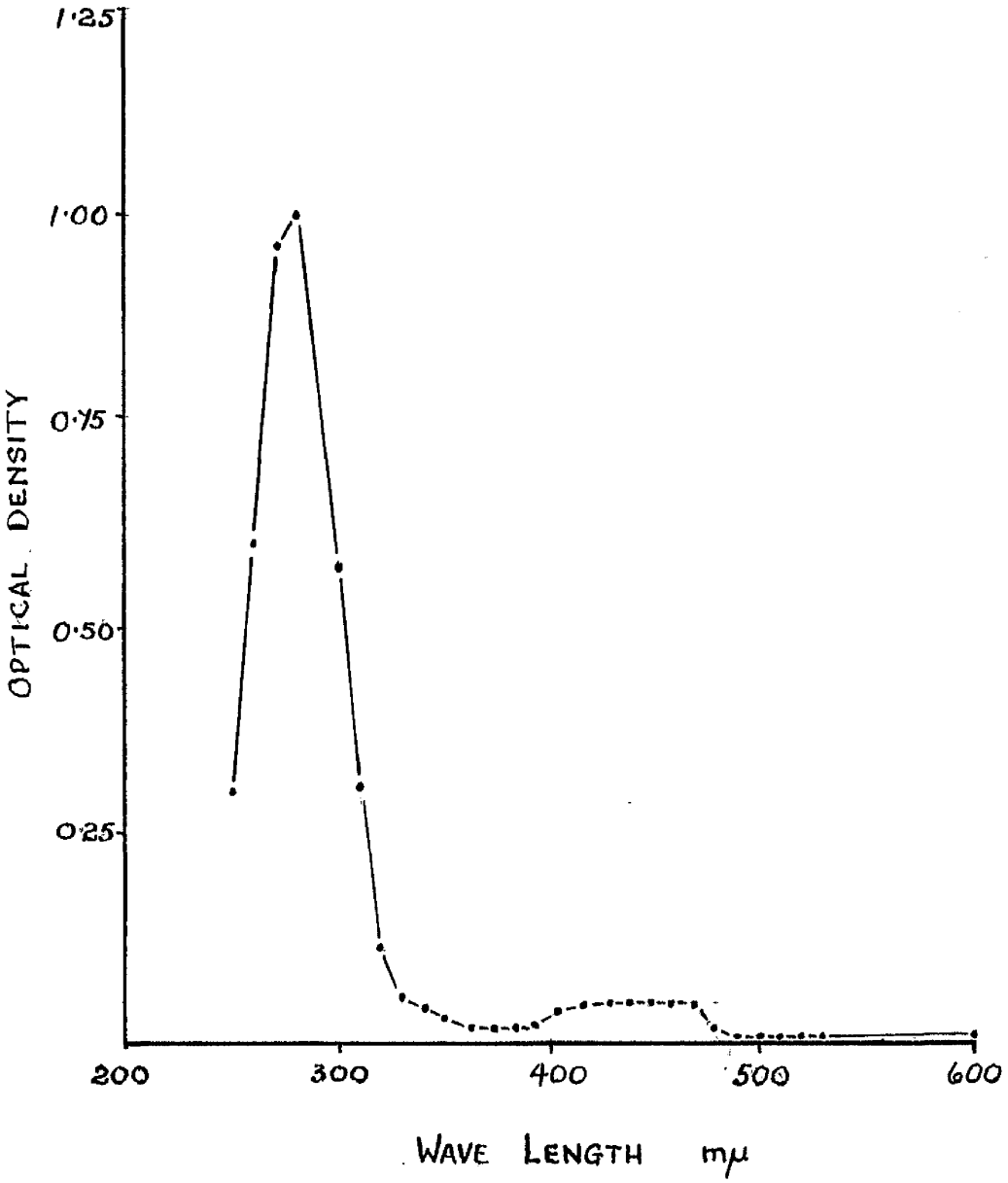


Fig. 25 Graph of absorption spectrum shown by yellow pigment from O. latus.

in chloroform solution gave a brown coloration on the addition of concentrated sulphuric acid.

Discussion

The results of the analysis of the pigment show that it has properties similar to the chromolipoid or lipofuscid group of pigments. These appear to be formed as oxidation products in the metabolism of fat (Ciaccio 1915). The presence of a similar pigment in cells surrounding the enteric canal of leeches has been reported (Verne 1926), although the presence of the pigments in various vertebrate tissues has been more completely investigated. Prenant (1913) gives one of the few accounts of this type of pigment in insects in his work on pigmentation in wings of Lepidoptera. The occurrence and physical properties of a number of similar pigments found in the marine annelid Thoracophelia mucronata has been investigated (Fox et al, 1948). The physical function of such pigments, however, remains unknown. It has been suggested that they become progressively oxidised to soluble compounds serving in this way as reserve fuel (Fox 1953). The decrease in pigmentation in specimens of O. latus deprived of food tends to support this theory. The /

The apparent intensification at 5°C. is possibly due to the fact that, although feeding continues at this temperature, movement is noticeably reduced.

Under normal conditions the fact that the degree of oxidation continues with advancing age confirms the suggestion that these pigments are essentially catabolic waste products. The physiological differences which cause deposition of the pigment in particular species in comparison with otherwise closely related but unpigmented species are unknown. For inhabitants of the upper soil layers there is probably a survival value in the possession of such pigments, unpigmented species being particularly conspicuous against the darker background of their natural habitat. It is of interest to note that the unpigmented young of this species tend to be found at lower levels in the soil. The place of the pigment in the biochemical life of these insects remains a question for future investigation.

Summary

1. The occurrence and distribution of yellow pigment in Onychiurus latus is recorded.
2. The pigment was found to be fat soluble and associated with fat body tissue in this species.
3. At low temperatures pigmentation was intensified whilst absence of food caused diminution of the colour.
4. The results of physical and chemical tests show that the pigment belongs to the group of fatty compounds known as chromolipoids which are considered to be oxidative products of lipids.
5. The possible function and place in metabolism of these products is discussed.

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Appendix I Extraction technique

The multiple funnel extraction apparatus.

A general view of the apparatus is shown in Plate 6 and details of the individual unit in Figure 26. The apparatus contains eight rows each of which accommodates six sampling units, the whole apparatus having a capacity for 48 samples. The material for the frame and sampling tubes was 16 gauge aluminium.

The samples were taken in the aluminium tubes which measure 1½ inches in outside diameter and 5½ cm. in height giving a sample of volume 50 c.cm. and 10 square cm. in cross-sectional area. A specially constructed handle was employed to insert the sampling tube in the soil and to withdraw the tube with the sample. After sampling the tube was placed in position in a laminated plastic plate in the apparatus where it was held by means of a rubber band so that it was suspended over the glass funnel with a space of approximately 5 mm. between the lower end of the tube and the funnel. Heat was applied to the samples by means of a current passing through a length of 18 gauge resistance wire in a polished hemi-tubular reflector along each row. The resistance wires in each row were connected in series with the mains electricity supply transformed to 12 volts. The collecting tube, attached/

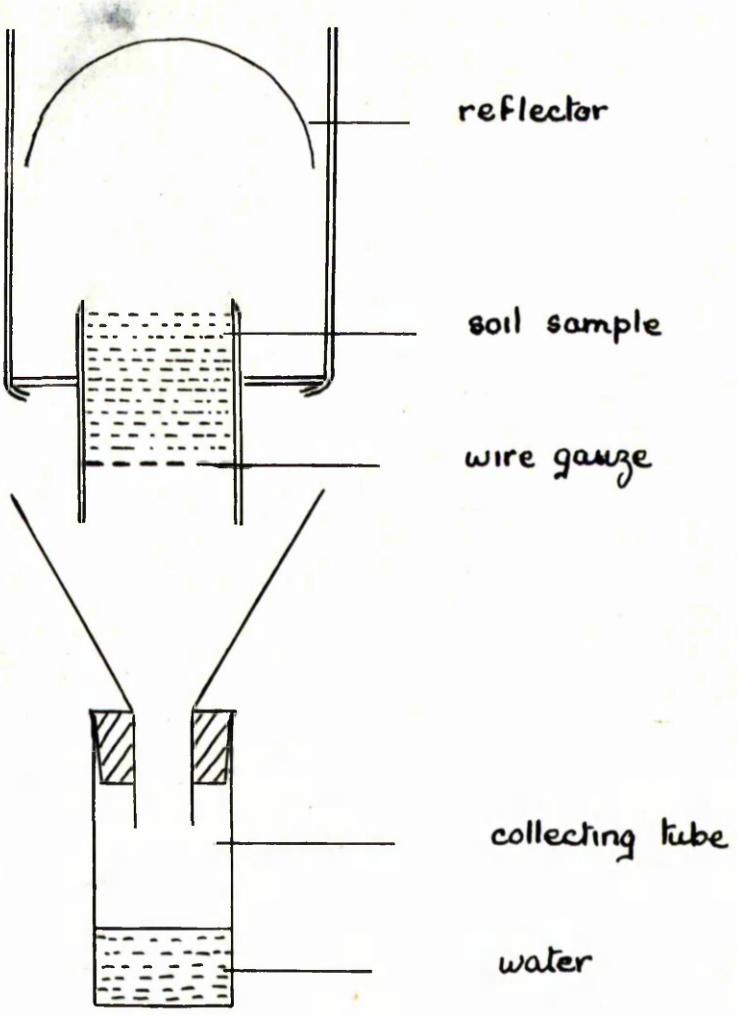


Fig. 26 Funnel extraction apparatus: Diagram of unit.

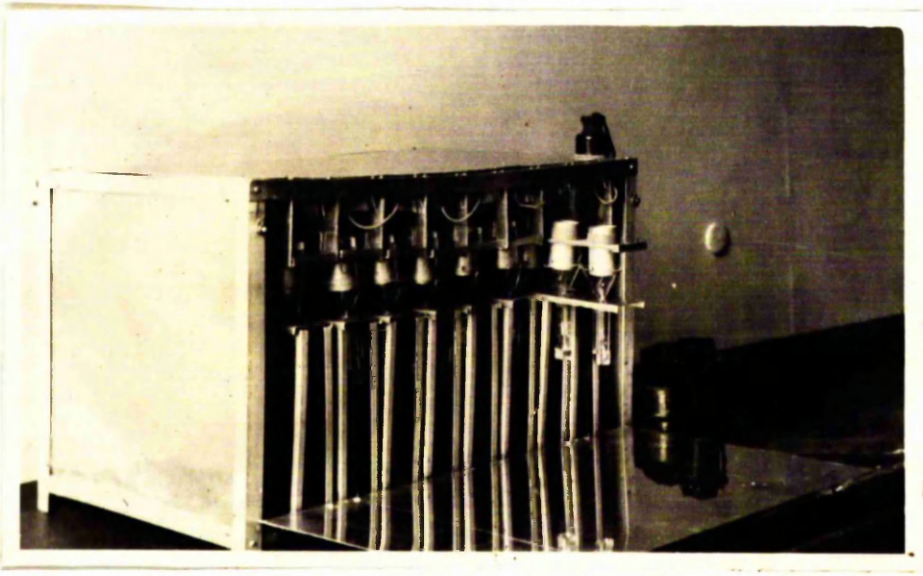


Plate 6 Funnel extraction apparatus (after Macfadyen, 1953).

to the glass funnel, contained water which was used in preference to alcohol, formalin or other fixatives which may have a deterrent effect on downward migration of the animals in the sample. The possibility of deterioration of specimens due to fungal contamination in the collecting tubes was avoided by removal of the tubes after four to five days and replacement by fresh tubes. The extraction was normally completed in from six to ten days. Before final removal from the apparatus the sampling tubes and funnels were washed down with water and then with 70 per cent alcohol to remove any specimens remaining on the sides of the system.

Measurements were made of the temperature and humidity changes at the upper and lower ends of one sample during extraction (Figure 27). A special sampling tube with small holes in the side at the upper lower ends of the sample was made so that temperature could be read directly by a small (4 inches long) mercury thermometer : relative humidity was measured by cobalt thiocyanate papers according to the method of Solomon (1945, 1957). The room temperature, which is said by MacFadyen (1953) to cause considerable change in the physical conditions in the /

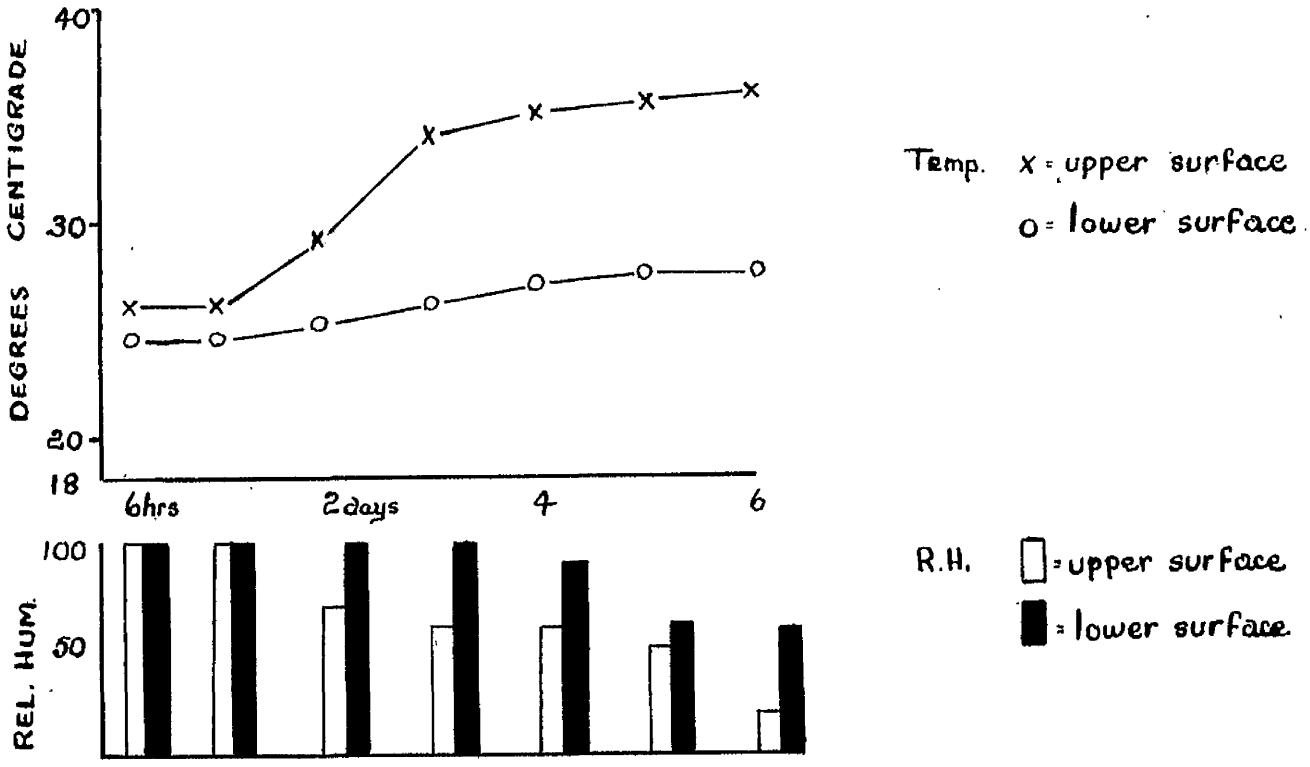


Fig. 27 Physical measurements of temperature and relative humidity of sample in the funnel extraction apparatus.

funnel apparatus, fluctuated only slightly during the period between 17.5°C. and 18.0°C. The temperature difference between the room air temperature and the lower surface of the sample, and between the lower and upper surface of the sample, was approximately 8 centigrade degrees in each case which is similar to the figures given by Macfadyen (1953) for his apparatus.

The efficiency of the apparatus in extracting Collembola compared with a direct count was not tested but a comparison by Macfadyen (1953) of a similar apparatus showed that about one third of the Collembola in the sample was extracted. Efficiency is possibly higher with samples of larger pore structure, such as those studied in the present investigations, but, in any case, the results are considered to be sufficiently consistent to make valid comparisons of the populations.

The flotation extraction apparatus

The apparatus which is similar to that described by Raw (1955) is shown in Plate 7. Details of the processes involved in this extraction method can be followed by reference to Figure 28. The soil sample was first thoroughly broken up in a container containing a solution/

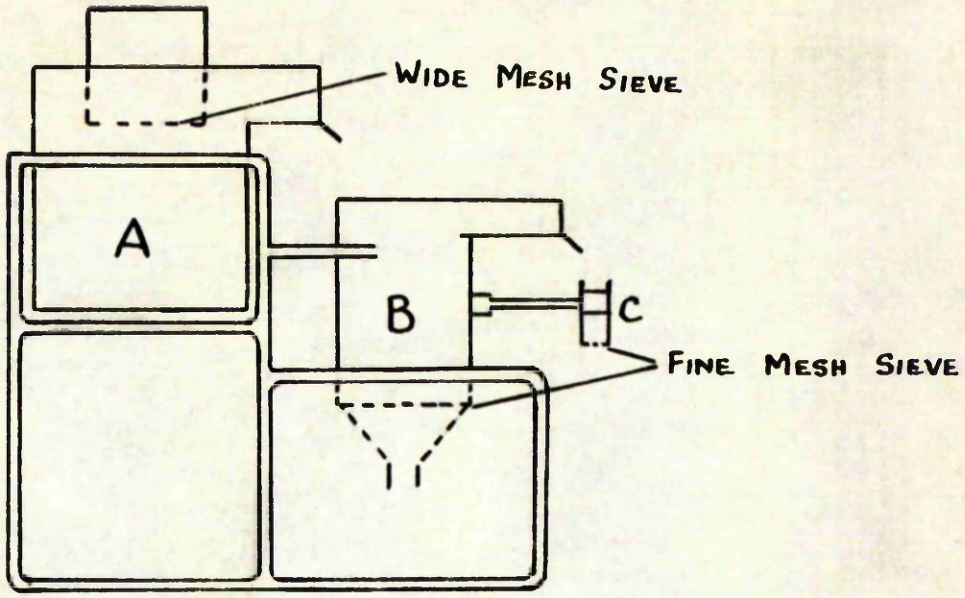


Fig. 28 Diagram of flotation-extraction apparatus.

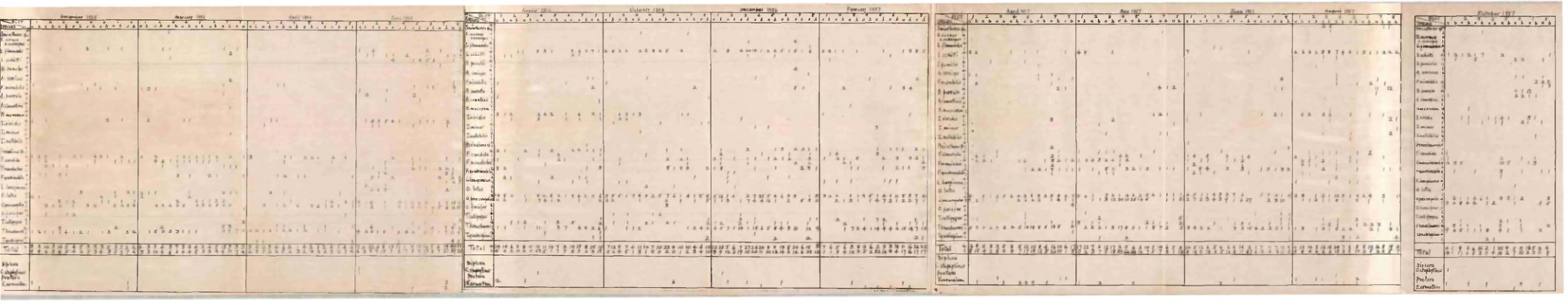
Plate 7 The flotation-extraction apparatus.

in water of 50g. sodium hexametaphosphate and 20g. sodium carbonate per litre. This facilated dispersion of the soil particles by transfer of sodium and calcium ions. The sample was then transferred to the wide mesh sieve and washed into the settling can A. Stones and other large pieces of material were removed from the sieve after thorough washing. The sample was transferred to the "ladell" can B by pivoting the settling can. In the "laddel" can the aqueous solution was allowed to filter through the fine mesh sieve and the can was then filled with a saturated magnesium sulphate solution. Compressed air was blown through the sample to ensure thorough mixing. The mineral soil particles were then allowed to settle and the organic material in the sample was floated from the surface of the solution into tube C which had a fine mesh at the lower end. In the present work little plant material was present in the sample and subsequent separation of the animals was done by direct sorting in a "Perspex" dish under a low-power binocular microscope.

Appendix II. Numerical Data

Table 32. Collembola and other Apterygota obtained from seasonal samplings of bracken soil.

u - upper sample l - lower sample.



Bracken

		28/9/56 Volume mm³	28/9/56 Number	26/1/57 Volume mm³	26/1/57 Number	23/5/57 Volume mm³	23/5/57 Number	Total Volume mm³	Total Number
1. Smithurus viridis	U		0		0		0		0
	L		0		0		0		0
2. Smithurinus flammeolus	U		0	0.0400	1		0	0.0400	1
	L		0		0		0		0
3. Smithurinus aureus f.ochropus	U		0		0		0		0
	L		0		0		0		0
4. Smithurides schötti	U	0.3930	10	1.8080	46	0.1179	3	2.3189	59
	L		0		0	0.0393	1	0.0393	1
5. Smithurides pumilis	U		0	0.0786	2		0	0.0786	2
	L		0		0		0		0
6. Arrhopalites sericus	U		0		0		0		0
	L		0		0	0.0360	1	0.0360	1
7. Brachystomella parvula	U	0.2800	10	0.0560	2	0.1960	7	0.5320	19
	L	0.0560	2		0	0.0840	3	0.1400	5
8. Hypogastrura denticulata	U		0		0	0.0360	1	0.0360	1
	L		0		0		0		0
9. Anurida comellinii	U		0		0		0		0
	L		0		0		0		0
10. Neanura muscorum	U	3.1200	1		0		0	3.1200	1
	L		0		0		0		0
11. Friesea mirabilis	U		0	0.0060	1	0.0060	1	0.0120	2
	L		0		0	0.0120	2	0.0120	2
12. Isotoma viridis	U	0.1800	3	1.4400	1	0.1024	4	1.7224	8
	L		0		0		0		0
13. I.notabilis	U		0		0		0		0
	L		0		0		0		0
14. Isotomiella minor	U	0.0700	1		0		0	0.0700	1
	L		0		0		0		0
15. Folsomia candida	U	0.0325	13	0.0275	11	0.0125	5	0.0725	29
	L	0.0175	7	0.0050	2	0.0250	10	0.0475	19
16. F.fimetaria	U		0		0		0		0
	L		0		0		0		0

Nardus

28/9/56 Volume mm³	28/9/56 Number	26/1/57 Volume mm³	26/1/57 Number	23/5/57 Volume mm³	23/5/57 Number	Total Volume mm³	Total Number
	0		0		0		0
	0		0		0		0
0.0400	1	0.0800	2	0.2400	6	0.3600	9
	0		0	0.0400	1	0.0400	1
	0		0	0.0400	1	0.0400	1
	0		0		0		0
0.1572	4	2.1220	54	0.3537	9	2.6329	67
	0		0	0.0393	1	0.0393	1
	0	0.2751	7	0.1572	4	0.4323	11
	0		0		0		0
	0		1		0		1
	0		0		0		0
0.3360	12	0.9240	33	0.7840	28	2.0440	73
	0		0		0		0
	0		0	0.0720	2	0.0720	2
	0	0.0360	1		0	0.0360	1
	0		0		0		0
0.1760	1		0		0	0.1760	1
	0		0		0		0
	0		0		0		0
0.0480	8	0.0720	12		0	0.1200	20
	0	0.0420	7		0	0.0420	7
0.2400	4	5.7600	4	0.1024	4	6.1024	12
	0		0	0.0512	2	0.0152	2
	0	0.2200	5	0.1320	3	0.3520	8
	0		0		0		0
0.0050	2		0	0.0075	3	0.0125	5
	0		0	0.0075	3	0.0075	5
0.0050	2	0.0300	12	0.0225	9	0.0575	23
	0	0.0225	9	0.0075	3	0.0300	12
	0		0		0		0
	0		0		0		0

Meadow

28/9/56 Volume mm³	28/9/56 Number	26/1/57 Volume mm³	26/1/57 Number	23/5/57 Volume mm³	23/5/57 Number	Total Volume mm³	Total Number
	0		0		0		0
	0		0	0.0400	1	0.0400	1
	0	0.1200	3	0.1600	4	0.2800	7
	0		0		0		0
	0		0		0		0
	0		0		0		0
	0		0		0		0
0.1179	3	0.7074	18	0.0393	1	0.8646	22
	0		0	0.0786	2	0.0786	2
	0		0		0		0
	0		0		0		0
0.0840	3		0	0.1960	7	0.2800	10
	0		0		0		0
0.5040	14	0.3240	9	0.5400	15	1.3680	38
0.1080	3	0.0360	1		0	0.1440	4
	0		0		0		0
	0	0.1760	1	0.1760	1	0.3520	2
	0		0		0		0
	0		0		0		0
0.0360	6	0.1080	18	0.0120	2	0.1560	26
0.0300	5	0.1860	31	0.0060	1	0.2220	37
0.7800	13	40.3200	28	1.1776	46	42.2776	87
	0	5.7600	4	0.0768	3	5.8368	7
	0		0		0		0
	0		0		0		0
	0		0		0		0
	0		0		0		0
	0		0		0		0
	0		0		0		0
	0		9		0	0.0400	16
0.0175	7	0.0225	3	0.0025	1	0.0550	22
0.0225	9	0.0300	12				

		Bracken								Nardus								Meadow							
		28/9/56		26/1/57		23/5/57		Total		28/9/56		26/1/57		23/5/57		Total		28/9/56		26/1/57		23/5/57		Total	
		Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number	Volume mm3	Number
17. F.sanolachei	U	0.3430	7	1.6660	34	0.1470	3	2.1560	44	0.0980	2	1.5190	31	0.5880	12	2.2050	45		0	0.1470	3	0.4990	10	0.6460	13
	L	0.0490	1		0		0	0.0490	1	0.1470	3	0.0490	1		0	0.1960	4		0		0		0		0
18. F.quadriocu-lata	U	0.3080	7	0.9680	22	1.3200	30	2.5960	59	0.3080	7	1.4080	32	2.9040	66	4.6200	105	0.6160	14	0.4840	11	0.0440	1	1.1440	26
	L	0.0440	1		0	0.0440	1	0.0880	2		0		0	0.1320	3	0.1320	3		0	0.1320	3	0.0440	1	0.1760	4
19. Lepidocyrtus lanuginosus	U		0		0		0		0		0		0		0		0		0		0		0		0
	L		0		0		0		0		0		0	0.0236	1	0.0256	1		0		0		0		0
20. Onychiurus armatus	U		0		0		0		0		0		0		0		0	0.1320	3		0		0	0.1320	3
	L		0		0		0		0		0		0		0		0		0		0		0		0
21. O.latus	U		0		0		0		0	0.0880	2	0.0960	2	0.0800	2	0.2640	6		0		0		0		0
	L	0.0880	2		0		0	0.0880	2		0		0		0		0		0		0		0		0
22. O.prosesepatus	U	0.9680	22	1.6800	35	0.6400	16	3.2880	73	0.7480	17	1.0560	22	0.2800	7	2.0840	46		0		0		0		0
	L	0.4400	10	0.5760	12	0.4000	10	1.4160	32	0.1760	4	0.8160	17	0.3200	8	1.3120	29		0		0		0		0
23. O.uliginatus	U		0		0		0		0		0		0		0		0	1.3200	30	1.0560	22	0.4400	11	2.8160	63
	L		0		0		0		0		0		0		0		0		0		0		0		0
24. Tullbergia krausbaueri	U	0.0028	2	0.0112	8	0.0015	3	0.0155	13	0.0014	1	0.0042	3	0.0015	3	0.0071	7	0.0028	2	0.0126	9	0.0020	4	0.0174	15
	L	0.0256	14	0.0764	67	0.0305	61	0.1325	142	0.0154	11	0.0994	71	0.0110	22	0.1258	104	0.0224	16	0.1498	107	0.0255	51	0.1977	174
25. T.callipygos	U		0		0		0		0		0	0.0440	1		0	0.0440	1		0		0		0		0
	L	0.0440	1	0.0440	1	0.0880	2	0.1760	4	0.0440	1	0.4400	10	0.1320	3	0.6160	14	0.0440	1		2		0	0.1320	3
26. T.quadrispina	U		0		0	0.1320	3	0.1320	3	0.0440	1		0		0	0.0440	1		0		0		0		0
	L	0.0880	2	0.0880	2	1.5840	36	1.7600	40	0.2640	6		0	0.8360	19	1.1000	25	0.2640	6		0		0	0.2640	6
Total Collembola	U	6.5494	76	8.5707	164	5.0541	76	16.1899	316	2.9410	63	15.1152	221	7.3669	182	21.4937	466	4.1011	95	49.8593	130	3.5593	91	50.0216	297
	L	3.9843	40		84		127	3.9843	251		26		116		66	3.9294	208		40		161		61	7.4981	266
Diplura Campodea staphylinus	U		0		0		0		0		0		0		0		0		0		0		0		0
	L		0		2		1		3		0		0		0		0		0		0		1		1
Protura Eosentomon armatum	U		1		0		1		2		0		1		0		1		0		3		0		3
	L		0		0		3		3		0		3		5		8		0		1		0		1

Table 71: Comparison of populations on three sampling occasions. Total numbers of of Collembola and other Apterygota and volume of Collembola in 12 samples.

U - Upper Samples L - Lower Samples.