Studies on the biology of moorland Collembola

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Work on the biology of Collembola (Springtails) was carried out between October 1959 and October 1962, on the Moor House National Nature Reserve, in Westmorland. This is an area of high Pennine moorland (1840ft. O.D.) which experiences a sub-Arctic climate.

Population studies were made on Limestone grassland, Alluvial grassland and Heather moor, by means of a statistical sampling method. Juncus squarrosus grassland and the erosion and recolonisation of blanket bog were also studied from the points of view of population densities and species differences.

In an attempt to explain the fluctuations in numbers recorded, biological data was also obtained from laboratory cultures of selected species. Observations on reproductive behaviour, fecundity, egg development, frequency of moulting, sex ratios and age distributions were made. Breeding experiments on members of the Onychiurus armatus species group were carried out, and these revealed what appears to be an unusual form of parthenogenesis; these experiments also showed that in some species, at least, the criteria for the division of the O. armatus species group, which have been questioned by some continental workers, are valid.

Regular sampling of the selected vegetation types provided data on horizontal distribution (aggregations), vertical distribution and seasonal variations in the numbers and biomass of Collembola.

Limestone grassland carried the highest mean annual population density (52.92 x 10^3 per m^2) and Juncus squarrosus grassland the lowest (20.93 x 10^3 per m^2).

A flotation extractor, to remove Collembola from organic soils, was designed and built, and this may prove an important step forward in the technique of studying the moorland fauna.

The work forms a contribution to the study of moorland ecology, but it is clear that to obtain a comprehensive picture of the ecological importance of Collembola on moorland, a great deal of work will be necessary in the future.

Studies on the biology of moorland Collembola

by

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..... being a thesis presented in candidature for the degree of Doctor of Philosophy in the Durham Colleges in the University of Durham, September, 1962.

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INTRODUCTION

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INTRODUCTION

The micro-arthropods of British uplands have received little attention from workers in this country. This thesis contributes towards filling this gap in our knowledge by providing information on the Collembola, or springtails, of a restricted area in the northern Pennines, namely the Moor House National Nature Reserve, in Westmorland.

The Collembola are usually given the status of an order, in the Sub-Class Apterygota (Insecta), although there is some diversity of opinion concerning their relationships with other Apterygote groups and the Pterygote insects in general. Imms (1936) considers that they are best regarded as a specialised offshoot from the base of the early Symphylan stock, but stresses the remoteness of the group from the main evolutionary line of the Insecta. Ewing (1942), Wygodzinsky (1943), Jeannel (1949), Paclt (1954) and Ross (1955) give more recent assessments of the taxonomic position of the group but, for the most part, support the conclusions of Imms.

Whilst it is generally considered that the group retains rather primitive features, Gisin (1943), Delamare-Debouteville (1950) and Paclt (1956) have suggested that

many of these are adaptations to life in the soil; Delamare-Debouteville points out that the persistence of primitive characteristics is typical of soil-living groups and attributes this to the stability of the soil as an environment. Gilyarov (1949) suggests that aerial habitats were first colonised by insects via the soil. Collembola actually living in the soil spaces seldom exceed 3 mm. in length but the surface and litter-living forms may reach a length of 6-7 mm.

Numerically the Collembola usually take second place only to the Acari in the air-breathing fauna of the soil, and on occasions (Stockli 1943, 1946) they have been found to be even more numerous than the mites. Probably as a result of the frequency with which they are found in soil samples, there is an extensive literature on the group, although in Great Britain few ecological studies have been made.

The literature on the fauna of soils deals mainly with mineral soils, and is of interest primarily from the point of view of comparison with the moorland peats. However, data is included here on two types of mineral soils occurring on the Moor House Reserve, namely the mulls of the Limestone grassland and the Alluvial grassland of the streamsides. Information on the Collembola of acid peat soils, with the exception of a single paper by

Murphy (1955), occurs only in the continental literature.

Records of Collembola from northern England exist in the publications of Bagnall (1910 et seq.), Gisin (1956) and Murphy (1955, 1958, 1960). For other upland and moorland areas records may be found in the publications of Carpenter and Evans (1899), Evans (1901), Bagnall (1914 et seq.), Womersley (1926 et seq.), Davies (1934) and Milne (1960). With the exception of that of Milne (1960) all these papers are of a taxonomic nature but contain brief notes on the ecology of the species concerned. Murphy (1955), who worked on the Moor House Reserve before the present study was begun, has provided the only ecological information available in this country concerning the Collembola of high moorland, although Jackson (1928) and Macfadyen (1952) dealt with the fauna of fen land, which has a similar soil-type and plant cover.

Due to the advances in the taxonomy of the Collembola, generally, and the revised species concept applied to certain groups, it is often difficult or impossible to make comparisons with the published data of many of the earlier workers. However, this has been done wherever possible.

The work recorded in this thesis falls into two major categories; firstly, the information derived from field work and regular sampling of the area; and secondly,

information obtained from laboratory cultures of various selected species. Integration of the two aspects of the study has been made where relevant.

In this thesis botanical nomenclature follows Clapham et al (1952) for higher plants, Watson (1953) for lichens and Watson (1955) for mosses; soil nomenclature follows the classification of Kubiena (1953).

PART A.

THE BACKGROUND

I. THE STUDY AREA

I. THE STUDY AREA

1) Introduction.

The Moor House National Nature Reserve (N.R.S0) is located in the northern Pennines (Nat. Grid Ref. NY 758329), 10 miles south of Alston, Cumberland, although the Reserve itself lies in Westmorland. Situated to the south-east of Cross Fell, much of the Reserve is over 1800ft. O.D., and includes the three principal fells of Great Dun (2780 ft.), Little Dun (2,701 ft.) and Knock (2604 ft.). The three fells form the peak of the western escarpment, and to the east the ground slopes more gently over an area of the Reserve forming part of the headwaters of the River Tees. The entire area is much dissected by streams which, in the west, run into the River Eden. Fig. 1 shows the part of the Reserve where most of the work was carried out; the sampling sites are numbered and these are referred to later in the text.

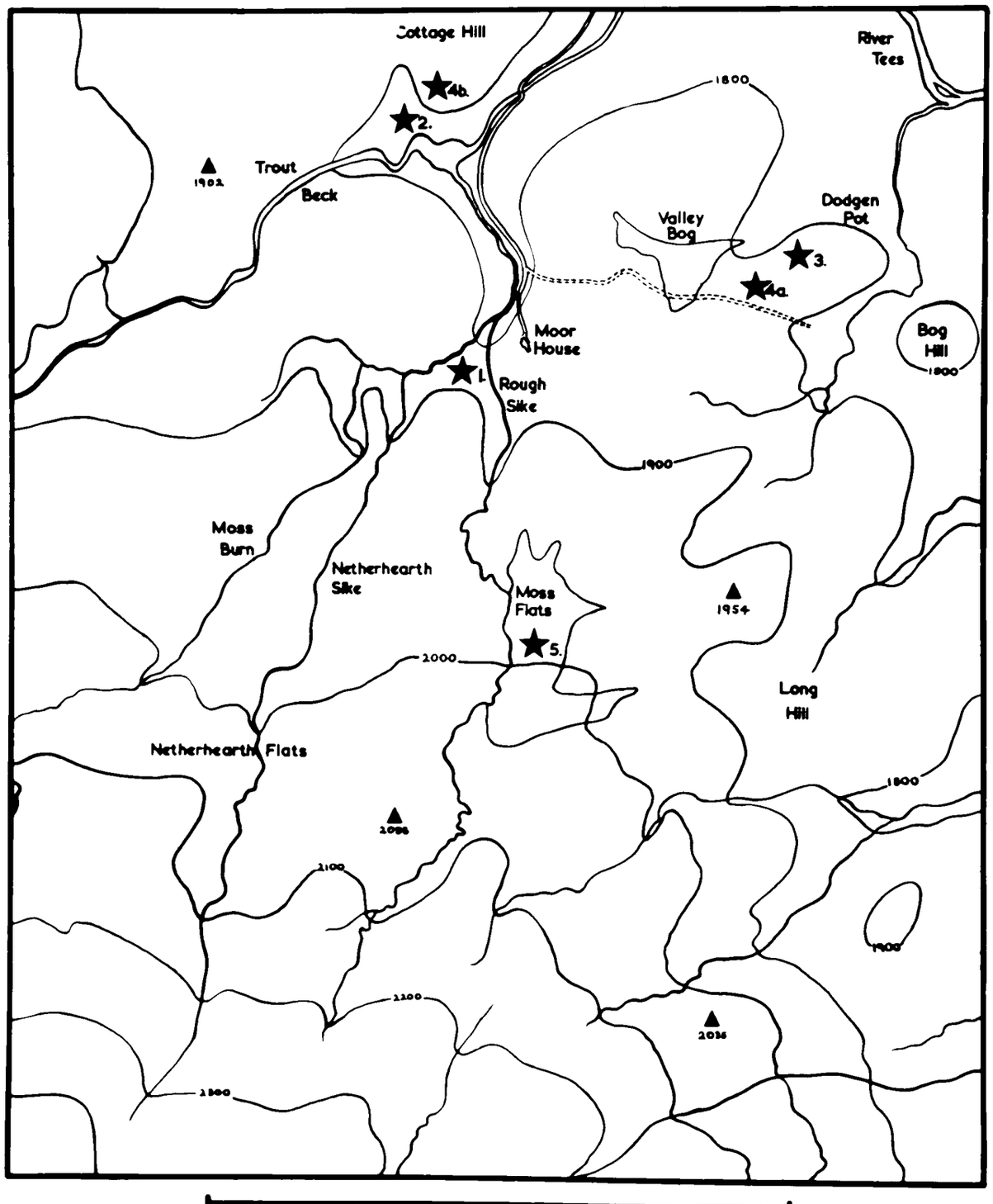
The climate is characteristically cold and wet (Manley 1952), and the whole area is overlain by blanket peat in various stages of erosion and regeneration. At present the forces of erosion appear to be predominant, and the Reserve is part of moorland forming a typical Grousemoor, in which the original water-table has been lowered. Mull soils are rare, and are restricted to the

Fig. 1.

Map of part of the eastern slopes of the Moor House Reserve. The sample sites are indicated by black stars, and the numbers refer to the different vegetation and soil types mentioned in the text.

Fig. 1.

Moor House Reserve – Sample sites.



1 mile.

limestone outcrops and the stream sides. The whole area, apart from special enclosures, is grazed by sheep throughout the summer.

General descriptions of the Reserve have been made by Conway (1955), Nicholson (1957), Svendsen (1957) and Coulson (1959).

2) The pedalogical background.

The geology of the area has been studied by Dunham (1948) and by Johnson (1958), and according to these authors, the area lies on the Yoredale series of Carboniferous limestones, sandstones and shales. The latter author has produced maps of both the geology and the pedology of the Reserve.

Since the area is covered almost entirely by a layer of glacial drift, and above this by blanket peat, the basement rock has little effect on the soil structure except where it has been laid bare by the forces of erosion. These areas are few, and here the outcrops project from the surface of the drift, and there is little chance of the establishment of soils derived directly from the rock. Areas from which the peat has been eroded, and where the drift lies upon limestone, have a soil referable to a Eutrophic or Mesotrophic Braunerde (Kubiena 1953). Typical examples of this may be found on the Reserve in House Field, and at Green Hole.

Except along the stream sides, the rest of the Reserve is covered by deep peat, and the soil present over most of the area is Dystrophic Peat Ranker. In areas where the peat has been disturbed, along the edge of the moor or along stream sides, peat slips occur which lose their original plant cover and become covered by grasses. In such 'moor-edge zones' the soil type can be referred to as Peat Anmoor.

In the wide range of temporary and semi-permanent soils found along the stream sides, a fourth important soil type occurs. This is an azonal soil and in some places, eg. Trout Beck Flats, it forms alluvial fans. It is formed by an admixture of mineral particles from the stream beds, and peat eroded during the formation of haggs which drain into the streams; a much finer and more acid soil than the Braunerde, it supports a similar vegetation.

The whole area may be considered to be both climatically and geologically strongly podsolising.

3) The botanical background.

Lewis (1904) included the Reserve in a survey of the botany of the northern Pennines and his general conclusions may still be applied to the area. The moor is almost entirely 'blanket bog', overlying peats reaching a thickness of 12-14 ft. At the present time, much of the

bog is thought not to be in an actively growing condition, as in this state it should have a more or less continuous Sphagnum cover (Pearsall 1950); at Moor House this occurs only in a few restricted places. Over the rest of the moor the Sphagnum cover is discontinuous or absent, resulting in a vegetation type referred to by Pearsall as 'mixed moor'. However, this is close to the continental concept of 'Hochmoore' (raised bog), and Valley Bog, one of the few areas at Moor House believed to be still actively growing, may be of this type (Murphy 1955). The difference between blanket bog and Hochmoore lies in the mode of peat production; whereas in the former peat is probably built up by a steady, uniform growth, Osvald (1923) has suggested that the raised bog is built up by a complex of raised hummocks and water-filled hollows succeeding each other.

Lewis (1904) divides the eastern slopes of the area into three types, distinguished primarily by the relative abundance of Eriophorum:

i) An upper zone of Calluna/Vaccinium moor, developed on dry slopes and shallow peats.

ii) Lower lying Calluna/Eriophorum moor, growing on deeper peats. This is mixed moor, although it should be recognised that the term encompasses a variety of habitats;

some may be very wet, having large amounts of Sphagnum and very little heather litter present, e.g. Cottage Hill, north of Troutbeck (Fig. 1), whilst other areas may be relatively dry, with little Sphagnum and an accumulation of heather litter, e.g. Burnt Hill.

iii) Eriophorum bog, where the peat becomes very wet, denudation is rapid and bare peat is common, e.g. Moss Flats. This type of vegetation is typical of the erosion complex, where hagg formation has become so exaggerated that patches of the original vegetation remain only as hummocks on the bare peat, which is in places recolonised by Eriophorum angustifolium and E. vaginatum.

Areas of shallow peat (Peat Anmoor) in the moor edge zones support a flora dominated by grasses, particularly Juncus squarrosus and Festuca ovina. Grasses are also dominant on the mull soils of the stream sides and limestone-drift areas; here Festuca ovina and Agrostis tenuis are the commonest species.

Further details of the plant cover will be found in the following section on the specific sampling sites.

4) The sampling sites.

Five main sampling sites were selected, these being typical of the major habitats found on the Reserve.

a) The Limestone Grassland Site (Plate 1).

Situated between Rough Sike and Moss Burn (1. Fig. 1), the site has a soil type referable to a Eutrophic or Mesotrophic Braunerde. The depth of the soil rarely exceeds 50 cm., due to the bedrock, Tynebottom Limestone, being close to the surface. The soil is well aerated, both earthworms and moles being present, and arthropods may be found throughout the soil profile. The drainage is good, and the pH of the soil varies from 4.9 (Banage 1960) to 6.6 (A. Eddy, pers. comm.). A typical upland grassland, the area is dominated by Festuca ovina (Plate 2a), whilst Agrostis canina and A. tenuis are also present, though less commonly. The site is typical Festuca-Agrostis grassland (Pearsall 1950) and it is cropped by sheep during the summer months. The vegetation mat is some 3 cm. thick, and during sampling this was separated from the soil proper.

b) The Alluvial Grassland site (Plate 3).

This site is located in the angle formed by the junction of Troutbeck and Nether Hearth Sike (2. Fig. 1). The azonal soil is a mixture of peat and mineral particles, and here again both earthworms and moles are present. A well-aerated soil, it is somewhat denser than that of the limestone grass-land, and the microcavities are much

PLATE 1.

The Limestone Grassland site looking westwards.

PLATE 2.

a) The vegetation of the limestone grassland; typical *Festuca*-*Agrostis* grassland with *Thymus drucei* in flower. x $\frac{1}{4}$.

b) Outcropping limestone on the limestone grassland, with *Rhacomitrium lanuginosum* and *Cladonia sylvatica*. x $\frac{1}{4}$.

PLATE 3.

a) The Alluvial grassland site looking south.

b) The Juncus squarrosus site (Dodgen Pot), facing north; the Juncus squarrosus area lies between the Calluna moor in the background and the Juncus effusus in the foreground.

smaller than in that soil. The vegetation is very similar to that of the limestone grassland, but there are no lichens, whereas Cladonia rangiferina is found commonly on the braunerde. The grass is cropped by sheep during the summer and the vegetation mat is similar in thickness to that of the limestone site; here again, it is separated from the soil proper during sampling. The plant cover may be said to be intermediate between the species-rich Festuca-Agrostis limestone grasslands and the poor Festuca-Agrostis grasslands of the high level acid podsols. The pH ranges from 4.5 to 6.0 (A. Eddy, pers. comm.).

c) The Calluna site (Plate 4).

An area of mixed moor was selected to the north-west of Dodgen Pot Sike (3. Fig. 1), this being the same area sampled by Banage (1960) for Nematodes. Calluna vulgaris was the dominant plant, Eriophorum vaginatum, E. angustifolium, Empetrum nigrum, Vaccinium myrtilis and Rubus chamaemorus occurring commonly. Sphagnum rubellum was found to be the dominant Sphagnum species, and Cladonia sylvatica, C. impexa and C. uncialis were plentiful. Hypogymnia physodes occurred as an epiphyte on the Calluna. The soil profile was that of a typical Dystrophic Peat Ranker. The water table was found to be lower than in some areas of mixed moor, e.g. the Cottage Hill site, and the Sphagnum cover was less complete,

PLATE 4.

The Dodgen Pot *Calluna* site.

a) Close up of the vegetation cover; *Calluna vulgaris*, *Eriophorum vaginatum* and *Rubus chamaemorus* (top centre). x $\frac{1}{4}$.
The rule is 30 cm. long.

b) General view of the sampling site, looking west.

there being much more heather litter present than in that area. This facilitated sampling, as the litter was much more easily sampled than the moss. Banage (1960) records the pH of this site as 4.5 - 4.9.

d) The Juncus squarrosus site (Plate 3).

A moor-edge zone (4a. Fig. 1) just below the Calluna site described was first sampled during 1960, but due to frequent previous sampling it was decided to utilise a new site after one set of samples had been taken. The new area (4b. Fig. 1) was located below the Cottage Hill Calluna site, on a peat-slip above the alluvial flats of Troutbeck. The following description applies equally to both sites sampled.

The soil-type may be referred to a Peat Anmoor, and cores taken tended to break off at a depth of about 3 cm., where the fermentation layer merged into dense black peat, which is not penetrated by arthropods. The vegetation is dominated by Juncus squarrosus and Festuca ovina, with Agrostis canina, A. tenuis and Deschampsia flexuosa occurring frequently. Galium hercynium, Nardus stricta and Potentilla erecta were present, together with Sphagnum mosses (mainly S. recurvum), Polytrichum commune and the liverwort Lophocolea bidentata. Like the other two grassland areas this is cropped by sheep. The pH is 4.5-4.6 (Banage 1960).

e) The erosion complex of Moss Flats (plate 5).

The site selected for the study of the fauna of the erosion complex was an area of Moss Flats (5. Fig. 1) which lies near the head of Rough Sike. Here the blanket bog is dissected by haggs into tabular masses, at times to such an extent as to leave only small heather-covered hummocks on a mass of bare peat. When a hagg is first formed, loose peat falls into the channel and is washed away; the vegetation tends to bind the surface peat, and a lip is formed on the edge of the hagg. As it dries out its cover of Calluna is lost, together with the mosses, and the lip becomes covered with Cladonia coccifera agg.. Because of the erosion of peat from beneath the lip, this comes to form an overhang (Plate 6a), and the peat here is no longer waterlogged; this makes it possible for arthropods to enter into its spongy mass.

The improved drainage and the exposure, both resulting from the formation of the hagg, allows the edge of the blanket bog to dry out and mosses are not normally found closer than one metre from the edge of the overhang.

Later in the erosion cycle the dissection of the bog becomes so extensive that only small hummocks of vegetation remain on exposed areas of bare peat (Plate 6b). Each hummock or anti-hagg (Bower 1959) has a gradual slope of bare peat up to its front, that is to say, the side

PLATE 5.

Typical peat erosion down to the bedrock, on the northern side of Moss Flats. The stream is 1 metre wide.

PLATE 6.

a) The hagg lip or overhang, with its cover of Cladonia coccifera agg.. x $\frac{1}{6}$

b) A residual hummock on Moss Flats, looking south; the prevailing wind is from the right side of the photograph. x $\frac{1}{25}$

The rule is 30 cm. long.

facing the prevailing winds. Here the hummock has a 'scarp' slope of bare peat; the dip slope of the hummock is covered by vegetation, and this is the remains of the original blanket bog. Mosses are generally absent, due to the drier, more exposed nature of the hummock, and Calluna vulgaris, Erica spp., and Empetrum nigrum are usually the only species found on the dip slope; above the scarp slope a small overhang is sometimes present, and like the hagg lips this is covered by Cladonia coccifera agg..

Surrounding the hummocks the bare peat surface is covered by the remains of birch trees (Betula) long buried in the peat and now uncovered by the processes of erosion. Some of the drainage channels have cut into the peat as far down as the bedrock, which in this area is sandstone, and in places damp runnels are formed in which small fragments of sandstone occur plentifully (Plates 5 & 8b).

In some places recolonisation of the bare peat is taking place. Eriophorum angustifolium (Plate 7a) is the first plant to gain a foothold in this habitat, and when it has formed a mat on the surface the more tussocky E. vaginatum (Plate 7b) may become established. It is thought that once such a plant cover becomes permanent Calluna is able to flourish once more.

PLATE 7.

a) Eriophorum angustifolium growing on bare peat on Moss Flats. x $\frac{1}{10}$

b) Eriophorum vaginatum tussocks growing on bare peat on Moss Flats; E. angustifolium in the background. x $\frac{1}{10}$

The rule is 30 cm. long.

When the bare peat is left undisturbed for some time in areas where birch roots are not projecting from the surface, an algal mat forms. As this dries it cracks, and gives rise to large flakes (Plate 8a), some 12 ins. in diameter. Beneath these Collembola soon become established.

Banage (1960) cites a pH of 4.3-4.6 for the bare peat.

f) Other sampling sites.

Apart from sampling regularly in the sites described above, qualitative samples were taken from the following habitats:

i) Juncus effusus (Plate 3b). The litter layer formed at the base of this rush was sampled regularly throughout the period of the field work. The site selected was the alluvial flats of Troutbeck, close to the alluvial grassland site.

ii) Mixed Moor on Cottage Hill. This was a wetter site than that above Dodgen Pot Sike and, apart from qualitative collecting, samples for microdistribution were taken here.

iii) Polytrichum. Beds of P. commune (Plate 9b) occurring on the Calluna site, the limestone grassland site, the two Juncus sites, and elsewhere on the Reserve were sampled several times.

PLATE 8.

a) Bare peat cracking and flaking on Moss Flats; on the top right of the photograph the algal mat is flaking away from the mass of peat. x $\frac{1}{4}$.

b) Fragments of sandstone on the bare peat on Moss Flats; the typical habitat of Isotoma antennalis. x $\frac{1}{4}$.

iv) Areas of Sphagnum, both on Valley Bog and in flushes surrounding Moss Flats (Plate 9a), were frequently sampled.

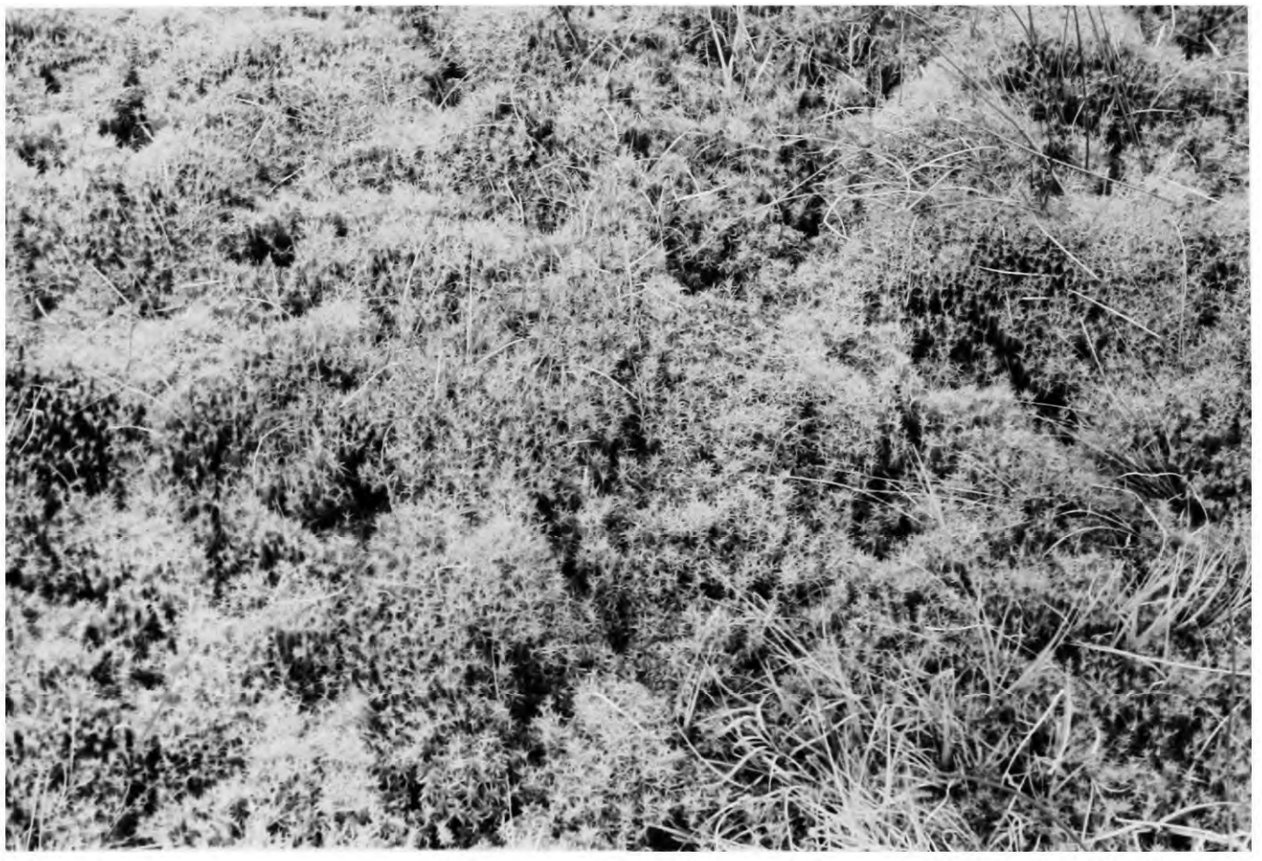
v) Water bodies. The surfaces of pools on the open moor and on the various streams on the Reserve were examined from time to time.

Habitats similar to the main sampling sites were collected over frequently, and collections were made in the upper regions of Crowdundle Beck, on the western side of the Reserve.

PLATE 9.

a) Sphagnum flush on the northern side of Moss Flats.
The foreground is 4 metres in width.

b) Polytrichum bed in Sphagnum flush. x ¼.



II. THE MOORLAND HABITAT

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The ecological investigation of moorland animals, of which this work forms a part, was begun in the hope that with its rigorous climate and limited flora, moorland would provide a relatively simple natural habitat in which an analysis of the fauna could be carried out. Subsequent work has shown that the interaction of the climate, which gives rise to processes of erosion and regeneration, with the effects brought about by man in sheep and grouse management, has produced a highly complex system (Cragg 1961).

1) Climate.

a) Introduction.

Manley (1936) has compared the climate of the northern Pennines with that of the sub-Arctic climate at sea level, and Pearsall (1950), by comparing January and July mean temperatures with those of Ben Nevis, shows that the Moor House Reserve is typical of the montane zone of Great Britain. Further information concerning the Moor House climate exists in the literature (Manley 1943, Green 1958, 1959). Since 1952, when the field station was first opened, meteorological data have been collected regularly. The data presented here are taken from the Meteorological Summary for Moor House where the station is at a height of 1,840 ft. O.D.. Table 1

Table 1. Summary of meteorological data for Moor House, 1960 and 1961.

	1960	1961
Annual rainfall (ins.)	72.8 (185cm.)	78.4 (199cm.)
Mean daily temperature °F.	41.6 (5.4°C.)	41.9 (5.5°C.)
Number of rain days ≠	250	241
Period of snow cover (days)	61	55
Days of ground frost	143	153
Average daily sunshine (hrs.)	3.14	2.80

≠ Days on which rain fell.

summarises the general climatic data for 1960 and 1961.

b) Temperature.

The monthly mean maximum and mean minimum temperatures during the two years of field work are shown in Fig. 2. Similar temperature conditions prevailed over both years (see Table 1) but January and February 1961 were appreciably warmer than the same months in 1960.

Due to variable weather conditions, where damp misty days are followed by dry cloudless ones, there is a wide range of daily temperatures, and frost occurred in all months in 1960 and 1961.

c) Precipitation and evaporation.

Pearsall (1950) records that an average annual rainfall of 50-55 in. (127-140 cm.) is sufficient to give rise to conditions of bog growth. Table 1 shows that the Moor House Reserve lies well within the limits of bog growth, with an annual rainfall of over 70 in. (178 cm.). Table 2 shows the precipitation and evaporation which occurred during 1960 and 1961. In only two months, May and June 1960, did the potential evaporation exceed the precipitation.

Fig. 2.

Monthly mean maximum and minimum temperatures recorded at the Moor House Meteorological Station, 1840 feet O.D., for 1960 and 1961.

Fig. 2.

Monthly mean maximum and minimum temperatures — Moor House 1960-61.

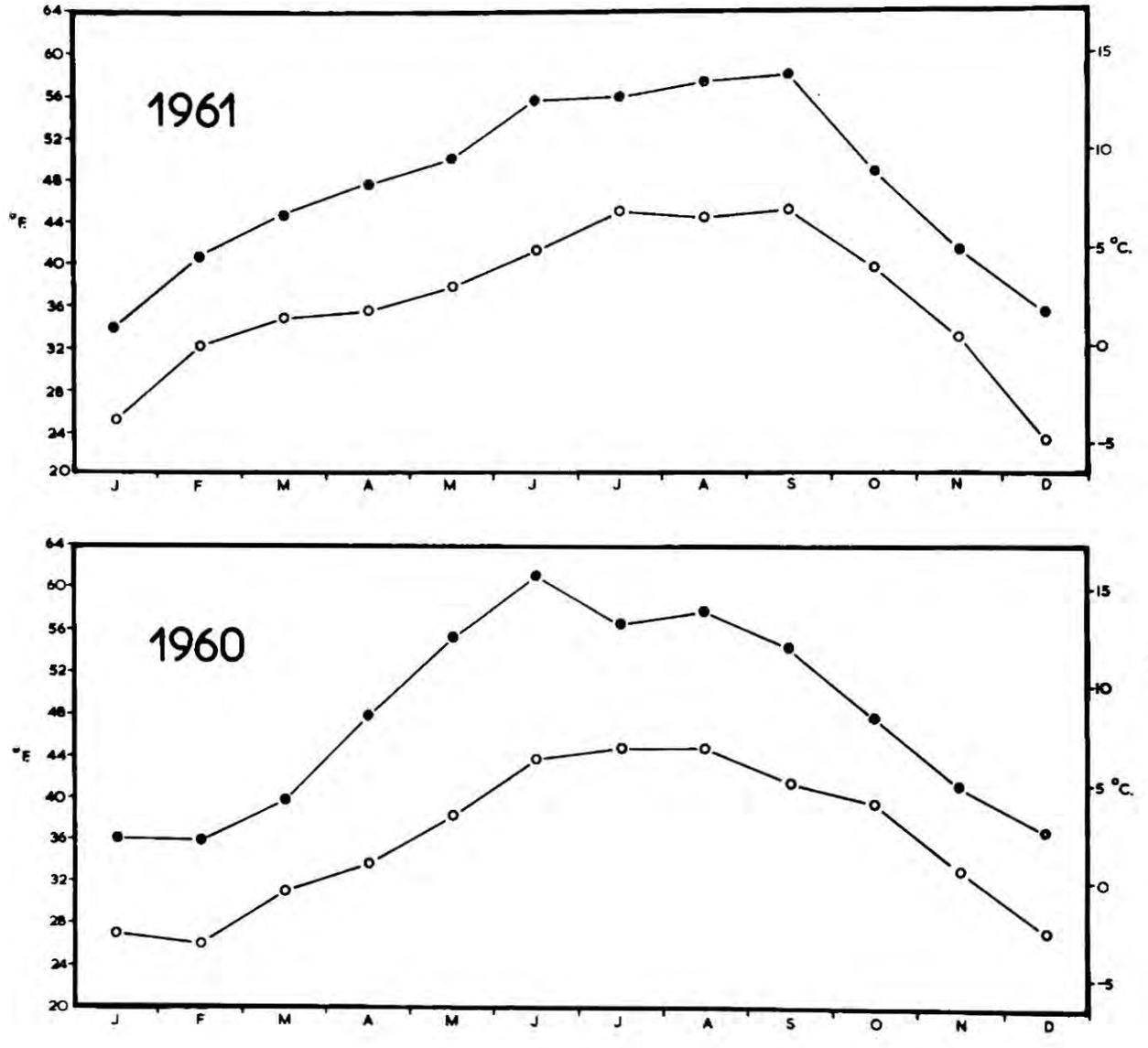


Table 2. Monthly Precipitation and Potential Evaporation (in ins.), 1960 and 1961.

Data from Meteorological Summaries for Moor House, 1960 and 1961.

Month	1960 Precip-itation	1960 Evapor-ation	1961 Precip-itation	1961 Evapor-ation
January	8.4	0.5	10.1	1.0
February	7.4	0.6	6.7	0.5
March	2.7	0.9	4.9	2.1
April	5.1	1.9	4.6	1.5
May	2.5 ≠	3.0 ≠	3.5	2.5
June	3.0 ≠	3.7 ≠	3.3	2.2
July	7.9	2.0	7.7	2.2
August	4.3	2.2	8.7	1.5
September	3.3	0.9	5.1	1.5
October	8.4	0.6	11.4	0.5
November	12.3	0.2	6.3	-0.2
December	7.5	0.2	6.1	0.3
Total Year	72.8	16.7	78.4	15.6

≠ Only two months where evaporation exceeded precipitation.

d) Relative Humidity.

The Relative Humidity of the atmosphere is associated with the rainfall, and as would be expected from the rainfall figures in Table 2, high values are recorded at Moor House. The average Relative Humidity at 0900 G.M.T. at Moor House in 1960 was 89.3% and in 1961, 89.8%, compared with an annual average of about 80% at sea level (Manley 1952).

2) Soil water content.

a) Introduction.

Crump (1913) has shown that the 'relative humidity' of peaty soils depends on the humus content, and Pearsall (1950) has used the water/humus ratio as a measure of this. Banage (1960) has pointed out that confusion might arise from the use of the term 'relative humidity', and has proposed in its place the term 'index of humidity'; this term is adopted here, and is applied to both organic and mineral soils. The indices of humidity for peat and mineral soils are not strictly comparable, but serve to show the relative water content (see footnote to Table 7).

b) Measurement and drainage.

On all sampling dates after and including 23 May, 1960, measurements of soil water content were made on all

sample units collected. This provided a long series of data which is summarised in Tables 3-7. The sample units were weighed before extraction of the Collembola, and later they were dried at a temperature of 105°C. to constant weight.

Whilst the mineral soils were relatively well drained, all the peat soils were liable to waterlogging, and because of this arthropods were rarely found below 3 cm. deep (see page 237). Where erosion occurred on the moor, the peat soils were better drained, as is indicated in Table 4. Conway and Millar (1960) have provided data on the drainage of small peat catchment areas at Moor House, and have shown that the uneroded moor has a considerable water storage capacity in its surface layers, as compared with an eroded catchment area.

3) The relationships of the soil types.

Pearsall (1950) has summarised the relationships of upland soils, and following this scheme Table 8 gives a classification of some of the Moor House soil types. The indices of humidity are averages for a period of twelve months, and values of pH are taken from Banage (1960) and A. Eddy (pers. comm.).

Table 3. Water content of samples from heather litter on mixed moor.
The figures are indices of humidity.

Date	Upper 3 cm.
23.1.61	7.36
20.2.61	9.18
18.3.61	6.50
18.4.61	8.27
15.5.61	7.73
5.6.61	5.67
5.7.61	8.01
28.7.61	9.81
28.8.61	7.53
25.9.61	9.42
23.10.61	9.35
22.11.61	7.12
11.12.61	8.92

Figures are means of 15 sample units in all cases.

Table 4. Water content of samples from different vegetation types on the erosion and recolonisation complex on Moss Flats.

The figures are indices of humidity.

Date	Hummock top	Hagg lip	Eriophorum angustifolium	Eriophorum vaginatum
27.2.61	3.63	2.52	4.39	4.01
29.5.61	1.04	1.09	3.61	3.44
5.9.61	3.26	1.75	4.32	3.60
4.12.61	3.40	2.96	5.70	7.25

Figures are means of 15 sample units each 3 cm. deep, except for Eriophorum vaginatum where the figures are means of 8 units 6 cm. deep.

Table 5. Water content of samples from Juncus squarrosus.

The figures are indices of humidity.

Date	Upper 3 cm.	Lower 3 cm.
20.2.61	5.78	5.07
15.5.61	5.50	-
28.8.61	6.56	-
11.12.61	7.55	-

Figures are means of 15 sample units in all cases.

Table 6. Water content of samples from cropped Limestone grassland.

The figures are indices of humidity.≠

Date	Upper 3 cm.	Lower 3 cm.
23.5.60	0.89	0.73
27.6.60	0.57	0.54
18.7.60	1.07	0.76
22.8.60	1.08	0.71
26.9.60	1.16	0.80
24.10.60	1.46	0.87
14.11.60	1.70	1.12
16.1.61	1.77	1.02
13.2.61	1.34	0.86
13.3.61	1.68	0.65
10.4.61	1.57	0.97
8.5.61	1.73	1.08
5.6.61	0.64	0.51
5.7.61	1.38	0.92
28.7.61	1.42	0.90
28.8.61	1.39	1.05
25.9.61	1.45	0.99
23.10.61	1.87	1.17
22.11.61	1.66	1.14
11.12.61	1.94	1.14

Figures are means of 15 sample units in all cases.

≠ See footnote to Table 7.

Table 7. Water content of samples from grazed alluvial grassland.

The figures are indices of humidity.≠

Date	Upper 3 cm.	Lower 3 cm.
6.6.60	0.47	0.34
4.7.60	0.53	0.32
25.7.60	0.76	0.51
29.8.60	0.81	0.60
26.9.60	1.08	0.60
24.10.60	1.11	0.72
14.11.60	1.18	0.72
16.1.61	1.11	0.72
13.2.61	0.91	0.71
13.3.61	1.00	0.70
10.4.61	1.03	0.68
8.5.61	1.19	0.76

Figures are means of 15 sample units in all cases.

≠ Note. In both mineral soils the 'index of humidity' is equivalent to the ratio $\frac{\text{water}}{\text{dry weight}}$, and is thus not a true 'index of humidity'; the water content is shown in this way purely for purposes of comparison with the water content of the organic soils. An index of humidity of 1 is equivalent to a 50% water content, of 2 to a 67% water content, 3 to a 75% water content, etc.

Table 8. Classification of Moor House soil types.

Soil	pH	Index of humidity	Group	Classification of Kubiena (1953)
Bare peat with *E. angustifolium*	4.3-4.6	4.51	Blanket peat	Dystrophic Peat Ranker
Heather litter on mixed moor	4.5-4.9	8.11	Blanket bog	Dystrophic Peat Ranker
Juncus squarrosus	4.5-4.6	6.35	Peat mor	Peat Anmoor
Alluvial grassland	4.5-6.0	0.93≠	Flush	-
Limestone grassland	4.9-6.6	1.34≠	Mull (Lime poor)	Mesotrophic Braunerde

≠ See footnote to Table 7.

III. TAXONOMY AND SYSTEMATICS

III. TAXONOMY AND SYSTEMATICS

1) Introduction.

In this section a check-list of the Collembola of the Moor House Reserve is given, together with notes on their taxonomy and autecology. Murphy (1958, 1959, 1960) has provided redescriptions of species from this area, which were previously inadequately known, but where it was considered necessary, further taxonomic notes were added . Localities are quoted for each species, extensively for the rarer ones, whilst for the commoner species a few typical records have been selected

During the present work 56 species of Collembola have been collected, including three which were new to the Moor House Reserve and one which was new to the British Isles. Several instances have arisen where it was found necessary to revise the Moor House check-list, and this is indicated ih the notes on the species in question. Several species recorded by Murphy at Moor House have failed to appear in the collections made by the present writer, but this may be due to a change in status of the species concerned.

2) The present state of Collembolan systematics.

The classification of the Collembola is essentially due to Borner (1906) although great advances have been made in the taxonomy of the specific level during the past two decades. Such are these advances, that in some cases, e.g. the Onychiuridae, present workers are unable to make comparisons with much of the published data of the earlier workers because of the existence of species groups. Again not all these advances are universally recognised; for example, Stach (1954) writes of the sub-division of the Onychiurus armatus species group, by Gisin (1952): "The rest of the species erected by Gisin and enumerated here, seem to be only insignificant ecological or local modifications. Therefore I do not think that such a separation of the species Onychiurus armatus (Tulb.) is desirable or right". Since each school of thought has its following, some confusion is still present in the current literature. Clearly from the ecological standpoint, it is essential that even the smallest differences between individuals and distinct populations are emphasised; should two members of a species group subsequently prove to be conspecific the data can be pooled, but data may be wasted after an initial pooling should specific differences ultimately be established.

It is for this reason that the narrow species concept of Gisin has been utilised in the present work. However, use of generic names is purposely conservative, and again follows Gisin. The proposals of Bagnall (1949 et seq.), concerning new genera of restricted scope, are rejected since they are considered to be often of an arbitrary nature and premature in that the taxonomy of Collembola is still based entirely on morphological characters. Even so, the taxonomy is sufficiently advanced for little further progress to be made on a purely descriptive morphological basis, and the remaining problems will be solved only by breeding experiments. Some such experiments are described later in this work, and these concern the splitting of the Onychiurus armatus species group.

3) The identification of the Moor House fauna.

a) Previous identification.

When this work was begun in 1959, D.H. Murphy kindly presented the writer with a species list of Collembola made from collecting on the Moor House Reserve. This contained 62 species of which three were new to science (Murphy 1959, 1960). This species list largely reduced the initial work, and together with the Durham

University collection of Collembola proved invaluable during routine identification.

b) Techniques.

Collections were normally preserved in 70% alcohol, to which a little glycerol was added to prevent accidental desiccation. For specialised taxonomic purposes rather better results were obtained by fixation in Gisin's fixative for two days before mounting. The formula for this is as follows:

95% alcohol	750 ml.
Diethyl ether	240 ml.
Glacial acetic acid	30 ml.
40% formalin	3 ml.

The insects were killed by direct introduction into the fixative.

Manipulation of individual Collembola was carried out by means of a piece of fine fuse wire flattened into a minute spatula by hammering; this was mounted in a glass rod. Orientation of the various parts of an individual on a slide was achieved by means of an eye-lash mounted in wax on a dissecting needle.

For routine work temporary mounts were made in lacto-phenol, and specimens which it was desired to keep were ringed with gold size on a turntable. More

permanent preparations were made using Goto's modification of Polyvinyl lactophenol. This is made up as follows:

i) 16 g. of Phenol detached crystals are dissolved in 14 ml. of Lactic acid.

ii) 5 g. of Polyvinyl alcohol (Bush, Beach & Gent Beacon Brand W/28/02) are mixed with 20 ml. of distilled water, which is added dropwise, to form a thick paste. This is then heated on a water bath.

iii) The Lactophenol is then added and the mixture reheated whilst stirring, until transparent.

This mounting medium has the advantage of drying relatively quickly, and there was no necessity to ring with wax as in the method recommended by Gisin (1960). Collembola were found to clear very well in this medium if warmed gently, and it is possible to mount them directly from life, or from most of the entomological preservatives, such as acetic acid, lactic acid, glycerol, formalin, alcohol or even water. Salmon (1951) has indicated that the refractive index, clearing power and drying time can be altered by varying the proportions of the constituents.

c) The literature used.

Before the publication of Gisin's 'Collembolenfauna Europas', in 1960, identifications were carried out

using the same author's earlier key, (Gisin 1944), in conjunction with Stach (1947 to 1960) and Salmon (1951). The earlier major taxonomic works of Linnaniemi (1912) and Handschin (1929) were also consulted regularly. The preceding works are of general taxonomic importance, and papers of a more specialised nature will be referred to under the species concerned. Early in the work the keys of Womersley (1930) and Maynard (1951) were found to be useful.

The publication of the very comprehensive 'Collembolenfauna Europas' greatly facilitated indentification of specimens, and the production, by the same author, of monthly additions and corrections in the form of his 'Summarische nachtrage' is a service greatly appreciated.

4) Taxonomic notes and the autecology of the Collembola of Moor House.

In the following list the species are arranged in accordance with modern practice, following exactly the key of Gisin (1960). Some additions have been made in view of more recent literature, and synonyms are quoted where these are more descriptive of the Moor House material.

1. Hypogastrura scotica (Carpenter and Evans 1899).

Advances in the taxonomy of the Hypogastrura armata species group have given rise to the necessity for redescription of certain species. Murphy (1960) has redescribed H. scotica on the basis of material collected in the northern Pennines and Ireland, and has created a new species, H. gotoi Murphy 1960, to accommodate a single specimen from the Outer Hebrides, described by Goto (1957) as H. scotica. These two descriptions are so similar that the naming of a new species on the basis of a single specimen is not justified. H. gotoi Murphy 1960 is thus to be regarded as a synonym of H. scotica (Carpenter and Evans 1899).

The species was found to be restricted to peat soils, and occurred in both Sphagnum samples and heather litter in small numbers; it has also been recorded from Juncus effusus litter on alluvial grassland, where there was a high content of redistributed peat. Micro-distribution samples from the mixed moor indicate that the species prefers the drier Cladonia covered areas to the Sphagnum patches. Typical records:

Great Dodgen Pot (Heather litter) 20.2.61

Cottage Hill (Heather litter) 13.2.61

2. Hypogastrura denticulata (Bagnall 1941) sensu Gisin 1949.

This species is common in the litter found at the base of Juncus effusus and occurs frequently on the alluvial grasslands of the stream sides. It has been found also in Sphagnum and Polytrichum samples from all over the Reserve, in Eriophorum angustifolium and E. vaginatum samples from areas of peat erosion, and it has been taken on three occasions on the limestone grassland. It is a much commoner species than the previous member of this genus. Typical records:

Trout Beck Flats (Juncus effusus litter) 2.5.60

Moss Flats (Eriophorum angustifolium) 27.2.61

3. Willemia anophthalma Borner 1901.

A relatively uncommon species apparently almost entirely restricted to the peat soils of the moor; there is a single record of two individuals from limestone grassland. Typical records:

Dodgen Pot (Heather litter) 14.5.61

Moss Flats (Hagg lip) 27.2.61

House Field (Limestone grassland) 25.9.61

Gisin (1943) regards this species as typical of dry, raw humus, and the present writer has found it to be

more common in the heather litter of the drier, exposed hummocks on Moss Flats, than elsewhere. However, Strenzke (1949) has recorded it from moist habitats.

4. Friesea mirabilis (Tullberg 1871) var. reducta Stach 1949.

A common species found in all areas where samples were collected, both on the mineral soils and on the peat soils of the moor. Its highest densities are reached in the moor edge zones of Juncus squarrosus, where frequently it outnumbers all other species. Typical records:

House Field (Limestone grassland) 29.2.60

Great Dodgen Pot (Heather litter) 23.1.61

5. Brachystomella parvula (Schaffer 1896).

An uncommon species which has been collected with but one exception only from the drying hummocks of the erosion complex on Moss Flats. Typical records:

Moss Flats (Hummock top) 16.5.61

House Field (Limestone grassland) 14.11.60

6. Anurida pygmaea (Borner 1901)

A common species on the mineral soils and the peat soils of the moor; recorded from all the areas examined with the exceptions of Juncus squarrosus and

Eriophorum angustifolium. Typical records:

Trout Beck Flats (Alluvial grassland) 4.7.60

Dodgen Pot (Heather litter) 18.4.61

7. Anurida forsslundi (Gisin 1949).

Material referable to this species collected on Bog Hill by D.H. Murphy, on 27.8.53, has been described as Micranurida conjuncta sp.n., (Murphy 1960). Further examination of this material, and material collected by the present writer show it to be referable to Anurida forsslundi (Gisin 1949). This is the first record of the species from the British Isles.

It is a rare species and has been collected only from one area of mixed moor. Total records:

Cottage Hill (Heather litter) 13.2.61

Dodgen Pot (Heather litter) 20.2.61

8. Anurida granaria (Nicolet 1847).

Widespread though not common in the grassland areas, and in Sphagnum flushes; it has also been collected in Juncus effusus litter. Typical records:

Trout Beck Flats (Alluvial grassland) 13.2.61

Milburn Beck (Polytrichum on Limestone grassland) 23.3.61

9. Neanura muscorum (Templeton 1835).

This species is widespread and not uncommon on the peat soils of the moor, and occurs commonly in the Juncus effusus litter along the stream sides. Entirely absent from the mineral soils, it has been recorded occasionally from areas of peat erosion and from Eriophorum vaginatum. Typical records:

Dodgen Pot (Heather litter) 23.1.61

Trout Beck Flats (Juncus effusus litter) 29.5.61

10. Onychiurus absoloni (Borner 1901).

Gisin (1949, 1960) regards this species as a synonym of Onychiurus affinis Ågren 1903, and Stach (1954) discusses the possibilities of this synonymy. The description given by Gisin (1960) follows that of Ågren for O. affinis. Since the largest specimens examined from the Moor House Reserve possess four vesicles in the form of a rosette in the post-antennal organ, and have a pseudocellar formula of 32/133/33343, the material is more referable to the description of O. affinis Ågren 1903. However, the presence of 2 + 2 pseudocelli at the base of the antennae on Borner's description of O. absoloni suggests that he was considering juvenile individuals (see p. 183), as members of this group of Onychiurus typically possess 3 + 3 pseudocelli at the

antennal base, Whilst there is little reason to regard O. affinis as a separate species on present knowledge, this nomenclature is quoted here under the heading of O. absoloni as being more descriptive of the Moor House material.

This species was collected regularly but in small numbers in Juncus effusus litter; on two occasions it was found in Eriophorum vaginatum samples, and a single individual was collected from the limestone grassland. Typical records:

Trout Beck Flats (Juncus effusus litter) 4.7.61.

Moss Flats (Eriophorum vaginatum) 27.2.61 and 5.9.61

House Field (Limestone grassland) 13.1.61

11. Onychiurus procampatus Gisin 1956.

Abundant and widespread in all the mineral soils of the limestone areas and stream sides. Occasionally collected in Juncus effusus litter from areas of alluvial grassland, and also very occasionally taken in Sphagnum and Polytrichum samples. Entirely absent from peat soils. A cavernicolous form, it penetrates deep into the mineral soil, and always occurs together with O. tricampatus on the Reserve. Typical records:

House Field (Limestone grassland) 29.2.60

Trout Beck Flats (Alluvial grassland) 2.5.60

12. Onychiurus latus Gisin 1956

Widespread in all peat soils sampled, except in Eriophorum angustifolium from which the species was absent. It occurs commonly in Juncus effusus litter and in Sphagnum and Polytrichum samples. It is absent from mineral soils although it occurs in the mosses growing on limestone outcrops, where more acid conditions prevail. It is a surface form, never penetrating below the decomposition layer. Typical records:

Dodgen Pot (Heather litter) 23.1.61

Trout Beck Flats (Juncus effusus litter) 4.7.61

13. Onychiurus tricampatus Gisin 1956

This species typically has the pseudocellar formula 33/023/33343; a small percentage of individuals in the Moor House population has the pseudocellar formula 33/033/33343, and over 90% of these are males. At present there is no reason to regard these individuals as specifically different from O. tricampatus.

The species is abundant and widespread in all mineral soils of the limestone areas and the stream sides. It is occasionally collected in Juncus effusus litter from areas of alluvial grassland and also in Sphagnum and Polytrichum samples. The species is entirely absent

from peat soils. A cavernicolous form, it penetrates deep into the soil, and is always found together with O. procampatus. Typical records:

House Field (Limestone grassland) 29.2.60

Trout Beck Flats (Alluvial grassland) 2.5.60

14. (Onychiurus stachianus Bagnall 1939)

Murphy (1960) redescribes Onychiurus stachi Denis 1938 nec Bagnall 1935, on the basis of material collected on the Moor House Reserve. Examination of this material clearly shows it to have a post-antennal organ typical of the Sub-genus Protaphorura Absolon 1901. Onychiurus stachianus Bagnall 1939, of which O. stachi is a synonym (Stach 1954 and Gisin 1960), has a post-antennal organ typical of the Sub-genus Onychiurus s. str.. Thus this material is clearly not referable to Onychiurus stachianus Bagnall 1939. The individuals described under this heading by Murphy (1960) are first instars of Onychiurus procampatus Gisin 1956.

15. Tullbergia krausbaueri (Borner 1901)

Widespread and abundant in all mineral soils. Frequent in Juncus effusus litter from alluvial grassland. Very locally abundant in peat soils, where normally it is rare or absent. Typical records:

House Field (Limestone grassland) 29.2.60

Moss Flats (Eriophorum angustifolium) 16.5.60

16. Tullbergia affinis Borner 1902.

In the Moor House material, the tubercles of the post-antennal organ are divided and thus the species is referable to Tullbergia bipartita Handschin 1920, which Gisin (1960) sinks as a synonym of Tullbergia affinis Borner 1902. Stach (1954) regards the species as separate, since in eastern European material he claims that there is no division of the tubercles of the post-antennal organ. Some doubt remains, therefore, concerning this synonymy, and the junior synonym is quoted here as being more descriptive of the material.

The species is apparently restricted to mineral soils; it has been recorded only once from quantitative samples taken from limestone grassland which were extracted in the high gradient cylinder apparatus (see page 276). Crumbling samples of limestone grassland into an ordinary Tullgren funnel produced many more individuals, suggesting inefficiency in the extraction of this species from quantitative samples. Typical records:

House Field (Limestone grassland) 11.12.61

17. Tullbergia denisi (Bagnall 1935).

Frequent in samples collected from alluvial grassland, but rarer on the limestone grassland. Absent entirely from peat soils. Typical records:

Trout Beck Flats (Alluvial grassland) 6.6.60

House Field (Limestone grassland) 18.7.60

18. Tetracanthella wahlgreni Linnaniemi 1911.

Abundant and widely distributed on the heather moor, especially in patches of Cladonia and Hypogymnaea, and on the hagg lips. Recorded also from mineral soils, especially where Cladonia occurred, occasionally in Polytrichum samples and rarely in both Eriophorum angustifolium and E. vaginatum samples. Unrecorded from Juncus effusus litter and from J. squarrosus, the species is characteristic of the drier areas of the moor. Typical records:

Dodgen Pot (Heather litter) 20.2.61

Moss Flats (Hagg lip) 23.11.59

19. Tetracanthella brachyura Bagnall 1949.

This species is regarded as dubious by Gisin (1960). Murphy (1960) has redescribed the species on material from the Moor House Reserve and concludes that

it is closely related to Tetracanthella pyrenaica Cassagnau 1953.

Ecologically the species is very different from T. wahlgreni, the only other species of this genus occurring at Moor House, and nowhere have the two species been found together. T. brachyura is characteristic of two very wet areas, the Sphagnum subsecundum and S.palustre zones of Valley Bog, and the Juncus squarrosus areas which have a very high water content (see page 24). Not recorded from elsewhere on the Reserve. Typical records:

Dodgen Pot (Juncus squarrosus) 9.5.60

Trout Beck (Juncus squarrosus) 11.12.61

20. Folsomia brevicauda Agrell 1939.

Abundant and widely distributed on the peat soils of the moor, but much less common on the mineral soils, where, however, it occurs regularly. The species was recorded from all areas sampled. Typical records:

Dodgen Pot (Heather litter) 23.1.61

Trout Beck (Juncus squarrosus) 20.2.61.

21. Folsomia quadrioculata (Tullberg 1871).

Frequently recorded from the limestone grassland areas but uncommon on the alluvial grassland. Occasionally recorded from peat soils. Typical records:

House Field (Limestone grassland) 28.3.60

Dodgen Pot (Heather litter) 25.9.61

22. Folsomia manolachei Bagnall 1939.

Abundant in the mineral soils of the limestone areas and stream sides; common in samples of Juncus effusus litter. Not recorded from peat soils.

Typical records:

House Field (Limestone grassland) 29.2.60

Trout Beck Flats (Alluvial grassland) 2.5.60

23. Folsomia cf. brevifurca (Bagnall 1949).

Several specimens of a species of Folsomia near to F. brevifurca have been recorded from the Moor House Reserve. The material differs from this species in having the macrochaetae much longer than 0.4 times the length of the mucro (up to 6 times the length of the mucro). Gisin (1960) regards F. brevifurca as a dubious species. It is possible that the individuals referable to this form are juveniles of another species, since all specimens collected are sub-adult. The only species in which the juveniles are not frequently found is F.litsteri where the furcula is very different in structure. The species recorded here as Folsomia cf. brevifurca could

possibly be juvenile material of Folsomia litsteri, but this is regarded as improbable.

The species was recorded occasionally from mineral soils of the limestone areas and stream sides, but was absent from peat soils. Typical records:

House Field (Limestone grassland) 25.4.60

Trout Beck Flats (Alluvial grassland) 2.5.60

24. Folsomia litsteri Bagnall 1939.

Examination of material in the University of Durham Collection, labelled Folsomia fimetaria Linne. 1758, by D.H. Murphy, has proved to be of this species. Further material has been collected by the present writer from the Moor House Reserve.

The species was found to be rare and restricted to the mineral soils of the limestone areas and stream sides. Typical records:

House Field (Limestone grassland) 4.7.61

Trout Beck Flats (Alluvial grassland) 29.8.60

25. Isotomiella minor (Schaffer 1896).

Abundant in mineral soils of the limestone areas and stream sides, but sparsely distributed in the peat soils of the moor. Typical records:

House Field (Limestone grassland) 29.2.60

Trout Beck Flats (Alluvial grassland) 2.5.60

26. Agrenia bidenticulata (Tullberg 1876).

Abundant in all stream side areas where deposits of pebbles and gravel occurred, the species was never found more than a few centimetres from water. There are two records of a single individual from areas of Eriophorum angustifolium on Moss Flats; all other records are from the surface of running water. Typical records:

Rough Syke (Water surface) 25.7.60

Moss Flats (Eriophorum angustifolium) 27.2.61 and 4.12.61

27. Isotoma sensibilis (Tullberg 1876).

Widespread and abundant in all soil types. On peat soils the species was found to possess its characteristic purple colour, but on mineral soils and in some areas of Sphagnum and Polytrichum a high percentage of greenish-yellow and brown individuals occurred. Typical records:

Dodgen Pot (Heather litter) 23.1.61

House Field (Limestone grassland) 29.2.60

28. Isotoma notabilis Schaffer 1896.

Widespread in all soil types, but more frequent in mineral soils than elsewhere. Typical records:

House Field (Limestone grassland) 29.2.60

Dodgen Pot (Heather litter) 18.4.61

29. Isotoma viridis Bourlet 1839.

Common in both mineral and peat soils. Typical records:

House Field (Limestone grassland) 29.2.60

Dodgen Pot (Heather litter) 23.1.61

30. Isotoma antennalis (Bagnall 1940).

Murphy (1958) has redescribed this species from material collected on the Moor House Reserve, and has demonstrated its affinities to the Genus Isotoma rather than the Genus Isotomurus.

The species is characteristic of very wet peat soils and is often found on the surface of Sphagnum pools. It is typical of areas of peat erosion and recolonisation, occurring under stones on the bare peat and in areas of Eriophorum angustifolium and Eriophorum vaginatum. Typical records:

Dodgen Pot (Juncus squarrosus) 7.3.60

Moss Flats (Eriophorum angustifolium) 27.2.61

31. Isotoma olivacea Tullberg 1871.

Individuals referable to the original description of this species (Tullberg 1871) occurred sparsely in some areas of Sphagnum and Polytrichum. Material referable to Isotoma neglecta Schaffer 1900, which Gisin (1960) sinks as a synonym of I. olivacea, was found to be much more common on the Reserve. Whilst these may be purely ecological forms of one species, the junior synonym is quoted here as being more descriptive of the material from Moor House. All references to I. olivacea in this work refer to material referable to I. neglecta, due to the rarity of the typical form which was absent from quantitative samples.

The species occurred in small numbers on mineral soils of both limestone areas and the stream sides, and was abundant in Juncus effusus litter and in the nests of small rodents; it occurred also in areas of Sphagnum and Polytrichum, but was absent from the heather moor. Typical records:

Trout Beck Flats (Alluvial grassland) 2.5.60

Trout Beck Flats (Juncus effusus litter) 29.5.61

32. Isotoma infuscata (Murphy 1959).

Murphy (1959) has described this species on the basis of material collected on the Moor House Reserve,

and places it in the new Genus Sensiterga. The criteria upon which this genus is erected are not valid: the sensillae of the third antennal segment are not unique, as they occur in Isotoma olivacea (personal observation) and in Isotoma violacea Tullberg 1876 (Gisin, pers. comm.), although in both cases they are not so numerous as in I. infuscata. Fusion of the last two abdominal segments occurs in other members of the Genus Isotoma, eg. I. sensibilis, and many, if not all, members of the genus have these segments fused in the early instars. (Personal observation valid for I. sensibilis, I. viridis, I. antennalis and I. olivacea). Subsequent to these observations made by the present writer, and supported by Gisin (pers. comm.), Huther and Winter (1961) have expressed similar opinions and placed Sensiterga infuscata Murphy 1960 in the Genus Isotoma. Its affinities are with the I. olivacea, I. albella, I. violacea, I. hiemalis group, and Gisin (Summarische nachtrage No. 25) places it between I. violacea and I. hiemalis.

The species was found to be widespread in all areas of Sphagnum and Polytrichum, and there was a single record from limestone grassland. Typical records:

Moss Flats (Polytrichum) 2.11.59

House Field (Limestone grassland) 22.11.61

33. Isotomurus palustris (Muller 1776).

Material referable to this species occurs in all areas of Sphagnum throughout the Reserve, together with individuals referable to Isotomurus plumosus Bagnall 1940. Since intermediates between these two forms occur it seems probable that the Moor House population forms a single species, and that the differences are a purely phenotypic effect. Individuals of the varieties 'prasina' and 'aquatilis' have been recorded frequently; the former is the more common away from water surfaces.

The species occurred regularly in Sphagnum samples and in wet situations throughout the Reserve; it has been recorded very occasionally from mineral soils and the heather litter of the peat moor. Typical records:

Moss Flats (Polytrichum) 7.3.60

Trout Beck Flats (Alluvial grassland) 24.10.60

34. Entomobrya nicoleti (Lubbock 1867).

The majority of individuals collected on the Moor House Reserve had very few dark markings, and some lacked markings entirely. South (1961) figures a specimen which is typical of the Reserve (p.393 Fig. 16). The lack of markings led to the individuals in the Durham University Collection being labelled as Entomobrya lanuginosa Nicolet 1841, by D.H. Murphy.

The species occurred in small numbers on the cropped vegetation of the mineral soils, in the heather litter, in Sphagnum and Polytrichum samples and in Eriophorum angustifolium. It was more common in uncropped Festuca and in Eriophorum vaginatum. Typical records:

House Field (Limestone grassland) 29.2.60

Trout Beck Flats (Alluvial grassland) 2.5.60

35. Entomobrya multifasciata (Tullberg 1871).

Only four individuals of this species were recorded during the course of the field work; the following is a complete list:

House Field (Limestone grassland) 28.8.61 (1)

Trout Beck Flats (Alluvial grassland) 16.1.61 (1)

Dodgen Pot (Juncus squarrosus) 7.3.60 (1)

Moss Flats (Polytrichum) 29.9.59 (1)

36. Willowsia buski (Lubbock 1869).

Recorded in small numbers from samples of heather litter. Elsewhere individuals have been found on limestone grassland, in Sphagnum and Polytrichum samples, and on the hagg lips and hummock tops of the erosion

complex. Typical records:

Dodgen Pot (Heather litter) 25.9.61

Moss Flats (Hummock top) 16.5.60

37. Lepidocyrtus cyaneus Tullberg 1871

The species occurred commonly in some areas of Sphagnum and Polytrichum and sparsely on Juncus squarrosus. There is a single record of one individual from Eriophorum angustifolium. Typical records:

Moss Flats (Polytrichum) 2.11.59

Dodgen Pot (Juncus squarrosus) 9.5.60

38. Lepidocyrtus lanuginosus (Gmelin 1788).

Murphy (University of Durham Collection) named material of this species collected at Moor House Lepidocyrtus curvicollis Bourlet 1839. Material from Little High Wood, Durham, which was collected for purposes of comparison, seemed more referable to L. curvicollis, and samples of both populations were sent to Dr. H. Gisin for confirmation of identification. He confirmed that the Moor House material was referable to L. lanuginosus and material from Little High Wood, Durham, to L. curvicollis.

The difference between L. lanuginosus and L. curvicollis lies in the shape of the second thoracic segment (Gisin 1952). Both species were cultured,

and eggs obtained; the hatching periods of the eggs of the two species at different temperatures were found to be identical (see Fig. 12). In the first instar individuals obtained, the shape of the second thoracic segment was found to be the same in both species. No other differences, such as those described in other members of the genus by Yosii (1959), could be found in the adults. It was therefore thought possible that the two populations, of apparently two separate species, could be conspecific, the so-called specific differences being purely phenotypic.

It was found difficult to rear these species from eggs, in culture, and so leaf litter from Durham, containing the eggs of L. curvicollis was taken to Moor House, and Juncus effusus litter containing the eggs of L. lanuginosus was transported to Durham. The litter was kept in galvanised iron containers sunk into the ground and covered by layers of muslin, to prevent entry or exit of Collembola. Three such containers were set up at Durham and at Moor House on 14 November, 1960. Examination of litter from both areas showed that only a few adult Lepidocyrtus sp. were present in the litter, and by hand sorting as many as possible of these individuals were removed from the experimental litter. Both species were known to lay eggs in October and November,

so it was very probable that the experimental litter contained eggs, although these were not seen. On 10 April, 1961, samples were taken from each of the three culture containers at Durham and at Moor House; no adults were present in the samples, but eggs had hatched and early instars were present. On 25 September, 1961, all the litter was collected from the culture containers and the Collembola extracted.

Control litter from Durham contained only L. curvicollis and from Moor House only L. lanuginosus, as was to be expected. Only six individuals were extracted from the litter kept at Moor House, and these were found to have the second thoracic segment of the L. lanuginosus type. Litter from Moor House kept at Durham contained individuals intermediate between the two so-called species. None of the material was fully adult, and this together with the precaution of examining the litter on 10.4.61, precluded the possibility of individuals having remained in the litter over the period of the experiment.

Apparently the environment has effect on the shape of the second thoracic segment, and the two populations are to be regarded as conspecific (environmental effects on body structure in Collembola has been clearly demonstrated by Cassagnau 1955 et seq.).

The material from the experiment has been shown to Dr. H. Gisin, who agrees with the conclusion. Whilst the two populations of Lepidocyrtus sp. at Moor House and Durham are now to be regarded as conspecific, L. curvicollis from Swiss caves appears to be a much bigger insect, and may well be specifically distinct.

In the following text the material from Durham is referred to as L. cf. curvicollis and the Moor House material as L. lanuginosus.

39. Pseudosinella alba (Packard 1873).

A rare species recorded on only four occasions from the Reserve. The following is a complete list of records:

House Field (Limestone grassland) 23.5.60 (2),
28.7.61 (1), 11.12.61 (1).

Trout Beck Flats (Juncus effusus litter) 25.9.61(1)

The two individuals taken in the same 10 sq. cm. sample unit on 23 May, 1960, were adult; however, whilst one individual possessed the normal 2 + 2 ocelli, the other individual had no ocelli, although in all other respects it was referable to this species.

40. Tomocerus minor (Lubbock 1862).

Frequently recorded from peat soils of all types and from areas of Sphagnum and Polytrichum on all parts of the Reserve. Common in Juncus effusus litter from alluvial grassland. There are no records from the mineral soils. Typical records:

Dodgen Pot (Heather litter) 18.3.61

Moss Flats (Eriophorum vaginatum) 4.12.61

41. Neelus minimus Willem 1900.

Recorded frequently but in small numbers from the heather moor and occasionally from the mineral soils of the limestone areas and streamsides. Typical records:

Dodgen Pot (Heather litter) 18.3.61.

House Field (Limestone grassland) 16.1.61

42. Sminthurides pumilis (Krausbauer 1898).

Frequently recorded in the spring and summer months on the mineral soils of the limestone areas and streamsides; absent in samples from peat soils. Typical records:

House Field (Limestone grassland) 25.4.60

Trout Beck Flats (Alluvial grassland) 2.5.60

43. Sminthurides malmgreni (Tullberg 1876).

Common in very wet areas, especially on the surface of Sphagnum pools and in their immediate vicinity. Recorded also from Eriophorum angustifolium and from Polytrichum samples. Typical records:

Moss Flats (Polytrichum) 17.9.59

Moss Flats (Eriophorum angustifolium) 29.5.61

44. Sminthurides schoetti (Axelson 1903).

Recorded frequently from both peat and mineral soils and in Sphagnum and Polytrichum samples. Usually absent from samples taken in winter. Typical records:

House Field (Limestone grassland) 28.3.60

Dodgen Pot (Heather litter) 20.2.61

45. Sminthurides signatus (Krausbauer 1898) sensu Murphy 1960.

Murphy (1960) has provided a redescription of this species based on material collected on the Moor House Reserve.

A rare species on the Reserve, it has been recorded only from areas of erosion on Moss Flats. Typical record:

Moss Flats (Hummock top) 29.5.61

46. Sminthurides parvulus (Krausbauer 1898).

Frequently recorded on peat soils of all types, but in small numbers; also in Sphagnum and Polytrichum samples. Unrecorded from mineral soils. Typical records:

Dodgen Pot (Heather litter) 28.7.61

Moss Flats (Eriophorum vaginatum) 27.2.61

47. Arrhopalites caecus (Tullberg 1871).

A single record from limestone grassland.

House Field (Limestone grassland) 25.4.60

48. Arrhopalites pricipalis Stach 1945.

Recorded in small numbers from peat soils and in Sphagnum and Polytrichum. Typical records:

Dodgen Pot (Heather litter) 20. 2. 61

Moss Flats (Polytrichum) 29.9.59

49. Sminthurinus elegans (Fitch 1863).

Frequently recorded during the summer months on the mineral soils of the limestone areas and the stream sides, but more common in sweepings from the uncropped grassland vegetation. Typical records:

House Field (Limestone grassland) 22.8.60

Trout Beck Flats (Alluvial grassland) 2.5.60

50. Sminthurinus aureus (Lubbock 1862).

Common during the summer months on the grasslands of the limestone areas and the stream sides, and in sweepings from uncropped grassland. Typical records:

House Field (limestone grassland) 22.8.60

Trout Beck Flats (Alluvial grassland) 26.9.60

51. Sminthurinus niger (Lubbock 1867).

Murphy (1960) has examined material from several British localities and considers that the material is conspecific with that examined by Stach (1956); probably this description applies to Lubbock's original species.

Recorded in very small numbers from mineral soils of both the limestone areas and the stream sides, in spring and summer. Typical records:

House Field (Limestone grassland) 22.8.60

Trout Beck Flats (Alluvial grassland) 2.5.60

52. Bourletiella insignis (Reuter 1876).

Recorded on only one occasion from a Sphagnum sample.

Valley Bog (Sphagnum) 5.6.61

53. Bourletiella clavigera Gisin 1958.

A description of this species based on material collected on the Moor House Reserve, has been given by Murphy (1960), under the heading of Bourletiella (Heterosminthurus) craggi sp.n.. This name is to be regarded as a synonym of B. clavigera Gisin 1958.

Recorded commonly from all vegetation types during the summer months. Typical records:

Dodgen Pot (Heather litter) 28.7.61

House Field (Limestone grassland) 26.9.60

54. Bourletiella hortensis (Fitch 1863).

Murphy (1960) comments upon material collected at Moor House, and indicates that this is referable to the descriptions of Jeannot (1954) and Gisin (1957) and not to Stach (1956); this last author's description refers to Bourletiella viridescens Stach 1920 sensu Gisin 1948.

Recorded infrequently from areas of peat erosion on Moss Flats. Typical record:

Moss Flats (Eriophorum angustifolium) 29.5.61

55. Bourletiella viridescens Stach 1920 sensu Gisin 1948.

Murphy (1960) discusses the possible synonymy of this species with Bourletiella lutea (Lubbock 1867) on a

basis of material collected from the Moor House Reserve; there is, however, insufficient evidence to regard the two species as synonymous.

The species was found commonly on the grassland vegetation throughout the summer months. Typical records:

House Field (Limestone grassland) 22.8.60

Trout Beck Flats (Alluvial grassland) 22.9.60

56. Dicyrtoma minuta (O. Fabricius 1783).

Widely distributed but infrequent on all peat soils and in Sphagnum and Polytrichum samples. Common in Juncus effusus litter. Much more common during the summer months but adults were occasionally taken in winter. Typical records:

Dodgen Pot (Heather litter) 28.8.61

Trout Beck Flats (Juncus effusus litter) 29.5.61

57. Dicyrtoma fusca (Lucas 1842).

Widely distributed but infrequent in all peat soils and in Sphagnum and Polytrichum samples. Occasionally recorded in Juncus effusus litter from alluvial grassland. Very rare during the winter months. Typical records:

Dodgen Pot (Heather litter) 5.7.61

Trout Beck Flats (Juncus effusus litter) 29.5.61

PART B.

GENERAL BIOLOGY

1. TECHNIQUES OF STUDY

PART B. GENERAL BIOLOGY

I. TECHNIQUES OF STUDY

1) Introduction.

It is almost impossible to make observations of the behaviour of Collembola in the field and it is very difficult to find their eggs in samples of soil and litter brought into the laboratory. Since it was hoped in the early stages of the work to obtain information on the life histories of several species from regular sampling, laboratory cultures were started in order to try and substantiate and add to data obtained from the field. Agrell (1949) has stressed the value of such an approach.

2) Qualitative collecting and extracting.

Collections of vegetation, litter and soil were made when Collembola were required, and if these were not to be extracted immediately they were stored in the cold room at 10°C. where it was found that they could be kept alive for several weeks. Depending upon the amount of material required, extractions were carried out in one of two large Tullgren funnels. The smaller of the two was heated by a 100 watt electric light bulb,

and was used mainly for the extraction of Collembola from mosses and lichens; its volume was about two litres. The larger funnel was heated by a 1000 watt radiator element, and the amount of heat produced was controlled by a sliding rheostat. This apparatus was used mainly for very wet litter and soil. It was found that the latter was more easily and more efficiently extracted by crumbling samples into the apparatus. To avoid the danger of fire in the extraction of peat soils and dry litter, the heating was limited; an additional precaution was taken in making the main structure of the funnel of asbestos and aluminium.

The insects which fell from the funnel were collected on the surface of the water in a deep petri dish which was filled to a depth of about one inch. This prevented individuals being caught in the mucus produced by earthworms, molluscs and enchytreids which sank to the bottom. In the early stages of using the apparatus the insects were collected on damp plaster of Paris medium, but even when small mesh gauze was used in the apparatus some small earthworms, molluscs and enchytreids managed to get through, resulting in the damage of many of the Collembola. The use of a water film on which to collect the insects necessitated the

early removal of the larger species such as Tomocerus minor and Isotoma viridis, as they broke the water film, became trapped, and died if left too long.

After extraction the Collembola were transferred to culture vessels of the type described in the next section.

3) Rearing.

Several of the early methods used for culturing soil arthropods in the laboratory involved the isolation of a small part of the natural habitat in a containing vessel. Davidson (1934) working on Sminthurus viridis used large breeding cages in which the insects had access to clover seedlings, and for egg-laying experiments the same author used plant pots containing soil, on the surface of which the insects were retained by means of a covered lamp-glass. Strebel (1932) used smaller glass vessels containing material from the place where the insects were collected; Davis and Harris (1936) and Uchida and Chiba (1958) utilised similar containers. To a large extent this type of culturing defeats the original purpose of bringing the insects into the laboratory, as it is difficult to find both the insects and their eggs in the debris.

On a much smaller scale, Michael (1884) used cavity micro-slides, containing a ring of damp filter

paper which was enclosed by a cover slip. Robertson (1945) and Jones (1951) used perforated plastic strips, one side of which was covered by filter paper on which the insects lived, and the other by a series of cover slips. The whole strip was placed in an atmosphere of high relative humidity. Connington and Solomon (quoted in Murphy and Doncaster 1957) utilised a similar device, but substituted bolting silk for the filter paper. Schaller (1953) cultured Collembola in cells cut out of a block of plaster, and Schuster (1956) used porous clay pipe filters set in sand, on which to rear Oribatid mites. Britt (1951) kept Collembola in glass vials with moist filter paper, but later added drops of water, in place of the moist filter paper, because of its frequent contamination by fungi.

Searls' (1928) method, of which minor modifications have been made by Edwards (1955), was the first used by the present writer. Here, a dark coloured soil was mixed with leaf mould, and ground in a mortar. After being sieved through a fine gauze this was mixed with plaster of Paris in the ratio of one to two, water was added, and the resulting creamy paste was left to set in screw-top jars in which half an inch of plaster of Paris had already been allowed to set. It is not

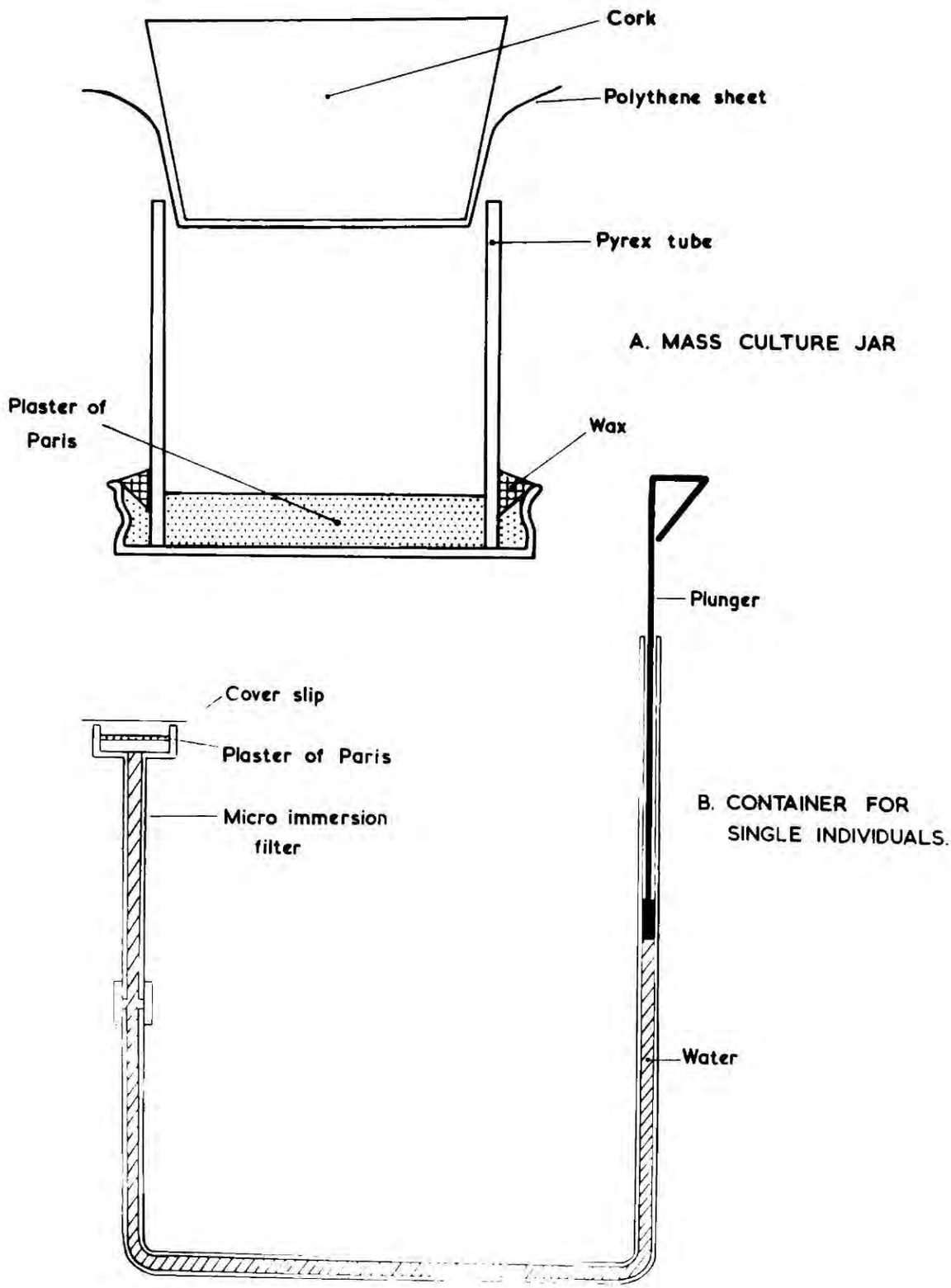
necessary to add food to such a culture medium, as Collembola apparently find sufficient nutritive material in the small particles of humus projecting from the surface, and from the fungi which grow on them. However, this type of method has the disadvantage that fungal mycelia in which Collembola are easily trapped soon begin to grow on the medium, and sometimes this covers the substrate if the jars are not checked daily. In addition the eggs of small soil arthropods are easily taken in with the sieved soil, and on hatching contaminate the culture with insects of a species other than that originally introduced.

A method of culturing very similar to that used by Choudhuri (1958) was found to be much more satisfactory. This method, based on those used by Michner (1946), Jenkins (1947) and Lipovsky (1953) involves a jar from which the bottom has been removed and replaced by a plug of a mixture of plaster of Paris and powdered charcoal. In practice 5 cm. lengths of Pyrex glass tubing 5 cm. in diameter were used, and these were embedded in a mixture of plaster of Paris and powdered charcoal, retained in an aluminium lid 6 cm. in diameter, (Fig. 3). On drying, to prevent evaporation from the plaster block, the gap between the aluminium lid and the glass was filled with wax. The container was enclosed by a cork, which, to

Fig. 3.

The types of containers used to culture Collembola.

Fig. 3.


Cork
Polythene sheet
Pyrex tube
A. MASS CULTURE JAR
Plaster of Paris
Wax
Plunger
Cover slip
Plaster of Paris
Micro immersion filter
B. CONTAINER FOR SINGLE INDIVIDUALS.
Water

prevent fungi growing on it, was covered by a piece of stretched polythene sheet. In Michner's container the walls were also covered with plaster of Paris mixture, to prevent droplet formation; this was found to be unnecessary as Collembola very seldom became trapped in the droplets. The surface of the plaster of Paris was flamed before the introduction of the insects and distilled water was used at all times to moisten the surface; this procedure kept the culture free of fungi and bacterial growths except for those introduced with the food.

Many types of food have been used for feeding small arthropods in culture, ranging over yeast, bread, moss prothalli, bracken spores, pollen, fungal mycelia, potato slices and "Truefood". Moistened yeast pellets were found to be quite satisfactory material on which to feed the insects, provided that the cultures were examined regularly; fungal mycelia sometimes grew out from the yeast over the sterilised substrate and when this happened the yeast was brushed to remove it.

Individual Collembola were cultured in 2 x $\frac{3}{4}$ inch. specimen tubes filled to within $\frac{1}{2}$ inch of the top with plaster of Paris/charcoal mixture, and covered by a $\frac{3}{4}$ inch diameter cover slip retained by a film of vaseline. Eggs were also kept in tubes of this type, but these were covered by polythene bungs.

The method of Murphy and Doncaster (1957) in which individual Collembola were kept in micro-immersion filters enclosed by a cover slip was used for some time, but eventually dispensed with as being unnecessarily elaborate. The high relative humidity of the atmosphere in the filter was maintained by keeping the water at the level of the scintered glass, by means of a plunger (Fig. 3).

Cultures were kept at constant temperatures by enclosing the culture vessels in large jars which were submerged in tanks of water where an even temperature was maintained by means of a thermostat. Except where otherwise stated, individuals were reared at 15°C.

II. BEHAVIOUR AND REPRODUCTION

II. BEHAVIOUR AND REPRODUCTION.

1) Introduction.

When Collembola are extracted from the medium in which they have been collected they frequently moult either on the meniscus of the collecting vessel or immediately on introducing them to the culture jar. Strebel (1932) has remarked upon the fact that Collembola often moult when mechanically stimulated. Occasionally all the insects in a culture vessel moult more or less simultaneously, particularly in members of the Isotomidae and Poduridae. Isotoma sensibilis, I. olivacea and Hypogastrura denticulata have all behaved in this way on more than one occasion. Both Ripper (1930) and Strebel (1932) have remarked upon such moulting 'societies' and suggested that moulting is stimulated by physical contact.

After introducing individuals into a culture jar it can often be seen after only a few hours that their intestines contain particles of charcoal, and examination of the faeces also reveals the presence of plaster of Paris. Often, too, yeasts appear to be passed through the gut unchanged. When the eggs hatch the first instar individuals begin to feed immediately, and often their

intestine appears as a black line, the lumen being filled with particles of charcoal. These observations suggest that Collembola take into the gut materials which may contain, or have on their surface, the nutritive material required, for example fungal hyphae. Thus everything that is found in the gut must not be regarded as food.

Apart from the normal faecal pellet produced, a second type occurs. This is pale yellow or orange in colour, and consists of minute crystalline spheres of a highly refractile nature. These are almost certainly the excretory materials which congregate in the cells of the epithelium of the mid-gut, and which are periodically discharged into the lumen. Willem (1900), Folsom and Welles (1906), Ichikawa (1931), Boelitz (1933) and Toth (1941, 1942) have discussed the origin and fate of excretory matter in Collembola. Spherical crystals of excretory matter occur in all faecal pellets, but the yellow 'faecal' pellets containing only excretory material, appear to retain their shape due to the presence of an outer pellicle. This pellicle could possibly be part of a peritrophic membrane, a structure which has not previously been recorded in Collembola.

2) The identification of the sexes.

Observation of reproductive behaviour in Collembola is made difficult by a marked lack of sexual dimorphism in most species. Handschin (1928), Ripper (1930), Agrell (1936), Davis and Harris (1936), Mayer (1957) and Choudhuri (1958) have pointed out the differences in the structure of the genital plate of the two sexes, but these are observable only by high power microscopic examination in prepared material. In the female the genital aperture is a transverse slit, bordered by bristles pointing posteriorly; the male genital plate is roughly circular and bears a longitudinal slit, the bristles being arranged radially. In Hypogastrura armata Britt (1950) has indicated that gravid females may be recognised by their distended abdomen, and Schaller (1953) recognised females of Orchesella spp. in the same way. The present writer has found this sexual recognition possible in species of the genera Hypogastrura and Onychiurus, but males could not be separated from non-gravid females by this means.

Willem (1925) and Denis (1926) have recorded that the tip of the abdomen is upturned in males of Archisotoma besselsi. Mayer (1957) casts doubt on the validity of this observation, and rightly points out that it could

be caused by the released furcula in the diagram of the male. Lindemann (1950) records the presence of patches of light coloured bristles in the males of Orchesella villosa and Poggendorf (1956) and Mayer (1957) have shown these to be present in males only during the sexual phases when spermatophores are deposited.

The Nearctic species Guthriella muskegis and Rhodanella minos from Somaliland show a marked sexual dimorphism (Paclt 1956), but these are exceptions within the group. Minor sexual differences can be seen in the different antennal segments of Australotomurus and in the presence of abdominal organs in the males of some species of the Genus Onychiurus. In the Symphypleona the male is often much smaller than the female, and sometimes the two sexes are distinguishable by their colours (Paclt 1956). In the genera Sminthurides, Sminthurinus and Dicyrtoma it is possible to separate the live females by means of their 'anal appendages', which are modified bristles.

Schaller (1953) has found it possible to separate the sexes of Tomocerus vulgaris and Orchesella villosa by means of their behaviour at times of reproduction: whereas the males were very active the females in both cases were lethargic. The present writer has observed females of T. minor to be inactive prior to egg laying,

but since similar behaviour occurs prior to moulting, in both sexes, it was found to be of no value in separating the sexes in this species.

3) Courtship behaviour.

The literature contains no comprehensive review of the present knowledge of reproductive behaviour in Collembola. In order to interpret the observations made during the present work a brief review of present knowledge is contained in this and the next two sections, together with original information.

In the literature the first record of courtship behaviour is that of Olfers (1862) where he describes the grasping of the antennae of the female with those of the male in Sminthurides aquaticus. Hermann (1865 a, b) describes the chasing of females of 'Podura' by the males, and Lubbock (1868) has outlined the courtship of Bourletiella lutea in most vivid terms: "It is very amusing to see these little creatures coquetting together. The male, which is much smaller than the female, runs round her, and they butt one another, standing face to face, and moving backward and forward like two playful lambs. Then the female pretends to run away and the male runs after her, with a queer appearance of anger,

gets in front and stands facing her again; then she turns coyly round, but he, quicker and more active, scuttles round too, and seems to whip her with his antennae; then for a bit they stand face to face, play with their antennae, and seem to be all in all to one another". Tullberg (1871) has described similar behaviour in Bourletiella bicincta.

In the Genus Sminthurides this type of courtship leads up to the interlocking of the antennae of the male and female. This has been considered at length by Reuter (1880, 1883), Oudemans (1888, 1890), Schött (1893), Levander (1894), Handschin (1928), Falkenhan (1932), Schaller (1953) and Mayer (1957) in Sminthurides aquaticus. Special bristles occur on the antennae of the male (Fig. 4) and these facilitate the attachment of the male to the antennae of the female; following upon this the female picks up the much smaller male and carries him above her head. The locking of the male's antennae upon those of the female is at first apparently resented by the latter, for by nodding movements of the head the male is often battered upon the substrate. Normally the male retains his purchase and the female eventually stops the nodding action. Carried in this position the male continues all the normal activities of life, such as

Fig. 4.

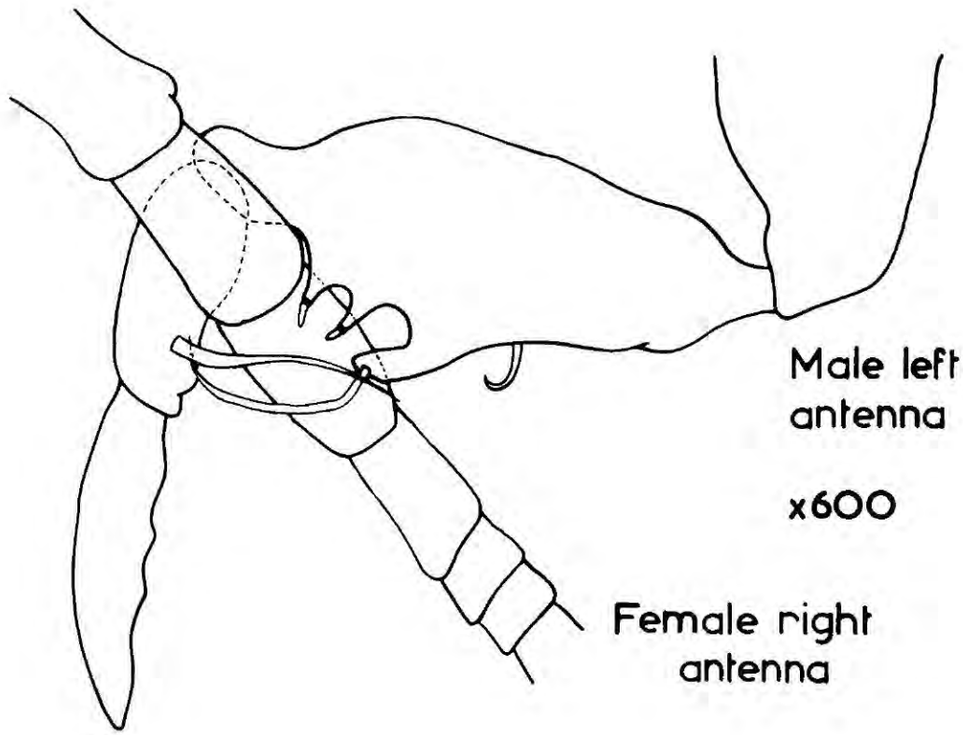
The method used in interlocking the antennae in the pre-coital behaviour of Sminthurides schoetti.

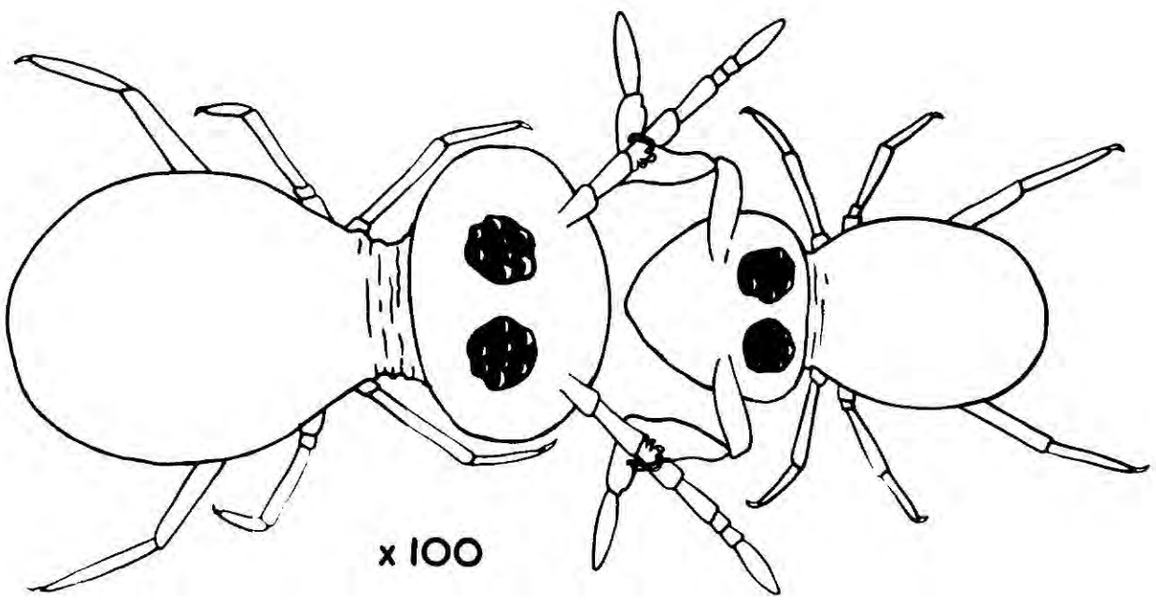
Top. Detail of the male left antenna gripping the right antenna of the female. x600.

Bottom. The postures assumed by the conjoined male and female. x100.

Fig.4.

The interlocking of the antennae in Sminthurides schoetti.





Conjoined male [right] and female [left].

eating, defaecating and cleaning itself, according to Mayer (1957). From time to time the male gives up the passive role of being carried and drags the female about (Strebel 1952). Mayer (1957) records that the male can descend to the substrate at any time, without releasing the antennae of the female, as a result of bending the antennae. All these aspects of the behaviour of S. aquaticus have been observed in S. schoetti and S. malmgreni during the present work.

In order to maintain a grip of the female's antennae, the antennae of the male must be bent at an angle of 90° between the 2nd and 3rd segments. Diagrams of this which occur in the literature are poor and in some cases erroneous eg. Reuter in Paclt (1956), and for this reason a diagram is given here (Fig. 4). This shows the orientation of the male and female antennae in conjoined individuals of Sminthurides schoetti; the posture has been observed to be identical in S. malmgreni; Stach (1951) gives a good diagram of the antennae of the male of S. cruciatus.

The interlocking of the antennae in the Genus Sminthurides is compared by Schaller (1953) to the interlocking of the pincers of pseudoscorpions (Arachnida), where the male drags the female over spermatophores.

Whilst no observations have been made of the deposition of spermatophores in the Genus Sminthurides, Strebel (unpublished work recorded in Schaller 1953) has recorded them from the closely related species Sminthurinus niger and Mayer (1957) and the present writer in other members of the Symphypleona. However, the males of all these species lack grasping antennae, although Strebel (1929) records 'love play' in the touching of the antennae in S. niger.

In the Arthropleona Strebel (1932) and Britt (1951) have recorded courtship behaviour involving the stimulation of both sexes by means of the antennae. In Orchesella villosa Schaller (1953) records the male touching the females with the antennae during the deposition of the spermatophores, but points out that the presence of females has no effect on their deposition, in that isolated males will produce them. This is also the case in Dicyrtoma minuta.

4) The spermatophores.

Schaller (1953) describes the spermatophores of Orchesella villosa as stiff upright stalks which are sometimes slightly bent at the upper end. The whole stalk is hyaline and colourless and at the top is the spermal drop which is also colourless and transparent.

This description applies equally well to the spermatophores of Tomocerus minor and Dicyrtoma minuta, which are described here, and to the spermatophores of several species described by Mayer (1957). Table 9 gives a summary of the dimensions of the known spermatophores of Collembola. The diameter of the sperm droplet varies with the relative humidity; those measurements given by the present writer are for spermatophores in about 100% relative humidity.

Whilst Schaller (1953) makes no mention of the structures which maintain the sperm droplet at the top to the stalk of the spermatophore, Mayer (1957) describes a double branching in the stalk of the spermatophores of O. villosa, and illustrates this together with the cone-shaped structure occurring at the tip of the spermatophore stalks in Sminthurus fuscus. In the two species examined by the present writer, two different mechanisms for maintaining the droplet at the top of the stalk have been observed. In Tomocerus minor the top of the stalk is curved over into a circle, and the sperm droplet hangs in it, or round it; in Dicyrtoma minuta the tip of the stalk carries a broader cone, the apex of which projects through the sperm droplet which is maintained at the tip of the stalk by the broader base of the cone (Fig. 5), as in Sminthurus fuscus (Mayer 1957).

Table 9. The dimensions of the spermatophores of Collembola.

Species	Authority	Diameter of droplet in microns	Length of stalk in microns
Entomobrya muscorum	Mayer 1957	40-53	180-248
Orchesella cincta	Mayer 1957	31-50	210-310
Orchesella flavescens	Mayer 1957	52-65	338-390
Orchesella villosa	Schaller 1953	49-72	313-481
Lepidocyrtus paradoxus	Mayer 1957	24-28	115-256
Tomocerus longicornis	Mayer 1957	82-136	490-1034
Tomocerus minor	Hale ≠	54.7 ± 1.1 (Range 50-60)	265.5 ± 1.6 (Range 230-280)
Tomocerus vulgaris	Schaller 1953	52-61	221-246
Sminthurinus aureus	Mayer 1957	17-26	81-130
Sminthurus viridis	Mayer 1957	78-93	698-755
Sminthurus fuscus	Mayer 1957	118-141	703-921
Dicyrtoma minuta	Mayer 1957	65-143	615-930
	Hale ≠	96.2 ± 2.8 (Range 80-110)	696.0 ± 2.9 (Range 650-750)
Dicyrtoma fusca	Mayer 1957	49-55	404-430

≠ The mean and standard error of 10 spermatophores of each species are shown, together with the range for comparison with the data of the previous workers.

Fig. 5.

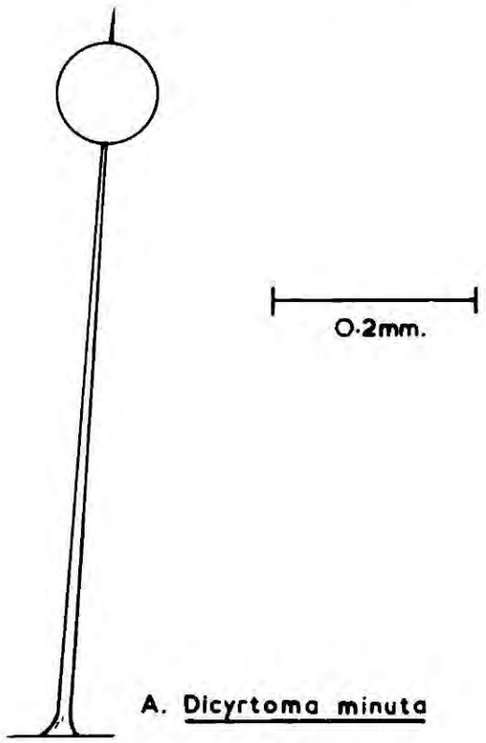
Spermatophores of Dicyrtoma minuta and Tomocerus minor.

Top. Appearance of newly deposited spermatophore.

Bottom. Detail of the support of the sperm droplet at the top of the stalk of the spermatophore.

Fig. 5.

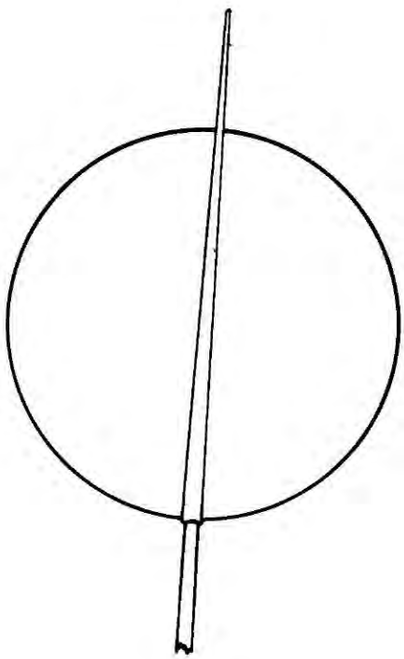
Spermatophores



0·2mm.

A. Dicyrtoma minuta

B. Tomocerus minor



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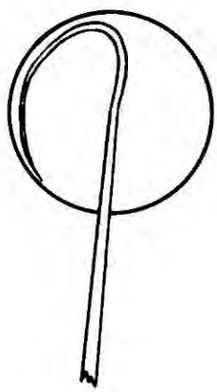


Detail of support
of sperm droplets

Schaller (1953) records that the sperms are retained within a pellicle on the stalks, and this is also the case in T. minor and D. minuta. However, it was found in both cases the pellicle did not burst on contact with water as was recorded by both Schaller (1953) and Mayer (1957). The pellicle was found to be remarkably resistant, and the whole spermatophore could be mounted in water, lactophenol or polyvinyl-lactophenol, without bursting; permanent preparations were made in this way without damage to the sperm globule. These observations suggest that it is only by mechanical fracture that the pellicle of the sperm globule can be broken.

The production of up to 300 spermatophores per male O. villosa was recorded by Schaller (1953), and Mayer (1957) records in the same species a maximum of 149 for a single period of deposition, up to 9 of which were recorded in the lifetime of a single individual. In D. minuta Mayer (1957) found an average of 50 spermatophores per male, at each deposition, with a maximum of 69; this compares with two counts of 53 and 55 in the present work. No estimate was possible in T. minor where spermatophores were produced in mass cultures.

According to Mayer (1957) spermatophores are deposited quite rapidly, a speed of 13 in 185 secs. having been recorded in O. villosa. The same author

also records males eating spermatophores which are more than 8-10 hours old, but apparently females do not do this.

The sperms of several species of Collembola have been described by Mayer (1957).

5) The transfer of the sperms.

Latreille (1832) and Kolanati (1858) having stated that the ventral tube carried the external opening of the sex organs, it was not until the observations of Lemoine (1882) and Lie-Petersen (1899) that sperm transfer was observed from the genital aperture which occurs three segments to the posterior of the ventral tube. Lemoine observed a drop of seminal fluid on the genital plate of a male Sminthurus fuscus; it was recorded that this was taken into the mouth by the female due to the fact that it was an immature individual where the genital plate was covered by a tegumen. It was concluded that the sperm passed through the intestine and penetrated to the ovaries via a special canal in front of the rectum. Lie-Petersen's observations concerned Bourletiella novemlineata and in translation were reported as follows:
"The male deposits a drop of sperm on the ground, frees himself from the head of the female, smears his mouth parts with seminal fluid with the help of his forelegs, pushes his head under the rear part of the female's

abdomen, and forces the sperm with the help of his mouthparts, into the sexual opening of the female". It was recorded that the genital aperture of the female opened to allow entry of the seminal fluid, and that the male repeated the dabbing of sperm onto the genital plate of the female on 18 occasions at 10 second intervals. Paclt (1956) casts doubt upon the validity of this observation on the basis that amongst other Collembola only indirect transfer has been observed, eg. Schaller (1953), Strebel (1932) and Britt (1951).

In Orchesella villosa and Tomocerus vulgaris the females strip off the sperm droplets from the stalked spermatophores in random movement (Schaller 1953), and according to this authority a droplet of liquid is exuded from the genital aperture of the female into which the sperm droplet supposedly bursts. In the light of the observations previously recorded (page 79) this seems unlikely, and the sperm droplets probably burst on contact with the cuticle of the female.

In an attempt to cast some light on the problem of the uptake of the sperm by females the following experiment was carried out. 12 females of Dicyrtoma minuta were isolated singly in culture tubes, and another twelve tubes were prepared which contained males. None

of the females produced eggs, and after 40 days it was assumed that they had not been previously fertilised. At this time two of the males had produced spermatophores, and after removing the male from each of these tubes a single female was introduced. The females were allowed to remain in the spermatophore-containing tubes for a period of five minutes, during which time they were continuously observed. Neither individual appeared to appreciate the presence of spermatophores and ran about the tube brushing against them with the underside of the body and the legs. In this way several sperm droplets were caused to burst on the body surface, purely by mechanical contact. After the period of five minutes the two females were returned to their own tubes, where after about 90 hours they began to produce eggs which eventually hatched. None of the other isolated females produced eggs. The period between contacting spermatophores and oviposition is comparable with that observed by Schaller of 3 hours to 3 days between 'dragging' and oviposition in Orchesella villosa.

From these observations it seems probable that in D. minuta:

1. The sperms make their own way, probably by a chemotactic response, to the genital aperture of the female, having once arrived on the body surface; or

2. The sperms are collected by some means and transferred to the genital aperture.

The only structures which appear capable of reaching most parts of the body in Dicyrtoma minuta are the filaments of the ventral tube (see Nutman 1941); when extruded these reach a length of almost twice that of the body. If the ventral tube is used in sperm collection, then the records of individuals taking sperm into the mouth ie. Lemoine (1882), Lie-Petersen (1899), Strebel in Schaller (1953), suggests the possible use of the ventral groove to pass the sperm to the filaments of the ventral tube. The ventral groove arises just behind the labium (Hoffman 1904, Ruppel 1953) and secretions of the cephalic gland are passed along it to the ventral tube. The filaments of the ventral tube could then be utilised to introduce the sperm to the genital aperture. As yet this is purely surmise, but it is a possibility worthy of future consideration.

Whilst in the experiments recorded here the males were absent during the uptake of sperm by females of Dicyrtoma minuta, Mayer (1957) is of the opinion that under natural circumstances the male is usually present during the uptake of spermatophores by the female; this is based on field observations of the species.

In Podura aquatica (Strebel 1932) and Hypogastrura armata (Britt 1951) apparently no spermatophores are produced, but the sperm droplets are deposited on the substrate and the female gathers the sperm by rubbing the genital plate over the droplet. In neither case was the presence of sperm in the sperm droplet verified. The possibility of direct transmission of sperm by the placing together of the genital plates of the male and female in Archisotoma besselsi (Willem 1925), is supported by the present writer in the case of Onychiurus tricampatus and O. furcifer. In two observations involving these species males have been seen in cavities in the substrate of the culture jar (caused by the formation of air bubbles as the plaster of Paris set) in the presence of another individual of the same species. In both cases a droplet of sperm was hanging from the genital plate, and this was removed and examined under the microscope; no definitive pellicle was present over the droplet, and motile sperms were found to be present in both cases. Movement of either individual in the confined space would have resulted in the sperm droplet bursting upon the other individual. The sex of the second individual was in neither case determined as this would have involved their being killed. Mayer (1957) records that

in Onychiurus armatus and Tullbergia quadrispina transfer of sperms occurs by the females picking up drops by means of the genital plate, deposition and acceptance of sperm being undirected by the other partner.

Sperm transfer in the Poduridae and Onychiuridae thus appears to be accomplished by the introduction of free sperm into the genital aperture of the female, either by collection from the substrate with no part being played by the male, or by the female brushing it off the genital plate of the male when in close proximity to it. No definite information exists for the Isotomidae, although the observation of Willem (1925) in Archisotoma besselsi suggests a transfer of sperm with the male taking an active part. In the Entomobryidae spermatophores occur, the sperm being taken up during random movement of the female. In the Sminthuridae spermatophores exist in the genera Sminthurinus, Sminthurus and Dicyrtoma and apparently both deliberate (Strebel in Schaller 1953, Mayer 1957) and accidental collection (Schaller 1953, present writer) occur; Lie-Petersen's observations suggest that some species of the Sminthuridae do not possess spermatophores, and this has been confirmed by Mayer (1957).

6) The eggs.

a) Oviposition.

i) Procedure.

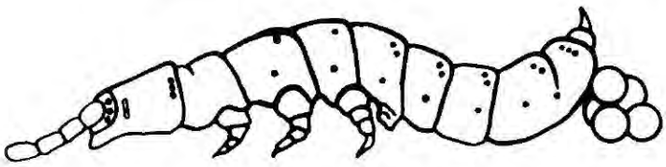
Davidson (1934) records that prior to oviposition in Sminthurus viridis a drop of 'anal fluid' is secreted from the anus and this is deposited on the soil surface so that the egg becomes coated with it as it is extruded; this implies that the abdomen tip is in contact with the substrate during the extrusion of the egg from the genital aperture. The present writer has observed oviposition in several individuals of the following species in culture: Hypogastrura denticulata, Onychiurus furcifer, O. latus, O. tricampatus, O. procampatus, Tullbergia krausbaueri, Lepidocyrtus lanuginosus, L. curvicollis, Isotoma sensibilis, Dicyrtoma fusca and D. minuta. In all cases the abdomen tip was elevated until the egg was extruded, and special postures were assumed by laying females apparently in order to prevent the egg from contacting the substrate until fully extruded (Fig. 6). Choudhuri (1958) records that the last abdominal segment is retracted in Onychiurus spp. during oviposition, but in the four species of the genus cultured in the present work this was never obvious. The same author states that "the genital aperture (is) lowered in order to

Fig. 6.

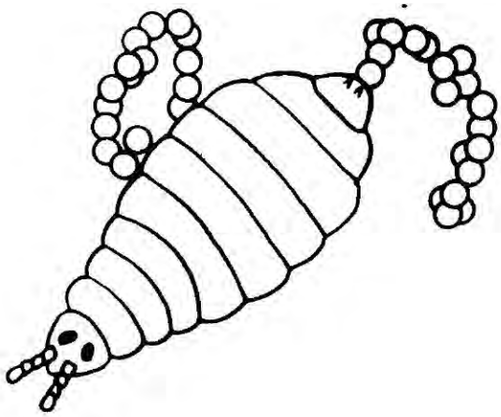
The postures assumed by females during oviposition. In all cases the genital plate is kept well clear of the substrate until the egg is extruded from the genital aperture. x30.

Fig. 6.

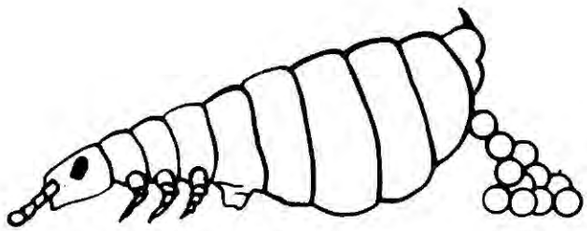
A. Onychiurus procampatus



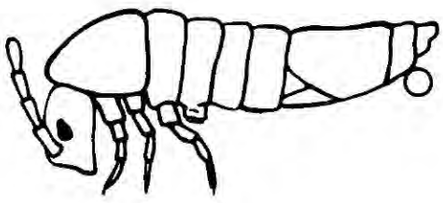
B. Tullbergia krausbauri



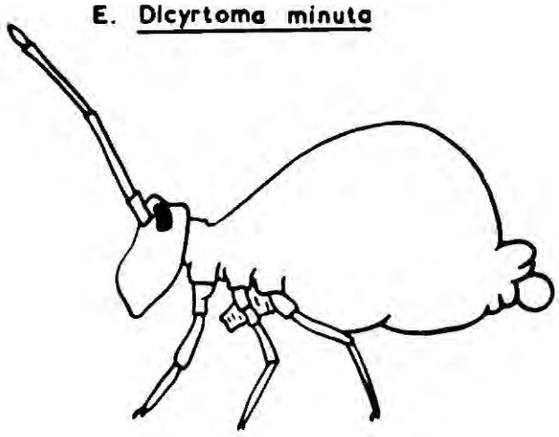
C. Hypogastrura denticulata



D. Lepidocyrtus lanuginosus



E. Dicyrtoma minuta



Postures of females during oviposition.

facilitate oviposition"; such is not the case, and in all species concerned the genital aperture apparently is deliberately elevated by the curling of the abdomen into a shallow U-shape.

During the process of extruding the egg from the genital plate female Collembola normally remain immobile. In Dicyrtoma fusca and D. minuta the abdomen tip pulsates during the process and particles of soil and faecal material move round the outside of the chorion, bathed in anal fluid; these particles move slightly at each pulsation and originate from the anus. In this way the egg may become entirely covered with dark particles before it is finally deposited. Deposition occurs with an abrupt cessation of the pulsating movement and the abdomen simultaneously drops onto the substrate. The female then rocks from side to side, whilst the claws retain their purchase and movement originates at the joints of the tibiotarsi and femurs; the rest of the body remains motionless. The rocking movement is exaggerated anteriorly and this causes a rotation between the genital plate and the egg. The insect breaks free after about 5 seconds and moves quickly away, picking up material from the substrate, and apparently eating it.

This activity is reminiscent of the 'displacement' activities of vertebrates (Armstrong 1950). Only in Dicyrtoma fusca and D. minuta were the eggs coated with faecal material during the laying process, as Davidson (1934) records in Sminthurus viridis.

In the other species observed, the eggs are laid in batches and as an egg is extruded it is deposited on the substrate by a slight jerking movement; the next egg is laid in a similar posture, with no contact between the two. The insects free themselves from a batch of eggs simply by walking away from it, and single eggs are detached from the genital plate by straightening out the abdomen so that the egg is brushed off by contact with the substrate. Occasionally single eggs were found in the cultures and these were probably due to a female being disturbed whilst laying. Wood (pers. comm.) has found this to be the case in Onychiurus 'armatus'.

ii) Duration of oviposition.

Choudhuri (1958) records a period of between 35 and 46 minutes for the production of an egg batch in Onychiurus spp.. In Table 10 the times recorded to produce egg batches are shown for seven species; those for Onychiurus latus and other Arthropleona agree closely with the times recorded by Choudhuri, whilst both species of Dicyrtoma take much longer to produce an egg-batch.

Table 10. Duration of oviposition in Collembola.

Species	Batch size	Time taken to lay batch in minutes	Average time to lay one egg in minutes
Hypogastrura denticulata	33	90	
	25	75	
	30	90	2.9
Onychiurus latus	15	40	
	12	30	2.6
Tullbergia krausbaueri	10	35	
	8	35	3.9
Isotoma sensibilis	20	45	
	12	30	2.3
Lepidocyrtus lanuginosus	35	120	3.4
Dicyrtoma minuta	25	1440	
	26	1440	
	27	1440	
	26	1440	55.4
Dicyrtoma fusca	17	1440	
	25	1440	
	18	1440	
	19	1440	79.4

iii) The situation in which eggs are laid.

The eggs of Collembola are usually laid in batches (Paclt 1956). In the cultures three species did not lay their eggs in batches. Tomocerus minor laid its eggs singly, wherever possible in a crevice approximately the same size as the egg itself. Dicyrtoma fusca and D. minuta distributed their eggs over the whole of the culture substrate and here again the eggs were placed in crevices and depressions. D. minuta deposited eggs in cultures where a pattern of scratches was provided on the surface; all eggs were laid in the grooves. Occasionally in all three species up to three eggs were found together in a cluster, but never more.

In the cultured species which lay their eggs in batches (Table 11), wherever possible the eggs are placed in a cavity. In the plaster of Paris medium holes left by air bubbles as it sets are a favourite situation for the deposition of eggs, and there is a suggestion that females lay more readily in culture jars containing such cavities.

b) The newly laid eggs.

Paclt (1956) states that the newly laid eggs of Collembola are shining white; this is not invariably the case as Milne (1960) found, and Choudhuri (1958) has described how colour changes occur during the

development of the eggs of Onychiurus spp.. The eggs of Isotoma viridis and Tomocerus minor are orange in colour when first laid, and later take on a brownish tinge, whereas the eggs of Neanura muscorum are a characteristic delicate shade of cream tinged with pink. Those of Hypogastrura denticulata are like small pearls when first laid and the eggs of Onychiurus latus, O. tricampatus and O. procampatus are similar but have a slightly whiter appearance and are less translucent. The eggs of Isotoma olivacea and I. infuscata are almost transparent on laying and the eggs of Lepidocyrtus lanuginosus and L. curvicollis have a white, almost opaque appearance. The eggs of Isotomurus palustris are bright yellow in colour. During further development the eggs of some species become coloured (Table 20).

c) Fecundity.

i) Introduction.

Lubbock (1873) reports that "the eggs are laid either singly, or in batches of from fifty to a hundred", and to date the literature contains little more precise information. The most comprehensive data available is for Sminthurus viridis, where Davidson (1934) records an average of 60 eggs per batch. Holdaway (1927) and

Maclagen (1932) have shown that the female of this species lays two egg batches at an interval of ten days. South (1959) records a mean of 53.5 for 11 egg batches of Entomobrya multifasciata.

In the same way that observations on the behaviour of Collembola is made difficult by the lack of a marked sexual dimorphism, so the design of experiments to determine the number of eggs laid is hindered. Four methods have been attempted in the present work to obtain information on the number of eggs produced by an individual female. These methods are:

1) The estimation of the average size of the egg batch;

2) The isolation of the gravid female until oviposition;

3) The dissection of the gravid female;

4) The setting up of a large number of small cultures containing two individuals, some 'pairs' thus being male and female (the sex of 'pairs' was determined on subsequent examination).

ii) Methods of determining the numbers of eggs laid at each period of oviposition.

1) The egg batch size.

Some information exists in the literature concerning the size of egg batches and this is summarised in Table 11. Some authors have indicated that their figures are means of a large number of egg batches,

Table 11. Size of egg batches of Collembola determined by previous workers.

Species	Authority	Comments	Batch size
Hypogastrura manubrialis	Ripper (1930)		30
Hypogastrura purpurascens	Strebel (1932)		20-30
Hypogastrura armata	Britt (1951)	Mean of 50 groups	28
	Wood (pers.comm.)		31
Neanura muscorum	Milne (1960)		1-2
Onychiurus furcifer	Milne (1960)		1-6
Onychiurus procampatus	Milne (1960)		1-2
Onychiurus latus	Milne (1960)		1-2
Onychiurus fimatus	Choudhuri (1958)	Maximum no. of eggs laid under optimum conditions	18
Onychiurus parthenogeneticus	Choudhuri (1958)		16
Onychiurus imperfectus	Choudhuri (1958)		18
Onychiurus armatus	Wood (pers.comm.)		10
Tullbergia krausbaueri	Milne (1960)		1-2
Folsomia candida	Milne (1960)		9-36
Isotoma viridis	Milne (1960)		27-54
Proisotoma sp.	Wood (pers.comm.)		17
Isotoma sp.	Wood (pers.comm.)		15
Isotomurus palustris	James (1933)	Mean of 3 batches	19
Entomobrya multifasciata	South (1959)	Mean of 11 batches	53.5
Pseudosinella violenta	Davis & Harris (1936)		45
Sminthurides aquaticus	Anders (1959)	Calculated: 45 females giving rise to 7020 young	15.9
Sminthurus viridis	Davidson (1934)		60

eg. Britt (1951), but for the most part the number of egg batches is not indicated and no confidence limits are given. Probably the only figures that can be relied upon to be accurate estimates of the egg batch size are those of Davidson (1934), Britt (1951) and South (1959), the others being either too large, eg. Choudhuri (1958) or too small, eg. Milne (1961), due to the methods used by these workers. However, there appears to be general agreement that the batch size in the Genus Hypogastrura lies between 20 and 30.

At the beginning of the present work several species were introduced into laboratory cultures in order to ascertain which species were most suitable for laboratory work. Several species produced eggs in mass cultures, and a summary of the batch size in those species laying in this way, is given in Table 12. Whilst some of the data is meagre because culturing of some species was discontinued, they are presented here since they are often an improvement on the existing data.

The data presented for Hypogastrura denticulata agrees well with previous estimates of egg batch size in the genus, but in other genera the agreement is not so good. Choudhuri's (1958) data for litter-giving (hemiedaphic) members of the Genus Onychiurus appears to

Table 12. Egg batch sizes of *Collembola* reared in laboratory cultures.

Species	Total eggs	Number of batches	Mean number of eggs per batch	Standard Error of the Mean ±
Hypogastrura denticulata	4330	145	30.2	2.6
Neanura muscorum	28	3	9.3	0.9
Onychiurus furcifer	774	54	14.3	0.9
Onychiurus procampatus	354	76	4.6	0.2
Onychiurus tricampatus	664	69	9.7	0.6
Onychiurus latus	621	41	15.1	0.9
Isotoma sensibilis	60	3	20.0	8.0
Isotoma viridis	172	8	21.5	3.5
Isotoma olivacea	1396	40	34.9	6.2
Isotomurus palustris	364	12	30.3	6.2
Lepidocyrtus cf. *curvicollis*	346	21	16.4	3.7
Lepidocyrtus lanuginosus	263	17	15.4	2.0

be a slight over-estimate, whilst Milne's (1961) data for the same genus is an underestimate for both soil-living (euedaphic) and litter-living species. The data presented here show a significant difference ($P < 0.05$) between the sizes of the batches of the euedaphic Onychiuridae (O. procampatus and O. tricampatus) and the hemiedaphic species (O. latus and O. furcifer). The difference is emphasised most in a comparison of O. latus and O. procampatus, where both the adult females and the eggs are identical in size. Possibly the reduction in the size of the egg batch in euedaphic species is correlated with a reduced predation (or other mortality factor) in the more confined spaces between the soil particles. There is also a significant difference between the egg batch sizes of O. procampatus and O. tricampatus.

The size of egg batches in the Isotomidae appears to be generally larger than that in the Entomobryidae in the present work, although Davis and Harris (1936) give a high figure for Pseudosinella violenta (Entomobryidae).

2) Isolation of the gravid female.

During the times of maximum egg laying in the field, presumably gravid adult individuals were collected

and isolated in single cultures; it was hoped that some of these would prove to be fertilised females, which would subsequently deposit eggs. For this to be successful, recent fertilisation (see page 82) was necessary, as females isolated alone fail to lay unfertilised eggs. Fifty cultures of each of eight species were set up; Table 13 gives the data obtained in this way.

Table 13. The number of eggs laid by isolated female Collembola.

Species	Total eggs	Number of cultures producing eggs	Mean number of eggs per female	Standard Error of the Mean ±
Hypogastrura denticulata	37	1	37	-
Isotoma viridis	51	1	51	-
Tomocerus minor	74	3	24.6	4.8
Lepidocyrtus curvicollis	76	2	38	∝
Dicyrtoma minuta	320	11	29.1	3.2
Dicyrtoma fusca	545	25	21.8	1.7

No eggs were obtained from Onychiurus latus or from Lepidocyrtus lanuginosus by this method. In the first three species in Table 13 the data were obtained in May, in the last three species in October.

Excepting for the two species of Dicyrtoma the method proved unsatisfactory for determining the number of eggs laid by an individual female during a single period of egg laying. However, these data show that the adult female is capable of producing appreciably more eggs than the data for egg batch sizes would suggest. This data also provides information on the three species that did not lay eggs in batches in the cultures, namely Tomocerus minor, Dicyrtoma minuta and D. fusca.

3) Dissection of the gravid female.

Of the four hundred insects isolated in the last experiment, half were used in other cultures after a period of three weeks, when it was assumed that no more eggs would be laid; the remaining two hundred were dissected. Some proved to be males, and in the majority of females the ovaries did not contain eggs. Only in the body cavities of females having laid eggs were more eggs found, these individuals being dissected within 48 hours of ceasing oviposition.

The single Hypogastrura denticulata which had laid 37 eggs contained 13 more, making a total of 50 eggs for the individual. In one female Dicyrtoma minuta which had laid 25 eggs, the right ovary was empty and the left contained 22 eggs; this gave a total of 47 eggs

for the insect. A second insect of this species which died after laying two eggs (not included in Table 13) was found to have 22 eggs in the right ovary, and 24 in the left, a total of 48 eggs. The other individuals of this species which were dissected were found to contain no more eggs. It seems probable that in this species and in D. fusca, the content of one ovary is laid before the other, and that some individuals had already laid the content of one ovary when collected from the field; thus the data given in Table 13 is probably an underestimate.

Again the data in this section are meagre, but it is recorded that a single female Hypogastrura denticulata may produce up to 50 eggs and a single Dicyrtoma minuta up to 48 eggs. It is recognised that although they are produced by the ovary, this is no indication that the eggs would ever be laid, as Phillipson (1959) has pointed out in Phalangidae. However, since batches of over 50 eggs have been recorded from H. denticulata in mass cultures during the present work, and isolated females of D. minuta have laid up to 44 eggs, it is possible that all these eggs could be laid.

4) Culturing 'pairs'.

The remaining individuals of the eight species of Collembola from the isolation experiment were each

provided with another individual of the same species; it was hoped that some of these 'pairs' would be male and female and subsequently give rise to fertile eggs. Where the sexes could be recognised ie. in the two species of Dicyrtoma, male/female pairings were made. Whilst conditions were maintained as similar as possible to those in the mass cultures where eggs were laid freely, this experiment proved to be a failure. Only one 'pair' produced eggs; this was a 'pair' of Onychiurus latus, and 21 eggs which subsequently proved to be fertile, were deposited in a single batch. Of the seventeen 'pairs' of O. latus set up, five proved to be male/female pairs on subsequent examination. The other species were not examined for the incidence of male/female pairs, as it was thought that this would provide little useful information.

iii) The number of periods of oviposition.

Holdaway (1927) and Maclagen (1932) have shown that two periods of oviposition occur in Sminthurus viridis at intervals of ten days, and Strebel (1932) reports that there are at least three batches of eggs produced in the lifetime of Hypogastrura purpurascens. Britt (1951) records that many female H. armata produced

two batches of eggs, and that one individual laid three batches and another four batches. Wood (pers. comm.) records at least two egg batches during the lifetime of Onychiurus armatus, and the present writer has found this to be the case in O. tricampatus. Schaller (1953) reports three periods of egg laying in Orchesella villosa and South (1959) records two females of Entomobrya multifasciata laying a total of eleven batches. On the basis of Lindemann's (1950) work, Handschin (1953) reports, in translation, as follows: "The lifetime up to the attainment of puberty takes in the case of Orchesella up to five months; full growth is attained between one and two months later and after this the animals live from five to six months until death. During the last period of life special processes occur; for one thing new egg-layings from time to time follow on an average the fifth moult, and indeed from time to time four to eight eggs may be laid, so that in the whole of an individual's lifetime 60-80 eggs may be laid".

It would appear then that the egg batch size and estimates of the number of eggs in the ovaries of a female at any given time would give an underestimate of the number of eggs produced in the lifetime of an average female, since each appears to lay more than once.

Thus the data given in Section II may be regarded as minimum estimates of the fecundity.

In two species, Hypogastrura denticulata and Isotoma olivacea, data are available from insects collected from the field before laying began. Histograms showing the numbers of eggs produced over different periods of the life of the insects in culture (Fig. 7) demonstrate that in H. denticulata probably three periods of peak egg production occurred, and in I. olivacea four such probable periods were evident. Insects in both cultures were of maximum (adult) size, and most probably had not laid previous to being introduced to the cultures; insects of the same species collected from the same habitat on previous dates did not lay until about the same time.

Handschin (1953) has recorded that Orchesella lays eggs before reaching a maximum size, and Britt (1951) has made similar observations in H. armata. Milne (1961) records sexual maturity as being reached in the penultimate instars of Onychiurus furcifer, O. latus, O. procampatus and T. krausbaueri, but since the data provided for the instar groupings is very meagre, and does not agree with that presented here for the same species (see page 139) this information is regarded as

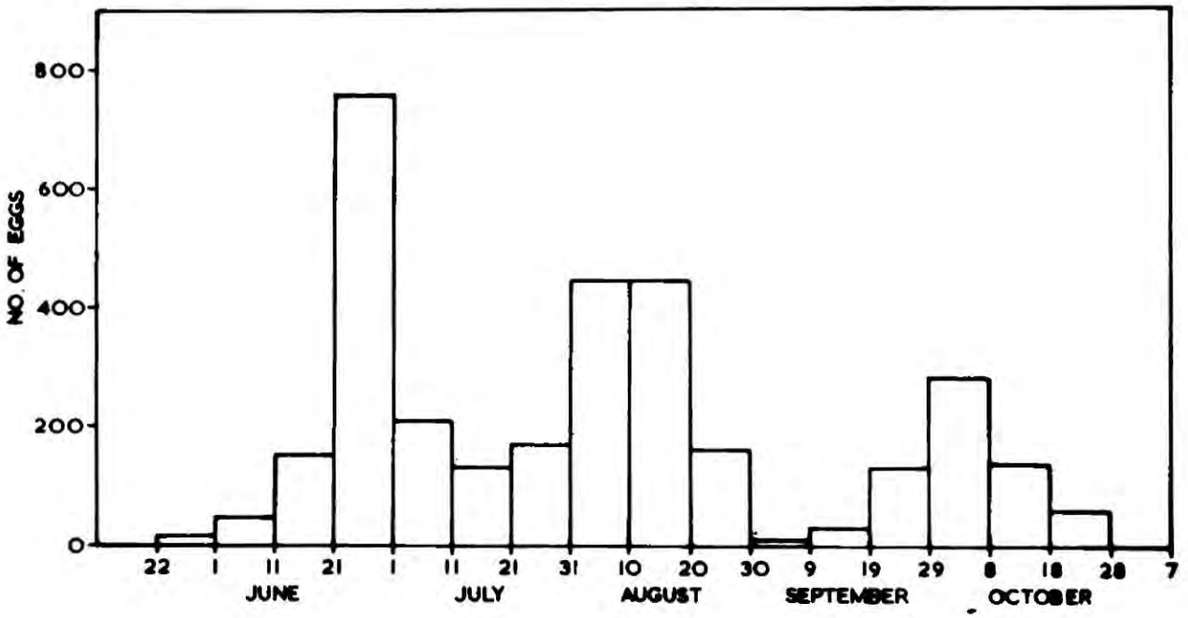
Fig. 7.

Histograms showing the number of eggs laid in cultures by about 100 females of Hypogastrura denticulata over a period of five months and by about 50 females of Isotoma olivacea over a period of two and a half months.

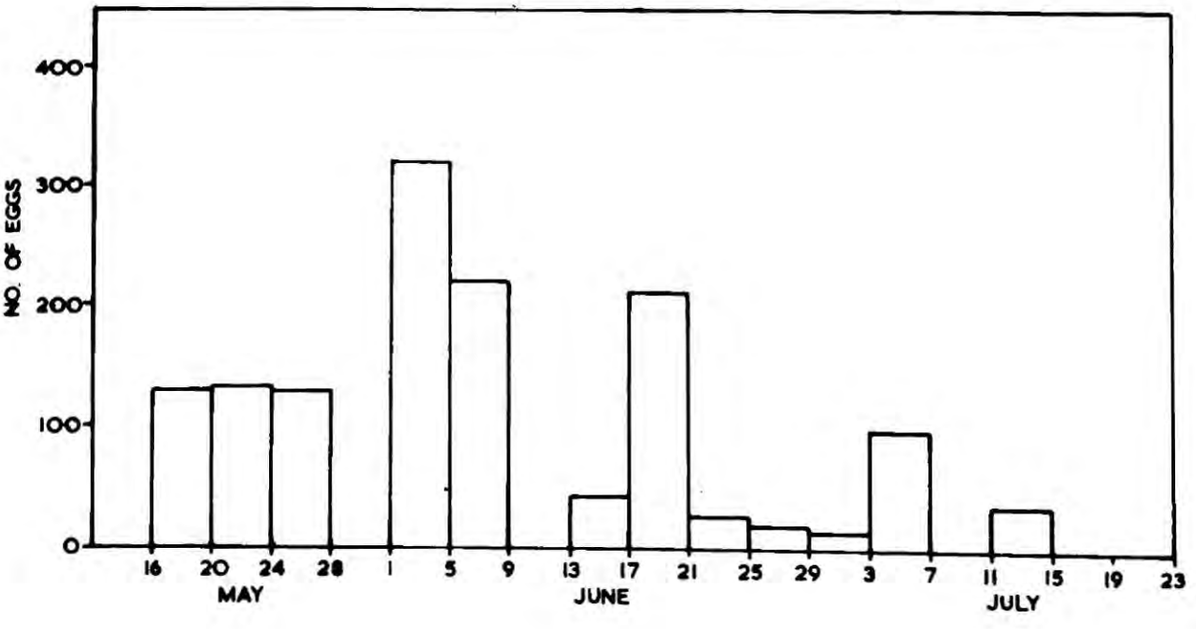
Fig. 7.

Egg laying in cultures.

Hypogastrura denticulata — eggs laid in 10 day periods.



Isotoma olivacea — eggs laid in 4 day periods.



unreliable. In the present work it has been shown that Lepidocyrtus cf. curvicollis reaches maturity before attaining maximum (adult) size. Fifth instar insects, some eight weeks old, laid eggs which were morphologically identical with those laid by adults (maximum size), and these eggs developed and hatched over an identical period. Table 14 shows the egg batch size of individuals not having attained maximum size compared with that of the adults, in L. cf. curvicollis.

Table 14. Egg batch size at different ages in Lepidocyrtus cf. curvicollis in culture.

Age & Instar	No. of eggs	No. of batches	Mean no. of eggs per batch	Difference and S.E. of difference	P
8 weeks (5th instar)	57	10	5.7	8.5 ± 3.4	0.05
12 weeks (8th instar)	71	5	14.2		
				22.1 ± 8.3	0.05
Adult	218	6	36.3		

Qualitative observations suggested that eggs were produced by individual females directly after moulting in both Dicyrtoma minuta and D. fusca, and in order to ascertain if this also occurred in members of the Arthropleona, a species which cultured easily and moulted

frequently was sought; Tullbergia krausbaueri was found to fit these requirements. Cultures were set up in 'pairs', newly hatched first instars being used. These cultures proved to be much more successful than those of the other species recorded previously (page 99), and data were obtained from twenty-three individuals. Table 15 shows in which instar the first eggs were produced, maximum size being reached in instar 4.

Table 15. Egg production in different instars of Tullbergia krausbaueri.

Instar	1	2	3	4	5	6	7	8	9	10
No. laying for first time	0	0	1	8	7	2	3	0	1	1

It was found that once a female had begun to lay, it laid directly after moulting at successive moults. Although several individuals refrained from laying after moulting on some occasions, if laying was resumed this always occurred directly after another moult.

Table 16 shows the mean number of eggs produced during each instar by twenty three females. The maximum number of eggs is laid in Instar 7 or 8, after which the number produced at each moult decreases. Thus even after attaining maximum size in Instar 4 (see later, page 138) the number of eggs laid at each moult increases

Table 16. Number of eggs produced in each instar in T. krausbaueri.

Instar	Total eggs	No. of batches	Mean no. eggs/batch		Standard error of mean
3	2	1	2.00		-
4	24	9	2.66		0.4
5	61	16	3.81		0.4
6	62	10	6.20		0.9
7	86	12	7.16		0.9
8	58	8	7.25		0.9
9	61	9	6.78		1.1
10	47	7	6.71		1.3
11	62	10	6.20		1.1
12	56	9	6.22		1.0
13	45	8	5.63		0.7
14	8	3	2.66		0.7
15	10	3	3.33	Average 3.55	1.5
16	14	3	4.66		0.9

until the 7th or 8th instar. It is of interest to compare these data for Tullbergia krausbaueri with the average egg batch sizes at different stages in the cultures shown in Fig. 7. These data are given in Table 17.

Table 17. Variations in egg batch size with age in H. denticulata and I. olivacea.

Species	Mean number of eggs per batch and standard error			
	1st peak	2nd peak	3rd peak	4th peak
Hypogastrura denticulata	21.5 ± 1.6	32.0 ± 5.3	25.0 ± 3.1	-
Isotoma olivacea	65.3 ± 19.1	41.9 ± 12.6	28.1 ± 10.6	14.7 ± 2.1

In both cases there is a tendency for the egg batch sizes to be reduced in older insects, as has been shown in T. krausbaueri (Table 16).

iv) The total number of eggs laid during life.

The data given in Table 12 for average batch size are open to criticism on the following lines: it cannot always be assumed that eggs in one cluster are the produce of a single female; Davidson (1934) has found clusters of up to 400 eggs in cultures of Sminthurus viridis and Britt (1951) points out that large clusters of eggs in cultures of Hypogastrura armata are the produce of more than one female. This has also been

suggested by Paclt (1956). In the present work clusters of up to 176 eggs have been found in Isotoma olivacea, and up to 160 in Hypogastrura denticulata. On four occasions in this last species eggs in which the chorion had split were allowed to remain in the cultures, and newly laid eggs were subsequently found in the same cluster; this supports the observations of the previous workers. This possibility of error was reduced by removing eggs from the cultures daily. Underestimation of the average batch size would be brought about by the laying female being disturbed; in the opinion of the present writer this is much the more common occurrence, and thus the figures given in Table 12 are probably a slight underestimate; that they are not a gross over-estimate is shown by comparison with Table 13, which gives an indication of the number of eggs that an individual is capable of laying during a single period of oviposition.

An estimate of the number of eggs laid by a female during life can be obtained by multiplying the average batch size by the number of periods of laying. It is thought that such a figure gives an indication of the minimum number of eggs that an individual female is capable of laying during life, and Table 18 summarises this information.

The fecundity of females in the field is difficult to estimate. Factors such as the incidence of fertilisation, mortality and the temperature of the environment (which affects the number of moults and thus the number of egg-laying periods) would have to be taken into consideration in the estimation of an average number of eggs per female during life. The temperature (8°C.) at which most of the cultures were maintained lies just below the mean temperatures experienced by laying females at Moor House in spring, and just above the mean temperature to which autumn layers are subject (see Fig. 2). The data presented here for 8°C. can probably be regarded as a minimum estimate under the field conditions prevailing at Moor House. The species maintained at 15°C. had the metabolism increased by a factor of 2.8 over those at 8°C.; that is to say that whereas the individuals of Hypogastrura denticulata had a period of 8.1 ± 0.4 days between moults at 15°C. this was increased to 22.6 ± 2.5 days at 8°C. (see page 148). Thus whilst members of the Genus Onychiurus could be expected to moult at least twice during the period in which eggs are laid at Moor House (May to October), thus probably producing two egg batches, Tullbergia krausbaueri would not moult on ten occasions as indicated in Table 19 during this period. Probably only in this last species, which would moult about six

Table 18. Estimates of fecundity in Collembola.

Species	Authority	Temp. of culture °C.	Mean no. of eggs in batch	Probable number of layings	Estimat no. of e laid during
H. manubrialis	Ripper 1930	22	30	3	90
H. purpurascens	Strebel 1932	-	20-30	3	60-90
H. denticulata	Hale	8	30.2 ± 2.6	3	90
H. armata	Britt 1951	24?	28	3	84
	Wood (p.c.)	16.7	31	3	93
N. muscorum	Hale	8	9.3 ± 0.9	?	?
O. furcifer	Hale	15	14.3 ± 0.9	2	28
O. procampatus	Hale	15	4.6 ± 0.2	2	9
O. latus	Hale	8	15.1 ± 0.1	?	?
O. tricampatus	Hale	15	9.7 ± 0.6	2	19
O. armatus	Wood (p.c.)	16.7	10	2	20
O. fimatus	Choudhuri 1958	-	18	2	36
O. parthenogeneticus	Choudhuri 1958	-	16	2	32
O. imperfectus	Choudhuri 1958	-	18	2	36
T. krausbaueri	Hale	15	5.5 ± 0.3	10	54

cont'd. overleaf.

Table 18 (continued).

Species	Authority	Temp. of culture °C.	Mean no, of eggs in batch	Probable number of layings	Estima no. of e laid dur lif
F. candida	Milne 1961	12	9-36	?	?
Proisotoma sp.	Wood (p.c.)	16.7	17	3	51
I. sensibilis	Hale	8	20.0 ± 8.0	3	60
Isotoma sp.	Wood (p.c.)	16	15	3	45
I. viridis	Hale	8	21.5 ± 3.5	3	64
I. olivacea	Hale	8	34.9 ± 6.1	3	90
I. palustris	Hale	8	30.3 ± 6.1	3	90
E.multifasciata	South (1959)	17	53.5	5-6	300
O. villosa	Lindemann(1950)		4-8	10	60-80
L. curvicollis	Hale	8	16.5 ± 3.6	3	48
L. lanuginosus	Hale	8	15.5 ± 2.0	3	46
P. violenta	Davis & Harris (1936)	25?	c45	?	?
T. minor	Hale	8	24.7 ± 4.8	?	?
S. aquaticus	Anders (1959)	-	c16	?	?
S. viridis	Davidson (1934)	-	60	2	120
D. minuta	Hale	8	29.1 ± 3.2	2	58
D. fusca	Hale	8	21.8 ± 1.7	2	43

times, laying a mean of about 33 eggs during the period of egg laying, are the data given in Table 18 an over-estimate for the situation in the field at Moor House.

d) Laying in the field.

In an attempt to determine at what time of the year Collembola laid under field conditions at Moor House, two separate cultures for each of sixteen species, were set up at monthly intervals over a period of one year (January to December 1960). Twenty individuals collected in the field were placed in each culture. The cultures were maintained at a constant temperature of 8°C. Egg laying in the cultures, within fourteen days of setting up, is indicated in Table 19 by a cross (X) for each culture, under the month in which the Collembola were collected. From this data, it is clear that most species lay in late spring and early summer, and that eggs are not laid during the winter. Cultures of species that were collected during the first four months of the year, and did not produce eggs within fourteen days of collection, laid at a later date, suggesting that oviposition is inhibited during the winter months, at Moor House. It was subsequently found that by raising the temperature at which the cultures collected in mid-winter were kept, oviposition could be brought about at an earlier date than in those maintained at 8°C. It

Table 19. Estimated dates of laying in the field at Moor House, 1960.

Species	Month J	F	M	A	M	J	J	A	S	O	N	D
Hypogastrura denticulata	-	-	-	-	X	XX	X	-	-	-	-	-
Neanura muscorum	-	-	-	-	-	XX	X	-	-	-	-	-
Onychiurus procampatus	-	-	-	-	-	XX	XX	XX	X	-	X	-
Onychiurus tricampatus	-	-	-	-	XX	XX	XX	XX	XX	XX	X	-
Onychiurus latus	-	-	-	-	XX	XX	-	-	-	-	-	-
Tullbergia krausbaueri	-	-	-	-	XX	XX	XX	XX	XX	X	-	-
Isotoma sensibilis	-	-	-	XX	XX	X	-	-	-	-	-	-
Isotoma viridis	-	-	-	X	XX	X	-	-	-	-	-	-
Isotoma olivacea	-	-	-	XX	XX	X	-	-	-	-	-	-
Isotoma infuscata	-	-	-	X	XX	-	-	-	-	-	-	-
Isotomurus palustris	-	-	-	XX	XX	X	-	-	-	-	-	-
Lepidocyrtus cf. curvicollis	-	-	-	-	-	X	-	-	X	XX	XX	-
Lepidocyrtus lanuginosus	-	-	-	-	X	-	-	-	-	XX	X	-
Tomocerus minor	-	-	-	X	XX	X	-	-	-	-	-	-
Dicyrtoma minuta	-	-	-	-	-	-	X	-	-	XX	XX	-
Dicyrtoma fusca	-	-	-	-	-	-	X	-	-	XX	XX	-

NOTE: - indicates no eggs laid.
With the milder spring in 1961 (Fig.2) laying was earlier.
X = Laying in one culture.
XX = Laying in both cultures.

would thus appear that low temperatures inhibit oviposition in the field.

In the two species of Dicyrtoma two egg-laying periods occur, in summer and autumn. These two periods coincide with two separate generations. Other species in Table 19 probably had only one generation in the year. In L. lanuginosus the majority of eggs is laid in autumn, but a few individuals survive the winter and lay in the following spring. In L. cf. curvicollis oviposition took place in sub-adults (Table 14) in June, but the majority of eggs were laid in autumn.

Plate 10 shows the eggs of N. muscorum laid in the field.

e) Development.

i) Morphological changes.

Directly the egg is laid, it begins to enlarge due to the uptake of water from the environment. In an atmosphere of 100% R.H. the eggs reach their maximum size in a few hours; further enlargement does not take place until the growth of the embryo begins after about 20% of the developmental period. In fertile eggs the first sign of development of the embryo is seen in the splitting of the chorion. That it is the growth of the embryo that

Plate 10.

Eggs of *Neanura muscorum* laid in the field on a root of *Calluna vulgaris*. The high humidity of the situation in which they were laid is indicated by the presence of leafy liverworts on the root. x25.

causes the chorion to split is demonstrated by the fact that in infertile eggs no split occurs, although initial enlargement by water uptake takes place. In most genera the chorion remains attached as two cap-shaped structures at opposite poles of the egg, but in members of the Genus Onychiurus which were cultured, the chorion remained closely attached to the next membrane (Fig. 8).

On the splitting of the chorion, the egg loses its spherical shape, and takes the form of a flattened spheroid except in the Entomobryidae and the two members of the Genus Dicyrtoma which were cultured. The two halves of the chorion remain attached to the lower membrane (serosal cuticle) throughout the course of the development of the egg. In all the species concerned in this study the chorion was found to be unpigmented, transparent and without any pattern or appended structures. South (1959), however, has found a species-characteristic pattern in the chorion caps of members of the Genus Entomobrya. The second membrane, which will be referred to as the serosal cuticle, was found in those cases examined to be patterned, and in some cases it bore appendages. In the case of the Isotomidae, the pattern was made up of small protruberances but no constant differences between species could be found. Eggs from the same egg batch tended to have a pattern of similar sized protruberances, but there was no consistancy between the eggs of different individuals of the same species.

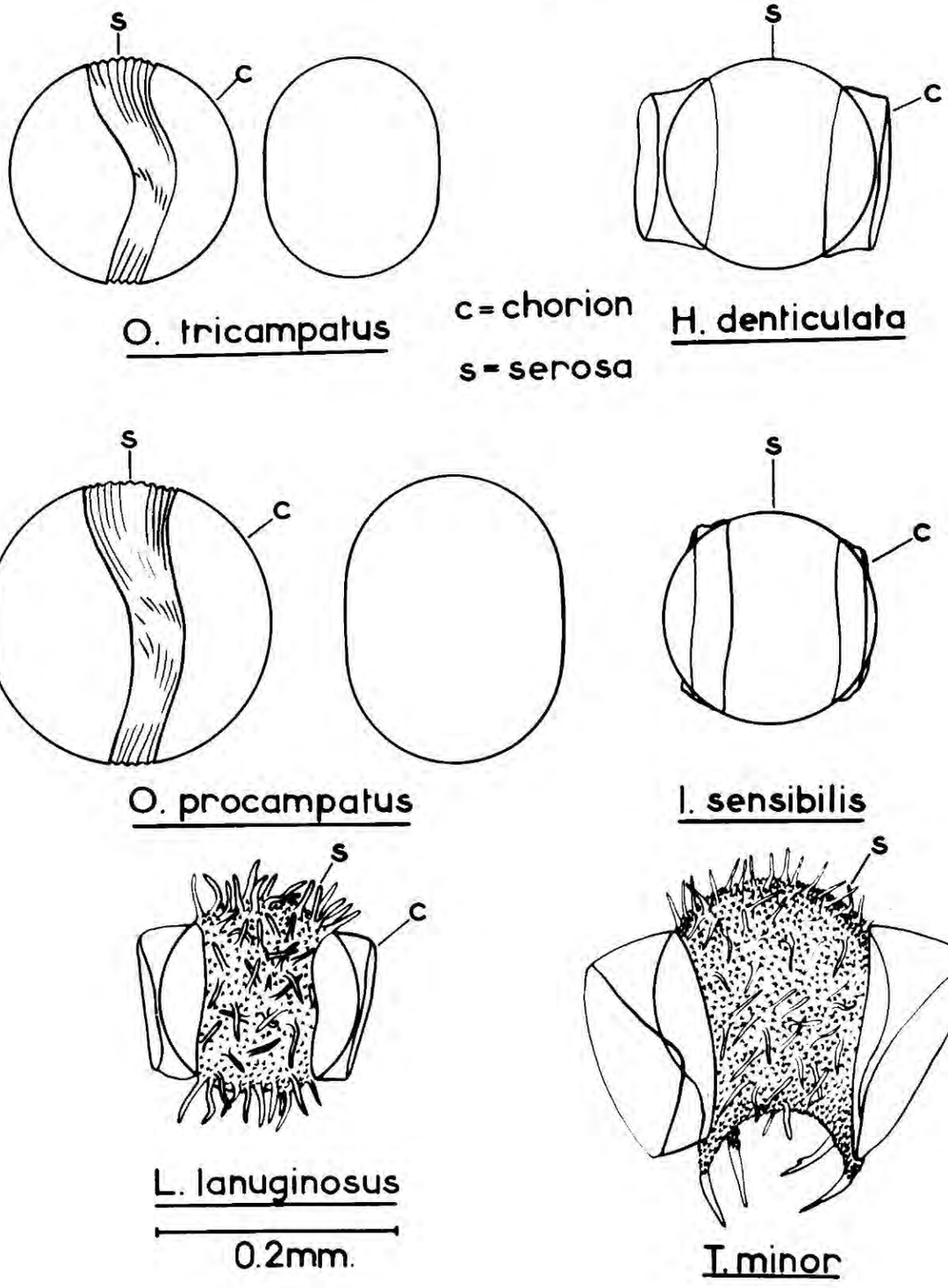
Fig. 8.

Developing eggs of several species of Collembola. In the two species of Onychiurus it can be seen that the chorion adheres closely to the serosal cuticle after splitting, whereas in the eggs of the other species figured, the chorion, after splitting, forms two caps at opposite poles of the eggs.

In the two species of Onychiurus the serosal cuticle is sculptured whereas in Hypogastrura denticulata and Isotoma sensibilis it is smooth; in Lepidocyrtus lanuginosus and Tomocerus minor the processes which grow out from the serosal cuticle, after the splitting of the chorion, are shown.

Fig.8.

Developing eggs.



All three members of the Entomobryidae cultured had numerous long hair-like appendages arising from the serosal cuticle. Nicolet (in Lubbock 1873) comments on these processes, which Handschin (1926) considers may serve as an anchorage underground. When the chorion first splits, the serosal cuticle can be seen to be perfectly smooth in all three species cultured. The hairs grow out from the serosal cuticle over a period of six days at 8°C., but no growth was observed beneath the chorion caps; only where the serosal cuticle was exposed to the air did hairs develop. In Tomocerus minor, four large spines grow out from the base of the egg in addition to the hairs. Uchida and Abukawa (1956), referring to Tomocerus minutus, record that "The chorion ..... forms a pair of lateral chambers each of which is soon provided with two curved spines". In fact there is no connection between the spines of the serosal cuticle and the chorion, as can be seen in Fig. 8. Each spine itself bears processes, and apically there is a long, claw-like region which curves under the egg; the length of each of the spines is approximately equivalent to the diameter of the egg. The fact that the processes are not produced by the egg until some days after it is laid may be correlated with a dispersal phase; Collembola laying this type of

egg are surface and vegetation dwellers (members of Gisin's (1943) 'atmobios'), and the eggs will probably be more subject to dispersal from the position of laying than eggs of, say, cavernicolous forms. The processes of the serosal cuticle, on their growing, could then act as anchors after dispersal of the eggs.

During further development, the eggs of the Isotomidae and Entomobryidae become coloured, after about 75% of the period of development has elapsed, apparently due to the formation of a pigment in the body fluid of the embryo. However, eye spots appear before the body colouration. The eggs of Hypogastrura denticulata remain colourless if kept in the dark, except for the eye spots which develop a dark pigment. If exposed to the light all species which are pigmented in the adult stage tend to develop surface pigmentation, and it was found that different coloured eggs could be produced dependent upon the time the eggs were exposed to light.

Table 20 gives a summary of the morphology of the eggs of the species cultured during the present work. Measurements are from twenty or more eggs from at least two females in all cases.

Table 20. Morphology of the eggs of Collembola.

Species	Colour of eggs on Laying	Colour of eggs on Hatching in dark	Diameter of eggs on Laying (mm.)	Diameter of eggs on Swelling (mm.)	Dimensions of eg on chorion splitting (mm.)	Dimensions of eg on hatch (mm
Hypogastrura denticulata	None	None	0.16	0.19	0.22	0.2
Neanura muscorum	Creamy pink	-	0.28	0.34	-	-
Onychiurus furcifer	None	None	0.19	0.21	0.22 x 0.19	0.23x0.19
Onychiurus procampatus	None	None	0.23	0.26	0.27 x 0.22	0.28x 0.22
Onychiurus tricampatus	None	None	0.17	0.20	0.20 x 0.17	0.21x 0.17
Onychiurus latus	None	None	0.23	0.26	0.27x 0.21	0.28x 0.21
Tullbergia krausbaueri	None	None	0.08	0.09	0.12 x 0.10	0.12 x0.10
Isotoma sensibilis	Orange red	Orange red	0.17	0.19	0.19 x 0.17	0.19 x 0.17
Isotoma viridis	Orange red	Orange red	0.20	-	-	-
Isotoma olivacea	None	Pink	0.17	0.19	0.19x 0.17	0.19x0.17

continued overleaf

Table 20 (cont'd.)

Species	Colour of eggs on Laying	Colour of eggs on Hatching in dark	Diameter of eggs on Laying (mm.)	Diameter of eggs on Swelling (mm.)	Dimensions of eg on chorion splitting (mm.)	Dimensions of eg on hatch (mm.
Isotoma infuscata	None	Pink	0.17	0.19	0.19 x 0.17	0.19x(
Isotomurus palustris	Yellow	Orange pink	0.17	0.19	0.19 x 0.17	0.19x 0.17
Lepidocyrtus cf. curvicollis	None	Pink	0.19	0.21	0.21 x 0.19	0.21x 0.19
Lepidocyrtus lanuginosus	None	Pink	0.19	0.21	0.21x 0.19	0.21x 0.19
Tomocerus minor	Orange	Pink	0.21	0.23	0.23	0.23
Dicyrtoma minuta	None	Pink	0.28	-	-	-
Dicyrtoma fusca	None	Pink	0.28	-	-	-

NOTE: Measurements taken to the nearest division of the micrometer eyepiece were such that no variations occurred.

ii) The hatching period.

1) Introduction.

Davidson (1934) has shown that the duration of development of Collembola within the egg is dependent on both temperature and humidity. The present work is concerned with those Collembola living in the litter and soil layers, where according to Thamdrup (1939) the relative humidity is greater than 90% even during dry periods. No account has been taken of variations in humidity, except to maintain 100% R.H. in culture jars containing eggs, in the experiments involving different temperature conditions.

2) Egg development at constant temperature.

Eggs laid in cultures were transferred on the day of laying to small culture tubes of the type described on page 68. These were then placed in constant temperature conditions and a range from 2°C. to 23°C. was utilised. 2°C, 4°C, 7°C, 12°C, 16° and 23°C. were the temperatures most used, but others occasionally became available and were used when the opportunity arose. The following fifteen species were involved in the series of experiments:

H. denticulata, O. furcifer, O. procampatus, O. latus, O. tricampatus, T. krausbaueri, I. viridis, I. olivacea, I. infuscata, I. palustris, L. cf. curvicollis, L. lanuginosus, T. minor, D. fusca and D. minuta.

Figs. 9 to 12 show the relationship between temperature and development time in these species.

The development time was measured from the day of laying to the day on which 50% of the eggs in a given batch had hatched. Usually about 20 eggs were placed in a culture tube, but this was not always possible; occasionally where eggs were abundant in the cultures up to 50 were used in each tube, as was the case in H. denticulata.

Table 21 shows the product of the egg development time in days and the temperature in degrees centigrade, for different temperatures. For each species this figure approximates to a constant, and average figures ($\overline{K}$) have been calculated for each species.

It was not considered valid to attribute different values of a constant (K) to different species, if eggs placed in a given temperature, at the same time, took the same time to develop. Thus the same constant (K) has been used in species where the average constant ($\overline{K}$) differs; minor differences in the constant temperatures over a period of time are thus allowed for; eg. O. furcifer, O. procampatus and O. tricampatus placed at 15°C. on the same date all had a 50% hatch after 24 days,

and thus a constant (K) of 380 (the mean of $\overline{K}$ for all three species), is applied to all three species. A similar procedure was also carried out for I. olivacea and I. infuscata and the two species of Lepidocyrtus, for the same reasons. Figures of K are given to the nearest 10 below 1000, and the nearest 100 above 1000 as it is considered that minor temperature fluctuations preclude a greater accuracy.

In the graphs (Figs. 9-12) the recorded development times are shown in relation to the constant K. In all cases the form of the graph is that of an hyperbola, and is in agreement with those figured by Davidson (1934) and Choudhuri (1958). The data suggest that development ceases between 0°C. and 2°C., in the species concerned in this work. Choudhuri (1958) and South (1959) give 4°C. as the minimum developmental temperature in Onychiurus spp. and Entomobrya spp. respectively. Davis and Harris (1936) provide a graph of the development time of Pseudosinella violenta which is the mirror image of the typical graph illustrated here; the data are only for temperatures above 25°C., at which temperatures the eggs of the species concerned in this work fail to develop. Choudhuri (1958) has shown that in Onychiurus spp. development time begins to increase above 25°C., and apparently the data of Davis and Harris (1936) concern only this atypical part of the graph.

Table 21. The product of the egg development time in days and the temperature in °C.. for different temperatures, to show that this figure is a constant (K).

Species	Temperature (°C.)												
	2/3	4	7	10	12	13	14	15	17/18	20	22/23	$\bar{K}$	K
Hypogastrura denticulata	300	392	392	-	408	-	-	420	442	-	506	408	400
Onychiurus furcifer	-	-	441	-	384	-	-	360	-	-	-	395	380
Onychiurus latus	-	424	441	-	408	-	-	-	442	-	506	444	440
Onychiurus procampatus	-	-	-	410	372	360	-	360	-	-	-	376	380
Onychiurus tricampatus	-	-	-	-	360	364	364	360	-	-	-	362	380
Tullbergia krausbaueri	-	-	-	500	-	-	-	510	-	520	-	510	500
Isotoma olivacea	159	180	182	-	216	-	-	-	204	-	230	195	180
Isotoma infuscata	-	180	154	-	-	-	-	-	144	-	-	159	180

cont'd. overleaf.

Table 21 (cont'd.)

Species	Temperature (°C.)												
	2/3	4	7	10	12	13	14	15	17/18	20	22/23	$\bar{K}$	K
Isotoma viridis	-	-	301	-	240	-	-	-	238	-	184	241	240
Isotomurus palustris	-	224	196	-	216	-	-	176	-	-	230	208	200
Lepidocyrtus lanuginosus	312	360	392	-	-	-	-	-	340	-	-	351	340
Lepidocyrtus cf. curvicollis	330	300	350	-	-	-	-	330	-	-	330	328	340
Tomocerus minor	-	368	385	-	-	-	-	-	340	-	330	356	360
Dicyrtoma fusca	-	-	1190	-	-	-	-	1270	-	-	1320	1260	1300

NOTE. $\bar{K}$ is the average of the product of development time in days and the temperature in degrees C.; K is the constant used in the calculations of development times in the field, and in the graphs. For the differences see text, page 119. Some additional points were added to the graphs (Figs. 9-12) as other constant temperatures became available.

Fig. 9.

The relationship between the developmental period in days and the temperature in degrees centigrade in eggs of Hypogastrura denticulata.

Fig.9

Egg development at constant temp. — Hypogastrura denticulata.

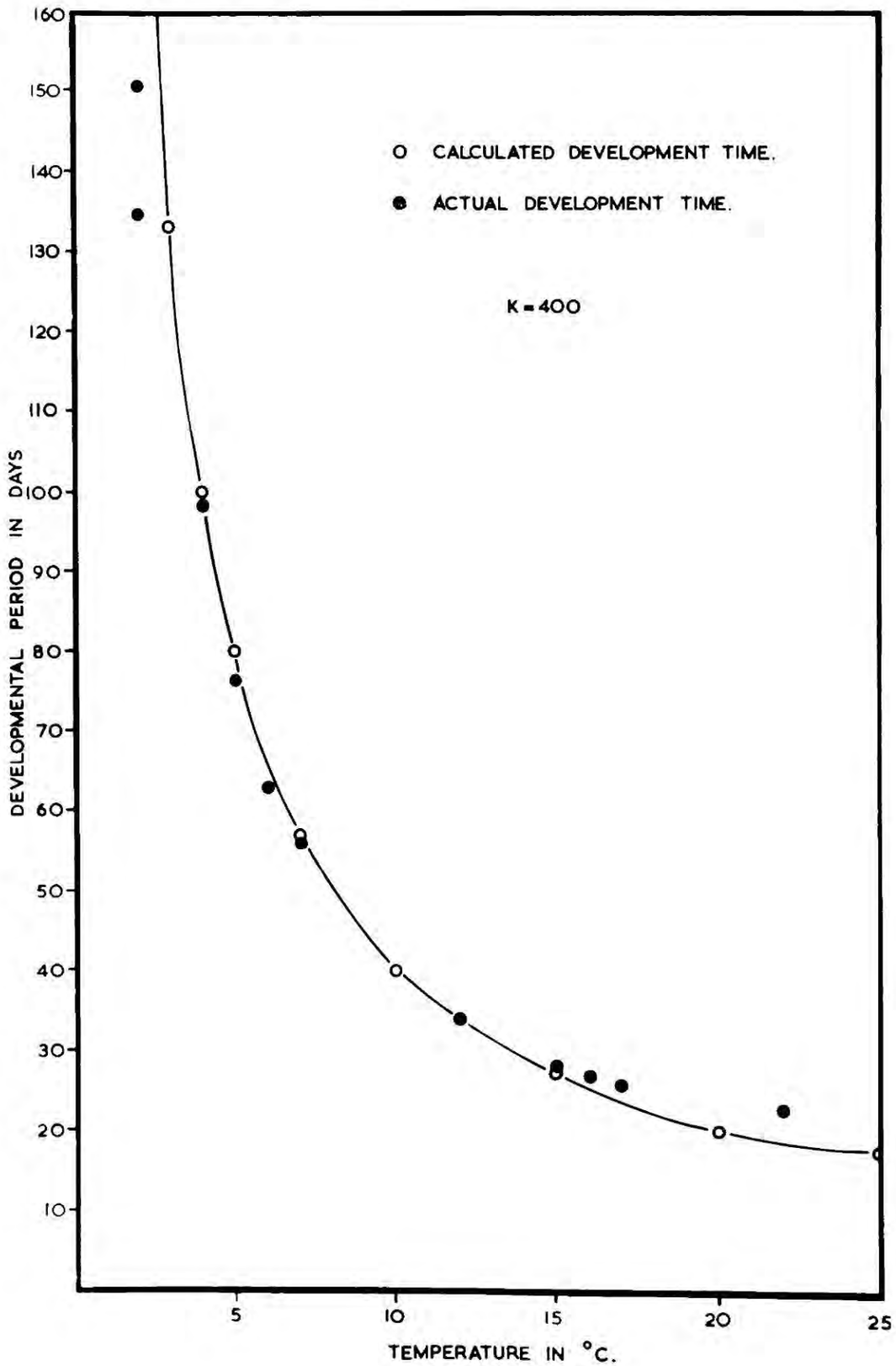


Fig. 10.

The relationship between the developmental period in days and the temperature in degrees centigrade in the eggs of four species of the Genus Onychiurus.

Fig.10.

Egg development at constant temperature.

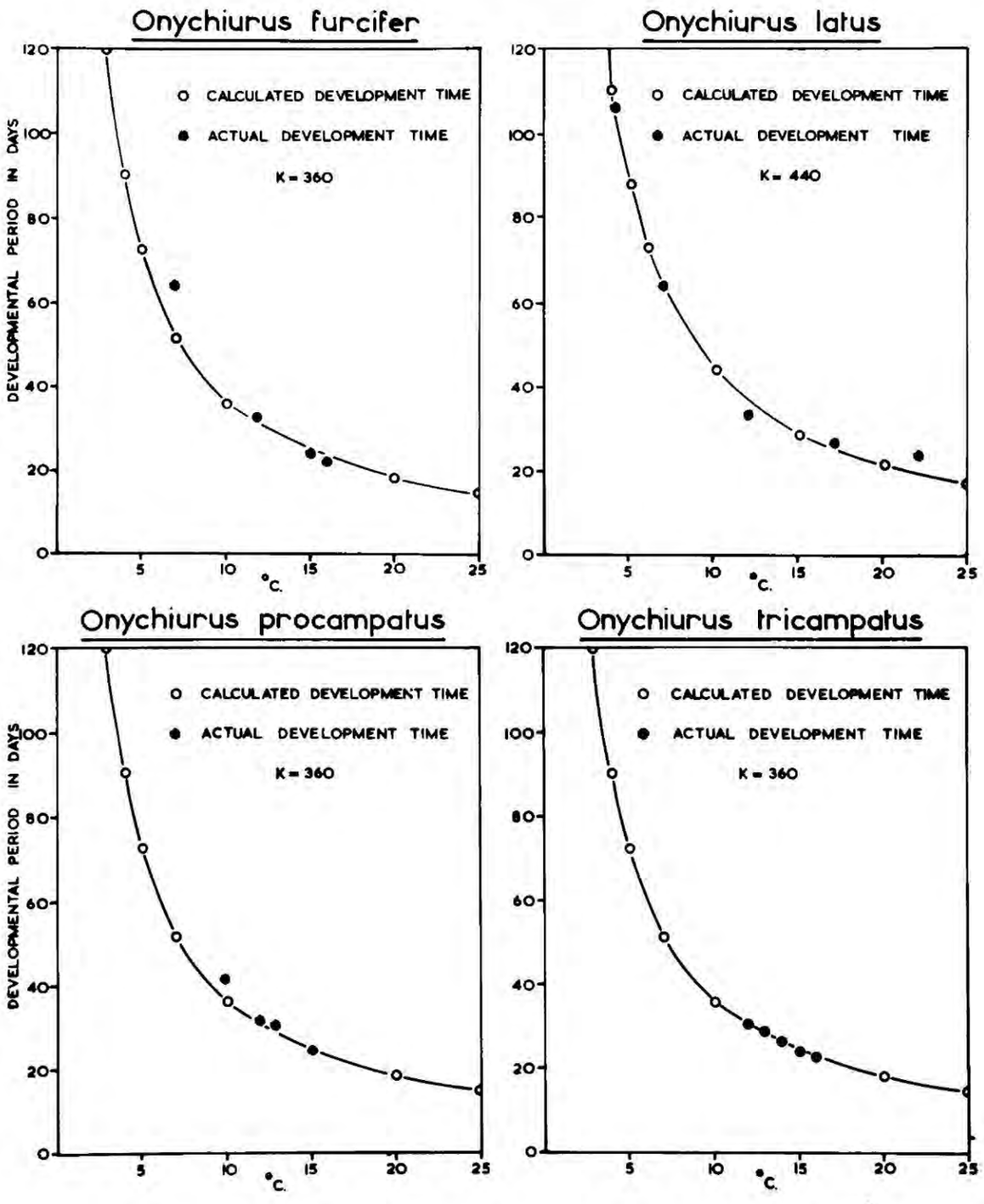


Fig. 11.

The relationship between the developmental period in days and the temperature in degrees centigrade in the eggs of three species of the Genus Isotoma and the closely related species Isotomurus palustris.

Fig.11.

Egg development at constant temperature.

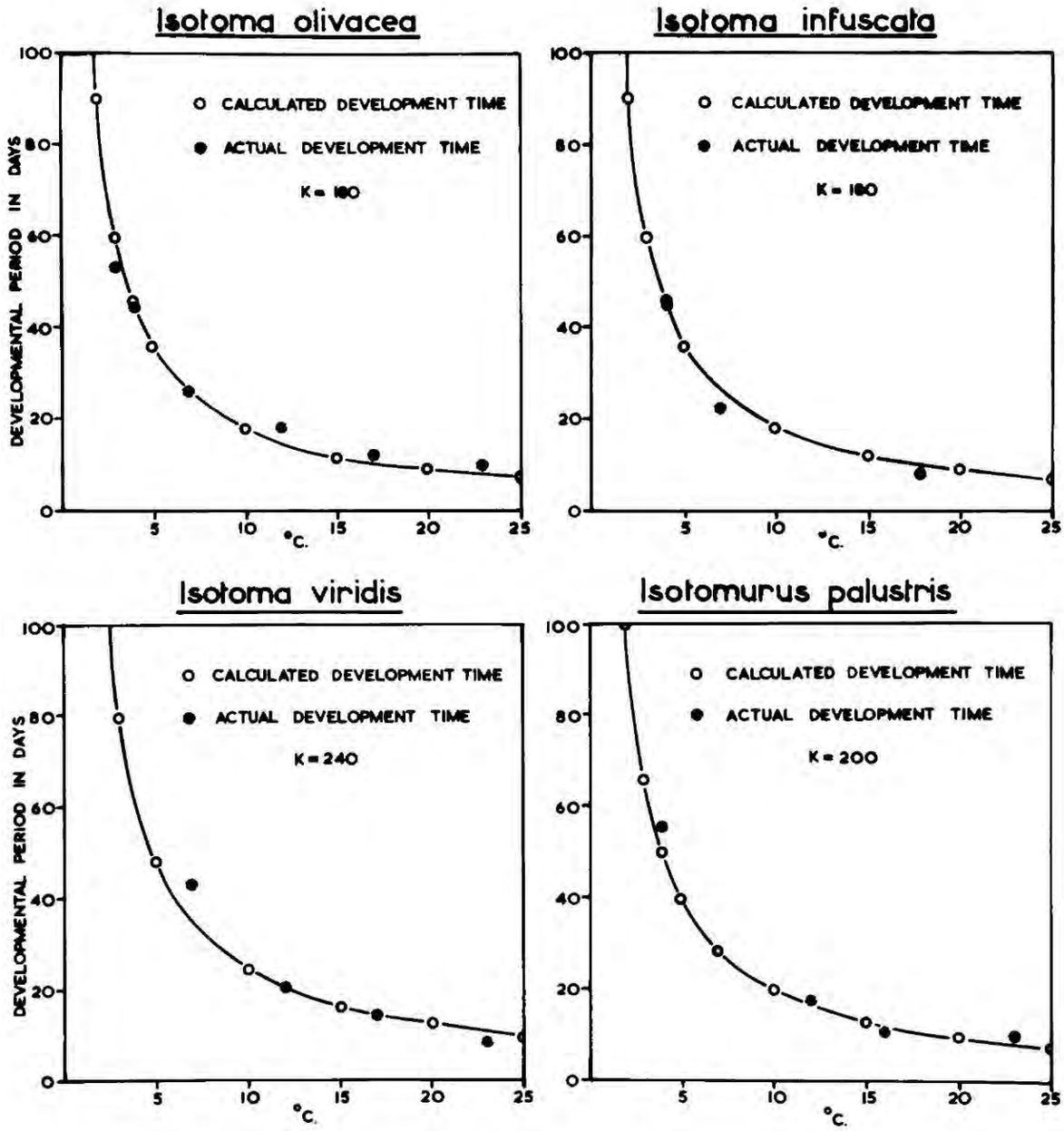
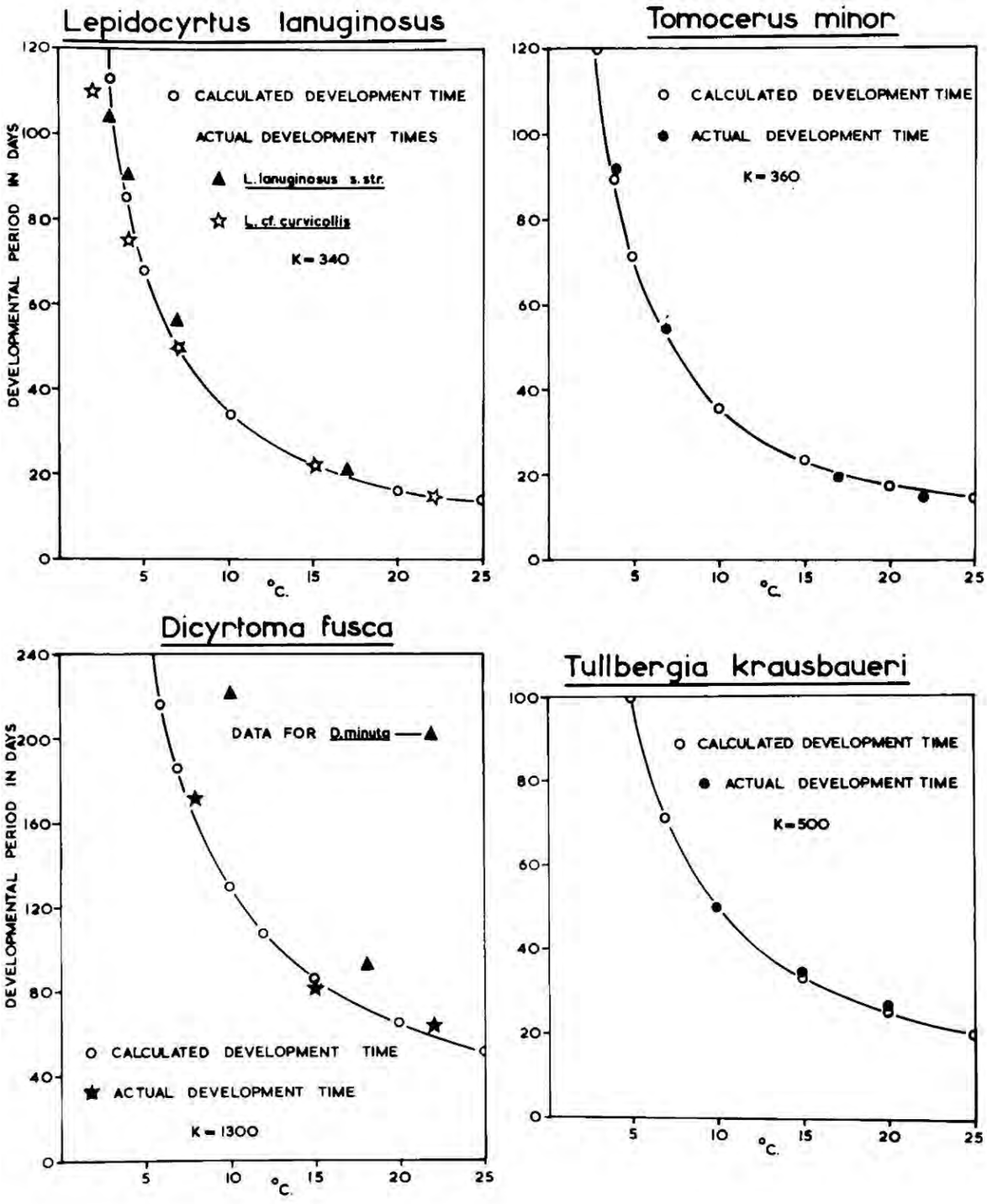


Fig. 12.

The relationship between the developmental period in days and the temperature in degrees centigrade in the eggs of Lepidocyrtus lanuginosus, Tomocerus minor, Dicyrtoma fusca and Tullbergia krausbaueri.

Fig.12

Egg development at constant temperature.



The egg developmental period appears to be unrelated to the food content (size) of the egg (compare Tables 20 and 21) or to any other obvious factor, such as availability to predators.

3) Egg development at fluctuating temperatures.

Eggs of seven species of Collembola (Table 22) were placed in culture tubes at the height of a Stevenson's screen, and subjected to the fluctuating outside air temperatures in Durham; The development times were observed as in the last section. Maximum and minimum daily temperatures were available at the screen. ½(max. + min.) temperatures were recorded daily over the development periods of all species. Table 22 shows the constants (K) calculated for both constant temperatures in the laboratory, and fluctuating temperatures in the field.

Table 22. Egg development constants for constant and fluctuating temperatures.

Species	K at constant temp.	K at fluctuating temp.
H. denticulata	400	370
O. latus	440	410
I. viridis	240	240
I. olivacea	180	180
I. palustris	200	180
L. cf. curvicollis		
a) at Durham	340	300
b) at Moor House	340	340
T. minor	360	290

The constants for fluctuating temperatures are the products of the development time in days and $\frac{1}{2}$(max. + min.) temperature in degrees centigrade. The agreement between the constants derived from the two different sources is such that prediction concerning hatching times in the field may be made, knowing the time of laying and the expected temperatures.

4) Egg development in the field.

In Table 19 it has been shown that the majority of species lay eggs in May and June, at Moor House; Fig. 2 shows the 1960 and 1961 temperatures during that period. From these data and the calculated constants, estimates for times of egg development in the field, at Moor House, have been calculated; these estimates are shown in Table 23. In order to test the accuracy of these estimates two batches of eggs of H. denticulata and two batches of O. latus were put out in the field at Moor House on 29 May, 1961. On 4 July, 1961, (after 36 days) 2 of 50 eggs of H. denticulata had hatched; none of the O. latus eggs had hatched. On 11 July, 1961, (after 43 days) all the H. denticulata had hatched, and 50% (23) of the O. latus eggs had hatched. All eggs had hatched by 17 July, 1961. These data give a period of about 40 days for the hatching of H. denticulata

in the field (calculated estimate over this period 41 days), and 43 days for O. latus (calculated estimate 46 days). It may be concluded that the estimates given in Table 23 for development times in the field are a slight overestimate.

In Table 19 it was shown that L. lanuginosus and the two species of Dicyrtoma laid the majority of their eggs in late autumn (October and November). The temperatures at Moor House at this time (Fig. 2) are so low that development would appear to be impossible until the following spring, and thus the eggs must survive the Moor House winter. In order to test this hypothesis, twenty tubes, each containing a single egg, of each of the three species, were set in the ground at Moor House, on a site similar to the Calluna sampling site (page 11), on 23 November, 1959. The eggs were laid in culture on 8 November, 1959, and kept at 2°C. until placing in the field at Moor House. The tubes were examined regularly throughout the winter, but it was not until 2 May, 1960 (175 days after laying) that any hatched. All the eggs of L. lanuginosus hatched by 9 May, 1960 (182 days after laying). The two species of Dicyrtoma hatched between 23 May, 1960 and 6 June, 1960. First instars were collected from the field populations for the first time in that year on the same dates as hatching was discovered

Table 23. Estimates of egg development times (days) in the field.

Species and Development Constant		Average of 10 years 1952-61. Development time: Laying 1 May	Laying 1 June	1960 Development time: Laying 1 May	Laying 1 June	1961 Development time Laying 1 May	Laying 1 June
Hypogastrura denticulata	(400)	50	40	44	35	53	41
Onychiurus procampatus	(380)	47	38	42	33	50	39
Onychiurus latus	(440)	56	44	47	40	57	46
Onychiurus tricampatus	(380)	47	38	42	33	50	39
Tullbergia krausbaueri	(500)	59	49	53	45	63	52
Isotoma viridis	(240)	32	25	29	21	35	26
Isotoma olivacea	(180)	25	19	22	16	28	20

continued overleaf.

Table 23 (cont'd.)

Species and Development Constant		Average of 10 years 1952-61. Development time: Laying 1 May	Laying 1 June	1960 Development time: Laying 1 May	Laying 1 June	1961 Development time: Laying 1 May	Laying 1 June
Isotoma infuscata	(180)	25	19	22	16	28	20
Isotomurus palustris	(200)	28	21	24	18	31	22
Lepidocyrtus lanuginosus	(340)	43	35	38	30	46	36
Tomocerus minor	(360)	45	37	40	32	48	38
½(max.+min.) temp. in °C.		7.20	9.57	8.20	11.30	6.50	9.20

Note. The first 30 days of the theoretical development time are calculated on the basis of the temperature for the given month, the rest of the development time on the mean temperature for the following month.

in the cultures. This clearly shows that the eggs of these three species survive the winter at Moor House, and the fact that most of the eggs are laid in autumn indicates that these species overwinter as eggs.

Overwintering eggs are at times subject to temperatures well below freezing point, but this seems to have no effect on them other than to halt development. In Table 24 the results of freezing batches of eggs of H. denticulata are shown; seven batches of eggs, about thirty each, were divided into two, one part being maintained at 4.5°C. and the other was frozen for 10 days at -7°C. before being placed at the same temperature.

Table 24. The effect of freezing on the eggs of H. denticulata.

Culture	Time in days for 50% of eggs frozen at -7°C. for 10 days and then at 4.5°C. to hatch	Time in days for 50% of eggs maintained at 4.5°C. to hatch	Increase due to freezing
1	104	93	+11
2	104	93	+11
3	106	92	+14
4	108	92	+16
5	100	89	+11
6	107	90	+17
7	107	92	+15
Average	105.1	91.6	+13.5

The development time was increased by an average of 13.5 days in the frozen eggs. Eggs frozen for a longer period at -7°C. were subject to high mortality. Occasionally some individual eggs seem less affected by low temperatures than others, and there is one record of a single egg in a batch hatching in 30 days at 15°C. (10 of which days were spent at -7°C.) whilst the rest of the eggs in the batch hatched at 42 days.

f) The process of hatching.

In those species of Collembola possessing pigmented eye spots, the onset of hatching can be forcast from the depth of the pigmentation. The embryo lies around the largest circumference of the egg, which at this time has the form of a flattened spheroid in all species except members of the Entomobryidae and the two species of Dicyrtoma. The caps of the split chorion also lie on the largest circumference, opposite the head and the tip of the abdomen of the embryo.

Maclagen (1932) points out the lack of hatching spines, or any similar structures in Collembola, and indicates that eclosion is brought about by the movement of the embryo within the serosal cuticle. In the four species of Onychiurus cultured the serosal cuticle was observed to be sculptured (Fig. 8), and the splitting of

the serosal cuticle on eclosion occurs along the line of the sculpturing. In all cases except the two species of Dicyrtoma, the split occurs across the smallest diameter of the egg, in a plane at right angles to a line joining the two chorion caps; thus the splitting of the serosal cuticle on eclosion is in the same plane as the earlier splitting of the chorion. In the two species of Dicyrtoma the eggs were normally covered by faecal material, and eclosion occurred by the individuals eating their way out of the top of the egg; no splitting of the cuticle was observed.

In the species normally hatching by splitting, the serosal cuticle first splits opposite the gap between the embryonal head and the tip of the abdomen. The head and the antennae are forced through the transverse slit and the legs are braced against the inside of the serosal cuticle; in this way the split is extended and the gap widened. Eclosion is often aided by the egg being anchored in some way to the substrate. In many cases this occurs by means of the projections of the serosal cuticle or by fungal hyphae which grow over the eggs. The sticking together of eggs in batches also aids eclosion, as the embryo is able to gain a purchase with its claws and drag the abdomen out of the serosal cuticle which remains

attached to the rest of the egg batch. The furcula is frequently used in freeing the abdomen, especially where the egg has not become attached.

On freeing itself from the serosal cuticle the hatched individual retracts the furcula if it has been used in the process of hatching, and it is immediately able to use it for jumping. Normally individuals take into their gut fungal mycelia and particles of the substrate within minutes of hatching.

III. THE HATCHED ANIMAL.

III. THE HATCHED ANIMAL.

1) Postembryonic development.

a) Introduction.

Agrell (1948) has provided information from field data on the number of ecdyses occurring before the attainment of the maximum size, in three species of Collembola, and has stressed the importance of following the growth in laboratory cultures, as a check on the information obtained from the field. Several other workers have studied the postembryonic development, and the available information on the numbers of pre-adult instars is summarised in Table 25.

Little information on the number of instars in different species of Collembola has been obtained by previous workers from measurement of individuals collected from the field. In this work a correlation is attempted between measurements of a field population, and measurements made upon cultured individuals which have moulted on an observed number of occasions. Samples were taken monthly over a period of two years, and three species of the Genus Onychiurus were selected for detailed study, namely O. latus, O. procampatus and O. tricampatus. At the same time cultures were maintained in the laboratory. Several other species were cultured and some data was obtained on various aspects of their life histories.

Table 25. Numbers of instars recorded by previous workers.

Species	Authority	Determination from Lab. culture	Determination from Field collecting	No. of instars To reproduction	No. of instars To maximu size
Hypogastrura manubrialis	Ripper 1930	X		6	-
Hypogastrura sahlbergi	Agrell 1948		X		8
Hypogastrura purpurascens	Strebel 1932	X		5	
Hypogastrura armata	Britt 1951	X		3-4	
Onychiurus furcifer	Milne 1960	X		4	5
Onychiurus fimatus	Choudhuri 1958	X			7
Onychiurus procampatus	Milne 1960	X		4	5
Onychiurus latus	Milne 1960	X		4	5
Onychiurus armatus	T.G. Wood (pers. comm.)	X			7
Onychiurus parthenogeneticus	Choudhuri 1958	X			6

Table 25 (cont'd).

Species	Authority	Determination from Lab. culture	Determination from Field collecting	No. of instars To reproduction	No. of instars To maximum size
Onychiurus imperfectus	Choudhuri 1958	X			7
Tullbergia krausbaueri	Milne 1960	X		3	4
Folsomia 4-oculata	Agrell 1948		X		9
Isotomurus palustris	James 1933	X			7
Entomobrya spp..	South 1961	X		5	
Orchesella cincta	Handschin 1926	X		5	
	Lindemann 1950	X		10-12	25-30
Pseudosinella violenta	Davis and Harris 1936	X			7
Tomocerus minutus	Uchida and Chiba 1958	X			c6
Sminthurides aquaticus	Falkenhan 1931	X		3	5
Arrhopalites pygmaeus	Agrell 1948		X		7
Sminthurus viridis	Maclagen 1932			7	

b) Determination of the number of instars by culturing.

i) Methods.

Newly hatched first instars were placed in individual containers of the type described (see page 68). The Collembola were fed with yeast which was replenished as required. The cultures were examined daily, and unless otherwise stated, were maintained at a constant temperature of 15°C.

It was found to be impossible to measure accurately the head length of live individuals, as was done by Choudhuri (1958) and Milne (1960). It was thus decided to rear larger numbers of individuals than did these workers, and to kill and mount a given number for precise measurement after each moult. Whilst this was time consuming due to the numbers involved, the data are regarded as more reliable than could have been obtained from measurements of live individuals. Only in the case of Hypogastrura denticulata, where single cultures proved unsuccessful, was any other method utilised. In this case, the early instars repeatedly died. It was thus decided to form a single mass culture of first instars hatched on the same day, and remove a small number of individuals after a set period of time, following the method of Davis and Harris (1936) and Uchida and Chiba (1958).

It was hoped that all individuals would moult simultaneously, as in the moulting colonies of Ripper (1930) and Strebel (1932), and this occurred (see page 70).

All measurements were made using a micrometer eyepiece which when using the 1/32" objective, gave 265 divisions to 1 mm.; all measurements were made to the nearest division of the scale, and later transformed to microns, in which form the measurements appear in the tables. Head length was chosen for measurement rather than the more usual head width, as measurements could then be made on individuals mounted for lateral viewing.

ii) Measurements of various species.

A. Hypogastrura denticulata.

Fifty newly hatched individuals were placed in a standard culture jar (see page 67), and five first instars were mounted for examination. After some days, 50 cuticles were cast within a period of 48 hours, and these were removed together with five individuals which were mounted and measured; the same procedure was carried out at each moult. Table 26 summarises the data obtained in this way. After the fifth moult no further increase in size occurred.

In Tables 26-35 a mean increment factor is calculated, and on the basis of the head capsule length of

the first instars, the expected head lengths in subsequent instars are calculated. There is close agreement between the calculated lengths and the actual lengths and thus agreement with Dyar's Rule. That Collembola grow in size according to Dyar's Rule has been previously shown by Agrell (1948) and Choudhuri (1958).

Some eggs were laid in the fifth instar, but the majority was not laid until the attainment of maximum size in the 6th instar.

Table 26. Head capsule length in Hypogastrura denticulata.

Instar	1	2	3	4	5	6
Observed head length (μ)	128 ± 0.37	151 ± 2.68	183 ± 0.46	222 ± 6.35	266 ± 3.87	304 ± 7.11
Rate of increase	-	1.18	1.21	1.21	1.20	1.15
Theoretical head length (μ) from Dyar's Rule	128	152	181	215	256	305

Mean increment factor from Dyar's Rule = 1.19.

These data agree well with those of previous workers on the members of this genus (Table 25). H. armata laid during an earlier instar than H. denticulata (Britt 1951), but H. purpurascens (Strebel 1932) and

H. manubrialis (Ripper 1930) laid during the 5th and 6th instars respectively, as occurred in H. denticulata. Agrell (1948) records H. sahlbergi reaching its maximum size in the 8th instar, two instars after H. denticulata; the same author's estimate of the progression factor for the growth of the head (1.13) in H. sahlbergi, falls below that calculated for H. denticulata (1.19) in the present work.

B. Tullbergia krausbaueri.

Ten individuals were killed and mounted after each moult, and it was found that no further growth took place after the third moult, i.e. the maximum size of the head capsule was reached in the fourth instar. It has been previously recorded (Table 15), that sexual maturity can be attained in the third instar, but more frequently maturity is reached in the 4th or 5th. Table 27 gives the results of measurements on the head capsule sizes of the four instars of Tullbergia krausbaueri.

Table 27. Head capsule length in Tullbergia krausbaueri.

Instar	1	2	3	4
Observed head length (μ)	64 ± ∝	76 ± 0.24	88 ± 0.21	106 ± 1.35
No. of individuals measured	10	14	13	13
Rate of increase	-	1.180	1.165	1.198
Theoretical head length from Dyar's Rule (μ)	64	76	89	106

Mean increment factor from Dyar's Rule = 1.18.

Milne (1960) has provided data on the body length, showing that T. krausbaueri reaches its maximum size in the 4th instar but no increment factor is given; this agrees with the data presented here for the length of the head capsule.

C. to F. Onychiurus spp..

First instar individuals were isolated singly on hatching. In all four species larger numbers of some instars were obtained than of others, due to mortality.

Milne (1960) found only four pre-adult instars in O. procampatus, O. latus and O. furcifer. In the first two species, data obtained in an early stage during the present work showed a greater number of instars before maximum size was reached. It was thus decided to culture the third species, O. furcifer, and determine the number of instars. Whilst the species is not strictly a moorland form, it does occur on upland areas, eg. near Melmerby, Cumberland, but was unrecorded from the Moor House Reserve. Material was collected from Melmerby and from Hamsterley, Co. Durham.

Tables 28 to 35 give a summary of the data concerning the number of instars passed through in order to attain maximum size in O. furcifer, O. procampatus, O. latus and O. tricampatus.

C. Onychiurus furcifer.

Table 28. Head capsule length in Ol furcifer, from cultures.

Instar	1	2	3	4	5	6	7
Observed mean head length(μ) and S.E. of mean	149 ± 0.71	172 ± 0.92	199 ± 2.26	232 ± 1.89	264 ± ∝	307 ± 2.67	354 ± ∝
No. of individuals measured	26	18	7	4	5	3	1
Rate of increase	-	1.154	1.153	1.166	1.138	1.161	1.154
Theoretical head length (μ) from Dyar's Rule	149	172	199	230	265	305	352

Mean increment factor from Dyar's Rule = 1.154

D. Onychiurus procampatus.

Table 29. Head capsule length in O. procampatus, from cultures.

Instar	1	2	3	4	5	6
Observed mean head length(μ) and S.E. of mean	170 ± 0.56	197 ± 1.46	227 ± 1.09	266 ± 1.46	302 ± ∝	347 ± 5.34
No. of individuals measured	12	5	4	5	3	4
Rate of increase	-	1.158	1.154	1.171	1.133	1.150
Theoretical head length(μ) from Dyar's Rule	170	196	226	261	301	347

Mean increment factor from Dyar's Rule = 1.153.

E. Onychiurus latus.

Table 30. Head capsule length in O. latus, from cultures

Instar	1	2	3	4	5	6	7
Observed mean head length (μ) and S.E. of mean	170 ±	198 ± 0.70	231 ± 1.89	262 ± 1.09	303 ± 1.54	339 ± 1.09	396 ± ∝
No. of individuals measured	5	43	5	4	3	4	1
Rate of increase	-	1.168	1.163	1.135	1.156	1.117	1.170
Theoretical head length (μ) from Dyar's Rule	170	196	225	260	299	345	397

Mean increment factor from Dyar's Rule = 1.152

F. Onychiurus tricampatus.

Table 31. Head capsule length in O. tricampatus, from cultures.

Instar	1	2	3	4	5	6
Observed mean head length (μ) and S.E. of mean	134 ± 1.80	151 ± 1.00	170 ± 1.20	200 ± ∝	230 ± 3.77	267 ± 2.67
No. of individuals measured	33	11	5	1	3	3
Rate of increase	-	1.122	1.127	1.178	1.150	1.159
Theoretical head length (μ) from Dyar's Rule	134	154	177	203	232	266

Mean increment factor from Dyar's Rule = 1.147.

c) Development of the chaetotaxy in successive instars.

Examination of the individuals of known instar in four species of the Genus Onychiurus showed that during the course of development the chaetotaxy of parts of the body was characteristic of the instar. The arrangement of the bristles in relation to the pseudocelli of the fifth abdominal segment was selected for detailed study, and the results are shown in Figs. 13, 14 & 15.

The ability to recognise a given instar on the basis of the chaetotaxy was found to be particularly useful in assigning individuals to a given instar when the measurement of head capsule size lay midway between two means. This was of particular value in drawing up Figs. 19-21 to show the age distribution, and was used in the case of some thirty individuals in assigning them to instar groups for the calculation of head capsule size from field data (Figs. 16 & 17).

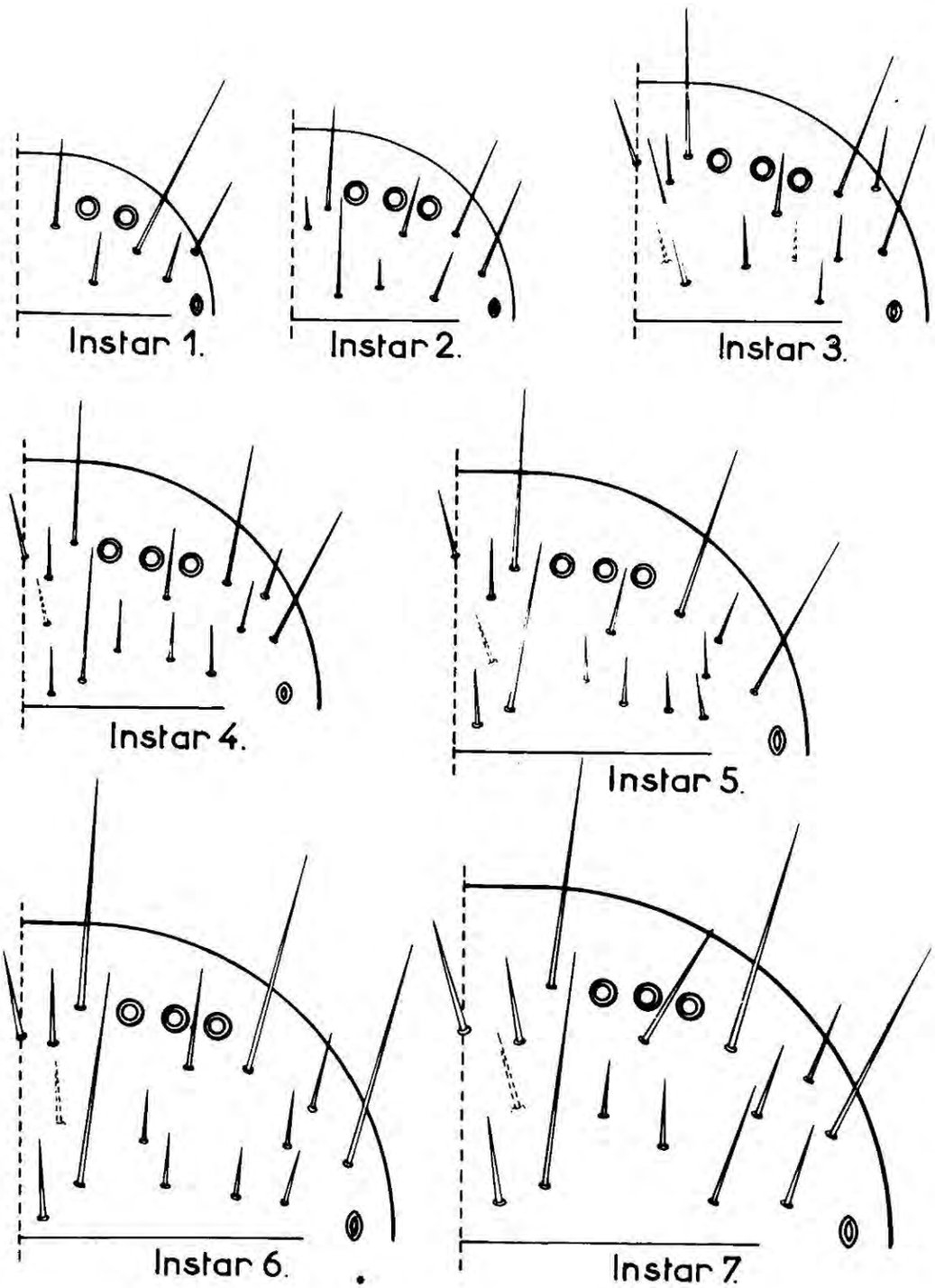
d) Determination of the number of instars from field data.

All individuals of O. procampatus and O. tricampatus extracted from 15 sample units on each of 24 sampling dates over a period of two years, were mounted on slides and the lengths of the head capsules were measured. The resulting data were plotted in the form of histograms (Fig. 16). From these distribution curves it is clear

Fig. 13.

The chaetotaxy of the fifth abdominal segment in Onychiurus latus. The number of chaetae increases at each moult and the number of pseudocelli on this segment increases from two to three at the first moult.

Fig.13.



Chaetotaxy of abdominal segment V.

Onychiurus latus.

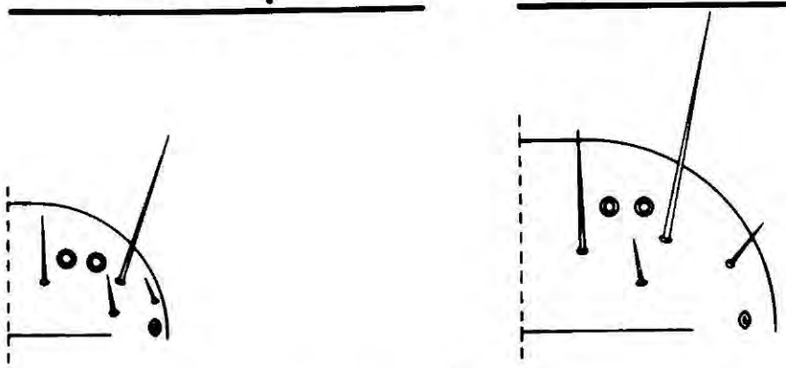
0.1mm

Fig. 14.

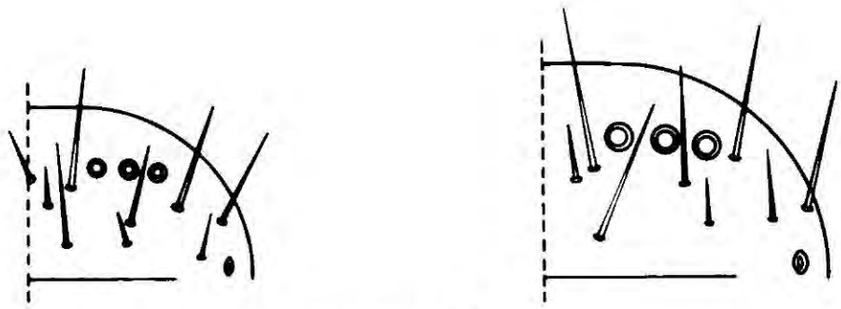
A comparison between the chaetotaxy of the fifth abdominal segment in Onychiurus procampatus and Onychiurus tricampatus at different stages of development.

Fig.14a.

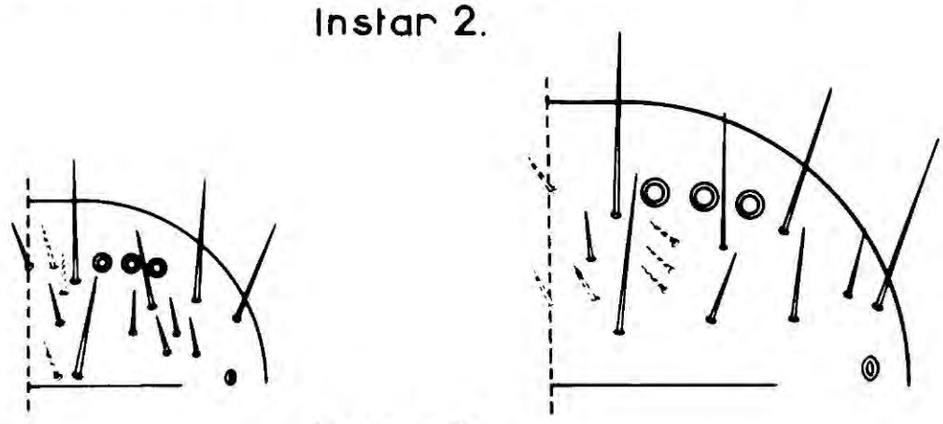
O. tricampatus. O. procampatus.



Instar 1.



Instar 2.



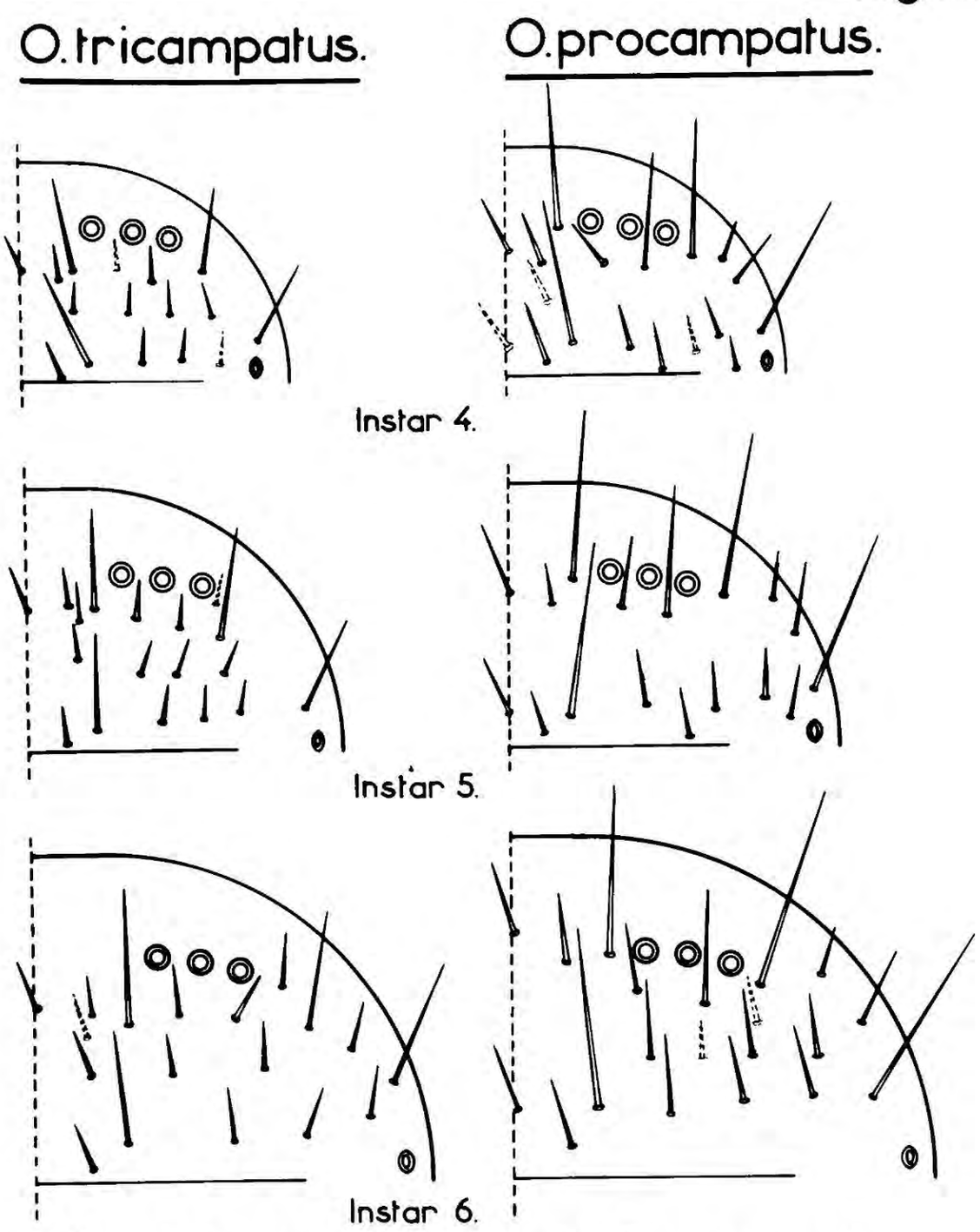
Instar 3.

Chaetotaxy of abdominal segment V.

Onychiurus tricampatus & O. procampatus.

0.1mm.

Fig.14b.



Chaetotaxy of abdominal segment V.

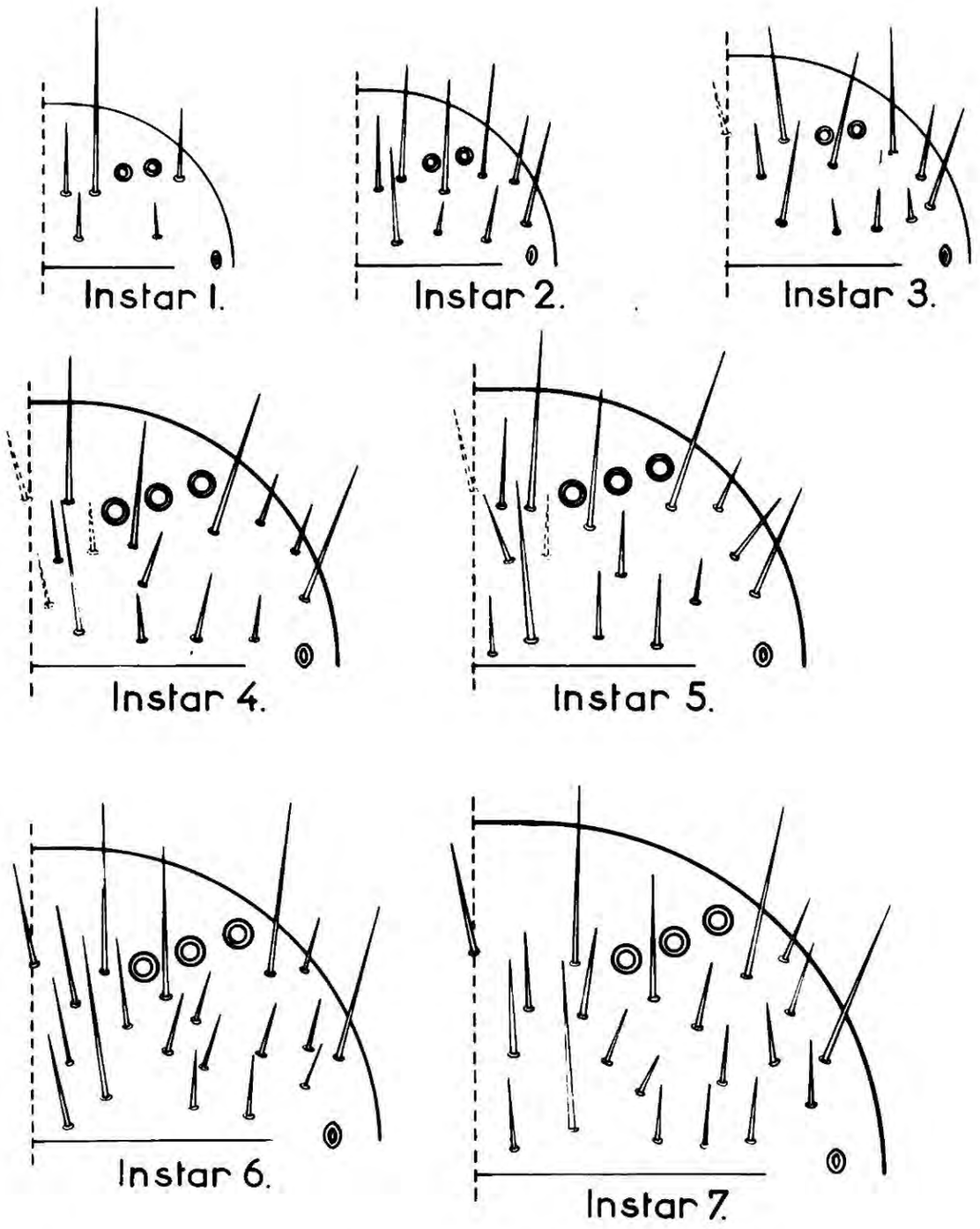
Onychiurus tricampatus & O. procampatus.

0.1mm.

Fig. 15.

The chaetotaxy of the fifth abdominal segment in Onychiurus furcifer. In contrast to the other three species of Onychiurus studied, the number of pseudocelli on the fifth abdominal segment does not increase from two to three until the third moult.

Fig.15.



Chaetotaxy of abdominal segment V.

Onychiurus furcifer.

0.1mm.

Fig. 16.

a. The distribution of head capsule sizes in Onychiurus procampatus; the six peaks correspond to six instars.

b. The distribution of head capsule sizes in Onychiurus tricampatus; the six peaks correspond to six instars.

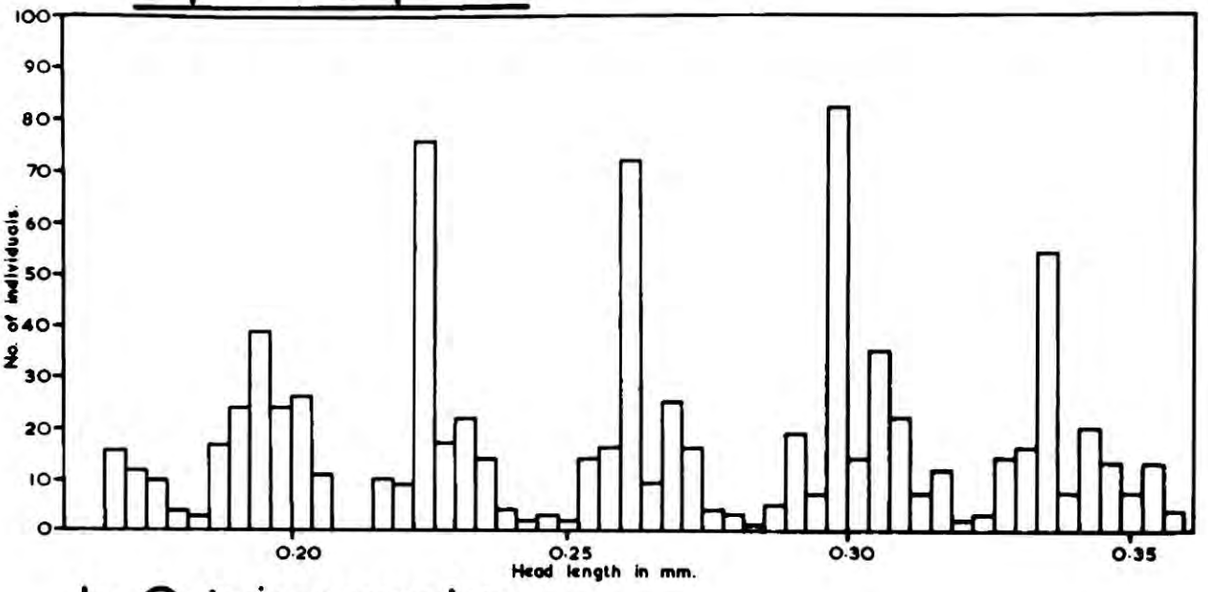
Note that in O. tricampatus the head capsule size of the adult is equal to that of the fourth instar in O. procampatus.

The data is from measurements of individuals collected at monthly intervals over a period of two years, from Moor House Reserve.

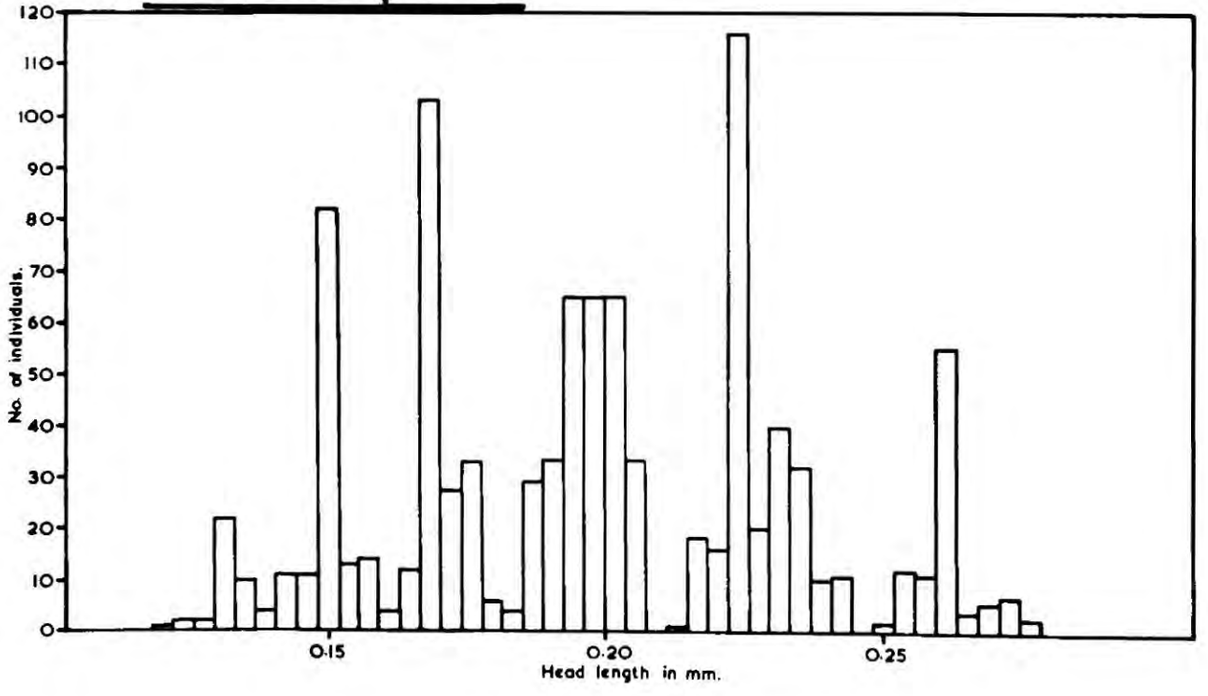
Fig. 16.

Distribution of head capsule sizes.

a. O. procampatus.



b. O. tricampatus.



that in each case six peaks occur, and these are indicative of the six instar groupings in each species. Calculation of the mean for each peak, placing intermediate individuals in their appropriate group by means of the chaetotaxy, as described in the last paragraph, was carried out, and the data are presented in Tables 32 and 33.

Table 32. Head capsule length in O. procampatus from field data.

Instar	1	2	3	4	5	6
Observed mean head length(μ) and S.E.of mean	172 ± 0.41	196 ± 0.48	229 ± 0.42	266 ± 0.54	305 ± 0.52	343 ± 0.68
No. of individuals measured	49	229	154	162	205	151
Rate of increase	-	1.139	1.165	1.163	1.148	1.124
Theoretical head length(μ) from Dyar's Rule	172	198	227	261	299	344

Mean increment factor from Dyar's Rule = 1.148

Table 33. Head capsule length in O. tricampatus from field data.

Instar	1	2	3	4	5	6
Observed mean head length (μ) and S.E. of mean	132 ± 0.60	150 ± 0.40	172 ± 0.35	199 ± 0.30	230 ± 0.41	264 ± 0.55
No. of individuals measured	42	192	149	292	264	100
Rate of increase	-	1.139	1.146	1.153	1.156	1.150
Theoretical head length (μ) from Dyar's Rule	132	152	174	200	230	264

Mean increment factor from Dyar's Rule = 1.149

In the case of O. latus, monthly samples were taken over a period of one year; on each occasion the sample was of an arbitrary size, and normally about 150 individuals were mounted and measured each month. The distribution curve shown in Fig. 17c demonstrates the seven peaks indicating the seven instar groupings. Intermediates were placed in their appropriate instar group on the basis of chaetotaxy, and the mean head capsule length for each instar calculated. The data are summarised in Table 34.

A similar procedure was carried out for O. furcifer, but this species was sampled on only three dates. Fig. 17d shows the distribution of the head capsule sizes for this species, and Table 35 summarises the data concerning the separate instars.

e) Correlation of data from cultures and from the field.

Comparison of Tables 30 and 34 for O. latus, Tables 29 and 32 for O. procampatus, Tables 31 and 33 for O. tricampatus and Tables 28 and 35 for O. furcifer, shows the close relationship of the data derived from the two separate sources. This is summarised in Table 36.

Table 36. Comparison of the number of instars and size increment factors for Onychiurus spp..

Species	Number of instars		Increment factor	
	Cultures	Field	Cultures	Field
O. latus	7	7	1.152	1.152
O. procampatus	6	6	1.153	1.148
O. tricampatus	6	6	1.147	1.149
O. furcifer	7	7	1.154	1.148

Fig. 17.

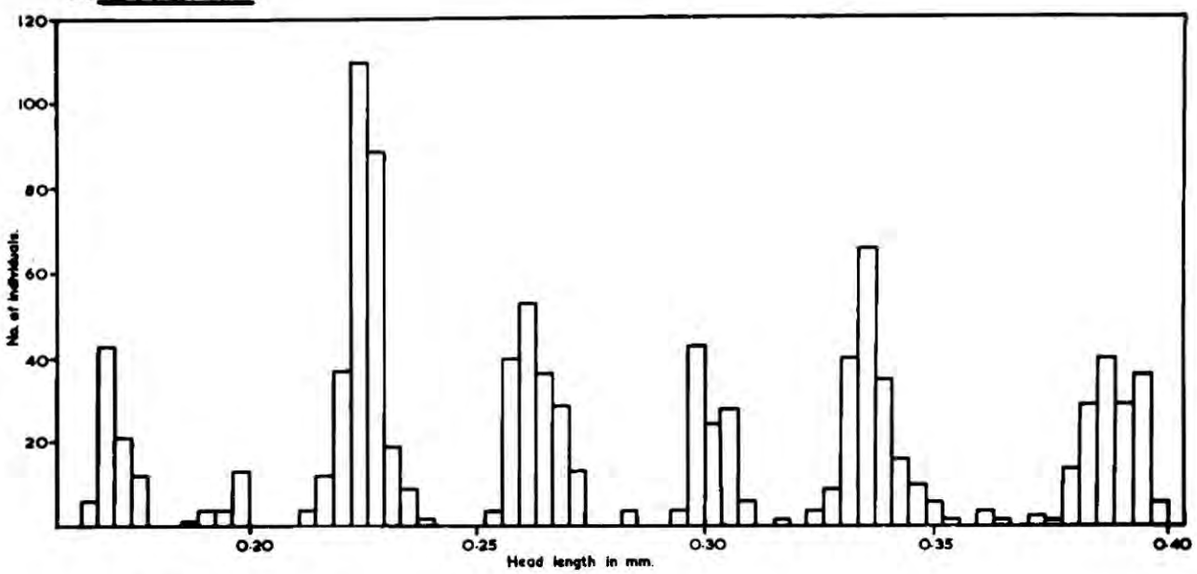
c. The distribution of head capsule sizes in Onychiurus latus; the seven peaks correspond to seven instars. The data is from measurements of individuals collected at monthly intervals over a period of one year, from Moor House Reserve.

d. The distribution of head capsule sizes in Onychiurus furcifer; the seven peaks correspond to seven instars. The data is from measurements of individuals collected on three sampling occasions from Melmerby, Cumberland and from Hamsterley, Co. Durham.

Fig.17.

Distribution of head capsule sizes.

c. O. latus.



d. O. furcifer.

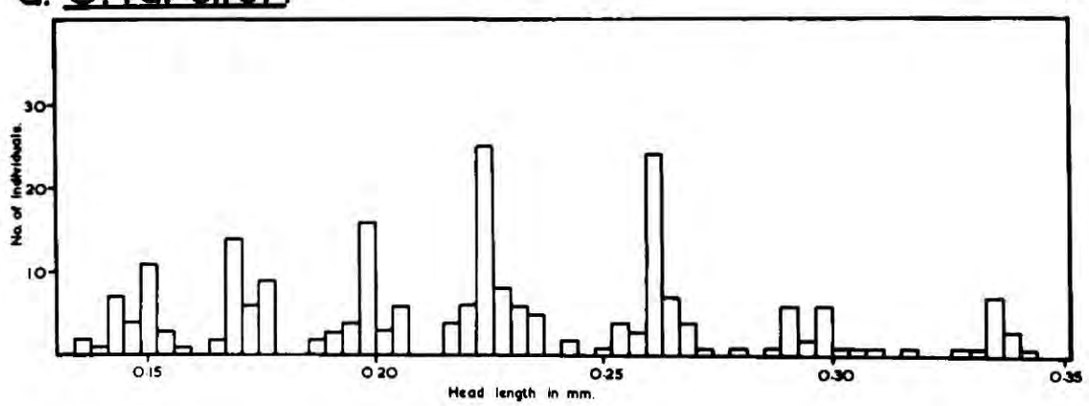


Table 34. Head capsule length in *O. latus*, from field data.

Instar	1	2	3	4	5	6	7
Observed mean head length(μ) and S.E. of mean	172 ± 0.19	200 ± 0.61	228 ± 0.24	266 ± 0.27	302 ± 0.27	345 ± 1.30	401 ± 0.31
No. of individuals measured	207	22	282	202	156	249	533
Rate of increase	-	1.160	1.140	1.169	1.135	1.141	1.164
Theoretical head length(μ) from Dyar's Rule	172	198	228	263	303	349	402

Mean increment factor from Dyar's Rule = 1.152

Table 35. Head capsule length in *O. furcifer*, from field data.

Instar	1	2	3	4	5	6	7
Observed mean head length(μ) and S.E. of mean	148 ± 1.03	173 ± 0.66	200 ± 0.88	228 ± 0.67	264 ± 0.86	299 ± 1.60	339 ± 1.68
No. of individuals measured	29	31	34	54	46	20	14
Rate of increase	-	1.166	1.158	1.140	1.156	1.134	1.132
Theoretical head length(μ) from Dyar's Rule	148	170	195	224	257	295	338

Mean increment factor from Dyar's Rule = 1.148

In all four species the number of instars was found to be the same in both laboratory cultures and field material. A close relationship was also found in the increment factor calculated from the two sources, and this was found to be similar in all four species. Choudhuri (1958) obtained a figure of 1.15 for three species of the Genus Onychiurus, namely O. parthenogeneticus, O. fimatus, and O. imperfectus, and the present data is in close agreement with this.

Milne (1960), working on O. procampatus, O. latus and O. furcifer found only five instars in each of the three species; no progression factor was calculated. The data presented here show this estimate to be inaccurate there being six instars in O. procampatus and O. tricampatus, and seven instars in O. latus and O. furcifer. This author kindly supplied material of O. procampatus, O. tricampatus and O. latus from his study area, and examination by the present writer showed that all individuals fitted closely the measurements and chaetotaxy described here. (O. tricampatus was not recorded by Milne from his study area, but specimens were found to be present in a sample of O. procampatus from this area).

f) The duration of the instars in culture.

From cultures, data were obtained for the frequency of moulting of the six species discussed in the last section.

Table 37 shows the number of days spent in each instar in H. denticulata until maximum size was reached; these data are for the mass culture at 15°C.

Table 37. Duration of instars of H. denticulata at 15°C.

Instars	1	2	3	4	5
Duration (days)	9	9	8	8	8

Thereafter moults occurred at intervals of 8.1 ± 0.42 days, on 21 occasions before the death of all individuals.

As has been mentioned previously (page 135) it was found difficult to rear individuals of H. denticulata singly in culture; eventually this was achieved, and moulting periods at 8°C. for individuals in isolation are shown in Table 38.

Table 38. Duration of instars of H. denticulata at 8°C.

Instars	1	2	3	4	5
Duration(days) and S.E. of mean	12.7 ± 1.0	17.4 ± 3.6	19.0 ± 1.7	17.3 ± 0.9	22.0 ± 1.5
No. of individuals examined	6	5	4	4	3

Moults occurred at intervals of 22.6 ± 2.5 days after attaining maximum size, at 8°C.

From Tables 37 and 38 it can be seen that at 15°C. 42 days elapse from hatching to achieving maximum size, and at 8°C. 88 days. A rise in temperature from 8°C. to 15°C. thus increases the rate of development by a factor of 2.1 and the rate of moulting in the adult stage by a factor of 2.8.

For T. krausbaueri more complete data are available for the frequency of moulting, and these are shown in Table 39.

Table 39. Duration of instars in T. krausbaueri at 15°C.

Instars	1	2	3
Duration (days) and S.E. of mean	10.5 ± 0.2	10.2 ± 0.3	13.2 ± 0.5
No. of individuals examined	40	33	27

Note. Whereas in the next four species the numbers examined for duration of instars corresponds to the numbers measured in the section on determination of the number of instars, in T. krausbaueri different cultures were used and thus the numbers do not correspond.

When the maximum size was reached in the fourth instar, moults occurred at intervals of 14.8 ± 0.2 days (184 intervals measured). Milne (1960) records ecdyses at intervals of 8-15 days in T. krausbaueri at 12°C. The same

author comments upon the irregularity of moulting in the adult stage, but the present writer found moulting to be regular (Table 40).

In Tables 38 and 39 there is a suggestion of a gradual increase in the duration of the interval between moults up to attaining the maximum size. This is significant in H. denticulata and there is a significant difference between the first two instars and the third in T. krausbaueri. In adult individuals of T. krausbaueri a similar trend continues, and this is shown in Table 40.

Table 40. Duration of adult instars in T. krausbaueri, at 15°C.

Instar	4	5	6	7	8	9	10	11	12	13
Duration in days and S.E. of mean	14.4 ± 0.4	13.7 ± 0.5	13.9 ± 0.5	15.9 ± 0.6	15.4 ± 0.7	14.1 ± 0.5	14.9 ± 0.5	14.1 ± 1.3	16.5 ± 1.1	15.9 ± 0.4
No. of individuals examined	26	20	16	16	16	15	15	14	10	7

Measurements were also made on the duration of the various instars of the four species of Onychiurus for which the number of instars was determined in the previous section. These data are shown in Tables 41 to 44.

Table 41. Duration of instars in O. furcifer at 15°C.

Instar	1	2	3	4	5	6
Duration in days and S.E. of mean	10.7 ± 0.6	11.5 ± 0.5	11.1 ± 0.4	11.3 ± 0.7	12.8 ± 1.1	14.0 ±
No. of individuals examined	38	20	13	9	4	1

Only one record of 15 days is available for moulting after the attainment of maximum size.

Table 42. Duration of instars in O. procampatus at 15°C.

Instar	1	2	3	4	5
Duration in days and S.E. of mean	13.7 ± 0.4	14.2 ± 0.6	16.0 ± 0.5	17.7 ± 0.7	20.9 ± 0.7
No. of individuals examined	25	20	16	11	8

The interval between moults in the adult stage was found to be 18.7 ± 1.0 days (12 measured).

Table 43. Duration of instars in O. latus at 15°C.

Instar	1	2	3	4	5	6
Duration in days and S.E. of mean	12.1 ± 0.2	13.7 ± 0.4	14.2 ± 0.6	18.5 ± 1.1	20.2 ± 1.7	22.0 ±
No. of individuals measured	60	17	12	8	5	1

No data are available concerning moulting in the adult stage.

Table 44. Duration of instars in O. tricampatus at 15°C.

Instar	1	2	3	4	5
Duration in days and S.E.of mean	10.5 ± 0.3	11.2 ± 0.5	12.0 ± 0.5	12.7 ± 1.0	18.7 ± 0.9
No. of individuals measured	23	12	7	6	3

No data are available concerning moulting in the adult stage.

In the four species of Onychiurus there is a marked tendency for the period between moults to increase in successive instars, up to the maximum size. Sufficient data is not available to show whether such an increase continues in the adult stage, although Handschin (1929) reports that it does so in Onychiurus spp.. Maclagen (1932) has demonstrated an increase in the duration of intervals between moults in successive sub-adult instars of Sminthurus viridis, as have Davis and Harris (1936) in Pseudosinella violenta. In Orchesella villosa Mayer (1957) finds no increase in the average duration between moults with age, but describes long and short inter-moult periods associated with the deposition of spermatophores by the male; in the female the inter-moult periods are of the same length.

Richards (1949) has shown that in some grasshoppers there is a regular relationship between the measurements of the successive instars only if account is taken of their varying duration; that is to say growth proceeds at a regular rate, and the longer the instar the greater the amount of growth. It has been shown here (Tables 26-35) that the increment factor for growth rate in Collembola is constant from moult to moult, and that Dyar's Rule is upheld; however, it has also been demonstrated (Tables 38-44) that the period between moults increases in successive instars. It has also been shown that the periods between moults is affected by temperature (Tables 37 and 38), and thus different periods between moults are to be expected at different times of the year under field conditions. However, Tables 32 to 35 and Figs. 16 and 17 suggest that individuals of the same instar are similar in head capsule size at all times of the year (and at different temperatures) and thus different intermoult periods are not represented by individuals of differing size. The field data of Agrell (1948) supports this, and thus the type of growth in Collembola must be regarded as of a different type to that in grasshoppers, in that Dyar's Rule is strictly followed. A possible explanation of this is that in Collembola the extension of the new cuticle at each moult is limited by physical factors within the cuticle itself, and that normally

maximum extension takes place.

g) The duration of instars in the field.

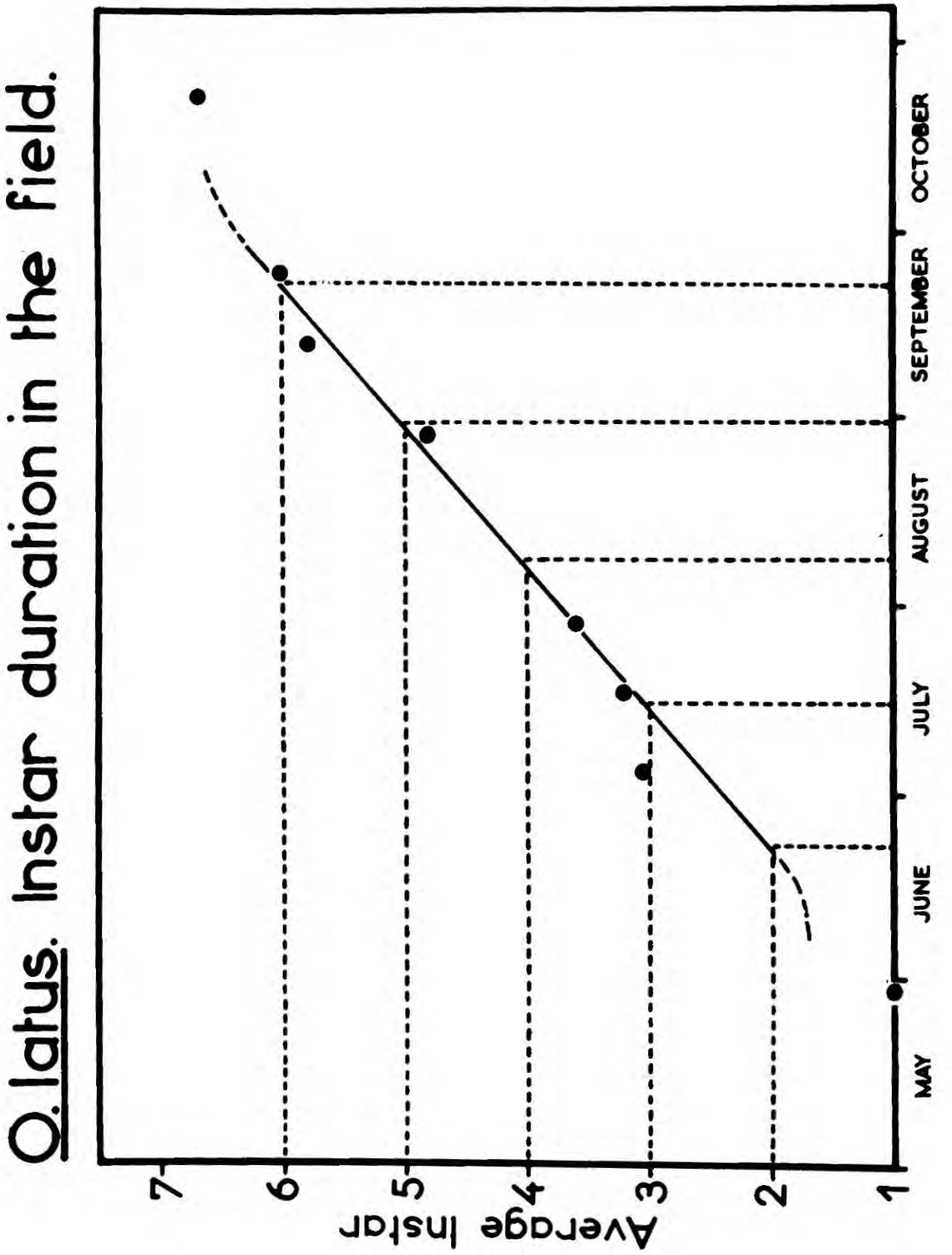
In only one case was it possible to determine the length of instars in the field. This was in O. latus, in 1961, when the adult population died during egg laying, in May, probably as a result of a late, hard frost. The almost simultaneous hatch of the eggs made it possible to follow the growth of the population in the field. This was done by measuring all the individuals from a randomly taken sample and from measurement of the head capsule length determining the percentages of the various instars on different dates. An 'average instar' was calculated for each date, and the resulting data plotted in the form of a graph (Fig. 18). From this graph it can be seen that a period of some 24 days occurs between each moult from instars two to six in the field. Table 43 indicates that at constant temperature there is a gradual increase in the time between moults in successive instars. In the field this is counteracted by an increase in the mean temperature, and this probably explains the straight line graph.

Over the period June-September, O. latus took 120 days from hatching to reach the fifth moult; the average mean air temperature over the period was 10.2°C. At 15°C. constant temperature it took 79 days to reach the

Fig. 18.

Graph to show the duration of instars of Onychiurus latus in the field, at Moor House, during 1961. The 'average instar' was calculated for all sampling dates after the first; the date upon which only first instars were collected cannot be included in the graph since the 'average instar' for this date cannot be calculated.

Fig.18.


O. latus. Instar duration in the field.
Average Instar
7
6
5
4
3
2
1
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

fifth moult in culture. Thus for a rise of 4.8°C. the rate of development increases by a factor of 1.52. This compares with an increase in the rate of development in H. denticulata by a factor of 2.1 for a rise in temperature of 7°C. (page 107). From these rather meagre data rough constants for development can be calculated from the product of the development time in days and the temperature in degrees centigrade (Table 45). The constants from separate sources agree sufficiently nearly to make their use justifiable in an estimate of the expected time of attaining maximum size in the field (Table 46).

Table 45. Constants (the product of the development time in days and the temperature in degrees centigrade) for the development of sub-adult instars.

Species	Constant temperature. 8°C.	15°C.	Mean field temperature. 10.2°C.
H. denticulata	704	630	-
O. latus	-	1180	1224

In Table 46 the constants derived from laboratory culturing at 15°C. are used. The number of days from hatching taken to attain maximum size is indicated under the appropriate

hatching date. The temperature figures are averages for the period 1952-61. In an average year O. latus takes 113 days to reach maximum size when hatched on 1 June. The calculated figure for 1961 is 116 days, and the actual figure estimated from the field population (Fig. 18) 120 days; there is thus a close relationship between the calculated data and the actual state of affairs in the field.

h) The process of moulting.

Davis and Harris (1936) have recorded that in Pseudosinella violenta the body becomes opaque and white prior to moulting. During the course of this work moulting has been observed in all the species cultured. The bases of the antennae first appear whitish, as the old cuticle separates from the new, and fluid moves between the two. The antennae are partially withdrawn from the old cuticle which also begins to separate from the new cuticle at the tip of the abdomen. At this stage a split usually occurs along the length of the top of the head. In those species possessing anal horns these are withdrawn from the old cuticle and thrust upwards in a more anterior position, so pulling backward the old cuticle. Undulating movements occur throughout the length of the body and the thorax and abdomen are alternately expanded and contracted.

Table 46. Calculated times to attain maximum size in the field, at Moor House, in days.

Species and Development constant (K)		Hatching date: 1 June	1 July	1 August	1 September	1 October	1 Novem
Hypogastrura denticulata	(630)	61	56	61	188	227	222
Tullbergia krausbaueri	(509)	50	45	49	67	212	209
Onychiurus procampatus	(1237)	119	145	286	295	294	277
Onychiurus latus	(1180)	113	127	277	278	284	272
Onychiurus tricampatus	(975)	91	91	224	266	266	254
½(max.+min.) temp. in °C. Mean of 10 years 1952-61.		9.57	11.28	11.13	9.62	6.74	3.02

The first 30 days of the development time are calculated on the basis of the mean temperature for that month, the following periods of 30 days on the mean temperatures for the appropriate months.

The split continues along the dorsal side of the moulting individual, and when it extends almost to the tip of the abdomen the thorax is pushed out through the split and the legs released. Normally the old cuticle is attached to the substrate, apparently by the claws. By bracing the legs against the substrate the antennae and head are then released, and strong wriggling movements begin in order to free the abdomen. The whole process of moulting normally takes from 10 to 15 minutes in culture.

In some of the species cultured the cast cuticle is normally eaten. In T. minor this occurred almost invariably, whilst in H. denticulata apparently no cuticles were eaten. All four species of Onychiurus cultured frequently eat the cast cuticle, though this occurred less frequently in T. krausbaueri. The eating of the cast cuticles made it necessary to examine cultures daily throughout the period of culturing.

i) The sex ratio.

Maclagen (1932) comments upon the disparity in the numerical relative production of the sexes in Sminthurus viridis where he records a ratio of 22 males to 100 females. In Pseudosinella violenta Davis and Harris (1936) record a sex ratio of 65 females to 35 males in 100 individuals examined, which is significantly

different from unity ($\chi^2 = 9.0$; d.f. = 1; $P < 0.005$). Falkenhan (1932) noticed that in Sminthurides aquaticus females normally produce offspring of one sex only, and Anders (1959) has carried out a genetical analysis of this which accounts for the disparity in the sex ratio. Choudhuri (1958) has produced additional evidence that the sex ratio is affected by temperature: at high temperatures the proportion of males in both Onychiurus fimatus and O. imperfectus was greater than that of females, whereas at low temperatures the reverse was true. These results are subject to review, due to the probable existence of a parthenogenetic form, at least in O. fimatus, which was not recognised by Choudhuri (1958) (see page 181).

During the course of the work at Moor House, sex ratios of four species have been determined. These are shown in Table 47.

Table 47. Sex ratios of Collembola taken at Moor House.

Species	No. of females counted	No. of males counted	χ^2	Probability of difference from equality
Hypogastrura denticulata	56	34	5.4	< 0.025
Onychiurus procampatus	362	0	181.0	< 0.005
Onychiurus latus	430	140	151.0	< 0.005
Onychiurus tricampatus	216	210	0.1	N.S.

N.S. = Not significant.

j) Life cycles and longevity.

Information concerning the life cycles of Collembola at Moor House has been derived from four main sources:

A) A knowledge of the time of egg laying (Table 19).

B) Examination of monthly samples for first instars, which were recognised by comparison with individuals hatched in culture.

C) Examination of the monthly samples for the presence of adults, and in some cases, eg. O. latus, O. procampatus and O. tricampatus, all other instars (Figs. 19-21).

D) A knowledge of the length of time from hatching to maturity.

From this information it appears that there are four main types of life-cycle:

1) Spring layers which mature through the summer and over-winter as adults which lay again the following spring. Into this category fall the majority of species. The onset of laying coincides with a rise in temperature in the spring (see page 111.), eg. H. denticulata, N. muscorum, O. latus, I. sensibilis, I. viridis, I. olivacea, I. infuscata, I. palustris, T. minor.

2) Spring layers which continue to lay throughout the summer and autumn, so that all life stages may be

found together in the field in summer, eg. O. procampatus, O. tricampatus, T. krausbaueri. These are cavernicolous soil forms in which the prolongation of the egg laying period is probably due to the stability of the soil as an environment, a fact commented upon by Delamare-Debouteville (1950).

3) Autumn layers which mainly die in early winter, over-wintering largely as eggs which hatch the following spring, with the rising temperatures. A few individuals over-winter, eg. Lepidocyrtus lanuginosus.

4) Collembola which have more than one complete generation a year, and over-winter mainly as eggs, eg. D. fusca, D. minuta. This category contains the majority of the Symphypleona.

Measurement of individuals of all species named was impracticable, and the three species of Onychiurus were selected for measurement. However, the qualitative observations on the other species are regarded as a reliable indication to their types of life cycle, and in Table 48 the probable number of generations is given for some Moor House species, together with the information on which the figures are based.

Fig. 21 shows the age distribution of O. latus during 1960 and 1961. This is a typical example of the first type of life history (Category 1), where the eggs

Table 48. The probable number of generations per year in the Collembola of Moor House.

Species	No. of days to reach maturity (Tables 23 & 46) Laying 1 May	Laying 1 June	Dates when first instars present in samples	Over-wintering condition	No. of periods of oviposition (Table 19)	Probable number of generation
Hypogastrura denticulata	111	96	May-Sept.	All stages	1	1 or 2
Neanura muscorum	-	-	May-Sept.	Mainly adults	1	1
Onychiurus procampatus	166	183	All months	All stages	1	1
Onychiurus tricampatus	138	129	All months	All stages	1	1 or 2
Onychiurus latus	169	171	May-July	Mainly adults	1	1
Tullbergia krausbaueri	109	94	All months	All stages	1	1 or 2
Isotoma sensibilis	-	-	April-Aug.	Mainly adults	1	1
Isotoma viridis	-	-	April-July	Mainly adults	1	1
Isotoma olivacea	-	-	April-Aug.	Mainly adults	1	1

continued overleaf.

Table 48 (cont'd.)

Species	No. of days to reach maturity (Tables 23 & 46) Laying 1 May	Laying 1 June	Dates when first instars present in samples	Over-wintering condition	No. of periods of oviposition (Table 19)	Probable number of generations
Isotoma infuscata	-	-	April-May	Mainly adults	1	1
Isotomurus palustris	-	-	April-July	Mainly adults	1	1
Lepidocyrtus lanuginosus	-	-	May	Mainly eggs	1	1
Tomocerus minor	-	-	May-June	Mainly adults	1	1
Dicyrtoma minuta	-	-	May & July	Mainly eggs	2	2
Dicyrtoma fusca	-	-	May & July	Mainly eggs	2	2

Fig. 19.

The age distribution of Onychiurus procampatus at Moor House during 1960 and 1961. Summer peaks in numbers in the second and third instars, and winter peaks in the adults can be seen.

Fig.19a.

Age distribution.

O. procampatus.

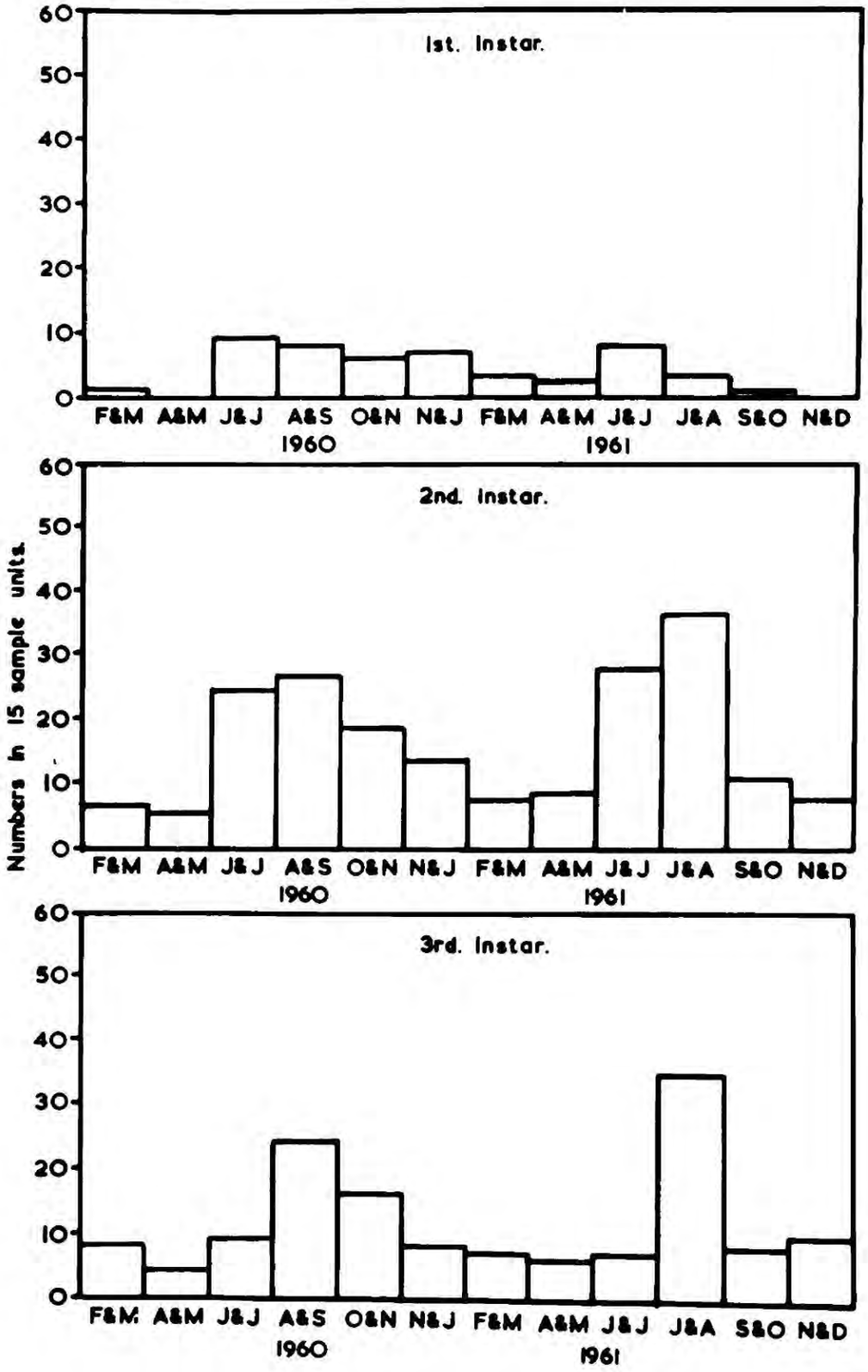


Fig.19b.

Age distribution.
O. procampatus.

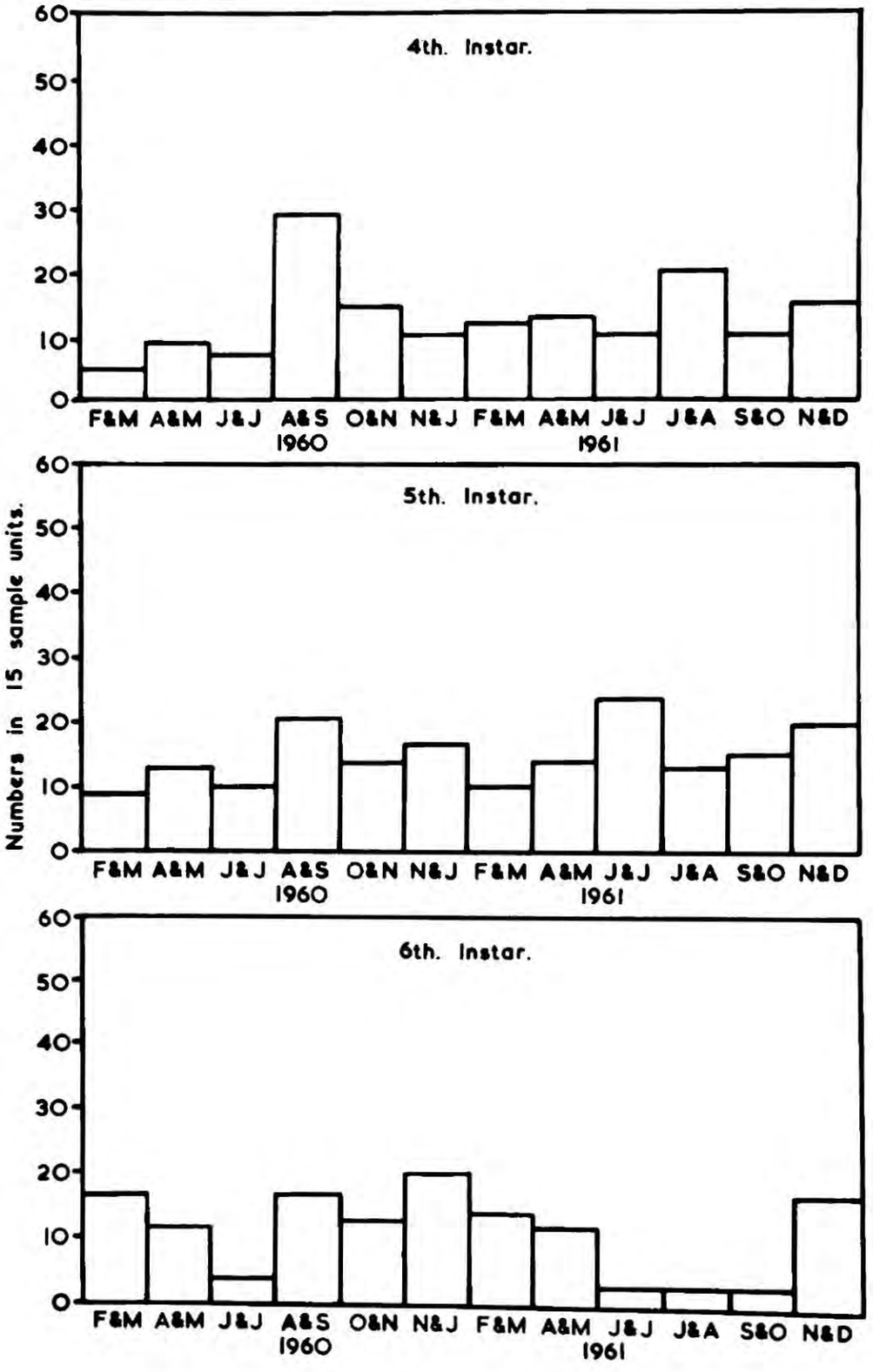


Fig. 20.

The age distribution of Onychiurus tricampatus at Moor House during 1960 and 1961. Summer peaks in numbers can be seen in second instar individuals and there is apparently a second peak in autumn; this could be caused by a second generation.

Fig. 20a.

Age distribution.

O. tricampatus.

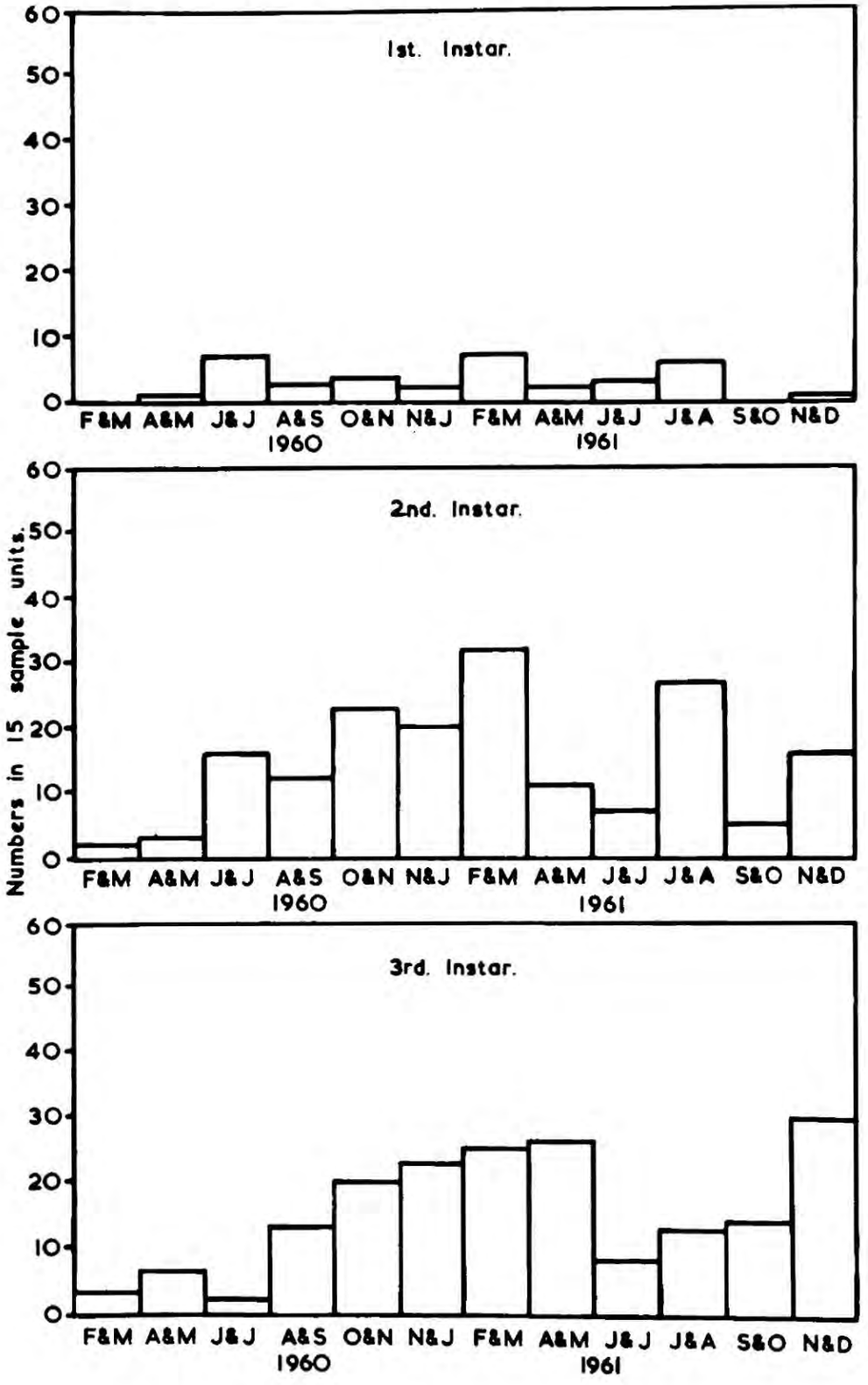


Fig.20b.

Age distribution.

O. tricampatus.

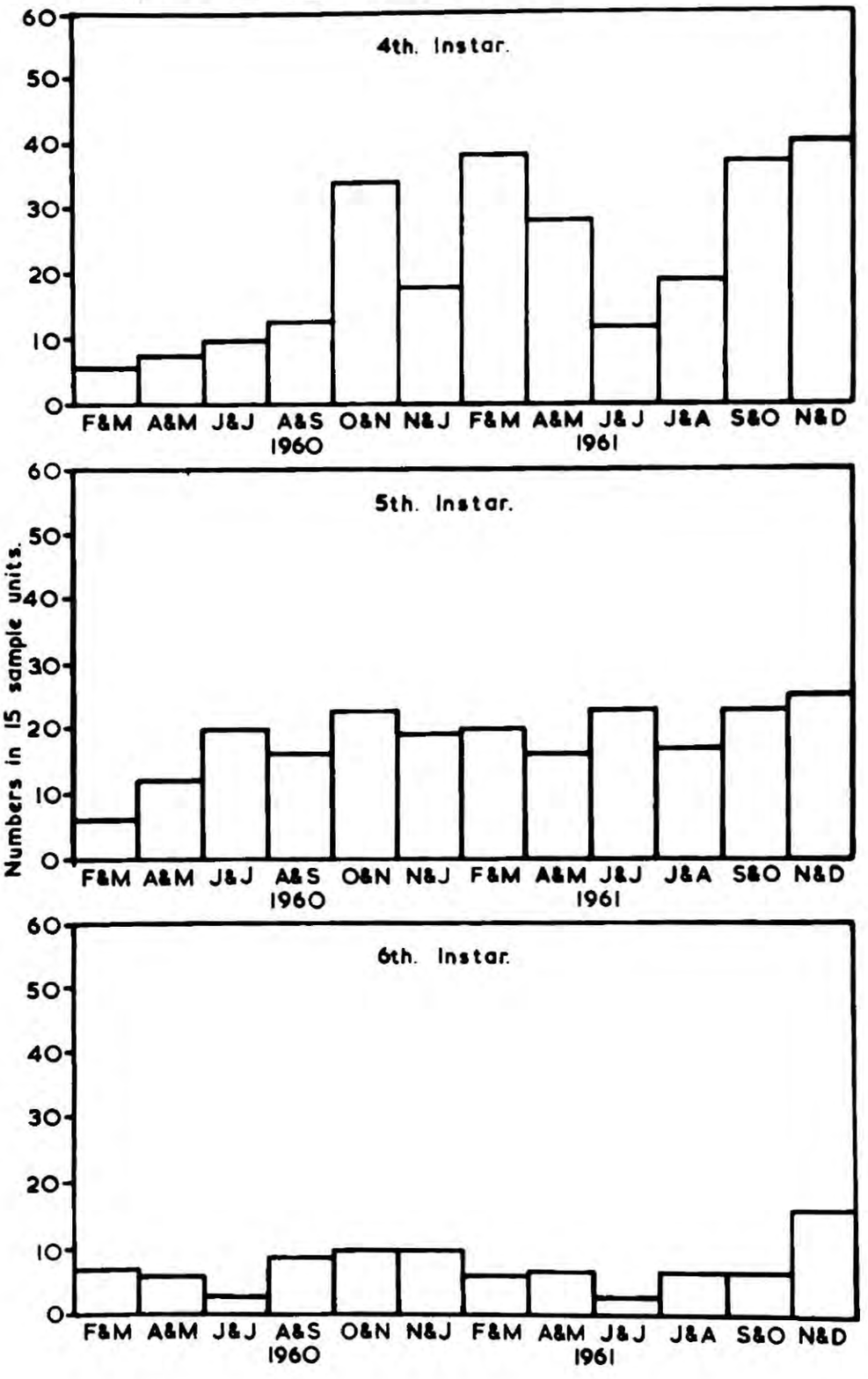


Fig. 21.

The age distribution of Onychiurus latus at Moor House during 1961 and 1962. It can be seen that there is a clearly defined single generation per year, with the eggs hatching in spring, growth occurring throughout the summer, and individuals wintering mainly as adults. The time scale is twice that of Figs. 19 and 20.

Fig. 21a.

Age distribution.

O. latus.

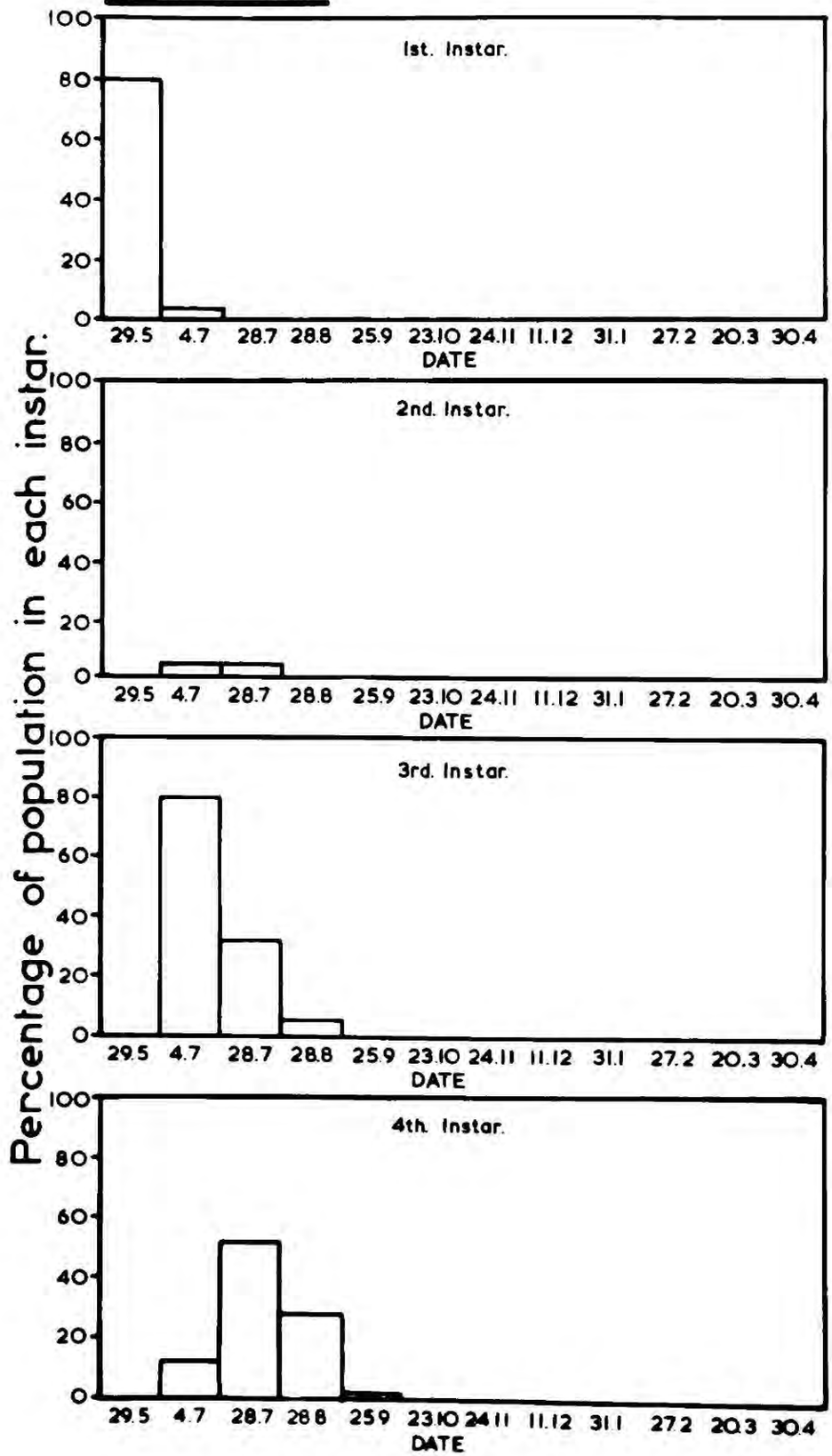
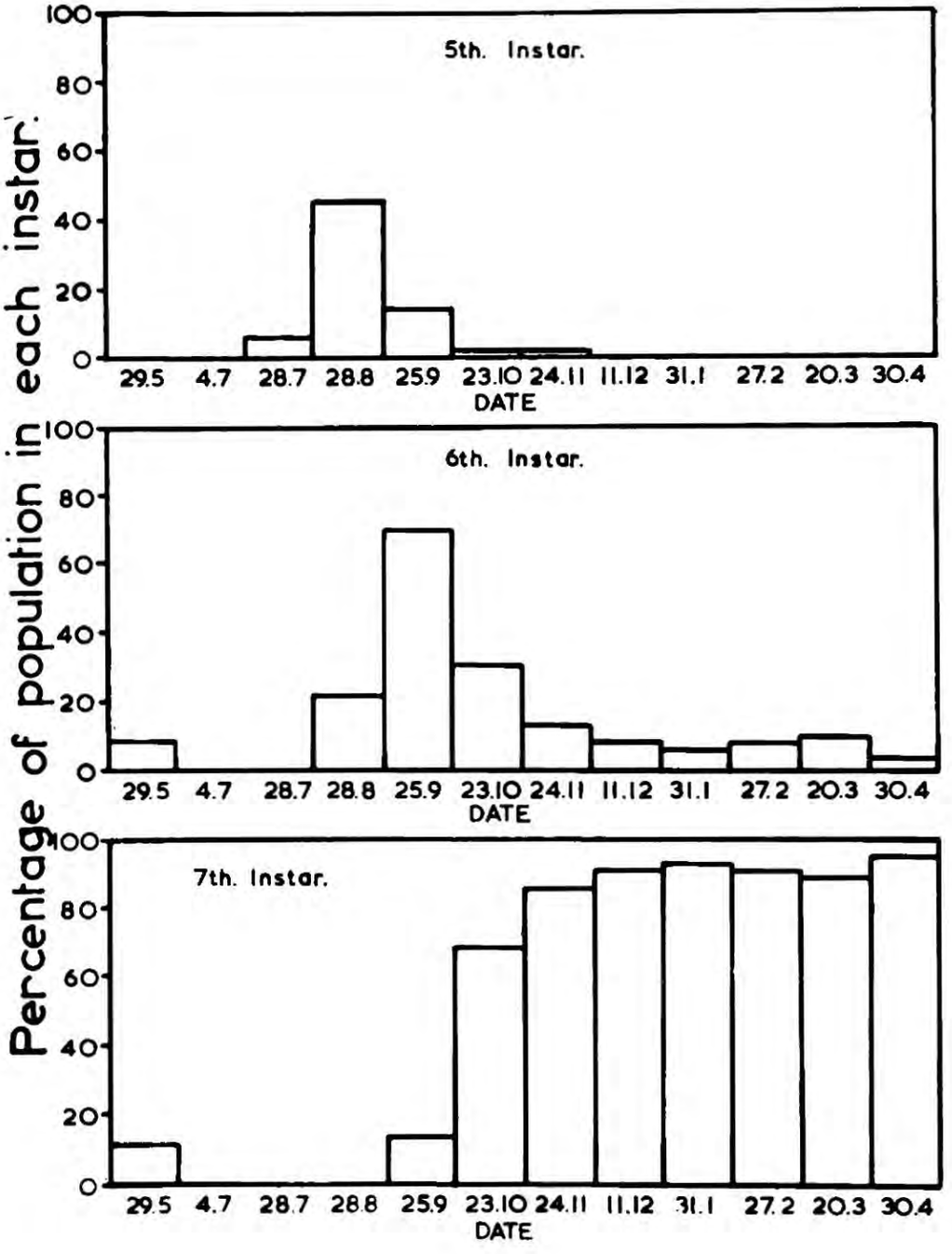


Fig. 21b.

Age distribution.

O. latus.



are laid in late spring, hatch in early summer and the insects reach their maximum size in late autumn (see also Fig. 17). Whilst they attain their maximum head capsule size in late autumn, the maximum weight is not attained until the following spring, as is shown in Table 49. The increase in weight in the adult individuals is most probably due to the maturation of the gonads. Individuals hatching in May 1961 produced eggs at the end of April 1962; this was found by bringing live insects into culture on each sampling date.

In contrast to the well defined life cycle in O. latus, which is a litter living species, the distribution of age groups throughout the years 1960 and 1961, for O. procampatus and O. tricampatus, does not give a clear picture of the life cycle. This is due mainly to the extended period of oviposition (Table 19), but to some extent to the disparity in the efficiency of extracting the earlier instars. Tables 41 and 44 show little difference in the duration of the first and second instars of O. procampatus and O. tricampatus and thus it would be expected that roughly equivalent numbers would be obtained over a full year. As can be seen in Figs. 19 and 20, this is not the case, and thus a disparity in extraction efficiency must occur, first instars being extracted less efficiently.

Table 49. Weight of O. latus during life cycle.

Date	Average instar	Weight of 100 individuals (mgm.)
29.5.60	1.0	0.83
4.7.61	3.1	2.32
17.7.61	3.2	2.51
28.7.61	3.6	3.01
28.8.61	4.8	4.99
12.9.61	5.8	9.98
25.9.61	6.0	11.25
23.10.61	6.7	17.67
24.11.61	6.8	20.81
11.12.61	6.9	21.82
31.1.62	6.9	30.10
27.2.62	6.9	30.47
20.3.62	6.8	30.69
30.4.62	6.9	31.44

In O. procampatus a summer peak can be observed in the numbers of second instar individuals (Fig. 19a), which corresponds with the laying in early spring, and there is a winter peak in the numbers of adults. In O. tricampatus a less obvious peak occurs in the early instars in summer and a second peak in autumn. It is possible that the second peak is caused by a second generation, for individuals hatching in late spring will reach maximum size by the end of August, and almost certainly mature before winter sets in. Laying occurs in cultures at 8°C. in October and November, and these eggs are probably laid by individuals that matured during autumn. In January and February 1961, high temperatures at Moor House caused an early hatch of overwintering eggs (see page 19). In O. tricampatus (Fig. 20a) a winter peak in the numbers of second instars (November to March) occurred, whilst no similar peak occurred in O. procampatus (Fig. 19a). Since the eggs of both species have a similar period of development (Fig. 10), this suggests that more overwintering eggs of O. tricampatus were present in the soil than that of O. procampatus, indicating a later laying in the former species; this later laying could be by a second generation. The data in Tables 23 and 46 support the possibility of two

generations in O. tricampatus and only a single generation in O. procampatus, since the former has an appreciably shorter life history (Table 48).

The only species in this work for which there is any precise information concerning the length of the life cycle in the field is O. latus. Fig. 21 shows that in this species the length of life from hatching to laying is 10-11 months, although a few individuals may live longer. Adults placed in culture at 8°C. at the time of laying have existed up to a maximum of 120 days after the usual time of laying, giving a maximum length of life of over 400 days. H. denticulata and other species having a similar type of life history have also been recorded as living over 120 days after collection from the field at the time of laying. It appears that most spring layers have a normal length of life of just under one year in the field at Moor House, although it is possible that some of the smaller species, eg. Folsomia spp., may have more than one generation a year at Moor House, (see page 258) and also a shorter life span. Agrell (1941) records two generations in Folsomia quadrioculata in arctic Sweden from measurements of material collected in the field.

At Moor House the low temperatures in winter and early spring prevent laying, and the low autumn temperatures retard development. It is possible that at times temperatures in the soil, and below snow, are above those of the air (Geiger 1950). The activity of Collembola may thus be greater than would be suggested by the air temperatures, on which development estimates here are based. Even so, it is doubtful if more than one complete generation occurs (Table 48) in any of the spring layers (Category 1) at Moor House. Qualitative examination of the monthly samples supports this.

In Tomocerus minor the single generation is clearly defined, and Agrell (1941) found this in T.vulgaris and Bellinger (1954) in T. flavescens, from examination of individuals collected from the field. According to Strebel (1938) members of the Genus Tomocerus may live up to 18 months. Folsom (1916) records 3-4 generations a year in Hypogastrura armata, and Britt (1951) records a maximum of 12 generations a year in the laboratory at 24°C. The latter author indicates that normally the life span is about 2 months in H. armata but overwintering individuals live for about 1 year. Ripper (1930) records a life span of 5-10 months for members of the Genus Hypogastrura.

In those species laying throughout the summer and autumn (Category 2), the usual life span is probably shorter than one year. However, in culture T. krausbaueri has lived for more than 1 year at 15°C., and a single individual of O. procampatus cultured at 8°C. was still alive 1250 days after being introduced to the culture as a sub-adult.

Autumn layers (Category 3) normally have a shorter life span in the field, since they hatch in spring, mature through the summer, and die after laying in autumn. The normal life span in the field for L. lanuginosus is probably in the region of 7-8 months.

In the rigorous moorland climate the only Collembola which appear regularly to have more than one generation a year are certain of the Symphypleona. Over-wintering as eggs D. minuta and D. fusca hatch in late spring and mature during the early summer when eggs are again laid; the resulting second generation lays eggs in the autumn and these over-winter. Individuals of these two species have a life span of about 3-4 months in the field at Moor House, as after a July hatch individuals were absent from November samples. The smaller Symphypleona, which normally overwinter as eggs, probably have a shorter life span and at least two generations during the summer.

Maclagen (1932) records a period of 48 days from hatching to maturity under field conditions in Sminthurus viridis, and a further 15 days for the life span of the adult.

In the sub-Arctic climate which prevails at Moor House, the Collembola probably have their life cycles extended over a period greater than that in any other habitat in the British Isles. Thus their activity in the general soil turnover may be regarded as at its minimum level.

k) Parthenogenesis.

Handschin (1928) referred to the possibility of parthenogenesis in the Collembola and stated that the periodic appearances of large numbers of a single species might be considered as circumstantial evidence for it. Isolation of individual females of various species by Strebel (1932, 1938), Falkenhan (1932), Schaller (1953) and Mayer (1957) resulted in no young individuals being produced. In only one case in Orchesella villosa (Lindemann 1950) did an isolated female produce eggs which subsequently developed, and Mayer (1957) explains this by suggesting that spermatophores were introduced to the culture with the food.

In Onychiurus parthenogeneticus Choudhuri (1958) parthenogenesis is the normal form of reproduction and males are absent in this species. Goto (1960) and Marshall and Kevan (1962) have demonstrated a facultative parthenogenesis in cultures of Folsomia candida.

During the course of the present work two examples of parthenogenesis have come to light. In Tullbergia krausbaueri individuals were isolated from the day of hatching and in four cases eggs were produced which subsequently developed and hatched. In three cases individuals cultured in pairs turned out to be pairs of females, and these also produced eggs which hatched. What is considered to be a form of parthenogenesis also occurred in Onychiurus procampatus (see page 179), and a similar state of affairs also exists in O. fimatus.

PART C.

THE TAXONOMIC STATUS OF SOME MEMBERS OF THE *ONYCHIURUS ARMATUS* SPECIES GROUP.

PART C.

THE TAXONOMIC STATUS OF SOME MEMBERS OF THE ONYCHIURUS ARMATUS SPECIES GROUP.

1) Introduction.

Gisin (1952), on the basis of material collected from the Alps, expressed the opinion that in the species Onychiurus armatus (Tullberg 1869) are included a diversity of species; twelve were named (Gisin 1952a) and later a thirteenth (Gisin 1952b). Gisin (1960) describes 38 species which are contained within the Onychiurus armatus species group. The main characters used in the separation of the species within the group are:

a) The location and number of pseudocelli on different segments of the body.

b) The arrangement of setae on the tergites of the first thoracic segment and those of abdominal segments five and six. Other minor characters involved are the relative lengths of the anal spines and the presence of an inner tooth on the claws.

The division of the O. armatus species group has been criticised by Stach (1954) and by Bodvarsson (1959). The former author considers most of Gisin's species to be 'insignificant ecological or local modifications', and the latter author writes as follows:

'As long as the biological conditions of the animals and the nature of the variations have not been studied experimentally, it seems the most appropriate to regard these forms as infrasubspecific and thus not to subject them to purely taxonomic treatment'. To a lesser extent Choudhuri (1958) criticised Gisin's subdivision of the group, but for the most part accepted his taxonomic criteria.

During the course of this work Gisin's criteria have been assessed experimentally in four species of the group, and found to be valid; the results are presented in this section.

2) The Moor House members of the O. armatus species group.

During the course of the work at Moor House three species of the O. armatus species group were encountered, namely O. procampatus, O. latus and O. tricampatus. O. latus was clearly a different species from the other two as was recognised by both Choudhuri (1958) and Milne (1960). (The former author considers it to be a synonym of O. aurantiacus Ridley 1880). The present work has shown that O. latus possesses one more instar than the other two species (Fig. 16a), its eggs take longer to develop (Fig. 10), and it also contains a yellow pigment

which the other two lack. In addition to these factors O. latus is ecologically different in that it is a litter living form characteristic of acidic areas, whereas the other two species penetrate deep into the soil and do not occur in acid peat conditions.

In the section on sex ratios it was seen that O. procampatus occurs at Moor House only as females, whereas O. tricampatus is present as both males and females. There is also a size difference between these two species (Figs. 16a and 16b), where the first instar of O.procampatus is equivalent in size to the third instar of O. tricampatus. It was found that O. procampatus laid larger eggs than O. tricampatus (Table 20), had a longer period of development to maturity, and had a different vertical distribution in the soil, (Tables 77 to 79). However, these two species always occurred together in samples from mull soils at Moor House.

3) The relationship between O. procampatus and O. tricampatus.

a) The occurrence together of the two species in the field.

Table 50 summarises the data concerning the numbers of these two species collected in different sampling areas,

Table 50. Numbers of *O. procampatus* and *O. tricampatus* obtained from different sampling sites.

Locality	Numbers			
	O. procampatus		*O. tricampatus*	
	Male	Female	Male	Female
1. Moor House, Limestone grassland, House Field.	0	362	210	216
2. Moor House, Limestone grassland, Green Hole.	0	64	27	49
3. Moor House, Limestone grassland, Milburn Beck.	0	10	28	32
4. Moor House Alluvial grassland, Trout Beck.	0	34	13	15
5. Cassop Vale, Co.Durham, Limestone grassland.	0	174	32	56
6. Melmerby, Cumberland, Limestone grassland.	32	68	2	3
7. Hartside, Cumberland, Limestone grassland.	0	14	8	13
8. Malham, Yorkshire, Limestone grassland.	0	176	33	42
9. Bowes Moor, Yorkshire, Limestone grassland.	0	11	3	13
10. Milngavie, Dunbartonshire. Sample from Dr. S. Milne.	0	12	1	0
11. Mewslade Bay, Gower, Glamorgan. Sample from A. Macfadyen and I. Healey.	0	25	7	21
12. Vorso, Denmark. Sample collected by H. Gisin.	0	4	2	3

In no locality during the course of this work was either species found alone.

b) Breeding experiments.

Whilst adult O. procampatus could be separated because of their larger size from O. tricampatus, this latter species could not be separated from earlier instars of O. procampatus, in life. It was found that on isolating O. procampatus adults no eggs were laid, despite the fact that no males existed in the samples of the species and thus parthenogenesis was to be expected. Mayr (1957) failed to get eggs from isolated individuals of O. armatus. Placing the adult O. procampatus into cultures which contained male O. tricampatus, eggs were subsequently produced. (The presence of male O. tricampatus was ascertained after the production of eggs by mounting and examining all individuals). In over 30 cultures containing both species, eggs were produced by O. procampatus, but in 10 cultures containing only O. procampatus (large females), no eggs were produced. In order to check that this was not merely a result of collecting at different times, samples were taken from Malham, Yorkshire; Cassop, Co. Durham and from Moor House, and pairs of cultures collected on the same day set up. One culture of a pair contained only adult O. procampatus, whilst the other culture contained a mixture of both species. No eggs were laid in any of the six cultures

containing only adult O. procampatus (large females) but eggs of this species were produced in all the six cultures containing both species. It thus appeared necessary for males of O. tricampatus to be present before females of O. procampatus would produce eggs.

c) The fate of the eggs.

Isolation of the eggs of O. procampatus and subsequent examination on hatching showed that all (over 150) the individuals produced were referable to O. procampatus; that is to say all were females and all were large individuals, the first instar being equivalent in dimensions to the third instar of O. tricampatus.

All the eggs laid by O. tricampatus females (over 200) hatched into individuals referable to O. tricampatus, and both males and females were present.

d) The production of fertile eggs.

Whilst eggs were not produced by O. procampatus (large females) in the absence of O. tricampatus (small) males, even when male O. tricampatus were present, a percentage of the eggs failed to develop, ie. the chorion never split, compared with 26% of the eggs laid by O. tricampatus. The fact that 43% of the eggs failed to develop in circumstances identical to those in which the

other 57% developed suggests infertility; if this is in fact so then they must be fertilised by O. tricampatus males.

e) The possibility of social facilitation.

The fact that no eggs were laid by individuals of O. procampatus in isolation, or in cultures containing only O. procampatus adults, suggests the possibility of social facilitation to egg laying. 10 individuals of O. procampatus were placed one in each of ten cultures of O. furcifer, but no eggs were laid by the O. procampatus females. No information was obtained on this topic.

f) The status of O. procampatus at Moor House.

O. procampatus (large females) always breeds true in cultures the individuals of which were collected from Moor House, Cassop and Malham. Since the population of this species at Moor House is entirely of females, which always give rise to females, apparently breeding is a form of parthenogenesis. However, it appears that the presence of O. tricampatus males is necessary in order that fertile eggs may be produced; true fertilisation, however, does not appear to take place, as O. procampatus has bred true for three generations in culture.

It seems probable that this is a case similar to that occurring in the grain beetles of the Genus Ptinus. Here, P. latro occurs always as females which are normally fertilised by the males of P. hirtellus, although males of other species can bring about 'fertilisation' (Moore, Woodroffe and Sanderson 1956). Apparently entry of the sperm into the egg of P. latro stimulates development mechanically, and there is no fusion of the nuclei or exchange of genetic material.

It would appear that O. procampatus and O. tricampatus are good species since there is apparently no transfer of genetic material, breeding in the former being a form of thelytokous parthenogenesis.

4) Normal sexual reproduction in O. procampatus.

In the material furnishing the types of O. procampatus, taken by Dr. H. Gisin from Engelalp, Bernese Alps, Switzerland, males were present, and specimens have been examined by the present writer. In the adult stage these were the size of the largest O. tricampatus and equivalent in size to the fourth instar of the large female O. procampatus from Moor House (Fig. 16). At Melmerby, Cumberland, adult O. procampatus both males and females, were collected which were identical

in size with the O. tricampatus and smaller than the large adult O. procampatus from Moor House; O. tricampatus occurred in the same samples. Cultures of the small O. procampatus were set up, and it was found to reproduce sexually laying small eggs identical in size with those of O. tricampatus. The first instars were also identical in size with those of O. tricampatus, but differed consistently in the pseudocellar formula and in the chaetotaxy. These bred true and the males were capable of stimulating development in the eggs of the large female O. procampatus. Thus two types of adult females occur in O. procampatus, large parthenogenetic forms and small sexually-reproducing individuals.

The fact that O. tricampatus was present in the same samples and no intermediates were found between the sexually reproducing individuals of O. procampatus and O. tricampatus suggests that these are good species.

5) Apparent parthenogenesis in other members of the O. armatus group.

Examination of over 200 individuals of O. fimatus collected in Durham showed that whilst all were identical from the point of view of pseudocellar formula and chaetotaxy, two different sizes of mature females occurred,

equivalent in head capsule length to the two forms of O. procampatus. Large mature females which laid large (0.23 mm. in diameter on laying) eggs in cultures set up, were present together with small females which laid small eggs (0.17 mm. in diameter on laying); small males were also present but there were no large males.

Choudhuri (1958) reports that in O. fimatus there are seven instars, one more than in O. procampatus and O. tricampatus. Only six size groupings, with a Dyar's increment factor of 1.15, were found in O. fimatus from Durham. The increment factor was identical with that found by Choudhuri, so possibly the last instar was absent from the Durham sample. Plotting all the individuals (large and small) of the sample, eight groupings of head capsule size occur. Choudhuri discarded all measurements of material collected in the field because it did not agree with the number of instars (7) found in the laboratory. The probable reason for lack of agreement is that the two size groupings were present in the field material whereas in the laboratory experiments eggs from only one size grouping were used. Examination of material of O. fimatus identified by Choudhuri has been carried out, and the presence of the two size groupings ascertained.

It thus appears that in O. fimatus there is a large, probably parthenogenetic female, and small sexually reproducing individuals.

Examination of O. quadriocellatus, taken from the Swiss Jura, showed a similar phenomenon with two sizes of females and small males, and Gisin (pers. comm.) has now observed this in the same species from another habitat.

6) Consistancy in the pseudocellar formula.

Bodvarsson (1959) states that the various species within the O. armatus species group are connected by individuals which are intermediate in morphological characters. Examples have not been encountered which support Bodvarsson's contention and it is likely that Bodvarsson has not taken into account variations in the pseudocellar formula and chaetotaxy in the various instars; if Gisin's taxonomic criteria are applied to individuals after the second instar (Table 51) complete separation can be made. Occasionally the pseudocelli of one side of an individual are duplicated in places, but provided both sides are examined carefully this can be recognised. Table 51 shows a comparison of the pseudocellar formulae of the three members of the O. armatus species group found at Moor House.

The present writer considers that the number and position of pseudocelli are not affected by the environment in the same way that certain characters are affected by temperature in other genera eg. Hypogastrura (Cassagnau 1955).

Table 51. Pseudocellar formulae in Moor House members of the O. armatus species group.

Instar	O. procampatus	D. latus	O. tricampatus
1	32/022/33332	32/022/33332	32/023/33332
2	33/022/3333 or 42 or 3	33/022/3333 or 42 or 3	33/02 or 33/33332 or 3
3	33/022/33343	33/022/33343	33/02 or 33/33343
4	33/022/33343	33/022/33343	33/02 or 33/33343
5	33/022/33343	33/022/33343	33/02 or 33/33343
6	33/022/33343	33/022/33343	33/02 or 33/33343
7	-	33/022/33343	-

Note: The pseudocellar formula applies to the distribution of pseudocelli on the dorsal side of an individual. The first two figures refer to the numbers at the base of the antennae and back of the head, the next three to the three thoracic segments and the last five figures to the first five abdominal segments.

7) Summary.

In some species at least, the criteria of Gisin (1952) for the division of the Onychiurus armatus species group are valid, since they are consistant from generation to generation and true intermediates do not exist. The taxonomy of the group is complicated by a form of thelytokous parthenogenesis which requires further investigation

PART D.

POPULATION ECOLOGY

I. SAMPLING AND EXTRACTION TECHNIQUES

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I. SAMPLING AND EXTRACTION TECHNIQUES.

1) Introduction.

Methods for removing micro-arthropods from soil samples have been reviewed in Kevan (1955), and these can be divided into two main categories. Firstly, there are those which rely on the movement of the animals along a physical gradient such as heat, desiccation or light (the so-called 'automatic' methods), and secondly, there are the 'mechanical' methods involving sieving or flotation where the animals are removed independent of their own activity.

The extraction of animals from soil samples still presents great problems, and especially in the case of the micro-arthropods, no accurate measure of efficiency of extraction has been found possible. In all cases assumptions have to be made concerning the reliability of the extraction technique; the main assumptions may be summarised as follows:

a) That the extraction processes are comparable on different dates ie. the relative numbers of different instars and species extracted at different times are assumed to be the same and the efficiency remains constant.

Factors such as different proportions of early and late instars (which would be able to move with different degrees of ease along the temperature gradient), varying water content of the samples, varying field temperatures (where the animals are less active when it is cold), and variations in the density of the plant cover through which the animals have to move to escape from the sample in automatic devices, affect the efficiency of extraction.

b) Comparison of numbers from different soil types must of necessity assume a similar efficiency of extraction, although variations in pore size, vegetation cover etc., may make escape from one soil type easier than from another.

c) In comparing the numbers of different groups of animals, whether they be different species or different phyla, again the extraction efficiency must be assumed to be equivalent for different groups. The use of different extraction techniques for various groups has shown large variations in the efficiencies of the types of apparatus, and thus such assumptions are clearly not justified.

d) In flotation devices, some groups float more easily than others eg. in Collembola, Folsomia spp. are very easily wetted whereas Onychiurus spp. are not. For comparative purposes it must be assumed that all groups float with equal ease.

In particular cases other assumptions must be made concerning the extraction of the fauna from soil samples, and at the outset of any work on the numbers of soil-living animals it must be recognised that, at least to some extent, the data obtained is a measure of the behaviour of the extraction apparatus rather than a reliable reflection of the state of affairs in the field. However, with careful selection of the extraction technique, and the knowledge gained from the experience of using it, relatively reliable, if to some extent subjective, results may be obtained. Clearly data obtained are minimum estimates and as such are of value.

2) The applicability of different extraction techniques to moorland soils.

Raw (1955) has described a flotation extraction process for soil micro-arthropods, but like all such methods this is based on the principle that organic material floats in magnesium sulphate solution of specific gravity 1.2, whereas mineral matter sinks. Clearly this would not be of use for the extraction of micro-arthropods from organic soils such as occur on moorlands. Initially, then, the possibility of using a mechanical method for extracting Collembola from peat soils was discarded, and other methods were tried out.

Hand-sorting peat samples was attempted, but this was found to be so laborious and time consuming that this method was dispensed with.

It was then decided that the most efficient automatic method of extraction available would be used. This proved to be the High Gradient Cylinder, details of which had not been published, but which were kindly supplied by Mr. A. Macfadyen, its designer. A description of the apparatus appeared later (Macfadyen 1961).

As has already been mentioned, automatic extraction devices depend on the movements of the animals themselves and this gives rise to certain errors. Flotation extraction methods are also subject to errors which, however, are not of the same magnitude. It was therefore decided to attempt to design a flotation method for the extraction of Collembola from peat and other organic soils.

3) The extraction techniques used.

a) The High Gradient Cylinder.

Macfadyen (1953, 1955, 1961) has described and compared several methods of extracting soil arthropods from soil samples. At the time when the present work was first started, Macfadyen (pers. comm.) had developed the High Gradient Cylinder which proved to be up to ten times

as efficient as an ordinary Tullgren Funnel (Macfadyen 1961); this type of extractor was thus chosen for the present work.

Fig. 22 shows a single unit of the High Gradient Cylinder. The sample unit is taken in a tufnal ring (see page 208) $\frac{1}{1000}$ m^2 in surface area and 3 cm. deep, whereas in the apparatus described by Macfadyen (1961) the core was $\frac{1}{200}$ m^2 in surface area and 3 cm. deep. The sample unit is inverted over a metal gauze fitted to the top of an aluminium canister which contains a little water, and sealed on by means of a rubber collar. The relative humidity within the canister into which the micro-arthropods fall is about 100%, and a steep temperature gradient can be maintained over the depth of the soil sample by heating from above and cooling the canister, from below, by means of a water bath through which a constant flow of cold water is maintained.

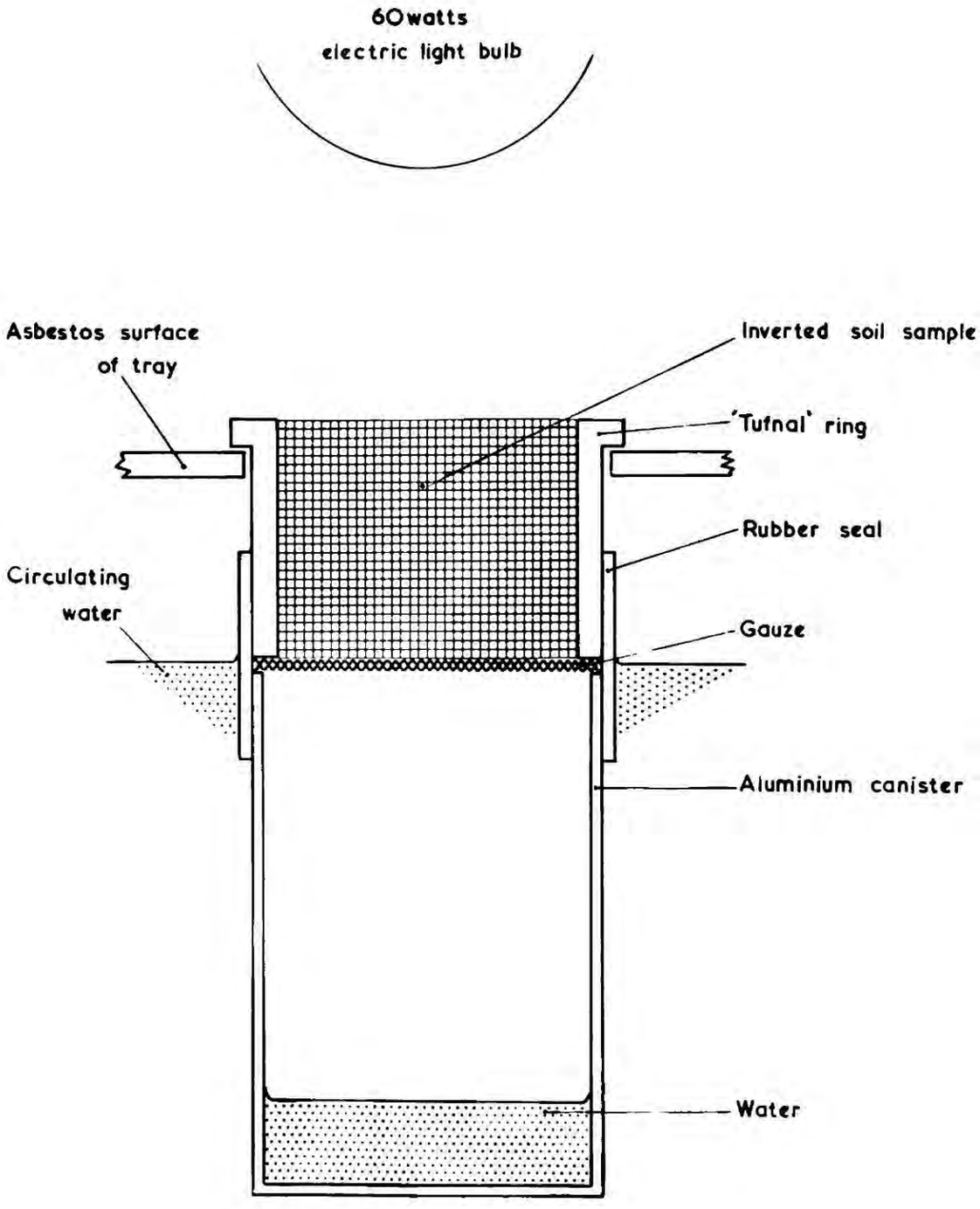
All the initial tests were carried out using a small 10 unit extractor built for the purpose. Plate 11 shows the apparatus built after deciding on the final design which was based on the results of these tests. It consists of two trays, each holding 16 canister units, each of which is heated from above by means of a 60 watt electric light bulb. The trays form the cold water baths

Fig. 22.

A single unit of the High Gradient Cylinder showing the orientation of the soil core.

Fig. 22.

The High Gradient Cylinder

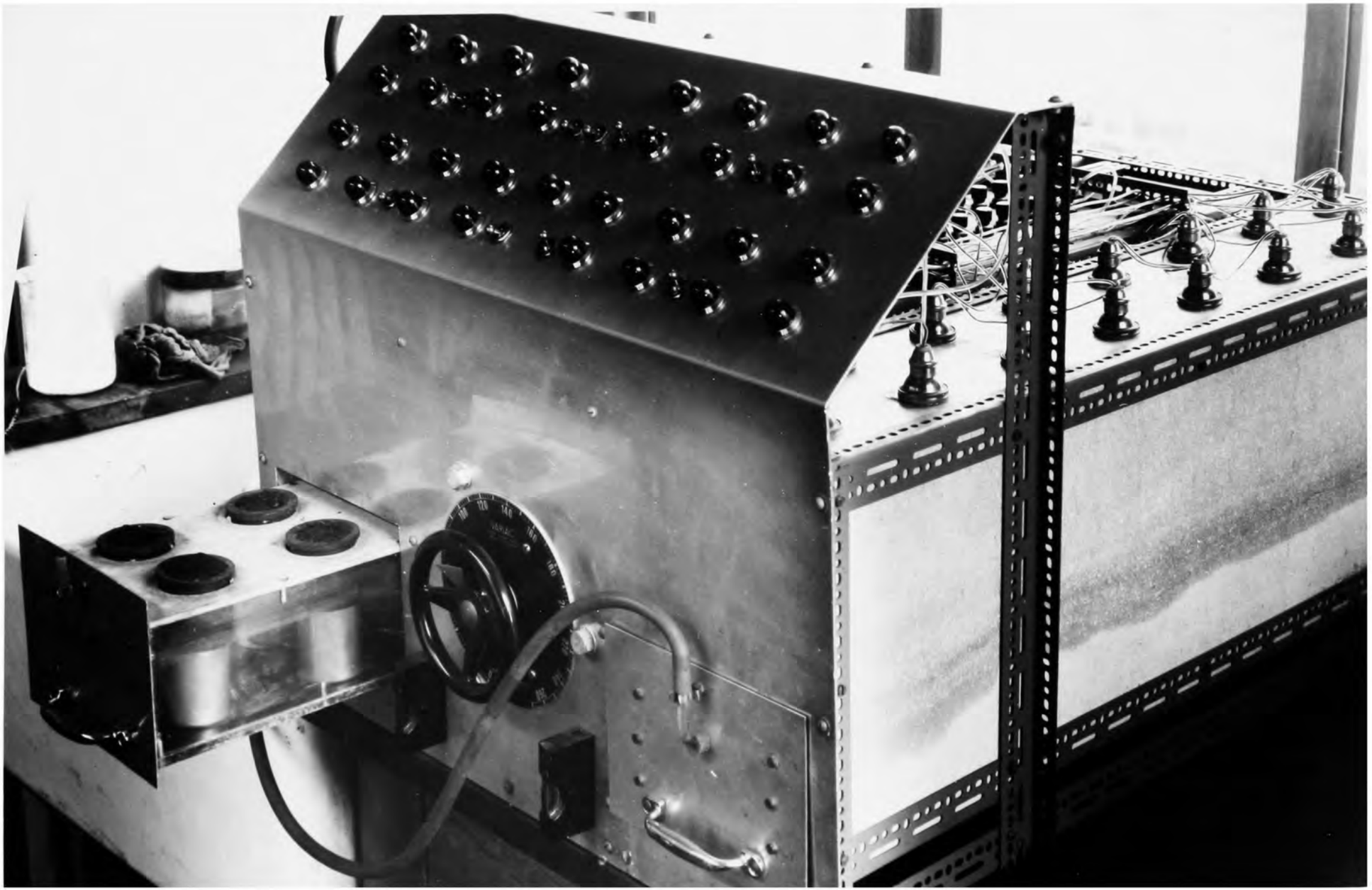


for the canisters, and water is circulated through the trays during extraction. A zenith Variac transformer (Type 100M) controls the voltage passing through the electric light bulbs, and in this way the temperature is controlled. A pilot light on the outside of the apparatus indicates when a bulb has ceased to function.

Several modifications of the original apparatus were found to be necessary. Due to the number of samples taken, and the frequency with which the different areas were sampled, it was found that the five day period recommended by Macfadyen (pers. comm.) was too long for an apparatus of only 32 units. Two extractions a week were required and thus the period of extraction was reduced to three days. It was also found that the recommended heat gradient of 20°C. over the depth of the soil sample, did not dry out the sample completely. With the relatively low temperature of 15°C. at the lower surface of the sample, Collembola remained in it even after a 5 day extraction if it was not completely dried out. A three stage extraction was eventually decided to be the best: for the first 12 hours of the extraction the Variac transformer was set at 60 volts; after 12 hours it was set at 100 volts for 24 hours and then at 140 volts until the sample dried out, a period which

PLATE 11.

The High Gradient Cylinder extractor, showing the method of fitting the canisters into the water trays. The Variac transformer is fitted between the two water trays, and above are the pilot lights which indicate whether or not the individual bulbs heating the apparatus are working.



varied between 12 and 24 hours depending upon the soil type. Table 52 shows the temperatures corresponding to the Variac reading.

Table 52. Temperature gradients during a three day extraction.

Time from beginning extraction (hours)	Variac reading (volts)	Temperature of cooled side of soil sample	Temperature of heated side of soil sample
0	60	19.0	19.0
12	60	19.0	34.0
13	100	18.5	55.0
20	100	19.5	58.5
25	100	18.8	58.5
36	100	18.8	55.5
37	140	21.0	76.0
48	140	20.0	79.0
60	140	20.0	80.0

Due to the shorter period of extraction it was not found necessary to use fixatives and fungicides in the canisters, and the micro-arthropods were not killed until after the extraction was completed, when 70% alcohol was added to the water in the canisters.

Because of the size of the apparatus and the fact that the samples were divided into two horizontal layers, when 30 unit samples were taken, half the units had to be stored for a period of three days before extraction; this was also the case when two sets of 15 units each were taken. It was found that storing in a refrigerator at 4°C. for a period of three days had little or no effect on the efficiency of extractions as is shown in Table 53; here the results of a 30 unit sample extracted over two periods of 3 days are shown. Table 54 shows the effect of extracting over two three day periods on the total numbers of Collembola from other soil types.

The data show that there was no significant difference between the numbers of individual species extracted from stored and unstored samples from Limestone grassland; nor was there a significant difference in the total numbers of Collembola extracted from stored and unstored samples from different collecting dates. On Alluvial grassland a significant difference was recorded in the numbers extracted from stored and unstored samples from two different extracting dates. However, at this stage (after 6 June, 1960), the sample size was reduced from 30 to 15 units and it was thus unnecessary to store samples from Alluvial grassland.

b) The flotation method developed.

Ladell (1936), Salt and Hollick (1944) and Raw (1955) have designed and developed flotation methods for separating animals from mineral soils. For the reason already explained (page 186) these methods are unsuitable for organic soils.

The main problem arising in devising a flotation method was in causing the peat and other organic material to sink in the liquid medium used for flotation, whilst at the same time maintaining the Collembola on the surface of the medium; even when soaked for periods up to a week some peat always remained floating when either water or magnesium sulphate were used. In the method described by Raw (1955) air was extracted from the sample by means of a vacuum desiccator, in order to disperse the soil particles. It was found that when peat soil samples were treated in this way most of the peat sank. Using a vacuum pump fitted to the water tap and a corked conical flask connected by means of a side arm to the pump, complete sinking of the peat sample contained in the flask was achieved by reduction of the pressure in it until the water boiled at room temperature. It was found that all the peat sank after a period of reduced pressure of some 30 secs. The effect of pressure reduction on the Collembola and other arthropods was then considered.

Table 53. The effect of storing for three days on the efficiency of extraction of various species of Collembola. Limestone grassland 25.4.60. The figures are means per sample unit 11.35 cm^2 in surface area and 6 cm. deep.

Species	*Onychiurus procampatus*	*Friesea mirabilis*	*Tullbergia krausbaueri*	*Folsomia manolachei*	*Folsomia* cf. *brevifurca*	*Isotoma viridis*	*Isotoma sensibilis*	*Isotoma notabilis*	*Isotomiella minor*	*Symphypleona*
Mean of first 15 units (A) 1-3 days	4.53	8.40	12.67	36.73	4.53	1.93	3.73	2.47	2.93	4.93
Mean of second 15 units (B) 4-6 days	4.46	6.93	11.40	26.67	3.20	2.13	4.13	3.53	2.60	5.07
Difference(B-A) between means and S.E. of difference	-0.07 ± 1.40	-1.47 ± 1.51	-1.27 ± 4.05	-10.06 ± 8.50	-1.33 ± 1.01	+0.20 ± 0.75	+0.40 ± 1.06	+1.06 ± 0.91	-0.33 ± 0.93	+0.14 ± 1.60

Note. None of the differences between the means are significant.

Table 54. The effect of storing for three days on the total extraction efficiency. The figures are means per sample unit 11.3 cm.^{2} in surface area and 6 cm. deep.

Soil Type	Limestone grassland						Alluvial grassland	
Date (1961)	29.2	28.3	25.4	23.5	27.6	18.7	2.5	6.6
Mean of first 15 units (A) 1-3 days	23.60	34.13	83.53	48.13	71.53	45.27	52.60	53.40
Mean of second 15 units (B) 4-6 days	29.53	40.53	70.66	47.13	76.07	51.80	38.93	39.00
Difference(B-A) between means and S.E. of difference	+5.93 ± 4.30	+6.40 ± 6.86	-12.87 ± 10.62	-1.00 ± 6.94	+4.54 ± 12.51	+6.53 ± 6.29	-13.67 ± 6.61	-14.40 ± 7.17

Note. None of the differences between the means are significant, except in the case of the two samples from Alluvial grassland.

Animals were extracted by means of a large Tullgren funnel, from a sample of leaf litter collected in Durham. Samples of the fauna extracted were placed in a conical flask with some water, and the contents were boiled under reduced pressure for some 30 secs. at room temperature. Table 55 shows the number remaining floating after this treatment, compared with the total introduced. As can be seen from the table, only 42% of the Collembola remained floating after pressure reduction.

At this stage the problem required a means of raising the Collembola to the surface once more, whilst at the same time keeping the peat at the bottom of the container. On many occasions whilst preserving Collembola, it was observed that they floated to the surface when water was added to the alcohol containing them, or when alcohol was added to water in which they had sunk; this method was tried but was unsuccessful because the peat also came to the surface.

It was decided to try bubbling air through the sample by means of an aerator; this was first tried on samples in which only Arthropods and water were present ie. the samples making up the data in Table 55. Table 56 shows the results of passing air in the form of very fine bubbles through the sample of water and Collembola.

Table 55. Numbers floating after pressure reduction.

Groups	Poduridae	Onychiuridae	Isotomidae	Entomobryidae	Sminthuridae	Total Collembola	Mites	Spiders	Coleoptera Larvae	Coleoptera	Diptera Larvae
Nos. introduced to flask	10	34	61	354	80	539	74	3	132	6	13
Nos. floating after pressure reduction	0	20	11	158	36	225	11	0	14	0	0
Percentage floating	0	59	18	45	45	42	15	0	11	0	0

After such treatment, in the absence of any soil particles, 99% of the total Collembola were on the surface of the water. It was also found that peat could be caused to sink in magnesium sulphate solution of specific gravity 1.2, by boiling under reduced pressure. Whilst it was unnecessary to use magnesium sulphate to recover Collembola (Table 56), most Arthropod groups were found to float better in it than in water. Tests were carried out to show the recovery of other Arthropod groups, using magnesium sulphate solution. Comparison of Tables 56 and 57 shows the greater efficiency achieved for the extraction of Arthropod groups other than Collembola.

Further tests showed that when Collembola were mixed with peat some means of stirring the sample was necessary in order to prevent individuals being trapped in the peat; continuous stirring, however, caused the Collembola to remain submerged due to the centrifugal effect of the stirrer. It was then decided to stir only for short periods, but to pass air bubbles through the sample continuously.

The final design of a single unit of the apparatus is shown in Fig. 23 and in Plate 12. The procedure for extraction is as follows:

1) The soil sample is first washed through sieves, in order to break it down, and this is then introduced

Table 56. Numbers floating in water after pressure reduction and aeration.

Collembola and other Arthropods	Poduridae	Onychiuridae	Isotomidae	Entomobryidae	Sminthuridae	Total Collembola	Mites	Spiders	Coleoptera Larvae	Coleoptera	Diptera Larvae
Numbers sunk before aeration	10	14	50	196	44	314	63	3	118	6	13
Numbers floating after aeration	10	12	48	196	43	309	44	2	93	4	1
Percentage floating	100	86	96	100	98	98	70	66.7	79	66.7	8

Table 57. Recovery of arthropods using magnesium sulphate solution.

Collembola and other Arthropods	Poduridae	Onychiuridae	Isotomidae	Entomobryidae	Sminthuridae	Total Collembola	Mites	Spiders	Coleoptera Larvae	Coleoptera	Diptera Larvae
Numbers introduced	1	24	210	323	240	798	297	11	135	18	29
Numbers floating after pressure reduction	1	19	116	205	166	507	198	10	99	16	26
Numbers sunk before aeration	0	5	94	116	73	288	92	1	35	2	2
Percentage floating	100	100	100	99	99	99	98	100	99	100	97

Fig. 23.

A single unit of the flotation extractor showing the parts described in the text.

Fig. 23.

Single unit of the flotation extractor.

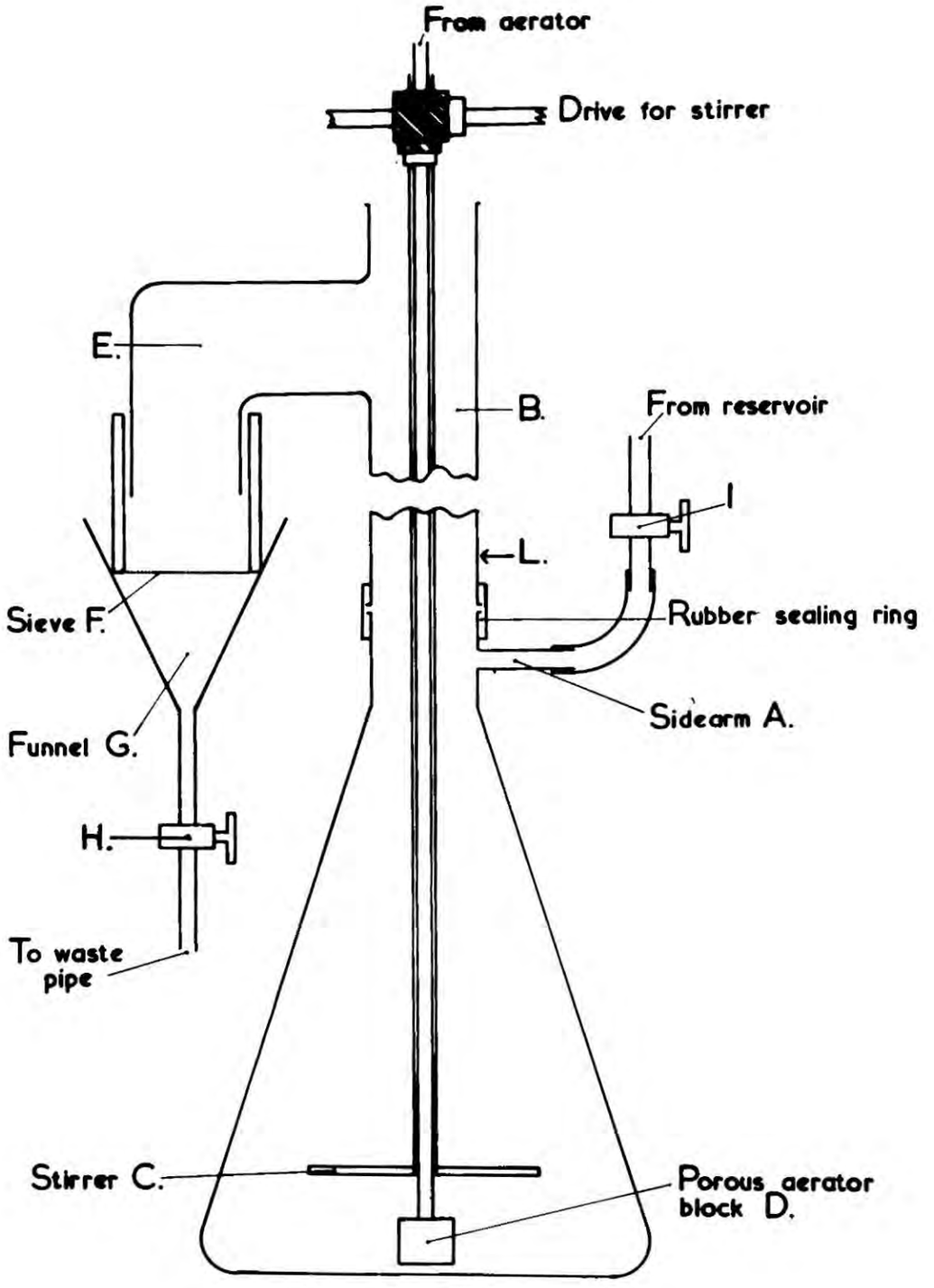
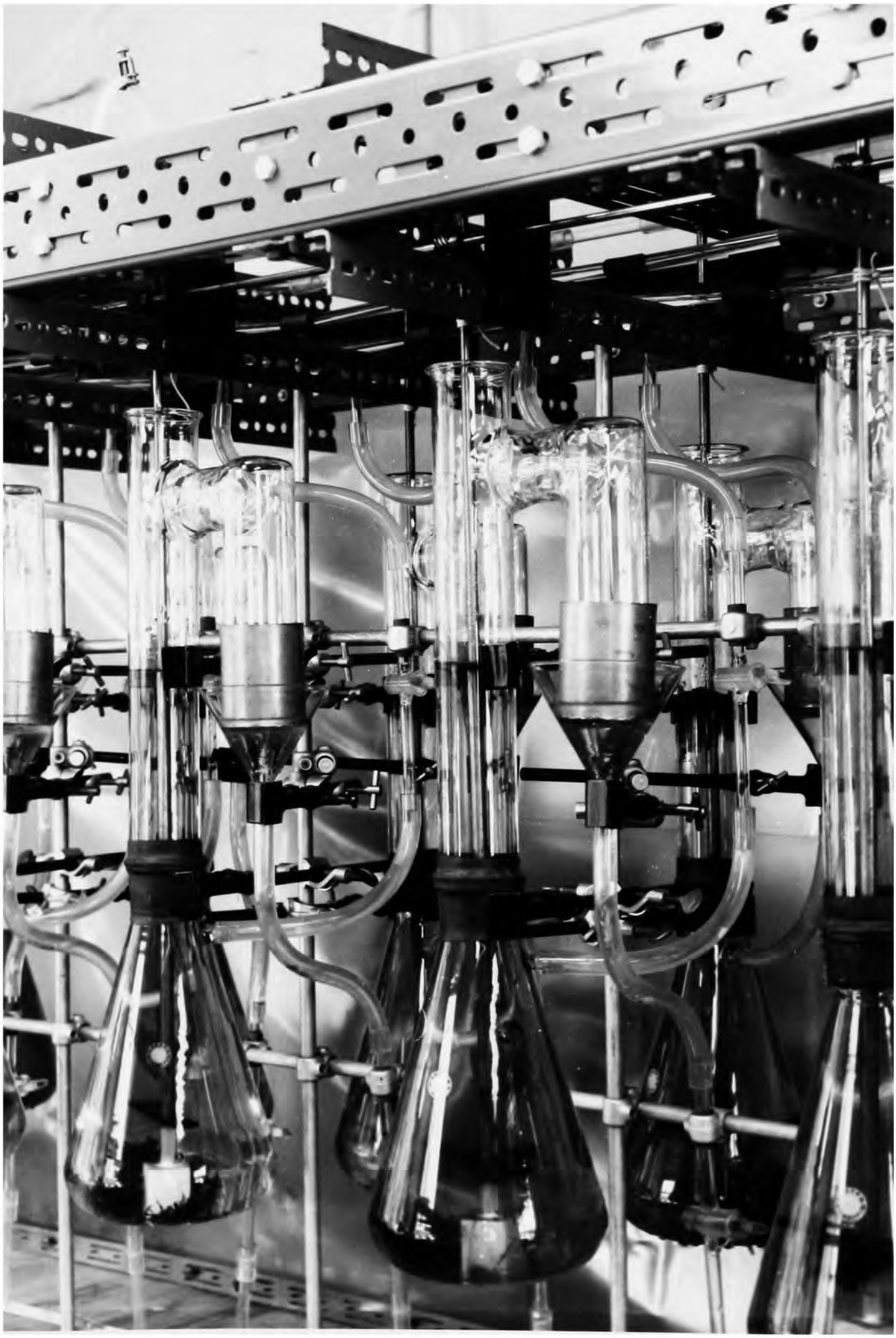


PLATE 12

Close-up of a single unit of the flotation extraction apparatus. The Mhor's clip to regulate the flow of air into the apparatus can be seen top left. The silver steel driving rod, carrying spiral gears, can be seen running in 'Tufnal' bearings along the top of the apparatus. The seals connecting the conical flasks to the vertical tubes are pieces of bicycle tyre inner tubing; the vertical tubes with side arms were specially produced by Pyrex Ltd.



into a 2 litre conical flask fitted with a sidearm.

2) The flask is corked, connected to a vacuum pump and the contents boiled under reduced pressure at room temperature for 30 secs.

3) The flask is then connected to the rest of the apparatus as shown in Fig. 23.

4) Water is run in through A by means of a tap I from a reservoir (top right of Plate 13) until it reaches the level L. Since many Collembola were extracted alive it was found necessary to maintain a low level in tube B during the extraction, in order to prevent escape from the top of the apparatus.

5) Air is now blown in through the aerator D, in a stream of very fine bubbles, and the stirrer C stirs for a period of 1 minute in every period of 5 minutes; this is achieved by means of a time switch (bottom right Plate 13).

6) At hourly intervals the level of the water in tube B is raised so that the floating material passes over into tube E, and from there into a fine mesh sieve F, of 360 mesh phosphor-bronze (aperture 0.042 mm.) The water passes through the funnel G and into a waste pipe running the length of the lower part of the apparatus.

7) Alcohol is poured into F from the side in order to kill the Collembola.

8) The level of water in B is then returned to the level L by means of increasing the rate of bubbling through D; this is carried out by releasing the Mhor's clips on the air control (top of apparatus in Plate 12), and when the clips are once again tightened the level returns to L.

After several trials it was found that no more Collembola passed into the sieve F after raising the level L on five occasions, so that a normal extraction should occupy 5 hours. The level of 70% alcohol in G was maintained by a tap H so that it covered the Collembola in sieve F.

The apparatus finally built contained 20 units and is illustrated in Plate 13. The stirrers were driven by means of spiral gears fitted at regular intervals along the length of two silver steel driving shafts; the shafts ran in 'Tufnal' bearings and were driven by an electric motor (bottom right Plate 13). Spiral gears were necessitated for driving the stirrers because of the concentric arrangement of the tube leading to the aerator and the stirring rod. A vacuum pump (bottom right Plate 13) supplied the air for aeration.

When the final apparatus was completed tests were carried out involving mixing a counted number of live Collembola with peat that had previously been thoroughly dried for several weeks in order to remove other Collembola.

The Collembola were thoroughly mixed with the moistened peat and extracted according to the procedure described. Table 58 shows the recovery of the Collembola from the manufactured samples.

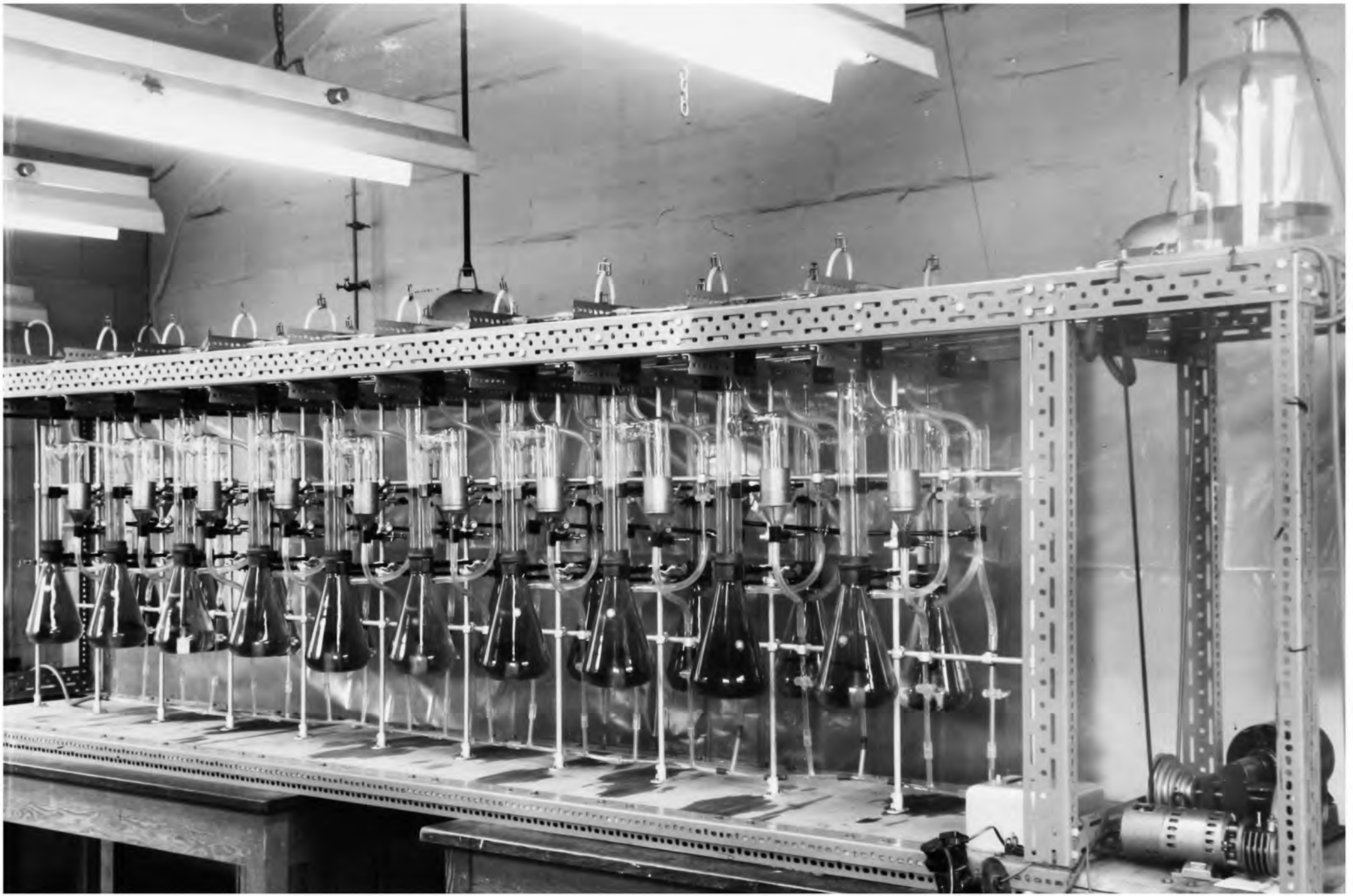
Table 58. Recovery of Collembola from manufactured peat samples.

Species	Onychiurus latus	Isotoma sp.	Tetracanthella wahlgreni	Lepidocyrtus lanuginosus	Dicyrtoma minuta	Dicyrtoma fusca	Total Collembola
Numbers placed in peat samples	6	6	100	46	8	20	186
Numbers recovered	6	6	96	46	8	20	182
Percentage recovered	100	100	96	100	100	100	98

There was thus a loss of the order of 2%. However, it is recognised that peat samples made up in this way are by no means identical with samples taken in the field and a greater error will no doubt occur due to the compacting of the peat and the difficulty in separating it when using soil samples from the field.

PLATE 13

The flotation apparatus carrying twenty single units. The glassware is supported by means of clamps on a chemi-frame and the mechanical part of the apparatus is supported by Dexion frame. Silver steel driving rods run the length of the top of the apparatus, and they carry spiral gears to drive the stirrers. The motor driving the stirrers can be seen bottom right, and in front of it is the pump which sends air through the apparatus; above these can be seen the reservoir supplying water (or magnesium sulphate) to the flasks. A time switch which controls the time during which stirring occurs can be seen to the left of the pump, bottom right.



c) A comparison of the two methods.

Three sets of 20 sample units each were collected, two from Heather litter and one from the Hagg Lip zone, and the Collembola were extracted using the flotation apparatus. These were collected at the same time as the monthly samples extracted by means of the high gradient cylinder. A direct comparison between the two extraction methods was thus possible. The data are compared in Tables 59, 60 and 61 and the significance of differences between the means resulting from these two methods is tested using the standard error of the difference; this is shown in the tables.

Whilst in all three cases the mean number of Collembola per sample unit was bigger in the case of the high gradient cylinder, there was no significant difference between the total means resulting from the two different extraction methods. With the exceptions of O. latus and I. viridis, a similar extraction efficiency can also be assumed for the individual species concerned in the extraction of Collembola from heather litter and hagg lip, by the two extraction methods. In the case of these two species, a significant difference between the numbers extracted from heather litter on both occasions was recorded (Tables 59 and 60), greater numbers being

extracted by the flotation method. I. viridis due to its large size and activity may escape during the preparation of the samples for extraction in the high gradient cylinder; O. latus is not sufficiently active to escape (it lacks a furcula) and its size may prevent its movement out of the sample unit; the large size of I. viridis may possibly inhibit movement out of the sample unit in the same way.

Ten sample units were hand sorted after extraction by each method, but no Collembola were found. Fifteen sample units from which the Collembola had been extracted by means of the high gradient cylinder were re-extracted using the flotation apparatus; again no further Collembola were recovered.

Whilst it is not claimed that hand sorting is an accurate measure of the presence in the sample of Collembola, from the total amount of data presented in this section it may be concluded that both the high gradient cylinder and the flotation apparatus have a high efficiency of extraction; it is, however, impossible to give a quantitative estimate of this efficiency.

Table 59. Comparison of the efficiency of the High Gradient Cylinder and the flotation extractors. Heather litter, 25.9.61. The figures are means per sample unit 11.35cm. in surface area and 3 cm. deep.

Species	Onychiurus latus	Friesea mirabilis	Isotoma sensibilis	Folsomia brevicauda	Isotoma viridis	Anurida pygmaea	Tetracanthella wahlgreni	Total Collembola
Means per sample unit from high gradient cylinder (A)	0.47	3.67	9.97	19.53	0.0	1.27	1.20	37.73
Means per sample unit from flotation extractor (B)	0.95	2.55	8.45	19.00	0.65	0.95	0.65	34.20
Difference (B-A) between means and S.E. of difference	+0.48 ± 0.12	-1.12 ± 0.88	-1.52 ± 2.21	-0.53 ± 4.97	+0.65 ± 0.26	-0.32 ± 0.51	-0.55 ± 0.61	-3.53 ± 6.14
Probability	<0.01	N.S.	N.S.	N.S.	<0.05	N.S.	N.S.	N.S.

Note: N.S. = Not significant.

Table 60. Comparison of the efficiency of the High Gradient Cylinder and the flotation extractors. Heather litter, 23.10.61. The figures are means per sample unit 11.35 cm^2 in surface area and 3 cm. deep.

Species	*Onychiurus latus*	*Friesea mirabilis*	*Isotoma sensibilis*	*Folsomia brevicauda*	*Isotoma viridis*	*Anurida pygmaea*	*Tetracanthella wahlgreni*	Total Collembola
Means per sample unit from high gradient cylinder (A)	0.40	2.53	9.80	18.33	0.00	1.07	2.13	34.90
Means per sample unit from flotation extractor (B)	0.90	2.60	9.10	16.90	0.50	1.25	1.75	33.65
Difference (B-A) between means and S.E. of difference	+0.50 ± 0.11	+0.07 ± 0.86	-0.70 ± 2.37	-1.43 ± 5.33	+0.50 ± 0.20	+0.18 ± 0.57	-0.38 ± 0.75	-1.25 ± 5.65
Probability	<0.001	N.S.	N.S.	N.S.	N.S.	<0.05	N.S.	N.S.

Note: N.S. = Not significant.

Table 61. Comparison of the efficiency of the High Gradient Cylinder and the flotation extractors. Cladonia covered hagg lip, 5.9.61. The figures are means per sample unit 11.35 cm^2 in surface area and 3 cm. deep.

Species	Tetracanthella wahlgreni	Isotoma sensibilis	Friesea mirabilis	Folsomia brevicauda	Total Collembola
Means per sample unit from high gradient cylinder (A)	48.20	38.40	0.47	12.67	100.8
Means per sample unit from flotation extractor (B)	48.40	32.20	1.15	7.90	90.55
Difference between means and S.E. of difference (B-A)	+ 0.20 ± 11.56	- 6.20 ± 7.76	+0.68 ± 0.42	-4.77 ± 4.34	- 10.25 ± 14.23

Note: None of the figures are significantly different.

4) Sampling.

a) The size of the sample unit.

Since it was required during the course of this work to estimate the variations in numbers of the commoner species, in addition to the total numbers of Collembola, a sample unit size which would yield numbers in the order of 20-200 was sought; a sample unit size of $\frac{1}{1000}$ m^2 was finally decided upon, and cores were taken to a depth of 6 cm.

In the construction of the sampling tool (Fig.24) it was found necessary to use 'Tufnal' cores which gave a surface area slightly larger than $\frac{1}{1000}$ m^2, as tubing of exactly the right diameter could not be purchased. The surface area of the sample units taken therefore was 11.35 sq. cm.

b) Taking the sample.

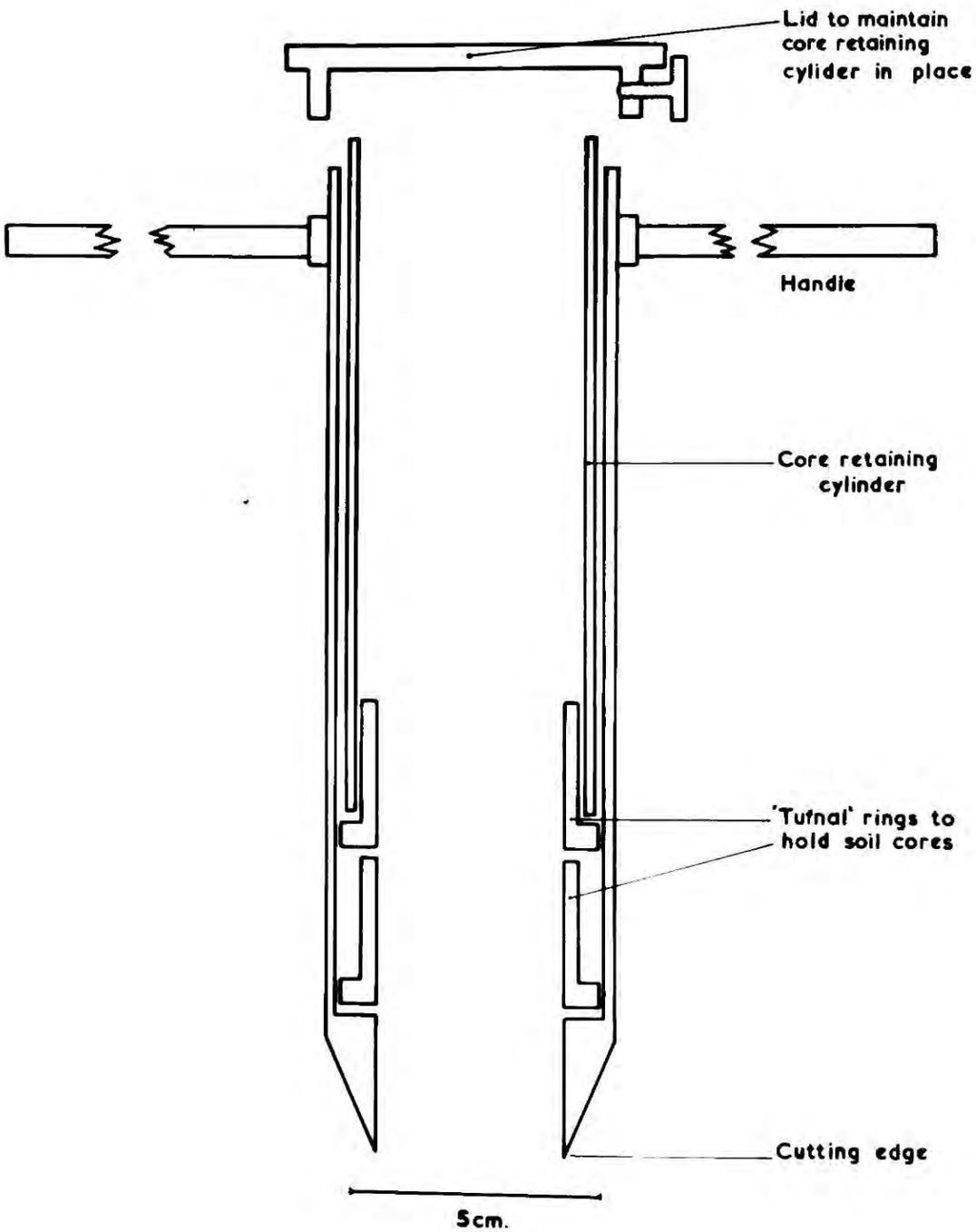
A soil sampler was designed to take 'Tufnal' cores of the type already described (page 188) and its construction was essentially similar to that described by Macfadyen (1961). A diagram of the sampler is shown in Fig. 24. Sample units of 3 cm. or 6 cm. in depth were normally taken and this involved the use of one (3 cm.) or two (6 cm.) 'Tufnal' rings. The rings were inserted

Fig. 24.

The soil sampler showing the fitting and means of retention of the tufnal rings, which surround the soil core.

Fig. 24.

The soil sampler.



into the sampler where they were held by means of a retaining cylinder clamped in place by a lid. The sampler was forced into the ground to the required depth by means of an alternate twisting action, 180° to the left then 180° to the right and so on.

Macfadyen (1957) points out that to estimate the size of a population by means of samples is to indulge in statistics, and one of the basic rules is that the samples themselves should be distributed without bias. In this work random samples were taken by throwing the containers of the 'Tufnal' rings and sampling 1 metre from the top of the container, along its axis.

c) The number of units.

It is considered of more value to take a large number of small sample units than a small number of large sample units, for the following reasons:

i. A larger number of units covers a greater range in the habitat, and is thus more representative.

ii. The statistical error is reduced since this varies as $\sqrt{\frac{1}{n}}$, where n is the number of sample units.

iii. The efficiency of extraction is greater in small sample units in the case of 'automatic' extraction techniques.

From a practical point of view it is usually necessary to compromise between the two due to the time

factor involved in dealing with a large number of sample units. Macfadyen (1957) recommends 30 sample units where the distribution of the organisms is patchy, and a unit size similar to that chosen here ($\frac{1}{1000}$ m^2). Initially during the course of this work 30 sample units were taken each month, on several soil types. The period between sampling dates was decided upon on the basis of what was known of the life cycles of Collembola, not more than two or three generations per year being expected at Moor House.

Sampling was started on a regular basis in February 1960, and it was soon found that there was not sufficient time available for the programme as planned. Accumulation of samples demanded some change in the programme, and the alternatives were:

i. To sample fewer soil types.

ii. To sample the same number of soil types less often.

iii. To take fewer sample units on each sampling date.

Testing the available data showed that reducing the number of sample units by half, to 15, did not alter either the mean or the standard error of the mean sufficient to affect appreciably the ultimate results. The data showing this are given in Tables 62 and 63. It was therefore decided to take only 15 sample units on subsequent occasions.

Table 62. The effect on reducing the number of sample units counted from 30 to 15 on the means and standard errors of total Collembola. The figures are means per sample unit 11.35 cm.^{2} in surface area and 6 cm. deep.

Soil type	Limestone grassland						Alluvial grassland	
Date	29.2	28.3	25.4	23.5	27.6	18.7	2.5	6.6
Mean of 15 units (A)	23.60	34.13	83.53	48.13	71.53	45.27	52.60	53.40
S.E. of 15 units	2.88	5.39	5.10	4.50	7.36	5.15	4.66	5.29
Mean of 30 units (B)	26.56	37.33	77.10	47.60	73.76	48.53	45.76	46.20
S.E. of 30 units	2.22	3.31	5.35	3.41	6.16	3.15	3.49	3.77
Difference (B-A) of means & S.E. of Difference	+2.96 ± 3.61	+3.20 ± 6.33	-6.43 ± 7.40	-0.53 ± 5.65	+2.23 ± 9.80	+3.26 ± 6.03	-6.84 ± 5.82	-7.2 ± 6.49

Note: None of the differences are significant.

Table 63. The effect of reducing the number of sample units counted from 30 to 15 on the means and confidence limits of different species of Collembola.

Sample from Limestone grassland 25.4.60. The figures are means per sample unit 11.35 cm.^{2} in surface area and 6 cm. deep.

Species	Onychiurus procampatus	Friesea mirabilis	Tullbergia krausbaueri	Folsomia manolachei	Folsomia cf. brevifurca	Isotoma viridis	Isotoma sensibilis	Isotoma notabilis	Isotomiella minor	Symphyleona
Mean of 15 units (A)	4.53	8.40	12.67	36.73	4.53	1.93	3.73	2.47	2.93	4.93
S.E. of 15 units	0.94	1.15	2.80	4.40	0.80	0.53	0.66	0.60	0.63	1.15
Mean of 30 units (B)	4.50	7.66	12.03	31.70	3.86	2.03	3.93	3.00	2.76	5.0
S.E. of 30 units	0.69	0.76	2.00	4.28	1.14	0.37	0.53	0.45	0.46	0.79
Difference (B-A) of means and S.E. of Difference	-0.03 ± 1.16	-0.74 ± 1.45	-0.64 ± 3.44	- 5.03 ± 6.14	-0.67 ± 1.39	+0.10 ± 0.64	+0.20 ± 0.84	+0.53 ± 0.75	-0.17 ± 0.78	+0.07 ± 1.39

Note: None of the differences are significant.

5) The treatment of the sample.

When the soil core was removed from the sampler it was placed together with the 'Tufnal' core(s) retaining it in an aluminium container. A second core was placed in the same container so that the vegetation surfaces were in contact. In this way the escape of Collembola into the can was prevented, although movement could take place between cores; it was assumed that if this took place at all it would not give rise to any appreciable error as the probability of movement in either direction would be equal, although the standard error could possibly be affected by such movement.

The sample was taken back to the laboratory in this way, and the first extraction normally began within six hours of collecting it. The sample units to be extracted later were stored at 4°C. until required.

When loading the soil cores into the extractor, 6 cm. cores were cut in half by means of a knife; the upper surface (ie. the upper surface in relation to the original orientation in the field, but lower surface during extraction) of the 3-6 cm. part of a core was scratched to counteract the effect of sealing the pores caused by cutting with a knife.

All soil cores were weighed before introducing them to the extractor, and again after drying them to constant weight (see page 21), in order to obtain data

on soil water content.

6) The sorting and counting process.

Each can removed from the high gradient cylinder extractor contained the Collembola from one core 3 cm. in depth. Alcohol was added to the water in the cans and the Collembola were thus preserved for counting. For counting purposes the contents of each can were poured into a petri dish of 10 cm. diameter, the bottom of which had been squared in centimetres, using a diamond pencil.

The Collembola were systematically removed from the dish by means of a minute spatula, first from the surface, then from the bottom and finally from around the edge of the dish. The whole area of the dish was thus covered twice, and individuals caught in the meniscus were recovered by the final search of the edge of the dish. The Collembola were transferred to a watch glass containing a few drops of water forming a convex meniscus. Touching them onto the water surface resulted in their removal from the spatula and they slipped down the convex surface of the meniscus to arrange themselves on the perimeter of the circle of water.

A single radial line was scratched on the bottom of the watch glass, and starting from this the Collembola were counted by rotating the watch glass under a binocular microscope. Each species was counted separately.

As a check on the method of counting three recounts were made on the sample units from a single extraction (collected 14.11.60), until the same numbers were obtained in different counts. Table 64 shows a comparison of the figures obtained from i) the normal count and ii) checks made by recording each individual as removed. It can be seen from this table that no significant errors arise from the counting process.

Table 64. Comparison of counting Collembola by rotating the watch glass with counted individuals removed one at a time. The figures are means per sample unit 11.35 cm.^{2} in surface area and 3 cm. dee

Species	Onychiurus procampatus	Friesea mirabilis	Tullbergia krausbaueri	Folsomia manolachei	Folsomia 4-oculata	Folsomia cf. brevifurca	Isotoma sensibilis	Isotoma viridis	Isotoma notabilis	Isotomiella minor	Symphypleona
Mean from first count	6.93	7.53	11.53	28.06	0.60	1.13	1.66	0.53	1.66	1.80	2.73
Mean from second check count	7.0	7.53	11.33	27.80	0.66	1.13	1.80	0.53	1.66	1.80	2.67
Difference between means and S.E. of Difference	0.07 ± 1.82	0.00	0.20 ± 5.04	0.26 ± 5.33	0.06 ± 0.32	0.00	0.14 ± 0.73	0.00	0.00	0.00	0.06 ± 1.26

II. HORIZONTAL DISTRIBUTION

II. HORIZONTAL DISTRIBUTION

1) Introduction.

Andrewartha and Birch (1954) have pointed out that most animal populations are distributed non-randomly, and tend to patchiness in their distribution rather than over-dispersion. Elton (1949) has stated that no habitat is homogeneous, and clearly heterogeneity of the habitat is likely to be reflected in the patchy distribution of animals. Thus, in a habitat as heterogeneous as the soil, patchiness is to be expected in the distribution of the animals living in it. Studies on the horizontal distribution of micro-arthropods have shown this to be the case. Glasgow (1939), Macfadyen (1952, 1957), Raw (1956), Hughes (1958), Kaczmarek (1960), Haarlov (1960) and Poole (1961) have all found that micro-arthropods tend to be aggregated in the soil.

Glasgow (1939) took samples in pairs so that the edge of one sample touched the edge of the other. Comparing the variance between pairs with the variance within pairs, the former was found to be much the greater, indicating an aggregated population; this was shown in four species, Onychiurus armatus, O. ambulans, Tullbergia quadrispina and T. krausbaueri. Macfadyen (1952) found indications of aggregation in Folsomia quadrioculata from comparison of paired samples, but concluded that

there was a very uniform distribution of micro-arthropods within each plant type examined. Kaczmarek (1960) defined the degree of aggregation by the percentage of samples in which the number of individuals was less than the mean, whilst Haarlov, (1960) and Poole (1961) detected aggregation by the use of the coefficient of dispersion (Salt and Hollick 1946).

The sizes of aggregations of Collembola have been estimated by Glasgow (1939); O. armatus aggregations were found to be between 3 in. (7.6 cm.) and 12 in. (30.5 cm.) in diameter, whilst in O. ambulans, T. quadrispina and T. krausbaueri the diameter was greater than 12 in.

Banage (1960) quotes three methods for the study of aggregation in soil animals:

i) Complete enumeration of all animals to a known depth followed by mapping their positions.

ii) Use of the 'tie line' technique of Hughes (1958), where paired samples are taken, one of which is taken at random and the other is 'tied' to it by a fixed distance; this is a development of the type of method used by Glasgow (1939).

iii) The analysis of results of random sampling.

Since this work was not designed to produce information on the spatial distribution of Collembola the only data available are from random sampling. No information on the size and possible distribution of aggregations can be derived from this, but an analysis of the available data is useful in that it could show the presence of aggregations.

2) The importance of the sample unit size.

Sample units may be either too large or too small to indicate the presence of aggregations within a population; that is to say a given sample unit may contain more than one aggregation or only a single individual (or none), and thus there exists for any population an optimum sample unit size for detecting aggregation. Greig-Smith (1952) has emphasised the importance of the quadrat size in studying the distribution of plants, and by random throws of coloured discs has shown that a single quadrat size is not sufficient to determine the randomness or otherwise of the distribution of a species. Cottam et al (1957) have also emphasised that any consideration of aggregation must be closely tied to the question of the area of the sample unit involved.

Whilst a given sample size may indicate that a population is distributed randomly, following a Poisson

expectation, this may not necessarily be the state of affairs within the population. However, if a given sample size detects aggregation, this is a real phenomenon, and aggregation exists within the population.

3) The detection of aggregation by random sampling.

a) The Coefficient of Dispersion.

Salt and Hollick (1946) introduced Fisher's Coefficient of Dispersion to their analysis of the distribution of wireworm populations. The coefficient may be expressed by the following formula:

$$C.D. = \frac{\sum(x - \bar{x})^2}{\bar{x}(n - 1)} \quad \text{or} \quad \frac{s^2}{\bar{x}}$$

where x is the number of individuals from each sample unit, $\bar{x}$ is the mean value of the sample units and n is the number of sample units. s^2 is the variance.
This is, in fact, the ratio of the variance to the mean; when this is equal to unity there is a random or Poisson distribution; when it is <1 there is an even distribution or over-dispersion; and when it is >1 there is aggregation or under-dispersion.

The significance of the divergence of the coefficient of dispersion from unity is regarded as

significant if it exceeds:

$$1 \pm 2\sqrt{\frac{2n}{(n-1)^2}}$$

where n is the number of sample units.
In this work, where samples of 15 units were used, the value of this is 1 ± 0.793, and where 30 units were used 1 ± 0.534.

The coefficients of dispersion were worked out for Collembola from three different soil types and in almost all cases it was found to be greater than unity for separate species (Tables 65-67). For the total Collembola the C.D. was greater than unity in all cases.

From these data it can be seen that the distribution does not follow a Poisson expectation, and that there is a marked aggregation or under-dispersion of both individual species and total Collembola. Haarlov (1960), using the same sample unit size as in this work, obtained much smaller values for the C.D. of individual species of Collembola; however, it is rightly pointed out that due to the scarcity of data (too few samples were taken) the conclusion that there is a random dispersion must be viewed with caution. Poole (1961) obtained values of C.D. (termed by this author 'relative variance'), similar to those in the present work.

Table 65. Coefficients of Dispersion for Collembola from Limestone Grassland 1960-61.

Species / Date	Onychiurus procampatus	Friesea mirabilis	Tullbergia krausbaueri	Folsomia manolachei	Isotoma sensibilis	Isotoma minor	Symphypleona	Total Collembola
29.2.60	1.64	2.34	4.92	3.63	6.86	3.01	-	5.39
28.3.60	3.86	3.82	5.42	6.19	1.75	2.44	2.48	8.85
25.4.60	3.15	2.24	9.90	17.32	2.12	2.29	3.71	11.15
23.5.60	1.63	1.83	20.07	6.74	3.20	1.71	0.96	7.33
27.6.60	1.98	3.20	19.19	8.32	1.99	6.53	1.69	15.44
18.7.60	2.04	1.62	3.11	7.50	1.68	5.14	1.71	6.14
22.8.60	8.06	5.22	6.24	1.22	3.60	5.53	2.42	11.43
26.9.60	4.72	5.68	7.04	8.84	2.13	1.25	2.64	9.98
24.10.60	2.57	2.26	13.96	11.86	1.61	2.19	1.94	6.95
14.11.60	3.48	4.11	29.66	5.82	1.94	3.91	4.95	16.15
28.11.60	6.60	1.92	15.09	15.99	1.27	2.93	1.39	20.73
16.1.61	3.21	2.59	6.68	17.86	2.13	2.76	9.30	21.04
13.2.61	2.29	1.32	12.43	15.92	9.60	7.48	13.98	21.32
13.3.61	4.89	2.76	10.71	3.34	6.84	1.15	5.04	11.78

continued overleaf.

Table 65. (continued).

Species / Date	Onychiurus procampatus	Friesea mirabilis	Tullbergia krausbaueri	Folsomia manolachei	Isotoma sensibilis	Isotoma minor	Symphyleona	Total Collembola
10.4.61	4.35	4.09	10.15	11.59	2.09	1.18	1.77	7.30
8.5.61	2.22	0.97	10.13	12.82	0.97	0.90	2.88	9.23
5.6.61	3.17	2.34	3.97	11.61	2.54	3.76	2.26	8.46
4.7.61	1.20	0.84	13.90	8.73	2.89	2.33	2.07	11.62
28.7.61	5.17	2.31	2.21	10.61	3.05	1.04	2.81	8.72
28.8.61	5.65	4.40	4.78	30.65	3.57	1.22	1.63	13.56
25.9.61	0.81	2.52	4.27	2.64	1.88	1.65	2.18	4.27
23.10.61	4.49	1.49	10.50	5.75	2.52	4.25	1.79	11.35
22.11.61	3.49	2.42	9.13	10.02	2.20	2.00	1.41	9.17
11.12.61	2.42	4.13	8.21	9.70	1.94	2.86	1.66	11.57
Average	3.46	2.77	10.07	10.20	2.93	2.90	3.16	11.20

Note. 15 unit samples were collected on all dates except those above the dotted line, where 30 unit samples were taken. Coefficients of dispersion which do not show significant aggregations are underlined.

Table 66. Coefficients of Dispersion for Collembola from Alluvial Grassland 1960-61.

Species / Date	Onychiurus procampatus	Friesea mirabilis	Tullbergia krausbaueri	Isotoma sensibilis	Isotomiella minor	Folsomia manolachei	Symphypleona	Total Collembola
2.5.60	4.12	1.44	10.08	4.05	3.52	7.89	3.07	7.97
6.6.60	5.43	2.15	14.24	4.59	3.15	5.18	4.21	9.21
4.7.60	6.53	2.69	3.36	3.14	4.94	10.62	1.47	5.48
25.7.60	2.14	1.01	7.34	3.98	1.93	16.82	1.62	12.10
29.8.60	2.35	2.40	12.89	2.50	4.82	6.52	1.33	16.17
26.9.60	4.26	2.96	14.37	2.24	7.63	8.93	0.97	16.37
24.10.60	8.90	1.86	8.20	1.02	1.07	7.05	-	11.20
14.11.60	12.48	4.92	10.36	2.79	5.65	2.73	-	12.19
16.1.61	9.29	2.70	10.00	1.91	6.49	2.85	3.95	13.09
13.2.61	7.48	4.62	19.52	1.93	3.24	4.27	2.39	17.62
13.3.61	3.62	4.17	10.33	2.27	0.91	7.22	2.14	9.44
10.4.61	3.07	2.51	5.54	0.85	1.09	12.38	1.16	10.08
8.5.61	2.16	1.36	3.46	3.38	1.43	8.57	-	28.17
Average	5.53	2.68	9.98	2.67	3.53	7.77	2.23	13.01

Note. 15 unit samples were collected on all dates except those above the dotted line, when 30 unit samples were taken. Coefficients of dispersion which do not show significant aggregations are underlined.

Table 67. Coefficients of Dispersion for Collembola from Heather litter site, 1961.

Species / Date	Friesea mirabilis	Isotoma sensibilis	Folsomia brevicauda	Total
23.1	5.87	3.30	14.82	12.11
20.2	1.65	8.59	10.38	15.70
18.3	3.95	4.51	30.44	27.60
18.4	0.85	2.81	24.44	19.11
14.5	4.23	8.07	37.51	25.02
5.6	1.81	8.06	6.42	9.31
5.7	1.28	9.12	8.97	1.21
28.7	2.81	6.98	12.12	12.10
28.8	5.32	2.57	22.35	21.20
25.9	2.40	3.90	12.89	10.27
23.10	1.91	5.57	15.26	9.45
22.11	1.79	5.47	24.96	23.68
11.12	3.44	4.19	46.15	42.24
Average	2.87	5.63	20.52	17.62

Note. 15 unit samples were collected on all dates. Coefficients of dispersion which do not show significant aggregations are underlined.

Table 68. Coefficients of Dispersion for Collembola from other sampling sites.

A. Hagg lip. (15 unit samples).

Species Date	Tetracanthella wahlgreni	Isotoma sensibilis	Friesea mirabilis	Folsomia brevicauda	Total Collembola
16.5.60	3.29	5.70	1.98	3.94	4.67
27.2.61	20.31	6.97	12.20	1.30	29.54
29.5.61	30.29	15.05	2.58	21.45	36.56
5.9.61	23.63	14.95	1.52	19.41	18.18
4.12.61	21.96	31.64	-	46.30	59.72
Average	19.90	14.86	4.57	18.48	29.73

B. Hummock top. (15 unit samples).

Species Date	Isotoma sensibilis	Friesea mirabilis	Folsomia brevicauda	Anurida pygmaea	Total Collembola
16.5.60	5.16	1.72	11.19	1.54	14.25
27.2.61	9.42	1.27	55.78	4.39	59.03
29.5.61	3.42	1.12	1.95	23.27	11.04
5.9.61	19.91	0.98	5.92	5.14	13.80
4.12.61	3.41	2.00	14.69	-	11.59
Average	8.27	1.42	17.91	8.64	21.94

Note. Coefficients of dispersion which do not show significant aggregations are underlined.

cont'd. over/

Table 68 (continued).

C. Juncus squarrosus. (15 unit samples).

Species Date	Friesea mirabilis	Isotoma sensibilis	Total Collembola
7.3.60	7.40	3.22	7.15
9.5.60	2.76	3.19	2.91
20.2.61	5.08	1.90	16.56
14.5.61	4.72	1.24	15.69
28.8.61	3.37	1.15	1.59
11.12.61	4.29	2.35	4.04
Average	4.77	2.53	7.99

Note. Coefficients of dispersion which do not show significant aggregations are underlined.

b) The frequency distribution.

The study of the frequency distribution of the sample unit values has been approached from two slightly differing points of view, due to the types of data available:

i. For the sample unit values of total Collembola on a given soil type comparison is made with the normal distribution curve; this is possible as no values of 0 occur in the sample unit values. Here the sample unit values are grouped into frequency distributions round their individual means, with multiples of the standard deviations as the class boundaries. The mean value is taken as zero, sample units smaller than the mean being indicated by negative S.D. classes and sample units larger than the mean by positive S.D. classes. The data for the three main sampling sites is shown in Tables 69, 70 and 71. In all three cases there is a significant difference from the expected normal distribution.

It can be seen that the distributions are skewed in all three cases, there being an excess of small negative deviates and large positive deviates. This is a typical frequency distribution where aggregation occurs within a population (see Poole 1961), where most sample units are from areas of relatively low density but some sample units are from high densities. O'Connor (1957), Peachey (1959) and Banage (1960) have found similar skewed distributions

Table 69. Frequency distribution of sample unit values about the mean (0). Limestone Grassland 1960-61.

S.D. Classes / Date	-3	-2	-1	0	+1	+2	+3	+4	+5
29.2.60	0	2	16	7	5	0	0	0	
28.3.60	0	3	13	10	3	1	0	0	
25.4.60	0	3	14	9	3	0	1	0	
23.5.60	0	4	13	8	3	2	0	0	
27.6.60	0	3	15	8	3	0	1	0	
18.7.60	0	5	10	10	5	0	0	0	
22.8.60	0	3	2	6	4	0	0	0	
26.9.60	0	2	7	4	2	0	0	0	
24.10.60	0	3	6	2	4	0	0	0	
14.11.60	0	2	7	4	1	1	0	0	
28.11.60	0	1	8	4	1	1	0	0	
16.1.61	0	3	5	6	0	1	0	0	
13.2.61	0	2	7	2	4	0	0	0	
13.3.61	0	3	5	5	1	1	0	0	
16.4.61	0	3	1	6	2	0	0	0	
8.5.61	0	2	6	5	1	1	0	0	
5.6.61	0	4	2	7	2	0	0	0	
5.7.61	0	2	7	4	1	1	0	0	
28.7.61	0	2	6	4	3	0	0	0	
28.8.61	0	2	8	3	1	1	0	0	
25.9.61	0	2	5	6	2	0	0	0	
23.10.61	0	1	11	1	0	2	0	0	
22.11.61	0	4	2	8	1	0	0	0	
11.12.61	0	3	3	7	2	0	0	0	
Total (Observed)	0	64	179	136	54	12	2	0	
Theoretical total	10	61	152	152	61	10			
	10.0	0.1	4.8	1.7	0.8	1.6			

Total $\chi^2 = 19.0$ d.f. = 5 $P < 0.05$

Table 70. Frequency distribution of sample unit values about the mean (0). Alluvial Grassland 1960-61.

S.D. classes	-3	-2	-1	0	+1	+2	+3	+4	+5
2.5.60	0	5	11	10	2	2	0	0	
6.6.60	0	2	18	4	3	3	0	0	
4.7.60	0	3	4	5	3	0	0	0	
25.7.60	0	2	9	2	1	1	0	0	
29.8.60	0	0	10	3	1	1	0	0	
26.9.60	0	1	8	2	3	1	0	0	
24.10.60	0	4	3	6	2	0	0	0	
14.11.60	0	3	4	6	2	0	0	0	
16.1.61	0	2	7	3	2	1	0	0	
13.2.61	0	2	7	4	1	1	0	0	
13.3.61	0	1	11	1	1	1	0	0	
10.4.61	0	1	7	5	1	1	0	0	
8.5.61	0	0	11	3	0	0	1	0	
Total (observed)	0	26	110	54	22	12	1	0	
Theoretical total	5	31	77	77	31	5			
	5.0	0.8	14.1	6.9	2.6	12.8			

Total χ^2 = 42.2 d.f. = 5 $P < 0.001$

Table 71. Frequency distribution of the sample unit values about the mean (0). Heather litter 1961.

S.D. classes	-3	-2	-1	0	+1	+2	+3	+4	+5
23.1.61	0	2	6	2	2	0	0	0	
20.2.61	0	0	10	3	1	1	0	0	
18.3.61	0	0	9	4	1	0	1	0	
18.4.61	0	0	10	3	1	1	0	0	
14.5.61	0	0	10	4	0	0	1	0	
5.6.61	0	1	9	3	1	1	0	0	
5.7.61	0	1	7	3	4	0	0	0	
28.7.61	0	2	6	2	5	0	0	0	
28.8.61	0	0	10	1	3	1	0	0	
25.9.61	0	2	7	4	1	1	0	0	
23.10.61	0	2	5	5	2	1	0	0	
22.11.61	0	0	11	4	0	0	1	0	
11.12.61	0	0	10	3	1	1	0	0	
Total (Observed)	0	10	110	41	22	7	3		
Theoretical total		31	66	66	31				
		14.2	29.3	9.5	2.6				

Total $\chi^2 = 55.6$ d.f. = 3 $P < 0.001$

in enchytreids and nematodes. The data presented here show the total Collembola to be aggregated in all the soil types considered.

ii. For sample unit values of individual species, where a number of sample units contained no individuals, comparison of the distribution was made with a Poisson frequency. In all cases examined the distribution of individual species was found not to follow a Poisson distribution. An excess of both low and high values was found, as compared with the Poisson expectation. This indicates aggregation of individuals, as in the case of the distribution of total Collembola.

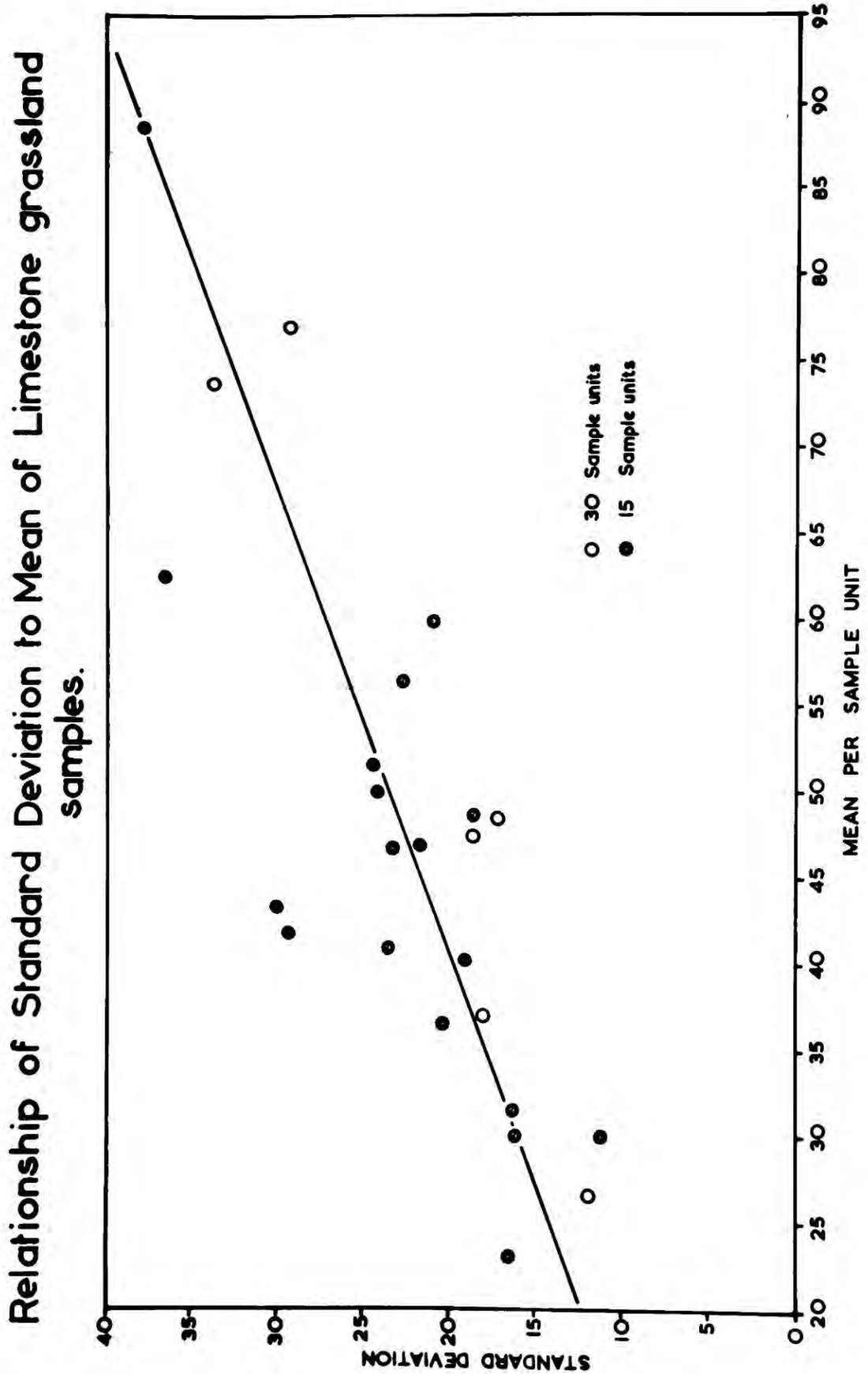
4) The statistical treatment of the data.

Since the raw data provided here show the sample unit values do not follow a normal distribution, a transformation of the data is indicated before using normal distribution statistics. Quenouville (1950) has shown that when the variance (or standard deviation) increases with the mean, a logarithmic transformation is the most suitable; Fig. 25 shows this to be the case for the data concerning total Collembola on Limestone grassland. However, since the use of normal distribution statistics on the raw data would tend to mask small differences rather than demonstrating differences which did not occur, no transformation has been made in this work; it was considered that errors

Fig. 25

Graph showing the relationship between the mean and the standard deviation in samples from Limestone grassland collected during 1960 and 1961. The line was fitted by eye.

Fig. 25.


Relationship of Standard Deviation to Mean of Limestone grassland samples.
STANDARD DEVIATION
MEAN PER SAMPLE UNIT
30 Sample units
15 Sample units
0
5
10
15
20
25
30
35
40
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95

arising, particularly from the extraction technique, would be sufficiently large not to justify the transformation.

5) The biological significance of aggregation.

Cole (1946) had advanced the hypothesis that whilst individual organisms occur clumped ie. in aggregations, ".... each group may be relatively or entirely independent of all similar groups and, therefore, (the groups are) randomly distributed". Considering a population consisting of several species, in which the individual species are known to be aggregated, random distribution of the total population would be expected if the above statement were true. That is to say that aggregations of any one species would be distributed at random with respect to an aggregation of any other species. The coefficient of dispersion and the distribution of sample unit values with respect to a normal distribution, show marked aggregation for total Collembola, which suggests aggregation of more than one species at a given centre. Poole (1961) points out that if this were not so the different species aggregations would tend to balance each other out and thus would result in a total distribution that was almost random. Thus it can be concluded that different species of Collembola tend to aggregate about the same centre of aggregation.

Two possibilities are evident to explain the formation of aggregations in soil micro-arthropods:

i. Aggregations result from the slow dispersion of individuals from an egg batch.

ii. Aggregations result from the coming together of individuals at, a) a food source, or b) as a result of being actively gregarious.

Evidence of aggregation resulting from egg batches is provided by rare species which are found aggregated. For example in sample units from heather litter, only 2 of 196 contained the species Willowsia buski; of these, one sample unit contained 12 individuals, the other a single one. All individuals were near-adults of the same size, and it seems probable that the aggregation was the result of an egg batch rather than the coming together of individuals, as the species is rare on this soil type.

Other aggregations are clearly the result of more than one egg batch; that is to say, the animals have come together, as the numbers far exceed those of the largest egg batch recorded. For example 210 individuals of Tetracanthella wahlgreni, 39 Isotoma sensibilis amd 218 Folsomia brevicauda (total 467), were counted in a single sample unit from the hagg lip zone on 4 December, 1961.

Poole (1961) has attempted to show that aggregations of Collembola are not related to egg clusters, by comparing the egg-batch size of three species with their coefficients of dispersion. The coefficient of dispersion varies

inversely with the egg batch size in all three cases. However, comparison with the data obtained during the present work (Table 72) shows no clear correlation, so that it is concluded that there is no evidence to suggest that aggregations do not arise as a result of egg batches.

Table 72. Comparison of egg batch size and coefficient of dispersion.

Species	Egg batch size	Coefficient of Dispersion	Authority
Tullbergia krausbaueri	1-2	20.70 - 41.50	Poole (1961)
	5.5 ± 0.3	2.21 - 29.66	Hale
Onychiurus procampatus	4.7 ± 0.2	0.81 - 12.48	Hale
Isotoma sensibilis	20.0 ± 8.0	0.97 - 31.64	Hale
Isotoma notabilis	6 - 10	21.50 - 38.20	Poole (1961)
Isotomurus plumosus	30 - 50	8.00 - 8.60	Poole (1961)

Aggregation in some cases appears to result from active gregariousness, where swarming occurs on snow or on water surfaces, as described by Davies (1932) and Paclt(1956).

Evidence for the overlapping of aggregations of different species (or aggregations consisting of different species) is provided by plotting the numbers of two different species in individual sample units against each

other. In Fig. 26 this is done for the two species occurring commonly on the hagg lip zone, where species other than T. wahlgreni and F. brevicauda are uncommon. There is a marked tendency for high numbers of each species to occur together, thus indicating interspecific aggregation.

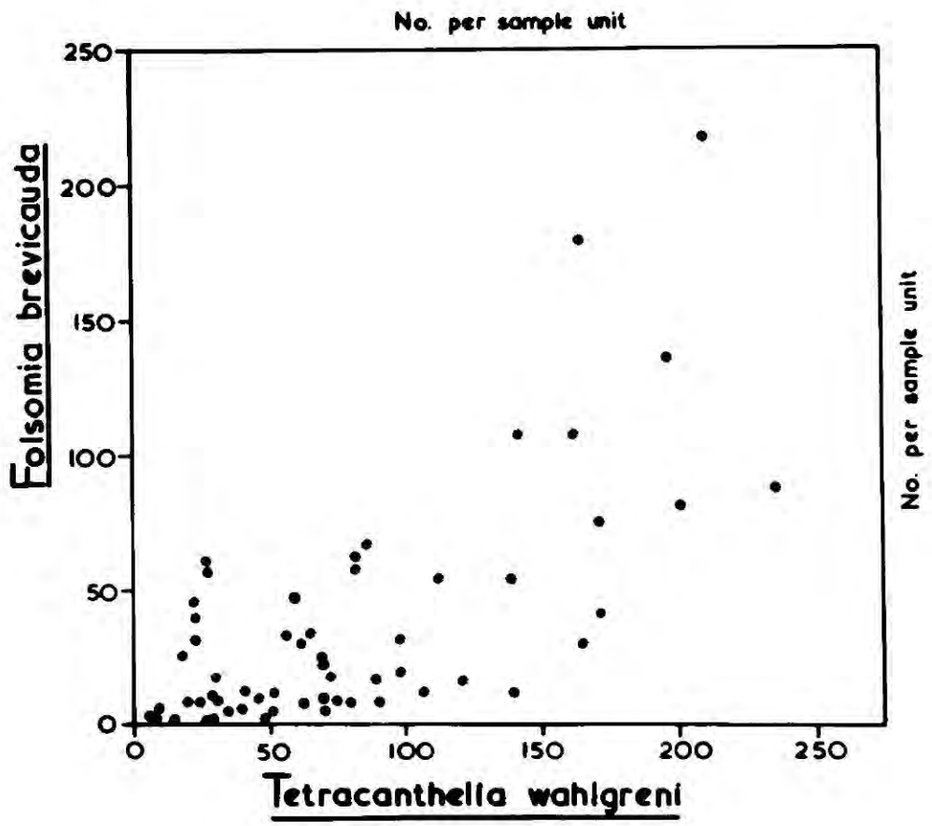
Whilst the available data casts little light on the actual formation of aggregations, it at least demonstrates their existence, and thus supports the findings of earlier workers. The fact that aggregations either overlap, or contain more than one species, suggests the coming together of individuals at a food source or similar micro-habitat in which optimum conditions prevail. However, no support can be given to the contention of Haarlov (1960) that the better the locomotary organs are developed, the less aggregated is the distribution of the species in question. The average coefficients of dispersion for Folsomia manolachei (10.20) and Isotoma sensibilis (2.93) (Table 65) which are very active species are relatively high, and the data do not suggest a lesser degree of aggregation than is found in any of the species with poorly developed locomotary organs, eg. Onychiurus procampatus (3.46), Tullbergia krausbaueri (10.07).

Fig. 26

The relationship between the numbers of Tetracanthella wahlgreni and Folsomia brevicauda occurring in the same sample units from the Hagg lip zone. There is a marked tendency for high numbers of each species to occur together, which suggests aggregation of the two species about the same centre.

Fig. 26.

Relationship between the numbers of two species occurring in the same sample units.



III. VERTICAL DISTRIBUTION

III. VERTICAL DISTRIBUTION

1) Introduction.

Macfadyen (1957) has commented upon the fact that life tends to be concentrated where two phases meet, because of the photosynthetic demands of the plants which form the primary food source. From the point of view of the soil micro-arthropods this has been demonstrated adequately by the investigations of Glasgow (1939), Agrell (1941), Gisin (1943), Nielsen (1949), Schaller (1949), van der Drift (1951), Murphy (1953), Bellinger (1954), Kuhnelt (1955) and Poole (1961), who have shown that the highest densities occur in the upper layers of the soil. Other authors have correlated the depth distribution and size of micro-arthropods with the structure of the soil in which they have been collected. Schimitschek (1938), Stockli (1946), Weis-Fogh (1948), Kuhnelt (1950), Macfadyen (1952), Elton and Miller (1954), Haarlov (1955, 1961), Murphy (1955) and Klima (1956) have considered micro-arthropods in relation to soil structure, and have shown that the highest densities occur where the pore spaces are largest. According to Haarlov (1955), the cavity size decreases with depth in mineral soils, and thus the results obtained again show high densities in the upper layers of the soil.

During the course of this work it was found that on peat soils Collembola usually did not occur at a depth greater than 3 cm., ie. they did not occur below the decomposition layer, in the peat proper. This was due mainly to waterlogging, and apparently below this depth pore spaces containing air are rare or absent; this can be demonstrated by squeezing peat from the 3-6 cm. layer under water, when few or no air bubbles appear. Samples were taken on one occasion only (April 1960) from the 3-6 cm. layer on the Heather litter site, the Juncus squarrosus site and from the bare peat site; Collembola were entirely absent. On the two mineral soils sampled, cores were regularly taken to a depth of 6 cm., and divided into two layers each 3 cm. deep. In both these soils, separation at this level divided the core into an upper layer containing the vegetation and the decomposition layer, and a lower layer consisting entirely of mineral matter permeated by plant roots.

All the data contained in this section are from 6 cm. cores, divided into two 3 cm. layers, which were collected from two types of mineral soil on Limestone grassland and Alluvial grassland.

2) Distribution in 0-3 cm. and 3-6 cm. layers.

In the samples collected from the two different soil types it was possible to determine the extent to which different species penetrated into the soil by counting the numbers in each of the two layers. The data resulting from such counts are shown in Table 73, and the figures listed are for total numbers over a period of one year. Only the more abundant species are shown.

As other workers have shown, the highest total density of Collembola occurs in the upper 3 cm. layer. Some species, Anurida pygmaea, Tullbergia krausbaueri, Tullbergia denisi, Folsomia brevifurca and Isotomiella minor have a higher density in the 3-6 cm. layer, and these are the true soil forms. Friesea mirabilis and Onychiurus procampatus penetrate into the lower layer, but the majority of the Isotomidae and the Symphypleona are surface forms which only occasionally penetrate into the 3-6 cm. layer, probably by entering earthworm burrows, or accidentally during sampling.

Sampling on the Limestone grassland site was carried out monthly over a period of two years, January 1960 to December 1961. In Table 74 comparison is made between the depth distribution of the species penetrating into the 3-6 cm. layer, in different years. Only those

Table 73. Depth distribution of Collembola on mineral soils.

Species	Limestone grassland 1960		Limestone grassland 1961		Alluvial grassland 1960-61	
	Nos. in 0-3 cm. / 3-6 cm.	% in lower 3 cm.	Nos. in 0-3 cm. / 3-6 cm.	% in lower 3 cm.	Nos. in 0-3 cm. / 3-6 cm.	% in lower 3 cm.
Friesea mirabilis	1361 / 391	22.3	896 / 308	25.6	753 / 142	15.9
Anurida pygmaea	32 / 50	61.0	77 / 93	54.7	41 / 50	55.0
Onychiurus procampatus	880 / 346	27.8	820 / 262	24.2	450 / 80	15.9
Tullbergia krausbaueri	1059 / 1382	54.2	484 / 812	62.7	2482 / 1861	42.9
Tullbergia denisi	-	-	-	-	5 / 33	86.8
Folsomia manolachei	4117 / 299	6.8	2121 / 232	9.9	1378 / 53	3.7
Folsomia 4-oculata	261 / 36	12.1	150 / 12	7.4	11 / 0	0.0
Folsomia cf. brevifurca	115 / 103	47.3	20 / 55	73.3	21 / 14	40.0
Isotoma sensibilis	538 / 13	2.7	411 / 23	5.3	572 / 9	1.6
Isotoma viridis	236 / 14	5.6	92 / 4	4.2	238 / 10	4.0
Isotoma notabilis	324 / 8	2.4	108 / 8	6.9	238 / 1	0.4
Isotomiella minor	395 / 595	60.1	100 / 276	73.4	232 / 235	50.3
Symphypleona	422 / 7	1.6	719 / 14	1.9	196 / 4	2.0
Total Collembola	9890 / 3604	26.7	6048 / 2051	25.3	7301 / 2572	25.7

Table 74. Comparison of depth distribution in different years; Limestone grassland, 1961 and 1962.

Species	1960		1961		χ^2 for 1 degree of freedom	P
	Nos. in 0-3 cm. layer	Nos. in 3-6 cm. layer	Nos. in 0-3 cm. layer	Nos. in 3-6 cm. layer		
Friesea mirabilis	1361	391	896	308	4.21	<0.05
Anurida pygmaea	32	50	77	93	0.89	>0.30
Onychiurus procampatus	880	346	820	262	5.27	<0.025
Tullbergia krausbaueri	1059	1382	484	812	12.73	<0.001
Folsomia cf. brevifurca	115	103	20	55	15.28	<0.001
Isotomiella minor	395	595	100	276	20.87	<0.001
Total Collembola	9890	3604	6048	2051	5.02	<0.05

Note. Comparison is made between the samples taken in two different years using 2 x 2 contingency table. Only those species occurring regularly in the 3-6 cm. layer, ie. where more than 10% of the numbers occur below 3 cm., are considered.

species whose density in the 3-6 cm. layer, exceeds 10% of the total are considered. With the exception of Anurida pygmaea, there is a significant difference in the depth distribution in the two years considered for all species, and for the total numbers of Collembola. During 1961 Friesea mirabilis, Tullbergia krausbaueri, Folsomia brevifurca and Isotomiella minor occurred more commonly in the deeper level, whilst Anurida pygmaea and Onychiurus procampatus occurred more frequently in the 0-3 cm. layer than in 1960. Total Collembola occurred more commonly in the 0-3 cm. layer in 1960, but this is only just significant, and the difference is between 26.7% and 25.3%.

The Alluvial grassland site was sampled monthly from May 1960 until May 1961, and in Table 75 comparison is made with samples collected on the Limestone grassland over the same period. With the exception of Anurida pygmaea there is a significant difference (which is shown in Table 75) between the two areas for all species concerned, and for total Collembola. This probably reflects to some extent the larger size of the pore spaces in the soil on the Limestone grassland, where, over the period concerned 28.3% of the population occurred in the 3-6 cm. layer as compared with 25.7% on the Alluvial grassland.

Table 75. Comparison of depth distribution on Limestone grassland and Alluvial grassland, May 1960 to May 1961.

Species	Limestone grassland		Alluvial grassland		χ^2	P
	Nos. in 0-3 cm. layer	Nos. in 3-6 cm. layer	Nos. in 0-3 cm. layer	Nos. in 3-6 cm. layer	for 1 degree of freedom	
Friesea mirabilis	1241	409	753	142	27.23	<0.001
Anurida pygmaea	39	73	41	50	2.20	>0.100
Onychiurus procampatus	924	387	450	80	41.48	<0.001
Tullbergia krausbaueri	1072	1455	2482	1861	139.54	<0.001
Folsomia cf. brevifurca	34	89	21	14	12.57	<0.001
Isotomiella minor	344	640	232	235	144.43	<0.001
Total Collembola	10364	4087	7301	2572	14.68	<0.001

Note. Comparison is made between samples taken on two different soil types during the same months, using a 2 x 2 contingency table. Only those species occurring regularly in the 3-6 cm. layer, ie. where more than 10% of the numbers occur below 3 cm., are considered.

3) 'Lebensformen' and vertical distribution.

Gisin (1943) constructed a classification of life-forms, in which the habitat in which the species lives is reflected to some extent in the modifications of body form which the species possesses. An assessment of this classification will be made in the light of the information listed in Table 73.

Gisin's system of life-forms of Collembola is as follows:

A. Atmobios; living in the larger plants.
8 + 8 eyes, furcula very long.

B. Hemiedaphon; pigment well developed; furcula of medium length.

a) Hydrophil; living on water surfaces.
Mucro with broad lamellae.

b) Mesophil; living in the upper layers of the soil.
Tennant hair pointed or clubbed.

c) Xerophil; living on bark, lichens and dry mossy areas.
Several clubbed tennant hairs.

C. Euedaphon; true soil dwellers.
Eyes reduced or absent. Pigment absent except possibly on eye-patches.

(Translation from Gisin 1943).

The species listed in Table 76 are regrouped according to Gisin's classification of life-forms, in Table 76. The percentage occurring in the 3-6 cm. layer on the Limestone grassland (1960 and 1961) and the Alluvial grassland are included, and it can be seen that there is a close correlation between the life forms and the vertical distribution. Those forms which possess well developed eyes and pigment occur in the upper layer (0-3 cm.) and those species without pigment and eyes occur mainly in the lower layer (3-6 cm.)

4) Seasonal variation in vertical distribution.

It has been shown that in both mites and Collembola changes in the vertical distribution of different species occur throughout the year (Volz 1934, Agrell 1934, Jacot 1936, 1940, Glasgow 1939, Baweja 1939, Strickland 1947, Belfield 1956, Schweizer 1956 and Stockli 1957). In most cases this is interpreted as a vertical migration during periods of adverse climatic conditions in the upper layers of the soil. Frenzel (1936) and Dhillon and Gibson (1962) found no evidence of seasonal changes in vertical distribution.

During the course of the present work the fact that monthly samples were taken at two levels made possible an analysis of the data from the point of view of seasonal vertical distribution. Only those species occurring

Table 76. Correlation between Gisin's 'Lebensformen' and vertical distribution.

Lebensformen (Life form)	Species	% in lower layer (3-6 cm.) of cores		
		Limestone grassland 1960	Limestone grassland 1961	Alluvial grassland
ATMOBIOS	Isotoma viridis	5.6	4.1	4.0
	Symphypleona	1.6	1.9	2.0
HEMIEDAPHON a) Mesophil	Friesea mirabilis	22.3	25.6	15.9
	Anurida pygmaea	61.0	54.7	55.0
	Folsomia manolachei	6.8	9.9	3.7
	Folsomia 4-oculata	12.1	7.4	0.0
	Isotoma notabilis	2.4	6.9	0.4
b)Xerophil	Isotoma sensibilis	2.7	5.3	1.6
EUEDAPHON	Onychiurus procampatus	27.8	24.2	15.9
	Tullbergia krausbaueri	54.2	62.3	42.9
	Tullbergia denisi	-	-	86.8
	Folsomia cf. brevifurca	44.3	73.3	40.0
	Isotomiella minor	60.1	73.4	50.3

commonly in both layers (0-3 cm. and 3-6 cm.) are considered, namely: Friesea mirabilis, Onychiurus procampatus, O. tricampatus, Tullbergia krausbaueri and Isotomiella minor. In Figs 27 and 28 the numbers occurring in the 3-6 cm. layer are plotted as a percentage of the total on each sampling date; the standard error of the mean is also indicated. On both the Limestone grassland (1960, 1961) and the Alluvial grassland, early summer and winter peaks occur, together with autumn and spring minima; thus there is a higher proportion of Collembola in the lower layer during early summer and winter, ie. during periods of adverse weather conditions. In most cases the standard errors indicate a significant difference between the maxima and minima, and it can be concluded that seasonal changes in vertical distribution occur in both soil types studied. Early summer and winter maxima for Collembola in the lower layers of the soil have been recorded by Ford (1937), Glasgow (1939), Poole (1961) and Dhillon and Gibson (1962); winter maxima only have been recorded by Strenzke (1951) and Macfadyen (1952) for both mites and Collembola.

Whilst the evidence strongly suggests a vertical migration in order to avoid adverse climatic conditions in the upper layers of the soil, in summer and winter, it is possible that these data show a differential mortality,

Fig. 27

Vertical distribution of Collembola on the Limestone grassland during 1960 and 1961. Note the early summer and winter peaks in the lower layer, which suggests a vertical migration due to adverse conditions in the upper layer.

Fig. 27.

Limestone grassland 1960-61.
Vertical distribution.

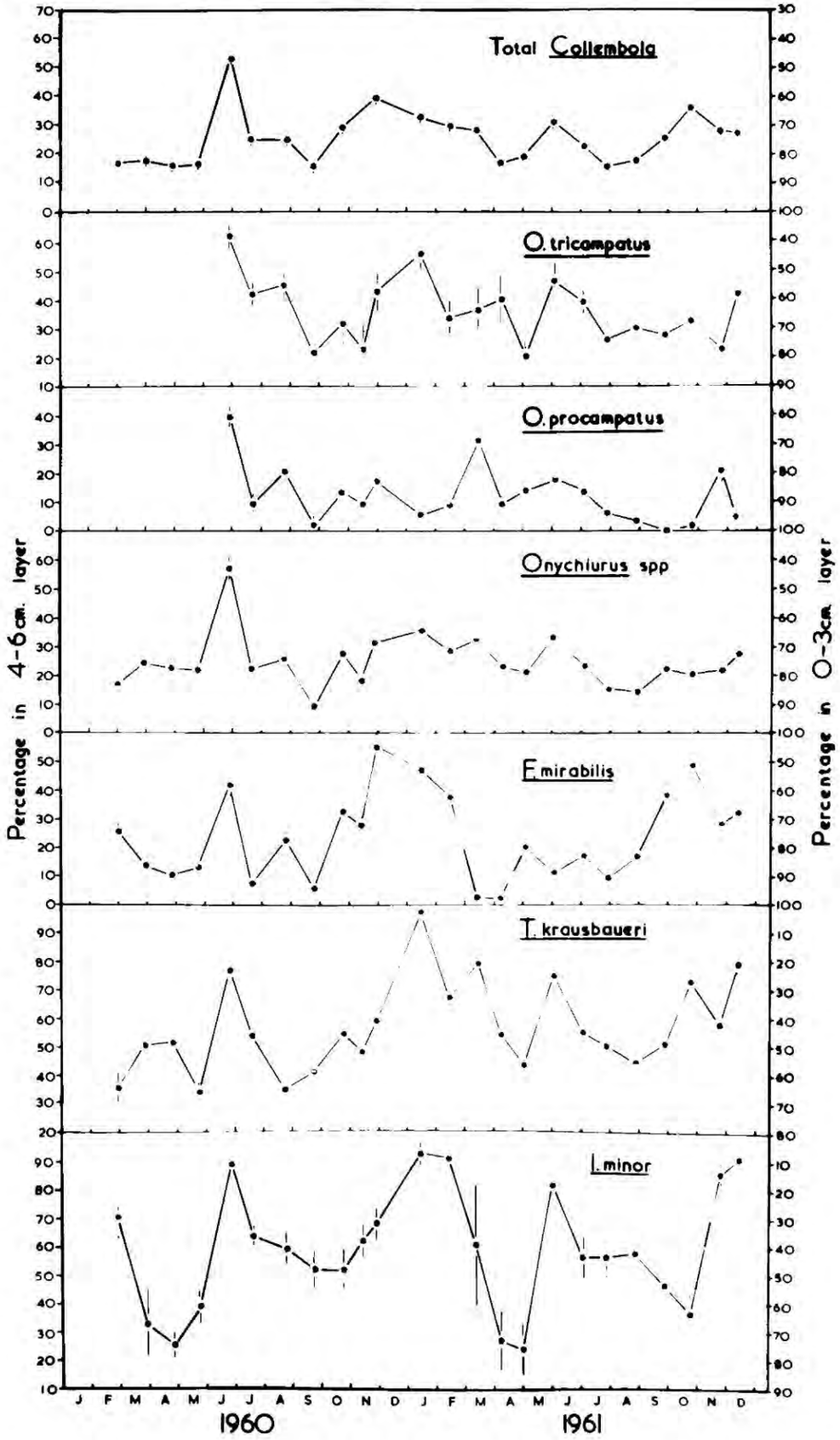
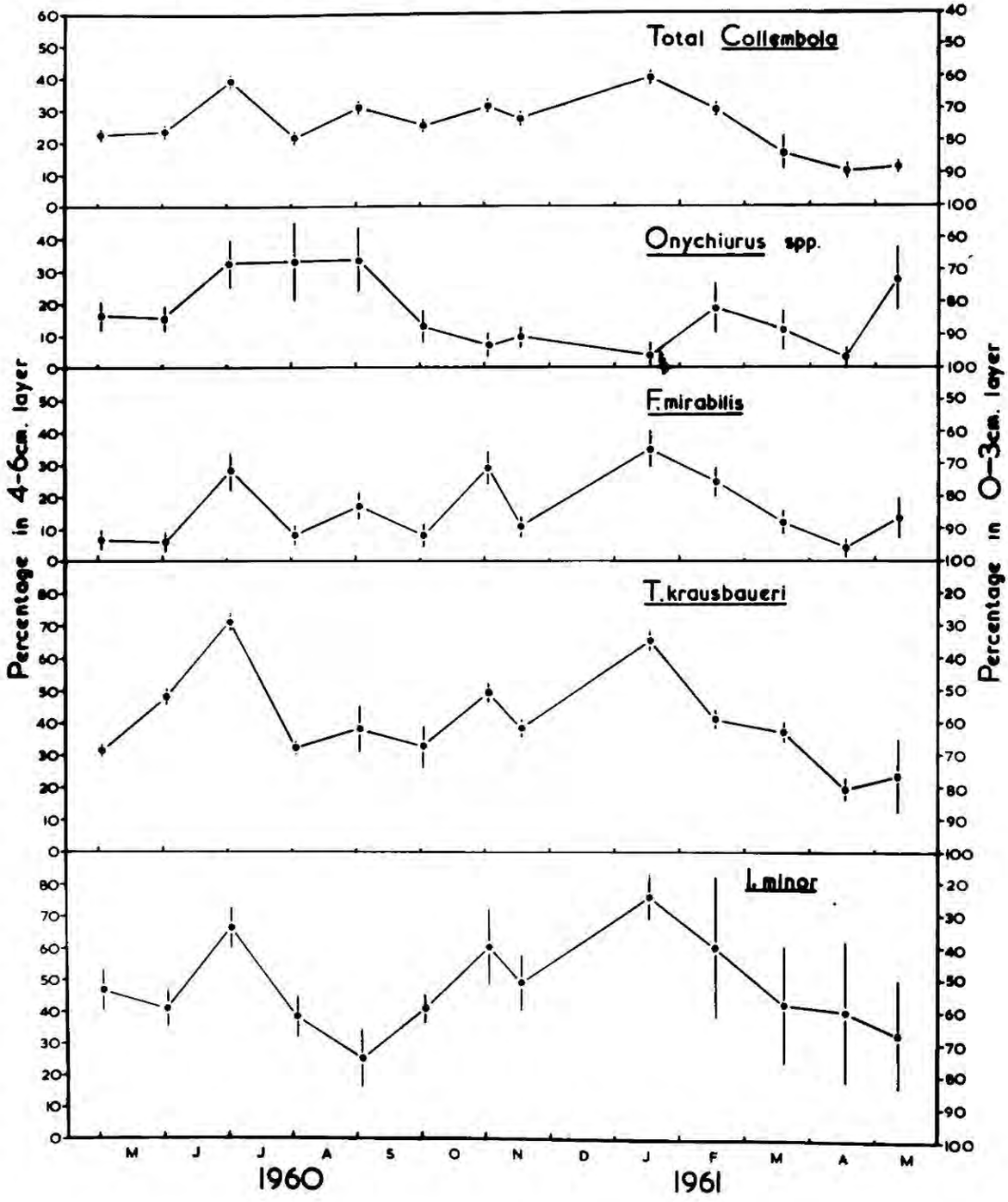


Fig. 28

Vertical distribution of Collembola on the Alluvial grassland during 1960-61. The time scale is different from that of Fig. 27. Note the early summer and winter peaks in the lower layer, which suggests a vertical migration due to adverse conditions in the upper layer.

Fig. 28.

Alluvial grassland 1960-61.
Vertical distribution.



or both this and vertical migration. The data available do not permit analysis to show which possibility is, in fact, the case.

5) A comparison of the vertical distribution of Onychiurus procampatus and O. tricampatus.

On both Limestone grassland and Alluvial grassland O. procampatus and O. tricampatus occur together in the same sample units. The possibility that these two members of the Genus Onychiurus are conspecific has been considered elsewhere (page 174), on both taxonomic and biological criteria, and the data presented here on the vertical distribution of the two species adds ecological evidence to that already provided.

Comparison of the total numbers of these two species in separate layers, indicates a significant difference in their depth distribution (Table 77).

Table 77. Depth distribution of O. procampatus and O. tricampatus; totals for February 1960 to December 1961.

Depth (cm.)	O. procampatus	O. tricampatus	Total
0-3	738	618	1356
3-6	113	352	465
Total	851	970	1821

$\chi^2 = 126.2$ d.f. = 1 $P < 0.001$

It is possible that this difference is merely a reflection of the differing sizes of the two species, where the larger O. procampatus is less able to penetrate into the soil. It can be seen from Fig. 17a and b that the head capsule sizes of the last four instars of O. tricampatus are exactly equivalent in size to the head capsules of the first four instars of O. procampatus; the dimensions of the body of these instars also coincide, so that instars 1, 2, 3 and 4 of O. procampatus are equal in size to instars 3, 4, 5 and 6 of O. tricampatus. Thus, comparison of the depth distribution of the four instars of equal dimensions should indicate whether or not the vertical distribution is a function of the different sizes of the two species. The data in Table 78 shows that there is a significant difference between the vertical distribution of individuals of equivalent size, and thus a factor other than size must affect the vertical distribution of the two species in question.

Table 78. Depth distribution of individuals of similar size in O. procampatus and O. tricampatus; totals for February 1960 to December 1961.

Depth (cm.)	O. procampatus	O. tricampatus	Total
0-3	493	478	971
3-6	68	264	332
Total	561	742	1303

$\chi^2 = 94.5$ d.f. = 1 $P < 0.001$

Comparison of the vertical distribution of the individual instars is made in Table 79. The significance of the difference has been tested by applying a 2 x 2 contingency to the data, and this is indicated in the Table. It can be seen that there is a significant difference between the vertical distribution of the two species during the first five instars, and thus an ecological difference occurs in addition to the taxonomic (morphological) and biological differences between O. procampatus and O. tricampatus.

Table 79. Comparison of the numbers of different instars of O. procampatus and O. tricampatus in the 0-3 cm. and 3-6 cm. layers. Limestone grassland 1960-61.

Species	Layer	Instar 1	2	3	4	5	6
Onychiurus procampatus	0-3 cm.	46	181	110	151	140	90
	3-6 cm.	11	30	10	17	25	20
Onychiurus tricampatus	0-3 cm.	23	117	110	173	139	56
	3-6 cm.	20	68	66	91	83	24
χ^2		8.5	26.9	39.3	32.5	23.3	3.6
P for 1 degree of freedom		<0.005	<0.001	<0.001	<0.001	<0.001	<0.05

IV. SEASONAL VARIATIONS IN NUMBERS

IV. SEASONAL VARIATIONS IN NUMBERS

1) Introduction.

Prior to the work of Glasgow (1939), population studies of Collembola had been directed mainly at describing the fluctuations in large groups of species. Glasgow showed that different species reached maximum and minimum numbers at different times of the year, and thus the discrepancies (Table 80) resulting when the work of different authors was compared could be explained. Table 80 summarises the work of previous authors, concerning the times of the year when peak populations of Collembola and mites occurred. Most workers found an autumn peak, with low numbers in summer, although under arctic conditions, Agrell (1941) and Hammer (1944) obtained summer peaks, as did Stockli (1957) in Switzerland, and Poole (1961) in Wales. Bellinger (1954) found maxima at different times of the year for different species and in this way these results compare with those of Glasgow.

Since all work on the seasonal fluctuations of Collembola has been limited to two years or less, it has been found difficult to demonstrate a regular annual cycle.

2) Sampling and the treatment of the data.

In the early stages of this work, thirty sample units were taken at random on each monthly sampling date.

Table 80. Summary of previous work on seasonal abundance of Collembola.

Author	Group	Peak populations			
		a. Spring	b. Summer	c. Autumn	d. Winter
Thompson (1924)	Total Arthropods	-	-	-	X
Edwards (1929)	Total Arthropods	-	-	Oct.	-
Ford (1937)	Collembola	-	-	-	Dec. -Feb.
Ionescu (1932)	Protura	-	-	Oct.	Jan.
Frenzel (1936)	Mites & Collembola	X	-	Oct.	Jan.
Baweja (1939)	Collembola	-	-	Nov.	-
Glasgow (1939)	Collembola	April	-	Oct.	Dec.
Agrell (1941)	Collembola	-	X (Arctic)	-	-
Hammer (1944)	Mites & Collembola	-	X (Arctic)	-	-
Weis-Fogh (1948)	Mites & Collembola	-	-	X	-
Strenzke (1949)	Collembola	-	July	-	Dec.
Schaller (1949)	Collembola	-	-	Oct. & Nov.	Jan.
Macfadyen (1952)	Mites & Collembola	-	-	-	Jan. & Feb.
Sheals (1957)	Mites & Collembola	-	-	Oct.	Dec.
Stockli (1957)	Mites & Collembola	-	X	-	-
Poole (1961)	Collembola	-	Aug.	-	Feb.
Dhillon & Gibson(1962)	Mites & Collembola	May	-	Sept.	-

X = season, but no month given. Spring = March to May, Summer = June to Aug. Autumn = Sept. to Nov. Winter = Dec. to February.

As described earlier (page 210) this was later reduced to fifteen units. Poole (1961) carried out a logarithmic transformation of the data in order to minimise the effects of large aggregations, and smoothed the curves for each species, and 'total Collembola' by taking 'running averages' of three samples. In the present work the data are plotted on an arithmetic scale (Figs 29 to 31) and bimonthly averages are superimposed upon these (Figs 29a to 31a), in order to smooth the curves. The monthly data are given together with the standard error of the mean for each sample.

For the purpose of studying seasonal variations in numbers, samples were taken as follows:

i. Limestone grassland; monthly samples for 24 months (Feb. 1960 to Dec. 1961). On the first six occasions 30 unit samples were taken, and subsequently 15 unit samples. The analysis is of 450 sample units.

ii. Alluvial grassland; monthly samples for 13 months (May 1960 to May 1961). On the first two occasions 30 unit samples were taken, and subsequently 15 unit samples. The analysis is of 225 sample units.

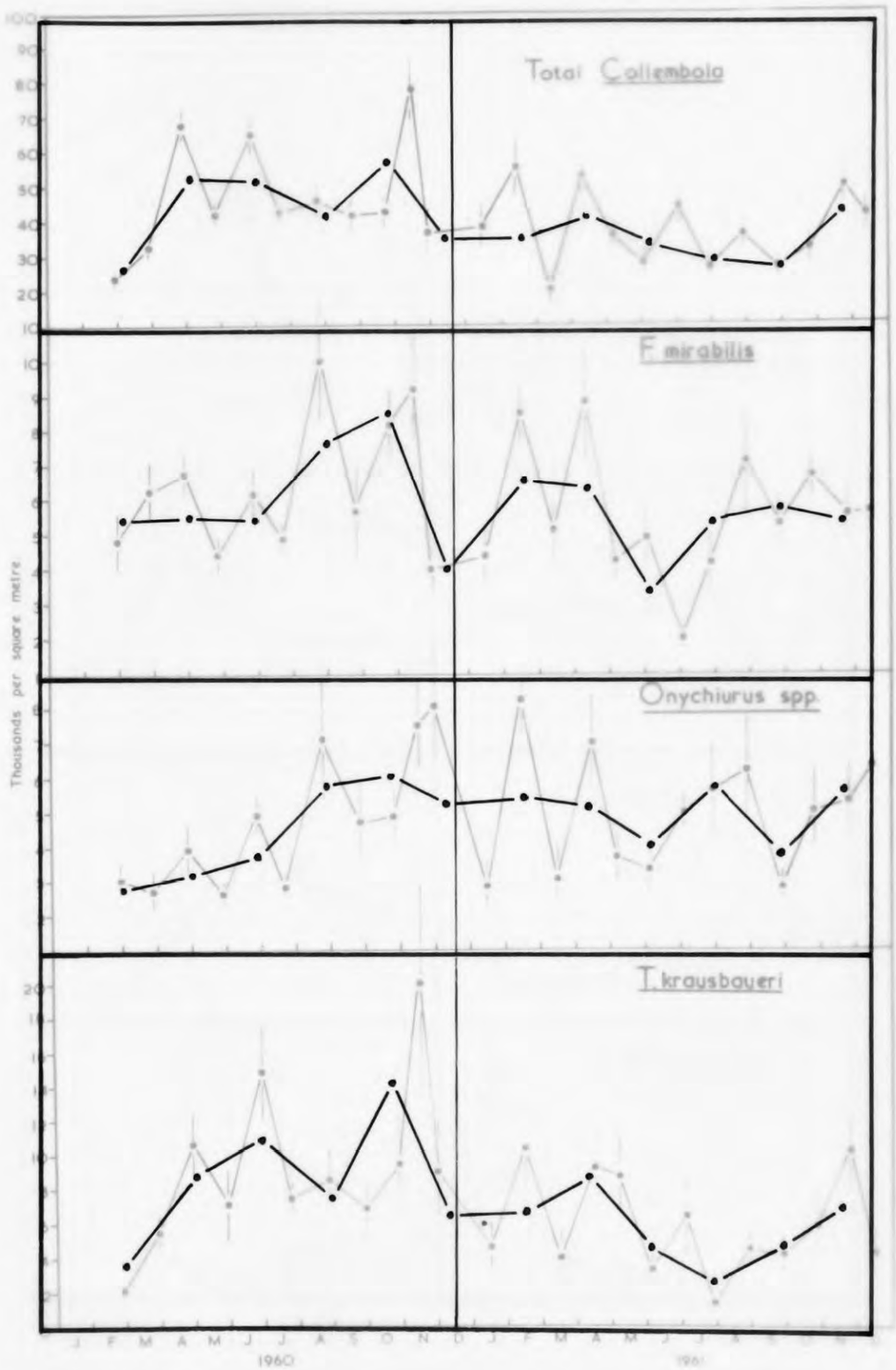
iii. Heather litter; monthly samples for 13 months (Jan. 1961 to Dec. 1961). All samples were of 15 units. The analysis is of 193 sample units.

Fig. 29.

Limestone grassland 1960-61. Seasonal variations in numbers. The graphs give data for two complete years (horizontal axis). It should be noted that scales of the numbers per square metre (vertical axis) are not the same for all species, and that in some cases the scales do not begin at 0.

Fig. 29a.

Limestone grassland 1960-61. Seasonal variations in numbers.



Bimonthly averages.

Fig. 29.

Limestone grassland 1960-61. Seasonal variations in numbers.

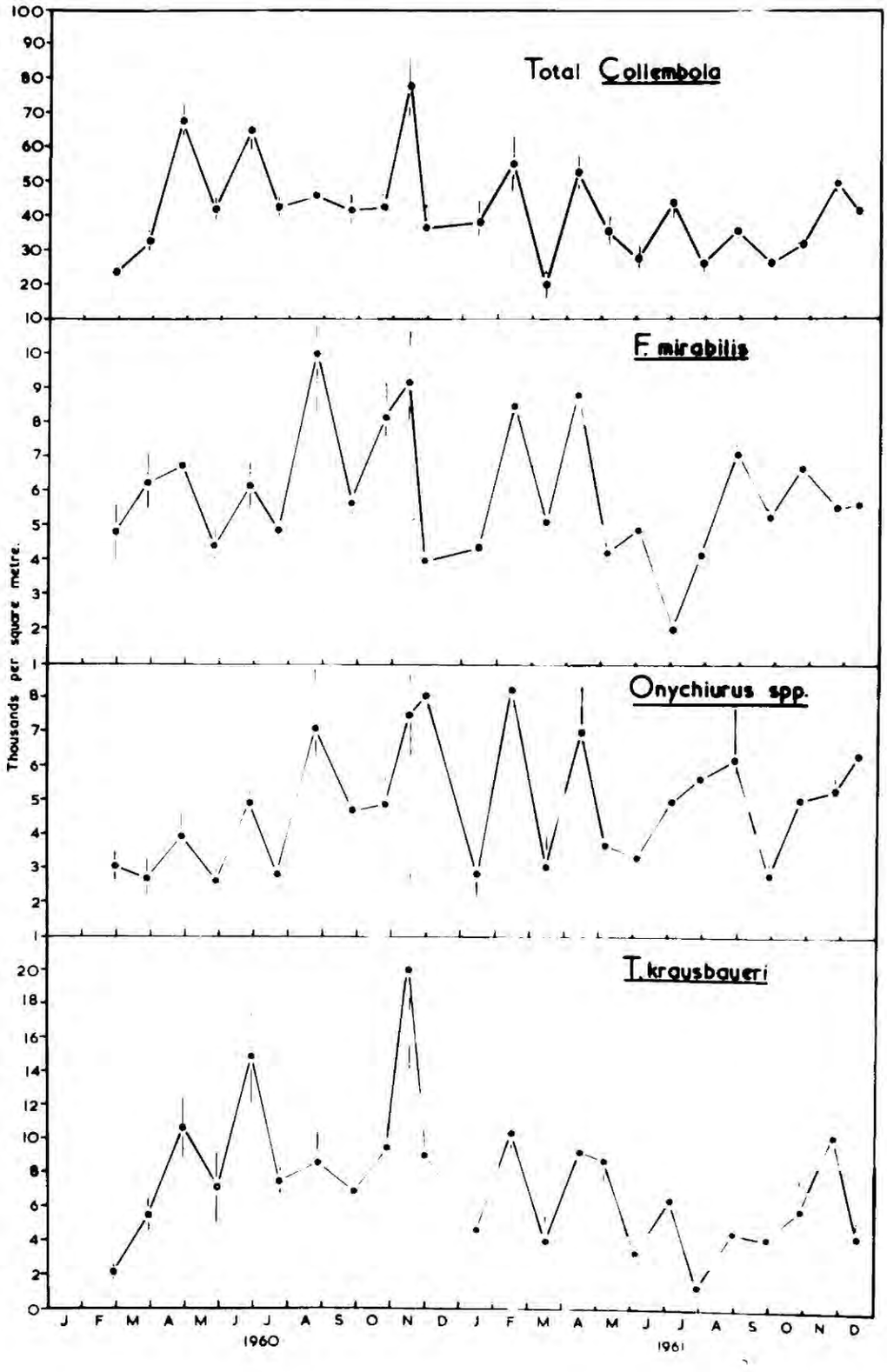
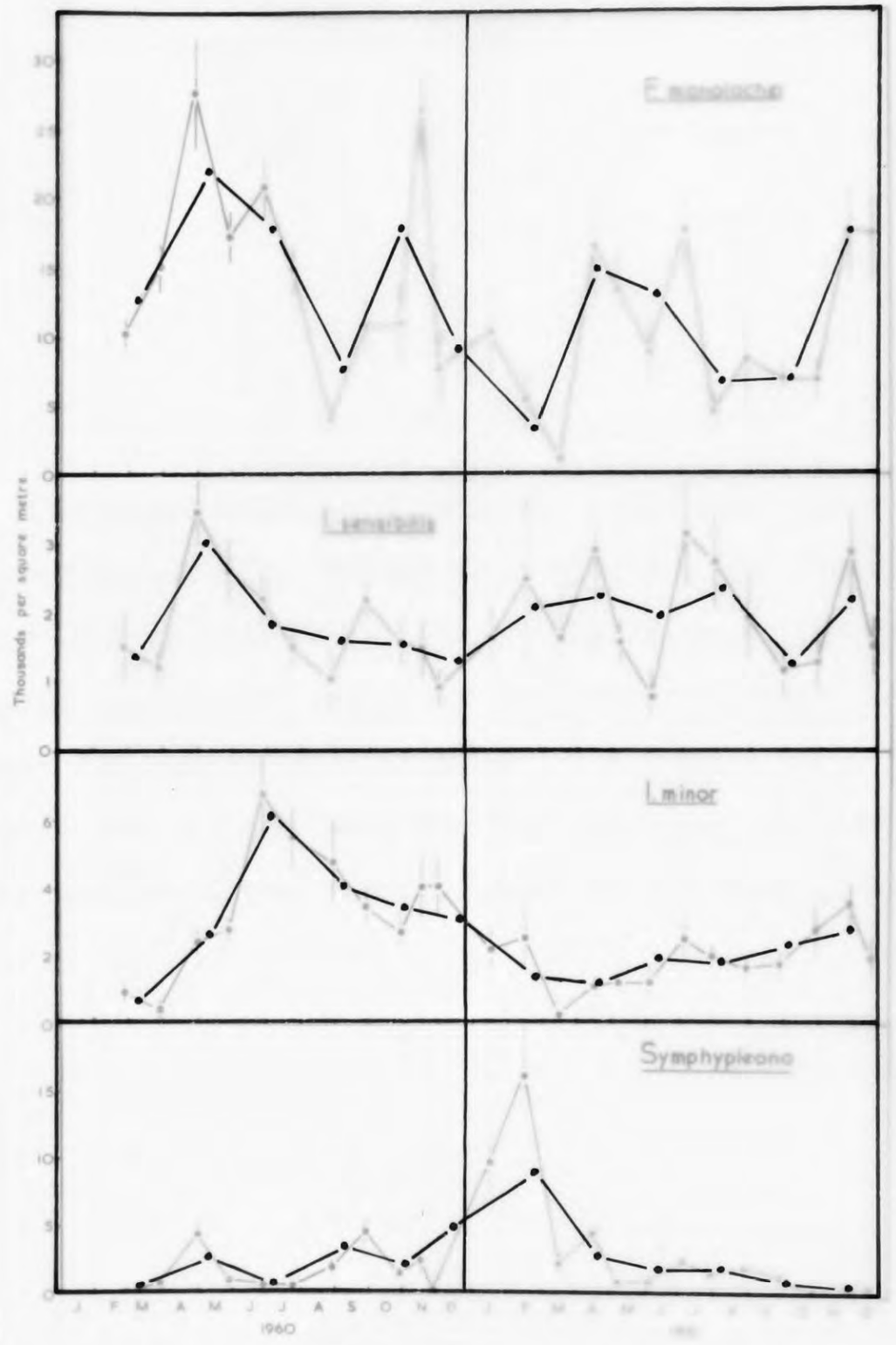


Fig. 29a.

Limestone grassland 1960-61.
Seasonal variations in numbers.



Bimonthly averages.

Fig. 29.

Limestone grassland 1960-61. Seasonal variations in numbers.

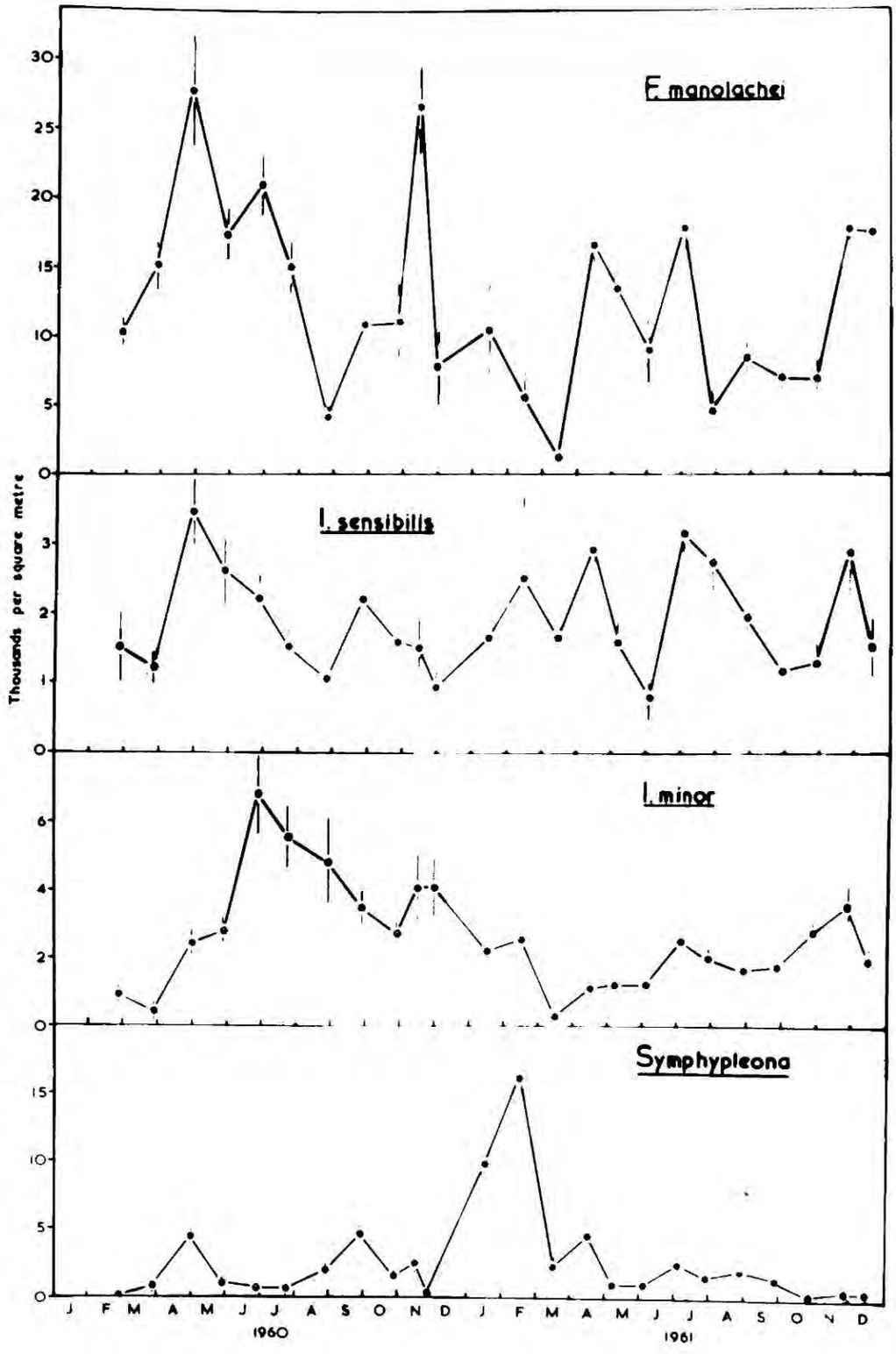
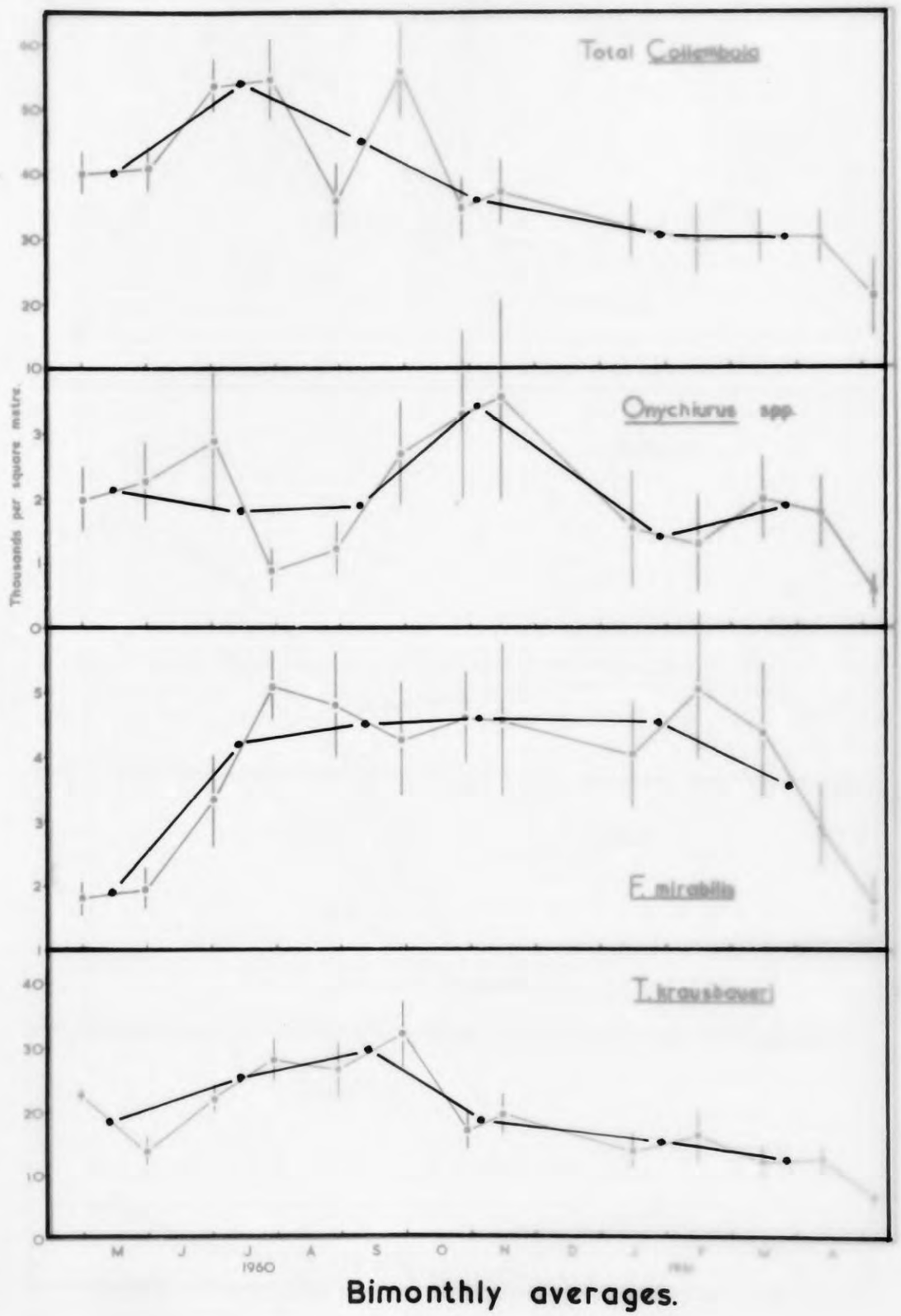


Fig. 30.

Alluvial grassland 1960-61. Seasonal variations in numbers. The graphs give data for one complete year, May 1960 to May 1961. It should be noted that the time scale (horizontal axis) is twice that of Fig. 29, and that the scales of the numbers per square metre (vertical axis) are not the same for all species; in some cases the scales of the vertical axis do not begin at 0.

Fig. 30a.

Alluvial grassland 1960-61.
Seasonal variations in numbers.



Bimonthly averages.

Fig. 30.

Alluvial grassland 1960-61.
Seasonal variations in numbers.

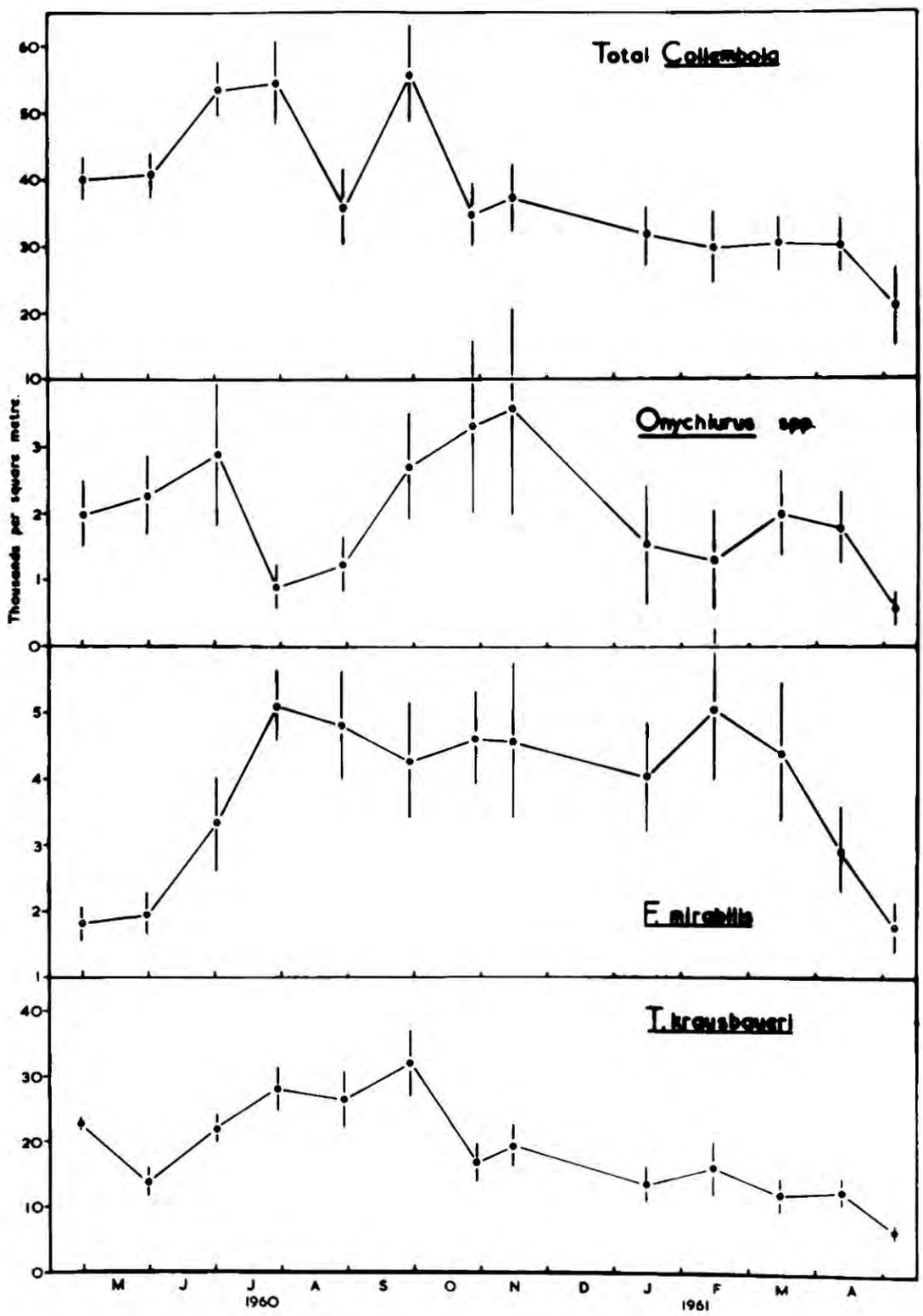
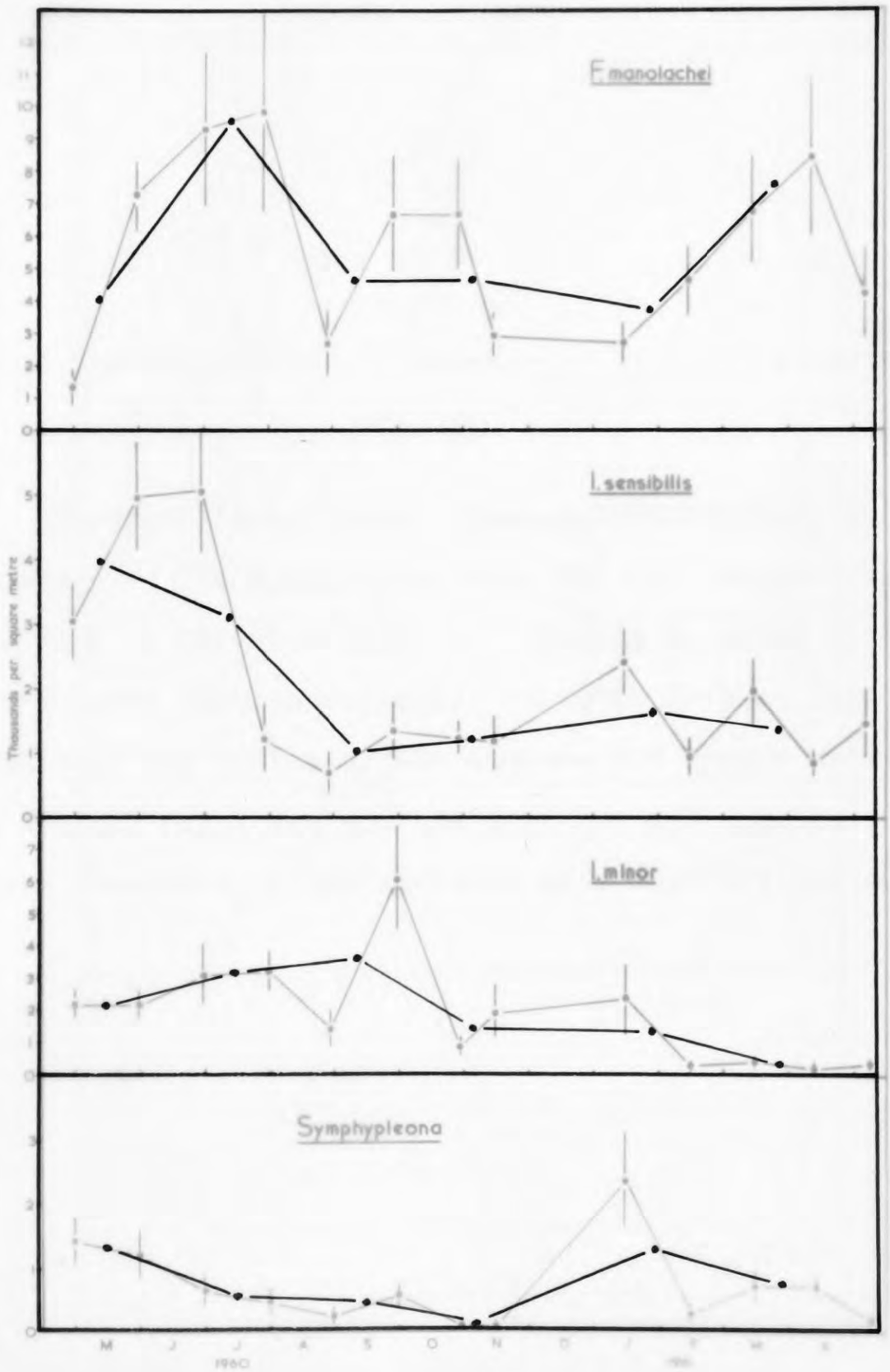


Fig 30a.

Alluvial grassland 1960-61.
Seasonal variations in numbers.



Bimonthly averages.

Fig. 30.

Alluvial grassland 1960-61.
Seasonal variations in numbers.

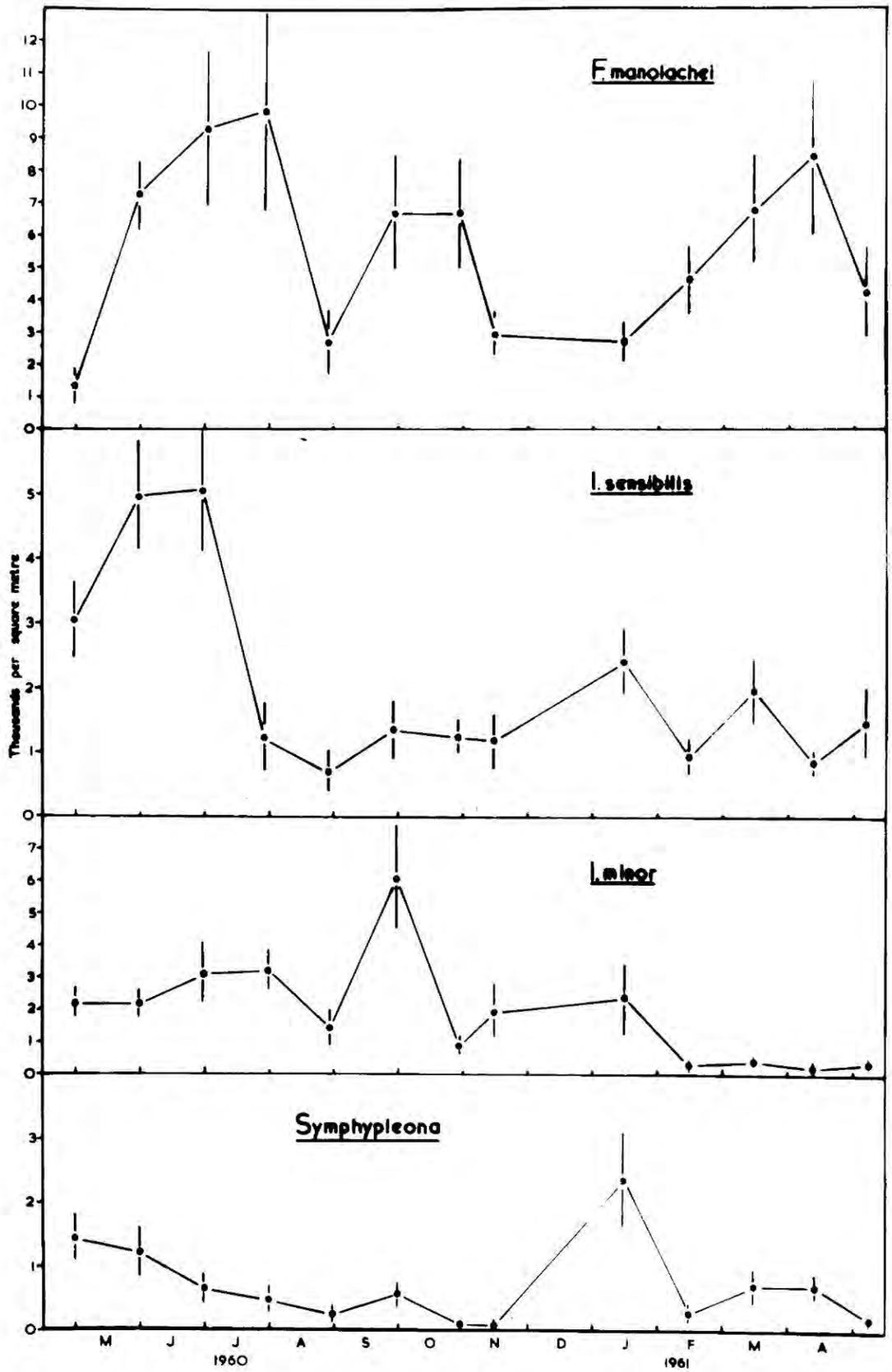
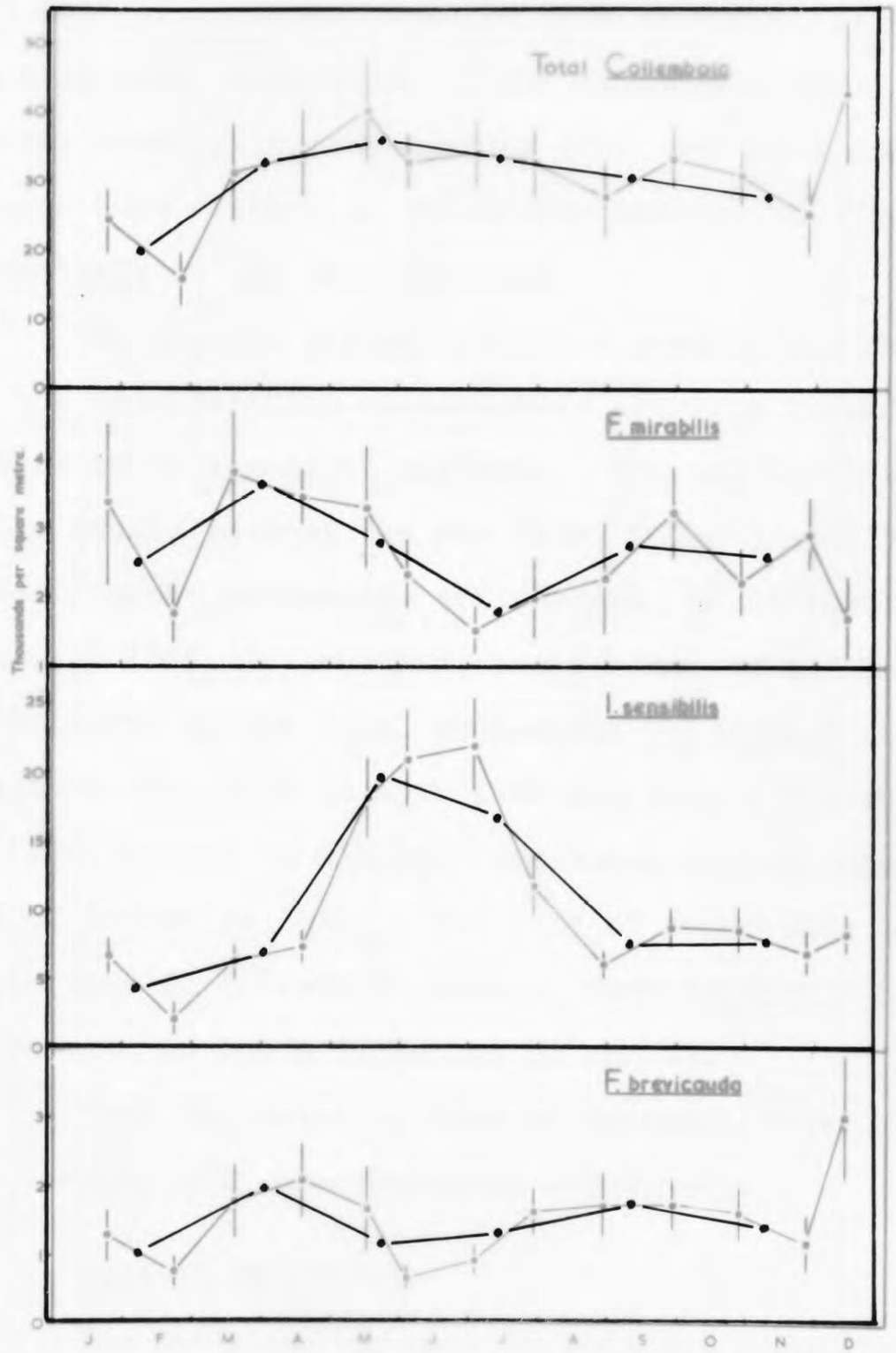


Fig. 31.

Heather litter 1961. Seasonal variations in numbers. The graphs give data for one complete year, January to December 1961. It should be noted that the time scale (horizontal axis) is twice that of Fig. 29, and that the scales of the numbers per square metre (vertical axis) are not the same for all species; in one case the scale of the vertical axis does not begin at 0.

Fig. 3 a.

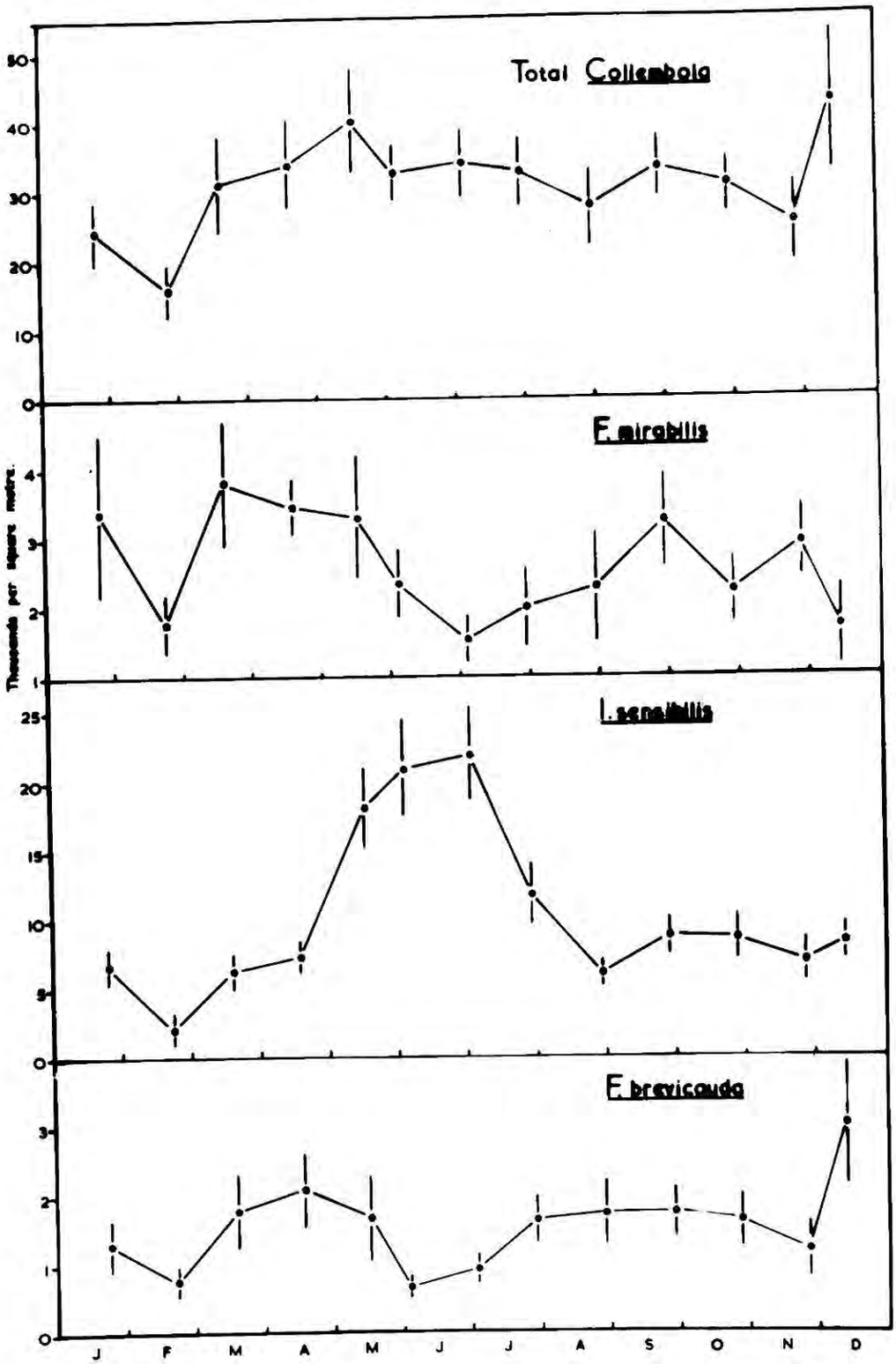
Heather litter 1961.
Seasonal variations in numbers.



Bimonthly averages.

Fig. 31.

Heather litter 1961.
Seasonal variations in numbers.



3) The analysis of the results of monthly sampling.

On both Limestone grassland and Alluvial grassland the six commonest species were selected for study; other species occurred in insufficient numbers. Fewer species occurred on the heather moor, and here only three species were present in sufficient numbers to justify an analysis of the data obtained.

No obvious pattern could be seen in the raw data, but the consideration of bimonthly averages reveals what appears to be a general pattern. The saw tooth effect of the graphs showing the raw data, which probably results from different extraction efficiencies on different dates (see page 184), is smoothed, and spring and autumn peaks are apparent in the total numbers of Collembola on Limestone grassland in both 1960 and 1961; spring peaks are also present on Alluvial grassland in 1960 and Heather litter in 1961. The time of occurrence of peak populations in different species, from bimonthly averages of the data is shown in Tables 81 and 82.

From the point of view of seasonal fluctuations each species will be considered separately:

1. Friesea mirabilis.

The early spring peak in 1961 was probably due to the hatching of overwintering eggs, due to the high temperatures prevailing in January and February 1961,

Table 81. The occurrence of peaks in numbers of *Collembola* on mineral soils at Moor House in 1960; from bimonthly averages of the data in Figs. 29a and 30a.

Species	Sampling site	Year	Month F	M	A	M	J	J	A	S	O	N	D	J
Friesea mirabilis	L.G.	1960									x			
	A.G.	1960									x			
Onychiurus spp.	L.G.	1960									x			
	A.G.	1960			x						x			
Tullbergia krausbaueri	L.G.	1960					x							
	A.G.	1960							x					
Folsomia manolachei	L.G.	1960			x						x			
	A.G.	1960					x							
Isotoma sensibilis	L.G.	1960			x									
	A.G.	1960			x									
Isotomiella minor	L.G.	1960					x							
	A.G.	1960							x					
Symphypleona	L.G.	1960			x									
	A.G.	1960			x									x
Total *Collembola*	L.G.	1960			x						x			
	A.G.	1960					x							

Table 82. The occurrence of peaks in numbers of Collembola at Moor House in 1961; from bimonthly averages of data in Figs. 29a, 30a and 31a.

Species	Sampling site	Year	Month												
			D	J	F	M	A	M	J	J	A	S	O	N	D	J
Friesea mirabilis	L.G.	1961			x							x				
	H.L.	1961				x					x					
Onychiurus spp.	L.G.	1961			x					x					x	
	A.G.	1961				x										
Tullbergia krausbaueri	L.G.	1961					x								x	
Folsomia manolachei	L.G.	1961					x								x	
	A.G.	1961			x											
Folsomia brevicauda	H.L.	1961				x					x					
Isotoma sensibilis	L.G.	1961					x				x				x	
	A.G.	1961		x												
	H.L.	1961						x								
Isotomiella minor	L.G.	1961							x						x	
Symphypleona	L.G.	1961			x											
	A.G.	1961	x													
Total Collembola	L.G.	1961					x								x	
	A.G.	1961														
	H.L.	1961						x								

at Moor House. (Large numbers of Symphypleona also hatched (Fig. 29) and some Lepidocyrtus lanuginosus, both of which normally overwinter as eggs).

2. Onychiurus spp..

O. procampatus and O. tricampatus are grouped together due to their not being recognised as separate species until six months after beginning the field work. The data suggest an autumn hatch of eggs laid during the summer and a spring hatch of overwintering eggs.

3. Tullbergia krausbaueri.

This species is probably similar to Onychiurus spp. in that there appears to be an autumn hatch of eggs laid during the summer and a spring hatch of overwintering eggs.

4. Folsomia manolachei.

The Limestone grassland data suggest spring and autumn generations and this is supported by examining the material for first instars; whilst no obvious peak in numbers occurred, first instars were found on Alluvial grassland in autumn.

5. Folsomia brevicauda.

This species occurs only on the peat moor in large numbers, and no significant differences were found in its numbers throughout the year (1961). However, peaks

occurred in the bimonthly averages in March/April and August/September 1961. These followed the trend in the numbers of F. manolachei on mineral soils, where spring and autumn peaks occurred.

6. Isotoma sensibilis.

In this species laying occurs only in spring (Table 19) and first instar individuals were present only in the April/May peak; thus probably only the spring peak is real.

7. Isotomiella minor.

The suggestion of two annual peaks in numbers in the 1961 data (Table 82) was not supported by the presence of early instars in the second autumn peak; first instars occurred only in the spring peak.

8. Symphypleona.

The high temperatures at Moor House in January and February 1961 caused an early hatch, and there was a February/March peak on the Limestone grassland and a December/January peak on the Alluvial grassland; the majority of these individuals were first instars.

Two major groupings can be made concerning the seasonal fluctuations in numbers of the above species:

i) Species normally having a single annual peak in numbers eg. Isotoma sensibilis.

ii) Species having spring and autumn peaks in numbers eg. Folsomia manolachei.

It would be expected that population peaks would occur shortly after the period of maximum oviposition, when temperatures are favourable to egg development. In the case of the species in the first group above eg. I. sensibilis, it has been shown that the period of maximum oviposition begins in April (Table 19). Since this data in Table 19 is accurate to within 1 month (monthly collections were made), eggs could have been laid in the field in early March. The population peak for 1960 occurs in April/May, and thus the correlation between egg laying and the population peak is a good one. At no other time were eggs laid, nor was there a second population peak.

No data concerning egg laying is available for members of the Genus Folsomia (second group), but the spring and autumn peaks suggest two generations a year. Data is also lacking concerning the egg laying periods of F. mirabilis.

The other species which have spring and autumn peaks, Onychiurus spp., T. krausbaueri and I. minor, are all members of the Euedaphon (see page 243). Table 19 shows that in O. procampatus, O. tricampatus and

T. krausbaueri the oviposition period extends from May to October or November. The autumn peak in numbers of these species is probably caused by the hatching of eggs laid throughout the summer, although there may be a second generation in O. tricampatus (see page 166).

It can be seen that by consideration of peaks occurring in bimonthly averages of the raw data, there is, in fact, an annual cycle, which can be correlated with the period of egg laying ih the species concerned.

4) Comparison with the results of previous workers.

Direct comparison of the Moor House data with that of other workers is difficult because of the short breeding season experienced under the prevailing sub-Arctic conditions. Most other work has been carried out on low-lying meadow land and woodland, where climatic conditions are less inclement.

Glasgow (1939) records an April peak for total Onychiuridae and a significant minimum in January between peaks in December and February/March, for totals of the three species 'O. armatus', Tullbergia quadrispina and T. krausbaueri. Such a minimum occurs also in the present work, for totals of O. procampatus and O.tricampatus on the Limestone grassland, and a minimum also occurs in T. krausbaueri. In the case of the Onychiurus spp.,

examination of the comparative numbers of different instars reveals that the February 1961 peak, following the January trough, is a result of an early hatch of over-wintering eggs; a significantly higher percentage of first and second instars of O. tricampatus occurs in February ($\chi^2 = 5.22$ for 1 degree of freedom; $P < 0.025$). Dhillon and Gibson (1962) have found April and December peaks in 'O. armatus' and Poole (1961) found an August maximum for T. krausbaueri.

For Isotoma spp., both Poole (1961) and Dhillon and Gibson (1962) found August peaks, but Bellinger (1954) found a May peak in Isotoma eunotabilis which agrees with the data presented here for other species of Isotoma; in other areas the same author found later peaks in the same species. The first two authors mentioned found an August peak in F. mirabilis which corresponds with that shown by the present data. Bellinger (1954) records April and August peaks in the Sminthurus fitchi, and Dhillon and Gibson (1962) found March, July and September peaks in the total Symphypleona; similar peaks were recorded in 1960 on Limestone grassland at Moor House.

5) Summary.

In general, the data provided concerning seasonal variations in numbers supports the views expressed as a

result of examination of biological data; that is that:

i. members of the Isotomidae probably have only one generation a year under the climatic conditions prevailing at Moor House.

ii. F. mirabilis, O. tricampatus, T. krausbaueri, Folsomia spp., and the Symphypleona may have two generations, but probably not more, under Moor House conditions.

V. THE FAUNA OF ERODING MOOR

V. THE FAUNA OF THE ERODING MOOR

1) Introduction.

As a result of erosion, the peat cover of the mixed moor has, in many areas, been dissected into haggs, and this has been described in the section on sampling sites (page 13). The presence of haggs influences the drainage in their immediate vicinity, and as a result, areas which vary considerably in both their water content and vegetation cover occur over short horizontal distances. It is thus possible to examine the habitat preferences of Collembola under natural conditions. Further, it is possible to deduce the succession of Collembola which occurs as the mixed moor is eroded, and eventually recolonised. A similar study of the Collembola associated with the pool and hummock system of bog growth on "Hochmoore" or raised bog has been made by Murphy (1955).

2) The sampling programme.

In order to compare the fauna of the erosion complex with that of the mixed moor, regular samples were taken over one year (January to December, 1961). This period coincided with the sampling of the mixed moor, so that a direct comparison was possible. In order to compare species differences, and differences in the

various vegetation types, the data for the year were pooled; this nullified variations arising from the comparison of data from different sampling dates, and from the annual cycle. The following four areas were selected for regular sampling on the erosion complex:

1. Hummock top
2. Hagg lip
3. An area of Eriophorum angustifolium
4. An area of Eriophorum vaginatum

It is suggested that these areas 1-4, which are described on pages 13 to 15, represent the successive stages which occur in the complex of erosion and recolonisation of blanket bog. Fig. 32 shows an idealised transect across the eroding blanket bog.

The Cladonia-covered hagg lip and the dry hummock top were sampled on four occasions during 1961, fifteen sample units of the type described on page 208 being taken on each occasion in each area. At the same time fifteen units were collected from Eriophorum angustifolium, and eight units 6 cm. deep from the Eriophorum vaginatum tussocks; only in this latter habitat did Collembola occur below 3 cm. deep. This gave data for 60 units each from Hagg lip, Hummock top and E. angustifolium, and 32 units for the E. vaginatum.

Fig. 32

Idealised section across the erosion and recolonisation complex.

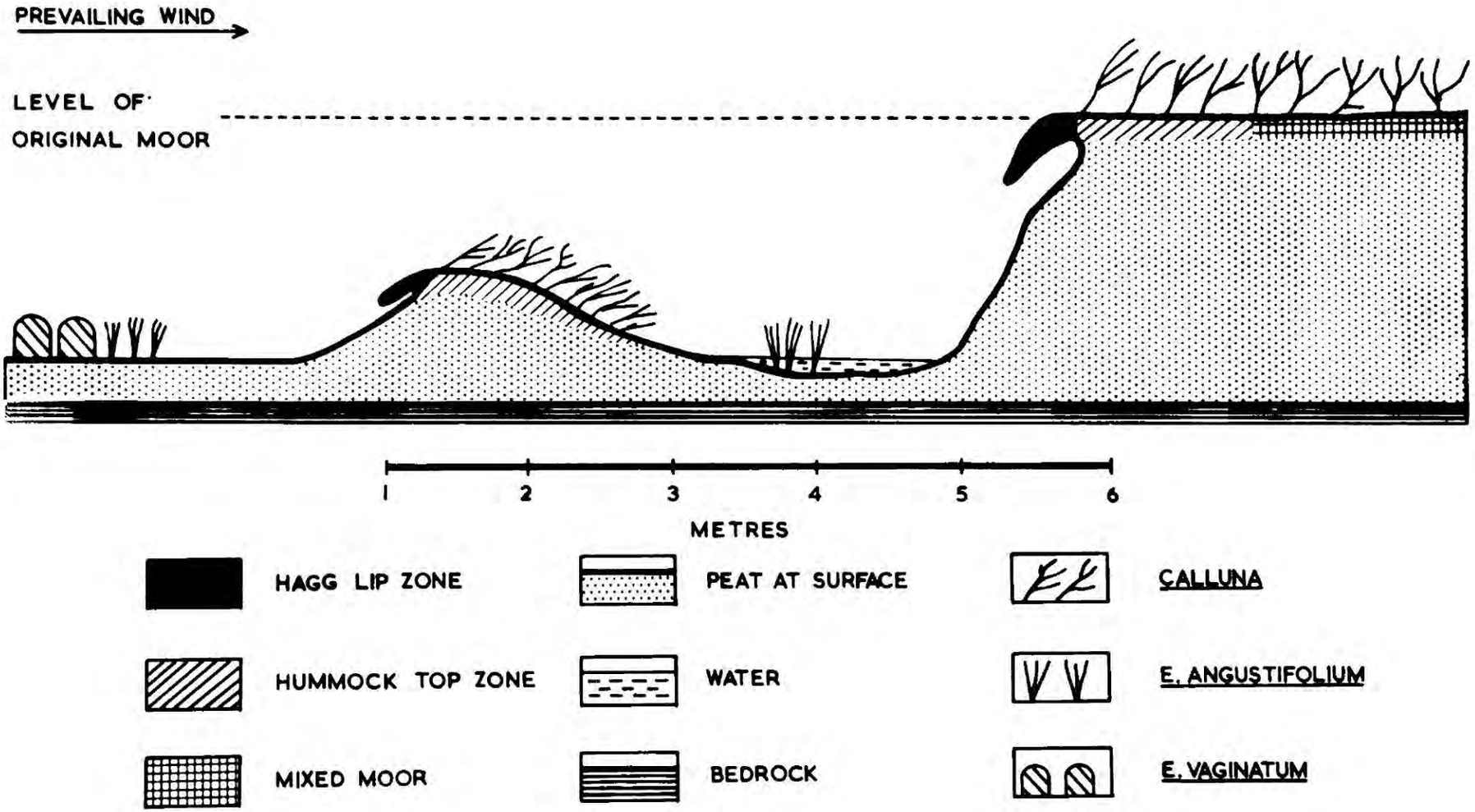

PREVAILING WIND
LEVEL OF ORIGINAL MOOR
1
2
3
4
5
6
METRES
HAGG LIP ZONE
HUMMOCK TOP ZONE
MIXED MOOR
PEAT AT SURFACE
WATER
BEDROCK
CALLUNA
E. ANGUSTIFOLIUM
E. VAGINATUM

Fig.32.

Table 83 shows a comparison of the mean values for 1961 of the water contents of the various sampling sites concerned in this section; these are means taken from Tables 4 and 5.

Table 83. Water content of sample units from the erosion complex compared with mixed moor. The figures are indices of humidity.

Mixed moor	Hummock top	Hagg lip	Eriophorum angustifolium	Eriophorum vaginatum
8.81	2.83	2.08	4.51	5.58

The high figure for mixed moor is due, in part, to the properties of water retention of the Sphagnum mosses.

3) Distribution of Collembola.

A. Erosion

Table 84 shows the average densities for the Collembola on the four sampling sites of the erosion complex, compared with the average density for mixed moor. The average density of Collembola was not significantly greater on the hummock tops than on the mixed moor (S.E. of difference less than twice the difference). The highest densities (three times that of any other area)

were found on the hagg lip. As conditions became drier the species 'spectrum' changed, and typical xerophil species became common. Thus, whilst Tetracanthella wahlgreni constituted less than 4% of the total numbers of Collembola on the mixed moor and hummock top, on the hagg lip over half the total numbers were of this species. Compared with the mixed moor significantly greater densities of Isotoma sensibilis ($P < 0.001$), and Folsomia brevicauda ($P < 0.001$) occurred on the hagg lip, where due to the lack of vegetation, the larger surface dwelling Collembola (the 'Atmobios' of Gisin 1943; see page 243) were absent.

The bare peat did not support a permanent population of Collembola but often individuals could be found below the hagg lip, from which they had presumably fallen.

B. Recolonisation

In some places an algal mat is formed on the bare peat. When conditions become drier in early summer, the surface of the peat cracks (Plate 8), and under these circumstances the algal mat flakes away from the solid mass of peat. Beneath these flakes high humidities are maintained, and Collembola rapidly colonise this temporary habitat. The most common species found

Table 84. Numbers of Collembola per 100 cm^2. (300 cc.) on the various sites sampled; the Standard Error of the mean is shown.

Species	Mixed moor 193 units	Hummock top 60 units	Hagg lip 60 units	Eriophorum angustifolium 60 units	Eriophorum vaginatum 32 units
Willemia anophthalma	0.4 ±0.1	0.4 ±0.3	1.8 ±0.5	0.0	0.0
Friesea mirabilis	25.9 ±1.9	13.6 ±1.6	13.8 ±2.9	0.3 ±0.2	30.6 ±9.5
Anurida pygmaea	5.0 ±0.8	21.4 ±6. 8	2.2 ±0.5	0.0	1.7 ±1.2
Neanura muscorum	1.1 ±0.3	0.4 ±0.3	0.2 ±0.2	0.0	0.6 ±0.4
Onychiurus latus	2.4 ±0.4	7.1 ±1.6	2.2 ±0.4	0.0	5.5 ±2.0
Tullbergia krausbaueri	0.4 ±0.2	0.0	5.6 ±1.3	0.0	2.8 ±1.5
Tetracanthella wahlgreni	7.3 ±2.2	13.8 ±5.8	675.8 ±47.3	0.2 ±0.2	0.6 ±0.4
Folsomia brevicauda	153.3 ±12.6	104.3 ±22.3	313.2 ±34.9	1.0 ±0.5	45.0 ±15.0
Isotoma sensibilis	102.9 ±5.5	200.4 ±16.4	236.2 ±25.7	0.3 ±0.2	100.5 ±24.0

continued overleaf.

Table 84 (continued).

Species	Mixed moor 193 units	Hummock top 60 units	Hagg lip 60 units	Eriophorum angusti-folium 60 units	Eriophorum vaginatum 32 units
Isotoma viridis	1.0 ±0.5	5.7 ±1.0	0.0	0.2 ±0.2	0.0
Isotoma antennalis	0.0	0.0	0.0	35.7 ±12.4	17.6 ±10.0
Entomobrya nicoleti	0.1 ±0.1	0.0	0.0	0.2 ±0.2	16.5 ±9.1
Lepidocyrtus lanuginosus	1.5 ±0.3	17.6 ±5.5	1.0 ±0.5	0.2 ±0.2	1.7 ±1.0
Tomocerus minor	0.4 ±0.2	0.6 ±0.3	0.0	0.7 ±0.4	7.7 ±2.9
Neelus minimus	1.4 ±0.3	1.0 ±0.8	0.0	0.0	0.0
Total Collembola	310.3 ±16.5	388.5 ±38.9	1252.0 ±88.3	47.2 ±18.2	244.4 ±27.2

Note: For comparison with continental data, and particularly with that of Murphy (1955), the data can be fitted directly to the scale of abundance used by Gisin (1943), where: 1 ≡ 1-2; 2 ≡ 3-6; 3 ≡ 7-20; 4 ≡ 21-50; 5 ≡ 51-200; 6 ≡ 201; except for the Eriophorum vaginatum data which should be divided by a factor of 2.

here was Isotoma antennalis, which occurred in greater numbers than all other species. A habitat very similar to this occurred beneath pieces of sandstone lying on the peat (Plate 8), where the effects of erosion had exposed the bedrock; here again I. antennalis outnumbered all other species. Artificial conditions very similar to these were created by putting down pieces of wood and metal sheets, and when these were sufficiently near to an area already inhabited by I. antennalis, colonies became established beneath them in less than a month. Thus it would appear that bare peat, which was impenetrable to Collembola because of waterlogging, lacked a population only because it did not supply sufficient protection from adverse climatic conditions.

Eriophorum angustifolium often becomes established on areas of algal mat and where pools form on the surface of bare peat. Whilst several species of Collembola have been collected from this habitat, again I. antennalis outnumbered all others (Table 84) and was found to be typical of habitats where very wet conditions prevailed; it may thus be regarded as a hydrophil species (see page 243).

Where Eriophorum vaginatum was established there was a similar density of Isotoma antennalis to that on the Eriophorum angustifolium, but some species typical of the

mixed moor were present. Folsomia brevicauda, Isotoma sensibilis and Friesea mirabilis were the commonest species, and the last two species maintained similar densities in this habitat and on the mixed moor. Entomobrya nicoleti was characteristic of this habitat. The total density of Collembola occurring on the Eriophorum vaginatum was lower than that of the mixed moor, and it was clear that the fauna was intermediate between that on the Eriophorum angustifolium and that on the mixed moor.

4) Discussion.

The processes of erosion of the blanket bog are associated with a general drying out of the area, and this is shown by the lower water content of the soil samples in the proceeding stages of erosion (Table 83, columns 1-3); a similar change in water status between the lower and higher parts of the growing bog studied by Murphy (1955) may be assumed. On the erosion complex the Collembola of the sites sampled ranged from a hydrophil fauna on the eroded peat, to a mesophil fauna on the blanket bog and a xerophil fauna on the hagg lip. On a smaller scale similar preferences are shown by the Collembola on transects made on a growing bog (Murphy 1955). The distribution of Collembola in both cases appears to be governed by physical factors which bring about alterations in the water content

of the habitat. Cragg (1961) has drawn comparisons between the present work and that of Murphy (1955).

To a large extent different vegetation types reflect the water content of the immediate environment, and where different vegetation types occur on the erosion complex and the mixed moor, different species and densities of Collembola occur. This may be summarised, showing the characteristic species of Collembola, in the following way:

Bare peat → Eriophorum angustifolium → Eriophorum vaginatum → Mixed moor → Hummock top → Hagg lip

Hydrophil fauna ——————→ Mesophil fauna ——→ Xerophil fauna

Isotoma antennalis — Folsomia brevicauda, Friesea mirabilis, Isotoma sensibilis — Tetracanthella wahlgreni

——————Increasing density ——————→

— Decreasing water content →

The whole process of erosion of the moor, and the subsequent recolonisation by a similar plant cover, may be regarded as a cyclic change in the blanket bog. Changes in the plant cover and water content of the habitat are associated with both density and species of Collembola; these changes can most easily be seen in the erosion of the hummocks on the bare peat, where in a matter of a few months a hummock top can be eroded to form a hagg lip, with its very different fauna. However, processes of recolon-

isation, and therefore the succession, are much slower, and must be measured in terms of years rather than months.

VI. THE FAUNA OF DIFFERENT SAMPLING AREAS

VI. THE FAUNA OF DIFFERENT SAMPLING AREAS

1) Introduction.

In this section the differences between the various sampling areas, with respect to total numbers, the numbers of various species and the species 'spectrum', are considered from the statistical point of view. This method of approach is used in preference to the sociological methods of continental workers eg. Agrell (1941), Cassagnau (1961), Haarlov (1960), in that it is not affinities between different species of Collembola, but differences in the faunas of various habitats, that it is desired to establish. Gisin (1943 et seq.) has used a scale of abundance (see page 267) to indicate the numbers of Collembola in different samples; in this work, the raw data is used for comparative purposes. In order to allow for seasonal fluctuations in numbers, the data for a period of twelve months have been pooled. In the case of the Limestone grassland, Heather litter and Juncus squarrosus areas, the data compared are for the same months, and in most cases for the same dates; this is also the case for the Limestone grassland and Alluvial grassland areas. However, the sampling of Alluvial grassland overlapped that of Heather litter and Juncus squarrosus for only five months.

In this section means per sample unit refer to the sample unit size of 11.35 cm^2., and are not corrected for an area of 10 cm^2; this was unnecessary for comparative purposes.

2) Qualitative differences.

Table 85 shows that six species, namely F.mirabilis, Onychiurus spp., T. krausbaueri, F. manolachei, I.sensibilis and I. minor dominated the fauna of the four main sampling sites. All these species were present in large numbers on the Limestone grassland and the Alluvial grass-land; in the Heather litter members of Gisin's (1943) "Euedaphon", namely O. procampatus, O. tricampatus, T. krausbaueri and I. minor were either absent or present in very small numbers, and F. manolachei was replaced by F. brevicauda. On the Juncus squarrosus grassland the numbers of F. brevicauda were greatly reduced, but members of the Symphypleona occurred more commonly.

Whilst obvious differences occur between the Juncus squarrosus and the Heather litter, and the two grassland areas, differences between these two latter areas are less obvious. Lousley (1950) has pointed out that plant rarities within a habitat are frequently better indicators of variations between habitats than are the commoner species, and this clearly also applies in the case of the Collembola of these two areas. Table 82 shows that

Table 85. Total numbers of Collembola collected in quantitative samples taken on the four main sampling sites in twelve months.

Species	Limestone grassland 195 sample units	Alluvial grassland 195 sample units	Heather litter 195 sample units	Juncus squarrosus 57 sample units
Hypogastrura scotica	0	0	1	0
Hypogastrura denticulata	7	158	0	1
Willemia anophthalma	2	0	8	0
Friesea mirabilis	1204	857	567	232
Brachystomella parvula	1	0	0	0
Anurida pygmaea	170	84	109	0
Anurida forsslundi	0	0	1	0
Anurida granaria	0	1	0	0
Neanura muscorum	0	0	25	0
Onychiurus absoloni	1	0	0	0
Onychiurus procampatus & tricampatus	1083	443	0	1
Onychiurus latus	0	0	52	7
Tullbergia krausbaueri	1296	4154	8	0
Tullbergia affinis	1	0	0	0
Tullbergia denisi	3	38	0	0
Tetracanthella wahlgreni	1	1	160	0
Tetracanthella brachyura	0	0	0	3
Folsomia brevicauda	0	0	3361	11

Table 85 (continued).

Species	Limestone grassland 195 sample units	Alluvial grassland 195 sample units	Heather litter 195 sample units	Juncus squarrosus 57 sample units
Folsomia 4-oculata	162	7	1	0
Folsomia manolachei	2285	1281	0	0
Folsomia cf. brevifurca	75	35	0	0
Folsomia litsteri	4	31	0	0
Isotomiella minor	376	419	0	0
Isotoma sensibilis	432	488	2254	231
Isotoma notabilis	116	193	7	1
Isotoma viridis	95	185	22	12
Isotoma antennalis	0	0	0	1
Isotoma olivacea	44	82	0	3
Isotoma infuscata	1	0	0	0
Isotomurus palustris	0	1	1	17
Entomobrya nicoleti	1	12	1	0
Entomobrya multifaciata	1	1	0	0
Willowsia buski	0	0	13	0
Lepidocyrtus cyaneus	0	0	0	2
Lepidocyrtus lanuginosus	1	10	32	0
Pseudosinella alba	2	0	0	0
Tomocerus minor	0	0	8	0

H. denticulata, T. denisi, F. litsteri, E. nicoleti, and L. lanuginosus occurred more frequently on the Alluvial grassland than on the Limestone grassland, whereas F. 4-oculata was commoner on the latter area. Two other species which occurred on the Limestone grassland, and were apparently absent from the Alluvial grassland were T. affinis and T. wahlgreni; the former was obtained frequently in crumbled samples of Limestone grassland from a Tullgren funnel (see page 42), but was absent in similar samples from other areas; T. wahlgreni occurred in very small numbers in the Cladonia rangiferina on the Limestone grassland, but both the lichen and this species of Collembola were absent from Alluvial grassland.

Species characteristic of the Heather litter are Neanura muscorum, Onychiurus latus, Tetracanthella wahlgreni which is associated with the lichens epiphytic on the Calluna stems, Folsomia brevicauda, Willowsia buski and Tomocerus minor. On the moor-edge zones of Juncus squarrosus, three species distinguish the fauna from those of the other three main sampling sites; Isotoma antennalis, Isotomurus palustris and Lepidocyrtus cyaneus were virtually absent elsewhere on the main sampling sites, but occurred commonly in qualitative samples from Juncus squarrosus.

Whilst this work is largely devoted to the Arthropleona, identification of Symphypleona has shown that several species appear to be characteristic of certain soil types. Thus, Sminthurides pumilis, Sminthurinus elegans, S. aureus, S. niger and Bourletiella viridescens have been recorded only from mineral soils, Sminthurides malmgreni, S. parvulus, Arrhopalites principalis, Dicyrtoma minuta and D. fusca from peat soils and Sminthurides signatus and Bourletiella hortensis from areas of peat erosion.

3) Quantitative differences.

Limestone grassland supports a higher density of Collembola than any of the other main sampling areas; Alluvial grassland, Heather litter and Juncus squarrosus grassland support progressively lower densities, the last area having an average density of less than half that of the Limestone grassland; this is shown in Table 86. This is in direct contrast to what has been shown for other groups of soil animals (Cragg 1961), where high densities have been recorded from Juncus squarrosus areas. The highest density recorded on Limestone grassland was on 14 November, 1960, when an average density of 77,950 ± 8,600 individuals per m^2 was estimated. Maxima for the

other main sampling areas are as follows:

Alluvial grassland (26.9.60)	55,860 ± 7,330 per m^2
Heather litter (11.12.61)	42,350 ± 10,250 per m^2
Juncus squarrosus (20.2.61)	38,890 ± 6,870 per m^2

When, however, the microdistribution of Collembola is considered, the specialised fauna associated with the hagg lip (see page 265) gives the highest densities yet recorded; on 4 December, 1961, 230,000 ± 28,400 individuals per m^2 was estimated, over 50% of which were Tetracanthella wahlgreni.

Consideration of the dominant species shows that:

1. Friesea mirabilis has a significantly different density on all areas, with the exception of the Alluvial grassland and the Juncus squarrosus areas (Tables 86 and 87A).

2. Onychiurus spp. have a significantly greater density on Limestone grassland than on Alluvial grassland, the species being virtually absent on the other sampling sites.

3. Tullbergia krausbaueri is significantly commoner on the Alluvial grassland than on the Limestone grassland, in contrast to the last species, but again is virtually absent on other sites.

4. Folsomia manolachei has a distribution similar to Onychiurus spp., and is replaced on the peat soils by F. brevicauda.

Table 86. Comparison of the mean annual numbers per sample unit 11.35 cm^2 of the commoner species of Collembola on the four main sampling sites; the standard error of the mean is also shown.

Species / Sampling site	Friesea mirabilis	Onychiurus spp.	Tullbergia krausbaueri	Folsomia manolachei	Folsomia brevicauda	Isotoma sensibilis	Isotomiella minor	Symphypleona	Total Collembola
Limestone grassland 1960 (units 6cm. deep)	6.87 ± 0.26	4.89 ± 0.23	9.99 ± 0.64	17.31 ± 0.81	0	2.16 ± 0.12	3.88 ± 0.23	1.68 ± 0.14	52.92 ± 1.35
Limestone grassland May 1960 to May 1961 cf. Alluvial grassland (units 6cm. deep)	6.93	5.54	10.65	15.41	0	2.14	4.15	3.41	52.86
Alluvial grassland May 1960 to May 1961 (units 6cm. deep)	3.98 ± 0.24	2.24 ± 0.25	19.30 ± 1.20	5.81 ± 0.56	0	2.58 ± 0.22	2.08 ± 0.24	0.89 ± 0.12	43.69 ± 1.64
Heather litter 1961 (units 3cm. deep)	2.94 ± 0.21	0	‡	0	17.41 ± 1.51	11.68 ± 0.78	0	0.87 ± 0.12	35.17 ± 1.90
Juncus squarrosus 1961 (units 3cm. deep)	4.07 ± 0.63	‡	0	0	‡	4.07 ± 0.37	0	11.74 ± 2.52	20.93 ± 2.86

Note. ‡ = less than 0.2 per sample unit.

Table 87. Differences between means and standard errors of the difference for species of Collembola on the various sampling sites.

Note. In the Table the Difference between means is shown, together with the Standard Error of the Difference, and the Probability (P) of the data being similar.

A.G. = Alluvial grassland

L.G. = Limestone grassland

J.sq. = Juncus squarrosus grassland

H.L. = Heather litter.

	A.G.	H.L.	J.Sq.	
A		2.95 ± 0.41 P = <0.001	3.23 ± 0.38 P = <0.001	2.10 ± 0.71 P = <0.010 L.G.
			1.40 ± 0.32 P = <0.010	0.09 ± 0.68 P = <0.900 A.G.
				1.13 ± 0.67 P = <0.010 H.L.

Friesea mirabilis

Table 87 (continued).

A.G.	H.L.	J.Sq.		
3.30 ± 0.41	5.55 ± 0.32	5.55 ± 0.32	L.G.	
P = <0.001	P = <0.001	P = <0.001		
	2.24 ± 0.26	2.24 ± 0.26	A.G.	B *Onychiurus* spp.
	P = <0.001	P = <0.001		
		-	H.L.	
A.G.	H.L.	J.Sq.		
8.65 ± 1.47	6.13 ± 0.62	6.13 ± 0.62	L.G.	
P = <0.001	P = <0.001	P = <0.001		
	19.30 ± 1.20	19.30 ± 1.20	A.G.	C *Tullbergia krausbaueri*
	P = <0.001	P = <0.001		
		-	H.L.	
A.G.	H.L.	J.Sq.		
9.60 ± 1.05	12.08 ± 0.91	12.08 ± 0.91	L.G.	
P = <0.001	P = <0.001	P = <0.001		
	5.81 ± 0.60	5.81 ± 0.60	A.G.	D *Folsomia manolachei*
	P = <0.001	P = <0.001		
		-	H.L.	

Table 87 (continued).

A.G.	H.L.	J.Sq.		
0.44 ± 0.28	9.46 ± 0.81	1.83 ± 0.42	L.G.	
P = <0.20	P = <0.001	P = <0.001		
	9.10 ± 0.81	1.47 ± 0.43	A.G.	E Isotoma sensibilis
	P = <0.001	P = <0.001		
		7.63 ± 0.86	H.L.	
		P = <0.001		

A.G.	H.L.	J.Sq.		
2.07 ± 0.39	1.93 ± 0.20	1.93 ± 0.20	L.G.	
P = <0.001	P = <0.001	P = <0.001		
	2.08 ± 0.24	2.08 ± 0.24	A.G.	F Isotomiella minor
	P = <0.001	P = <0.001		
		-	H.L.	

A.G.	H.L.	J.Sq.		
2.52 ± 0.46	2.89 ± 0.54	7.98 ± 2.58	L.G.	
P = <0.001	P = <0.001	P = <0.001		
	0.02 ± 0.16	10.85 ± 2.53	A.G.	G Total Symphypleona
	P = <0.900	P = <0.001		
		10.87 ± 2.53		
		P = <0.001		

Table 87 (continued)

A.G.	H.L.	J.Sq.		
9.17 ± 2.52	6.36 ± 2.63	20.60 ± 3.38	L.G.	
P = < 0.001	P = < 0.02	P = < 0.001		
	8.52 ± 2.51	22.76 ± 3.29	A.G.	H Total Collembola
	P = < 0.001	P = < 0.001		
		14.24 ± 3.43	H.L.	
		P = < 0.001		

5. Isotoma sensibilis is ubiquitous, the highest densities occurring on the Heather litter site; the density on Juncus squarrosus is significantly higher than those on the Alluvial and Limestone grasslands where there is no significant difference (Table 87E).

6. Isotomiella minor has a distribution similar to Onychiurus spp. and F. manolachei; the greatest densities occur on Limestone grassland.

7. Symphypleona have significantly higher densities on Juncus squarrosus than elsewhere.

The data concerning relative population densities of these species is summarised in Tables 86 and 87.

4) Annual differences within a single vegetation type.

The Limestone grassland is the only area for which there is more than one year's data. In Table 88 comparisons are made between the numbers of the commoner species in 1960 and 1961. In Friesea mirabilis, Onychiurus spp., and Isotoma sensibilis there is no significant difference between the average densities in different years. In Tullbergia krausbaueri, Folsomia manolachei and Isotomiella minor there is a significant decrease in numbers in 1961 as compared with 1960, whereas an increase occurs in the Symphypleona in 1961. The overall picture is of a reduction in the average density in 1961, as compared with 1960.

5) Microdistribution.

Whilst on the Limestone grassland and the Alluvial grassland it is difficult to see any obvious differences in the plant cover, which may give rise to different micro-habitats, on the other two areas differences could be seen. Thus on the Juncus squarrosus site possible differences could occur within and between the rosettes of J. squarrosus. On the Heather litter site, areas of Sphagnum rubellum could be differentiated clearly from patches of Cladonia spp.; in this latter case differences in the Collembola would be expected due to the differences in water content between the wet, mossy areas and the dry areas where lichens were abundant.

Table 88. Comparison of numbers and species of Collembola in different years on Limestone grassland, 1960 and 1961; the figures are means per sample unit 11.35 cm^2 and 6 cm. deep.

Species	Onychiurus	Friesea mirabilis	Tullbergia krausbaueri	Isotoma sensibilis	Isotomiella minor	Folsomia manolachei	Sympy-pleona	Total Collembol
Means per sample unit 1960 (A)	4.89	6.87	9.99	2.16	3.88	17.31	1.68	52.92
Means per sample unit 1961 (B)	5.55	6.17	6.13	2.22	1.93	12.08	3.76	41.53
Difference (B-A)	+0.67	-0.70	-3.86	+0.06	-1.95	-5.23	+2.08	-11.39
Standard Error of ± Difference	0.43	0.45	1.01	0.26	0.35	1.37	0.60	2.60
P	<0.900	<0.900	<0.001	<0.900	<0.001	<0.001	<0.001	<0.001

In order to ascertain whether or not there was a difference in the distribution of Collembola on the Juncus squarrosus site, in and between rosettes, samples, each of 15 units, were taken from both areas on the same date; a summary of the data is given in Table 89.

Table 89. Comparison of the distribution of Collembola in and between the Rosettes of Juncus squarrosus, 9.5.60. 15 sample units 11.35 cm^2 and 3 cm. deep were taken from each area.

Species	Friesea mirabilis	Isotoma sensibilis	Total Collembola
Mean per sample unit around rosettes	9.14	2.66	11.93
Mean per sample unit between rosettes	10.56	1.35	13.60
Difference between means and S.E. of difference	1.42 ± 2.17	1.31 ± 1.03	1.67 ± 2.71
P	>0.7	>0.4	>0.7

It can thus be seen that no significant differences occurred in the distribution of Collembola with respect to the rosettes, on the Juncus squarrosus site.

To examine possible differences occurring in different vegetation types on the heather moor, an analysis was made for the two species Folsomia brevicauda and Tetracanthella wahlgreni; in the random samples collected from Heather litter, 101 units contained Sphagnum rubellum and 21 units Cladonia spp.

Table 90 summarises the data.

Table 90. Comparison of the density of two species of Collembola in different microhabitats on Heather moor, from random samples. Sample units 11.35 cm^2 and 3 cm. deep.

Species	Folsomia brevicauda	Tetracanthella wahlgreni
Mean per sample unit in Sphagnum rubellum	19.31	0.42
Mean per sample unit in Cladonia spp..	10.95	5.05
Difference between means and S.E. of difference	8.36 ± 3.49	4.63 ± 1.65
P	<0.05	<0.02

From these data it can be seen that Folsomia brevicauda occurred in significantly higher densities in Sphagnum than in Cladonia, whereas the reverse is the case in Tetracanthella wahlgreni. This is also supported by data obtained from counts of Collembola from samples of 25 sq. cm. surface area taken from sites where Cladonia and Sphagnum were actually in contact; a comparison of 20 such units, extracted in an ordinary Tullgren funnel, is made in Table 91. Again F. brevicauda occurred in significantly higher densities in Sphagnum, and T. wahlgreni in significantly higher densities in Cladonia.

Table 91. Comparison of the numbers of two species of Collembola from 25 cm^2 sample units of Sphagnum and Cladonia in contact.

Species	Folsomia brevicauda	Tetracanthella wahlgreni
Mean per sample unit in Sphagnum rubellum (20 units)	21.50	1.15
Mean per sample unit in Cladonia spp. (20 units)	1.30	29.60
Difference between means and S.E. of difference	20.20 ± 10.86	28.45 ± 9.27
P	<0.1	<0.01

Thus differences occur within microhabitats on the Heather moor comparable with those seen on the erosion complex (see page 265).

VII. BIOMASS

VII. BIOMASS

1) Introduction.

Biomass estimations are the most widely used measure of the importance of populations, but there are certain difficulties in obtaining figures of biomass for Collembola; these are as follows:

i. Direct weighing is impossible for many groups, as in the live state the individuals possessing a furcula cannot be handled conveniently; weighing of preserved material is practically impossible, due to the retention of the liquid preservative in and between separate individuals.

ii. Different species are represented by individuals in various stages of development, and calculations based only on the weights of adults would provide a gross over-estimate.

iii. Varying proportions of species of different sizes occur on the various sampling sites, so it is not practicable to determine the weight of an average individual, and apply this to all sampling areas on different dates.

Ideally the biomass of all instars of all species present should be known before an estimate of the total biomass is made. However, this is clearly impracticable, and in practice a 'best estimate' has to be made.

Macfadyen (1952) estimated biomass in Collembola by measuring the volume of individual adults and multiplying this by a conversion factor obtained from direct weighing of selected adults; however, it is stressed that these figures only indicate the order of magnitude of the biomass. During the course of the present work it was decided to obtain biomass figures which were as accurate as possible for one or two species, and to estimate total biomass from these. On the Limestone grassland Onychiurus procampatus and O. tricampatus accounted for approximately half the total biomass. This estimate was made by observing the surface area covered when individuals of these two species were floated on water; it was approximately equal to that covered by the rest of the Collembola, in a sample from a given date. This rough approximation held for all dates on the Limestone grassland.

2) Weights of different instars.

In Figs. 16 and 17 it can be seen that the head capsules of the first six instars of O. procampatus are equal in size to the head capsules of the first six instars of O. latus. Not surprisingly the weights of the equivalent instars are also similar; 100 first instars of O. procampatus were found to be the same weight as 100 first instar O. latus; no second instars were weighed, but ten individuals of each of the other four instars were found

to be similar in weight in the two species. These data are shown in Table 92.

Table 92. Comparison of the weights (in microgrammes) of different instars in Onychiurus procampatus and O. latus.

Instar	1	2	3	4	5	6	7
Onychiurus procampatus	8.3	-	18.0	37.8	83.1	101.0	-
Onychiurus latus	8.3	-	18.0	36.9	82.5	110.0	314.4

The data for O. latus was plotted graphically (Fig. 33) and the average weight of each instar read from the graph. No direct weighings were made of individuals of O. tricampatus and the assumption was made that individuals of equivalent head capsule size would be equivalent in weight cf. O. procampatus and O. latus. Extrapolation of the graph (Fig. 33) thus gave estimates of weights of individuals having head capsule sizes equivalent to instars one and two of O. tricampatus. Table 93 gives the calculated average weights of different instars from Fig. 33.

Table 93. Calculated average weights (in microgrammes) of different instars of Onychiurus procampatus and O. tricampatus.

Species	Instars							
Onychiurus procampatus			1	2	3	4	5	6
Onychiurus tricampatus	1	2	3	4	5	6		
Weight per individual in ugms.	4.2	5.6	8.3	12.6	18.0	35.5	63.1	114.8

3) Biomass of the population of O. procampatus and O. tricampatus.

From a knowledge of the age distribution of O. procampatus and O. tricampatus (Figs. 19 and 20) and a knowledge of the average weights of different instars (Table 93), the biomass of the two species was calculated for different sampling dates. This is shown in Fig. 34. As would be expected the largest biomasses occur in early winter, at the end of the breeding season (Fig. 34a).

From these data estimates of the total biomass of Collembola on the various sampling sites can be made. It is stressed that these estimations are only approximations to the total biomass of Collembola, as it is assumed that the Onychiurus spp. account for half the total biomass on

Fig. 33.

The relationship between the head capsule size and weight in Onychiurus latus and O. tricampatus.

Relationship between head capsule size and weight in Onychiurus latus.

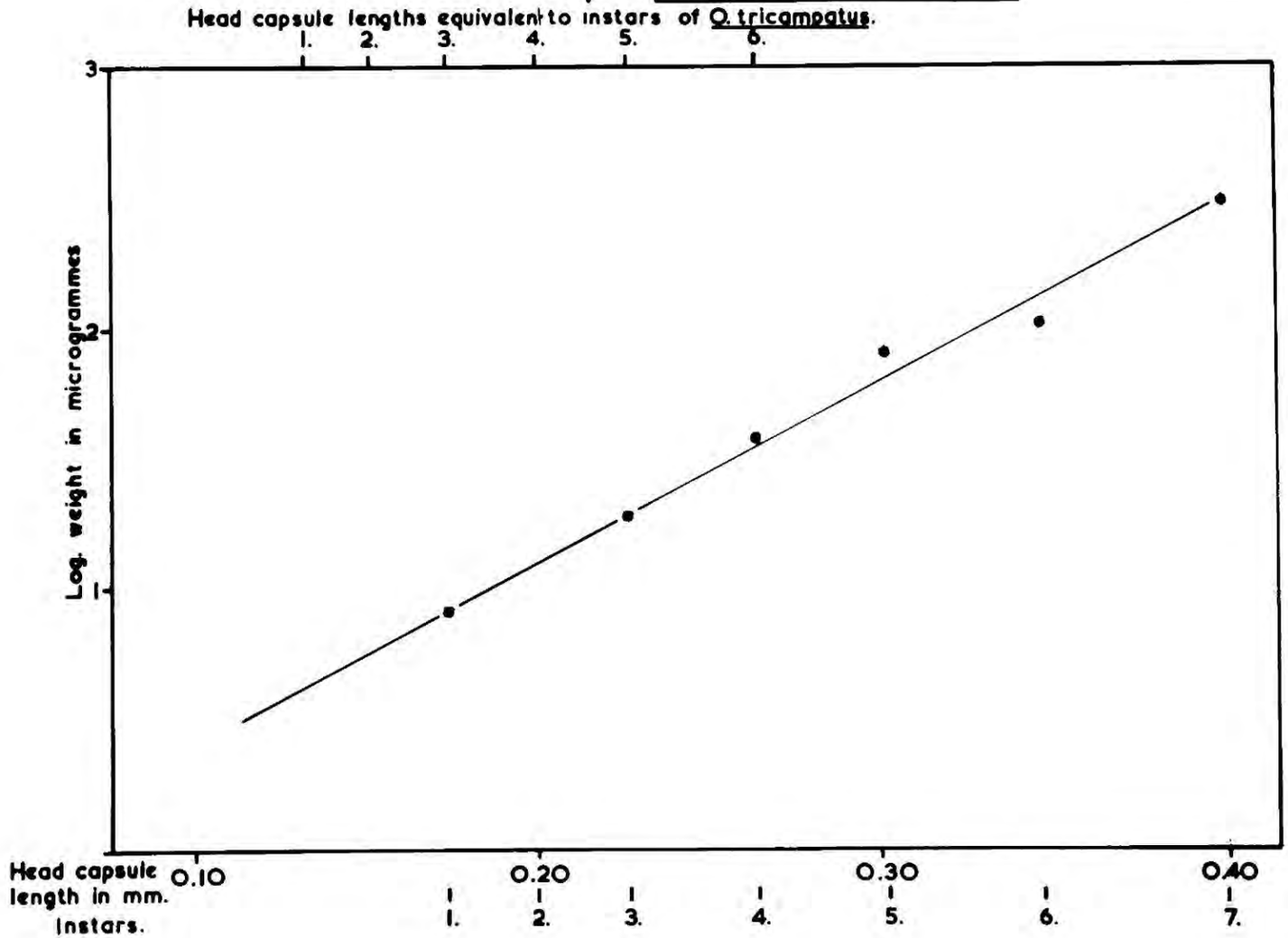


Fig. 33.

all occasions. Table 94 gives the data for maximum and minimum biomasses on different sampling sites.

The highest population density recorded of 230,000 ± 28,400 m^2 on an area of hagg lip, on 4 December, 1961, represented a biomass of about 2.53 g/sq.m. It can thus be seen that the biomass estimates in this work are appreciably smaller than those of Bornebusch (1930) and Macfadyen (1952, 1957).

4) The relative importance of Collembola in the soil.

On a basis of data provided by the present writer, Cragg (1961) has compared Collembola with other groups of moorland soil animals, with respect to biomass and respiration. A biomass of 0.6 g. per m^2 (this figure is to be regarded as a maximum) accounts for 0.3% of the total biomass on Limestone grassland, and a biomass of 0.1 g. per m^2 accounts for 0.1% of the total biomass on Juncus squarrosus. Calculations based on the respiratory determinations of Bornebusch (1930) show that on these two areas 1.1 mgms. and 0.3 mgms. of oxygen are respired per square metre per hour at 13°C; this accounts for 2.0% and 0.3% respectively of the total respiration.

Cragg (1961) points out that it is dangerous to make too detailed a comparison between the estimates of metabolic activity since the respiratory rates of the

Table 94. Maximum and minimum estimates of biomass on the four main sampling sites, in grammes per square metre.

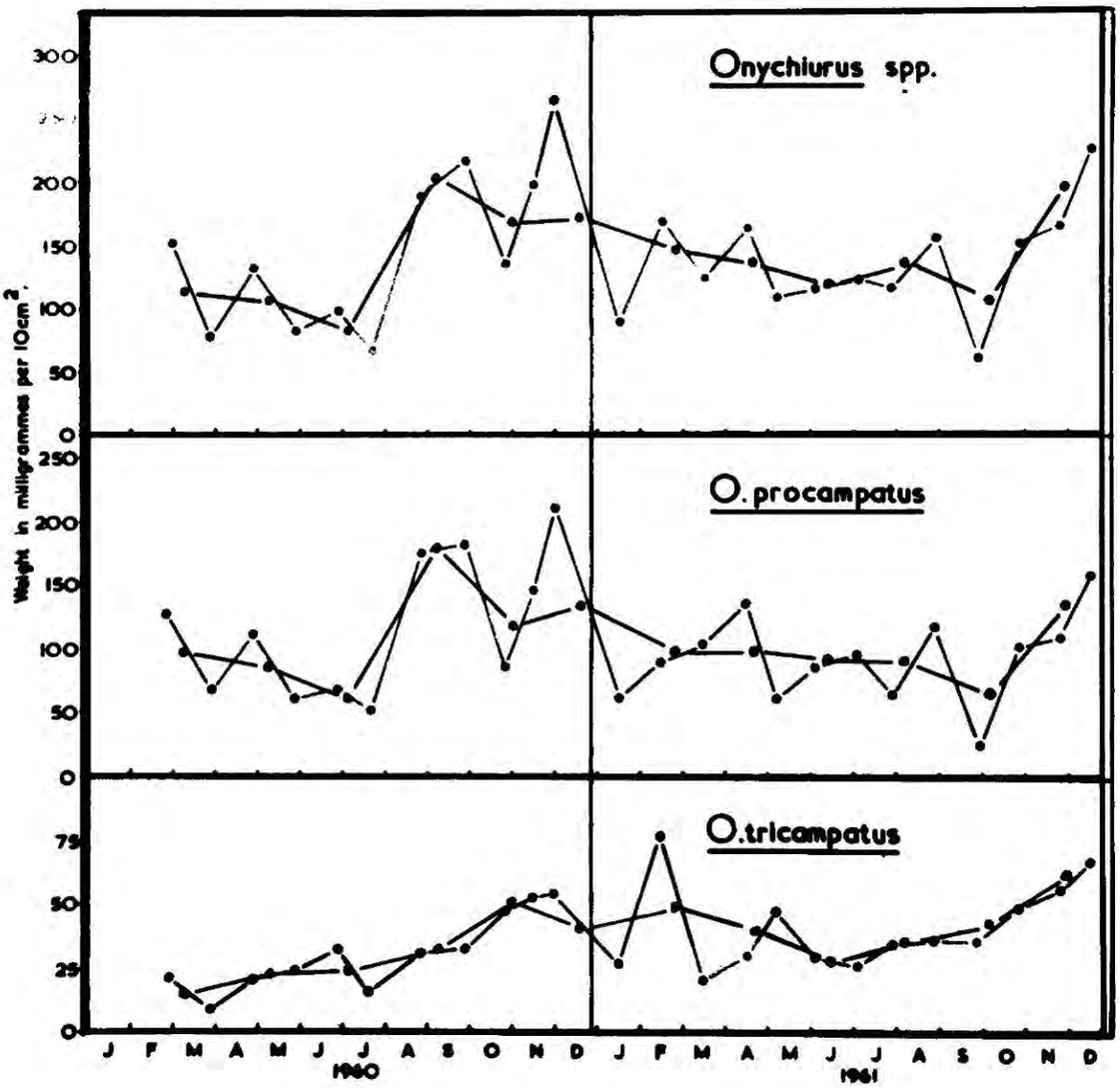
Sampling site	Maximum	Minimum	Average
Limestone grassland 1960	0.53	0.13	0.33
Limestone grassland 1961	0.45	0.13	0.29
Alluvial grassland 1960-61	0.54	0.19	0.37
Heather litter 1961	0.47	0.10	0.29
Juncus squarrosus 1961	0.24	0.06	0.15

Fig. 34.

Biomass of Onychiurus procampatus and O. tricampatus on Limestone grassland, Moor House 1960-61. Bimonthly averages of the data are shown in Fig. 34a.

Fig. 34a.

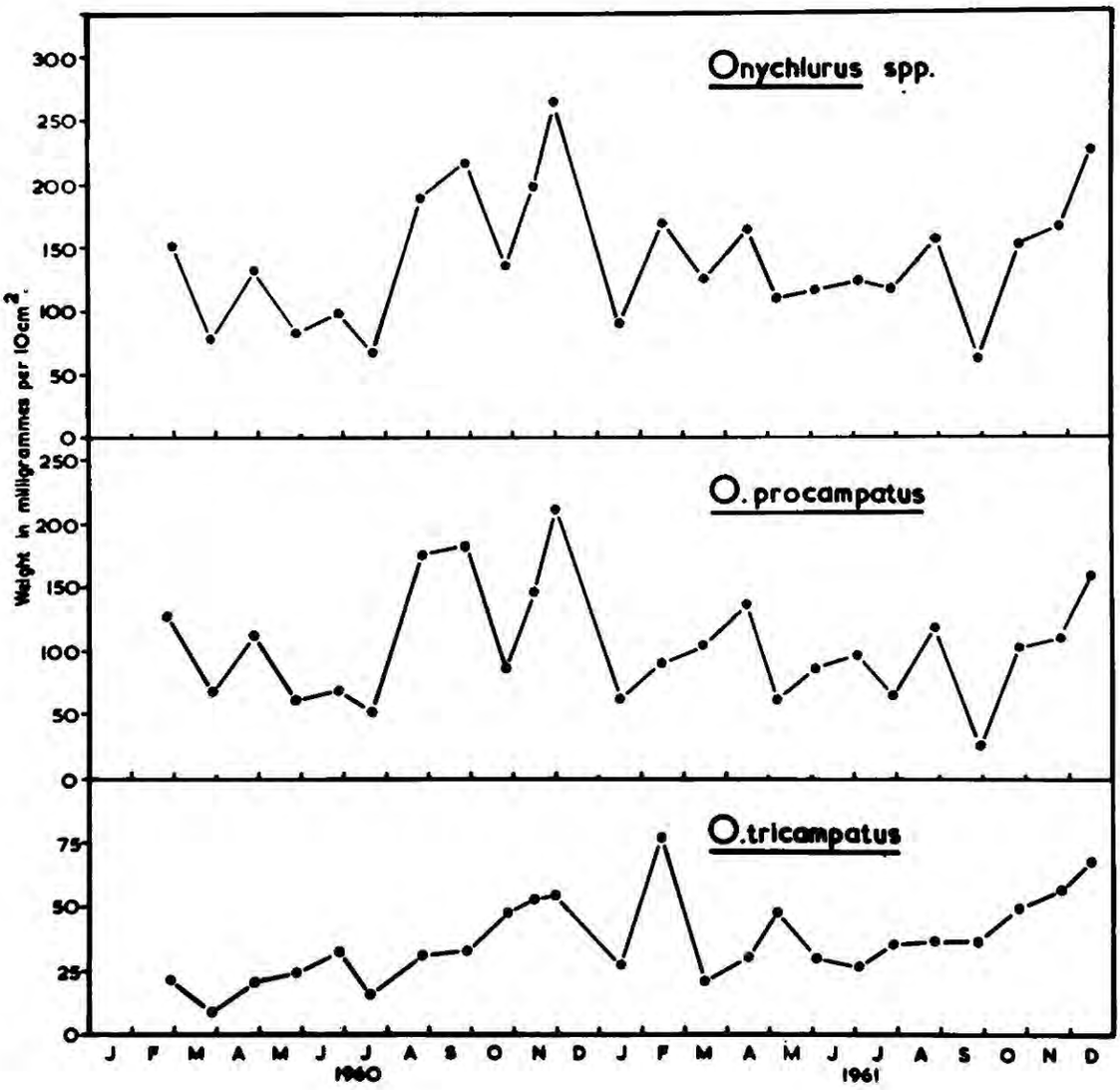
Biomass of Onychiurus spp.. Limestone grassland 1960-61.



Bimonthly averages.

Fig.34.

Biomass of Onychiurus spp.. Limestone grassland 1960-61.



animals under natural conditions are not known. Even so, it is clear that Collembola play a smaller part at high altitudes, than is suggested by the theoretical example for a meadow soil constructed by Macfadyen (1957), where Collembola account for 6.4% of the total biomass and 15.2% of the total metabolism in calories. Cragg (1961) has pointed out that this is largely due to the relative absence of earthworms and enchytreids in Macfadyen's example. It thus appears that the Collembola play a smaller part in the general soil turnover on high-altitude moorlands than their numerical abundance would suggest.

PART E.

GENERAL DISCUSSION

GENERAL DISCUSSION

1) Introduction.

In viewing the present work in relationship to a wider field of knowledge, this is probably best considered from the point of view of the role played by Collembola in moorland soils. In the following discussion this will be reviewed in terms of population density, general metabolism and the part played in actual soil formation.

2) Population densities.

Estimates of population densities which occur in the literature vary greatly, and a summary of the available information is given in Table 95. Glasgow (1939) has estimated that in some soils Collembola constitute up to 80 per cent of the total numbers of animals but due to size differences this is clearly no indication of their relative importance.

It has been shown (Table 86) that high average population densities of Collembola occur in an area of the northern Pennines which experiences a sub-Arctic climate, and these tend to be higher than the densities which are recorded in the literature for more low-lying areas; possibly this may be accounted for by the improved extraction technique used in the present work. However, it can be concluded that, purely from the point of view of total numbers, Collembola are at least as numerous on

Table 95. Estimates of population densities from different soil types.

Author	General habitat type	Vegetation and/or soil type	Density in thousands per m^2
van der Drift (1950)	Forest soil	Fagus mor	0.7
Poole (1961)		Pseudosuga litter	40.0 *
Forsslund (1945)	Heath	Vaccinium	15.0
Glasgow (1939)	Grasslands	Dactylis	27.0 *
Salt et al.(1948)		Pasture soil	43.0
Weis-Fogh (1948)		Sandy soil	8.5
Schaller (1949)		Limestone grassland	15.9 & 25.0
Dhillon and Gibson (1962)		Loam on boulder clay	33.0 *
Hale		Limestone grassland	52.92*(1960) 41.53*(1961)
		Alluvial grassland	43.69*(1960-61)
		Juncus squarrosus	20.93*
Strenske (1949)	Fen	Phragmites	20.0
Macfadyen (1952)	Fen	Molinia	25.0*
		Deschampsia	24.0*
		Juncus subnodulosus	7.2*
Hale	Mixed moor	Heather litter	35.17*(1961)

* Mean for twelve months.

Note. Only figures quoted in the literature after 1945 are given, as data collected previous to this date give very low estimates of population densities, due to the inefficiencies in the extraction methods used.

moorland areas as elsewhere, and that in all probability denser populations occur in this habitat.

3) Biomass and general metabolism.

The estimates of biomass given earlier tend to be smaller than the estimates appearing in the literature (Macfadyen 1952, 1962) for reasons already discussed. Whilst numerically Collembola constitute a large proportion of the fauna, from the point of view of total biomass they constitute only a small percentage. From data obtained during the present work, Cragg (1961) has compared the biomass and respiration of Collembola with other groups of the moorland soil fauna, and with the fauna of two of the sites studied by Bornebusch (1930). This data is summarised in Table 96. From this it can be seen that both from the point of view of biomass and general metabolism the Collembola form a relatively unimportant part of the fauna of Limestone grassland and Juncus squarrosus moor. However, on heather moor Collembola play a greater part in the general metabolism. Biomass figures for mixed moor are little below those for Limestone grassland, ie. about 0.4g/m^2, and Cragg (1961) has estimated that on this soil type Collembola account for 1.4 per cent of the total biomass. Thus it appears to be on mixed moor that Collembola are of most importance on upland soils, from the point of view of total metabolism.

Table 96. A comparison of biomass (live weight) and respiration for two of the Bornebusch (1930) sites and two of the Moor House sites. Modified from Cragg (1961).

Site	Collembola		Total fauna	
	g/m^2	Respiration ($mg.O_2/m^2/hr$ at 13°C.)	g/m^2	Respiration ($mg.O_2/m^2/hr$ at 13°C.)
Limestone grassland	0.6 (0.3%)	1.1 (2.0%)	189.7	54.9
Juncus squarrosus	0.1 (0.1%)	0.3 (0.3%)	78.0	107.0
Quercus mull Bornebusch (1930)	5.2 (5.8%)	9.6 (25.5%)	90.1	37.7
Picea raw humus Bornebusch (1930)	6.8 (13.6%)	20.0 (22.9%)	50.0	87.4

The figures quoted by Bornebusch (1930) are, in the opinion of the present writer, much too high. Biomass figures of the order of ten times those recorded from Moor House are claimed for densities fifty times smaller, even where many of the same species occur in both areas. Thus no good comparison can be made between the Moor House sites and the Bornebusch sites. However, it is worth noting that Macfadyen (1962) also quotes a high figure (13.4%) for the relative metabolic activity of Collembola in grassland soil; here, again, biomass estimates, on which the calculations of metabolic activity are based, are probably too high.

A further important point arising from the small percentage biomass of Collembola is that because of this they can form only a relatively unimportant potential source of food for predators, and, from the quantitative point of view, a relatively insignificant part of the total food web on moorland soils.

4) The life cycles of Collembola in a sub-Arctic climate and their effect on the contribution to the general soil turnover.

Apart from their metabolic activities during life, like any other soil animals Collembola contribute to the general soil turnover on dying, on the breakdown of the

body by soil micro-organisms. Thus, in areas where several generations occur each year this type of contribution is greater than where few generations occur. It has been shown that in the sub-Arctic climate of the northern Pennines only one, or at the most two generations occur each year, and that metabolism is accelerated by higher temperatures and retarded by lower temperatures. Clearly, then, the annual contribution of Collembola at high altitudes is in this way smaller than in areas having a milder climate.

Whilst many soil animals living under sub-Arctic conditions are active at low temperatures, this is particularly noticeable in the Collembola where there is apparently no diapause, and most species are fully active just above freezing point (Kuhnelt 1950). Choudhuri (1958) and South (1959) found threshold temperatures of about 4°C, below which no egg development occurred. The latter author also found that in the field Entomobrya multifasciata laid only when the temperatures exceeded 5°C., and laying ceased when temperatures fell below this level. It was found during the present work that eggs laid by Moor House Collembola would develop in a temperature as low as 2°C., and some individuals laid eggs at temperatures not exceeding 3°C. Whilst Choudhuri and South worked on Collembola from low-lying areas, the present work is related to Collembola living normally in a sub-Arctic climate;

it thus appears possible that there is a physiological mechanism allowing the Moor House forms to carry out biological processes at temperatures below those at which it is possible for the same processes to be carried out at lower altitudes, in a relatively warmer climate. It is thus possible that, whilst contributing relatively little to the soil by way of decaying animal remains, Collembola contribute relatively more to the soil turnover than other groups by remaining active at low temperatures.

5) The role of Collembola in soil formation.

In the living state Collembola contribute to the soil in two different ways. Firstly, they remove from it material which is ingested into the gut and, secondly, they produce faecal pellets which are added to the soil. Collembola have been recorded taking into their guts fungal mycelia, detritus, arthropod excreta and mineral particles and it is clear that everything that is ingested must not be regarded as food (see pages 70 and 71). In all probability particles are ingested for their fungal or bacterial content and their partial breakdown by Collembola may be an important factor in their being made more readily available to other decomposers. Stockli (1950), Dunger (1956, 1958) and Schuster (1956) have drawn attention to this aspect of soil formation by Collembola and mites and have considered their role in humus formation. Poole

(1959) has suggested that Collembola may play an important part in the dissemination of fungi, and in the breakdown of faeces of larger arthropods. Doeksen (pers. comm.) has demonstrated the presence of bacteria which break down chitin in the intestines of Collembola. It has been recorded in the present work that Collembola eat their own cuticles, and it is possible that they ingest chitinous material in the form of remnants of other arthropods. In this way Collembola may play an important role in making chitinous material re-available in the soil.

Zachariae (1962) has concluded that the contribution of Collembola to the mechanical and chemical breakdown of the soil is insignificant in forest soils. The weight of evidence suggests that this is, in fact, not the case. In addition to what has already been said there is the additional evidence of what has been termed by Muller (1879, 1884) "insect mull" soils. Probably the best known of these is the Alpine Pitch Rendzina of Kubiena (1953, 1955) where the A_1 and A_2 horizons are largely of coprogenous origin, with the presumed collembolan faeces forming layers up to 30 cm. deep. Schaller (1950) has calculated that populations of Collembola of the order of 100,000 per m^2 produce 183 cc. of faeces annually, which is equivalent to a soil layer 0.2 mm. in depth. However, this disregards breakdown by leaching and biological activity which, under the climatic conditions prevailing

in the northern Pennines, would occur relatively quickly. Zachariae (pers. comm.) has expressed the opinion that the Alpine Pitch Rendzina has been produced not by Collembola but by Enchytreidae; however, since no distinction can at present be made between the faecal pellets of the two groups, this cannot be regarded as established.

Kubiena (1955) has described how a coprogenous soil (peat moder) can be derived from undecomposed peat, if the water table is lowered. Whilst the possibility that Enchytreidae may be responsible to a large extent for the formation of coprogenous soils, since the density of mites and Collembola together exceeds that of Enchytreidae on the mixed moor, it seems reasonable to assume that they play at least an equal part in the accumulation of faecal material in such a situation.

On peat soils, the relative importance of Collembola is increased by the absence of earthworms and millipedes. According to Kubiena (1955), Blower (1956) and van der Drift (1951) millipedes are largely responsible for the formation of 'mull-like moder' in some forest soils.

Whilst on the face of it Collembola may not appear to be of great importance in the general soil turnover it may be that in the comminution of plant residues and in their activity in raw humus they play an indispensible role; this aspect of the activity of Collembola in the soil should

be carefully assessed in future work on the feeding activities of the group.

6) Conclusion.

The present study has involved the discussion of the relevant literature under the various aspects of the work, and a general discussion as to the relationship of Collembola to soil formation has been made. The work consists mainly of a factual addition to our meagre knowledge of the biology of Collembola, and in particular to our knowledge of upland forms. It is clear that to obtain a comprehensive picture of the ecological importance of Collembola on moorlands, a great deal of work will be necessary in the future, and particular problems have been outlined in the text. Suffice it to say that this thesis provides a fragment of information on moorland animals, and, as such, contributes to the study of moorland ecology. To quote from Cragg (1961), ".... provided that the aim of the main study is remembered .... what are the functions of these organisms in the biological history of moorlands?.... then fragmentation should increase our understanding, not lessen it".

SUMMARY

SUMMARY

1. A study of the Collembola of the Moor House National Nature Reserve, Westmorland, which experiences a sub-Arctic climate, is described.

2. 56 species of Collembola are recorded as being collected, three of which are new to the Moor House Reserve, and one, (Anurida forsslundi) to the British list. Notes on the taxonomy and autecology are given.

3. Reproductive behaviour is described and the conclusions of Mayer (1957), that spermatophores are not produced by members of the Poduridae and Onychiuridae, are supported.

4. Spermatophores of Tomocerus minor and Dicyrtoma minuta are described, and the methods of retention of the sperm droplets at the tips of the stalks, by a loop in the case of T. minor, and by a special conical structure in the case of D. minuta, are considered.

5. Methods of sperm transfer are discussed, and the possibility of the use of the ventral groove and ventral tube considered.

6. Oviposition is described; it may take from two minutes, in Isotoma sensibilis, to eighty minutes in Dicyrtoma minuta, to lay a single egg.

7. Mean egg batch sizes in mass cultures may vary from 4.6 in Onychiurus procampatus to 34.9 in Isotoma olivacea. Isolated females may lay more eggs, up to 51 being recorded in a single laying period by Isotoma viridis.

8. In Lepidocyrtus lanuginosus the mean egg batch size increases with age, from 5.7 at 8 weeks (fifth instar) to 36.3 in adults.

9. Tullbergia krausbaueri is able to lay in the third instar, but it is more usual for egg laying to begin in the fourth or fifth instar; thereafter eggs are laid after each moult up to the fifteenth.

10. In T. krausbaueri the number of eggs laid during each period of oviposition increases until the seventh or eighth instar, and afterwards decreases.

11. Estimates of the total number of eggs laid during life are made; it is suggested that most Moor House species have about three periods of oviposition during which about 90 eggs are laid.

12. Laying occurs mainly in spring, but in some species, eg. Onychiurus procampatus, O. tricampatus, Tullbergia krausbaueri, laying continues throughout the summer. Lepidocyrtus lanuginosus lays mainly in autumn. Dicyrtoma spp. have two periods of oviposition, in summer and autumn, corresponding with two generations.

13. Egg development is described, and development periods at different constant temperatures are recorded. It is shown that in thirteen species the product of the development time in days and the temperature in degrees centigrade is a constant.

14. Graphing the development time in days and the temperature in degrees centigrade, a hyperbola is obtained in all cases.

15. Constants are calculated for constant temperatures and for fluctuating temperatures, and it is shown that these can be used for forecasting the development time of eggs in the field.

16. Eggs of Hypogastrura denticulata were kept for ten days at -7°C. and then allowed to develop at 4.5°C. The frozen eggs, when placed at 4.5°C. took a mean length of time of 95.1 days to develop, as compared with 91.6 days in the unfrozen eggs.

17. The number of pre-adult instars is recorded for several species, the data being obtained from laboratory cultures and from the field, as follows:
H. denticulata 5, T. krausbaueri 3, O. furcifer 6, O.latus 6, O. procampatus 5 and O. tricampatus 5.

18. Dyar's rule is found to be upheld.

19. The differences in chaetotaxy in successive instars is described in O. furcifer, O. latus, O. procampatus and O. tricampatus.

20. The duration of different instars at 15°C. is recorded, and is found to increase with age.

21. Constants are calculated from the products of the development time in days and the temperature in degrees centigrade, for constant and fluctuating temperatures;

times taken to attain maximum size in the field are calculated from these constants and found to approximate to recorded times for field development.

22. Sex ratios in four species are determined; these vary from equality in O. tricampatus to 100% females in O. procampatus, where a form of parthenogenesis occurs.

23. The age distribution of O. procampatus and O.tricampatus is shown over two years, and that of O. latus over one year. In the first two species all age groups (instars) occur throughout the year; in O. latus first instars occur in May and June and the species overwinters only as adults.

24. It is shown that in some species at least, the criteria for the division of the Onychiurus armatus species group are valid. The taxonomy of the group is complicated by a form of thelytokous parthenogenesis.

25. For studying population ecology a modification of the Macfadyen high gradient cylinder was used to extract Collembola from soil cores. Population densities of up to 230,000 per square metre are recorded.

26. A flotation extraction technique for peat soils is described, and this is found to have the same extraction efficiency for total Collembola as the high gradient cylinder; O. latus and I. viridis are extracted more efficiently using the flotation apparatus.

27. The presence of aggregations in Collembola is demonstrated by the use of the Coefficient of Dispersion, and the fact that the frequency distribution of sample unit values differs significantly from normal. The biological significance of aggregation is discussed.

28. The vertical distribution of Collembola is considered with respect to 0-3 cm. and 3-6 cm. layers in mineral soils. Significantly higher proportions of Collembola are found in the lower layer in summer and winter. The evidence suggests a vertical migration, but it is possible that the data show only a differential mortality.

29. An ecological difference between O. procampatus and O. tricampatus is shown; individuals of similar size occur at different depths, the former species being a surface form, the latter dwelling deeper.

30. Spring and autumn peaks in population densities are shown in total Collembola, and these probably correspond to two generations in some species.

31. Population densities for single species show:

1) A single annual peak in Isotomidae, probably corresponding to a single generation.

2) Two annual peaks in F. mirabilis, O.tricampatus, T. krausbaueri, Folsomia spp., and total Symphypleona, probably corresponding to two generations.

32. In considering the Collembola of eroding moor it appears that their distribution is governed by physical

factors which bring about alterations in the water content of the habitat. The fauna varies from hydrophil (typified by I. antennalis) on wet areas recolonised by Eriophorum angustifolium, to xerophil (typified by Tetracanthella wahlgreni)on the dry hagg lip.

33. Qualitative and quantitative differences between the fauna of Limestone grassland, Alluvial grassland, Heather litter and Juncus squarrosus are considered; rarer species are better indicators than the commoner ones, of differences between vegetation types; a significant difference in total numbers of Collembola occurs between all four vegetation types; Limestone grassland carries the highest mean annual population density (52.92×10^3 per m^2) and Juncus squarrosus the lowest (20.93×10^3 per m^2).

34. No difference in population density occurred in the distribution of Collembola in and between the rosettes of Juncus squarrosus.

35. On the mixed moor T. wahlgreni is found to be associated with drier areas characterised by Cladonia, and F.brevicauda with wetter areas of Sphagnum.

36. Biomass figures are given for O. procampatus and O. tricampatus and estimates are made from these concerning total biomass of Collembola. Average biomass estimates are 0.31 g/m^2 for Limestone grassland, 0.37 g/m^2 for Alluvial grassland, 0.29 g/m^2 for Heather litter and 0.15 g/m^2 for Juncus squarrosus.

37. The role played by Collembola in moorland soils is discussed from the points of view of population density, general metabolism, and the part played in soil formation; whilst on the face of it Collembola do not appear to be of great importance in the general soil turnover, it may be that in the comminution of plant residues, and in their activity in raw humus, they play an indispensible role.

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