Investigations on protozoa with special reference to moorland forms

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INVESTIGATIONS ON PROTOZOA WITH SPECIAL REFERENCE TO MOORLAND FORMS.

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Thesis submitted for the degree of Doctor of Philosophy in the University of Durham.

October 1959.

Acknowledgments.

I am greatly indebted to Prof. J. B. Cragg for his advice and assistance throughout the research period, and it is also a pleasure to thank the members of the Zoology Department at Durham, for their help in many different ways.

I am very grateful to Dr. M. Robertson, F.R.S. and Dr. M. Pittam, of the Lister Institute of Preventive Medicine for their training and hospitality; to the Staff of the Moor House Nature Reserve for their help; to Prof. G. Deflandre for checking species of Testacea; to Mr. C. C. Hentschel and the members of the Botany and Zoology Department at Chelsea College of Science and Technology for their help during the final preparation of the thesis; and to all other people who have given assistance during the research.

This research was only made possible by the receipt of a Research Studentship from the Nature Conservancy, to whom I am deeply indebted.

Memorandum

The work included in this thesis has not been submitted for any other degree and it is entirely original except where acknowledged by a reference.

Contents

INTRODUCTION.

Most of the work on Protozoa has been confined to the laboratory. Apart from the aspects of economic importance, particularly medicine, the cytology, physiology and genetics of many groups have been comprehensively studied. With the introduction of the electron microscope there has been a spate of works on the ultra-structure of Protozoa (see Robertson 1958).

Ecological studies have lagged far behind other aspects. A number of studies on the seasonal succession in water-bodies have been carried out (Wang 1928, Lackey 1938, Webb 1956, Bamforth 1958) and in some cases the "community structure" is examined (Noland 1925, Picken 1937, Fauré-Fremiet 1950). These studies have been restricted largely to flagellates and ciliates. Soil Protozoa have been briefly studied, particularly at Rothamstead Experimental Station, by Cutler, Crump and Sandon (Cutler and Crump 1935 and Sandon 1927) and more recently by Singh (Singh 1955).

With regard to the Testacea the basic taxonomy, as with other Protozoa, was largely worked out during the late C.19 and early C.20. This has been enlarged since 1930, largely by the many works of Decloitre, Deflandre, van Oye, Thomas and Hoogenraad and de Groot (see Hoogenraad and de Groot 1940). The ecology of the group has been studied mainly by European workers, collecting from Sphagnum and other mosses in fens and bogs. From this, another aspect of the subject has developed in the study of "sub-fossil" tests in peat (see Grospietch 1953, Harnisch 1948).

In Great Britain a number of general lists of species have been recorded, mainly between 1900 and 1920. (Cash, Wailes and Hopkinson 1901-1919; Cash 1904, West 1901, 1903, 1905; Wailes 1910, 1912, 1956; Wailes and Penard 1911; Murray 1905, 1907; Brown 1909a,b, 1911a, b, 1912, 1913, 1931). These provide a species list for the country but give no information on the ecology of species, as the sites are described only in a very general way, with no indication of the environmental conditions.

As there has been relatively little work on the ecology of Testacea, particularly in Great Britain, and as these animals are common in *Sphagnum*, it was decided to study the Testacea associated with the *Sphagnum* regeneration complex on Valley Bog at the Moor House Nature Reserve. This complex has been described by Murphy (1955) and it provides a series of habitats, differing markedly in water-content and characterised by various *Sphagnum* species. The aims of this study were, 1. to find if a series of Testacea was present, related to the different stages in the moss succession, 2. to study some of the factors influencing the distribution of Testacea in this succession and 3. to study the relationship between Testacea and other organisms.

In contrast to the acid areas of Moor House, *Sphagnum* was examined from areas of base-rich vegetation at Sunbiggin Tarn in Westmorland. Here a very different testate fauna was observed. As a result of this a number of fen and bog areas with a wide range of chemical conditions were/

were studied to see if the two types of area carried characteristic faunas. The sites for study were selected in connection with the work of Gorham and Pearsall (1956) and Gorham (1956a, b) who give data on the chemical nature of a large number of Lake District sites. Only Sphagnum was examined to restrict the variability between samples, but de Graaf (1956, 1957) sampled various mosses and the present results correspond closely with his.

This survey of bog and fen areas in northern England (Section 1) is compared with continental work, begun largely by Harnisch (1925, 1927) and followed by Jung (1936a), Jung and Spatz (1938) and others. The most detailed work however, is that of de Graaf (1956, 1957). Harnisch (1927) postulated a series of testate associations characteristic of different habitats. These have been variously accepted and rejected, but they are now usually taken as being generally applicable, though in need of further study and re-organisation. In the comparison with the continental work, it has been necessary to examine the British, German and Scandinavian terminology associated with fens and bogs.

The general survey was carried out on a qualitative basis, but in the early stages of the research, a quantitative technique was devised. This method proved to be too time-taking for population estimation, but it was used to study the micro-distribution of Testacea on individual Sphagnum plants (Section 2.). This appears to be the first examination of its type, apart from a general survey by Heinis (1945) which produced few results.

The majority of earlier workers paid little attention to the variability in form of the species which they studied, and it seems possible that in some cases, aberrant or deformed specimens have been described as new species or varieties. Some basic work on variation and the effects of selection were carried out by Jennings (1916) and other members of the Johns Hopkins University in America. These appear to have had little effect on the taxonomic methods of other workers, and little or no effort has been made to relate variations in morphology to environmental conditions, except by Štěpánek (1952). The polytypic species, Nebela tincta provided a good subject for the study of the relationship between morphology and environment at Valley Bog, where it was distributed throughout the succession of Sphagnum (Section 3).

In Section 4, the ecology and taxonomy of a number of individual species is dealt with. The taxonomy is discussed when the identification is doubtful or there is difficulty with synonomy. Prof. G. Deflandre kindly checked the identification of about 50 species and these are listed in Appendix 3. Where there is disagreement, the case is discussed in Section 4. This is followed by a discussion on the factors effecting the distribution of Testacea and the taxonomic difficulties of the group.

Section 1.

The distribution of Testacea in Fen and Bog areas.

THE DISTRIBUTION OF TESTACEA IN FEN AND BOG AREAS.

Identification.

The main works used for identification of Testacea were Cash, Wailes and Hopkinson (1901-1919), Penard (1902) and Hoogenraad and de Groot (1940). For the genera Arcella, Centropyxis and Nebela, Deflandre (1928b, 1929, 1936) were used. The numerous papers of Decloitre and van Oye were referred to for individual species. In a number of cases, closely related species could not be separated and these are discussed in Section 4. Throughout the text these are grouped under specific names and are indicated by *. The asterisk is omitted when the species sensu stricto is referred to.

Sphagnum species were identified from Proctor (1955) and Dixon (1904), other plants by Clapham, Tutin and Warburg (1952).

Terminology.

It is essential to define a number of terms which are used, but it must be stressed that these are designed only for the areas studied and the general use of the terms will be discussed later.

Fen: A general term covering topogenous or soligenous areas, usually on mineral soils, with the water pH usually >5.0. These areas bear a rich vegetation with Phragmites and/or Carex spp. common, though they may be absent in poor fens.

Bog: A general term covering areas on peaty soil which are ombrogenous or fed by mineral-poor water with pH <5.0. The vegetation is poor in species, usually with a fairly complete Sphagnum cover often in hummocks, and many Ericaceae.

Lacustrine Bog: Soligenous areas of poor fen usually developed on a lake edge behind a Phragmites swamp, with little peat formed. The vegetation is poor in species relative to fen areas and mainly in the form of Molinia tussocks with Myrica gale and Narthecium. Sphagnum is sparse but may increase at a later stage of development.

Valley Bog: An area of bog, mainly soligenous but sometimes partly ombrogenous, with a flat or concave surface, developed in a valley or lake basin. A complete or nearly complete Sphagnum cover with typical bog vegetation is always present.

Raised Bog: Very acid, relatively dry, ombrogenous bog developed on valley or lacustrine bog. A complete or nearly complete Sphagnum cover, with many ericaceous shrubs and some pine and birch, is present.

Acid: The term is used, not in the chemical sense, but to mean any area with pH <5.0. (Conway 1949).

Methods

pH.

Measurements of pH were carried out on water squeezed from Sphagnum, usually within 24 hours of collection. Various electrical instruments were used. A Cambridge pH meter and a Pye Universal pH meter at Durham were used for the Moor House samples, a Cambridge pH meter at the Freshwater Biological Association Laboratory at Windermere for the Lake District samples, and a pH-probe (Analytical Measurements Ltd.) for samples from Sunbiggin Tarn and some Moor House samples. There will obviously/

obviously be variation in the accuracy of these instruments, but this will be outweighed by seasonal and local fluctuations (Paulson 1952, Rose 1953, Messikommer 1943).

The pH values of Gorham (1956 a, b) and Gorham and Pearsall (1956) recorded in the text, were taken by pressing a bottle into the soil, into shallow pools or from open water. The methods used are particularly important because many species of Sphagnum have the ability to alter the pH of the medium by ion-exchange to the preferred optimum of the species (Skene 1915, Ziegenspeck 1936, Conway 1949, Bell 1959). In a number of cases a marked fall in pH occurred where the Sphagnum was just above water level (pp.9-11). This may be due to the Sphagnum or to increased oxidation.

Water content.

The water content of each sample was recorded using the following scale, the figures in brackets representing the scale proposed by Jung (1936b). The latter was not used because the distinction between the different grades was too fine.

1. Submerged. (1 and 2)
2. Saturated, water running out without pressure. (3)
3. Wet, little pressure needed to release water. (4)
4. Fairly wet, firm pressure required to release water. (5 and 6)
5. Dry, strong pressure needed to release water. (7 and 8)

Sample collection and examination.

Samples were taken from all the obviously different habitats in the

areas,/

areas, and placed into arbitrary groups, based mainly on pH and water content.

Each sample was composed of about 6 strands of Sphagnum which were placed in 2" x 1" glass tubes and examined within a few days of collection, or preserved in 70% alcohol to be studied later. When examined, water was expressed into 3 watch glasses and observed under x30 and x100 magnifications. If the detritus or diatoms were very dense, portions were spread on slides and re-examined. Each species was recorded with an estimate of the abundance, as rare, few, common or abundant, and the state of the tests as full, encysted or empty. In most samples, both full and empty tests were present and no difference in their distribution was recorded.

THE SAMPLE AREAS.

Esthwaite North Fen, Westmorland.

The vegetation of this area, (Nat. Grid Ref. SD 355975, c60m. above sea level) has been described by Tansley (1939) and Pearsall (1918). Briefly, in the zone studied, it is composed of a succession from open water, through Phragmites reedswamp, Betula-Alnus-Salix carr and Molinia lacustrine bog, to grass and sedge meadow.

S.subsecundum is present in a flush at the edge of the Phragmites zone, where the reedswamp merges with Betula and Salix. Iris pseudacorus, Typha latifolia, Menyanthes trifoliata, Carex spp. and Filipendula ulmaria are obvious among the tall, dense vegetation. The Sphagnum/

Sphagnum is either submerged in shallow water, or is just emergent, the latter having a much reduced pH of 4.7-4.8, compared with 6.2-6.4 of the submerged Sphagnum. As it is close to the lake edge, this area will certainly be flooded regularly by lake water, pH 6.8-7.0. Gorham and Pearsall (1956) and Gorham (1956 a) recorded many pH values 5.1-7.6 from Esthwaite reedswamp and carr.

In the lacustrine bog, Molinia caerulea forms large tussocks, between which is a network of narrow peaty runnels. Myrica, Narthecium, and Filipendula occur locally and a few Salix are present. Sphagnum occurs in small patches between the Molinia tussocks where the water level is just at or above the surface of the peat, and also in a few small areas about 10-15 cm. above water-level. Gorham (1956 a) recorded pH values of 6.92-7.30 and Sphagnum squeezings taken in the course of the present survey gave pH 5.6-5.7.

The samples are grouped as follows.

Esthwaite 1. 7 samples S.subsecundum from Phragmites zone, water-content (W) 1, pH 6.2-6.4

" 2. 6 samples S.subsecundum from Phragmites zone, W 2, pH 4.7-4.8

" 3. 5 samples S.recurvum and S.rubellum between tussocks in Molinia zone, W 2, pH 5.6-5.9

" 4. 7 samples S.squarrosum and S.rubellum in Molinia zone, W 4.

Sunbiggin Tarn, Westmorland.

Two distinct areas near Sunbiggin Tarn, (Nat. Grid Ref. NY 677076, c250m. above sea level) were investigated. The first, a rich fen community on the edge of the Tarn, the other an area of calcareous springs about 0.5 km. south-west of the Tarn.

The fen bordering the limestone Tarn has been described by Holdgate (1955b) and in one area of Carex rostrata swamp south-east of the Tarn, are patches of S.contortum either submerged or just emergent. The latter will almost certainly be periodically submerged by Tarn water of pH 8.2 (Holdgate 1955b). Holdgate recorded the pH of the fen as 6.0-6.5 and in the present survey, submerged Sphagnum gave pH 6.5-7.0 while squeezings from the emergent Sphagnum gave pH c.5.3.

In an area of "upper fen" vegetation dominated by Filipendula ulmaria, again to the south-east of the Tarn, a small hummock of S.palustre was sampled.

The samples are grouped and named as follows.

Sunbiggin Tarn 1. 18 S.contortum samples from Carex rostrata fen, W 1-2, pH 5.3-7.0

" " 2. 5 samples of S.palustre from "upper fen", W 5, pH 3.3-3.5

The calcareous springs give rise to mounds of tuffa, and wet flushes of rich fen vegetation with Carex spp. and much Scorpidium scorpioides in very shallow water. Mounds of Sphagnum up to 60 cm. high rise from the flushes (Plate 1). Similar flush areas, without Sphagnum hummocks, have/

Plate 1. Sunbiggin Spring zone showing acid _Sphagnum_ hummocks rising from _Carex_-dominated calcareous flush.

have been described by Holdgate (1955a) with a pH 7.5-8.5. In the flushes studied the pH varied from 6.1-7.9 depending on the extent of open water.

S.subsecundum and S.plumulosum occur at the base of the hummocks and on saturated areas bordering the open water, associated with Scorpidium scorpioides. The pH of these sphagna was 4.1-5.4 but this will obviously fluctuate greatly with seasonal variation in the water level. The samples were taken on 2nd June, 1958.

Shallow areas of S.papillosum $<$15 cm. above water level are frequent with some Calluna and Erica mixed with Carex spp., the latter probably being rooted in deeper mineral-rich layers. In the well developed hummocks, S.rubellum is dominant. The pH falls rapidly above water-level and in the hummocks, it corresponds closely with the pH of hummocks in bog areas.

The spring area is of the type described by Sjörs (1950) as "mixed mire" with "moss islands" or hummocks of bog vegetation separated by a network of wetter fen.

Samples from the spring area are grouped and named as follows,

Sunbiggin Spring 1. 7 S.subsecundum samples, W 2, pH 4.1-5.4

" " 2. 9 S.plumulosum samples, W 2, pH 4.1-5.4

" " 3. 7 S.papillosum samples, W 3.

" " 4. 12 S.rubellum samples, W 4-5, pH 3.5-3.9

Nibthwaite Swamps.

Gorham and Pearsall (1956), in a table headed " -----transitional lacustrine swamps" give chemical data and the main vegetation of "Nibthwaite Swamp". No grid reference is given and in the present survey two areas on the south-west shore of Coniston Water, c40m. above sea level, were examined, the second probably being the one which Gorham and Pearsall sampled.

The first area (A), (Nat. Grid Ref. SD 389899,) is a small Molinia lacustrine bog, similar to that at Esthwaite. It is separated from the lake by a narrow Phragmites reedswamp and surrounded on the other sides by Betula and Salix. The Molinia is tussocky with some Narthecium Juncus and Salix. Small patches of Sphagnum are present between the Molinia tussocks and also on the edge of the Phragmites zone, where it is mixed with Carex spp. Water squeezed from saturated Sphagnum from both areas gave readings 4.4-5.2, but the area is liable to flooding by lake water, pH 6.8-7.0 (H.C. Gilson, personal communication).

This area differs from that described by Gorham and Pearsall in its species - poor vegetation and the lack of pools.

The second area (B), (Nat. Grid Ref. SD 288903,) has a richer flora and is also separated from the lake by a marginal Phragmites zone. On the main bog surface are two shallow pools with Carex spp., Menyanthes trifoliata Equisetum limosum, Utricularia minor and Eriophorum angustifolium. In the drier area Myrica, Narthecium and Eriophorum spp. are present with Molinia which appears to be less tussocky than at Esthwaite/

Esthwaite due to the more complete Sphagnum cover. Calluna is present on the dry areas near the Torver-Blawith Road, from which the bog is separated by a bank of Pteridium aquilinum. This area corresponds closely with that mentioned by Gorham and Pearsall (1956). They recorded a pH 6.43 for the pool water and in the present survey, water drained from submerged S.subsecundum gave pH 5.7.

The samples from the two bogs are grouped and named as follows.

Nibthwaite (A) 1. 8 samples S.subsecundum at margin of Phragmites zone and between Molinia tussocks, W 1-2, pH 4.4-5.2

" (B) 2. 4 samples S.subsecundum submerged in pool, W 1. pH 5.7

" " 3. 3 samples S.subsecundum beside pool, W 3-4.

" " 4. 4 samples S.nr. palustre from hummocks near road, W 5.

Lady Vane Pot, Moor House, Cumberland.

Lady Vane Pot (Nat. Grid Ref. NY 353345) is an artificial pond, area about 600 m^2, situated just outside the eastern boundary of the Moor House Nature Reserve. Well marked zones of Chara, Equisetum limosum, Potamogeton natans and Carex rostrata are present and there are signs of considerable iron staining. On the western edge of the pond is a sward of Sphagnum, about 1 m. wide, mixed with Juncus effusus and Carex rostrata. S.squarrosum occurs at the edge of the pond and within about 0.5 m. of the waters edge it mixes with S.recurvum. The latter is the sole species in the outer parts of the sward.

The S.squarrosum when sampled (8/VI/58, 24/IX/58, 24/XI/58) was not fully/

fully submerged and had a pH 5.2-6.6. It is probably flooded at certain times of the year by pond water, pH 8.1 (Gorham 1956b). The pH in the sward falls to about 4.2 further from the waters edge.

The samples are grouped and named as follows.

Lady Vane Pot 1. 7 samples S.squarrosum at waters edge, W 2, pH 5.2-6.6

" " " 2. 5 samples S.squarrosum, S.recurvum about 0.5 m. from the waters edge, W 3, pH 4.2-5.7

" " " 3. 5 samples S.recurvum, S.squarrosum c.1 m. from waters edge, W 4, pH 4.2

Blelham Bog, Westmorland.

This is a Molinia-Myrica-Sphagnum lacustrine bog (Plate 2) developed behind a narrow Phragmites-Carex reedswamp on the edge of Blelham Tarn, (Nat. Grid Ref. NY 367007, c40m above sea level). A carr of Alnus, Betula and Salix is also present. The bog is similar to that at Esthwaite though possibly at a later stage of development with more Myrica and Narthecium, and in the drier places Calluna. Some Phragmites occurs on the bog. Sphagnum is more extensive than at Esthwaite, with S.subsecundum between the Molinia tussocks and carpets of S.papillosum on the parts of the bog furthest from the Tarn. S.subsecundum is also present in small quantities on the edge of the Phragmites zone. The pH varied little between the Phragmites zone and the bog as shown below.

Plate 2. Belham lacustrine bog, looking away from the Tarn, showing Molinia and Myrica in the foreground, white heads of Narthecium in the centre and Phragmites in the background.

	Phragmites	Bog
Present survey	5.7	5.6-6.3
Gorham and Pearsall (1956)	5.6-6.0	4.8-5.9
Pearsall (1938)	5.5	5.4

The pH of the Tarn water is 6.8-7.0 (H.C.Gilson personal communication) or 6.2-7.3 (Pearsall and Mortimer 1939).

The samples are grouped and named as follows.

Blelham Bog 1. 7 samples S.subsecundum, 4 from Phragmites, 3 from between Molinia tussocks, W 1, pH 5.7-6.3

" " 2. 6 samples S.subsecundum, S.papillosum, 4 from Phragmites, 2 from Molinia zone, W 2-3.

" " 3. 6 samples S.papillosum from bog, W 4-5, pH 4.1.

Dale Park Swamp.

This area, (c.120m. above sea level, Nat. Grid Ref. SD 361935) is described by Gorham and Pearsall (1956) and Gorham (1956a) as a transitional lacustrine swamp with some drier bog areas. It is formed in a shallow lake basin and has a considerable Sphagnum cover. Some pools are present with S.cuspidatum and S.subsecundum plus Carex spp. and Eriophorum angustifolium. Narthecium is common on the pool edges with Drosera rotundifolia and in the drier places Oxycoccus, Calluna and much Myrica gale. The pH recorded from the pools was 4.2, Gorham (1956a) quoting 4.22 and 4.35.

In the North-West corner is a large marginal stream with S.recurvum

and/

and S.subsecundum submerged among Juncus effusus, Carex, Menyanthes, Potamogeton polygonifolius and Utricularia. Sphagnum squeezings gave a pH range 4.7-5.6. Gorham and Pearsall (1956) state that this zone "represents the original mineral soil water type" with a pH 5.75-6.06 and Gorham (1956a) records pH 6.19-6.86 for "the line of water movement".

A typical S.recurvum sward occurs at the edge of the marginal zone with Juncus effusus and some Carex and Myrica. In these areas little or no open water is present, though the Sphagnum is saturated. Here the pH is much lower than in the Sphagnum from the stream.

Samples are grouped and named as follows.

Dale Park 1. 7 samples S.subsecundum, S.cuspidatum, S.papillosum in bog pools, W 1, pH 4.2

" " 2. 6 samples S.subsecundum, S.cuspidatum, S.papillosum and S.capillaceum, W 2-3, pH 4.1-4.2

" " 3. 5 samples S.papillosum, S.capillaceum, W 4-5.

" " 4. 6 samples S.recurvum at edge of marginal stream, W 1-2, pH 3.9-4.1

" " 5. 8 samples S.recurvum, S.subsecundum in marginal stream, W 1-2, pH 4.7-5.6

Muckle Moss, Northumberland.

The vegetation and history of this moss (c.200m. above sea level, Nat. Grid Ref. NY 805669) have been fully described by Pearson (1954). It is a flat valley bog, about 2.5 km. long and 300 m. wide, developed in a shallow lake/

lake basin and bearing various plant communities which have been much affected by burning, draining and grazing.

The samples were taken mainly from the western end of the moss as this has been least affected by man and carries the most varied communities,some of which are listed below.

1. A central zone, surrounded by a horseshoe of pools of various size containing Sphagnum. Among Pinus and Betula is a mixed Sphagnum and Polytrichum cover with Eriophorum angustifolium, Carex and Calluna.

2. A hummock complex of Sphagnum in the north-west of the moss with a succession S.cuspidatum, S.recurvum, S.papillosum, S.magellanicum and S.capillaceum (= S.nemoreum). Pools are very rarely developed and the hummocks are topped with Calluna, Erica tetralix, Empetrum nigrum, Eriophorum vaginatum and Cladonia. Andromeda polyfolia is also present.

3. A Calluna-Eriophorum vaginatum community with Sphagnum. This community results from intense burning.

4. At the northern margin of the moss is a poorly developed lagg, in the form of a Betula-Salix carr with a ground cover of Sphagnum, mainly S.recurvum, with Carex spp.

pH readings from the pools on the bog surface show a rather low range of 3.6-3.8 (11/VI/58) and in the hummocks 3.2-3.5 was recorded. In the lagg zone saturated Sphagnum gave pH 5.2-5.3. These readings cannot be compared directly with those of Pearson (1954) as his samples were taken from 10 cm. below the peat surface. He recorded readings from the main bog as 3.0-4.7 and the lagg, 5.2

The samples are grouped and named as follows.

Muckle Moss 1. 7 samples S.palustre, S.cuspidatum, S.tenellum in pools, pH 3.6-3.8

" " 2. 5 samples S.palustre, S.cuspidatum, S.magellanicum, S.papillosum, S.capillaceum, W 2.

" " 3. 9 samples S.magellanicum, S.cuspidatum, S.palustre, W 3-4, pH 3.4-3.5

" " 4. 12 samples S.magellanicum, S. capillaceum, S.papillosum, W 4-5, pH 3.2-3.5

Muckle Moss Carr 1. 4 samples S.recurvum, W 2, pH 5.2-5.3

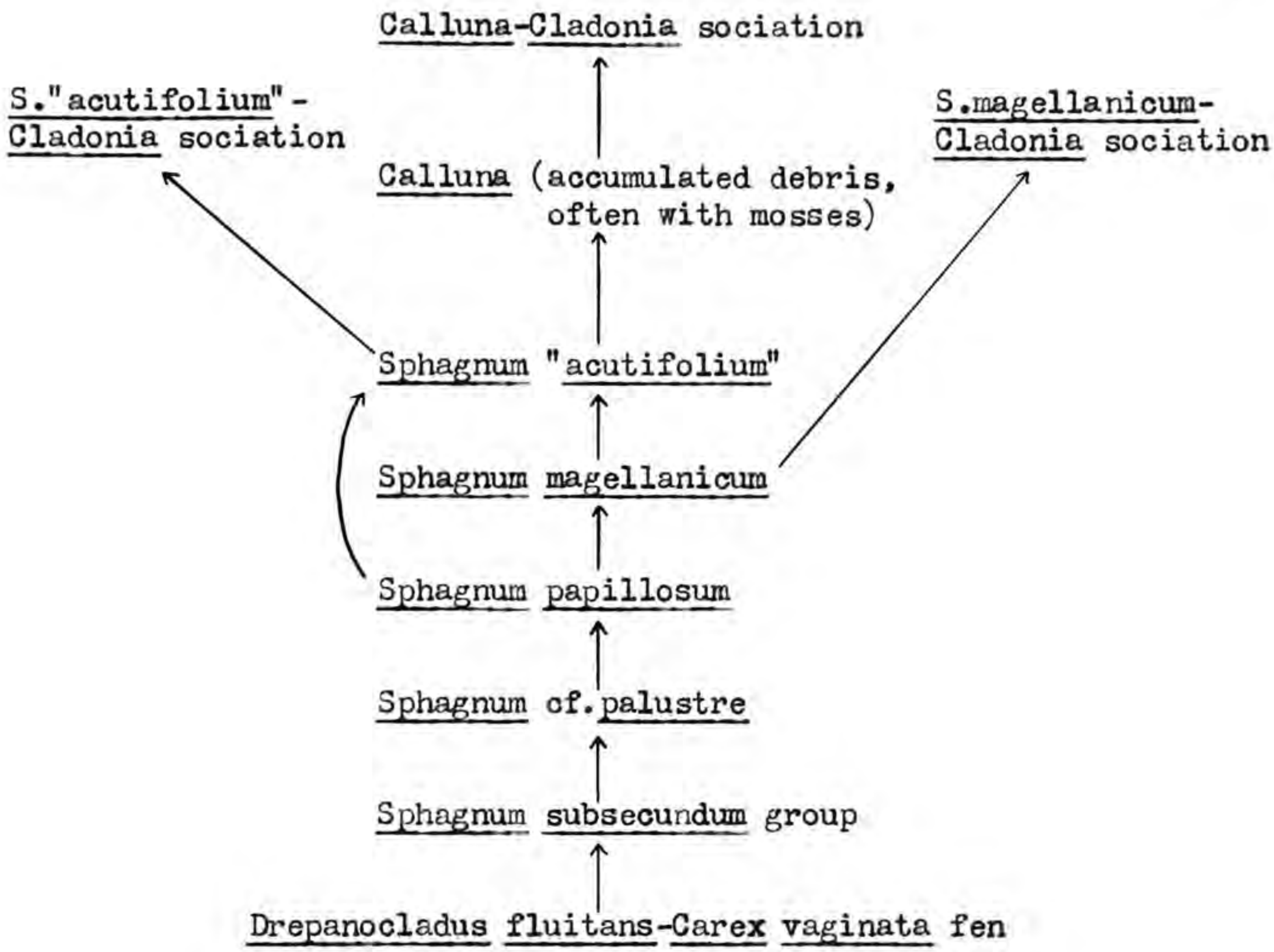
" " " 2. 6 samples S.recurvum, W 3-4, pH 3.8

" " " 3. 4 samples S.palustre, S. magellanicum, W 5.

Valley Bog, Moor House, Cumberland.

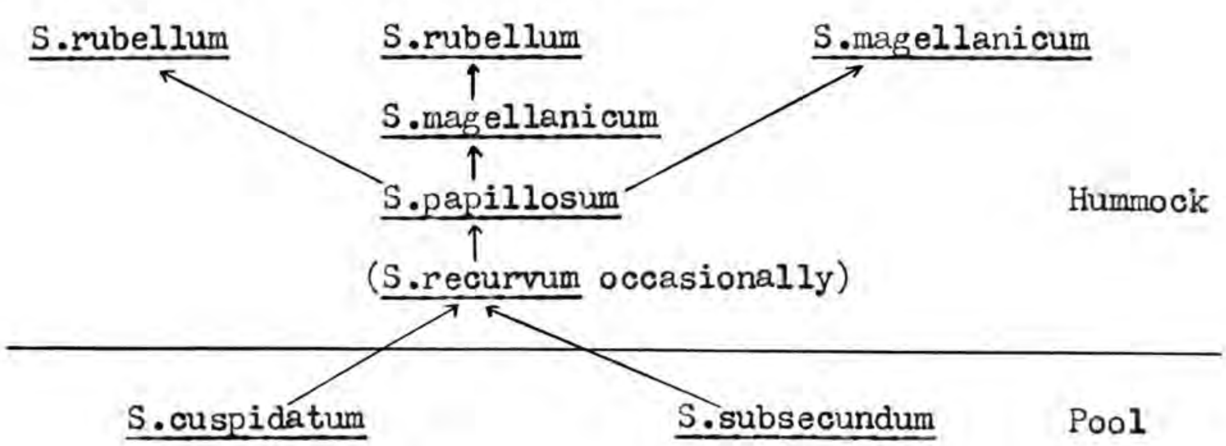
The Moor House Nature Reserve, (c550m. above sea level, Nat. Grid Ref. NY 761330) is an area of blanket bog and mixed-moor (Conway 1955). To the east of the field station is a small area of valley bog, developed in a shallow lake basin and with a small drainage area. The vegetation has been briefly described by Murphy (1955). An almost complete Sphagnum cover is present and in the centre of the bog it is developed into a series of pools and hummocks (Plate 3). The succession in these is listed by Murphy (1955) as follows:-

Plate 3. Valley Bog, Moor House showing pools, Sphagnum hummocks, dark patches of Calluna and much Eriophorum.



The term S."acutifolium" includes S.rubellum and S.nemoreum (=S. capillaceum).

Samples from this area were taken from the different species of Sphagnum which act as indicators of changing environmental conditions. Because of this the Sphagnum succession is described in greater detail than in other areas, and it may be listed as follows:-



This does not differ significantly from the succession of Murphy except in the inclusion of S.recurvum and S.cuspidatum, and it resembles the classic succession of Osvald (in Tansley 1939).

The light green S.cuspidatum inhabits the deeper hollows (< 30 cm.) situated on the north side of the valley, while the olive brown S.subsecundum is abundant in shallow areas of water in the centre of the bog often with Trichophorum caespitosum and Carex paupercula. During very dry periods, the water level of these pools may fall below the peat surface. A fall of about 10 cm. was recorded during the dry 1959 summer.

S.recurvum is occasionally present, at or just above water-level in the hummock complex, but it is more typical of flushes on the southern border of the bog, where it forms large swards, mixed with Polytrichum commune under Juncus effusus. In these areas water is moving just below the Sphagnum, and a few similar flushes are found at the east and west ends of the bog, particularly associated with sink holes.

The hummocks rise to a maximum of 70-80 cm., but the succession is seldom complete, the hummocks usually being dominated either by S. magellanicum or S.rubellum. The term S.rubellum is used here in the same sense as Murphy's S.acutifolium. Eriophorum vaginatum and E.angustifolium occur over most of the area, Oxycoccus on the sides of the hummocks, and Calluna and Cladonia on the drier areas.

pH measurements were taken at various times of the year and with different instruments, but they show a close similarity to pH values recorded from similar areas in this and other surveys. In the pool-hummock succession/

succession they varied from 4.0-4.6 in the pools and 3.4-4.0 in the hummocks. The flushes of S.recurvum showed a pH c.4.2. Gorham (1956b) sampled pools on Bog Hill, situated about 0.5 km. east of Valley Bog where there is a similar pool-hummock succession. In a dry period the pH was 3.68-3.90, and during wet weather 4.16-4.20.

The samples from Valley Bog are listed as follows:-

Valley Bog 1.	15	samples	S.subsecundum, W 1, pH 4.0-4.6
" " 2.	"	"	S.cuspidatum, W 1, pH 4.0-4.6
" " 3.	"	"	S.recurvum, W 2, pH 4.2
" " 4.	"	"	S.papillosum, W 2-3, pH 3.7-4.0
" " 5.	"	"	S.magellanicum, W 4-5, pH 3.4-3.8
" " 6.	"	"	S.rubellum, W 4-5, pH 3.4-3.7

An area of high pH was observed on Valley Bog. This was a flush about 10 m. east of the sink hole in the south-east corner of the bog. The vegetation contained Carex demissa, C.paupercula, Cardamine pratense, Eriophorum angustifolium, E.vaginatum, Potentilla erecta and Erica cinerea, with some Sphagnum hummocks, particularly S.rubellum. The pH of water from the base of one S.rubellum hummock was 6.0-7.0 (29/IV/59.).

A number of samples were taken from this flush. The results are not included in the discussion of testate associations but the list of species recorded is shown in Appendix 1.

Rusland Moss, Westmorland.

Rusland Moss is a raised bog, (c.12m. above sea level, Nat. Grid

Ref./

Ref. SD 335885,) much damaged by cutting and draining, with a well developed pine wood in one area. The region from which the samples were taken is dry, relative to other areas in the survey and bears a shrubby vegetation of Calluna, Myrica, Erica tetralix, Eriophorum angustifolium, E.vaginatum, Molinia and Narthecium with occasional pine and birch. There is a good Sphagnum cover with some Drosera rotundifolia and in the drier places Cladonia is common. A few shallow pools are present some on bare peat, others with S.cuspidatum and S.subsecundum, and hummocks up to 60 cm. high are developed.

Water squeezed from pool Sphagnum gave pH 3.8-4.0. Gorham and Pearsall (1956) and Gorham (1956a) give 3.99-4.35.

The samples are grouped and named as follows.

Rusland Moss 1. 8 samples S.subsecundum, S.cuspidatum, S.tenellum, S.nr.palustre, W 1, pH 3.8-4.0

" " 2. 7 samples S.cuspidatum, S.papillosum, S.nr. rubellum, W 2-3, pH 3.9-4.0

" " 3. 8 samples S.papillosum, S.nr.rubellum, W 4-5 .

Discussion of the sample areas.

Before the distribution of Testacea is considered, it is necessary to co-ordinate the data on the terminology and possible evolutionary sequence of the sample areas.

In English ecology the terms fen and bog are rather loosely used but are generally covered by definitions similar to those given on page 5 .

The term lacustrine bog was apparently coined by Pearsall (1938) for areas of vegetation developed behind reedswamps on the edge of small non-calcareous lakes and moorland pools. These have a vegetation of Molinia, Myrica, Narthecium, Erica tetralix and Eriophorum angustifolium with abundant Sphagnum. The Molinia is usually tussocky, a feature indicating the presence of relatively fresh water (Jefferies 1915). The pH ranges from 4.5-6.5. Gorham and Pearsall (1956) and Gorham (1956a) use the term in Lake District areas including parts of Esthwaite North Fen, Blelham Bog, Nibthwaite and Dale Park Swamps. These appear to form part of a series with increasing amounts of Sphagnum and decreasing Molinia, Dale Park also containing abundant Myrica. The Molinetum at Esthwaite "can barely be classed as fen, but is rather a stage in the development of bog" according to Tansley (1939). Pearsall (1938) also states that if lacustrine bogs were left untouched they would probably develop into raised bogs.

According to Tansley (1939), valley bogs develop where water draining from relatively acidic rocks, stagnates in a flat-bottomed valley or depression. Rose (1953) has surveyed a large number of bog areas in southern/

southern and central England, and found that the centre of these valley bogs is usually occupied by a poor fen or carr with pH <7.4. Bog vegetation with *Sphagnum* hummocks and Ericaceae (pH c.5.0) is usually confined to the sides of this and is succeeded by heath. The northern valley bogs lack this central fen area, the whole surface bearing an acid, *Sphagnum* dominated community.

The two valley bogs studied in this survey, namely Valley Bog and Muckle Moss, are of the typical northern type (Pearson 1954). These areas resemble Dale Park in morphology and vegetation, except for the distribution of *Myrica*, and all are soligenous and developed in shallow lake basins. This indicates the succession; open water----fen----lacustrine bog----valley bog, in these areas, the bog being fed by ground water which is held in the lake basin. Peat borings at Valley Bog and Muckle Moss show that oligotrophic peat is developed on top of eutrophic fen peat (M.Johnson personal communication, and Pearson 1954). Muckle Moss however is not a simple valley bog as there is a definite marginal lagg zone and a central complex of pools, possibly representing the remnants of the lake. These pools may also be drainage split-pools (Pearsall 1956), but these usually are at right angles to the slope whereas at Muckle Moss the pools are in the form of a horseshoe, open at the lower end.

Raised bogs are clearly distinguished communities with a considerable cover of ericaceous shrubs and usually some development of pine and birch. They are ombrogenous, with pH usually <4.0 and their surface is convex. At the/

the edge of the raised bog is frequently a soligenous lagg zone with a relatively rich vegetation and high pH. The term lagg is of Scandinavian origin and is now widely used in England.

Very few, if any, undamaged raised bogs remain in England the majority having been effected by peat cutting and burning. Rusland Moss is relatively uneffected in parts.

According to Tansley (1939), raised bogs usually develop on fens rather than valley bogs, but it seems likely that at some stage in the transition from fen to raised bog, the area will be of the valley bog type.

Other areas which were studied, but which do not fall into the above classes, are Sunbiggin Springs (p.10) and Lady Vane Pot (p.13). In the former, the vegetation is governed by calcareous springs (Holdgate 1955a), and falls into the category of mixed mire (Sjörs 1950). Lady Vane Pot is an artificial pond with a marginal Carex-Juncus zone of rich----poor fen, which passes rapidly into mixed-moor.

The chemical nature of these areas has been studied by Gorham (1956a, b), Gorham and Pearsall (1956) and Gorham in Holdgate (1955b). Full details of their analyses are not given but some representative figures are shown in Table 1.

Table 1. Chemical data from Gorham (1956a, b), Gorham (in Holdgate 1955b) and Gorham and Pearsall (1956).

	pH	Specific conductivity	Calcium (Mg./l.)
1. Bog Hill, Moor House (Sphagnum-Erioph.pool)	3.9	38	0.7
2. Rusland Moss.(Sphagnum, Erioph., Calluna)	4.12	43	1.2
3. Dale Park, older bog. (Sphagnum pool)	4.24	44	1.5
4. Dale Park. (Sphagnum-Carex swamp)	4.84	55	3.4
5. Blelham Bog. (Sphagnum, Rhynchospora alba, Narthecium)	5.55	45	3.5
6. Nibthwaite Swamp. (pool)	6.43	85	7.5
7. Esthwaite N.Fen. (between reedswamp and carr)	7.16	94	10.4
8. Esthwaite N.Fen. (Molinia-Myrica bog)	6.92	56	5.8
9. Lady Vane Pot, open water	8.1	156	30.5
10. Sunbiggin Tarn, open water.	8.2	-	2.34(Me/l)
11. Sunbiggin Tarn, spring water.	7.7	-	3.6 (" ")

The Bog Hill, Moor House data is included as the area is very similar to Valley Bog and is situated less than half a mile from it. It is probably slightly more ombrogenous than Valley Bog, but the pools bear similar faunas.

A tentative scheme of classification of the areas studied giving the possible lines of evolution and hydrology may be made as follows.

Sunbiggin Tarn, Carex fen.	Fen.	Topogenous.
Esthwaite, Phragmites reedswamp.		
Blelham and Nibthwaite reedswamps.		
Esthwaite, Molinia zone.	Lacustrine Bog.	
Nibthwaite (A), Molinia zone.		
Blelham, Molinia zone.		
Nibthwaite (B), Molinia zone.		Soligenous.
Dale Park, Molinia-Myrica zone.		
Muckle Moss.	Valley Bog.	
Valley Bog.		
Rusland Moss.	Raised Bog.	Ombrogenous.

RESULTS

The arrangement of sample groups.

The lists for individual areas are given in Appendix 1. The distribution in relation to the habitats sampled is shown in Fig. 1 and Table 2 in which the sample groups are arranged in a series: fen----bog pool---- bog hummock. The main factors used to decide the series were vegetation, pH and water content, but this arrangement is arbitrary and requires some explanation, particularly regarding pH.

The fen samples were of submerged or saturated Sphagnum, usually associated with relatively large water-bodies and with a pH >5.0. The observed pH of some samples is rather low but in all these cases the samples were just above water level and were liable to flooding by lake or spring water of higher pH. The pH of the medium can be altered by the Sphagnum to varying extents depending on the species. (Skene 1915, Ziegenspeck 1936, Conway 1949, Bell 1959) and it was noticeable that when Sphagnum was growing just above water level, there was a marked reduction in pH (pp. 9-11). This may be due to the activity of the Sphagnum or to increased oxidation. The fen samples are arranged approximately in a series, rich fen----lacustrine bog and poor fen, on the basis of vegetation rather than pH.

The bog areas show comparatively little variation in pH, the total range being 3.2-4.6 with the pools in the upper parts of the range and the hummocks in the lower. The bog samples are thus grouped largely on water content and vegetation. The areas are seldom associated with large water bodies and when these are present they exert little or no effect/

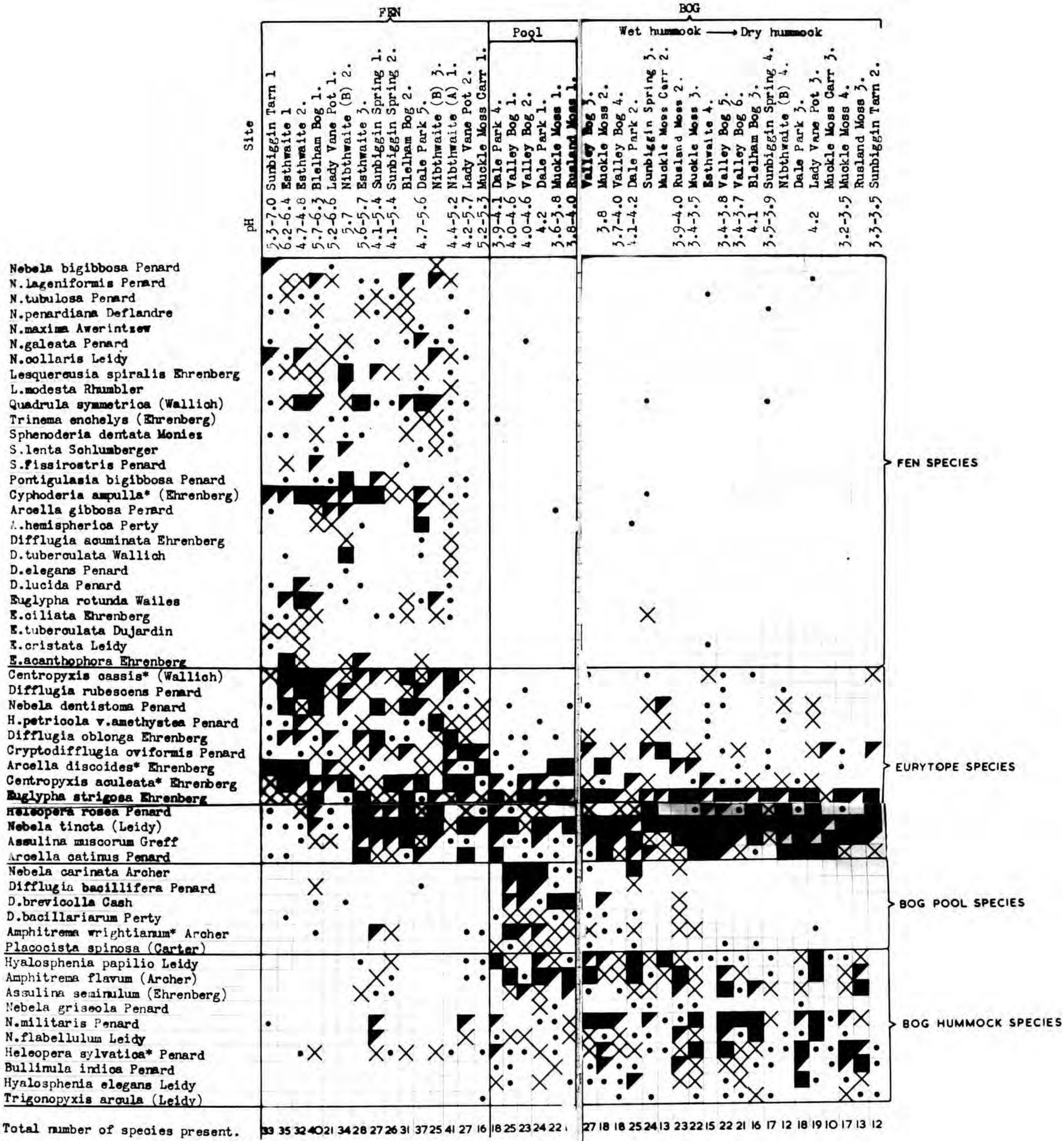


Fig. 1. The distribution of the common Testacea in fen and bog areas. The sites are arranged approximately in order of pH (see text).

• = present in 25% of the samples; ✕ = 26-50%; ◤ = 51-75%; ■ = 76-100%.

Table 2. The distribution of the uncommon Testacea. The sample sites are arranged as in Fig. 1.

	FEN														BOG																										
																Pool						Wet hummock ⟶ Dry hummock																			
	Sunbiggin Tarn 1.	Esthwaite 1.	Esthwaite 2.	Blelham Bog 1.	Lady Vane Pot 1.	Nibthwaite (B) 2.	Esthwaite 3.	Sunbiggin Spring 1.	Sunbiggin Spring 2.	Blelham Bog 2.	Dale Park 5.	Nibthwaite (B) 3.	Nibthwaite (A) 1.	Lady Vane Pot 2.	Muckle Moss Carr .	Dale Park 4.	Valley Bog 1.	Valley Bog 2.	Dale Park 1.	Muckle Moss 1.	Rusland Moss 1.	Valley Bog 3.	Muckle Moss 2.	Valley Bog 4.	Dale Park 2.	Sunbiggin Spring 3.	Muckle Moss Carr 2.	Rusland Moss 2.	Muckle Moss 3.	Esthwaite 4.	Valley Bog 5.	Valley Bog 6.	Blelham Bog 3.	Sunbiggin Spring 4.	Nibthwaite (B) 4.	Dale Park 3.	Lady Vane Pot 3.	Muckle Moss Carr 3.	Muckle Moss 4.	Rusland Moss 3.	Sunbiggin Tarn 2.
Cochliopodium vestitum Archer.						x																																			
Diplochlamys vestita Penard.		x	x																																						
Capsellina timida Brown.																																x									
Pseudochlamys patella Claparède.		x																																							
Arcella vulgaris Ehrenberg.						x											x	x	x						x			x													
A.arenaria Greef.					x					x									x						x			x								x					
Pyxidicula invisitata Awerinzew.				x						x			x																												
Difflugia lobostoma Leidy.						x																																			
D.nr.pristis Penard.									x				x																												
D.nr.pulex Penard.		x	x	x						x	x										x																				
D.oviformis Cash.						x																																			
D.urceolata Carter.						x																																			
Centropyxis discoides Penard.		x	x																																						
C.arcelloides Penard.				x																																					
Lequereusia epistomium Penard.	x																																								
Nebela griseola Penard.																			x	x					x	x		x	x							x					
N.parvula Cash.	x																																								
N.longicollis Penard.							x		x																																
N.speciosa Deflandre.	x											x	x																												
N.marginata Penard.																									x													x			
N.bipes (Carter) Murray.						x																																			
N.acolla Cash.																			x			x																			
Hyalosphenia subflava Cash.																																x									
Phrynganella hemispherica Penard*.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x	x		x			x	x			x	x
Cryptodifflugia eboracensis Wailes.							x				x		x		x							x					x														
Euglypha scutigera Penard.	x											x																													
E.denticulata Brown.	x																									x								x							
E.strigosa v.heterospina Penard.				x													x																								
E.bryophila Brown.		x																																							
E.filifera Penard.				x							x					x																									
Placocista jurassica Penard.			x																																						
Corythion Taránek*.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Campascus minutus Penard.		x																																							
Plagiophrys parvipunctata Penard.																						x																			
Lecythium hyalinum (Ehrenberg).																																x									
Pseudodifflugia nr.fulva (Archer).		x	x	x		x				x			x																												

Table 2. The distribution of the uncommon Testacea. Phrynganella hemispherica* and Corythion* are included because they are species complexes and no information
distribution of the component species can be obtained.

effect on the sample sites. In many cases, these areas were partly or wholly ombrogenous.

Testate associations.

The distribution shown in Fig. 1 for the common or characteristic species indicates that the Testacea may be grouped into the following associations.

1. Fen association.
2. Bog association. a. bog pool.
   b. bog hummock.

1. Fen association.

This association contains a group of about 25 characteristic species which are restricted to base-rich habitats with pH > 5.0. The species occurring most regularly are: Quadrula symmetrica, (14 sample groups) Nebela lageniformis (10), N.tubulosa (9), Lesquereusia spiralis (9), Euglypha ciliata (9), N.penardiana (8), N.galeata (8), N.collaris sensu stricto (8), Sphenoderia dentata (8), Euglypha rotunda (8), Pontigulasia bigibbosa (8). Cyphoderia ampulla and C.trochus var ampullacea were present in 14 sample groups but were not separated (p.109).

The fen species did not occur in very large numbers in any of the samples, usually only a few specimens being present in each watch glass, whereas in the bog associations species of Testacea were often abundant. A number of other species, though present only in a small number of samples, were restricted to the fens. These belong mainly to the genera Arcella, Euglypha, Difflugia and Sphenoderia (Fig. 1).

The characteristic fen species were accompanied by a number of eurytope species (p.32), particularly Centropyxis cassis*, Difflugia rubescens, D.oblonga and Centropyxis aculeata*.

No division into rich fen and lacustrine bog associations is apparent but this may be shown in detailed transects through such a plant succession. However it is noticeable that a base-rich area of spring origin i.e. Sunbiggin Springs, bears the same fauna as areas of lacustrine origin.

Muckle Moss Carr 1 is the only area with pH >5.0 which does not carry a definite fen association. Water squeezed from the S.recurvum gave pH 5.2-5.3. It differs from the other fen areas in that it is not associated with a large water-body or spring and has no actual open water, receiving drainage water from surrounding slopes.

Two generalisations, dealt with more fully later, can be made concerning the fen association. 1. The fen areas usually contain more species than bog areas (p.48) and 2. where foreign matter is used in test formation, it is mainly in the form of mineral particles (p.49).

2. Bog association.

In bog areas where pH <5.0, a greater variety of habitats in respect of water content is found, than in fen areas. A number of associations can be identified. These form a series in which divisions are arbitrary and the succession in the Sphagnum complex of Valley Bog shows this clearly (Fig. 2). In general the species present use peat particles and diatom frustules rather than mineral particles, in the test formation (p.49).

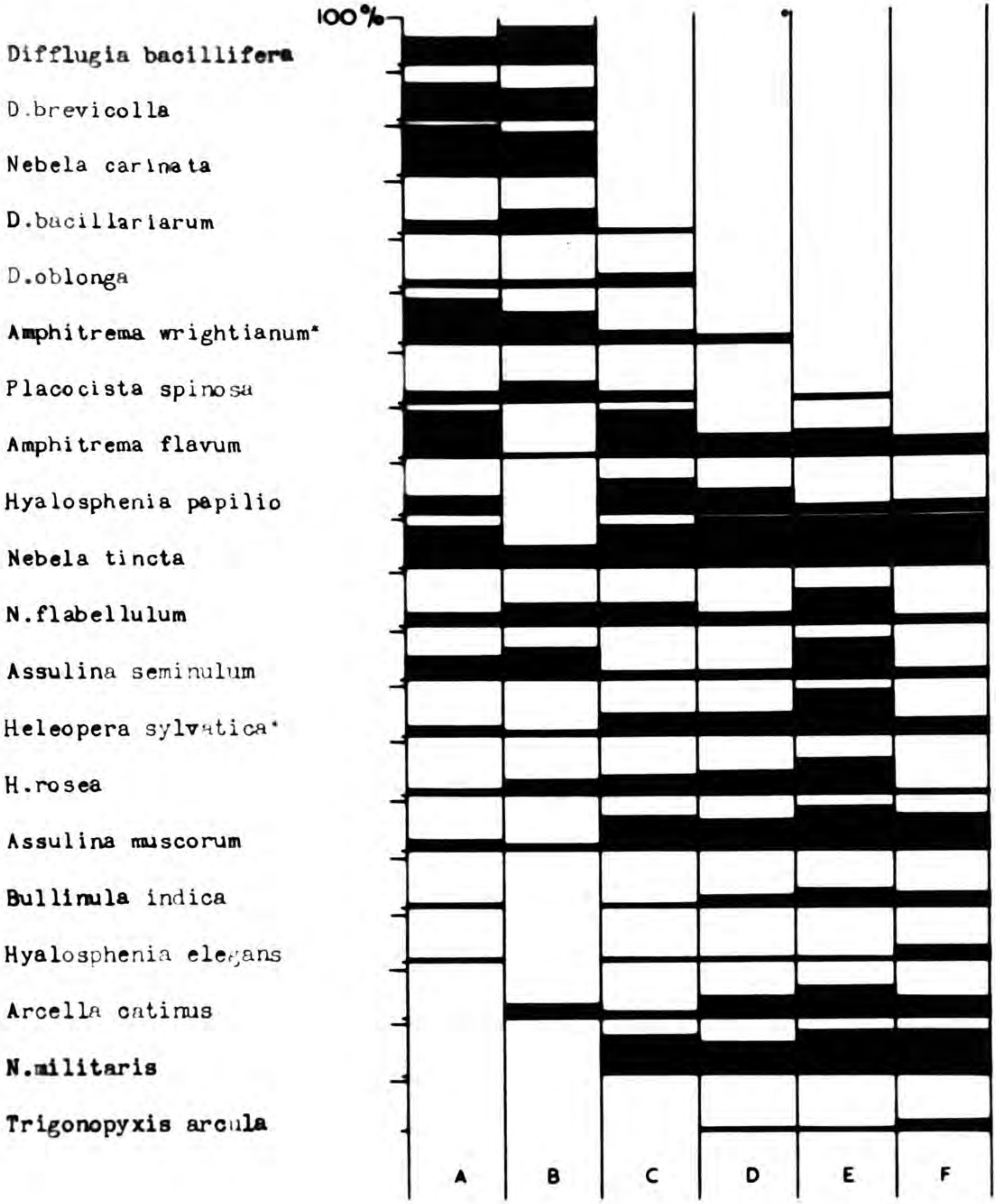


Fig. 2. The distribution of the common Testacea in Valley Bog, Moor House. The solid area indicates the % occurrence of the species in the 15 samples of each Sphagnum species. A = S.cuspidatum; B = S.subsecundum, C = S.recurvum; D = S.papillosum; E = S.magellanicum; F = S.rubellum.

a. Bog pool.

The pools of valley and raised bogs contain a large number of species, but six or seven of these appear to be restricted to this habitat. These are Amphitrema stenostoma, A.wrightianum, Difflugia bacillifera, D.bacillariarum, D.brevicolla, Nebela carinata and possibly Placocista spinosa. Other species commonly present in the pools are Amphitrema flavum, Hyalosphenia papilio and Nebela tincta. In general the largest bog species are found in the pools (p.86).

b. Bog hummocks.

The pools are clearly demarcated from the other Sphagnum-bearing habitats in bogs, but in the hummocks the different habitats grade into each other and cannot be clearly demarcated. Similarly many Testacea are present throughout the hummocks and it is not possible to distinguish different associations on the presence or absence of certain species (Figs. 1 and 2). It is possible however to distinguish associations characteristic of the two extremes of the series, on the regularity of occurrence and number of individuals present.

The fauna of wet Sphagnum is usually dominated by Amphitrema flavum and Hyalosphenia papilio, with Arcella catinus, Nebela tincta, N.militaris, Assulina muscorum, Heleopera rosea and Euglypha strigosa frequently present. The pool species mentioned above are almost entirely absent. This wet Sphagnum group occurs in the lower parts of the hummocks in bogs, in swards of wet Sphagnum, particularly S.recurvum, in bogs, and in the moss situated just above base-rich water, but not directly affected by it. This last/

last case is seen at Esthwaite, Nibthwaite and particularly Sunbiggin Springs where acid hummocks rise from the spring water. These hummocks carry typical "bog hummock" species of Testacea. Thus a general area of fen vegetation may contain bog Testacea in the species list, if small ombrogenous sites are present.

In the driest parts of the hummocks the water is difficult to express from the Sphagnum, which is usually S.rubellum, S.capillaceum, or S.magellanicum. Here the main Testacea are Nebela tincta, Assulina muscorum, Arcella catinus, Heleopera sylvatica*, Euglypha strigosa, and Nebela militaris. Bullinula indica and Trigonopyxis arcula though present only in small numbers, also appear to be typical of dry hummocks. Hyalosphenia papilio and Amphitrema flavum are present in some of these hummocks, but only in small numbers, a large proportion of the tests being empty.

Eurytope species.

Certain species are present in both bog and fen habitats, but some forms show distinct bog or fen "affinities". Difflugia rubescens, Nebela dentistoma, Centropyxis cassis*, Heleopera petricola var. amethystea, and Difflugia oblonga are more common in fen than in bog areas (Fig. 1) and they may be indicators of alkaline influence in acid waters. For example in Muckle Moss Carr, with pH 5.2, Nebela dentistoma and Heleopera petricola var. amethystea are present among a number of bog species.

Cryptodifflugia oviformis, Arcella discoides*, Centropyxis aculeata*, Euglypha strigosa and Heleopera rosea appear to be truly eurytopic (Fig. 1), but/

but Euglypha strigosa occurs in larger numbers in bog areas. Corythion* and Phryganella hemispherica* are not included as they are complex aggregates.

Nebela tincta, Assulina muscorum and Arcella catinus though frequently present in fen areas occur more regularly, and in larger numbers, in the acid sites. N.tincta however is present in a variety of forms which have distinct distributions (pp. 91-93).

Other associations.

It is probable that some of the associations named above will be subdivided when the ecology of Testacea is better known. Thus in Valley Bog, Moor House, two distinct pool types were present containing either S.subsecundum or S.cuspidatum. Amphitrema flavum and Hyalosphenia papilio occurred more frequently in the latter than in the former (Table 3).

In general the subsecundum pools are shallow (<15 cm.), tend to dry up in summer and contain much loose peaty material, whereas the cuspidatum pools are up to 30 cm. deep, only dry up during exceptionally dry weather and the Sphagnum is relatively free from detritus. The difference in detritus content may be related to the growth habit of the sphagna, S.subsecundum being rather prostrate and slow growing thus it remains near to the peat surface, while S.cuspidatum has a vigorous growth and a long stem and therefore it is clear of the peat surface.

It is possible that the distribution of these two testates is related to the presence of zoochlorellae in their protoplasm and it may be significant that both occur most frequently in S.recurvum at Moor House, this/

this Sphagnum also being relatively free from detritus, especially in the head region where these Testacea occur (p.74).

Table 3. The number of samples (maximum 20) in which A.flavum and H.papilio occurred in the two pool-types at Valley Bog, showing the more frequent occurrence of the Testacea in S.cuspidatum.

	S.subsecundum	S.cuspidatum
Amphitrema flavum	2	18
Hyalosphenia papilio	0	7

Discussion of testate associations recorded in the present and previous surveys.

1. The classification of bogs and fens.

In this section the results obtained are compared with the previous studies on fen and bog Testacea. To make this possible it is necessary to ensure that all areas are arranged on a common classification. This is particularly necessary as there is no standard nomenclature for such areas.

The present study areas have already been discussed (p. 23) and they are here compared with Scandinavian and German sites.

In Scandinavian terminology, "mire" or "myr" are used to cover all types of peat land and vegetation (Sjörs 1950, Godwin and Conway 1939, Osvald 1949), while "fen" is used to describe soligenous areas of peat, whether alkaline or acid. The reedswamp at Esthwaite and the Carex rostrata zone at Sunbiggin Tarn are comparable to the Scandinavian "rich fen" while the reedswamps of Blelham and Nibthwaite, having slightly less rich vegetation are probably intermediate between "rich" and "poor fen" (Osvald 1949, Sjörs 1950, du Rietz 1950). As these sites are greatly affected by the lake water, they fall into the category of "topogenous" or "limnogenous mire sites" of Sjörs (1950) and Jessen (1949). The lacustrine bogs at Esthwaite, Blelham and Nibthwaite fall into the category of poor fen.

"Bog" or "Moss" appear to have similar meanings in Great Britain and Scandinavia, but they may be slightly more restricted to ombrogenous

areas/

areas in the latter (Osvald 1949). Jessen (1949) in studying Irish bogs on the Scandinavian basis, divided the climatically controlled bogs into 1. soligenous and 2. ombrogenous, the latter being sub-divided into blanket and raised bogs. This closely resembles the recognised British terminology.

Most work on the ecology of Testacea has been carried out in Germany and it is necessary to compare their terminology with that given above. The German term "moore" appears to correspond with the Scandinavian mire. Harnisch (1929) describes a "moore" as a continuous area of humidity-loving vegetation under the influence of terrestrial or telluric water, which produces (living moor) or has produced (dead moor) a massive carbon-rich deposit. There does not appear to be an English term which corresponds to this definition, "moor" in English having been used for a wide variety of vegetation types (Tansley 1939).

The Governing Body of the Prussian Botanical Society (Der Vorstand des Preussischen botanischer Vereinis, 1913) issued a directive on the study of East Prussian moores. In this they gave details of the features of German Flachmoore or Niedermoore, and Hochmoore, which correspond to the English fen and raised bog types. Gross (1913) followed this and in England, Pearsall (1938), Tansley (1939), Godwin and Conway (1939) and many others regard the term Hochmoore as synonymous with our raised bog, but in a number of papers it is inferred from the floral lists that Hochmoore is more widely used. These lists include a number of fen species such as Triglochin palustre, Primula farinosa, Pedicularis palustris,/

palustris, Ranunculus flamula, Orchis maculata, Salix spp., Epilobium sp. and particularly Carex spp. among the typical bog forms. In some cases there is also mention of Flachmoore influence or the presence of a "swamp flora." (Scheffelt 1921, Haberli 1918, Klieber 1911, Jung 1936b, Heinis 1945, Ertl 1955). The pH of some of these areas appears to be rather high if they are true raised bogs, Ertl (1955) quoting 4.13-4.5 and Hoogenraad and Jirovec (1944) giving 5.6. The obvious explanation of these features is that the authors have not discriminated between the acid raised central part of the bog (Hochflache) and the lagg zone.

Hochmoore means literally "high moor" as opposed to Niedermoore or "low moor" and Osvald (1923) and Harnisch (1929) state that in the British Isles the former are widespread and of various types, listing Eriophorum vaginatum and E.angustifolium association; Scirpus caespitosus (= Trichophorum caespitosum) association; Vaccinium myrtilis association; Calluna vulgaris association and Grimia (= Rhacomitrium) hypnoides association. These indicate that the term Hochmoore may be used in a relatively wide sense to cover blanket bog, and is not necessarily restricted to raised bog. However in the same work, Harnisch lists the Hochmoore vegetation as Sphagnum spp., especially S.rubellum, S.magellanicum and S.fuscum, Eriophorum vaginatum, Trichophorum caespitosum, Rhynchospora alba, Scheuzeria palustris, Oxycoccus quadripetalus, Andromeda polyfolia, Calluna vulgaris, Vaccinium uliginosum, V.vitis-idaea, Empetrum nigrum, Drosera, Ledum palustre, Rubus chamaemorus, Pinus spp. Betula spp. and Cladonia. This is a typical raised bog flora, excluding the lagg zone.

The term Zwischenmoore (= Uebergangsmoore ?), literally "transition moor", has been used in a number of testate studies and it appears to cover a wide variety of communities between Flachmoore and Hochmoore. Der Vorstand des Preussischen botanischer Vereinis (1913) lists typical Zwischenmoore plants as Ledum palustre, Vaccinium uliginosum, Carex pauciflora, Menyanthes trifoliata, Chamaedaphne calyculata, and Aspidium cristatum. These are usually mixed with typical Hochmoore plants, mainly Ericaceae and Sphagnum, or Flachmoore forms such as Carex spp. Phragmites and Typha latifolia. Unfortunately the characteristic Zwischenmoore plants named above are absent or rare in this country, except for Menyanthes which has a very wide ecological range.

The above is one of the few detailed lists for Zwischenmoore, most authors defining Zwischenmoore as intermediate between Flachmoore and Hochmoore and as mesotrophic. (Harnisch 1925, 1929, Tansley 1939, Gross 1913, Messikommer 1943).

de Graaf (1957) in the Netherlands described two Sphagnum zones with pH range 4.0-6.0, and bearing a mixture of fen and bog plants. He classes this as a transitional peat series or Zwischenmoore. Messikommer (1943) in Switzerland also gives the pH range for a Zwischenmoore with considerable Flachmoore influence as 5.6-6.6.

The term thus appears to cover a wide range of communities and in the present study, the Molinia and Molinia-Myrica lacustrine bogs and the Sphagnum-dominated valley bogs would come under the heading Zwischenmoore. There do not appear to be any common features except that they are neither true fens nor raised bogs. The pH of free water in these areas probably ranges from 4.0-6.0.

The following Table attempts to show the theoretical relationship between the main terms used in Great Britain, Germany and Scandinavia.

<table>
<tr><td rowspan="2">Great Britain</td><td colspan="2">Fen</td><td colspan="2">Bog</td></tr>
<tr><td>Fen</td><td>Lacustrine bog</td><td>Valley bog</td><td>Raised bog</td></tr>
<tr><td rowspan="2">Scandinavia</td><td colspan="4">Mire</td></tr>
<tr><td>Rich fen</td><td colspan="2">Poor fen</td><td>Bog or moss</td></tr>
<tr><td rowspan="2">Germany</td><td colspan="4">Moore</td></tr>
<tr><td>Flach- or Niedermoore</td><td colspan="2">Zwischenmoore or Uebergangsmoore</td><td>Hochmoore</td></tr>
</table>

2. The distribution of Testacea.

In a number of studies on Testacea the areas have been inadaquately described and the faunas from different habitats have not been separated. Because of this, it is impossible to compare these faunas with the areas investigated here and they offer little information on the ecology of Testacea. (Klieber 1911, Haberli 1918, Scheffelt 1921, Hoogenraad and Jirovec 1944, Heinis 1945, Ertl 1955).

Harnisch (1925, 1927) surveyed a series of Flachmoore, Zwischenmoore and Hochmoore. On his results, and those of previous workers, he postulated a series of rhizopod associations characteristic of various habitats in Central Europe. These form a useful framework around which to discuss the present results and to compare them with other works. The general application of Harnisch's associations will also be reviewed.

The associations postulated by Harnisch (1927) are:

Type 1. Waldmoostype. A varied fauna of Difflugia spp. Centropyxis spp., Arcella spp., Nebela collaris (in the broadest sense p. 105) N.militaris, N.americana, Euglypha spp., Assulina muscorum, A.seminulum, Corythion and Trinema spp. The typical Sphagnum-dwelling species Hyalosphenia papilio, H.elegans, Amphitrema flavum, A.wrightianum are absent. This association occurs in the non-peat-forming Sphagneta of woods, lake edges, heaths and old Hochmoore.

Type 2. Hyalosphenia type. This contains the species of Type 1, plus Hyalosphenia papilio and H.elegans, the former usually being dominant. This type occurs mainly in Zwischenmoore, but also in young bogs and dead Hochmoore.

Type 3. Amphitrema type. This is typified by the presence of Amphitrema spp. and is found in Hochmoore. It is divided into two sub-types

3a. Flavum type, in which A.flavum only occurs.

3b. Wrightianum type, in which A.flavum and A.wrightianum are present but no difference in the distribution of the two sub-types is noted.

There are naturally intermediate stages between the types and occasionally specimens of Hyalosphenia and Amphitrema species may be found in Waldmoos type associations. The communities in general show development of bog conditions, and are based largely on the presence and absence of Hyalosphenia and Amphitrema species.

The faunas recorded in the present survey may be compared with the types of Harnisch as follows.

Fen association. ---Waldmoos type (1), with very occasional Amphitrema and Hyalosphenia specimens.

Bog association.

pool ---Amphitrema wrightianum type (3b)

wet hummock ---A.flavum type (3a)

dry hummock ---Waldmoos type (1) with very occasional H.papilio and A.flavum, and some H.elegans.

A true Hyalosphenia type is present only in Dale Park 4. This is an area of saturated Sphagnum (pH 3.9-4.1) between a relatively base-rich drain (pH 4.7-5.6) and the acid bog (pH 4.1-4.2). The intermediate zone is probably more affected by the drain than is indicated by the pH. The only typical bog pool species present are Difflugia bacillariarum and Placocista spinosa which occur in small numbers. H.papilio is present in large numbers and Amphitrema species are absent.

In the following discussion, relevant works are discussed and the lists of Testacea are compared with the characteristic species in the present survey in Table 4. The faunas are also classed on the system of Harnisch in this Table.

Harnisch (1925, 1929) also gave lists of the typical species in Hochmoore, and this corresponds closely with the list of bog species in the present survey (Table 4). The only discrepancy is in the presence of Nebela collaris, but Harnisch uses the term in the broadest sense (p.105).

Prior to Harnisch, Steinecke (1913) studied well defined areas of pine wood; alder, Carex and Iris Flachmoore; Zwischenmoore and different areas of Hochmoore. He found relatively few species in the Flachmoore and Zwischenmoore but on the system of Harnisch (1927) these belonged to

Waldmoos/

Table 4.

	Harnisch (1925, 1929)	Steinecke (1913)	Gauger and Ziegenspeck (1931)	Jung (1936a) 1	2	3	4	Jung (1936b)	Jung and (1938) 1	2	3	Spatz 4	5	Thunmark (1942)	Messikommer (1943)	Paulson (1952) 1	2	3	4	de Graaf (1956) 1	2	3	4	de Graaf (1957) 1	2	3
	B	B	B+I	B				B+I	F	F	F	I	W	F	F	F	I	B	B	F	F	I	B	F	F	I+B
				Wet			Dry						Dry					Wet	Dry							
Nebela bigibbosa																										
N.lageniformis											o	o	o	o										o	+	
N.tubulosa								o			o	+														
N.penardiana											o	o														
N.maxima																										
N.galeata											o	+		o	o										o	o
N.collaris	+		o								o	+	o	o	+	o	o	o			o	+	o	o	+	+
Lesquereusia spiralis		o							o		+	+		+	+					o				o	o	
L.modesta		o									o	o		+										o	o	
Quadrula symmetrica								o			+	o		+											o	o
Trinema enchelys		o	o						o	o	+	o	o	o	+	o				o	+	+	o	+	o	o
Sphenoderia dentata		o						o			o	+	o		o	o								o	o	o
S.lenta								o			o	+	o	o		o					o	o		o	o	o
S.fissirostris								o			o	o	o									o			o	o
Pontigulasia bigibbosa									o		o	o									o					
Cyphoderia ampulla								o	o	o	o	+		+	o									+	+	o
Arcella gibbosa										o	o	o				o	o	o			o					
A.hemispherica										+	o			+						o	+	o		o	+	
Difflugia acuminata										+	o	o		+	o					o	o			+		
D.tuberculata									o		o															
D.elegans				o				o			o	o			o									o		
D.lucida											+	o												o	o	o
Euglypha rotunda		o						o			o	o														
E.ciliata		o						o				o		o	o	o	o			o	o	+	o	o	o	o
E.tuberculata																										
E.cristata								o			o	o			o	o									o	o
E.acanthophora										+	o	o		o								o		o	o	o
Centropyxis cassis							o	+	+	o	+	+	o							o	o					
Difflugia rubescens								o			+	o										o				
Nebela dentistoma								o		o	o	+										o	o	+	o	o
H.pet.v.amethystea								o							o					o					+	o
Difflugia oblonga				+	o	o		o	o		o	o		o	o	o		o						o		
Cryptod. oviformis								o				o				+	o	o				o		o	o	+
Arcella discoides		o	o	+	o	o	o				o	o				o		o		o	o	o		o	o	
Centropyxis aculeata			o	+				o	o	+	+	+		o	+	o	o			o	o			+	o	o
Euglypha strigosa		o	o	o	o	+	o	+	o		o	+	+			+	o	o	o	o		o	+			o
Heleopera rosea		o						o			o	+	o													
Nebela tincta		o			o	o	+	+					+			o	o	o	o			o	+		o	o
Assulina muscorum	+	o	o		o	+	o	o			o	+	+			+	+	+	+			+	+		+	+
Arcella catinus		+	o		o	o	o	o					o			o	o	o	o			o	o	o	+	+
Nebela carinata	+	o	o	o	o	o		o			o	o			o					o	o	+				
Difflugia bacillifera	+	o						o			o										+	o				
D.brevicolla								o																		
D.bacillariarum														+							o	o		o	o	o
Amphitrema wrightianum	+	o	o	+	+	+		o		o	o															o
Placocista spinosa								o																		
Hyalosphenia papilio	+	+	+	o	+	+	o	+			o	+				+	+	+	o		o	+			+	+
Amphitrema flavum	+	+	+	o	+	+		o		o	o	+				o		+	o						o	o
Assulina seminulum	+	o	+		o	o	o	o					o					o	o	o	o	o	o		o	o
Nebela griseola																					o	+				
N.militaris	+	o	+		o	o	o	o				o	o			o	o	o	o		o	+	+		+	o
N.flabellulum																										o
Heleopera sylvatica		o	o			o	o	o			o	o	+		o	o	o	o			o	o			o	o
Bullinula indica						o	o	o													o		o			o
Hyalosphenia elegans	+	+	+		+	+	o	o									o	o	o		o	o			o	+
Trigonopyxis arcula		o	o				o	o			o	o	+			o		o	o				+			
Harnisch's classification	3b	3a	3b	3b	3b	3b	1-2	3b	1	1	3b	3a	1	1	1	1-2	2	3a	1	1	1-2	2	1	1	1-2	3a
% Fen	10	27.2	12.5	11.1	-	-	-	28.5	55.5	54.5	57.8	59.4	37.5	81.2	66.6	35	23	12.5	-	41.6	38	29.1	25	66.6	51.6	40
% Bog	80	45.4	56.2	44.4	53.8	60	53.8	37.1	-	18.1	18.4	16.4	25	6.2	13.3	25	30.7	43.7	60	16.6	47.6	37.5	33.3	4.7	22.5	33.3

Table 4. The characteristic fen, eurytope and bog species are listed and compared with the species lists of other workers. Species which the authors record as characteristic, dominant or abundant are marked +, others o. Harnisch (1925, 1929) only records characteristic species. The % bog and fen is shown and the areas are approximately classed as bog (B) wood (W), intermediate or Zwischenmoore (I) and fen (F).

Waldmoos and Hyalosphenia types respectively. Characteristic Hochmoore species listed by Steinecke are shown in Table 4.

In the study of the succession of an ombrogenous Hochmoore, Gauger (1931) and Gauger and Ziegenspeck (1931) gave a detailed account of the botany of the area, which included zones of Zwischenmoore. They listed Salix spp., Tilia cordata, Carex rostrata, C.goodenoughii, Scirpus silvaticum, Phragmites communis and Daphne mezereum which are not normally associated with Hochmoore. The pH however, did not rise above 4.21 even in the Zwischenmoore, and the testates, related to this, were all typical bog forms (Table 4).

Jung (1936a) recorded a typical bog fauna (Table 4) for a German Hochmoore in which he recognised four main habitats, showing a general reduction of moisture. These he termed 1. Pool- 2. Regeneration- 3. Climax- 4. Erosion-complex. A similar succession, with photographs, is recorded by Harnisch (1929) and Osvald (1923). The distribution of Testacea in these habitats (Table 4) shows a close resemblance to the pool-hummock succession in the present survey (Fig. 1).

Other Hochmoore, with some Zwischenmoore influence, are briefly described by Jung (1936b), and though full details are not given the fauna is dominated by bog species. The fen species occur only in small numbers (Table 4).

Jung and Spatz (1938) studied a series of lake margin habitats passing through 1. open water, 2. Equisetum zone, 3. Magnocaricetum, 4. Eriophorum-Sphagnum zone and 5. acid wood. The later stages in the succession/

succession are not fully described, but the first three fall into the category of fen. The Eriophorum-Sphagnum zone is of an intermediate type leading to the relatively dry wood, the latter being the climax rather than bog.

The different habitats contain a mixture of fen and bog Testacea, but in general there is an increase of bog species as the series becomes drier and more acid (Table 4). It is possible that the presence of bog species in the fen areas is due to the occurrence of ombrogenous hummocks of Sphagnum. This work shows the necessity of identifying the habitats fully.

Two relatively base-rich areas have been studied by Thunmark (1942) in Southern Sweden, and Messikommer (1943) in Switzerland. The former examined large numbers of sites effected by iron-deposition and bearing a Flachmoore-Zwischenmoore vegetation. The pH range is given as 5.1-6.6 and the Testacea (Table 4) belong to the fen group of species in the present survey.

Messikommer (1943) studied areas of Zwischenmoore with strong Flachmoore influence, and the pH range is given as 5.6-6.7. The Testacea clearly belong to the fen group of species (Table 4).

Unfortunately neither Thunmark nor Messikommer drew any conclusions on the distribution of Testacea in their areas, or discussed their identifications. This is probably because they were interested mainly in other micro-organisms.

Paulson (1952) investigated a Swedish mire which comprised a small raised bog with relatively dry surface and poorly developed Sphagnum hummocks./

hummocks. A marginal zone of pine, fir and birch and a lagg zone (1 and 2 in Table 4) surround the bog. The pH of the lagg is unusually low (4.0-5.0) but the flora is rich. In places in the lagg the Sphagnum is quite dry, which probably accounts for the presence of bog species. On the bog, a wet hollow (3) and a Sphagnum magellanicum hummock (4) were sampled. The pH values are 3.7-4.2 and 3.5-4.0 respectively.

The list of Testacea recorded by Paulson (Table 4) contains both fen and bog species, but the fen forms are almost restricted to the lagg. No true bog pool fauna is present, probably because the hollow examined was not submerged.

The most outstanding modern studies on the ecology of Testacea are those of de Graaf (1956, 1957) in the Netherlands. In the first work he studied an area with a central lakelet (pH >5.0), surrounded by small pools showing "peat moor" (= Hochmoore) development with Sphagneta. The sites may be grouped as follows,

1. "Periphyton benthos" with algae and some Sphagnum, pH 5.4-5.5.
2. "Swimming and submerged Sphagnum", mainly S.cuspidatum, pH 5.0-5.8.
3. "Sphagnetum", including both wet and dry Sphagnum, pH 4.5-5.0.
4. "Ericetum", with relatively dry Sphagnum, pH 4.3-4.5.

The Testacea recorded in this succession are shown in Table 4, and indicate the gradual increase of bog species as the habitats become more acid. The main succession is considered by de Graaf to be typical of Zwischenmoore and Hochmoore and he also stated that in alkaline waters the/

the initial stages will differ by the inclusion of Flachmoore forms. This latter type of community is described in de Graaf (1957), and in Table 4 it is seen that many more fen species are included.

de Graaf (1957) studied an area of quaking bog developed behind a series of lakes. There is a typical fen flora at the lake margin, followed by

1. a Scorpidium scorpioides mat with a fen flora (pH 6.0-7.2).
2. the first Sphagnum zone with base-tolerent Sphagnum species, (pH 4.9-6.0).
3. the second Sphagnum zone with S.recurvum, S.acutifolium, S.palustre, Molinia, Myrica and Erica (pH 4.0-5.2).

The faunas of these habitats are shown in Table 4 and the fen---bog succession of the present survey closely resembles these. However a complete bog fauna is not developed in de Graaf's area.

de Graaf (1957) mentions the fauna of very dry bog hummocks. This he describes as a "Bullinula indica community" after the findings of Jung (1934). This community is without Amphitrema or Hyalosphenia species and similar results are described by de Graaf (1956), Paulson (1952), Jung and Spatz (1938) and Jung (1936a). In the present survey this community is described on p. 32, and it belongs to the Waldmoos type of Harnisch.

3. Conclusions.

A comparison of the results of the present survey with those of previous workers (Table 4), indicates that there is a well marked succession of Testacea following the sere from fen, through intermediate stages,/

stages, to raised bog. In the early stages of the succession there is little apparent variation in the testate fauna despite the difference in the floral communities studied. All these associations correspond with the Waldmoos type of Harnisch (1927), mainly as a result of the absence of Hyalosphenia and Amphitrema species. The change from fen to bog Testacea occurs in the region of pH 5.0, but too great an emphasis should not be placed on this figure because of seasonal fluctuation in acidity. This transition is marked in the hydrosere by dominance of Sphagnum spp. which form a complete cover.

In the present survey the testate fauna showed a rapid change at this stage with little or no clearly defined "transition fauna" and seldom a mixture of fen and bog species. Some workers (Paulson 1952, de Graaf 1956, 1957) record a transition fauna with Hyalosphenia species, especially H.papilio. This corresponds to the Hyalosphenia type of Harnisch, stated to be typical of Zwischenmoore. This fauna has not been shown to be widespread, while Zwischenmoore are a large and varied group of communities (p.38).

The bog fauna described in the present survey is very similar to those previously recorded by various workers (Steinecke 1913, Harnisch 1925, 1927, 1929, Jung 1936a, b, Jung and Spatz 1938, Gauger 1931, Gauger and Ziegenspeck 1931) and these correspond to the types of Harnisch, as indicated in Table 4.

It can be seen that the association types of Harnisch (1927) are largely based on the presence, and particularly dominance, of Amphitrema and/

and

Hyalosphenia species, all faunas without these being classed as Waldmoos type. He stated that this type occurred in non-moor-forming Sphagneta of woods, lake margins, heaths and old Hochmoore. The above discussion has shown that the faunas of fens and dry hummocks, though both classed as Waldmoos type, are very different from each other and should be separated.

Hyalosphenia type, though present in certain areas, is not widespread and the Amphitrema type is, as stated by Harnisch, typical of Hochmoore, if this term is used in a broad sense to include acid areas of the valley bog type.

The flavum and wrightianum types have different distributions which were apparently not recorded by Harnisch (1927). It would seem advisable to divide the pool fauna from that of the hummock on the occurrence of a number of species (p. 31) rather than on the presence or absence of one species. In this way the patchy distribution of species and the number of samples examined, effect the type less.

It must be remembered that the association types which Harnisch postulated, were for Central Europe, but they seem to be generally applicable. One limitation of the system of Harnisch is that it describes associations characteristic of areas, rather than of environmental conditions. It has been shown earlier that certain areas of fen vegetation contain acid Sphagnum zones in which bog Testacea occur. In this way an area of fen or lacustrine bog will contain both bog and fen Testacea. Thus it is more realistic to describe testate communities occurring in fen or bog conditions, often in very restricted habitats, than to describe them for large areas such as Flachmoore or Zwischenmoore.

<u>The number of species present in different areas.</u>

The figures for the total number of species present in the different areas shown in Fig. 1, indicate that there is a gradual fall from fen -- bog pool -- bog hummock. The mean number of species ($\pm$ 95% Confidence Limits) for the sample groups are as follows;

30.1 ($\pm$ 3.53) for the 15 fen sample groups.

21.3 ($\pm$ 2.20) for the first 13 bog sample groups.

16.6 ($\pm$ 2.26) for the last 13 bog sample groups.

The 95% Confidence Limits indicate that the means are significantly different.

If the number of species present in a sample are plotted against the pH of the sample, a positive correlation is shown, with a correlation coefficient P = between 0.05 and 0.02 (Fig. 3). The correlation is probably not causal, the pH being an indicator of the environmental conditions, representing a change from eutrophic to oligotrophic conditions. This change is usually associated with paucity of species.

These results agree with de Graaf (1957) who showed a clear decrease in the number of species in both microflora and microfauna with rising acidity. Jung (1936a) earlier made a similar statement, but added that there is a decrease in species associated with increasing humidity. This is rather difficult to reconcile with his first statement, as in bog areas there is a general tendency for the acidity to rise as the humidity falls. This is clearly shown in the fall in pH of samples ascending a <u>Sphagnum</u> hummock, and thus the two statements appear to be contradictory.

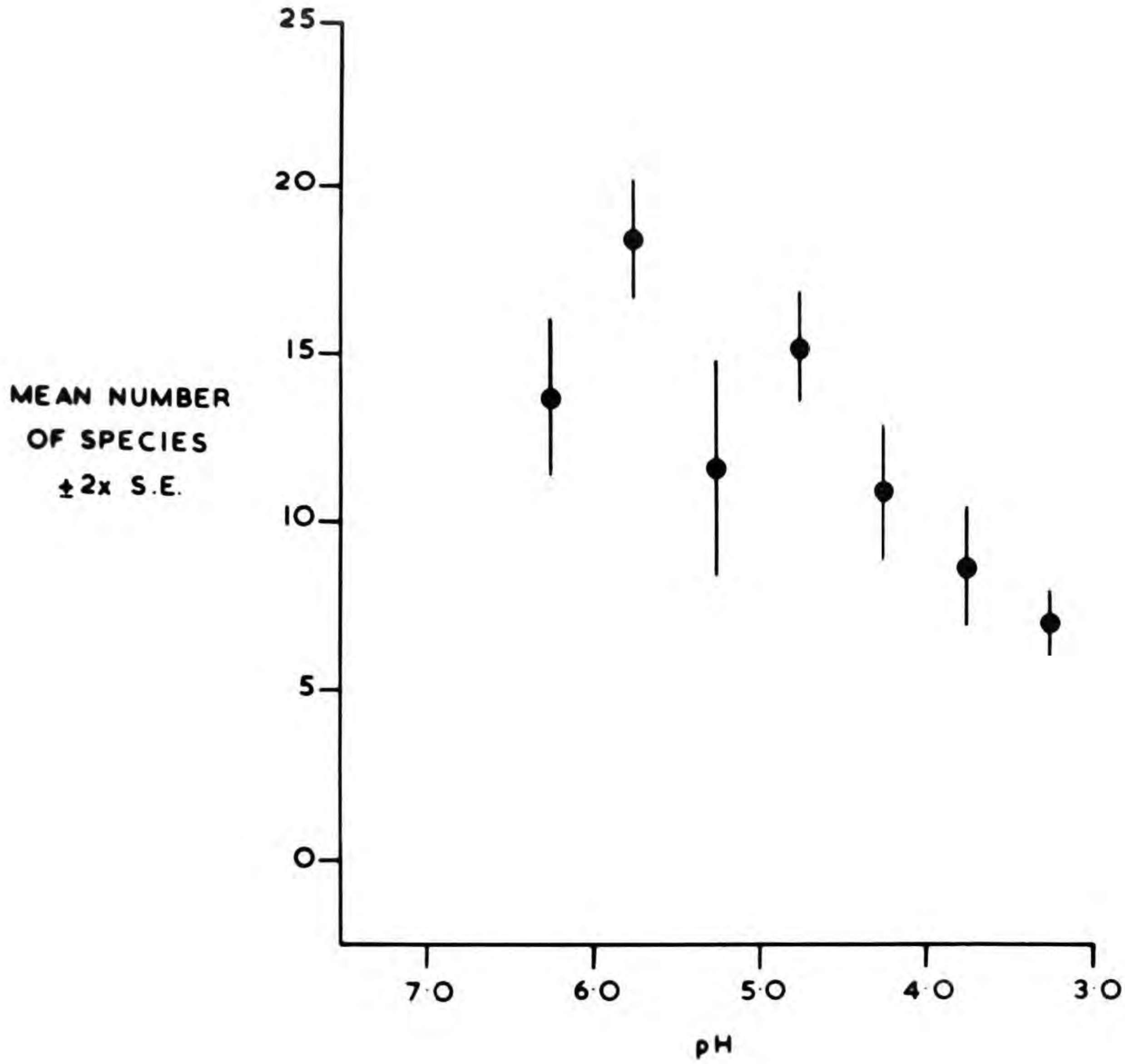


Fig. 3. The relationship between pH and the number of species present.

Test structure.

Species whose tests are membranous (Arcella, Hyalosphenia, Cryptodifflugia and Amphitrema flavum) or covered with silica plates (Euglypha, Cyphoderia, Sphenoderia, Placocista, Trinema, Corythion, and Assulina) do not appear to show any habitat preference related to their structure. Species incorporating foreign material in their tests show a marked distribution effected by the material used (Table 5). The majority of species in bog areas which use foreign matter, utilise peat particles, diatom frustules and other detritus with very few mineral particles. Species occurring in fen areas tend to use mineral particles rather than organic matter. It is however rather surprising that none of the fen species utilise diatoms to any considerable extent, although these are very common in fens.

In 1864, Wallich recorded that in Difflugia (used in a very wide sense) the test structure differed greatly in various habitats due to the availability of materials. Little attention has been paid to this aspect since then, except by Štěpánek (1952) who uses it as did Wallich, in the reclassification of Difflugia.

Table 5. The test structure of species living in different habitats.

M = minerals, D = detritus including diatoms.

	M	M+D	D+M	D	
Lesquereusia modesta	x				Fen
Pontigulasia bigibbosa	x				Fen
Difflugia acuminata	x				Fen
D.elegans		x			Fen
D.tuberculata	x				Fen
D.lucida	x				Fen
Centropyxis cassis*		x			Eurytope
D.rubescens			x		Eurytope
D.oblonga	x				Eurytope
Centropyxis aculeata*			x		Eurytope
Heleopera rosea			x		Eurytope
D.bacillifera			x ——	x	Bog
D.brevicolla			x		Bog
D.bacillariarum				x	Bog
Amphitrema wrightianum*			x		Bog
Heleopera sylvatica*			x		Bog
Bullinula indica			x		Bog
Trigonopyxis arcula			x		Bog

The relationship between Testacea and Sphagnum species.

The suggestion that species of Testacea are related to the species of *Sphagnum* on which they occur has been generally rejected in recent years (Heinis 1945, Hoogenraad 1935, Fantham and Porter 1945). In the present survey there was no indication of a close relationship. Fig. 2 shows that the majority of Testacea are found on a number of *Sphagnum* species in Valley Bog, and in comparing samples of one *Sphagnum* species from different areas it is seen that a *Sphagnum* species may carry different associations. This is best seen for samples of *S.subsecundum* which in Valley Bog 1, contain a typical bog pool association but in Blelham Bog 1, Esthwaite 1 and 2, and Sunbiggin Tarn 1, contain fen Testacea (Fig. 1). However the influence of *Sphagnum* on the pH may have some effect on the Testacea present, although they are not responsible for specific faunas.

It is probable that the Testacea are related to the conditions occurring in the *Sphagnum*, and though the species of *Sphagnum* are limited in their distribution and are able to control their environment to a certain extent, the tolerence limits of the *Sphagnum* and Testacea do not coincide.

Food and predators.

Before going into details on the feeding of Testacea, it is necessary to give some indication of the composition of the aquatic microflora and microfauna present on the Sphagnum.

Naked amoebae are present in small numbers particularly in the wetter habitats, where large species ($> 100\mu$), including Amoeba verrucosa, occurred. In fen areas, numbers of amoebae of the Biomyxa, Penardia type were observed. Actinophrys sol and Actinosphaerium eichornii were the commonest Heliozoa, occurring mainly in pool Sphagnum. Ciliata of various types were always present and were abundant in the pools. Complete lists were not made but the following forms were recognised in various samples; Spathidium spathula, Lacrymaria olor, Dileptus anser, Loxophyllum sp., Paramecium bursaria, Paramecium sp., Frontonia sp., Colpidium sp., Bursaria sp., Spirostomum sp., Stentor caerulea, Stentor sp., Halteria sp., Uroleptus sp., Holosticha sp., Oxytricha sp., Opercularia ? sp.,

Many small flagellates were present but unidentified, Euglena and other Euglenoidea were frequently observed.

Rotifera numerically form a large part of the microfauna, and are present in all areas, members of the Fam. Bdelloidea being common, particularly in the hummocks.

Gastrotricha; Tardigrada; Cladocera, mainly Chydorus sphaericus and Alonella spp.; Turbellaria about 2 mm. in length; Enchytraeidae, mainly Enchytraeoides sphagnetorum ; chironomid larvae and mites were occasionally present in small numbers. Nematodes were present in most samples in considerable/

considerable numbers and all the feeding-types were represented. Copepoda, mainly small Harpacticoidea (Canthocamptus sp.?) were present in many samples, but only occasionally in large numbers.

Large numbers of diatoms were present in all the wet and submerged samples, the fen areas containing a wide range of species. Desmids were also abundant in the fens but filamentous algae, Cyanophyceae and Chlorophyceae were present in most areas, reaching large numbers only in a few samples. Fungal spores and hyphae were present in small quantities and teleutospores were also observed. It was not possible to obtain an accurate idea of the presence of bacteria, but large rods, 1-2μ long were abundant in some samples.

Numbers of pollen grains, eggs of nematodes, rotifers and tardigrades, harpacticoid spermathecae, cladoceran ephippia and various cysts, spores and other unidentifiable objects were present in most samples.

The food of Testacea.

During the examination of samples, all recognisable objects contained in the protoplasm of Testacea and other Protozoa, or in the guts of higher animals, were recorded and these observations provided the following data.

Nebela. The test structure indicates that members of this genus prey on Euglypha, Assulina, Corythion and other small Testacea, utilising their plates to form their own tests. The mouth plates of Euglypha spp., with their characteristically dentate tips, can often be recognised.

In the protoplasm of N.tincta, specimens of Amphitrema flavum and Cryptodifflugia/

Cryptodifflugia oviformis were observed along with various cysts, diatoms, brown fungal teleutospores and many brown and green unidentifiable objects. Specimens of N.tincta s.s., 70-90 μ long (p.86) seldom bear silica plates and it is suggested that they feed on bacteria and occasionally very small Testacea such as Corythion* and Cryptodifflugia oviformis.

N.carinata and most of the other large nebelids have been observed with algae and diatoms in their protoplasm. This is probably associated with their presence in aquatic habitats where chlorophyll-bearing organisms are abundant. However, as mentioned above, these species also feed on other Testacea and on a few occasions, N.galeata and other large species, have been seen with Testacea in their protoplasm.

Heleopera. H.rosea and H.petricola have been observed with silica plates on their tests, these presumably having been obtained from other Testacea. On two occasions H.rosea was seen with Amphitrema flavum in the protoplasm, brown and green particles are also frequent. H.sylvatica which is smaller than the other species, inhabits the drier Sphagnum and rarely has silica plates in the test indicating that it may be a bacterial feeder, like N.tincta s.s.

Hyalosphenia papilio. Though this species contains zoochlorellae it is often observed with brown particles in the protoplasm. These have never been identifiable and no recognisable remains of other Testacea have been observed. No particles have been seen in Amphitrema flavum which also contains zoochlorellae.

Difflugia, Lesquereusia and Pontigulasia appear to be mainly diatom and/

and algal feeders, but it is difficult to distinguish particles in their protoplasm due to the thickness of the test.

Pseudodifflugia, Centropyxis aculeata*, Phryganella hemispherica* and Arcella spp. have all been observed with numbers of diatoms in their protoplasm.

It has not been possible to identify particles in the smaller species, namely Corythion, Trinema, Assulina, Sphenoderia, Euglypha and Cryptodifflugia. It is therefore suggested that they are bacterial feeders or possibly saprophagous.

A big disadvantage in assessing the feeding habits of Testacea by their protoplasmic contents, is that certain food, such as ciliates, would not be recognised because of disintegration.

In general it appears that Testacea are mainly omnivorous. The large forms utilise most organisms of suitable size, but feed mainly on chlorophyllous organisms which are abundant in wet habitats. In the drier areas few diatoms and algae are present and it is probable that the small Testacea are mainly bacterial feeders. Larger species in these habitats probably feed on the small testates, rotifers and ciliates. The unspecialised feeding of Testacea is recognised by various authors (Sandon 1932, Jung and Spatz 1938, Deflandre 1936, MacKinlay 1936) largely based on casual observation.

Of the other Protozoa, the naked amoebae, Heliozoa and many ciliates have been observed with diatoms and algae, and occasionally other microfunal members. Many of the ciliates are also baterial feeders (Sandon 1932).

Predators of Testacea

Many large Testacea have been seen to feed on small ones, but the only observed case of predation by other Protozoa, was of an amoeba about 200μ in diameter with a Nebela tincta 120μ long in the protoplasm.

In the Metazoa, the rotifers are bacterial or occasionally algal feeders, and the majority of nematodes had stylet mouth parts although some predatory mononchids were present. No recognisable contents were found in the digestive tracts of nematodes, turbellaria, copepods or mites. Two of the six specimens of Enchytraeoides sphagnetorum examined, were seen to contain specimens of Cryptodifflugia oviformis and Corythion* among the masses of peat particles. It is probable that these testates were ingested with the general detritus. The only chironomid larva examined, contained masses of algae and the gut contents of Cladocera were regularly green in colour although no identifiable particles were present.

There does not appear to be any metazoan which preys on Testacea to any considerable extent, the "potential predators" such as Mononchus being relatively scarce.

One possible group of predators are the Fungi (Dreschler 1935-1948 in Peach 1955). A number of empty tests of Nebela tincta, Assulina muscorum and Amphitrema flavum were seen to contain brown, fungal aseptate mycelium, which unfortunately could not be identified. No living Testacea were observed to contain fungal hyphae which might have been expected if the fungi were preying or parasitising the amoebae. The number of occurrences of fungi in tests was relatively few and this is probably/

probably not a major cause of mortality.

Conclusions

From this rather scanty information, it may be deduced that in wet Sphagnum, diatoms and algae, presumably with bacteria, form the basis of the food web. In the drier areas, where diatoms and algae are largely absent, bacteria are the main food. The latter habitat thus resembles more closely the usual concept of "soil" with the lack of chlorophyll-containing organisms, most of the microfauna being smaller than their aquatic relatives and are bacterial feeders (Birch and Clark 1953, Kuhnelt 1955).

It has not been possible to assess the effect of organisms living in the air-spaces between the Sphagnum, but no major predator of Testacea was observed in the aquatic microfauna although there is considerable predation within the Testacea.

Section 2.

The distribution of Testacea on individual *Sphagnum* plants.

THE DISTRIBUTION OF TESTACEA ON INDIVIDUAL SPHAGNUM PLANTS.

Individual Sphagnum plants show a marked vertical zonation, with a compact head below which is a green portion of varying length, with well developed branches and leaves. This grades into the lowest section where the few remaining branches and leaves are brown in colour. Little peat is found in the upper sections but in the lowest few cm. the amount of peat attached to the plant increases greatly. This zonation is found to a variable extent in all Sphagnum species but it is probably most marked in S.recurvum, particularly where there is no water-movement.

Heinis (1945) divided Sphagnum plants into three sections, each of 10 cm. He did not find a marked vertical distribution of Testacea, but most species were present in the top 10 cm. The lack of information from this survey probably arose from the large sections examined, as it is shown below that Testacea are in most cases limited on a much smaller scale than that examined by Heinis.

Preliminary survey.

S.recurvum plants, from Valley Bog, Moor House, about 10 cm. long were divided into 3 equal sections (upper, middle and lower). Water was expressed from these sections into watch glasses and examined under x30 and x100 magnification. The data obtained (Table 13) indicated the occurrence of a well marked zonation of Testacea. The number of species increased with depth and in the upper section, the majority of tests were occupied; in the middle section only about 50% were full, and in the lower section most of the tests were empty.

After 7 plants had been examined, it was decided to carry out a more detailed survey using a quantitative method.

Detailed survey.

Method

The method finally adopted may be summarised as follows

1. Collection of samples.
2. Preparation of each sample by maceration.
3. Extraction by centrifuging through a filter.
4. Concentration of the filtrate.
5. Counting the Testacea in a graduated cell.

1. Samples were collected in the field by cutting off the head of the Sphagnum plant and dividing the remaining stalk into 2 cm. lengths ("levels"), each portion being placed in a tube containing 4% formalin. Throughout the survey the head sample was treated as being comparable with other samples.

2. Using forceps, the leaves were removed from the branches of each sample, thus releasing the Testacea caught between the leaves and in the axils.

3. The macerated Sphagnum was placed in a 5 cm. long bolting-silk "thimble", with c.500 meshes per sq.cm. The mesh thus has a side of about 350 μ, allowing all tests to pass through. This thimble was then placed in a centrifuge tube containing water (Fig. 4), and centrifuged at 1500 revs. per minute for 5, 1 minute periods. The samples were agitated between each period of centrifuging.

4. The filtrate containing the testates was concentrated to 2 ml. by removal of the supernatant fluid with a pipette.

Fig. 4. Centrifuge tube (A) containing a bolting silk thimble (B) supported by a brass ring (C) and containing the macerated Sphagnum.(D)

5. The concentrate was agitated to suspend the testates, then 4 sub-samples of 0.5 ml. were taken, placed in a graduated cell and the tests counted under x30 and x100 magnifications. Because of the structure of the cell (Fig. 5) higher magnifications could not be used. All large tests ($> 100\mu$) on the slide were counted, but smaller specimens were counted from a given area of the slide and the total number of tests per slide calculated.

The above method was the one finally adopted and was used for the majority of the samples, but in the first 3 samples the tests were extracted by washing. The macerated Sphagnum was placed on a bolting-silk filter in a glass funnel and washed with a fine jet of distilled water (400 ml.). 100 ml. of the filtrate was concentrated, sampled and counted as above. The main difficulties with this method were that the washing was not uniform and it was difficult to repeat in a like manner with each sample. Considerable time was also taken in washing and particularly in concentrating the filtrate. The efficiency of this method did not appear to differ from that finally adopted (p.59), so the results are taken as comparable.

A cell (Fig. 5), with a grid for counting, was constructed as follows. The floor of the cell consisted of a photographic plate on which the grid, 25 x 20 cm., had been reproduced. Each square of the grid corresponded with the field under x100 magnification. The emulsion was protected by a cover slip. By mounting another cover slip on two glass strips, each 1 mm. deep and 20 mm. long, placed 25 mm. apart, the cell had a volume of 0.5 ml. (25 x 20 x 1 mm.).

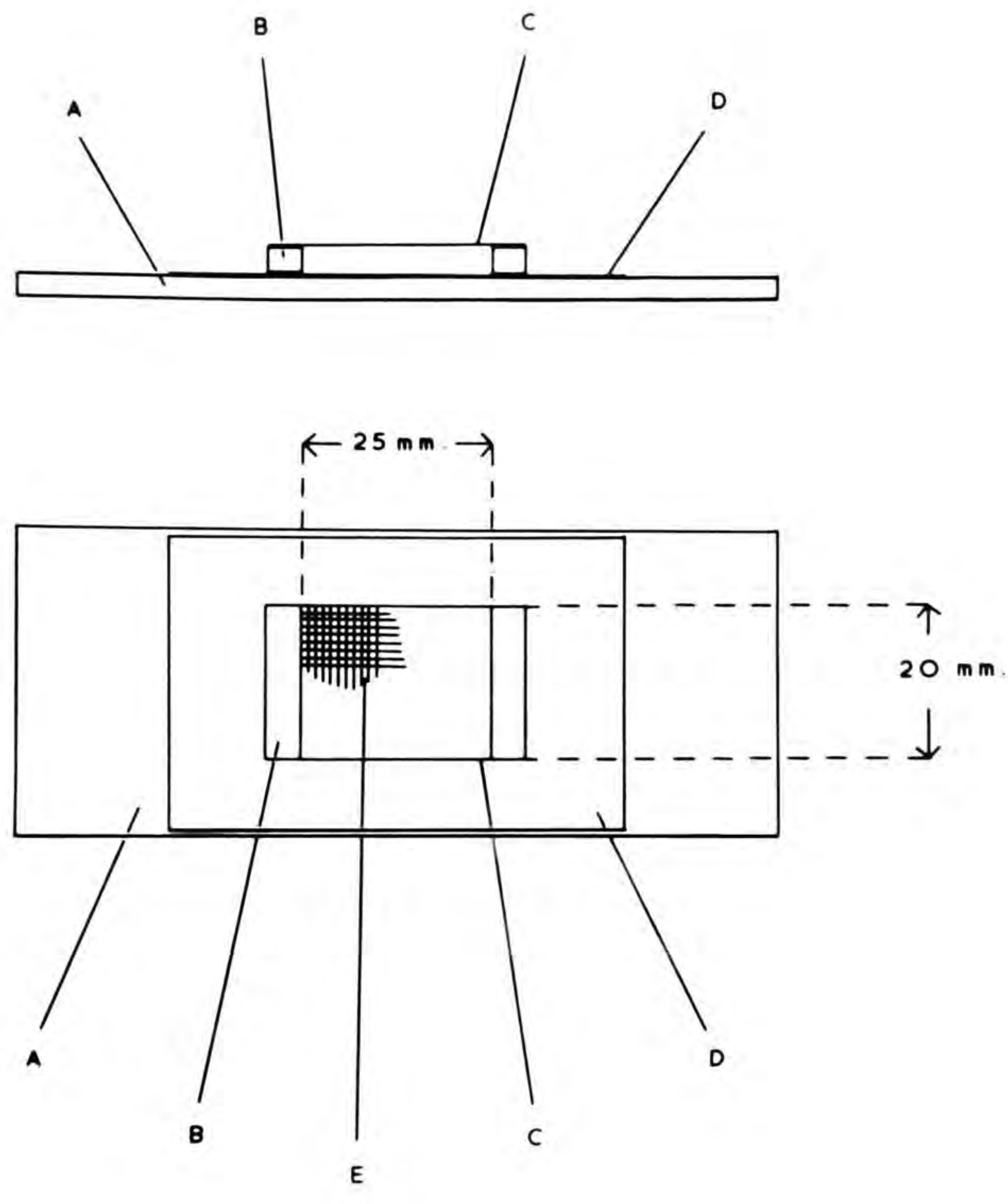


Fig. 5. The counting cell. A, photographic plate. B, 1 mm. deep glass support. C, cover slip forming the cell roof. D, cover slip protecting emulsion on the photographic plate. E, grid.

The grid lines were very thin and slightly out of focus when the cell floor was examined, thus they did not interfere with counting. A suspension could be easily injected or withdrawn and the cell readily cleaned with filter paper.

The cell volume was ascertained by weighing it, then filling it with water until the manisci reached the edges. It was then re-weighed. This process was repeated a number of times and the volume calculated as 0.498 ± 0.009 ml. A number of pipettes were graduated from the original cell and one was kept as a standard to test the volume of other cells.

Sources of error in the method.

Errors in extraction.

In the extraction there were two possible errors. The first was that 5, 1 minute periods of centrifuging or washing with 400 ml. water were not sufficient to extract all the animals. To test this, the number extracted by each 1 minute period of centrifuging, and after each 100 ml. of washing, were counted. The results shown in Tables 6 and 7 indicate that the methods removed the majority of extractable tests.

Table 6. The % of tests extracted after each 100 ml. washing. The figures in brackets indicate the number of tests extracted.

	Washing 1	2	3	4	
Experiment 1.					
Nebela tincta	88.2	5.9	-	5.9	(68)
Amphitrema flavum	84.0	16.0	-	-	(355)
*A.wrightianum**	80.0	16.0	-	4.0	(475)
Cryptodifflugia oviformis	74.0	13.0	6.5	6.5	(366)
Experiment 2.					
Nebela tincta	66.6	33.3	-	(12)	
*Amphitrema wrightianum**	100.0	-	-	(19)	
Cryptodifflugia oviformis	87.5	-	12.5	(152)	

Table 7. The % of tests extracted after each of 4, 1 minute periods of centrifuging. Bracketed figures show the number of tests extracted.

	Extraction 1	2	3	4	
Nebela tincta	96.0	-	2.0	2.0	(48)
Rotifera	96.0	4.0	-	-	(28)

The second possible source of error in extraction, was that some tests might be so lodged in the Sphagnum, that they were not extracted. After extraction, the macerated Sphagnum was carefully examined under x30 magnification. The results (Table 8) showed that some tests were not extracted, these usually being situated in the junction of a branch to the stem, where a few leaves had not been removed. Results could only be obtained for one species, but they indicate that the method of extraction was adaquate for the purposes.

Table 8. The number of tests remaining after extraction by centrifuging.

		No. extracted	No. remaining	% efficiency
Sample 1.	Hyalosphenia papilio	47	12	79.6
" 2.	" "	86	23	79.9
" 3.	" "	72	8	90.0
" 4.	" "	44	5	89.7

The extraction did not release small species living in the hyaline cells of the Sphagnum leaves (Paulson 1952). In Valley Bog, Cryptodifflugia oviformis (length 20 μ) was the only species observed to do this.

Examination of the supernatant fluid after concentration of the filtrate showed that no tests were being lost at this stage and there was no indication that maceration and centrifuging damaged the tests.

Errors in counting.

(a) Distribution in the cell.

When placed in the cell the larger tests were readily visible using x30 magnification, and all the specimens in the cell were counted ("cell counts"). Smaller species ($\langle 100\mu$) had to be counted under x100 magnification. Because of this, and as there were large numbers of small tests, the individuals from a restricted area of the cell were counted ("Block counts"). If the latter counts were to give an accurate estimate of the population, then the tests must be randomly distributed in the cell. A non-random distribution could be caused by differential sedimentation.

To test for a random distribution, a number of cells were examined under x100 magnification and the distribution of the tests recorded on sheets, with a grid comparable with that in the cell (Fig. 6). The grids were then divided into 8 equal areas (blocks) and an Analysis of Variance calculated for the 3 commonest species, Cryptodifflugia oviformis (c. 20 μ long), Amphitrema flavum (c. 50μ) and Nebela tincta (c. 120μ). The Analysis of Variance for C.oviformis is shown in Table 9. The value of F does not reach the 10% level in either case, thus the specimens of C.oviformis may be taken to be randomly distributed in the cell, with no significant difference between samples.

Similar results were obtained for Amphitrema flavum and Nebela tincta , showing that there is no differential sedimentation, even in the larger species.

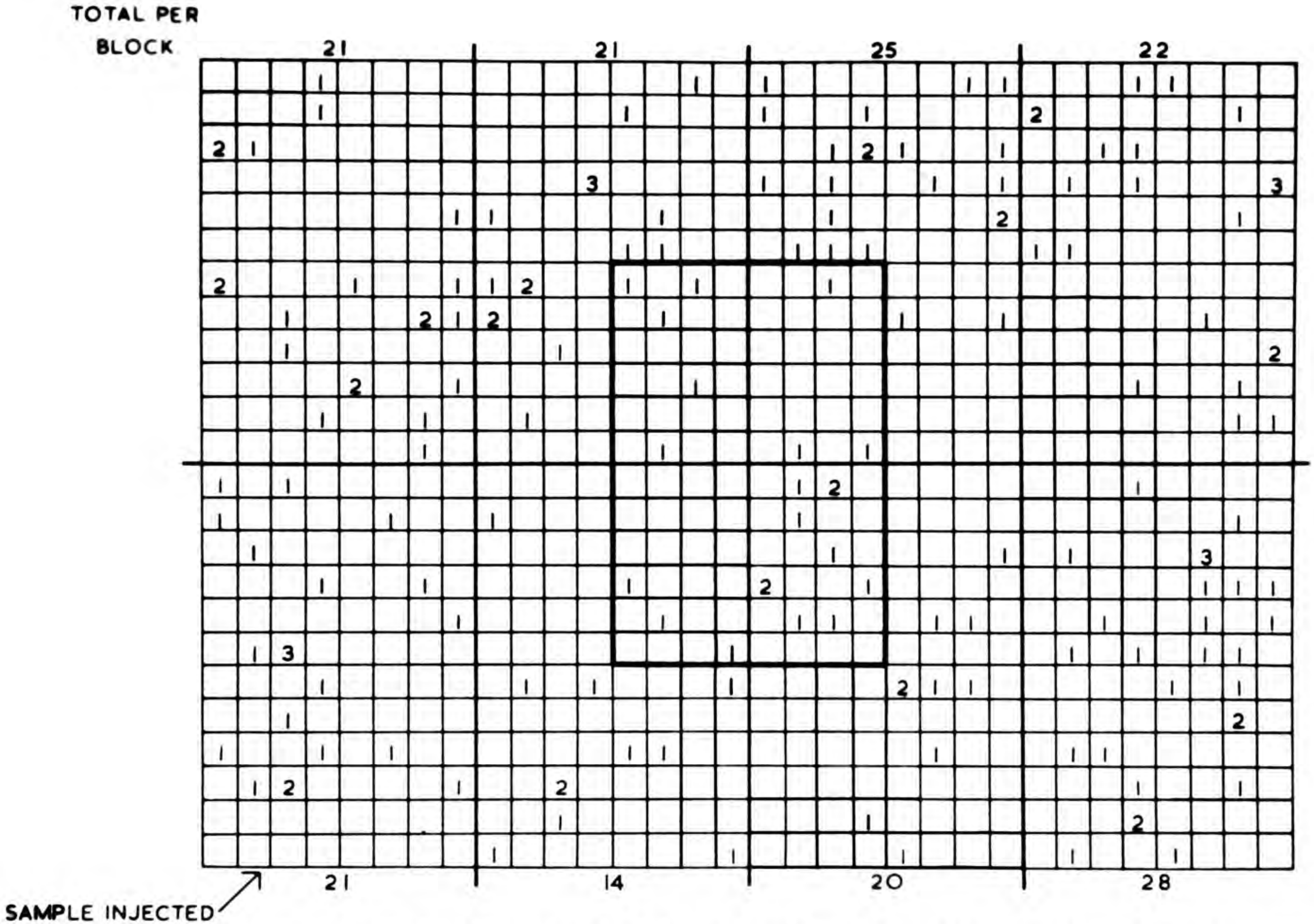


Fig. 6. The cell grid showing the distribution of tests of Cryptodifflugia oviformis. The 8 blocks used in the Analysis of Variance are marked, the central area is that used for "block" counts.

Table 9. Table of Analysis of Variance for the distribution of *Cryptodifflugia oviformis* in the counting cell.

	°Freedom	Sum of squares	Var. estimate	F
Between sample var.	3	60.75	20.25	1.00
" block "	7	296.50	42.36	1.78
Residual var.	21	500.25	23.82	
Total	31	857.50		

A comparison of block and cell counts was also made using a suspension of *Amphitrema flavum*. The results are shown in Table 10. The 95% Confidence Limits overlap indicating that the differences are not significant.

The remaining tests in the suspension were also counted (166) giving a total of 232 specimens counted from the suspension. This compares with the estimates of 298 and 220.

Table 10. Comparison of block and cell counts of *Amphitrema flavum*.

	No. of tests in each count	Calc. no. in original suspension $\pm$ 95% C.L.
Block	0; 4; 2; 3; 1; 0; 1;	298 ± 99.5
Cell	13; 9; 9; 12; 12;	220 ± 15.0

(b) Errors in sub-sampling.

To see if the suspension was sedimenting or aggregating during sub-sampling, thus causing the sub-samples to differ from one another,

-tests/

χ^2-tests were carried out on a series of sub-samples. These were not significant at the 5% level (Table 11). This shows that the range in each set of sub-samples is within the range expected from a random distribution.

Table 11. χ^2-tests on sub-sample variation.

Mean	No. of samples	χ^2
1.6	7	8.3
6.6	10	8.5
21.6	5	3.5
24.2	10	10.9
76.5	4	5.3
116.6	5	4.5
204.7	4	6.5

c). <u>Counting samples of different size</u>.

Another possible source of error was that when extreme numbers of tests per cell were counted, the counts were inaccurate. This was tested by taking a suspension of Testacea and diluting or concentrating portions of it to a known extent. These were then sampled, the number of tests in the original suspension calculated, and the estimates compared. Because large numbers of animals were required, only the figures for *Cryptodifflugia oviformis* could be used in the calculations.

The results are shown in Fig. 7 and the 95% Confidence Limits indicate that a significantly lower estimate of the population is obtained when large numbers of animals per cell are counted. This assumes that the higher estimates of the population are most accurate. Original data are shown in Table 12.

Table 12. Population estimates from counts of different concentration.

Conc.	Counts	Mean $\pm$ S.E.	Estimate $\pm$ 95% C.L.
N/4	21,18,21,19,29.	21.6 $\pm$ 1.72	1728 $\pm$ 348.5
N	84,74,87,61.	76.5 $\pm$ 4.79	1530 $\pm$ 265.5
2N	103,111,119,116,134.	116.6 $\pm$ 4.58	1166 $\pm$ 117.7
4N	211,178,228,202.	204.7 $\pm$ 8.24	1023 $\pm$ 114.1

The 95% Confidence Limits are a multiplication of the Standard Error. Where more than 30 samples are used, 2x S.E. is taken. When less than 30 samples are used, the number of samples (n) is found in the t-test tables at 0.05 probability to give the multiplication factor. Where C.L. do not overlap, the means are significantly different.

The inaccurate population estimates obtained when large numbers of animals were counted (Fig. 7) were probably due to the difficulties in counting resulting from the increased amounts of detritus present. This correlation/

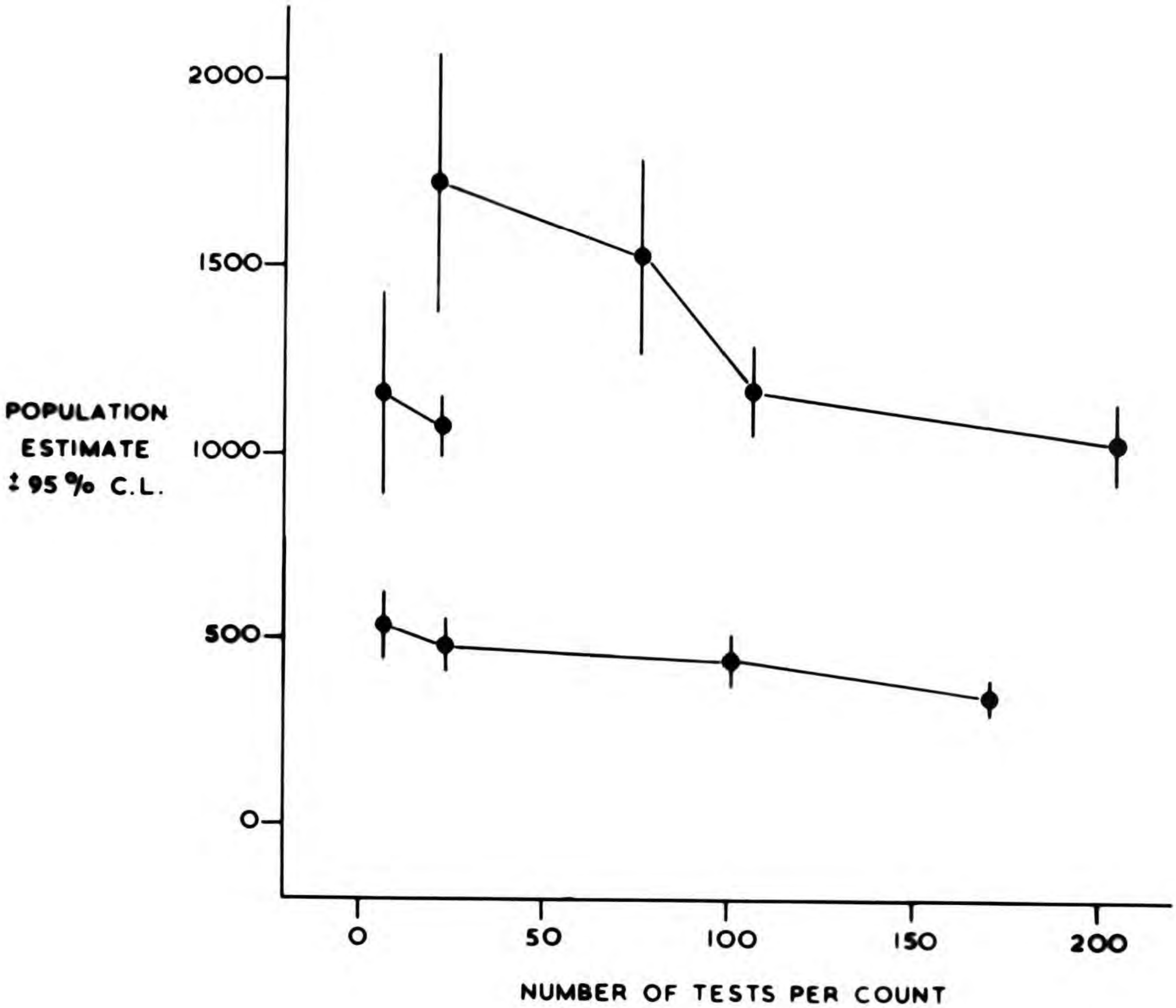


Fig. 7. Population estimates obtained from counts of varying concentrations of *Cryptodifflugia oviformis*.

correlation between large numbers of tests per cell and large quantities of detritus, was due to the concentration of the suspension and does not occur in nature. However in the survey, large quantities of detritus were avoided by dilution of the sample. Lund et al (1958) state that "---the accuracy of a count varies indirectly as the square root of the number counted" and therefore it is to be expected that the larger the count, the more accurate the estimate will be.

Results of the detailed survey.

Treatment of results.

Only the results obtained from the quantitative sampling of 12 *S.recurvum* plants will be discussed in detail. 11 other plants of *S.recurvum* were examined in the same way but the results from these are not included in detail because the *Sphagnum* varied in length and in some cases they were taken from atypical habitats. The results of these however, completely confirm the data obtained from the 12 plants examined here.

The results of the preliminary survey (Table 13) also verify those of the detailed survey, but as they do not add any information they are only mentioned briefly.

In dealing with the distribution of individual species, the results were first examined using an Analysis of Variance, to see if there were significant differences between levels. This was seldom shown because of the great "between sample variation" (p.83), although the proportion of tests found at a given level was fairly constant. A χ^2-test was therefore carried out on the results obtained for each species of Testacea on each of the 12 plants. In the majority of cases it was only required to find if the species inhabited the lower levels rather than one particular level, therefore the total number of tests in the lowest three levels was compared with the total from the upper 3. (Table 16).

The distribution of *Hyalosphenia papilio*, *Nebela tincta* and *Amphitrema flavum* was more restricted and the number of tests in pairs of levels or individual levels was used. (Figs. 8-10).

The full results of these χ^2-tests are shown in Table 16 and an example of a complete calculation is shown in Appendix 2. Though this method is unwieldy it overcomes the difficulty of the "between sample variation".

The distributions of the 4 commonest species are graphed (Figs. 8-11), but the Standard Errors of the Means are only included in one graph (Fig. 8). This is because the Standard Errors are large due to "between sample variation" (p.83) and tend to obscure the graphs. Also, as mentioned above, the proportion of tests present at a level or levels is fairly constant, despite the "between sample variation", and this has been shown by χ^2-tests.

General results.

The number of species present in each level, increases greatly with depth, the lowest levels usually containing 2-3x the number of species present in the head (Table 14). The majority of species are restricted to a few levels, or if the species is present at most of the levels, the full tests show an optimum in a restricted area (Table 14).

The optimum for the empty tests is lower down the stem than that for full ones (Tables 14, 15. Figs. 8-11) probably due to the empty tests being washed down the Sphagnum stems. The empty tests appear to suffer little damage and each Sphagnum plant usually carries more empty than full tests. Empty tests are preserved in the peat and attempts have been made to correlate these with the peat formation, (Grospietsch 1952, 1953, Harnisch 1948). However membranous tests preserve better than those/

Table 13. Preliminary survey. Presence of Testacea (full + empty tests) in three levels of S.recurvum, 7 samples at each level.

	Upper	Middle	Lower
Hyalosphenia papilio	5	4	5
Nebela tincta	6	6	5
Amphitrema flavum	6	6	6
Assulina muscorum	3	3	3
Amphitrema wrightianum*	1	4	2
Cryptodifflugia oviformis	2	4	6
Euglypha strigosa	3	5	6
Phryganella hemispherica*	1	1	6
Heleopera rosea	-	3	-
Corythion*	-	2	7
Nebela militaris	-	2	6
Difflugia bacillariarum	-	1	-
Centropyxis aculeata*	-	-	1
Heleopera sylvatica*	-	-	4
Nebela flabellulum	-	-	4
Nebela dentistoma	-	-	3
Difflugia oblonga	-	-	3
Placocista spinosa	-	-	2
Centropyxis cassis*	-	-	1
Nebela acolla	-	-	1
Plagiophrys parvipunctata	-	-	1
Hyalosphenia elegans	-	-	1
Total no. of species	8	12	20

Table 14. The presence of species recorded at the 6 levels in the detailed examination of 12 S.recurvum plants. F = full tests. E = empty. In some cases full and empty tests were inseperable.

		Level 1	2	3	4	5	6
Hyalosphenia papilio	F	12	11	5	4	2	2
	E	5	7	6	6	7	5
Nebela tincta	F	11	12	12	12	11	9
	E	5	12	12	12	12	11
Amphitrema flavum	F	10	10	8	6	6	5
	E	1	8	7	7	8	8
Assulina muscorum	F	6	1	4	1	2	-
	E	1	-	3	3	2	2
Amphitrema wrightianum*	F	1	2	4	5	4	5
	E	-	-	1	4	1	6
Cryptodifflugia oviformis	F	1	2	5	6	9	9
	E	1	1	2	4	10	9
Euglypha strigosa	F	1	-	6	6	4	6
	E	-	-	5	6	8	11
Cryptodiff. eboracensis	F E	1	-	2	4	6	8
Heleopera rosea	F	-	-	3	7	6	5
	E	-	-	1	3	4	5
Corythion*	F	-	-	3	5	5	9
	E	1	-	5	9	10	9
Lecythium hyalinum	F	-	-	2	2	1	1
	E	-	-	-	-	-	-
Centropyxis aculeata*	F	-	-	2	3	4	2
	E	-	-	1	2	5	5
Bullinula indica	F E	-	-	1	2	1	-
Pseudodifflugia	F E	-	-	1	5	8	7

continued

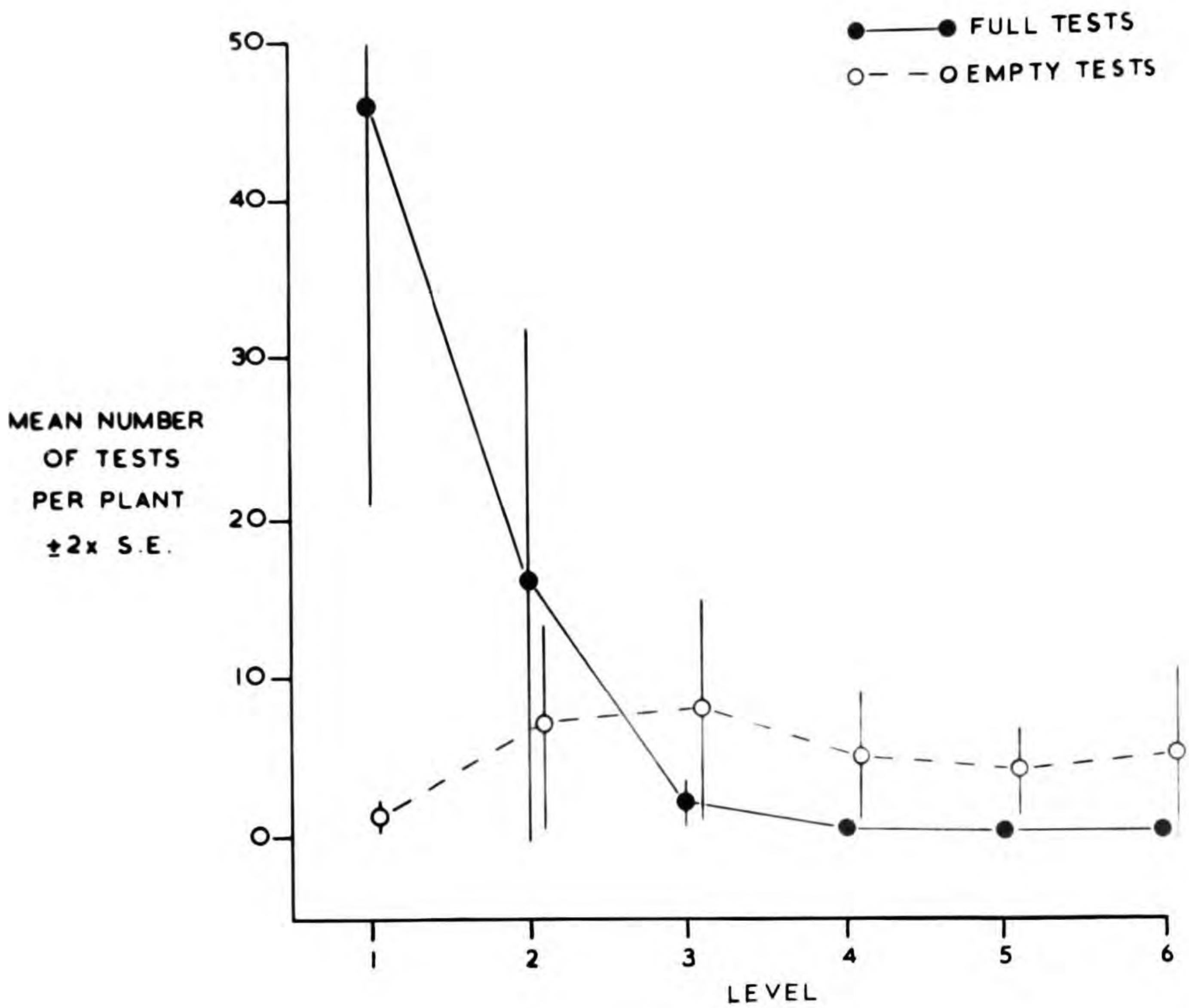
		Level 1	2	3	4	5	6
Nebela flabellulum	F	-	-	1	3	4	5
	E	-	-	1	-	3	6
Heleopera sylvatica*	F	-	-	1	4	3	3
	E	-	1	1	6	5	7
Difflugia oblonga	F	-	-	-	2	3	4
	E	-	-	-	-	3	4
Nebela militaris	F	-	-	-	2	2	4
	E	-	-	-	3	3	8
Difflugia brevicolla	F	-	-	-	2	3	2
	E	-	-	-	-	3	2
Placocista spinosa	F	-	-	-	1	2	2
	E	-	-	-	-	1	-
Phryganella hemisph*	F E	-	-	-	1	3	7
Difflugia rubescens	F	-	-	-	-	2	2
	E	-	-	-	2	1	2
Centropyxis cassis*	F	-	-	-	-	2	3
	E	-	1	-	-	2	3
Nebela dentistoma	F	-	-	-	-	1	3
	E	-	-	-	-	-	1
Assulina seminulum	F	-	-	-	-	1	-
	E	-	-	-	-	-	-
Hyalosphenia elegans	F	-	-	-	-	1	-
	E	-	-	-	-	1	-
Nebela parvula	F	-	-	-	-	-	1
	E	-	-	-	-	-	-
Nebela tubulosa	F	-	-	-	-	-	1
	E	-	-	-	1	-	-
Trigonopyxis arcula	F E	-	-	-	2	2	2
Total no. of species	F	7	6	13	17	22	21
	E	6	6	12	14	19	18
	F + E	1	-	3	5	5	4

those bearing mineral particles, thus giving biased results. In the present survey the majority of tests were membranous or bore silica plates; only Difflugia oblonga had a test of mineral particles and this was present only in small numbers. Nothing may therefore be concluded concerning the rates of disintegration.

One general conclusion which is indicated by this survey is the need to take samples from the whole length of the Sphagnum strand to obtain a true picture of the Testacea present.

Hyalosphenia papilio and Amphitrema flavum.

Direct observation of a strand of S.recurvum under x30 magnification will often reveal large numbers of H.papilio situated on the upper parts of the plant. The vertical sectioning showed that full tests were largely confined to the head and top 2cm. 95% of the 783 full tests were found in these 2 levels. The numbers in the head were significantly higher ($<5\%$ level of significance) than those in level 2, in 8 of the 12 plants (Fig. 8). The distribution of empty tests was not well marked. Encysted individuals were found in large numbers in 2 of the heads, 54 specimens in each, and this indicates that H.papilio responds to unfavourable conditions by encysting rather than by migrating to a lower level.



	Levels	χ^2 tests Sig.	Not sig.	No animals
Full	1 > 2	8	4	0
	" < "	0		
	1,2 > 3,4	12	0	0
	" < "	0		
	3,4 > 5,6	2	5	5
	" < "	0		
Empty	1,2,3 > 4,5,6	3	4	3
	" < "	2		

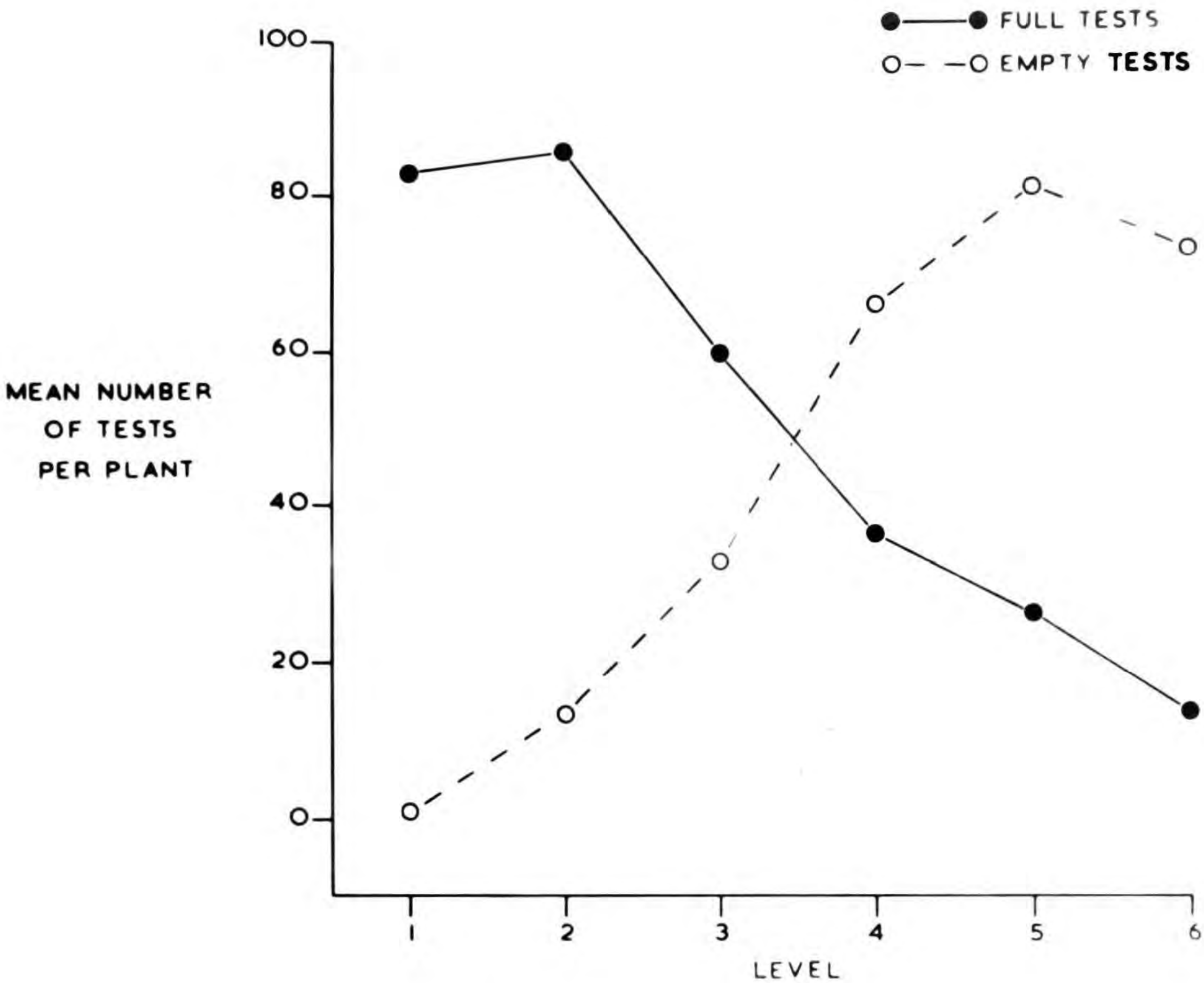
Fig. 8. The distribution of Hyalosphenia papilio on S.recurvum and the results of χ^2 tests.

The full tests of A.flavum appear to be slightly less restricted to the upper layers of the Sphagnum (Fig. 9) than those of H.papilio. However the living specimens in the upper layers were full of protoplasm and the symbiotic zoochlorellae were bright green in colour, but in lower samples there was a decreasing amount of protoplasm and the zoochlorellae were pale. Because of this, in the lower levels, it was often difficult to differentiate between tests containing protoplasm and empty tests containing particles of detritus. It is probable that the optimum zone for this species is more restricted than is shown in Fig. 9.

H.papilio and A.flavum are the two species showing the most marked preference for the upper layers of the Sphagnum. Both have membranous tests, without foreign particles and contain zoochlorellae in their protoplasm.

It is suggested that their distribution is a response to light in order to maintain their symbionts. To find if either species would live in areas of restricted light, a $0.3m^2$. sheet of blackened perspex, supported by canes, was placed in a S.recurvum flush about 2 cm. above the Sphagnum heads. It was hoped to compare the numbers of H.papilio and A.flavum occurring outside and underneath the shade. This was not possible on a quantitative basis, because, under the shade, the Sphagnum became elongated and the head greatly reduced in size, so that comparable samples could not be taken. However an examination of the Testacea, after the "shade" had been in position for 7 months showed that large numbers of tests of H.papilio and A.flavum were present in both cases,

but/



		χ^2 tests Sig.	Not sig.	No animals
Full	1,2 > 3,4	8	4	0
	" < "	0		
	3,4 > 5,6	12	0	0
	" < "	0		
Empty	1,2 > 3,4	2	5	5
	" < "	0		
	3,4 > 5,6	3	4	3
	" < "	2		

Fig. 9. The distribution of Amphitrema flavum on S.recurvum.

but tests from the shaded area were mainly empty, the full tests that were present, containing comparatively little protoplasm and the zoochlorellae were pale yellow-green in colour. In comparison, the Testacea from unshaded areas, were normal in respect of protoplasm and zoochlorellae, and most of the tests were full. The only other common species was Nebela tincta which appeared to be unaffected by shading. This species does not contain symbiotic algae.

A number of samples taken from naturally shaded areas did not give a clear picture, because actual numbers could not be compared due to etiolation. Also Sphagnum does not grow in heavily shaded areas.

These results indicate that light may be an important factor governing the distribution of H.papilio and A.flavum, because of the symbiotic algae which they contain. However it is difficult to reconcile this with the distribution of A.wrightianum* (Tables 13-15). This species also contains symbiotic algae, but differs from H.papilio and A. flavum in having foreign particles attached to the test. Though present in much smaller numbers than the other two species, the figures indicate an optimum in the middle and lower levels of the Sphagnum.

Other chlorophyll-containing organisms were present, particularly diatoms, but these occurred in relatively few samples, varying greatly in number (maximum of 9433 in one sample). They were present at all levels and common even in the lowest, but there, like A.flavum, they did not appear to be healthy.

Table 15. The distribution of Amphitrema wrightianum*. (a) Totals for 12 plants. (b) The results of χ^2-tests on individual plants.

(a)

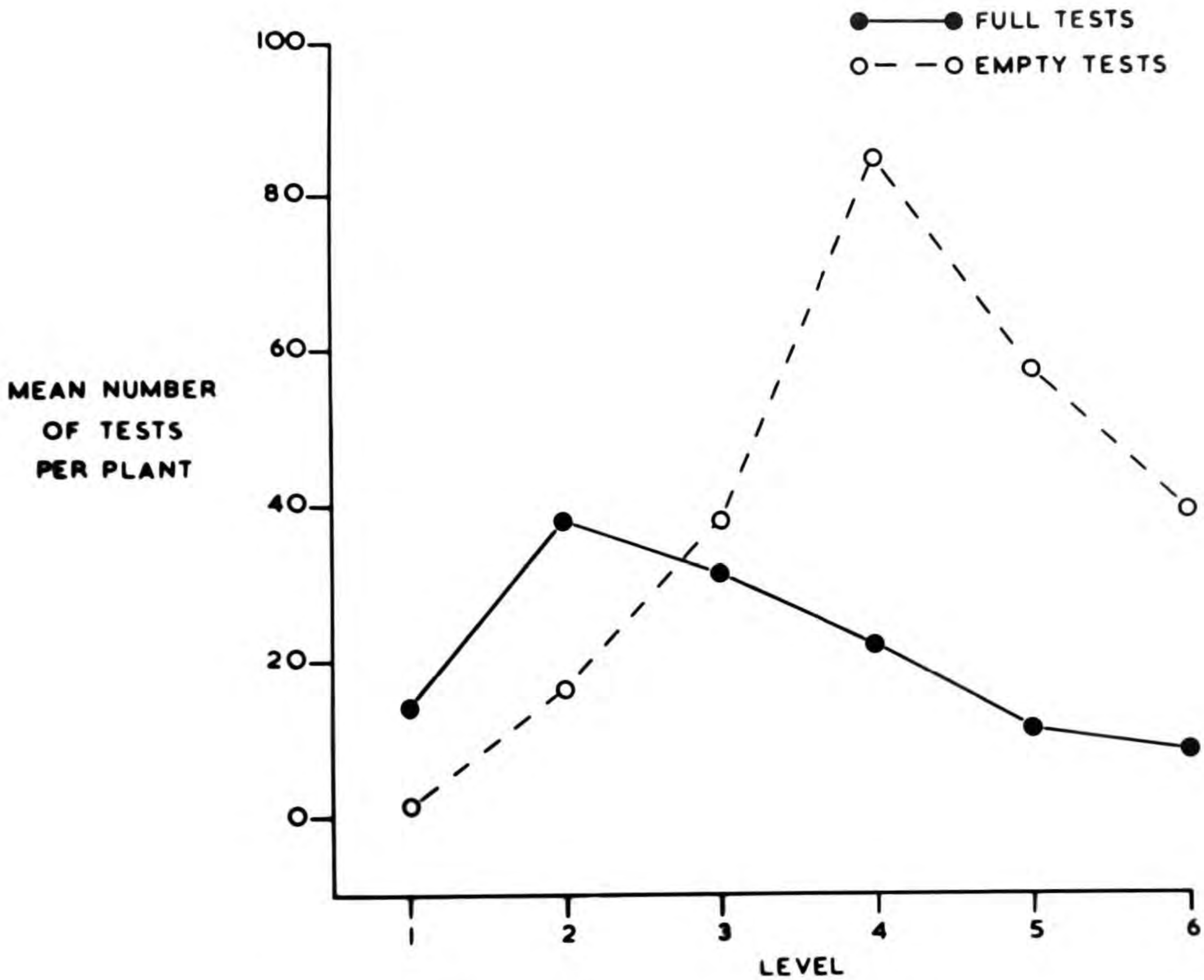
Level	Number of tests Full	Empty
1	9.5	-
2	114	-
3	294	114
4	209	104
5	294	19
6	119	166

(b)

	Levels compared	Result of χ^2-tests Sig.(5% L.C.)	Not sig.	No animals
Full	1+2 > 3+4	0	1	5
	" < "	6		
	3+4 > 5+6	4	0	3
	" < "	5		
Empty	1+2 > 3+4	0	0	7
	" < "	5		
	3+4 > 5+6	2	2	5
	" < "	3		

Nebela tincta.

The result of χ^2-tests showed that the distribution given in Fig. 10 was fairly accurate, with the majority of the full tests in levels 2, 3 and/



		χ^2 tests		No animals
		Sig.	Not sig.	
Full	1 > 2 " < "	1 6	5	0
	1,2 > 3,4 " < "	4 6	2	0
	3,4 > 5,6 " < "	10 2	0	0
Empty	1,2 > 3,4 " < "	0 9	3	0
	3 > 4 " < "	1 7	4	0
	4 > 5 " < "	5 3	4	0
	5 > 6 " < "	7 2	3	0

Fig. 10. The distribution of Nebela tincta on S.recurvum.

and 4. Empty tests occur mainly in the lower levels and χ^2-tests (Fig. 12) indicate that the peak in level 4 does not occur regularly, but is the result of an unusually high population in one sample. On examination of the original data it was seen that 432 empty tests were present in one sample at level 4.

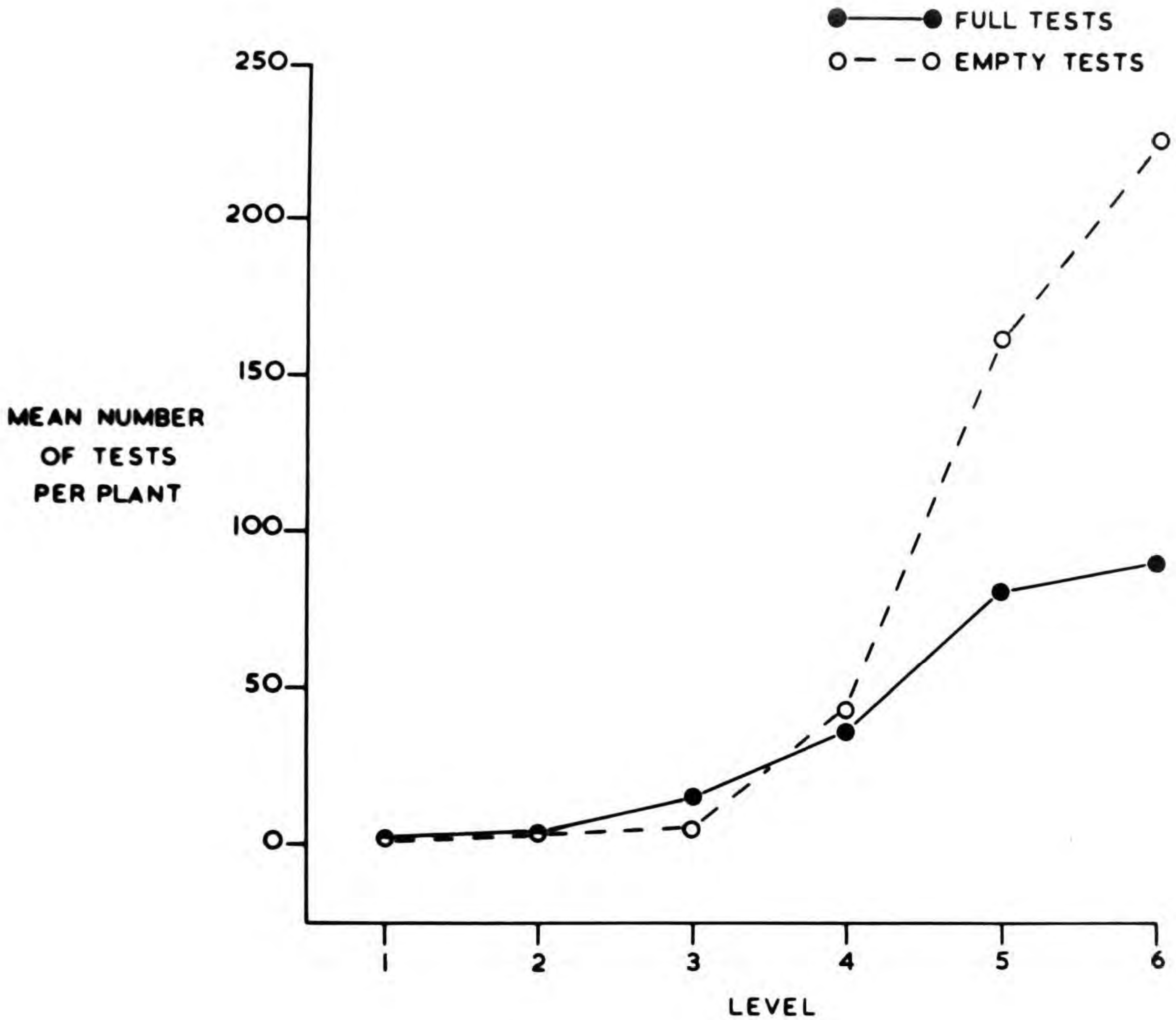
Cryptodifflugia oviformis.

This is one of the many species concentrated in the lower parts of the Sphagnum strands (Fig. 11), but it is the only one apart from C.eboracensis (Table 16) which occurs in large numbers.

Other species.

A number of species, though not common, showed distinct distributions which correspond with those described above. Full details are not given, but the results of χ^2-tests and the total number of specimens recorded are shown in Table 16.

Assulina muscorum is similar to Amphitrema flavum in its distribution and clearly shows the different distribution of full and empty tests. Full tests of Euglypha strigosa reach an optimum in the middle and bottom levels, but again the empty tests reach their maximum in the lowest levels. The remaining 7 species show very similar distributions with maxima of both full and empty tests in the lowest levels, thus resembling Cryptodifflugia oviformis (Fig. 11). The results of the χ^2-tests are all similar to those of Centropyxis aculeata* and are therefore not included in Table 16.



		χ^2 tests Sig.	Not sig.	No animals
Full	1,2,3 > 4,5,6	1	0	1
	" < "	10		
Empty	1,2,3 > 4,5,6	0	0	2
	" < "	10		

Fig. 11. The distribution of Cryptodifflugia oviformis on S.recurvum.

Table 16. Total numbers of individuals from 12 plants of <u>S.recurvum</u> and results of χ^2-tests on the individual plants.

<u>Assulina muscorum</u>

Level	Full	Empty
1	565*	38
2	38	0
3	66	57
4	9.5	28.5
5	19	28.5
6	0	47.5

	Level	χ^2-tests Sig.	Not sig.	No animals
Full	1,2,3 > 4,5,6.	7	0	4
	" < "	1		
Empty	1,2,3 > 4,5,6.	1	0	6
	" < "	5		

<u>Euglypha strigosa</u>

Level	Full	Empty
1	9.5	0
2	0	0
3	123.5	76
4	227	114
5	143	207
6	114	485

	Level	χ^2-tests Sig.	Not sig.	No animals
Full	1,2 > 3,4	1	0	3
	" < "	8		
	3,4 > 5,6	6	1	2
	" < "	3		
Empty	1,2 > 3,4	0	0	4
	" < "	8		
	3,4 > 5,6	1	1	0
	" < "	10		

<u>Centropyxis aculeata*</u>

Level	Full	Empty
1	0	0
2	0	0
3	6	4
4	23	5
5	13	10
6	4	23

	Level	χ^2-tests Sig.	Not sig.	No animals
Full	1,2,3 > 4,5,6	0	1	7
	" < "	4		
Empty	1,2,3 > 4,5,6	0	2	5
	" < "	5		

<u>Heleopera rosea</u>

Level	Full	Empty
1	0	0
2	0	0
3	8	1
4	26	6
5	18	15
6	15	9

<u>Nebela militaris</u>

Level	Full	Empty
1	0	0
2	0	0
3	0	0
4	19	38
5	57	60
6	66	296

Heleopera sylvatica*

Level	Full	Empty
1	0	0
2	0	4
3	9.5	9.5
4	36	64
5	24	133
6	23	203

Difflugia oblonga

Level	Full	Empty
1	0	0
2	0	0
3	0	0
4	3	0
5	16	11
6	29	53

Nebela flabellulum

Level	Full	Empty
1	0	0
2	0	0
3	2	1
4	8	4
5	31	19
6	32	32

Cryptodifflugia oviformis

Level	Full + Empty°
1	9.5
2	0
3	19
4	124
5	798
6	1482

* Mainly due to 1 sample containing 380 tests

° Full and empty tests were indistinguishable.

Discussion

It has been suggested (p.76) that reaction to light may govern the distribution of Hyalosphenia papilio and Amphitrema flavum, but there are no obvious factors controlling the distribution of other species. There is no apparent correlation between the distribution on a Sphagnum plant and the distribution in the pool-hummock succession. The upper layers of S.recurvum are liable to dessication and it might be expected that pool-dwelling species would tend to live in the lower levels, with zerophile species occupying the upper layers, but this was not the case.

The amount of detritus increases with depth, and it is composed mainly of small peat particles and Sphagnum leaves, the former sometimes being incorporated into the test of certain species. These species (Centropyxis aculeata*, Bullinula indica, Pseudodifflugia sp., Difflugia brevicolla, Phryganella hemispherica*, Difflugia rubescens, Amphitrema wrightianum*, Centropyxis cassis*, Heleopora sylvatica*, H.rosea and Trigonopyxis arcula) are almost completely restricted to the lower half of the Sphagnum plant where most of the detritus is present. (Tables 13,14).

In many studies on Protozoa, food has been shown to be an important factor influencing their distribution (Picken 1937, Noland 1925, Fauré-Fremiet 1950, Webb 1956). On pages 53-55 it is shown that Testacea are mainly omnivorous, indicating that food will have relatively little effect on their vertical distribution. A possible exception to this is that, if the bacterial population increases with depth and the accumulation of detritus, bacterial-feeding Testacea will be directly effected.

Regarding the possibility of seasonal variation in the vertical distribution, the preliminary survey was carried out from March-May 1957, and the detailed survey from May-October 1957, and similar distributions were shown in both cases. Also no marked variation was observed within each group of samples.

As mentioned earlier (p.58) the only work on vertical distribution in Sphagnum has been carried out by Heinis (1945) with little result. Volz (1951) however, examined the vertical distribution of Testacea in beech and oak woods. He recorded a separation of species living in different levels, but no chlorophyll-containing species were named. In general, small numbers of individuals were recorded in the undecomposed leaf layer; the population increased as the litter was humified, then decreased again as the mineral content became greater with depth. This corresponds with the observation of Sandon (1927) that Testacea are largely confined to soils with high humus content.

Volz (1951) also recorded that empty tests were more abundant than full ones, and that their maximum number was recorded at a lower level than that of living animals. Similar findings are recorded in the present survey.

Aggregation

The Standard Errors shown in Fig. 8 indicate considerable variation in the numbers of Testacea present in different samples. χ^2-tests were carried out for each species on the number of individuals present in each of 12 Sphagnum strands and the results were significant at the 0.1% level in all cases, showing that aggregation occurred.

This could be due to seasonal fluctuations, but samples taken on the same day also gave significant χ^2-tests. In one case 18 heads of S.recurvum from an area of about 0.1 m^2 were examined for Hyalosphenia papilio. The numbers observed (mean 38 $\pm$ 7.3) gave $\chi^2 = 459$ which is significant at 0.01% Level.

Assuming that the aggregation is not an artifact of the sampling technique, it may be caused by migration of animals, or variations in the reproductive or mortality rates. The latter is almost certainly the case and it has been noticed that the population is greatly increased when the Sphagnum has been under dung. This is probably due to the increase in bacteria and bacterial-feeding organisms, and also diatoms and algae, thus providing an increased food supply for the Testacea.

Population estimate.

It is not possible to give accurate estimates of the population, because the number of samples is very small; they were taken at different periods of the year, and the population is not randomly distributed. However the following figures give some indication of the "order of magnitude" of the testate population in a S.recurvum sward. Data obtained from the other Sphagnum plants previously mentioned (p.69) corresponds well with these estimates.

There do not appear to be any estimates of testate populations from Sphagnum, but Volz (1951) records the populations from beech and oak woods. Two examples are given by him of populations of living animals with 8,260,000 and 7,804,000 individuals per m^2 respectively, for two wood-types.

The figures below are based on the total number of full tests per stem analysed. The mean number of stems of S.recurvum per 0.01 m^2 is 138 $\pm$ 4.4, from 10 quadrats.

	No. per stem	Thousands per m^2
Hyalosphenia papilio	63 $\pm$ 18.5	869 $\pm$ 255
Nebela tincta	124 $\pm$ 21.0	1,711 $\pm$ 290
Cryptodifflugia oviformis	228 $\pm$ 116.0	3,146 $\pm$ 1,600
Amphitrema flavum	309 $\pm$ 90.0	4,264 $\pm$ 1,242
Cryptodifflugia eboracensis	200 $\pm$ 102.3	2,760 $\pm$ 1,407
Difflugia oblonga	4 $\pm$ 2.0	55 $\pm$ 30
Assulina muscorum	51 $\pm$ 32.9	704 $\pm$ 454
Nebela flabellulum	6.1 $\pm$ 1.8	84 $\pm$ 25

	No. per stem	Thousands per m^2
N.militaris	11.7 ± 5.2	161 ± 72
*Heleopera sylvatica**	7.5 ± 8.4	104 ± 116
H.rosea	5.5 ± 1.5	76 ± 20
*Centropyxis aculeata**	3.7 ± 1.9	52 ± 26
*Corythion**	71.0 ± 21.4	980 ± 295
Euglypha strigosa	24.5 ± 15.2	365 ± 209
*Amphitrema wrightianum**	86.6 ± 20.0	1,135 ± 276

This gives the number of Testacea per m^2 as c.16,500,000 ± 6,000,000.

Section 3.

The size of Testacea.

SIZE IN TESTACEA

It has long been recognised that species of soil micro-organisms living in the water-film are smaller than species living in aquatic habitats, and in some cases the soil is inhabited by small forms of larger species. (Kuhnelt 1955, Birch and Clark 1953, Lund 1945).

In the present survey it was noticeable that large species of Testacea tended to inhabit the pool Sphagnum, only relatively small species living in the drier hummocks (Table 17). Three of the largest species, Arcella catinus, Bullinula indica and Trigonopyxis arcula, occurring in the drier parts of the hummocks are dorso-ventrally flattened.

Nebela tincta

N.tincta occurred throughout the pool-hummock succession in Valley Bog in various forms which correspond to those described in the literature as N.tincta (Leidy) Awerintzew, N.tincta forma stenostoma Jung and N.tincta var.major Deflandre. The features of the three forms are given as follows.

N.tincta sensu stricto (= N.bursella Vejdovsky).

Length 70-90μ, breadth 50-65μ. Ovoid or slightly pyriform in shape, transparent or with few platelets, mouth usually truncate, lateral pores always present (Fig. 12.) Lengths given by other authors are 76-92μ Leidy (1879); 70-80μ Taránek (1882); 76-100μ Hoogenraad and de Groot (1940); 70-80μ Penard (1902); 70-120μ Awerintzew (1906); 85-90μ Cash et al (1901-1919); ± 77.5μ van Oye (1933); 70-90μ Deflandre (1936).

Table 17. The length of pool and hummock Testacea in Valley Bog. For flattened species, diameter* and height° are given.

	Observed size	Hoogenraad and de Groot (1940)
Pool		
Difflugia bacillifera	150-192 µ	120-180 µ
Amphitrema wrightianum*	60-87	53-71
Difflugia oblonga	132-156	60-580
D.bacillariarum	72-120	90-133
D.brevicolla	114	96-100
Nebela carinata	150-258	150-243
Placocista spinosa	144-180	93-155
Hummock		
Hyalosphenia papilio	112-126	92-130
Amphitrema flavum	50-75	50-68
Heleopera rosea	100-138	94-134
Assulina seminulum	78-132	67-107
Arcella catinus	99-132*,36-66°	80-135*
Nebela flabellulum	76-90	72-96
Nebela militaris	66-84	59-79
Hyalosphenia elegans	75	85-100
Euglypha strigosa	63-99	51-85
Assulina muscorum	40-52	33-60
Heleopera sylvatica*	60-84	50-75
Trigonopyxis arcula	115-120*,c.50°	59-180*
Bullinula indica	c.150*, c.80°	120-183*

N.tincta var.major.

Deflandre (1936) and Gauthier-Lievre (1953) figure this variety as broader than N.tincta s.s., ovoid to circular, covered by platelets, truncate mouth, and the pores present but rarely visible due to the platelets. The length recorded by Deflandre and Gauthier-Lievre is 90-120μ but the description corresponds exactly with specimens of length 125-156μ in the present survey. (Fig. 12.)

N.tincta f.stenostoma.

Jung (1936b) gives the size 100-130μ x 70-93μ . Pyriform in shape with a constricted neck and smaller mouth than N.tincta s.s. relative to the size. It is covered with plates, has a truncate mouth, and the pores are poorly visible due to the plates. (Fig. 12.)

Transects with about six samples in each were taken up the Sphagnum succession of Valley Bog to see if the size of the species was related to its distribution. From each sample, 20 specimens were taken and their length, breadth and mouth width were measured using a micrometer eye-piece. Some of the samples had to be rejected as there were insufficient specimens present, thus the number of specimens examined from each level is different (Table 18).

Fig. 12 shows the variation in form of specimens of N.tincta from Valley Bog. (Figs. 12-16 are grouped together after p. 92 for convenience).

Table 18. The number of specimens of N.tincta measured from different levels in the Sphagnum succession of Valley Bog.

Height above water-level (").	0	1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	22
Number of specimens.	160	180	140	120	120	140	160	60	80	20

The size variation of N.tincta shown in Fig. 13 and the bimodal distribution in Fig. 14, indicate that a form of length c.75-90 μ is clearly separated from specimens of length c.100-150 μ. The small group belongs to N.tincta s.s. and the presence of the lateral pores and the transparency of the test fit the general description. Further evidence that N.tincta s.s. is distinct from a larger form or forms was obtained from samples from Muckle Moss and Rusland Moss. In these it was noticed that the population of N.tincta contained two size groups, this being confirmed when 50 specimens from each sample were measured (Table 19). The lowest size group in each case corresponds to N.tincta s.s.

The main group of specimens (100-150μ) in Fig. 13 does not appear to be divided into the two forms, stenostoma and major. There is a definite change in shape from pyriform (stenostoma) to ovoid-circular (major) as indicated by the ratio, length:breadth (L/B). This is a measure of the "shape" of the test, nearing unity with a change from pyriform to ovoid. The mouth width of all the specimens was not measured, but the length and mouth width of 740 specimens are compared in Fig. 15. This indicates that between/

Table 19. The length in μ of 50 specimens from samples from Muckle and Rusland Mosses.

Length in μ	Area and height of sample above water level (")		
	Muckle Moss		Rusland Moss
	1	3	18
140-149	15	8	-
130-139	16	17	-
120-129	5	11	-
110-119	1	4	14
100-109	1	-	14
90-99	1	2	3
80-89	9	7	4
70-79	2	1	15

between the lengths 100-c.125μ the mouth is proportionally smaller than in tests of length 75-90μ or 130 μ, although there is considerable overlap. The middle group corresponds with Jung's stenostoma, but again it does not appear to be morphologically distinct from the var. major.

It thus appears that f.stenostoma and var. major are not distinguishable though there is a distinct but gradual change in the shape and mouth size. It is possible that the chosen morphological characters of the two forms overlap to such an extent that they are not separable although they may be genetically distinct. It is also possible that the two forms have been named without recognition of the intermediate stages and that they constitute a single, variable variety. Prof. G. Deflandre (personal communication) after examining specimens of the various forms from Moor House/

House stated that "N.tincta f.stenostoma Jung seems to be included in the variations but you are right when you find that it is difficult (if possible??) to separate it from var.major".

Hoogenraad and de Groot (1937) in a biometric survey of a number of Testacea examined N.tincta. They gave the typical size as 78-97μ, but also gave data for two mixed populations.

1. With size groups 78-102 and 102-121μ long.
2. With lengths 70-86 and 84-108μ.

The first population (1) in particular resembles a mixture of N.tincta s.s. and N.tincta f.stenostoma.

The distribution of N.tincta on Valley Bog.

When the transect samples are grouped in height above water level, the size of the specimens shows a gradual decrease as the hummock is ascended, with N.tincta s.s. dominant in the hummock tops (Fig. 16). The three samples from Muckle and Rusland Mosses (Table 19) show a similar relationship between size and height above water-level. Even if stenostoma and major are regarded as distinct forms, there is still a size change within each form (Fig. 16).

Possible explanations for the change in size.

1. The size change is not related to any change in the Sphagnum species as it occurs in hummocks composed of one or more Sphagnum species. Table 20 shows the change in a transect up a hummock composed entirely of S.rubellum.

Table 20. The size of specimens of N.tincta from a hummock of S.rubellum.

Length in μ	Height above water level in " 1	4	7	10
120-129	5	5	-	-
110-119	13	9	2	-
100-109	2	4	4	-
90-99	-	-	-	-
80-89	-	2	12	19
70-79	-	-	2	1

2. The possibility of the change being seasonal is ruled out because transects taken in April, July, September and October 1958 all showed the same relationship between size and height above water-level.

3. A possible migration of small or young forms down the hummock, increasing in size during the migration, is extremely doubtful because of the distance involved. A return migration in the life cycle is also necessitated. Also in asexual reproduction the daughter individual is the same size as the parent. Thus the size change is not related to the life-cycle of the species.

4. There is an obvious correlation between the size of the test and the water-content of the habitat. As the water-content has been shown to effect the size of other organisms (Kuhnelt 1955, Lund 1945), experiments were made to find if this was the limiting factor.

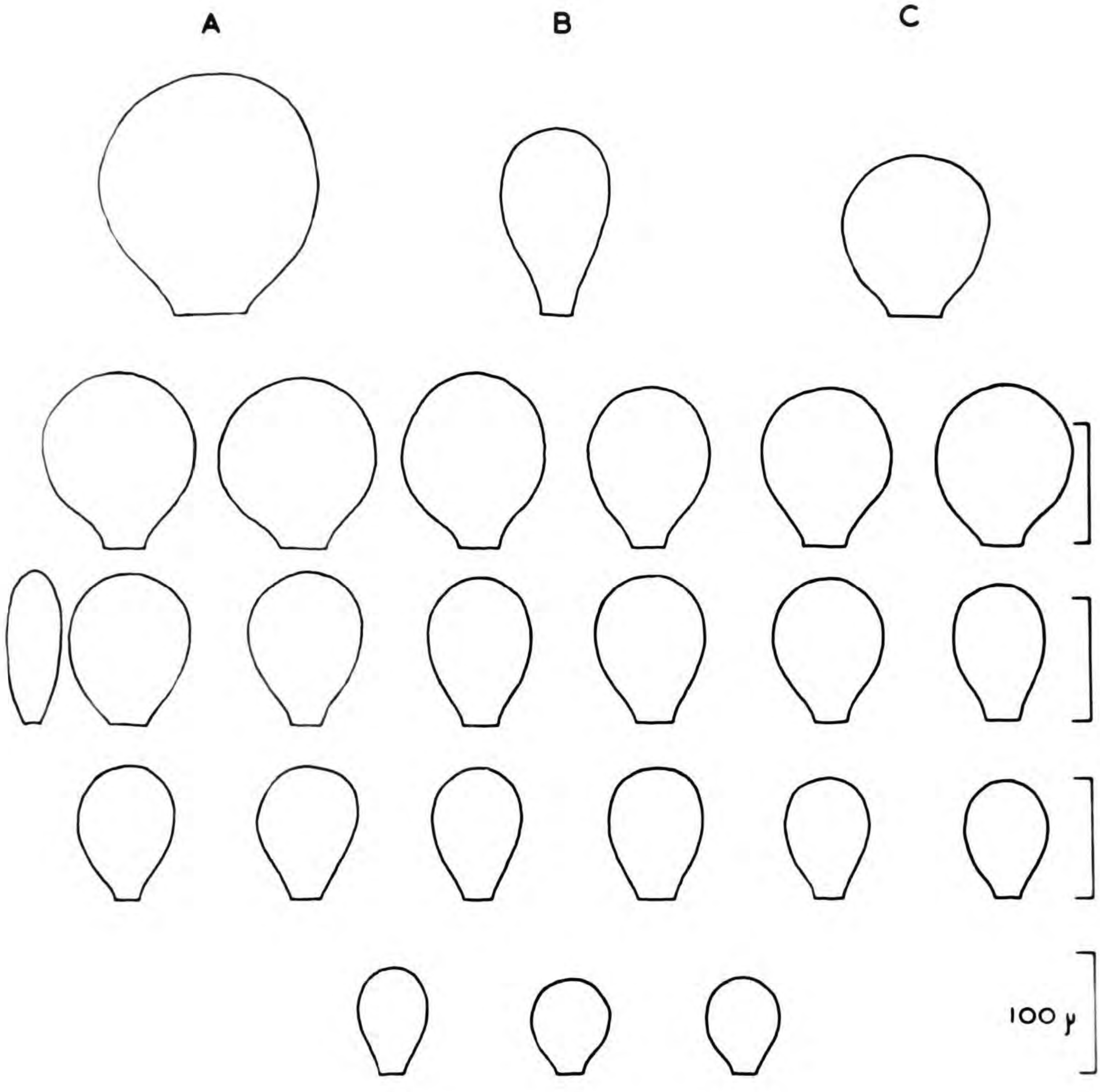


Fig. 12. A. Nebela tincta v.major (after Deflandre 1936);
B. N.tincta f.stenostoma (after Jung 1936);
C. N.tincta s.s. (after Deflandre 1936), followed by a series of tests of N.tincta from Valley Bog, Moor House, arranged in order of length. One specimen is shown in side view. (Drawn with camera lucida). A,B,C not to scale

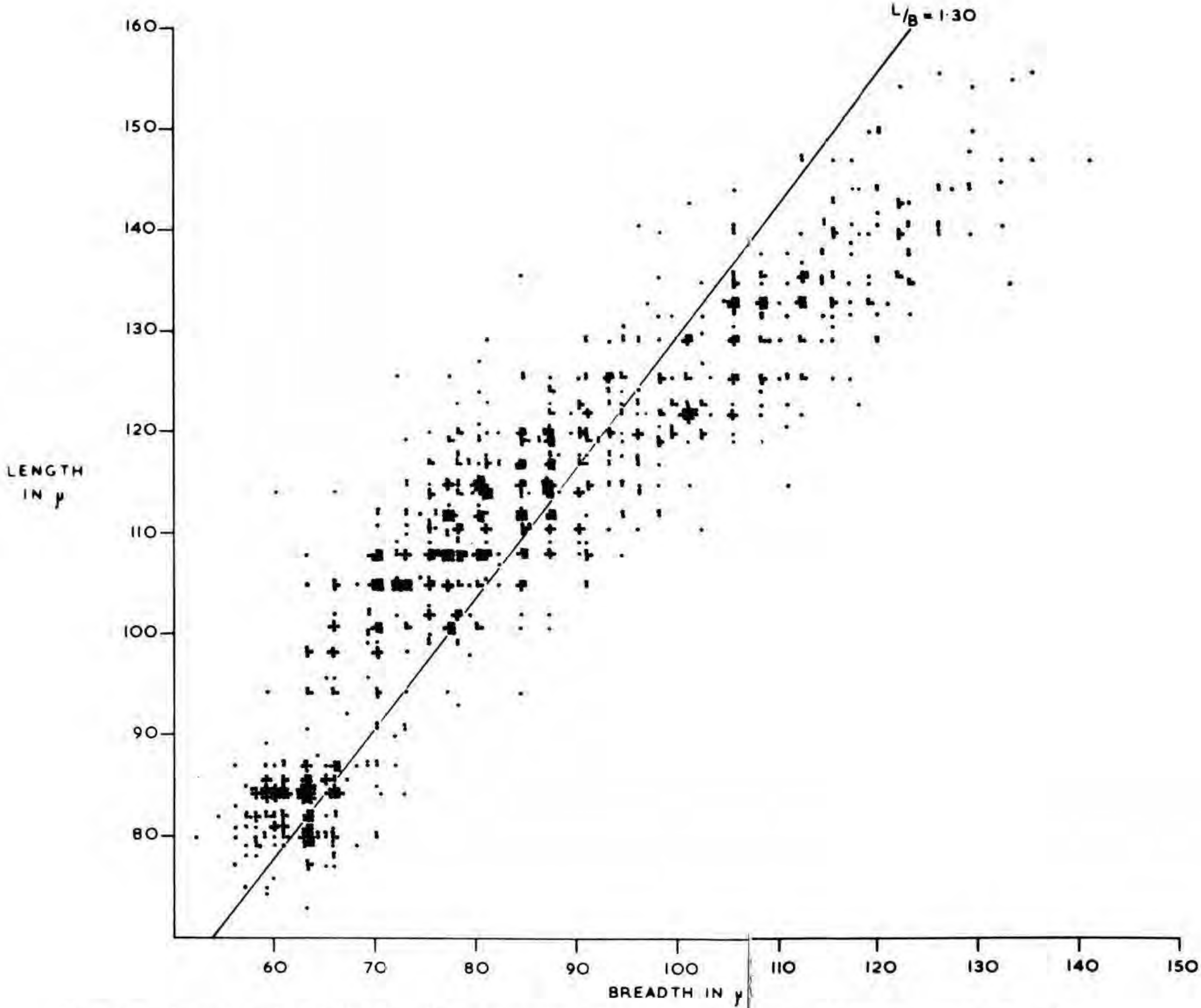


Fig. 13. Measurements of the length and breadth of 1,080 specimens of N.tincta from Valley Bog, Moor House.

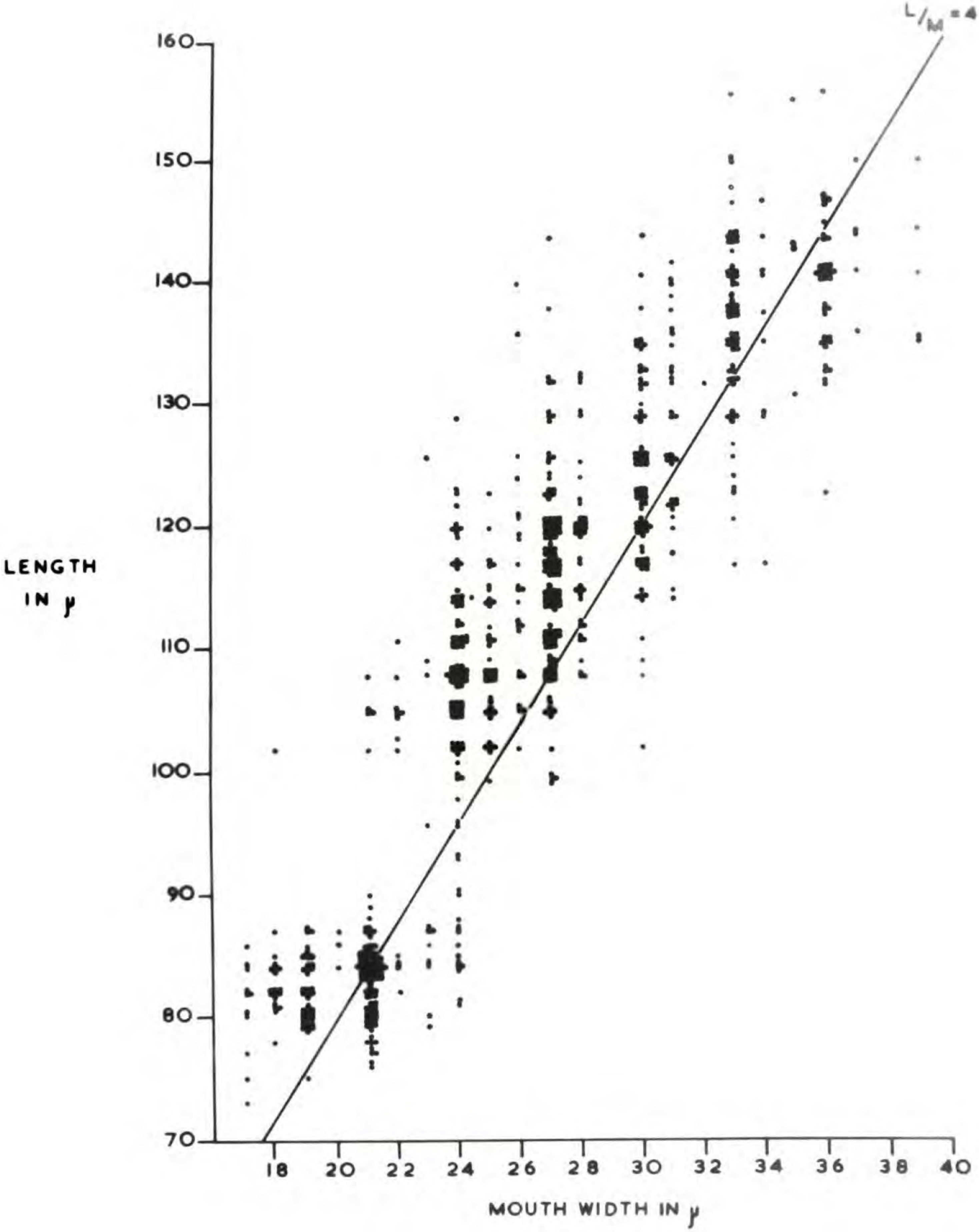


Fig. 15. The relationship between length and mouth width in 740 tests of N.tincta.

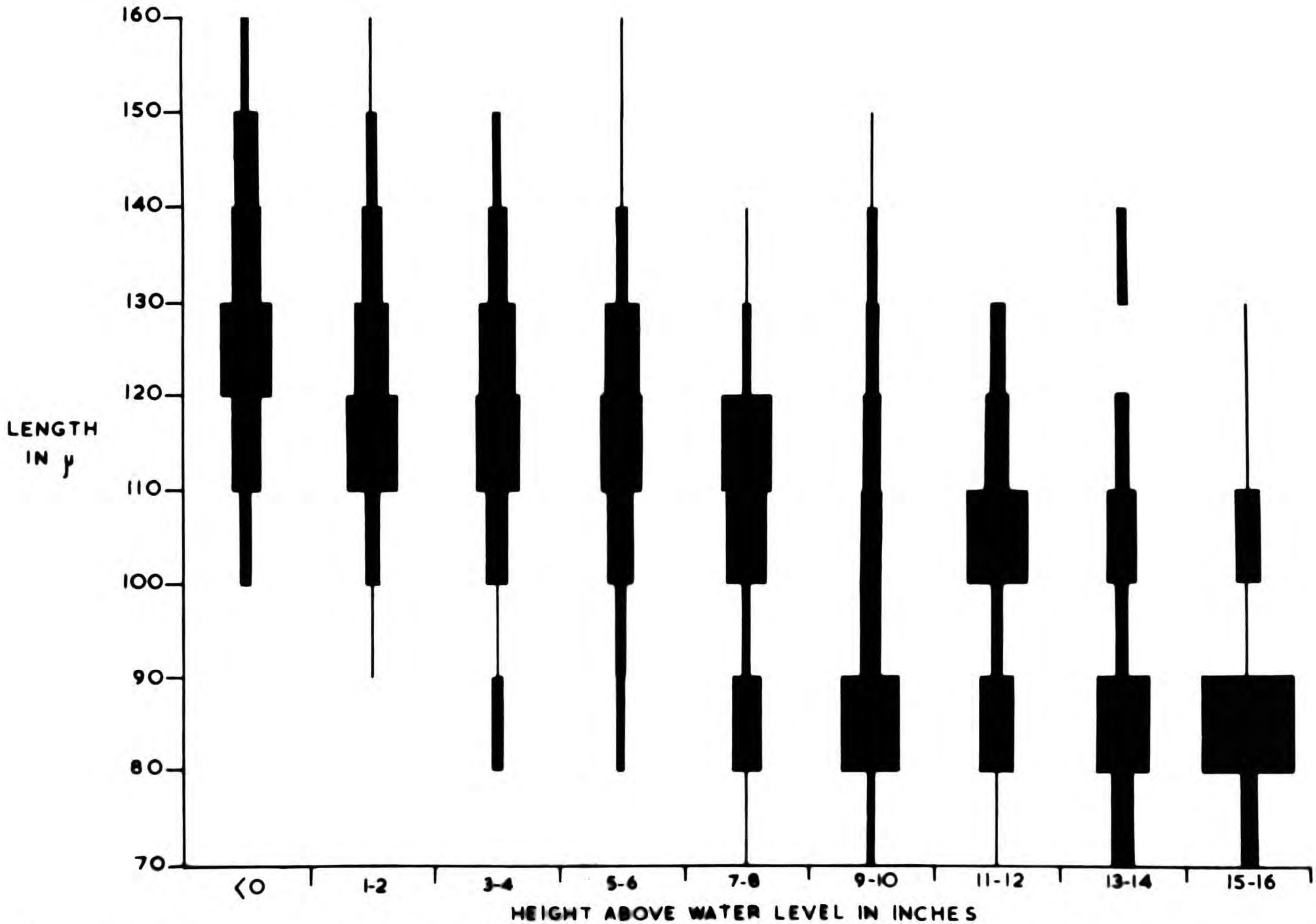


Fig. 16. The length distribution of tests of N. tincta at different levels in Valley Bog. Table 18 shows the number of tests examined at each level and the columns are arranged as a percentage of this.

Experiments.

1. Hummock Sphagnum was brought back to the laboratory and placed in polythene bags, in the open air, and saturated with sterile Moor House water. The size of N.tincta before and after the experiments was taken. Frequently sufficient numbers of N.tincta could not be obtained, and though in one case a marked increase in size was obtained, the results must be regarded as inconclusive.

2. The transplanting of Sphagnum was repeated under more natural conditions at Moor House. A number of hummocks were examined in order to obtain a large population of N.tincta of uniform size. Clumps of Sphagnum were immersed in a pool on Valley Bog and surrounded by glass tubes, diameter c.8 cm. The pool contained very little Sphagnum and no specimens of N.tincta were found, indicating that there would be little or no interference or contamination from other populations. 20 specimens were measured on the day of transplanting and at approximately monthly intervals. During the period of the experiment (13/V/59 - 11/VII/59) the water level in the pool fell 15 cm. due to the dry weather.

S.rubellum taken from a dry hummock, and S.recurvum from a wet flush were used in the experiment. At the beginning, both were submerged, but during June, July and August the S.rubellum was only "saturated" and the S.recurvum was "wet". This was due to the fall in water-level and, in the case of S.recurvum, to the active growth of the moss.

Results

The results of the experiments are shown in Fig. 17 and the 95% Confidence/

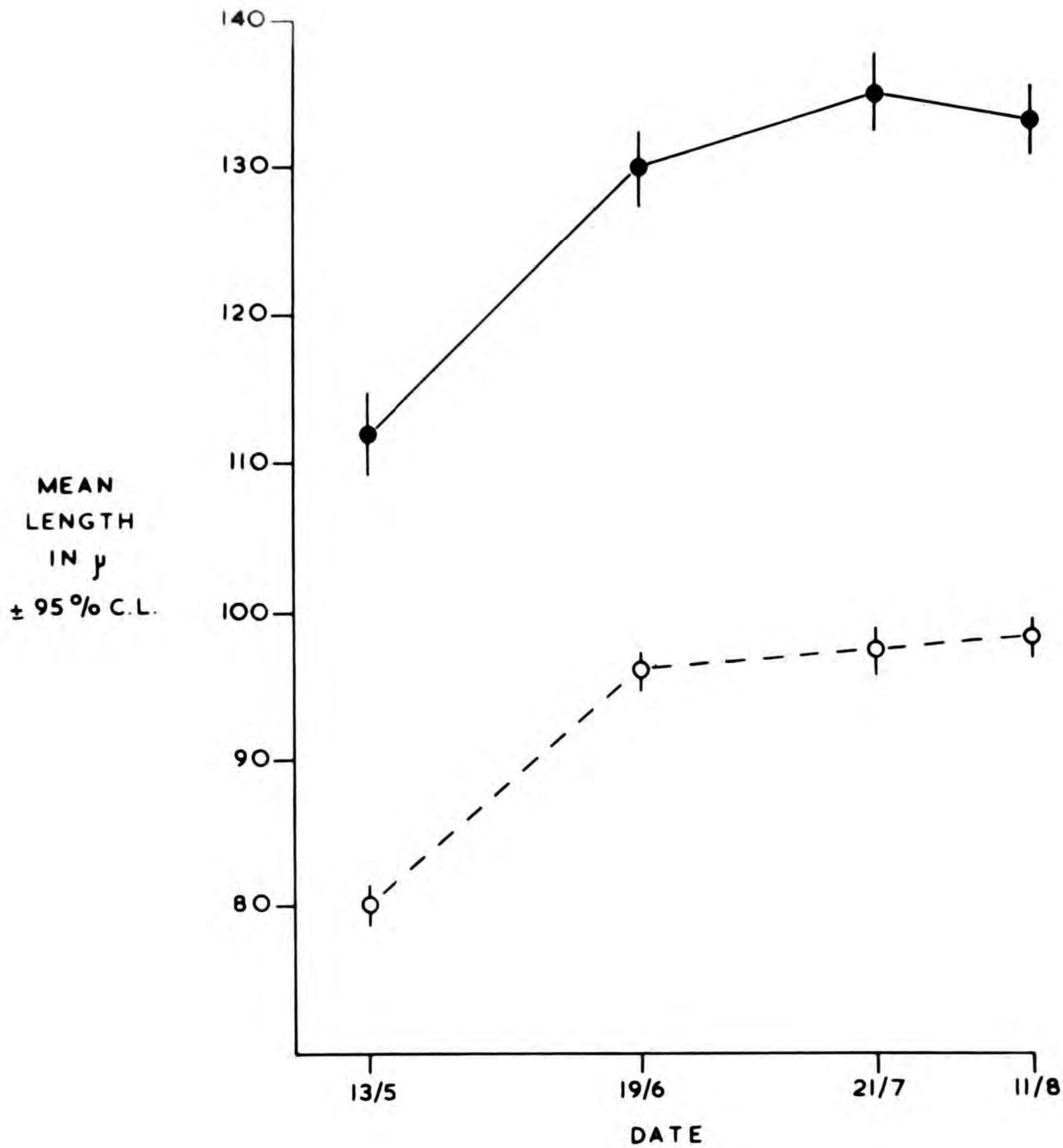


Fig. 17. The change in size of tests (20 in each sample) of <u>N.tincta</u> in flooded <u>S.rubellum</u> (lower curve) and <u>S.recurvum</u> (upper curve).

Confidence Limits indicate that in each case the initial rise is statistically significant. In S.rubellum the length increased from a mean of 80.1 to about 97µ, the last three points not being significantly different from each other. All the specimens were typically N.tincta s.s. in shape and structure although there was an increase in the number of silica plates on the test of the larger specimens. The lateral pores were always present. The size to which the population grew was at the extreme for the species in Valley Bog, but other workers record a greater size range (p.86).

In the S.recurvum the size increased from 112 to c.133µ, but the shape remained pyriform as shown by Fig. 18. The earlier data (Fig. 13) indicate that a change from pyriform to ovoid would occur with this increase in size. No other changes were observed in these tests. The general microflora and fauna did not appear to change greatly apart from an increase in the numbers of ciliates and diatoms.

These experiments indicate that a change in size is related to the water content of the habitat as suggested by the hummock transects, but the evidence regarding the taxonomy is conflicting. Both populations increased in size, then stopped. Two explanations for this are obvious.
1. the populations had reached the maximum size possible genetically or
2. that the cause of cessation of size increase was environmental, resulting from the lack of free water as the Sphagnum was not submerged.

The S.rubellum population increased to about the recognised limits of N.tincta s.s. (105µ) and showed no change to f.stenostoma. The S.recurvum population/

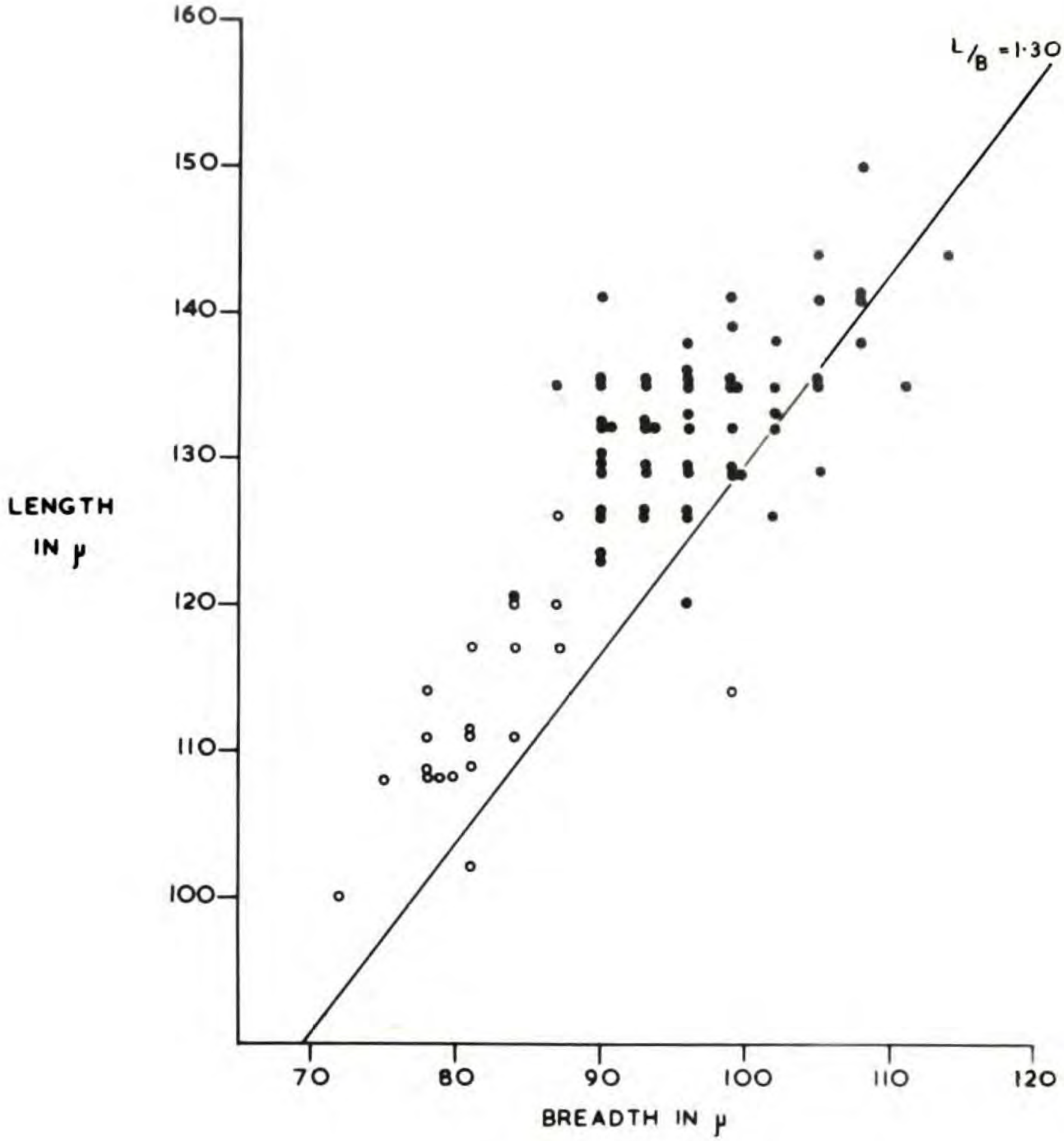


Fig. 18. The length and breadth of tests from a population of <u>N.tincta</u> from <u>S.recurvum</u> before (open circle) and after (solid circle) flooding.

population did not reach the limits of the larger group shown in Fig. 13 i.e. 150 μ. This may be due to the Sphagnum not being fully submerged, but it could also mean that the upper limit of f. stenostoma had been reached and a genetic restriction was imposed. It is noticeable that these forms did not change shape with increasing length (Fig. 18) as might have been expected. This suggests that stenostoma may be distinct from major, despite the lack of separation of morphological characters. Before a final decision can be made further experimental work is necessary.

Discussion.

Despite the taxonomic uncertainty it is shown that the size of N.tincta sensu lato varies with the water content of the Sphagnum and also that the larger species of Testacea inhabit the aquatic habitats.

Deflandre (1936) mentions that the larger species of Nebela occur in aquatic habitats and later (Deflandre 1937) stated that as a general rule, the largest species of all genera are purely aquatic. Decloitre (1950) states that smaller and flattened species tend to inhabit "aerophytic" sites, but no data are given. Regarding the change in size within a species, Jung (1936b) stated that Assulina muscorum becomes smaller as the water content of the habitat decreases, but he only measured 21 animals. As mentioned earlier (p.85), the dwarfing of micro-organisms in drier habitats is widely recognised for other plants and animals, but most attention has been paid to soil diatoms, especially by Lund (1945). He surveys the earlier work related to the occurrence of small/

small diatom species or small forms of larger species in the soil. In considering the limiting factors he rejects the nutritional and chemical factors and suggests that smallness is of ecological value in "facilitating apposition to the moisture film surrounding the soil particles, movement in the soil and distribution as wind borne dust".

With regard to the movement of Testacea in the water film, when active, the test is held at right angles to the substrate, thus the depth of the water film is obviously a limiting factor and in a number of cases the test is dorso-ventrally (oral-aborally) flattened (p.86). The water film on Sphagnum cannot be measured as most of the moisture is held in the concave surfaces of the leaves and between the pendant branches which adhere to the main stem. It is in these sites that the Testacea live and they will obviously be restricted when drying occurs and thus small forms will be able to move more freely than large ones. There is no indication that leaf size of the Sphagnum is an important factor, as the size change in N.tincta occurred irrespective of Sphagnum species.

The method of size increase.

Many organisms, especially Protozoa have been shown to vary considerably under different environmental conditions. The variation in size and rostrum lengths in the Cladocera, Daphnia and Bosmina, has been attributed, partly at least, to seasonal and temperature changes (Wesenburg-Lund 1910, Brooks 1946). Variations in the spine length of Ceratium due to similar environmental effects, are well documented. The great effect on size and shape of different foods has been shown in Tetrahymena/

Tetrahymena (Glaucoma) vorax (Kidder, Lilly and Claff 1940) and other ciliates and amoebae (in Kudo 1954), while Deflandre (1937) records differences in volume of 1:64 of specimens in culture, though the species is not given. Moewus (1933) studied a number of "species" of Chlamydomonas and found that when they were cultured in different media, they were extremely variable. Within the various forms of a single species, he was able to recognise many previously described species.

In Testacea, the variability of the form and test structure of different "species" was recorded as early as 1864 by Wallich. A number of studies were carried out at the beginning of this century to ascertain whether species were fixed in form or could be altered by selection in culture. Some of the early data (Jennings 1908, 1909, Ackert 1916) showed that in natural populations of Paramecium, there were a series of size races which in clonal culture, produced progeny of a standard mean size. Selection of small and large individuals within the clone produced cultures of the same mean size as the original population, rather than being related to the size of the immediate parent. The age of the individual probably has a considerable effect on the results, as small individuals tend to be younger than large ones, thus the selection was for different age groups rather than size.

Jennings (1916) later worked on Difflugia corona which shows considerable variation in size, shape, spine number and other test features. He found that by selection from a clone, he could produce forms with particular characters such as large size or many spines. These

forms/

forms produced similar offspring but after a number of generations they tended to revert to "normal". This work was corroborated by a number of other workers from the Johns Hopkins University. Root (1917) on Centropyxis aculeata and Hegner (1918) on Arcella dentata showed that selection for morphological characters in the progeny of a single individual was effective. Reynolds (1924) obtained similar results in Arcella polypora but here physiological characters were used. Individuals would fuse with portions of protoplasm, if they came from individuals, of the same species, kept in "identical environments". If the protoplasm came from individuals under "different environment" it was rejected. However the change was reversed if the donor, after culture in "different environment" is placed in "identical environment" prior to the experiment.

These data indicated that the environment, acting by selection on the successive generations of a variable, vegetatively reproducing species, can alter the form of the species, but the alteration is probably only temporary.

In the natural populations of Nebela tincta described above, even if it is assumed that N.tincta s.s., f.stenostoma and var.major are distinct forms, size change still occurs within the distinct taxa as suggested by the morphometric study and confirmed by experiment. This change may occur in two ways.

1. By the increased size of all individuals resulting from the removal of the restriction of a limited water film. No selection is involved and the increase in size could occur in the members of the original population or in their progeny. This is similar to the effect of feeding on ciliates and other organisms.

2. By the selection for large individuals in the progeny of the original population, this selection being related to the increased water-film and is similar to the experiments of Jennings (1916) and others.

Against the first suggestion it may be said that growth of the individual during the life history has not been recorded. In binary fission the test is laid down by the parent and apparently does not change during its life, compared with the plasticity of the ciliate. Binary fission is usually regarded as the natural mode of reproduction, but other methods have been observed. Sporulation has been recorded by Taylor (1947) in Amoeba kerri and by Cavellini (1926 a,b) for Centropyxis aculeata and Arcella vulgaris. Although these are isolated, and even doubtful examples, they do provide a method by which all the members of the population could increase in size.

With regard to the second suggestion, what advantage do large individuals have over small ones in wet areas? Smallness is obviously advantageous when the water-film is restricted, but why should it be a disadvantage to the individual when the water-film is increased? This is implicit in the argument for selection of large individuals within each taxon. It may be argued however that size is related to some other character which is advantageous to large individuals in wet areas.

Obviously, further experiments are necessary to elucidate the problem of size change in Nebela tincta.

Section 4.

The taxonomy and ecology of individual species.

NOTES ON THE TAXONOMY AND ECOLOGY OF INDIVIDUAL SPECIES

Taxonomic notes are given when the status of the species is in any way doubtful or there is confusion due to synonomy. Prof. G. Deflandre of the École Pratique des Hautes Études in Paris, kindly examined about 70 slides of specimens prepared during the survey. In the large majority of cases he confirmed the nomenclature. Details are given in Appendix 3. The cases of incorrect identification or synonomy are discussed below. All authorities are given in Fig. 1 and Table 2.

Ecological comments are only given where they supplement the distribution shown in Fig. 1, or where there is disagreement between the present findings and those of previous authors. The distribution of many species in relation to the water content of the habitat has been studied by a number of workers, particularly Bartos (1940, 1949, 1950). As this aspect is relatively well documented and the findings of the present survey correspond with those of earlier workers, details of this distribution are not given unless there are marked discrepancies. Most of this data can be seen in Figs. 1 and 2, in which the sample groups are arranged approximately in a series of decreasing water content.

Arcella catinus.

There has been some discussion on the synonomy of A.catinus Penard, A.artocrea Penard and A.artocrea Leidy. The species observed here is similar to the first two species but not A.artocrea Leidy. This agrees with Hoogenraad and de Groot (1940).

A.catinus is more characteristic of bog areas than is indicated in Fig. 1. This agrees with the observations of other authors. It was often abundant in dry samples but Deflandre (1928b) and Bartos (1940) regard it as occurring mainly in wet Sphagnum.

A.discoides*.

The nomenclature of Hoogenraad and de Groot (1940) is followed here, the species including A.polypora Penard. Considerable size variation was observed but the data are not sufficient to draw any conclusions. Many specimens corresponded to A.discoides var. scutelliformis Playfair.

Difflugia bacillariarum and D.elegans.

In many works on Testacea there are discussions on whether or not to place these forms together as one species. They have the same size and shape but the test of the former is composed of diatom frustules and the latter of mineral particles. There are however intermediates, using both types of material. In the present survey tests entirely of mineral particles occurred in the fens (D.elegans) while those with a mixture or only diatoms were present in bog areas (D.bacillariarum). Although D.bacillariarum occasionally bore mineral particles, the uniformity of D.elegans was never attained. Prof. Deflandre classed the intermediate forms as D.bacillariarum and favours the separation of the species.

It is possible that some earlier workers include both species under one or other of the specific names, which may account for the occasional anomolous results in Table 4.

D.oblonga, D.bacillifera and D.brevicolla.

The situation here is similar to the Difflugia species just discussed. D.oblonga and D.bacillifera are similar in shape and size, but differ in that the former has a test composed of minerals and the latter of diatoms or a mixture of both. D.brevicolla is more broadly pyriform than D.oblonga and has a slightly constricted neck. The test is composed of mineral and other foreign particles. Štěpánek (1952) suggested the fusion of a number of species of Difflugia into an ultra-species Difflugia U oblonga, including in it D.oblonga bacillifera and D.oblonga brevicolla. He suggested this because he found intermediate forms between these species and D.oblonga. The general question of these taxonomic difficulties will be discussed later (p.115).

In the present survey, both D.bacillifera and D.brevicolla have been found in the same samples as D.oblonga and have been morphologically distinct. They are thus retained as species as suggested by Prof. Deflandre.

D.acuminata.

Štěpánek (1952) included this in his D.U.oblonga because of intermediate forms, the main difference between D.oblonga and D.acuminata being the extension of the fundus of the latter into a spine. In the present survey both species were found in a number of samples but were distinct, thus the specific names are retained.

D.rubescens.

The length of this species is usually given as 60-105 μ (Leidy 1879 Penard 1902, Jung 1936b, Hoogenraad and de Groot 1940) but in the present survey two size groups were indicated. Although a full morphological examination was not carried out, 34 specimens were measured giving the lengths 72-84 μ (24 specimens) and 112-132 μ (12 specimens). All the specimens had the red protoplasm characteristic of the species.

D.pulex.

The term used here may include Cryptodifflugia sacculus Penard as well as D.pulex. They are similar in size and shape, Penard (1902) giving lengths 22-25 μ for D.pulex and 17-26 μ for C.sacculus.

Bullinula indica.

The specimen examined by Prof. Deflandre was only visible in side view. From this Prof. Deflandre suggested that it was probably Plagiopyxis sp. rather than Bullinula. However the diameters given by Thomas (1958) and Chardez (1956) for the four Plagiopyxis sp. are always $<$110 μ. The specimens observed in northern England were always c. 150 μ and also bore a series of pores round the lip of the mouth, a feature absent in Plagiopyxis spp. It is therefore felt that the identification is valid.

Centropyxis aculeata*.

This is a variable species measuring 70-200 μ in length. Many specimens/

specimens were almost circular as in the species sensu stricto, but var. oblonga Deflandre was also present but not separated in the identification. According to Prof. Deflandre, C.hirsuta Deflandre has also been included in the term C.aculeata* as used here. The former species falls into the size range of C.aculeata but has a slightly deeper test.

C.cassis*

The term is used to cover a number of species which could not be separated. It probably includes at least C.cassis s.s., C.aerophila, Deflandre, C.constricta Ehrenberg and C.kolkwitz van Oye. Paulson (1952) encountered similar difficulties. The majority of specimens were 50-120 µ long, 30-90 µ wide and 30-60 µ high and they varied in shape from almost circular, to tests with almost parallel sides.

Pontigulasia biggibosa

This species appears to be synonymous with P.compressa (Carter) Cash, but not P.compressa Rhumbler (Hoogenraad and de Groot 1940).

Lesquereusia spiralis and L.modesta

Štěpánek (1952) suggests that these species should be grouped under the ultra-species L.U spiralis, as L.spiralis spiralis and L.spiralis modesta. The main distinguishing feature of the two species is the test composition. The former is composed of vermiform plates, possibly modified diatom frustules, while the latter bears mineral grains. In the/

the present survey there was some overlap in the test formation but as there was little difficulty in assigning specimens to one or other of the species, the specific names were retained.

Nebela collaris

This name has been used in the literature to cover a wide variety of forms and has probably included such closely related species as N.tincta, N.bohemica Taránek, N.flabellulum and N.penardiana among others. In the present survey there was little difficulty in distinguishing it from other species and all the specimens (length 102-150 μ, breadth 76-96 μ) fitted the description of Deflandre (1936) very closely. It resembles N.tincta f.stenostoma but it is separated from this by the wider, curved mouth and lack of lateral pores. Prof. Deflandre after examining specimens from northern England writes "--it is good to reserve the name N.collaris for the typical specimens with curved mouth and I also think that it is a well characterised species, not very variable".

With regard to the ecology of N.collaris, it was found to be a typical fen species in the present survey. Other workers have recorded it from a wide range of habitats and pH's (Table 4). The distribution with regard to the water content of the habitat is also contradictory. In the present survey N.collaris was restricted to very wet or submerged Sphagnum, corresponding with Deflandre (1936), van Oye (1949), Hoogenraad and de Groot (1940), Heinis (1910), Bonnet (1953) and Bartos (1949). On the other hand Harnisch (1925) and de Graaf (1956, 1957) stated that it is typical of the drier moss.

Thus there is much discrepancy regarding the ecology of this species and it probably arises from taxonomic difficulties. Harnisch (1927) when using the term in his association types states that it is used in the broadest sense. Hoogenraad and de Groot (1937) in a morphometric survey, were able to separate it from N.tincta s.s. N.militaris, N.flabellulum and other closely related species, but they conclude that it includes N.bohemica Taránek. According to MacKinlay (1936), Penard states that N.collaris includes N.bohemica, N.crenulata and N.collaris. Jung (1936b) also suggests that a full statistical study on the collaris-tincta-parvula-bohemica-flabellulum group is essential.

N.lageniformis

The distinction between this species and N.wailesi Deflandre (= N.lageniformis var.minor Wailes) is questionable (Hoogenraad and de Groot 1940, van Oye 1948, 1958). The lengths of the species are given by Deflandre (1936) as 125-130 μ for N.lageniformis and 75-100 μ for N.wailesi. The latter is also stated as being slightly narrower than the former. Van Oye (1949, 1958) extended the recorded size limits in his investigations in Java and the Belgian Congo, and the ranges overlap. In the present survey the observed range was 105-147 μ which corresponds to Deflandre's N.lageniformis in Europe.

Hyalosphenia papilio

Among specimens examined from Valley Bog, after the original survey of that area, a number of individuals corresponding to H.papilio var. stenostoma Deflandre were found. In the populations of H.papilio observed, slightly deformed specimens were frequently seen, usually having indentations in the fundus and a slight constriction of the mouth. The var. stenostoma is among these and it may be merely composed of extremely deformed individuals rather than a constant morphological variety. A single specimen of H.papilio f. multiporifera Jung was also observed.

Heleopera sylvatica*

In the earlier stages of the research, due to the variability in size and shape, it was not found possible to distinguish between H. sylvatica and H.petricola Leidy in many cases. These species are thus grouped under the former name. Despite this taxonomic difficulty it appears that these species occur more regularly in bog than in fen areas. There was also some indication that H.sylvatica s.s. inhabits drier sites than the larger H.petricola s.s. This corresponds with Bartos (1940, 1949, 1950), Brown (1911b) and de Graaf (1956).

Phryganella hemispherica*

Under this term are grouped a wide variety of forms, varying from colourless specimens 40μ in diameter, to dark specimens composed of mineral/

mineral particles and c.180 μ in diameter. It is probable that it includes at least P.hemispherica Penard (41-55μ) (= P.acropodia Hertwig and Lesser), P.nidulus Penard (160-221μ) and Difflugia globulosa Dujardin (24-260μ according to various authors). Because of the complex of species nothing can be said on their distribution, but it was noticeable that the larger, mineral bearing forms inhabited the fens.

Cryptodifflugia eboracensis.

Hoogenraad and de Groot (1940) state that they found a series of intermediates between C.oviformis and C.eboracensis and they therefore doubt the existance of the latter as a true species. Deflandre (1928a), on the other hand, raised the new genus Wailesella to hold eboracensis. In the present survey the forms were distinct even when they occurred in the same sample, but they are so similar in structure, form and size that it seems unnecessary to raise a new genus. The only difference between the two species is that in C.oviformis, the mouth is terminal while it is sub-terminal in C.eboracensis.

Sphenoderia spp.

The synonomy of S.dentata with Euglypha dentata Vejdovsky and Tracheleuglypha dentata (Vejdovsky) Deflandre, is complicated and is reviewed by Deflandre (1928a). In the present survey the first name is retained.

The three species of Sphenoderia recorded in northern England though/

though seldom common, were almost restricted to the fen areas (pH >5.0). The pH values of various workers (in de Graaf 1956) and of de Graaf (1956, 1957) for each species are as follows,

S.dentata.	5.3-6.5 various workers;		4.0-7.3 de Graaf.	
S.lenta.	4.3-6.6 "	"	4.0-7.2 "	"
S.fissirostris.	5.5-6.2 "	"	4.0-6.0 "	"

It is difficult to reconcile these figures with those of the present survey, but Fig. 1 shows that none of these species was recorded regularly in bog areas by previous workers.

Trinema-Corythion*.

Here again a taxonomic difficulty was encountered. Members of these genera were found in all areas, but it was usually impossible to distinguish between the various species, due to their variability and the difficulty in observing the component plates on which the taxonomy is based. The same difficulty was encountered by Paulson (1952).

Large specimens of Trinema enchelys were readily identified and these occurred only in fen areas.

Cyphoderia ampulla*.

When specimens of Cyphoderia were first examined they were seen to belong to C.ampulla, as indicated by the shape and non-imbricating plates. Specimens examined by Prof. Deflandre belonged to C.trochus var. amphoralis (= C.amphoralis Wailes and Penard) which has a similar shape to C.ampulla but with imbricating plates. Following this, 50 specimens from/

from Nibthwaite, Sunbiggin, Blelham, Esthwaite and Dale Park, were examined under oil-immersion. It was found that 10 were C.ampulla (= C.margaritacea Ehrenberg) and 40 C.trochus var.amphoralis. Thus the term C.ampulla* here covers both species but there appears to be little difference in their distributions, both being restricted to fens.

Amphitrema wrightianum*

The main taxonomic difference between this species and A.stenostoma Nüsslin is the presence (A.wrightianum) or absence (A.stenostoma) of a small collar encircling the mouth. The collar was frequently visible but in some specimens, because of the foreign matter attached to the test, the mouth openings could not be observed and the species were not separated. However Fig. 1 indicates that they live in bog pools and both species were identified from this habitat. This distribution is in accord with the findings of previous workers (de Graaf 1957, Harnisch 1925, 1927).

Section 5.

Discussion and Summary.

DISCUSSION.

1. Factors effecting the distribution of Testacea.

It has been shown that most species of Testacea have limited distributions on individual Sphagnum plants, in the pool-hummock succession and in different bogs and fens. A large number of environmental factors may effect the distribution and these are discussed separately, but only very general conclusions can be drawn, as the detailed biology of Testacea under natural conditions is not known.

Altitude.

The sample areas covered an altitudinal range from c.12 to c.200 m. above sea level and there was no indication that this effected the distribution in any way.

Chemical composition of the water.

It has been shown that there is a close correlation between pH and the distribution of Testacea. Data on this relationship have been collected since the work of Harnisch (1927) but only de Graaf (1956, 1957) has made a systematic study over wide pH ranges. Evidence for the correlation with pH has accumulated because it is the most easily measured chemical component of the environment, but there is no experimental confirmation that the correlation is causal. Other components vary over the same range, thus there is a close correlation between the distribution of Testacea with, for example, the Calcium content of the water (Table 1).

The regularity with which individual species occur over a given range of pH and the short distance over which a change of species occurs, as/

as in Sunbiggin Springs indicate that the distribution is directly effected by the chemical composition of the water. In other Protozoa, the pH of the culture medium is recognised as being important, and many ciliates and flagellates will only grow over a restricted pH range (in Kudo 1954). Calcium and Magnesium have been shown to effect the metabolism of ciliates (Mast and Pace 1939).

Water content of the habitat.

As with pH much data has been collected to show that the range of individual species of Testacea coincides with a certain moisture content of the *Sphagnum*. It is shown that large species occur only in submerged or saturated *Sphagnum* and also that the size of an individual species varies with the water content of the moss. Other workers on Testacea (Jung 1936a, Deflandre 1936, 1937 and Decloitre 1950) and other micro-organisms (Lund 1945) describe a similar relationship. Thus this factor appears to directly effect the distribution of Testacea, but it only acts on the large species or individuals and some species appear to be modified, by flattening of the test, to inhabit dry areas.

The water content of the habitat may be altered by drying and it may be suggested that resistance to dessication is important in the distribution of Testacea. The data of Fantham and Porter (1945) contradicts this as they record that many species are able to survive very long periods in dry moss some examples are given below

Difflugia acuminata	7 years 128 days
D.oblonga	7 " 362 "
Lesquereusia spiralis	8 " 131 "

Nebela tincta	5 years	53 days
Hyalosphenia elegans	5 "	116 "

Test materials.

Where specific foreign matter, such as diatoms or mineral particles are used in test construction, the availability of these will effect the distribution of the species. This is particularly important in Difflugia and it has been shown that species using mineral particles in their tests tend to inhabit fen areas and those with diatoms or peat particles are usually restricted to bogs (p. 49). However there is a need to find by experiment, whether a species will utilise other material if the normal source is excluded. Stump (1936) showed that Pontigulasia vas (Leidy) Schouteden would not reproduce unless the test materials were present in the culture.

Food.

The majority of the larger Testacea are omnivorous, feeding on plants, animals and detritus of suitable size, however, if certain species are exclusively diatom feeders, then these will be restricted to the fully aquatic habitats. Nebela species prey on smaller species having silica plates, but as these occur in all habitats they are not liable to restrict the distribution of Nebela. Also McKinlay (1936) has shown that it is possible to culture N.collaris entirely on algal food. Thus it may be concluded that food probably has little effect on the distribution of Testacea.

Predators.

No specific predators of Testacea were observed in the brief survey that was carried out, but the nematode Mononchus, and Fungi may be important. Crustacea are said to effect culture of Testacea (Fantham and Porter 1945) but this may be through interference due to the activity of the Crustacea.

Light.

Where symbiotic zoochlorellae are present, light is probably an important factor in the distribution of the species, and this is indicated in the microdistribution of Hyalosphenia papilio and Amphitrema flavum.

2. Taxonomy of Testacea.

In the literature on the taxonomy of Testacea it is possible that many species and varieties have been described on a single or very few specimens. The variability has not been ascertained and no attention is paid to the effect of the environment on the size and structure. One outstanding example of the uncritical naming of species is given by Deflandre (1931) who points out that Hyalosphenia coogeeana Playfair is actually the lorica of the rotifer Callidina (Habrotrocha) angusticollis Murray.

The size and structure of the test are usually taken as "good" morphological characters, but there has been little or no experimental work to show the effect of the natural environment on these characters. Information/

Information on the selection of particles for test construction is especially required, particularly in species pairs which are differentiated on the test structure. Examples are Difflugia bacillifera and D.oblonga, D.bacillariarum and D.elegans, Lesquereusia spiralis and L.modesta.

Štěpánek (1952) examined test form in relation to the environment and claimed to have found many intermediate forms in the genus Difflugia, particularly those related to D.oblonga. Unfortunately he gives little exact data and it is not corroborated by experiment. He suggests the erection of an ultra-species, Difflugia U oblonga and lists a number of other forms such as D.bacillifera, D.acuminata and D.brevicolla as sub-species or varieties. One difficulty with this system is that it is not possible to tell what rank these different forms should have as the criteria are entirely subjective. It is thus unneccessary to erect new taxonomic groups such as ultra-species.

The suggestions of Štěpánek (1952) have not been widely accepted and in the present work the "old" taxonomy has been retained as a full series of intermediate forms have not been observed in many cases, even when the separate "species" occur in the same sample (pp.102-5). The morphometric study of Hoogenraad and de Groot (1937) indicated that the species which he examined were valid and Deflandre (1937) states that in his experience, the majority of the earlier described common species are "good".

Thus there is a need for more accurate work on the biology of Testacea and the relation of form to environment, before changes in nomenclature/

nomenclature are made. Experimental work, particularly on the selection of test materials, is required, especially in the species pairs named above.

Summary.

1. Sphagnum samples were examined from a series of fen and bog sites. These provided habitats ranging in pH from 3.2 to 7.0 and differing greatly in water-content. The sites were in Northumberland, the Pennines and the Lake District, those in the Lake District being selected from the data of Gorham and Pearsall (1956) and Gorham (1956a,b).

2. The survey was carried out on a qualitative basis and showed the presence of species associations, a. in fens with pH >5.0, b. in bogs with pH 5.0, the latter with a distinct pool association, and hummocks showing a series of indistinct associations.

3. The characteristic species in the fens were; Quadrula symmetrica, Nebela lageniformis, N.tubulosa, N.penardiana, N.galeata, N.collaris sensu stricto, Lesquereusia spiralis, Euglypha ciliata, Sphenoderia dentata, Euglypha rotunda, Pontigulasia bigibbosa, Cyphoderia ampulla* and C.trochus var.ampullacea.

4. The typical bog pool species were; Amphitrema wrightianum, A.stenostoma, Nebela carinata, Difflugia bacillifera, D.brevicolla, D.bacillariarum, and Placocista spinosa.

5. In the wet parts of the hummocks the dominant species were; Amphitrema flavum, Hyalosphenia papilio, Arcella catinus, Nebela tincta sensu lato, N.militaris, Assulina muscorum, Heleopera rosea, and Euglypha strigosa.

6. In the dry parts of the hummocks the dominant species were; Nebela tincta sensu stricto, Arcella catinus, Heleopera sylvatica*, Euglypha/

Euglypha strigosa and Nebela militaris. Bullinula indica and Trigonopyxis arcula are typical of this habitat.

7. Some species were present in both fens and bogs, but these usually showed affinities to fens (Difflugia rubescens, Nebela dentistoma, Centropyxis cassis*, Heleopera petricola var. amethystea and D.oblonga) or to bogs (N.tincta, Assulina muscorum and Arcella catinus). Truly eurytope species are Cryptodifflugia oviformis, Arcella discoides*, Centropyxis aculeata* and Heleopera rosea.

8. The observed associations are compared with the findings of previous workers, particularly in Europe and Scandinavia. This shows that the distribution of individual species, and the associations in well-defined habitats, are similar in all these areas.

9. In particular the association types described by Harnisch (1927) are discussed, and it is concluded that though they are generally applicable, they are not detailed enough and need reorganising.

10. A positive correlation between the number of species and the pH of the habitat is demonstrated.

11. No direct correlation between Sphagnum species and species of Testacea was observed.

12. A brief study of the food relationships in the micro-flora and -fauna, indicates that Testacea are mainly omnivorous, diatoms forming the basis of the food-web in wet areas, bacteria probably being more important in drier habitats. No major predator of Testacea could be distinguished, although Mononchus and Fungi may be important. Within the Testacea, considerable predation occurs.

13. The vertical distribution of Testacea on Sphagnum was studied using a quantitative technique which was examined for errors. The method was, briefly, to section the stem of the plant, macerate each section, extract the tests by centrifuging through a filter, concentrate the filtrate and count the tests on a grid cell.

14. The survey showed that the number of species present, increased with depth, 8 species being recorded in the Sphagnum head and 25 at 10-12 cm. The distribution of each species was restricted, and empty tests occurred lower down the stem than full ones, probably due to water-movement.

15. Hyalosphenia papilio and Amphitrema flavum are restricted to the upper layers and experiments suggest that this may be related to the presence of zoochlorellae in their protoplasm.

16. There is no indication of a seasonal change in the vertical distribution, but there is evidence that the distribution of detritus may effect the distribution of Testacea which use foreign matter in test construction.

17. It is shown that Testacea are not randomly distributed throughout a sward of Sphagnum, but a very approximate estimate of number of Testacea per m^2 of S.recurvum, gives a figure of 16 ± 6 million.

18. A morphometric study of the polytypic species Nebela tincta was made. This species occurs throughout the regeneration complex of Valley Bog and the study showed that N.tincta sensu stricto is distinct from a group of larger individuals (100-150μ long). These larger individuals/

individuals may be divided into f.stenostoma (100-130μ) and var. major 130-150μ).

19. Transects up the Sphagnum hummocks showed that N.tincta s.s. occurred in the dry areas, stenostoma-type individuals in wet moss, and the larger, major-type individuals in the pools. Some overlap occurred but even within each size group, the largest individuals tended to be present in the wettest areas.

20. Transplanting of Sphagnum from dry to wet areas, caused an increase in size of individuals of the N.tincta populations, but the experiments were not sufficient to elucidate the taxonomic problem.

21. The question of the factors causing the size increase are discussed. The evidence indicates that "smallness" is of advantage in the dry habitats as it enables the animal to move in the restricted water-film. This corresponds with the conclusions of Lund (1945) on diatoms.

22. The taxonomy and nomenclature of certain species are discussed where there may be confusion, and in the discussion it is suggested that critical work on the variability of Testacea in relation to environment is necessary.

23. In the discussion of the factors effecting the distribution of Testacea, it is concluded that altitude has no effect, food probably little effect, but pH, water-content, availability of test materials, and in some cases light may control the distribution.

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Appendix 1.

The lists of species recorded from the different areas are given below. As most authors differ in their systems of classification, the species are listed in alphabetical order. The areas are grouped in the order in which they were described in Section 1.

1. Esthwaite North Fen.

Arcella catinus, A.hemispherica, A.discoides*, Assulina muscorum, A.seminulum, Campascus minutus, Centropyxis aculeata*, C.cassis*, C.discoides, Corythion*, Cryptodifflugia eboracensis, C.oviformis, Cyphoderia ampulla*, C.trochus var.amphoralis, Diplochlamys vestita, Difflugia bacillariarum, D.lucida, D.pulex, D.oblonga, D.rubescens, D.tuberculata, Euglypha acanthophora, E.bryophila, E.ciliata, E.cristata, E.rotunda, E.strigosa, Heleopera petricola var.amethystea, H.rosea, H.sylvatica*, Hyalosphenia papilio, Lesquereusia spiralis, Nebela collaris, N.dentistoma, N.lageniformis, N.longicollis, N.penardiana, N.tincta, N.tubulosa, Phrynganella hemispherica*, Pontigulasia bigibbosa, Placocista jurassica, Pseudochlamys patella, Pseudodifflugia fulva, Quadrula symmetrica, Sphenoderia dentata, S.fissirostris. Total = 47 species and varieties.

2. Sunbiggin Tarn.

Amphitrema flavum, A.wrightianum*, Arcella catinus, A.discoides var. scutelliformis, A.gibbosa, Assulina muscorum, A.seminulum, Bullinula indica, Centropyxis aculeata*, C.cassis*, Corythion*, Cryptodifflugia oviformis, Cyphoderia ampulla*, C.trochus var.amphoralis, Difflugia lucida, D.oblonga, D.pristis, Euglypha ciliata, E.cristata, E.denticulata, E.scutigera, E.strigosa, E.tuberculata, Heleopera petricola var. amethystea, H.rosea, H.sylvatica*, Hyalosphenia papilio, Lesquereusia spiralis, L.epistomium, Nebela collaris, N.dentistoma, N.bigibbosa, N.griseola, N.tincta, N.flabellulum, N.militaris, N.longicollis, N.parvula, N.lageniformis, N.penardiana, N.tubulosa, N.speciosa, N.galeata, Phryganella hemispherica*, Potigulasia bigibbosa, Quadrula symmetrica, Sphenoderia dentata, Trigonopyxis arcula. Total number of species and varieties = 48.

3. Nibthwaite swamps.

A. Arcella discoides*, A.hemispherica, A.gibbosa, Assulina muscorum, Centropyxis aculeata*, C.cassis*, Corythion*, Cryptodifflugia oviformis, C.eboracensis, Cyphoderia ampulla*, C.trochus var.amphoralis, Difflugia oblonga, D.acuminata, D.rubescens, D.elegans, D.tuberculata, D.lucida, D.pristis, Euglypha ciliata, E.strigosa, E.rotunda, Heleopera petricola, H.petricola var.amethystea, H.sylvatica*, Lesquereusia spiralis, L.modesta, Nebela dentistoma, N.collaris, N.tincta, N.tubulosa, N.speciosa, N.lageniformis, N.galeata, N.maxima, Phryganella hemispherica, Pontigulasia bigibbosa, Pseudodifflugia fulva, Pyxidicula invisitata, Quadrula symmetrica, Sphenoderia lenta, S.dentata, Trinema enchelys, Total = 42 species and varieties.

B. Arcella discoides*, A.vulgaris, A.gibbosa, Assulina muscorum, Centropyxis aculeata*, C.cassis*, Cochliopodium vestita, Corythion*, Cryptodifflugia oviformis, Cyphoderia ampulla*, C.trochus var.amphoralis, Difflugia oblonga, D.acuminata, D.rubescens, D.elegans, D.brevicolla, D.tuberculata, D.oviformis, D.lobostoma, D.urceolata, Euglypha ciliata, E.scutigera, E.rotunda, E.strigosa, Heleopera petricola, H.petricola var. amethystea, H.sylvatica*, H.rosea, Lesquereusia spiralis, L.modesta, Nebela collaris, N.tincta, N.dentistoma, N.flabellulum, N.speciosa, N.lageniformis, N.galeata, N.bigibbosa, N.bipes, Phryganella hemispherica*, Pontigulasia bigibbosa, Pesudodifflugia fulva, Quadrula symmetrica, Sphenoderia dentata, S.lenta, Trinema enchelys. Total of 46 species and varieties.

4. Lady Vane Pot.

Amphitrema flavum, A.wrightianum*, Arcella discoides*, A.catinus, A.arenaria, A.hemispherica, A.gibbosa, Assulina muscorum, Centropyxis aculeata*, C.cassis*, Corythion*, Cryptodifflugia oviformis, Cyphoderia ampulla*, Difflugia oblonga, D.rubescens, D.lucida ?, Euglypha strigosa, Heleopera petricola, H.petricola var.amethystea, H.sylvatica*, H.rosea, Hyalosphenia papilio, H.elegans, Nebela dentistoma, N.collaris, N.tincta, N.flabellulum, N.militaris, N.penardiana, N.lageniformis, N.bigibbosa, Phryganella hemispherica*, Pontigulasia bigibbosa, Quadrula symmetrica, Trinema enchelys. Total number of species and varieties = 35.

5. Blelham Tarn Swamp.

Amphitrema wrightianum*, Arcella catinus, A.hemispherica, A.arenaria, A.gibbosa, Assulina muscorum, A.seminulum, Bullinula indica, Centropyxis aculeata*, C.arcelloides, C.cassis*, Corythion*, Cryptodifflugia oviformis, Cyphoderia ampulla*, C.trochus var. amphoralis, Difflugia oblonga, D.bacillifera, D.rubescens, D.pulex, D.brevicolla, Euglypha filifera, E.ciliata, E.rotunda, E.strigosa, E.strigosa var.heterospina, Heleopera petricola, H.petricola var.amethystea, H.sylvatica*, H.rosea, Lesquereusia spiralis, L.modesta, Nebela dentistoma, N.tincta, N.flabellulum, N.militaris, N.penardiana, N.tubulosa, N.galeata, N.lageniformis, N.maxima, Phryganella hemispherica*, Placocista spinosa, Pontigulasia bigibbosa, Pseudodifflugia fulva, Pyxidicula invisitata, Quadrula symmetrica, Sphenoderia dentata, S.lenta, S.fissirostris, Trigonopyxis arcula, Trinema enchelys. Total of 51 species and varieties.

6. Dale Park Swamp.

Amphitrema flavum, A.stenostoma, A. wrightianum, Arcella catinus, A.vulgaris, A.discoides*, A.arenaria, A.hemispherica, A.gibbosa, Assulina muscorum, A.seminulum, Bullinula indica, Centropyxis aculeata*, C.cassis*, Corythion*, Cryptodifflugia oviformis, C.eboracensis, Cyphoderia ampulla*, C.trochus var.amphoralis, Difflugia oblonga, D.acuminata, D.bacillariarum, D.rubescens, D.pulex, D.tuberculata, D.brevicolla, Euglypha strigosa, E.rotunda, E.filifera, E.acanthophora, Heleopera petricola, H.petricola var.amethystea, H.sylvatica*, H.rosea, Hyalosphenia papilio, H.elegans, Lesquereusia spiralis, L.modesta, Nebela dentistoma, N.tincta, N.flabellulum, N.militaris, N.acolla, N.marginata, N.galeata, N.maxima, N.griseola, N.carinata, Phryganella hemispherica*, Placocista spinosa, Sphenoderia lenta, Trinema enchelys. A total of 53 species and varieties.

7. Muckle Moss

Amphitrema flavum, A.wrightianum*, Arcella catinus, A.discoides*, A.gibbosa, Assulina muscorum, A.seminulum, Bullinula indica, Centropyxis aculeata*, C.cassis*, Corythion*, Cryptodifflugia oviformis, C.eboracensis, Difflugia oblonga, D.bacillifera, D.brevicolla, D.bacillariarum, Euglypha strigosa, Heleopera rosea, H.sylvatica*, H.petricola var.

amethystea, Hyalosphenia papilio, H.elegans, Nebela tincta, N.flabellulum, N.militaris, N.dentistoma, N.griseola, N.carinata, N.marginata, Phryganella hemispherica*, Trigonopyxis arcula. Total = 32 species and varieties.

8. Valley Bog, Moor House.

Recorded in the regeneration succession are: Amphitrema flavum, A.wrightianum, A.stenostoma, Arcella catinus, A.discoides, A.vulgaris, Assulina muscorum, A.seminulum, Bullinula indica, Centropyxis aculeata*, C.cassis*, Capsellina timida, Corythion*, Cryptodifflugia oviformis, C.eboracensis, Difflugia oblonga, D.bacillifera, D.brevicolla, D.bacillariarum, D.rubescens, Euglypha strigosa, E.strigosa var. heterospina, Heleopera petricola, H.rosea, H.sylvatica, Hyalosphenia papilio, H.elegans, H.subflava, Lecythium hyalinum, Leptochlamys sp., Nebela dentistoma, N.tincta, N.acolla, N.flabellulum, N.militaris, N.galeata, N.carinata, Phryganella hemispherica*, Placocista spinosa, Plagiophrys parvipunctata, Trigonopyxis arcula. A total of 41 species and varieties.

Also recorded from Valley Bog; Arcella hemispherica, Campascus minutus, Cyphoderia ampulla*, Heleopera petricola var. amethystea, Nebela lageniformis, N.tubulosa, N.tubulata, Pyxidicula invisitata, Quadrula symmetrica, Sphenoderia lenta, S.dentata, Trinema enchelys. These were present in a flush, pH 6.0-7.0, at the eastern end of the bog (p. 21) and they are not discussed in the text. The total number of species and varieties recorded from Valley Bog is 53.

9. Rusland Moss.

Amphitrema flavum, A.wrightianum, A.stenostoma, Arcella catinus, A.discoides*, A.arenaria var. crenulata, A.vulgaris, Assulina muscorum, A.seminulum, Bullinula indica, Corythion*, Difflugia bacillariarum, D.brevicolla, Euglypha strigosa, Heleopera petricola, H.sylvatica*, Hyalosphenia papilio, H.elegans, Nebela tincta, N.flabellulum, N.militaris, N.dentistoma, N.carinata, N.griseola, Phryganella hemisphaerica*, Pseudodifflugia fulva, Trigonopyxis arcula. A total of 27 species and varieties.

Appendix 2.

An example of a χ^2-test carried out on the vertical distribution of Testacea in S.recurvum plants. The distribution of full tests of Nebela tincta is given below.

	Sphagnum plants											
	1	2	3	4	5	6	7	8	9	10	11	12
Level 1	8	24	8	3	13	26	21	47	5	10	-	1
" 2	56	8	212	21	15	21	18	71	8	15	4	8
" 3	8	16	36	19	7	1	68	72	51	40	31	26
" 4	12	4	4	26	7	14	24	39	51	47	16	21
" 5	4	-	12	8	8	10	20	10	24	28	4	6
" 6	4	-	-	-	3	13	4	15	12	35	6	6

For the χ^2-test, the levels are grouped in pairs. Thus in plant 1, the number of tests in level 1 + 2 = 64, level 3 + 4 = 20 and level 5 + 6 = 8.

Comparison of top and middle pairs.

$$\chi^2 = \frac{(\text{Observed - Expected})^2}{\text{Expected}} + \frac{(\text{Observed - Expected})^2}{\text{Expected}}$$

$$\chi^2 = \frac{(64 - 42)^2}{42} + \frac{(20 - 42)^2}{42}$$

$$\chi^2 = 11.5 + 11.5$$

χ^2 = 23 which is significant at the 0.1% level.

Thus the top pair of levels contain a significantly greater number of tests than the middle pair. If this examination is carried out for each pair of levels in each plant, the following table may be made;

	χ^2-tests		
	Significant	Not significant	No animals
Levels 1+2 > 3+4	4	2	-
" 1+2 < 3+4	6		
" 3+4 > 5+6	10	-	-
" 3+4 < 5+6	2		

Appendix 3.

Prof. G. Deflandre, after examining specimens, confirmed the following identifications;

Amphitrema flavum, A.wrightianum, Arcella catinus, A.discoides var. scutelliformis, A.hemispherica, Assulina muscorum, A.seminulum, Difflugia oblonga, D.bacillifera, D.brevicolla, D.bacillariarum, D.elegans, D.acuminata, D.tuberculata, D.rubescens, Euglypha cristata, E.tuberculata, Heleopera petricola, H.petricola var. amethystea, H.rosea, Hyalosphenia papilio, H.elegans, Lesquereusia spiralis, L.modesta, L.epistomium, Nebela tincta, N.collaris, N.galeata, N.tubulosa, N. penardiana, N.bigibbosa, N.dentistoma, N.speciosa, N.carinata, N.flabellulum, Placocista spinosa, P.jurassica, Pontigulasia bigibbosa, Pyxidicula invisitata, Sphenoderia dentata, Trinema enchelys, Trigonopyxis arcula.

The discrepancies (Centropyxis aculeata*, C.cassis*, Cyphoderia ampulla*, Bullinula indica and Phrynganella hemispherica*) are discussed in the section on taxonomy of individual species.