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AN ILLUSTRATED INTRODUCTION TO THE TESTATE RHIZOPODS IN *SPHAGNUM*, WITH SPECIAL REFERENCE TO THE AREA AROUND MALHAM TARN, YORKSHIRE

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Keys, descriptions and illustrations are given for the identification of the commoner species of testate rhizopods in *Sphagnum*. A discussion of their ecology includes an account of some features of their microhabitat in relation to the horizontal and vertical distribution of species. Some suggestions are made for the use of testate rhizopods in teaching.

Introduction

THE assemblage of animals living on the leaves of *Sphagnum* is unlike the fauna of any other habitat. Nearly all the animals are small enough to inhabit the film of water in the concavity of a *Sphagnum* leaf, which may be only 300μ in diameter. The plant provides a microhabitat with unusual chemical and physical conditions, showing great variation from the top of the plant to the bottom. Its fauna includes several groups that are rarely seen elsewhere, and is dominated by the shelled amoebae, or testate rhizopods, of which many species may be found on a single branch of *Sphagnum*. The microecosystem of a *Sphagnum* leaf can provide an elegant introduction to the study of protozoology as well as to various ecological topics. A handful of *Sphagnum* in a polythene bag is easily transported and maintained; a drop of the clear water squeezed from it contains little debris and abundant animals; and it might be more widely used in teaching if it were not for the difficulty of naming the animals. Many species of testate rhizopods are easily recognized, and in the first part of this paper we illustrate and describe some of the commoner and more distinctive forms found in the Malham Tarn area and elsewhere. The second part of the paper discusses some aspects of the ecology of the inhabitants of *Sphagnum*.

Identification

Books

Both of the books written in English and devoted to the systematics of testate rhizopods are out of print. Because of their beautiful coloured plates they are now very valuable, and hence not available to most amateurs. They are: *Freshwater Rhizopods of North America*, by J. Leidy, published by the United States Geological Survey in 1879; and *British Freshwater Rhizopods and Heliozoa*, by J. Cash, G. H. Wailes and J. Hopkinson, published in five volumes by the Ray Society in 1905–1921. Many British species are mentioned in the key to testate rhizopods in *Freshwater Biology*, by H. B. Ward and G. C. Whipple (1959). *Wechseltierchen*, by Th. Grospietsch, in German, is very useful. This key is based on those books, together with the revisions of the genera *Arcella* (1928), *Centropyxis* (1929) and *Nebela* (1936) by G. Deflandre. Other works on the identification of testate rhizopods are those of Hoogenraad and de Groot (1940) in Dutch, and Harnisch (1960) in German. In the British Museum

(Natural History) is a collection of slides prepared by Penard, a valuable source of reference for serious students of the group.

We include here only the more distinctive species found in *Sphagnum*, excluding any that are rare or difficult. The keys, descriptions and illustrations should make it possible to recognize most of the commoner species. There remain a number which can only be identified by experts. If one of these difficult species turns up in an elementary study it can be described and given a code name for the purpose in hand.

Preparation of material

Rhizopods can be found in the water squeezed from wet *Sphagnum*. A good hunting ground is the water that oozes into the footprints of a heavy-footed person walking on a *Sphagnum* carpet. For more exact work a few strands of *Sphagnum*, consisting of the deeper, brown part, where dead rhizopod tests accumulate, as well as the green tops, can be taken in a polythene bag to the laboratory and there wrung out over a small petri dish, a watch glass, or a slide. When this extract is examined under a binocular microscope, it will be seen to contain a variety of lively animals, which, because of their conspicuous movements, are more obvious than the testate rhizopods; rotifers, nematodes, mites, ciliates, gastrotrichs and tardigrades are likely to appear. If the extract is left undisturbed for several hours, the rhizopods may begin to put out their pseudopodia and move about. Detailed examination of the testate rhizopods is best carried out on a slide under a coverslip, so that when a promising animal is found one can switch to a high-power objective. Drawings of the animal, seen from all aspects, are a valuable aid to observation and identification. Size is a character used in identification, and it is often necessary to measure the tests. This measurement is easily done with a graticule in the eyepiece of the microscope, but if that is not available it is possible to use a micrometer slide to measure the diameter of the field of view of a particular microscope for each of its objectives; the dimensions of an object can then be calculated as a fraction of the diameter of the field of view.

To make permanent preparations of testate rhizopods it is necessary to transfer individual animals from the water in which they were found to a drop of mounting medium on a clean slide. This is a delicate job best done under a good binocular dissecting microscope. The rhizopod is located, in a drop of water without a coverslip, under the dissecting microscope, and can be transferred either on a needle or in a fine pipette. A suitable needle can be made by gluing the head of a fine insect pin into a handle of glass tubing ("Five-minute" Epoxy is a suitable glue) or by holding a short length of hair in fine forceps. The rhizopod is chivied to the edge of its drop of water and then pushed out of the drop, so that it lies at the end of a trail of water. From here the animal can be edged into a drop of mountant on the same slide, if the rest of the extract from which it came can be cleaned off. If not, the rhizopod must be transferred to a fresh slide. Its trail of water evaporates, and just before it begins to dry up the rhizopod can be picked up on the tip of a needle or hair wet with mountant, and transferred to a small drop of mountant on another slide. Alternatively the rhizopod can be picked up in a narrow-mouthed teat pipette, drawn out in a flame to a capillary not much wider than a hair. The contents of the pipette are discharged just beside the drop of mountant, and a needle is used to edge the rhizopod, with as little water as possible, into a suitable position in the middle of the drop of mountant. Very small, transparent species that are difficult to see can be made more easily visible by allowing them to dry until a tiny air bubble fills the test, but the timing is critical; if allowed to dry completely they cannot be moved without breaking up.

A good mountant is polyvinyl lactophenol, to which animals can be transferred direct from water. The rhizopod should be kept in view under the dissecting microscope while a round coverslip is carefully placed over it, and when the coverslip has settled a ring of ink can be marked gently on to the coverslip around the specimen, so that it is easily located. Examination under a compound microscope will show whether the rhizopod is oriented at a suitable angle. If not, its position can be altered by gently shifting the coverslip. A generous quantity of mountant should be used to allow for some shrinkage.

The animals

Testate rhizopods belong to the order Testacea, and differ from other members of the class Rhizopoda in their ability to make a shell, or test. These tests persist long after their occupants have died, and most of the tests that one finds are empty. Those that contain a living animal are recognizable by the granular appearance of the protoplasm which contains numerous inclusions so that it is sometimes difficult to make out details of the test wall. Many testate rhizopods can encyst, and, particularly if the *Sphagnum* has dried, one often finds tests in which the protoplasm has rounded up. It is rare to see a testate rhizopod protrude pseudopodia from the mouth of its test, and although the form of the pseudopodia is used in classification most identification has to rest on characters of the test alone.

The test may consist of transparent secretion or it may be composed of regular or irregular plates or scales, or of more or less neatly arranged mineral or organic particles picked up from the environment. It is usually easy to see how the test is made; but there are some genera, such as *Trinema* and *Corythion*, in which the scales, if they are present, may be so small and delicate that they are hardly visible, or they may appear simply as slight irregularities on the surface of the test. There are a few forms of *Nebela* which fail to produce the mosaic of irregular plates that characterize the genus, and although in shape they are identical with typical species of *Nebela* occurring in the same place, their tests appear to be made of secretion only.

Tests can show intraspecific variation in shape as well as in composition. Where the range of variation is particularly wide, as in *Centropyxis aerophila* or *Trinema lineare*, the taxonomic status of the various forms is doubtful and we have sometimes lumped together a group of species. Variation in test shape causes particular confusion in the genus *Nebela*, where the widespread and important species *N. collaris* may occur in a range of shapes some of which resemble other species very closely. Fortunately other features can be taken into consideration here, and despite the apparent similarity of these species we have included several of them because of their ecological importance.

The species dealt with in this paper include all the more obvious ones that turned up during a week's searching at Malham Tarn, together with others that are common elsewhere and may be found at Malham. Those marked with an asterisk in the list that follows have been recorded from Malham but little is known about their habitat distribution there. It should be emphasized that this is not a complete list of British testate rhizopods; it includes only those species that we consider are common and easily found in *Sphagnum*.

Notes on the distribution of species are taken from Heal (1961, 1962) and Schönborn (1962, 1963).

List of species described

Family Arcellidae
- 1.1 *Arcella catinus* Penard*
- 1.2 *A. discoides* Ehrenberg*
- 1.3 *A. gibbosa* Penard
- 1.4 *A. hemispherica* Perty
- 1.5 *A. vulgaris* Ehrenberg*

Family Centropyxidae
- 2.1 *Trigonopyxis arcula* (Leidy)*
- 3.1 *Bullinularia indica* Penard*
- 4.1 *Centropyxis arcelloides* Penard*
- 4.2 *C. aculeata* group*
- 4.3 *C. cassis* group*

Family Difflugiidae
- 5.1 *Difflugia urceolata* Carter*
- 5.2 *D. tuberculata* Wallich
- 5.3 *D. acuminata* Ehrenberg
- 5.4 *D. bacillariarum* Perty
- 5.5 *D. rubescens* Penard
- 5.6 *D. bacillifera* Penard
- 5.7 *D. oblonga* Ehrenberg

Family Nebelidae
- 6.1 *Hyalosphenia elegans* Leidy*
- 6.2 *H. papilio* Leidy*

- 7.1 *Heleopera rosea* Penard*
- 7.2 *H. petricola* Leidy*
- 7.3 *H. sylvatica* Penard*
- 7.4 *H. sphagni* (Leidy)

- 8.1 *Lesquereusia modesta* Rhumbler
- 8.2 *L. spiralis* (Ehrenberg) Bütschli

- 9.1 *Quadrulella symmetrica* (Wallich)

- 10.1 *Nebela griseola* Penard
- 10.2 *N. barbata* Leidy
- 10.3 *N. dentistoma* Penard
- 10.4 *N. vitraea* Penard
- 10.5 *N. lageniformis* Penard
- 10.6 *N. galeata* Penard
- 10.7 *N. marginata* Penard
- 10.8 *N. carinata* (Archer)
- 10.9 *N. bigibbosa* Penard
- 10.10 *N. flabellulum* Leidy*
- 10.11 *N. tincta* (Leidy)*
- 10.12 *N. parvula* Cash
- 10.13 *N. minor* Penard
- 10.14 *N. collaris* (Ehrenberg)
- 10.15 *N. militaris* Penard*
- 10.16 *N. penardiana* Deflandre
- 10.17 *N. tubulosa* Penard

Family Euglyphidae
- 11.1 *Trinema lineare* Penard
- 11.2 *T. enchelys* (Ehrenberg)

- 12.1 *Corythion dubium* Taranek*

- 13.1 *Sphenoderia lenta* Schlumberger

- 14.1 *Placocista spinosa* (Carter)

- 15.1 *Assulina seminulum* (Ehrenberg)
- 15.2 *A. muscorum* Greeff*

- 16.1 *Euglypha acanthophora* (Ehrenberg)
- 16.2 *E. tuberculata* Dujardin*
- 16.3 *E. strigosa* (Ehrenberg)*
- 16.4 *E. rotunda* Wailes
- 16.5 *E. compressa* Carter
- 16.6 *E. ciliata* (Ehrenberg)*

Family Cyphoderiidae
- 17.1 *Cyphoderia ampulla* (Ehrenberg)

Family Amphitremidae
- 18.1 *Amphitrema flavum* (Archer)*
- 18.2 *A. wrightianum* Archer
- 18.3 *A. stenostoma* Nuesslin

Key to some genera of testate rhizopods in *Sphagnum*

1	Test of secretion, without visible plates or particles	2
—	Test with plates or particles	7
2	Test a domed disc or hemisphere with a central mouth (test usually yellow-brown and with a finely-patterned surface)	*Arcella*
—	Test a different shape; mouth not central	3
3	Test oblong with a small mouth at each end	*Amphitrema*
—	Only one mouth	4
4	Test less than 50μ long; mouth subterminal* or oblique	*Trinema/Corythion*
—	Test more than 80μ long, or, if smaller, mouth terminal*	5
5	Test round in cross section with a curved neck and an oblique mouth	*Cyphoderia*
—	Test strongly flattened; mouth at right angles to long axis	6
6	Test pinkish or yellowish	*Hyalosphenia*
—	Test quite colourless, consisting of regular plates that are hard to see if the contents are opaque	*Euglypha*
7	Test coated with foreign particles	8
—	Test a neat mosaic set in cement, or a patterned arrangement of regular plates, without untidily-stuck-on particles	14
8	Test appearing asymmetrical, with a curved tube on one side leading to the mouth	*Lesquereusia*
—	Not like this	9
9	Test oblong with a small mouth at each end	*Amphitrema*
—	One mouth only	10
10	Test neat, the posterior part decorated with larger particles	*Heleopera*
—	Particles similar throughout test	11
11	Test ovoid or elongate with a terminal* mouth	*Difflugia*
—	Test ovoid or flattened with the mouth on one side	12
12	Mouth a curved slit with an irregular row of pores beside it	*Bullinularia*
—	Mouth not slit-shaped; no pores	13
13	Mouth three- or four-sided	*Trigonopyxis*
—	Mouth round, oval or crescent-shaped	*Centropyxis*

14	Test a mosaic, neat but not geometrically patterned	15
—	Test of rounded or oval plates arranged in very regular rows	17
15	Mouth subterminal* or oblique; small, colourless, transparent test	*Corythion/Trinema*
—	Mouth terminal*	16
16	Plates four-sided	*Quadrulella*
—	Plates rounded, elongate, or irregular	*Nebela*
17	Colourless; mouth bordered by a membranous collar	*Sphenoderia*
—	Not as above	18
18	Mouth bordered by plates with toothed margins (test colourless, flattened, often bearing spines)	*Euglypha*
—	Mouth plates not toothed	19
19	Test bordered with flattened spines	*Placocista*
—	Test without spines	20
20	Test flattened, with mouth at right angles to long axis	*Assulina*
—	Test round in cross-section, with a curved neck and an oblique mouth	*Cyphoderia*

Family Arcellidae

(1) *Arcella*

There are about 30 species of *Arcella*. In nearly all of them the circular test is amber-coloured and its surface is finely patterned with hexagons, spots or striations. Most species have two nuclei, but a few species have only one and some have as many as 200. All of them are shaped like a radially symmetrical hat, and they range in height from the flat, beret-like *A. discoides* to *A. apicata*, shaped like a bishop's mitre. The shape in side view is important in identification (see Fig. 1), and the profile can be seen by turning the specimen over with a needle in a drop of water under a dissecting microscope. Permanent preparations, if mounted mouth-down, should bear a sketch of the profile on the slide label.

Key to some sphagnicolous species of *Arcella*

1	Disc not quite circular, flat-topped; mouth always ringed with pores	*A. catinus* (1.1)
—	Disc usually circular, evenly domed; mouth usually without pores	2
2	Saucer-shaped or flatter	*A. discoides* (1.2)
—	Bowl-shaped or deeper	3
3	Convex surface puffy with irregular bulges and hollows	*A. gibbosa* (1.3)
—	Convex surface an evenly-curved dome	4

* A "terminal" mouth is right at the end of the test, at right angles to the long axis of the test (as in *Nebela*, plate I, j). A "subterminal" mouth is at or near one end but is not symmetrically at right angles to the long axis (as in *Trinema lineare*, figure 4).

4 Diameter less than 60μ; a hemisphere or deeper *A. hemispherica* (1.4)
— Diameter greater than 100μ; usually shallower than a hemisphere *A. vulgaris* (1.5)

1.1 *Arcella catinus* Penard (Plate II, a) (77–116μ diameter)

The outline of the test is usually not quite circular and this, with the flattened top, the radiating swellings which are often present on the convex surface (and which appear as folds when the test is flattened under a coverslip), and the ring of about 12–25 pores around the mouth, makes the species easily recognized. Other species, such as *A. discoides*, have forms with pores around the mouth, but do not show the irregular outline and radial swellings of *A. catinus*.

1.2 *Arcella discoides* Ehrenberg (Plate II, b) (53–168μ)

This is a rather variable species. The typical form is 100–150μ in diameter, the shape of a shallow saucer, and may or may not have pores around the mouth. Some forms are deeper, with a height as much as one-third of the diameter.

1.3 *Arcella gibbosa* Penard (70–125μ)

This hemispherical species has distinctive undulations on the surface; the dome is covered with bulges and hollows. Seen under a coverslip these give the impression of a series of polygons in different focal planes. Similar irregularities are found occasionally in varieties of other species, which differ in the shape of the profile, in size, or in the shape of the mouth.

1.4 *Arcella hemispherica* Perty (45–56μ)

Nearly always smaller than *A. gibbosa* or *A. vulgaris*, *A. hemispherica* is the shape of half, or even three-fifths, of a sphere. The profile is more regularly hemispherical than is that of *A. vulgaris*.

1.5 *Arcella vulgaris* Ehrenberg (100–145μ)

This species is usually a little shallower than a hemisphere, and a gentle marginal undulation makes it look like a pudding basin with a slightly swollen rim. The amber or brown colour of the test and its hexagonal patterning are often rather obvious.

Family Centropyxidae

(2) *Trigonopyxis*

2.1 *Trigonopyxis arcula* (Leidy) (Plate I, a) (100–150μ)

T. arcula is the only British species in the genus *Trigonopyxis*. The test is red-brown and is composed of mineral and organic particles forming a neat hemisphere. The shape of the mouth distinguishes it from *Centropyxis*; it is usually triangular, although four-sided mouths are sometimes found. In *Centropyxis* the margin of the mouth is reflexed inwards, but in *Trigonopyxis* the edges of the mouth are flat, although the whole mouth area may be recessed a little into the hemisphere.

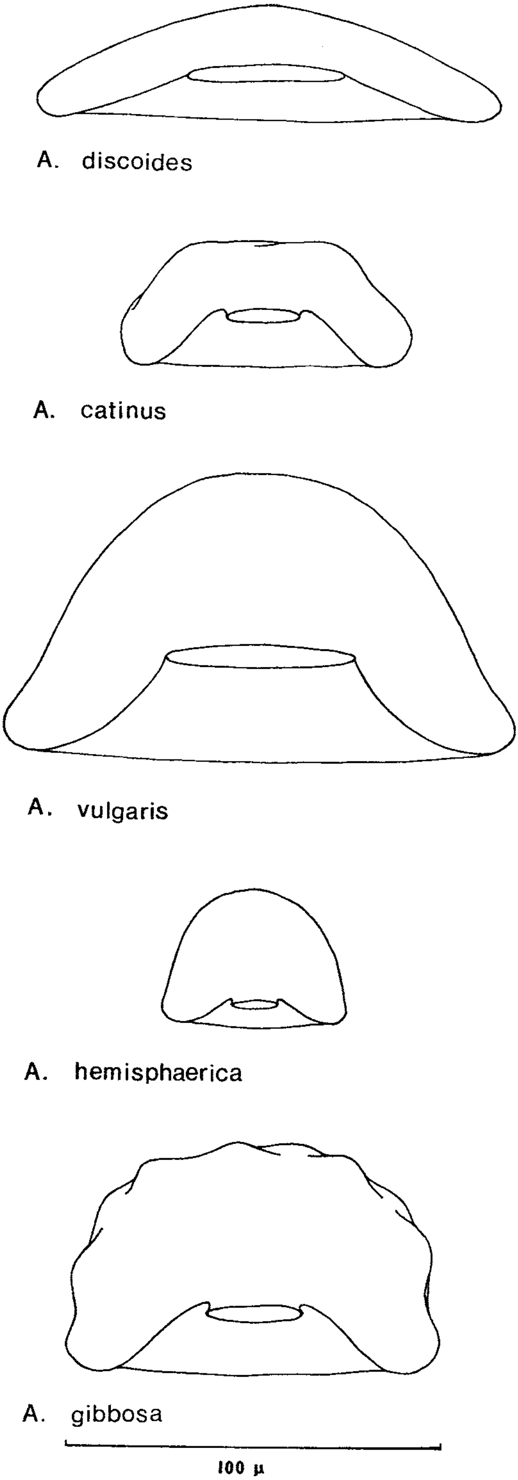


FIG. 1.
Profiles of some species of *Arcella* (after Deflandre, 1928).

(3) *Bullinularia*

3.1 *Bullinularia indica* Penard (Plate I, b) (120–250 μ)

This species is the only British member of its genus. The test is ovoid, rather opaque brown, and composed of mineral particles rather neatly cemented together. The curved, slit-shaped mouth, often with one lip overlapping the other, is distinctive, although because of the opacity of the test the structure is at first difficult to see. The irregular row of pores beside the mouth will confirm the identification.

(4) *Centropyxis*

The test is hemispherical or ovate, with the flattened ventral surface invaginated at the mouth and the dorsal surface rounded. The test is composed of secretion and is usually covered with mineral or organic particles. The colour ranges from opaque brown to translucent pale greenish grey.

This very large genus is divided into two subgenera: the subgenus *Centropyxis*, which contains the bilaterally symmetrical species in which the mouth is not central; and the subgenus *Cyclopyxis*, with the radially symmetrical species, which parallel species of *Arcella* in shape. The subgenus *Centropyxis* includes some difficult species, and we describe two groups, each of which represents a complex of species and varieties that can only be sorted out by experts.

Key

1	Test hemispherical with a central mouth	*C. arcelloides* (4.1)
—	Test bilaterally symmetrical; mouth not central	2
2	Test with some spines posteriorly	*C. aculeata* group (4.2)
—	Test without spines	*C. cassis* group (4.3)

4.1 *Centropyxis* (*Cyclopyxis*) *arcelloides* Penard (80–110 μ)

C. arcelloides is hemispherical with a large, circular, slightly invaginated mouth. In shape it resembles *Arcella hemispherica*, but it can be distinguished from that species by its larger size and by the composition of the test, which is covered with mineral particles.

4.2 *Centropyxis* (*Centropyxis*) *aculeata* group (Plate I, c)

C. aculeata is 120–150 μ in diameter; others in this group may be larger or smaller.

Members of the *C. aculeata* species group are flattened, especially in the anterior region. The mouth is round or oval and is anterior, and the posterior side of the test is produced into spines, usually varying in number from two to about ten, which point outwards and upwards. The test consists of secretion with mineral and organic particles, and its colour ranges from translucent grey-green to dark brown.

This group includes *C. aculeata* (Ehrenberg) and its varieties and *C. hirsuta* Deflandre.

4.3 *Centropyxis* (*Centropyxis*) *cassis* group (Plate II, c)

C. cassis is 60–86 μ long; others in this group may be larger or smaller.

Members of this group are usually oval with the mouth right at the anterior end, although some forms are wider, with an almost circular outline. There is great variation in the amount of mineral and organic material in the test, and the colour varies accordingly from translucent greenish-grey to dark brown. Sometimes larger particles are incorporated into the anterior edge of the mouth or added to the posterior end of the test.

This group includes *C. aerophila* Deflandre and its varieties, *C. orbicularis* Deflandre, *C. constricta* Ehrenberg and *C. platystoma* (Penard) as well as *C. cassis* (Wallich).

Family Difflugiidae

(5) *Difflugia*

The *Difflugias* make rather untidy tests, usually of mineral particles but sometimes of organic material; the test of *D. bacillifera* and some other species is covered with diatom frustules. The tests of most species are of round cross-section, not compressed, and the mouth is terminal (Fig. 2). Members of this genus are particularly abundant in the mud and ooze of ponds. Those that occur in *Sphagnum* are found in the deeper layers where materials for test building are available.

Many species of *Difflugia* occasionally turn up in *Sphagnum*. We describe only those that are characteristically found there (*D. bacillifera*) or are particularly distinctive.

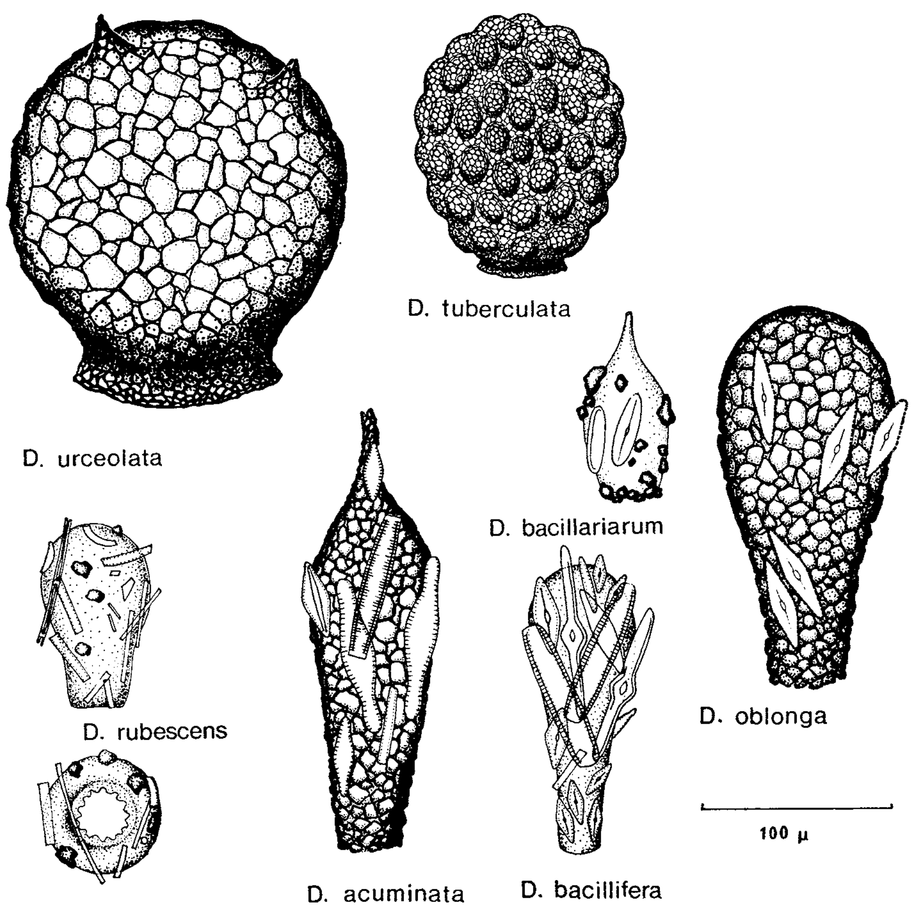


FIG. 2.

Some species of *Difflugia*. *D. tuberculata* after Green (1963); *D. acuminata* after Leidy (1879); others after Cash, Wailes and Hopkinson (1905–1921).

Key

1	Test more or less spherical	2
—	Test markedly elongate	3
2	Mouth bordered by a conspicuous flared rim	*D. urceolata* (5.1)
—	Test thrown into numerous little blisters	*D. tuberculata* (5.2)
3	Test pointed posteriorly	4
—	Test rounded posteriorly	5
4	Test 3–4 times as long as broad	*D. acuminata* (5.3)
—	Test relatively broader, about twice as long as broad, usually coated with diatom frustules	*D. bacillariarum* (5.4)
5	Mouth margin inturned, usually scalloped; cytoplasm with red granules	*D. rubescens* (5.5)
—	Mouth margin simple, straight; cytoplasm not red	6
6	Test coated with diatom frustules	*D. bacillifera* (5.6)
—	Test coated with mineral particles	*D. oblonga* (5.7)

5.1 *Difflugia urceolata* Carter (150–220 μ)

The test is opaque, coated with mineral particles, and more or less spherical or ovoid, sometimes with one or two blunt spines posteriorly. It is recognized by the flared rim around the mouth.

D. urceolata is not common in Britain.

5.2 *Difflugia tuberculata* Wallich (about 130–140 μ)

The test of *D. tuberculata* is shaped like a mulberry; it is spherical or broadly ovoid and is covered with little swellings where the test bulges out. There is a small simple collar around the polygonal mouth.

D. tuberculata occurs in fen *Sphagnum*, and is not very common.

5.3 *Difflugia acuminata* Ehrenberg (100–400 μ)

The test is about three or four times as long as it is broad, and narrows gradually to the simple round mouth. Posteriorly the test is drawn out into a point. It is composed of mineral particles, sometimes with diatoms. It can be distinguished from *D. bacillariarum* by its more elongate shape and its often larger size.

5.4 *Difflugia bacillariarum* Perty (90–130 μ)

The test is rather delicate and transparent, bearing a thin covering of diatom frustules and mineral particles. It is relatively broader than that of *D. acuminata*, seldom more than twice as long as broad, and the sides slope evenly towards the mouth. The posterior end is pointed, and the point is sometimes curved a little to one side and often has a hole at the tip.

D. bacillariarum is characteristic of bog pools.

5.5 *Difflugia rubescens* Penard (66–105 μ)

The delicate, rather transparent test is thinly coated with diatom frustules and foreign particles. It is pear-shaped and about twice as long as broad. It differs from

D. bacillariarum in its rounded posterior end, and is characterized by the brick-red cytoplasmic granules visible in living individuals and by the margin of the mouth, which is usually incurved and crenulate, or scalloped.

D. rubescens is a eurytope species occurring most commonly in fen *Sphagnum*.

5.6 *Difflugia bacillifera* Penard (120–180 μ)

D. bacillifera's test is coated with diatom frustules, with which it is sometimes very thickly encrusted. It is about three or four times as long as broad, with a rounded posterior end, and tapers to a nearly cylindrical neck. This species differs from *D. rubescens* in its lack of red pigment and in its simple round mouth. *D. oblonga* is a rather similar shape but has a test of mineral particles.

D. bacillifera is a characteristic member of the testacean association of bog pools, and it is unlike other species of *Difflugia* in that *Sphagnum* is its typical habitat.

5.7 *Difflugia oblonga* Ehrenberg (100–400 μ)

This is a common and very variable species. The test is coated mainly or entirely with opaque mineral particles. It is elongate, usually about 2–3 times as long as broad, rounded posteriorly and tapering evenly to the round mouth.

D. oblonga is a eurytope species but is commoner in fens than in bog areas.

Family Nebelidae

(6) *Hyalosphenia*

Elegant species with a test which is clear, homogeneous and pale yellowish pink or colourless, flattened and narrowing towards the terminal mouth. The cytoplasm contains zoochlorellae.

Key

1	Test flask-shaped, narrow-necked, with regular or irregular surface undulations	*H. elegans* (6.1)
—	Test smooth, narrowing gradually towards the mouth	*H. papilio* (6.2)

6.1 *Hyalosphenia elegans* Leidy (Plate I, d) (90–110 μ)

The flask-like shape and the dented surface of *H. elegans* make it a very distinctive species. It is characteristic of bog hummocks, and at Malham it is common on Tarn Moss.

6.2 *Hyalosphenia papilio* Leidy (Plate I, e) (90–130 μ)

The shape of the smooth, clear, delicately-coloured test is quite different from that of *H. elegans*. The posterior end is semicircular, and the straight sides converge gradually from the widest point to the slightly-curved mouth. On each side, at the widest point, is a small pore, which may be difficult to see. *H. papilio* is particularly striking if it is seen alive with the cytoplasm, dotted with green zoochlorellae, attached to the inside of the test by slender filaments. Cash describes the movements of this species as "fairy-like".

H. papilio is characteristic of wet *Sphagnum* in bog hummocks, where it was one of the commonest species in Heal's (1961) survey. It was found in the upper, green parts of the plants. At Malham it occurs just south of Spiggot Hill.

(7) *Heleopera*

Test flattened, oblong in broad view, narrowing only a little towards the terminal mouth and consisting of small transparent irregular plates rather untidily cemented together. The posterior end is usually decorated with larger sand grains and other particles stuck to the outside. The genus is easily recognized, but except for the brightly-coloured forms it is more difficult to distinguish between the species.

Key

1	Test wine-red with orange-yellow lips	*H. rosea* (7.1)
—	Test violet, greyish, yellowish or colourless	2
2	Test violet or amethyst-coloured with yellowish lips	*H. petricola* var. *amethystea* (7.2)
—	Test greyish, yellowish or colourless	3
3	Test usually less than 80 μ long, transparent, colourless, at least twice as long as broad; outline of side walls continuing in a smooth curve around mouth	*H. sylvatica* (7.3)
—	Test often more than 80 μ long, less transparent, broader	4
4	Test colourless, untidy, with numerous mineral particles; lips thickened, almost straight, meeting side walls in a rounded angle	*H. petricola* (7.2)
—	Test tinged with golden yellow, with fewer mineral particles; large, neat, almost circular; mouth smoothly curved, scarcely angled at the corners, its lips scarcely thickened	*H. sphagni* (7.4)

7.1 *Heleopera rosea* Penard (Plate I, f) (120–135 μ)

H. rosea is distinct from the other species of *Heleopera* in its wine-red or rose-red colour. It has the bluntly-angled mouth of *H. petricola,* and the lips are thickened and orange-yellow or brown. Heal (1961) found *H. rosea* in *Sphagnum* in both fens and bogs.

7.2 *Heleopera petricola* Leidy (Plate I, g) (80–125 μ)

H. petricola varies in size and colour, but is characterized by the shape of the mouth which is straight or only slightly curved, with a rounded but definite angle at each end. The lips are thickened. These features of the mouth distinguish *H. petricola* from the other species mentioned here except *H. rosea,* which is known by its colour.

Heleopera petricola var. *amethystea* Penard resembles the typical form in shape and size but is a clear amethyst colour. The lips may be yellow or light brown. Heal (1961) found this variety in both fen and bog *Sphagnum,* but it was commoner in fens.

7.3 *Heleopera sylvatica* Penard (50–75 μ)

This is a small, transparent species, with a narrower test than the others. The mouth is markedly curved, so that the ends of the mouth are scarcely angled at all, but curve round smoothly to the side walls.

7.4 *Heleopera sphagni* (Leidy) (100–145μ)

The large, neatly-made, broadly ovoid test is tinted yellow or brown. The mouth is without the thickened lips of *H. petricola* and *H. rosea*, and is usually strongly convex so that it continues the curve of the sides. The test sometimes looks almost circular. The cytoplasm contains zoochlorellae, and this species inhabits the upper, green parts of the *Sphagnum*.

Harnisch (1960) calls this species *H. picta* Leidy.

(8) *Lesquereusia*

The curious shape of the test is characteristic of this genus. It is somewhat compressed and in broad view it looks asymmetrical. On one side, leading to the mouth, is a tubular vestibule, separated from the main body of the test by an incomplete cross-wall. The test consists of mineral particles or a mosaic of minute curved rods.

Key

1	Test opaque, encrusted with sand grains	*L. modesta* (8.1)
—	Test translucent, a neat mosaic of curved rods	*L. spiralis* (8.2)

8.1 *Lesquereusia modesta* Rhumbler (95–150μ)

This species, with the distinctive "spiral" shape of its genus, is known from the other species by its rather rough, opaque brown test composed of sand grains. Heal (1961) found *L. modesta* in fen *Sphagnum*.

8.2 *Lesquereusia spiralis* (Ehrenberg) Bütschli (Plate I, h) (100–150μ)

L. spiralis differs from *L. modesta* in the composition of its test, which is translucent and consists of minute curved rods cemented together in a neat mosaic. The outline of the test is therefore more regular than that of *L. modesta*, and its characteristic shape is more easily seen. *L. spiralis* is common in fen *Sphagnum*.

(9) *Quadrulella*

Quadrulella (once known as *Quadrula*) is sometimes treated as a subgenus of *Nebela* (Deflandre, 1936). As in *Nebela* the test is strongly compressed, elongate, and rounded at the posterior end; and it tapers gently towards the terminal mouth. As in *Nebela* it consists of transparent plates cemented together in a rather neat mosaic. It differs from *Nebela* in the shape of the plates, which are four-sided in *Quadrulella* and rounded or elongate in *Nebela*.

9.1 *Quadrulella symmetrica* (Wallich) (Plate II, d) (68–120μ)

This species varies from the shape illustrated in plate II to one with a longer neck like *Nebela militaris*. The four-sided plates are colourless and transparent and are usually arranged in a mosaic pattern that is sometimes very regular. In some specimens the plates may overlap one another a little.

(10) *Nebela*

This is the most characteristic genus of testate rhizopods in *Sphagnum*. The test is usually strongly flattened. In broad view it is rounded posteriorly, narrowing gradually or abruptly towards the mouth (Fig. 3). In *N. barbata* the test bears whiskers, in *N. carinata* and *N. marginata* there is a marginal keel, and in many there are pores, which are often difficult to see, opening on the angles at the sides. One species, *N. bigibbosa*, has large pores on the broad face. The test is smooth and composed of irregular, oval or rod-shaped siliceous plates, often rounded, touching, overlapping, or, more often, set as a neat mosaic in conspicuous cement. The test is transparent and colourless or tinged with pink, yellow or grey.

Sometimes the plates composing the test of *Nebela* can be seen to be derived from the tests of prey organisms such as *Euglypha*, *Quadrulella* or diatoms.

Heal (1963) has made a morphometric study of some of the more difficult species of *Nebela*.

Key to some species of *Nebela* living in *Sphagnum*
(to be used in conjunction with Fig. 3)

1	Edge of mouth formed of particles and recurved, forming a lip	*N. griseola* (10.1)
—	Edge of mouth not recurved	2
2	Mouth edged with plates	3
—	Mouth with smooth edges of secretion	5
3	Test flask-shaped, with a distinct neck; usually bearing scattered siliceous whiskers	*N. barbata* (10.2)
—	Test narrowing gradually towards the mouth	4
4	Plates not touching one another, the cement between often studded with minute holes	*N. dentistoma* (10.3)
—	Plates touching one another, reinforced at their angles by small additional plates on the inner face of the test	*N. vitraea* (10.4)
5	Test flask-shaped, with a distinct, more or less parallel-sided neck	*N. lageniformis* (10.5)
—	Test narrowing steadily to the mouth	6
6	Posterior end of test edged with a flat keel or an inflated ridge	7
—	Posterior end of test without a keel or ridge	9
7	Test edged with an inflated ridge	*N. galeata* (10.6)
—	Test edged with a sharp keel	8
8	Keel narrow, extending less than halfway to the mouth	*N. marginata* (10.7)
—	Keel broad, extending more than halfway to the mouth	*N. carinata* (10.8)
9	A pair of large, conspicuous pores on the broad face of the test	*N. bigibbosa* (10.9)
—	Without pores on the broad face of the test	10

10 Test as broad as long, or broader, narrowing abruptly to the mouth — *N. flabellulum* (10.10)
— Breadth of test less than distance from mouth to posterior end — 11

11 Test usually less than twice as long as broad; mouth length less than one-third maximum width of test — 12
— Test more than twice as long as broad; mouth more than one-third maximum width of test — 13

12 With a pair of lateral pores, faintly visible as breaks in the side wall, near the mouth — *N. tincta* (10.11)
— Usually without lateral pores; 78–90μ — *N. parvula* (10.12)

13 Without lateral pores — 14
— With a pair of lateral pores, faintly visible as breaks in the side walls near the mouth — 15

14 80–100μ — *N. minor* (10.13)
— 107–184μ — *N. collaris* (10.14)

15 50–72μ — *N. militaris* (10.15)
— 140–175μ — *N. penardiana* (10.16)
— 190–215μ — *N. tubulosa* (10.17)

10.1 *Nebela griseola* Penard (70–85μ)

The test is pear-shaped, slightly compressed, greyish and rather opaque, consisting of rather untidy plates. It is recognized by its stony mouth which is recurved outwards to form a distinct lip. *N. griseola* occurs in the *Sphagnum* of bog hummocks.

10.2 *Nebela barbata* Leidy (80–160μ)

N. barbata has a slightly flattened, flask-shaped test with a relatively long narrow neck. The colourless, polygonal or rounded plates that compose the test extend to the edge of the mouth; there is no smooth lip of secretion. Sticking out all over the surface of the test are long siliceous "whiskers", which are easily seen in water but are said to be invisible when the test is mounted in Canada balsam. In some specimens the neck is curved.

N. barbata is not a very common species.

10.3 *Nebela dentistoma* Penard (66–115μ)

The broad, compressed test tapers gradually to the rather wide mouth, which is edged with plates or, rarely, with an uneven lip of secretion. The rounded plates of the test do not touch one another; the spaces between them are occupied by cement, and in many specimens this has a very characteristic appearance because there are small round holes in it. The test is colourless or blue-grey, never tinged with yellow or brown. *N. dentistoma* is similar in shape and size to *N. vitraea*, but the latter is sometimes yellow and can always be distinguished by the small extra plates that reinforce the junctions between the main plates of its test.

N. dentistoma is found in *Sphagnum* in both fen and bog areas, but is commoner in fens.

10.4 *Nebela vitraea* Penard (95–231 μ)

N. vitraea resembles *N. dentistoma* in shape and in the presence of plates bordering the mouth. Its test is glassy and colourless or clear yellow, a colour that is never seen in *N. dentistoma*. The two species differ in the detailed patterning of the plates. In *N. vitraea* adjacent plates touch one another and minute extra plates inside the test reinforce the angles where several larger plates meet. In *N. dentistoma* these minute extra plates are not found, and the cement is often pitted with small round holes around the main plates.

10.5 *Nebela lageniformis* Penard (125–130 μ)

The test is slightly compressed and flask-shaped, with an almost parallel-sided neck. The slightly curved mouth has a thin lip of secretion. The test consists of rounded plates neatly cemented together, and it is transparent and colourless or yellow-tinted. A smaller (75–100 μ) more slender form with a thicker lip has been described as another species, *N. wailesi* Deflandre.

10.6 *Nebela galeata* Penard (180–200 μ)

The pear-shaped test is swollen in the centre and more strongly compressed at the edges, so that a thick rim surrounds it. This distinctive shape can be seen in side view or, in broad view, by focusing up and down. The mouth is slightly curved with thin lips of secretion. The rounded plates are neatly arranged, touching or overlapping, and the test is transparent and usually colourless. The lateral pores are often difficult to see, but they are sometimes marked by a small bulge on each side.

N. galeata is found in fen *Sphagnum*.

10.7 *Nebela marginata* Penard (140–170 μ)

The test, often tinted yellow-grey or brown, is flattened and pear-shaped with a thin lip of secretion at the slightly-curved mouth. A narrow keel around the posterior part of the test extends about halfway towards the mouth. This species resembles *N. carinata*, but has a shorter and narrower keel.

10.8 *Nebela carinata* (Archer) (140–180 μ)

The test is transparent and of variable shape. It is compressed, and characterized by the keel extending around the posterior end and (usually) about two-thirds of the way to the mouth. The plates forming the keel are a little smaller than those of the rest of the test. The keel of *N. carinata* is wider and longer than that of the similar species *N. marginata*.

10.9 *Nebela bigibbosa* Penard (135–170 μ)

The test of *N. bigibbosa* is yellowish, compressed and pear-shaped in broad view, with a slightly-curved mouth with lips of secretion. The species is recognized by the two pairs of large pores, each in a lateral depression about one-third of the distance from the mouth, and connecting with the corresponding pore on the opposite face by a tube through the thickness of the test. A small inconspicuous lateral pore is also present in each side wall at about the same level as the large pores.

This species occurs in fen *Sphagnum*.

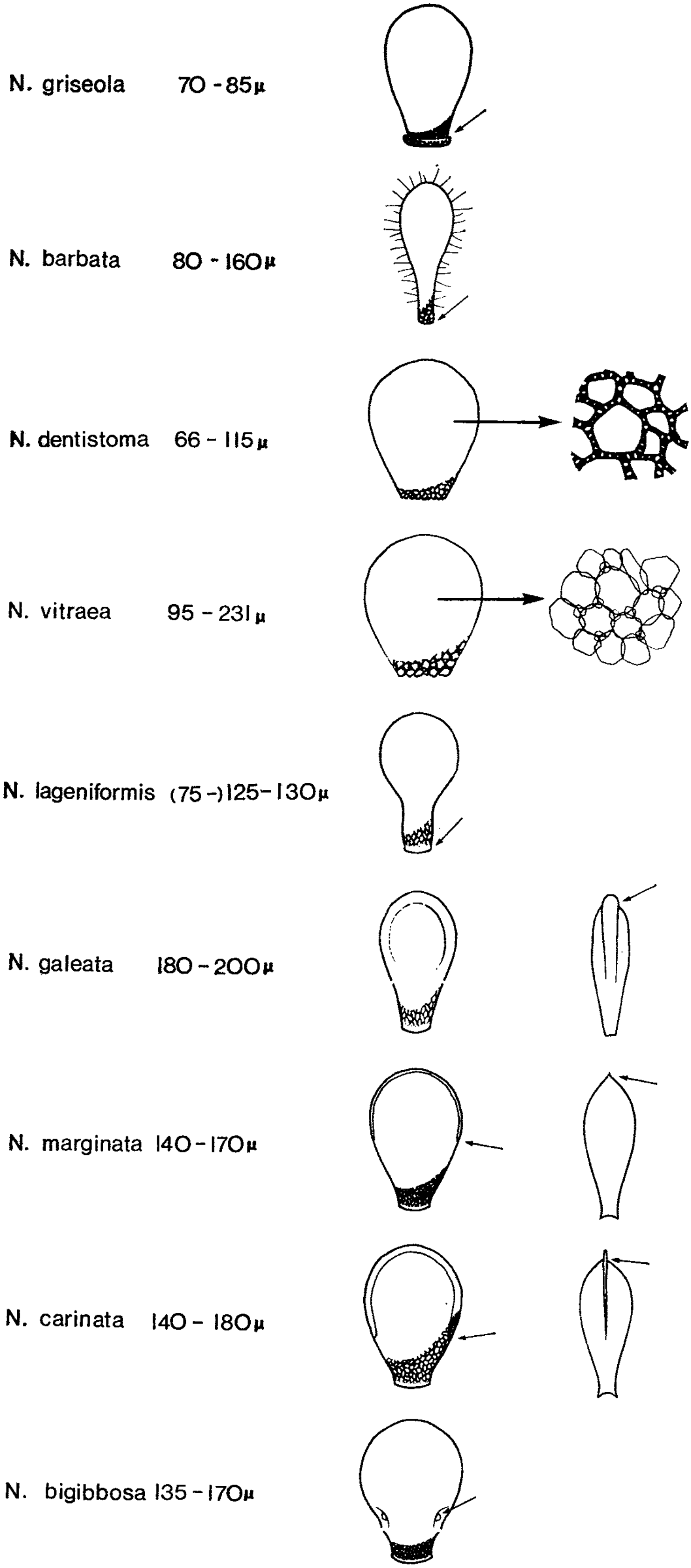


FIG. 3.
Some species of *Nebela* (after Deflandre, 1936).

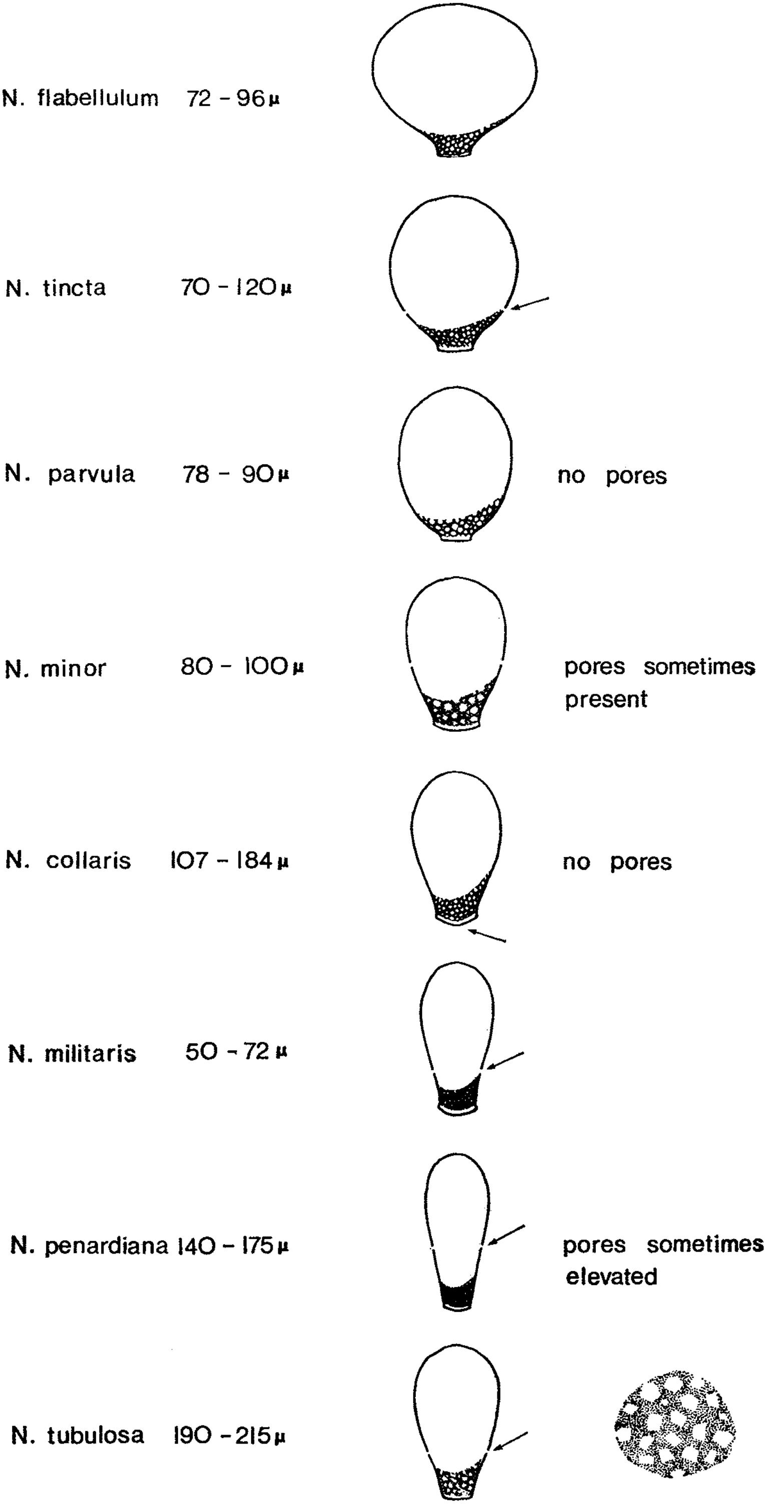

N. flabellulum 72 - 96μ
N. tincta 70 - 120μ
N. parvula 78 - 90μ
no pores
N. minor 80 - 100μ
pores sometimes present
N. collaris 107 - 184μ
no pores
N. militaris 50 - 72μ
N. penardiana 140 - 175μ
pores sometimes elevated
N. tubulosa 190 - 215μ

FIG. 3 cont.

10.10 *Nebela flabellulum* Leidy (72–96 μ) (Plate I, i)

The very transparent test consists of a neat mosaic of rounded plates in yellowish cement. It is slightly compressed and very broad, narrowing abruptly to a very short neck. The mouth, straight or very slightly curved, has an unthickened lip of secretion. A few other species occasionally produce forms in which, as here, the distance from side to side is greater than the distance from mouth to posterior end; but this species can be distinguished from them by the shape of the mouth and neck. It does not have lateral pores.

N. flabellulum occurs in *Sphagnum* in bog hummocks.

10.11 *Nebela tincta* (Leidy) (70–120 μ) (Plate I, j)

The test is very transparent and the plates are sometimes difficult to see. It is slightly compressed, and broad, tapering gently to a straight or slightly curved mouth. A pair of lateral pores is always present but sometimes inconspicuous.

N. tincta is common in *Sphagnum*, and is found more often in bogs than in fens.

10.12 *Nebela parvula* Cash (78–90 μ)

The test is slightly compressed and ovoid in broad view, tapering to a straight mouth with thin, smooth lips of secretion. Like *N. collaris*, this species is without lateral pores. It differs from *N. collaris* in its smaller size, more transparent test (composed of thin, irregular, polygonal plates) and in its less pear-shaped outline.

10.13 *Nebela minor* Penard (80–100 μ)

The test is pear-shaped and tapers gradually to a wide, rather curved mouth with a smooth, slightly thickened lip of secretion. *N. minor* can be distinguished from the similar *N. collaris* by its smaller size and its relatively broader mouth (and by the lateral pores which are occasionally present).

10.14 *Nebela collaris* (Ehrenberg) (107–184 μ)

N. collaris is variable, and several species have been included under this name in the past. The compressed test is pear-shaped, narrowing gradually to the broad, curved mouth which has thick lips of secretion. The curved mouth, together with the absence of lateral pores, distinguishes *N. collaris* from related species. The test is usually yellowish, and consists of a mosaic of rounded or elongate plates.

N. collaris is common in fen *Sphagnum*.

10.15 *Nebela militaris* Penard (50–72 μ) (Plate II, e)

This small species is easily recognized by its elongate shape, its strongly curved mouth with a well-differentiated lip, and its lateral pores, which are usually easy to see. The transparent test is composed of thin rounded plates, sometimes rather sparse, embedded in clear yellowish or pinkish cement.

N. militaris is common in the wet *Sphagnum* of bog hummocks, and at Malham it occurs widely on Tarn Moss.

10.16 *Nebela penardiana* Deflandre (140–175 μ)

The test is compressed and in broad view it is shaped like a long, narrow pear, the straight sides tapering gently towards a curved mouth with thickened lips of secretion. The lateral pores are sometimes accentuated by small deflections of the side walls.

The rounded plates often overlap one another, and the test is usually colourless and transparent, unlike that of *N. tubulosa* which is larger but a similar shape.

N. penardiana occurs in fen *Sphagnum.*

10.17 *Nebela tubulosa* Penard (190–215μ)

The large test of *N. tubulosa* is compressed and in broad view is shaped like an elongate pear. The mouth is slightly curved, with unthickened lips of secretion. The lateral pores are usually accentuated by small deflections of the side walls. The appearance of the test surface is distinctive: the irregular, polygonal or rounded plates are set some distance apart in thick, rough-surfaced cement which is coloured yellowish or brownish and is often darker towards the mouth.

Family Euglyphidae

(11) and (12) *Trinema* and *Corythion*

These two genera both include very small species with tests so transparent that their plates are often difficult or impossible to see unless a phase contrast microscope is available. The two genera are treated together here because to separate them it would be necessary to see whether the plates touch one another (*Trinema*) or not (*Corythion*).

Key

1	Mouth oblique or terminal	*Trinema lineare*
—	Test flattened, the mouth on the flat ventral surface	2
2	Plates circular, sometimes overlapping or surrounded by rings of dots	*Trinema enchelys*
—	Plates oval, never overlapping	*Corythion dubium*

11.1 *Trinema lineare* Penard (18–35μ) (Fig. 4)

This is a very variable species. Its test is always very small, colourless and transparent, and it looks clear because the plates are so difficult to see. The test is ovoid and not flattened. The mouth is usually obliquely set at one end, but its position varies and it is occasionally almost terminal. The edges of the mouth curve inwards.

Tests of *T. lineare* are very numerous in some samples of *Sphagnum*, but beginners often fail to see it. At Malham it is common on Tarn Moss.

11.2 and 12.1 *Trinema enchelys* (Ehrenberg) (usually 40–60μ)
and *Corythion dubium* Taránek (usually 30–45μ) (Plate II, f)

It is impossible to separate these two species unless one can see the plates. The tests of both are alike in shape; they are usually compressed, oval or nearly circular in broad view and often narrower at the anterior end. The mouth is circular or oval, on a flat surface, and its edges curve inwards.

The plates of *T. enchelys* are sometimes obvious. They are circular and regularly arranged, and sometimes those around the mouth are smaller than the others. Sometimes the plates overlap, and sometimes each one is surrounded by a ring of minute dots.

In *C. dubium* the plates are less often seen. They differ from those of *T. enchelys* in their oval shape and their irregular arrangement, and in the fact that they do not overlap.

Both *T. enchelys* and *C. dubium* are common in *Sphagnum*.

(13) *Sphenoderia*

13.1 *Sphenoderia lenta* Schlumberger (30–64μ) (Fig. 4)

The test of *Sphenoderia lenta* is small, colourless and transparent. It is ovoid or spherical, composed of rather large round or oval overlapping plates which are regularly arranged and usually easy to see. At the mouth is a transparent membranous collar which is flattened, so that the aperture would appear slit-shaped if one could look into the mouth from the anterior end. *Assulina muscorum*, which sometimes has a rather similar membranous collar, differs from *S. lenta* in the shape and colour of its test (Plate II) and in its more numerous, less regular plates.

S. lenta is found in fen *Sphagnum*.

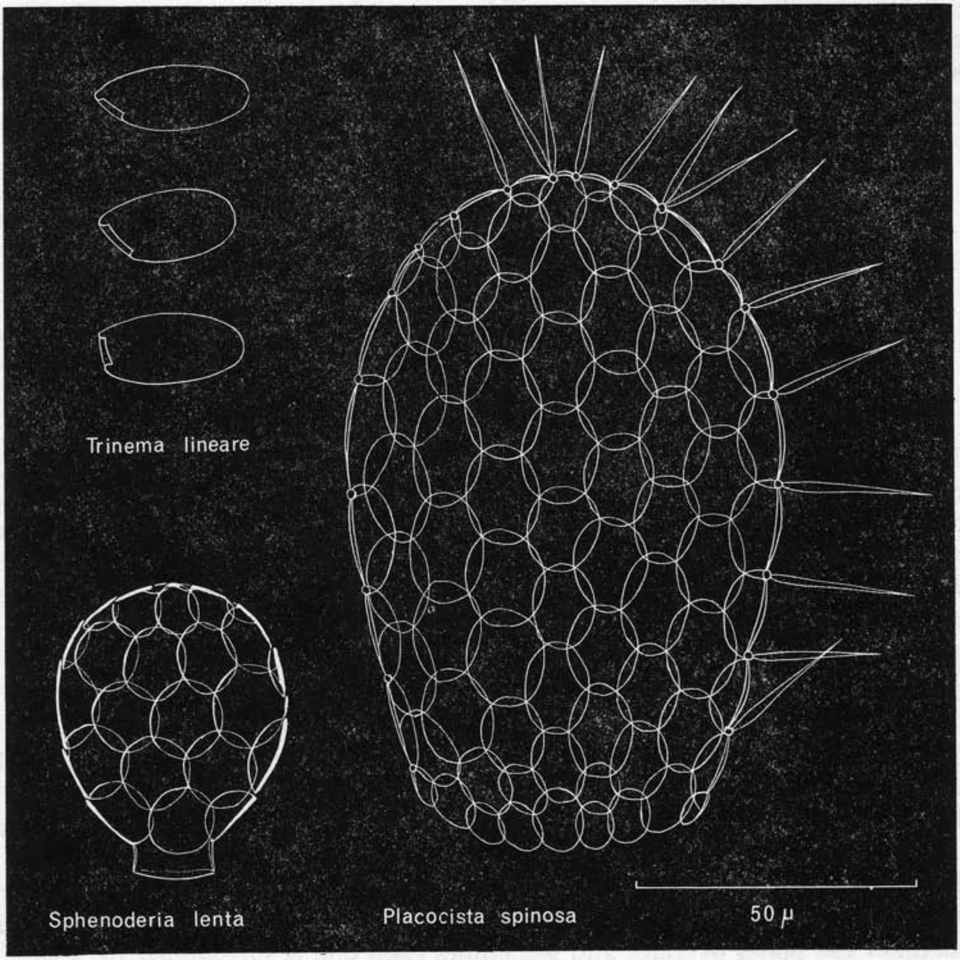


FIG. 4.

Sphenoderia lenta and *Trinema lineare* after Cash, Wailes and Hopkinson (1905–1921) and *Placocista spinosa* after Leidy (1879).

(14) *Placocista*

14.1 *Placocista spinosa* (Carter) (116–174μ) (Fig. 4)

The test is colourless, transparent and compressed. The mouth is terminal and has a straight or uneven border of secretion. The absence of special toothed plates at the mouth distinguishes *Placocista* from *Euglypha*, which is very like it in shape and structure of the test. The plates of *P. spinosa* are oval, overlapping, and regularly arranged in rows. The test is bordered by a row of flattened spines, often arranged in pairs. Zoochlorellae are often found in the cytoplasm.

P. spinosa is found in the *Sphagnum* of bog pools, where it inhabits the upper, green layer.

(15) *Assulina*

The test of *Assulina* is compressed and colourless or rich brown, with a terminal mouth bordered by a ragged membranous collar. The plates are neatly arranged in rows, sometimes with geometrical regularity.

Key

1	Larger species, 60–100μ or more	*A. seminulum* (15.1)
—	Smaller species, 28–58μ	*A. muscorum* (15.2)

15.1 *Assulina seminulum* (Ehrenberg) (60–90 (– 150) μ)

The test of *A. seminulum* is often colourless, or sometimes brown, and composed of geometrically regularly arranged overlapping oval plates. It differs from *A. muscorum* in its larger size and in its shape: *A. seminulum* nearly always has a relatively broader test than *A. muscorum.*

A. seminulum is found in bog hummocks.

15.2 *Assulina muscorum* Greeff (28–58μ) (Plate II, g)

A. muscorum is usually russet or red-brown, and rarely colourless. The small oval plates are arranged neatly in rows, often with occasional irregularities. The test is smaller and relatively narrower than that of *A. seminulum.*

A. muscorum is very common, occurring in both bog and fen *Sphagnum.*

(16) *Euglypha*

Members of the genus *Euglypha* are easily recognized by the transparent, colourless test with very regularly arranged rows of oval plates, and special toothed plates edging the terminal mouth. Because the tests are often very small and very transparent they are easily overlooked at first, and the plates may be difficult to see without a phase contrast microscope.

Several species of *Euglypha* are common in *Sphagnum*, and to be sure of their identification it is necessary to see whether the test is compressed or round in cross-section, and to have a head-on view of the mouth, to see whether its outline is circular or oval. Some species, such as *E. strigosa*, have a round mouth even though the test is compressed (Fig. 5).

Sometimes in the cytoplasm of living individuals one can see extra test-plates, probably destined for the daughter cell after division.

The genus *Euglypha* has been revised by Decloitre (1962).

Key

1	Test with a few stout spines, each consisting of a modified plate, pointing backwards at the posterior end	*E. acanthophora* (16.1)
—	Test with scattered thin articulated spines, or without spines	2
2	Test not compressed; without spines	*E. tuberculata* (16.2)
—	Test compressed, with or without spines	3
3	Mouth-scales thickened; test usually with spines	*E. strigosa* (16.3)
—	Mouth-scales not thickened	4
4	Mouth circular; smaller species (22–52 μ) without spines	*E. rotunda* (16.4)
—	Mouth oval; larger species, usually with spines	5
5	Spines robust, always confined to margin of test; test strongly compressed with sharply-angled margins; 70–132 μ	*E. compressa* (16.5)
—	Spines less robust, usually marginal but sometimes scattered over broad face of test; marginal angles less sharp; 40–90 μ	*E. ciliata* (16.6)

16.1 *Euglypha acanthophora* (Ehrenberg) (55–80 μ)

The distinctive spines make this species easy to recognize (Fig. 5). There are 3–7 of them, large and easily seen, consisting of prolongations of the plates of the test. They all originate separately near the posterior end and point backwards. The test is circular in cross-section, not compressed.

E. acanthophora occurs in fen *Sphagnum*.

16.2 *Euglypha tuberculata* Dujardin (45–100 μ)

E. tuberculata is recognized by its uncompressed, spineless test and by the shape of the plates, which are round or more broadly oval than those of the other species. The mouth is bordered by 8–12 finely-toothed plates.

E. tuberculata occurs in fen *Sphagnum*.

16.3 *Euglypha strigosa* (Ehrenberg) (45–100 μ)

E. strigosa is one of the commonest species in its genus. The test is compressed, and the mouth is circular, and bordered with 10–14 toothed plates which are noticeably thicker than those forming the rest of the test. Their thickness is best seen at each end of the mouth, where the mouth plates are seen edgeways on and can be compared with the thinner plates just posterior to them. *E. strigosa* usually bears slender transparent spines scattered over the surface of the test (or occasionally confined to its margins).

The thickened mouth scales distinguish *E. strigosa* from *E. rotunda* and *E. ciliata*, the two other common species with a compressed test. The circular mouth of *E. strigosa* is also a useful character in identification but is troublesome to see.

Heal (1961) found *E. strigosa* in both fens and bogs; it was particularly abundant in bog hummocks.

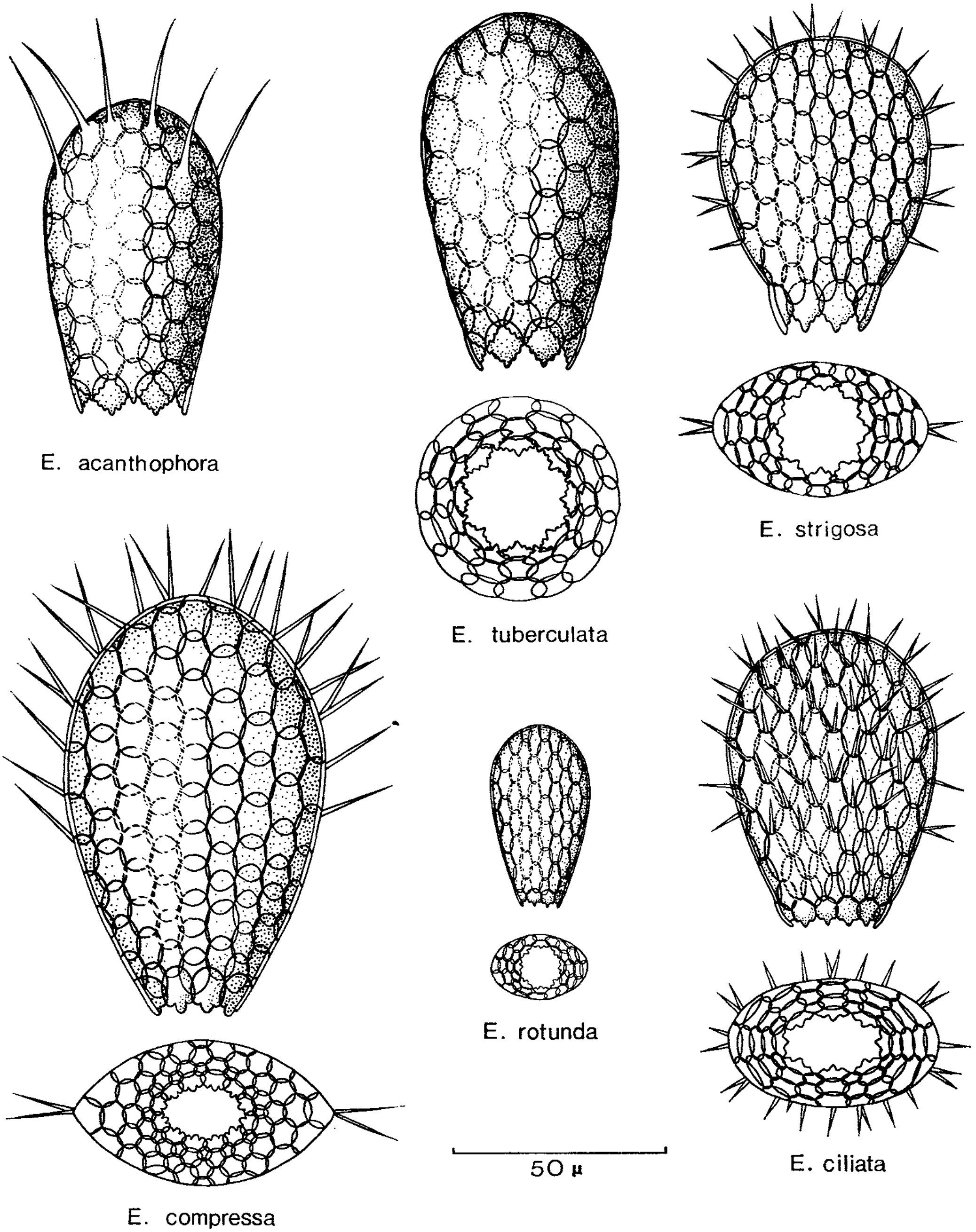


FIG. 5.

Side views and end views of some species of *Euglypha* (after Cash, Wailes and Hopkinson, 1905–1921). This form of *E. strigosa* has spines at the margins only; usually in this species the spines are scattered over the surface of the test.

16.4 *Euglypha rotunda* Wailes (22–52 μ)

E. rotunda is a small species with a compressed spineless test and a round mouth. It differs from spineless forms of *E. strigosa* in the plates of the mouth: there are only eight in *E. rotunda*, they are unthickened, and they are less complex. In *E. rotunda* the mouth plates have only one little tooth on each side of the point; in *E. strigosa* there may be two or three.

E. rotunda is common in fen *Sphagnum*.

16.5 *Euglypha compressa* Carter (70–132 μ)

The test is compressed, with rather sharply-angled margins, and the mouth is oval, edged with unthickened, bluntly-toothed plates. The plates of the test are oval and relatively large (9–12 μ long) and the spines, if present, are always confined to the margin and are robust, 5–35 μ long, often flattened and occasionally leaf-shaped.

E. compressa is often larger than *E. ciliata* and has larger plates and more robust spines. The angled margins of its test and the blunt teeth on the mouth plates also help to distinguish it.

16.6 *Euglypha ciliata* (Ehrenberg) (40–90 μ) (Plate II, h)

The test is compressed and elliptical in cross-section, and the oval mouth is bordered by 8–14 unthickened plates each with one or two teeth on each side of the point. The test usually bears slender transparent spines, 6–10 μ long, scattered over the surface, or, occasionally, confined to the margin.

E. ciliata is distinguished from *E. tuberculata* by its compressed test and from *E. strigosa* by its unthickened mouth plates. The rare spineless forms of *E. ciliata* usually differ from *E. rotunda* in their larger size and more elaborately toothed mouth plates, and can be distinguished with certainty by the oval shape of the mouth. *E. ciliata* can be distinguished from *E. compressa* by its more slender spines, often distributed over the broad faces of the test; by its smaller test plates; and by the rounded test margins, giving it an elliptical cross-section.

E. ciliata is common in fen *Sphagnum*.

Family Cyphoderiidae

(17) *Cyphoderia*

17.1 *Cyphoderia ampulla* (Ehrenberg) (usually 100–140 μ) (Plate II, i)

The test is a characteristic shape, round in cross-section and elongate, with the terminal mouth set obliquely on a curved neck. The test is yellowish or colourless, translucent, and consists of a thin membrane on which round or oval plates are regularly arranged in diagonal rows, usually touching but never overlapping. These plates are small and hard to see and the test gives the impression of being finely cross-hatched.

C. ampulla (with the very similar *C. trochus*, which has overlapping plates) is common in fen *Sphagnum*.

Family Amphitremidae

(18) *Amphitrema*

The test is compressed, oval, with a small mouth at each end. It is transparent, consisting of clear secretion, and in some species particles are stuck to it. The cytoplasm usually contains zoochlorellae.

Key

1	Test brownish, without particles	*A. flavum* (18.1)
—	Test colourless, with foreign particles stuck to it	2
2	Test drawn out into a short tube-like collar at each mouth	*A. wrightianum* (18.2)
—	Mouths without collars	*A. stenostoma* (18.3)

18.1 *Amphitrema flavum* (Archer) (45–77 μ) (Plate II, j)

The small, almost rectangular, amber-brown tests of *A. flavum* are easily recognized by the presence of two mouths. It is a common species in bog *Sphagnum*, particularly in the wetter parts of hummocks. At Malham it occurs just south of Spiggot Hill. Heal (1962) has shown that living individuals are commoner in the upper parts of *Sphagnum* than they are in the deeper regions, as would be expected for a species with zoochlorellae that depend on light for photosynthesis. Further, the zoochlorellae were darker green in specimens from the top of the *Sphagnum* than they were in specimens taken from deeper down.

18.2 *Amphitrema wrightianum* Archer (50–95 μ)

The test of *A. wrightianum* is compressed and oval, with shoulders that slope more gently than those of *A. flavum*. At each end is a small mouth with a short but distinct collar. The colourless test is often almost hidden by the mineral particles and diatom frustules that are stuck to it. These may obscure the collar, in which case it is difficult to distinguish this species from the collarless species *A. stenostoma*.

Heal (1961) treated *A. wrightianum* and *A. stenostoma* together, and found them less abundant than *A. flavum*, occurring in bog pools. They were found at intermediate depths in the *Sphagnum* (Heal, 1962).

18.3 *Amphitrema stenostoma* Nuesslin (usually 45–97 μ)

A. stenostoma is very like *A. wrightianum* and they are often found together. *A. stenostoma* is distinguished from *A. wrightianum* by the absence of any collar around the mouths. When the mouth region is thickly clothed with foreign particles this difference may not be visible and the two species cannot be separated without clearing away the particles.

Ecology

The study of the self-contained ecosystem of a *Sphagnum* plant has some of the advantages of a visit to another inhabited planet; it enables one to appreciate ecological principles which are obscured by familiarity in the macroscopic world we know.

Size

One of these principles is the importance of size. On a *Sphagnum* plant the moisture is held within the cells and between the leaves, and although some very tiny flagellates can enter the cells, most species inhabit the water between the leaves and in their inrolled tips. The observed association of larger testate rhizopods with wetter *Sphagnum* (Heal, 1963) is probably due to the larger space available in a thicker water film, and will be discussed later in connection with "moisture" (page 832).

Figure 6 shows the size of some animals found in a species of *Sphagnum* in which the leaf surfaces were about 400 μ apart. It is clear that this space was quite large enough for most protozoans, but rather small for metazoans; although many metazoan species were present most of them were near this maximum convenient size, and the great majority of very tiny species were Protozoa.

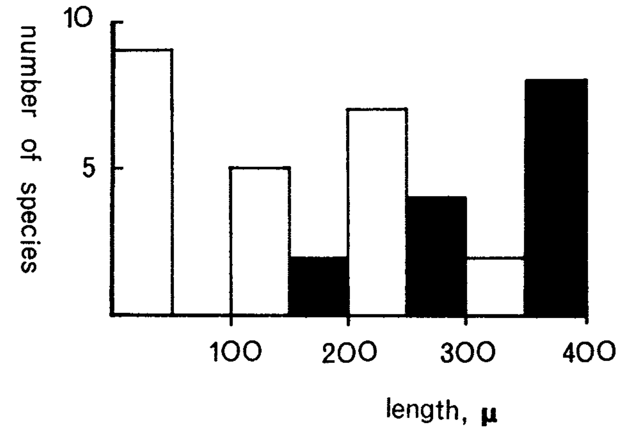


FIG. 6.

Length-frequency histogram for the species of protozoans (white blocks) and metazoans (black blocks) in a sample of *Sphagnum* from the Lake District.

Food

Protozoans can feed on metazoans. It is not unusual to find rotifers in the food vacuoles of various types of amoebae. Clearly there are limits to the size of prey that any given form can engulf, and if the predator is encased in an inelastic cuticle or test these limits are particularly strict. Testate rhizopods usually have wide enough mouths to permit their pseudopodia to withdraw inside, carrying protozoan or algal cells. An obvious exception is the genus *Amphitrema* (Plate II, j), in which the mouth at each end of the test is seldom more than 10 μ in diameter. But *Amphitrema* has another feeding method. Food vacuoles are not seen in the cytoplasm of *A. flavum*, and it apparently relies solely on its zoochlorellae (Schönborn, 1963).

An alternative to engulfing the prey whole is to break open its cells and simply suck in the contents. This can be done by forms with the right tools for the job: tardigrades, nematodes and mites all have stylets with which they can penetrate and suck the contents from algal or animal cells, thus feeding on organisms too large for them to swallow. That is an important adaptation in a habitat where the possible size range is so small, and the primary consumers cannot be much larger than the primary producers.

The community of organisms living on *Sphagnum* is remarkably self-sufficient, in that it depends relatively little on materials imported from outside. Its primary producers, most of them unicellular green algae, live in the film of water or as symbionts in the cytoplasm of protozoans. Among the many groups of animals living here the testate rhizopods are important both as primary and secondary consumers: they feed on the algal cells, on other animals or on each other, alive or dead, and some of the smaller forms (such as *Corythion*, *Trinema* and *Euglypha*) probably feed mainly on bacteria. Most testate rhizopods are transparent and it is sometimes possible to recognize the food that they have eaten from the remains in their cytoplasm.

Test construction

The community of organisms living on *Sphagnum* seems to require only light, carbon dioxide, oxygen and water from outside the system. But the importation of materials from outside is clearly essential for test construction. Some of the rhizopods derive the materials for their tests from the organisms on which they feed: *Nebela* uses the plates of *Euglypha*, and both *Nebela* and *Difflugia* sometimes incorporate diatom frustules into their tests. Fragments of dead *Sphagnum*, too, are often used as test material. The mineral particles that are so important in the tests of *Difflugia*, *Heleopera* and *Centropyxis* must be derived ultimately from airborne dust or material brought by inflowing water.

Microclimate

The physical and chemical microclimate within a *Sphagnum* carpet is unique, and the unusual assemblage of animals living there belong to groups that can tolerate this peculiar, often extreme, environment. Conditions may fluctuate sharply through space and time, and the distribution of living individuals of the various species of rhizopods often shows a close correlation with them.

Temperature

The surface temperature of a *Sphagnum* carpet fluctuates widely during a 24-hour period. By day the surface becomes very hot, heated by radiation more than enough to compensate for the heat lost by evaporation from the wet surface. But *Sphagnum* is a poor conductor of heat; the temperature of the lower layers changes much more slowly and by the middle of a sunny day a steep temperature gradient is found in the top 10 cm. (Fig. 7). In the late afternoon the intensity of the radiation falling on the surface decreases. The surface cools sooner than the deeper layers and the temperature gradient is reversed: the surface is cooler than the deeper layers. Nørgaard's 24-hour series of temperature profiles for a Danish *Sphagnum* bog (Fig. 8) shows very clearly how the temperature 10 cm. below the surface varies little (18–22 °C. in this instance) while the surface is hotter by day (41 °C.) and cooler by night (7 °C.) (Nørgaard, 1951). These extreme surface temperatures may make that region uninhabitable for some species of rhizopods. But the temperature gradients are steep, and a few millimetres down the climate will be less extreme. The effects of these ephemeral changes of temperature on the fauna are difficult to analyse and poorly understood. The abrupt change of temperature with depth may be matched by horizontal variations. These very high surface temperatures were measured in patches of *Sphagnum* in full sunlight; shaded areas would be cooler. Popp (1962) has shown that the daily march of temperature change on the south face of a *Sphagnum* hummock is very different from that on the north face.

Moisture

The moisture content of *Sphagnum* is important in determining the distribution and condition of testate rhizopods. Some *Sphagnum* plants are totally submerged in bog pools. From this extreme the wetness varies through those bordering the pool to the plants on bog hummocks, well above water level, in which the fauna is confined to the film of water on the plant. Occasionally the plants dry out completely, becoming white and papery. When this happens the *Sphagnum* dies and its rhizopods can presumably only survive by encysting or migrating down to wetter layers. Little is known about the possible vertical migration of testate rhizopods, but encystment is a common phenomenon. Heal (1962) has shown that in *Hyalosphenia papilio* and *Nebela tincta* the vertical distribution of cysts is the same as that of unencysted living individuals, which indicates that these species respond to adverse conditions by encysting rather than by migrating.

The few centimetres between a bog pool and a hummock may separate microhabitats that differ widely in the wetness of their *Sphagnum*. The small-scale distribu-

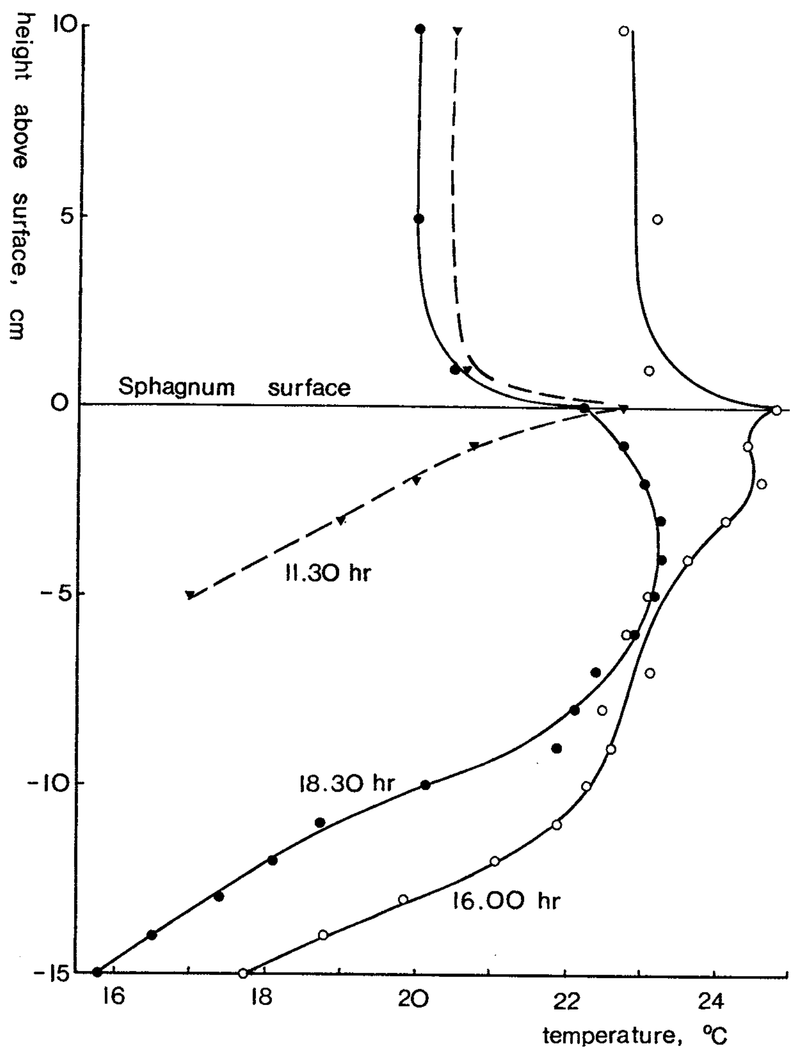


FIG. 7.

Temperature profiles across the surface of *Sphagnum* on Tarn Moss, measured with a thermocouple at 11.30 a.m., 4 p.m. and 6.30 p.m. B.S.T., on a sunny day in July 1972.

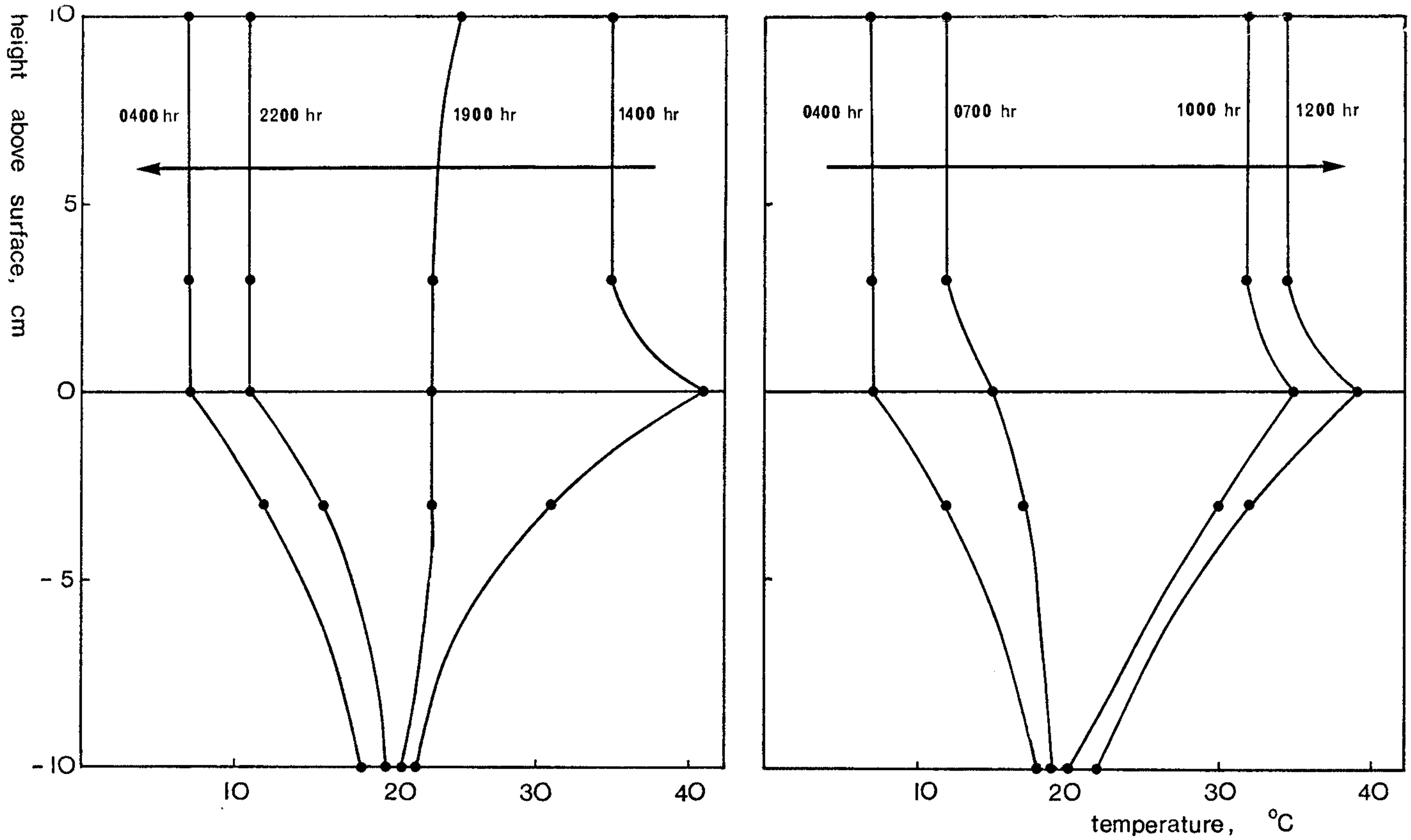


Fig. 8.

Temperature profiles across the surface of a Danish *Sphagnum* bog, taken at intervals through a 24-hour period (after Nørgaard, 1951). The surface cooled during the afternoon and night (left-hand diagram) and warmed up during the morning (right-hand diagram).

tion of several species of testate rhizopods is so closely correlated with the wetness of their habitat that they can be classified on this basis as:

hydrophiles: inhabiting plants submerged in water;

hygrophiles: living in moist plants;

and xerophiles: living in relatively dry habitats.

Xerophiles are typically found in such periodically dry habitats as tufts of moss on walls and trees, but many xerophiles also occur in *Sphagnum*. The xerophile testacean fauna of *Sphagnum* hummocks resembles that of humus soils, where living space is similarly restricted.

The biological features associated with these different situations have been little studied. Xerophiles must withstand desiccation: they can be expected to be capable of encysting; many of them have small mouths, often on the flat side of the test (so that as they move forward the water film distorts to accommodate them) (Grospietsch, 1965); they are usually small species, able to survive in the thin film of water on drying moss. Hygrophiles will be subjected to desiccation less frequently and will normally inhabit an ample water film in which the tests can be spiny and can be carried upright without distorting the meniscus. Such species are typically larger than xerophiles although species in *Sphagnum* must still be small enough to inhabit the space between the leaves; unless the plants are submerged the space outside the leaves is not accessible to them. In such species the nutritional advantages of a large mouth to the test may outweigh the risk of losing water through it during dry periods. In hydrophiles, inhabiting free water, encystment will probably be less common and species that engulf their food can afford to have large mouths. They are not limited to the water film on the *Sphagnum* leaves, and it is in very wet habitats that the largest species are found (Heal, 1963).

Bonnet (1958) suggested that the vertical distribution of testate rhizopods reflected their horizontal distribution with respect to this ecological classification: xerophiles were found in the *Sphagnum* heads, the region most liable to dry up, and hydrophiles in the deeper layers that are always wet. This hypothesis was examined by Heal (1962), who found many species that did not conform with it. He found the xerophile *Assulina muscorum* to be commonest near the tops of the plants and the hygrophile *Nebela dentistoma* commonest at the bottom, as Bonnet had done. But the main species that Heal found near the top were the hygrophiles or hydrophiles *Amphitrema flavum* and *Hyalosphenia papilio*. The xerophiles *Bullinularia indica*, *Trigonopyxis arcula*, *Euglypha strigosa*, *Nebela militaris* and *Heleopera sylvatica* were restricted to regions lower on the plant. Clearly other factors are important in the distribution of these species, as Heal was able to show.

Light

The *Sphagnum* heads, packed close together, intercept most of the light; light intensity falls off steeply with depth (Fig. 9), and the region light enough for photosynthesis is only a few centimetres deep. Except in submerged *Sphagnum* the upper, green layer is poor in the detritus on which most testate rhizopods can be seen to feed, and it is only those species that can derive nourishment from their symbiotic zoochlorellae that are found at this level: *Hyalosphenia papilio*, *Placocista spinosa*, *Heleopera sphagni*, *Amphitrema flavum* and *A. stenostoma* (Schönborn, 1963). All of these species have rather transparent tests. *Amphitrema flavum* is exceptional in that food particles have not been found in its cytoplasm. Whereas the other species supplement their diets by eating detritus, *A. flavum* seems to rely entirely on its symbionts.

Most species of rhizopods live deeper down, where the decomposition of the dead *Sphagnum* gives rise to detritus on which they can feed (Schönborn, 1963), mineral particles are available for test construction (Heal, 1962), the temperature is more equable and drought is less frequent. Heal (1962) found that *Amphitrema wrightianum* (with which he included some *A. stenostoma*), although it contains zoochlorellae, occurred in its greatest numbers a few cm. below the surface (Fig. 10). *A. wrightianum* and *A. stenostoma*, unlike *A. flavum*, have particles on their tests, and Heal interprets their vertical distribution as a compromise between the requirement for light, maximal at the surface, and particles for test construction, most abundant at depth. Schönborn (1965) was able to trace the digestion of their zoochlorellae by *Hyalosphenia papilio*, *Heleopera sphagni* and *Amphitrema flavum*, by staining these rhizopods with neutral red. He showed, too, that these rhizopods were so closely dependent on their symbionts that they died out when their habitat was artificially darkened with a wooden cover.

Oxygen

Although measurements are not available it is clear that the concentration of oxygen must show a steep vertical gradient. At the surface the water will be in equilibrium with air and perhaps locally supersaturated with oxygen when the

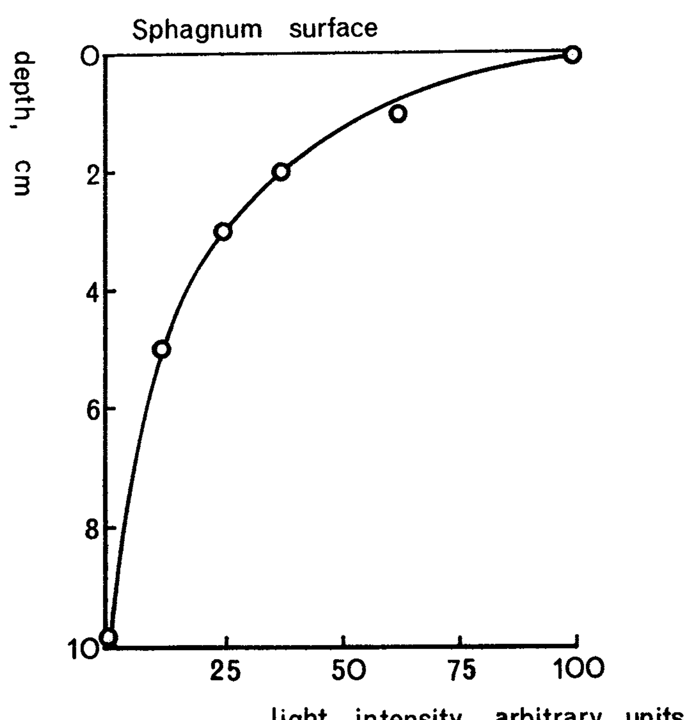


FIG. 9.

The change of light intensity with depth in *Sphagnum* carpet on Tarn Moss, measured with a Griffin Environmental Comparator.

Sphagnum is photosynthesizing. In the compact mass of dead *Sphagnum* about 20 cm. down, where living testaceans are absent but their empty tests are abundant, there must be very little free oxygen. There is no photosynthesis here and oxygen can only reach this region from above by diffusion, a process that is very much slower in water than it is in air. Below the water level bacteria and fungi use up the oxygen before it can penetrate far. The shortage of oxygen may limit the depth at which aerobic species can live.

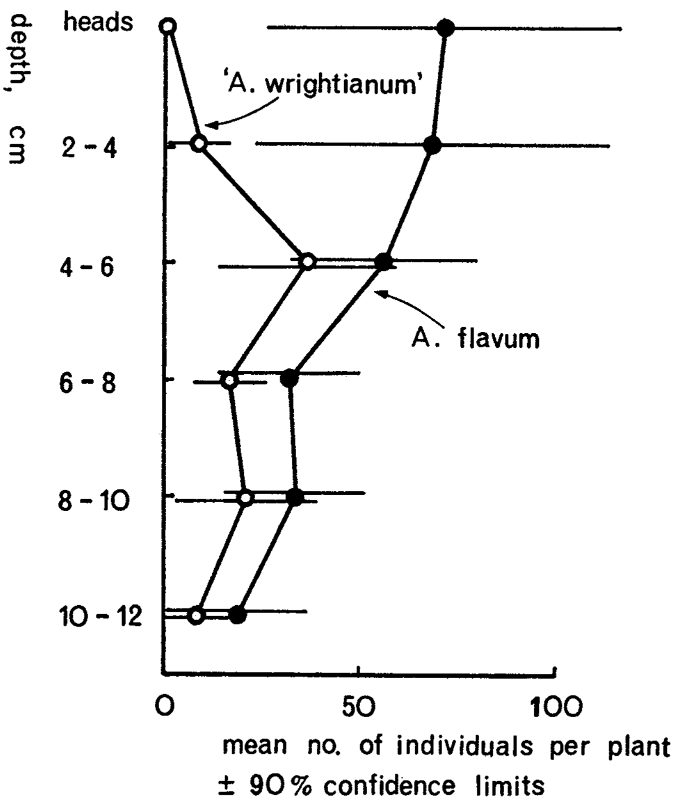


FIG. 10.

The vertical distribution in *Sphagnum* of living individuals of *Amphitrema flavum* and of "*A. wrightianum*" (with some *A. stenostoma*) (after Heal, 1962).

pH

Sphagnum bogs are often very acid, commonly with a pH between 3·2 and 4·6 (Heal, 1961). Many protozoans cannot survive in such conditions and even among the testate rhizopods many species are found only in more alkaline habitats. In a survey of the testate rhizopods in a variety of habitats in northern England Heal (1961) found an association of about 25 species characteristic of fen areas (pH greater than 5), about 16 species characteristic of bog pools or hummocks (pH 3·2 to 4·6) and a further 13 "eurytope" species (occurring in both bogs and fens). pH, as well as water content, may influence the small-scale distribution of species when (as sometimes happens) acid hummocks emerge from alkaline flushes.

Distribution patterns

An ecological classification that may well prove to be of wide application results from Schönborn's (1963) study of the testate rhizopods in a *Sphagnum* moor in Brandenburg. His integration of vertical and horizontal distribution patterns is expressed diagrammatically in Figure 11. Schönborn considered water content and light as the two factors of overriding importance in governing the distribution of testate rhizopods. He recognized two vertical zones inhabited by living testaceans, an upper horizon, including the green part of the *Sphagnum*, and a middle horizon

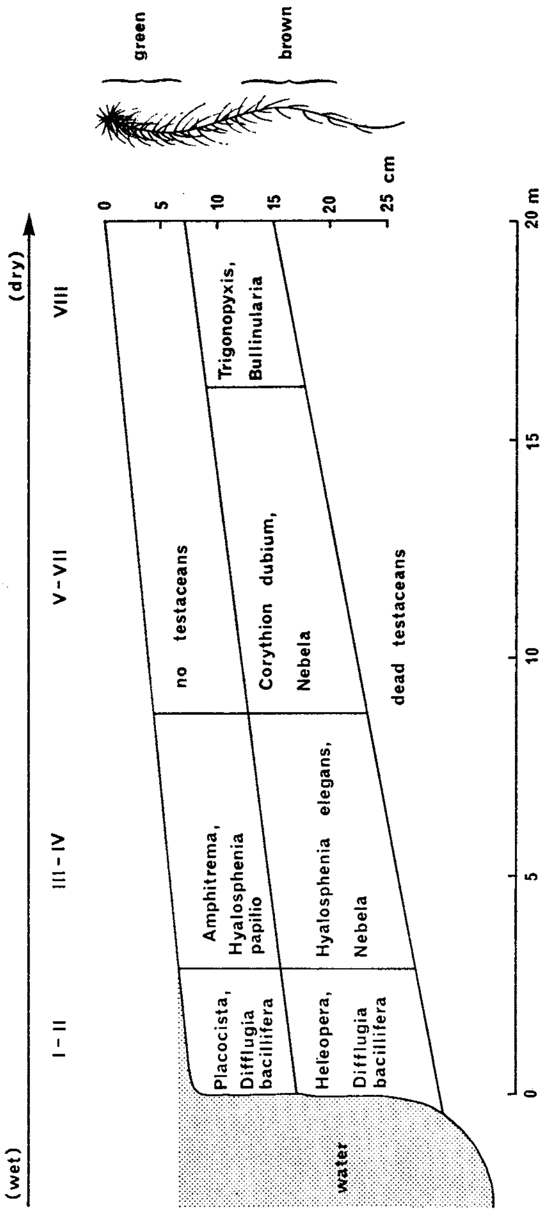


Fig. 11.

A diagram showing the distribution of associations of living testate rhizopods in a *Sphagnum* bog (after Schönborn, 1963). The associations are named after the characteristic species (which are not necessarily the commonest).

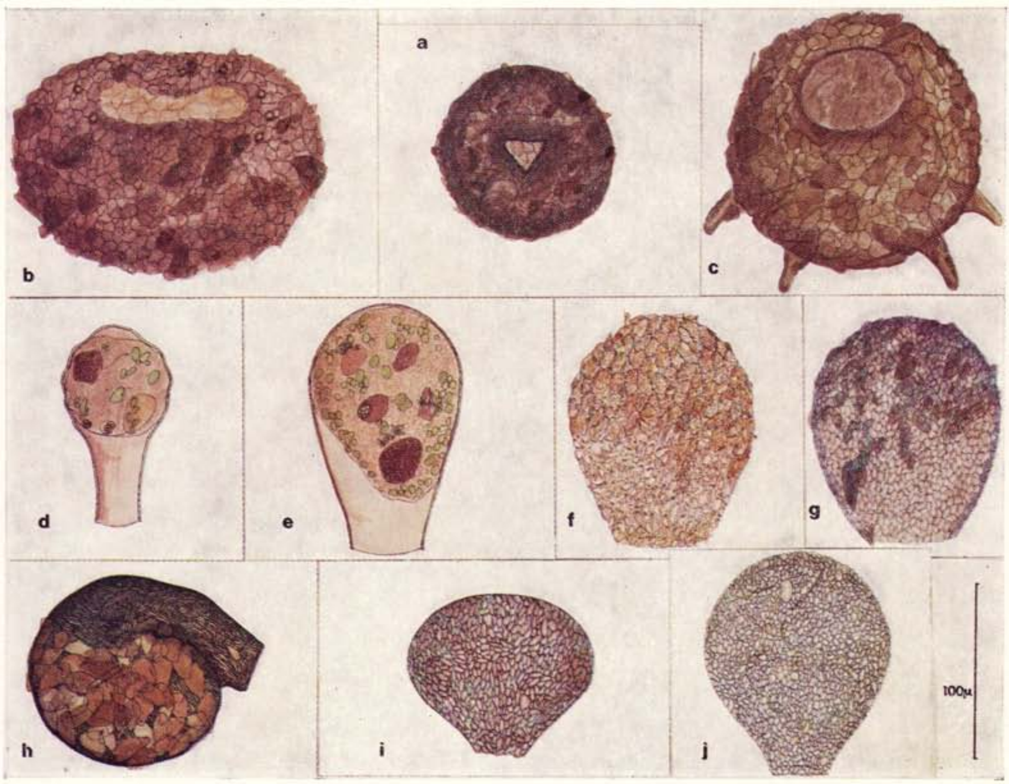
where the *Sphagnum* is brown and decomposing. The lower horizon contains the empty tests of all species. The rhizopod communities also vary horizontally and Schönborn recognized four types of community associated with different degrees of wetness, from submerged or floating *Sphagnum* (which he called I and II) to the *Sphagnum* on the crown of the moor (VIII). The submerged *Sphagnum* is clothed with a rich growth of microscopic organisms and both upper and middle horizons there have rich testacean faunas. In the upper horizon where photosynthesis is possible live species with zoochlorellae (*Placocista spinosa*, *Hyalosphenia papilio*), together with species without symbionts such as *Difflugia bacillifera* and *Nebela carinata* (Table).

Table. *The distribution of the commoner testate rhizopods in the upper and middle horizons of a* Sphagnum *bog in relation to the wetness of the habitat* (*from Schönborn, 1963*). *See Figure 11.*

Wet		Dry	
I–II	III–IV	V–VII	VIII
UPPER HORIZON: *Placocista spinosa* *Difflugia bacillifera* Hyalosphenia papilio Difflugia globulosa Nebela carinata Arcella catinus Arcella discoides Centropyxis spp. Euglypha compressa	*Amphitrema flavum* *Amphitrema stenostoma* *Hyalosphenia papilio* Heleopera sphagni Centropyxis sp.		
MIDDLE HORIZON: *Heleopera petricola* *Difflugia bacillifera* Difflugia globulosa Nebela carinata Arcella catinus Arcella discoides Centropyxis spp. Euglypha compressa	*Hyalosphenia elegans* *Nebela* collaris Nebela tincta Nebela militaris Nebela minor Arcella catinus Centropyxis sp. Assulina muscorum Assulina seminulum	*Corythion dubium* *Nebela* collaris Nebela tincta Nebela militaris Bullinularia indica Arcella catinus Euglypha compressa Assulina muscorum	*Trigonopyxis arcula* *Bullinularia indica* Centropyxis sp. Phryganella hemisphaerica Euglypha compressa Assulina muscorum

The middle horizon supports a fauna that differs mainly in the absence of the zoochlorella-bearing species. In drier regions the difference between the two horizons is more marked. Here the upper horizon is without the detritus, resulting from the decomposition of *Sphagnum*, that forms a major food source for species in the middle horizon. The only species important in the upper horizon are those with zoochlorellae: *Hyalosphenia papilio*, *Heleopera sphagni*, *Amphitrema flavum* and *A. stenostoma*. These are confined to rather wet areas, and in the driest areas (V–VII, VIII) the upper horizon (no doubt subject to extreme fluctuations in temperature and moisture content) is without testaceans. The middle horizon in wet *Sphagnum* (III–IV) has a rich fauna in which *Hyalosphenia elegans* and species of *Nebela* (*N. collaris*, *N. tincta*, *N. militaris* and *N. minor*) are characteristic. In drier areas (V–VII) the middle horizon is without *H. elegans*, but most of the species of *Nebela* (*N. collaris*, *N. tincta*, *N. militaris*) persist and in addition *Corythion dubium* is abundant. The middle horizon at the peak of the moor (VIII) has a poorer fauna characterized by the xerophiles *Trigonopyxis arcula* and *Bullinularia indica*.

Because of competition between co-existing species with similar ecological require-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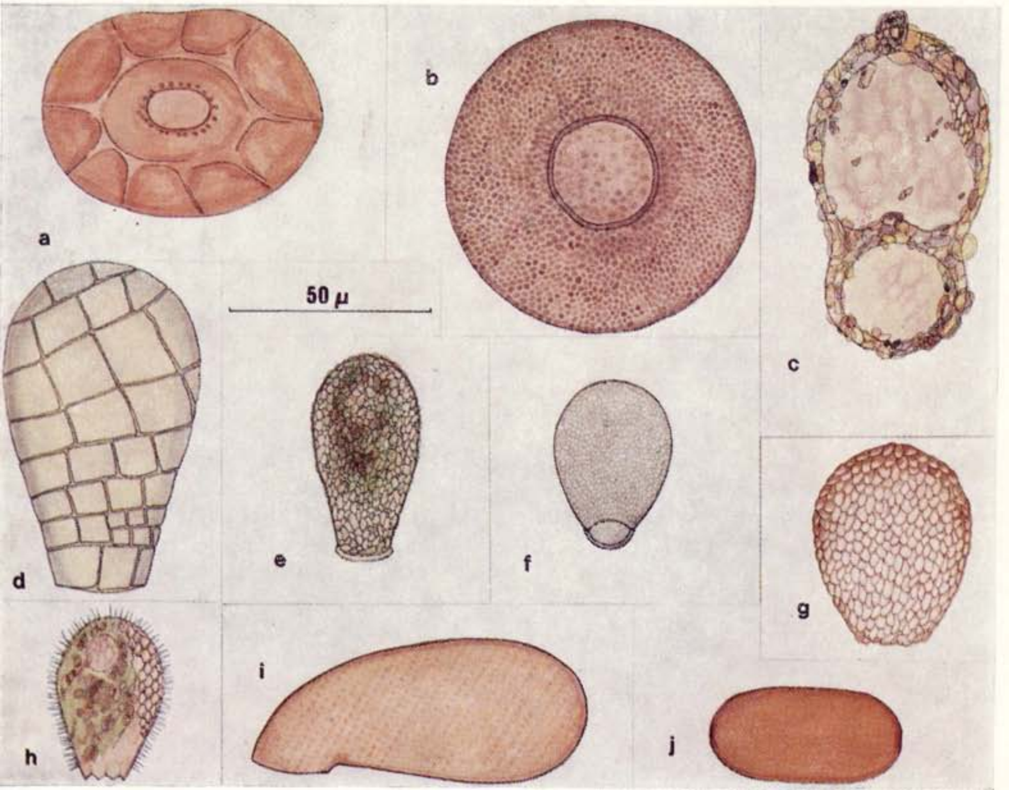
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PLATE I

(a) *Trigonopyxis arcula* (Leidy).
(b) *Bullinularia indica* Penard.
(c) *Centropyxis aculeata* (Ehrenberg).
(d) *Hyalosphenia elegans* Leidy.
(e) *Hyalosphenia papilio* Leidy.
(f) *Heleopera rosea* Penard.
(g) *Heleopera petricola* Leidy.
(h) *Lesquereusia spiralis* (Ehrenberg) Bütschli.
(i) *Nebela flabellulum* Leidy.
(j) *Nebela tincta* (Leidy) (a large form).

PLATE II

(a) *Arcella catinus* Penard.
(b) *Arcella discoides* Ehrenberg.
(c) *Centropyxis aerophila* Deflandre (a member of the "*Centropyxis cassis* group")
(d) *Quadrulella symmetrica* (Wallich).
(e) *Nebela militaris* Penard.
(f) *Corythion dubium* Taranek.
(g) *Assulina muscorum* Greeff.
(h) *Euglypha ciliata* (Ehrenberg).
(i) *Cyphoderia ampulla* (Ehrenberg).
(j) *Amphitrema flavum* (Archer).

ments there are likely to be ecological differences between the species within any genus and this may be reflected in differences in their distribution. Schönborn found *Hyalosphenia papilio* in the upper horizon and *H. elegans* in the middle horizon, and a similar vertical separation in the genus *Heleopera* between *H. sphagni* and *H. petricola*. Although he found both *Amphitrema flavum* and *A. stenostoma* in the upper horizon, Heal's more detailed analysis revealed that *A. wrightianum*/*A. stenostoma* reached its maximum density a few centimetres below that of *A. flavum* (Fig. 10). In the genus *Nebela*, *N. carinata* is separated horizontally from *N. collaris*, *N. tincta*, *N. militaris* and *N. minor* by its requirement for wetter *Sphagnum* (Schönborn, 1963), and Heal's (1961) study shows differences in distribution in relation to pH between *N. tincta* (a eurytope species), *N. militaris* (a bog hummock species) and *N. collaris* (a fen species, but the victim of taxonomic uncertainty). A disparity in size, as for instance between *N. militaris* and *N. tincta*, probably reduces the intensity of competition between them where they occur together.

Further studies

Little work has been done on testate rhizopods in Britain and there is great scope for research. A habitat classification like Schönborn's does not seem to have been attempted elsewhere, although Heal (1961) has shown that regions of different pH support different species of testate rhizopods. The problems of diurnal and seasonal changes in distribution have received little attention although Nørgaard's measurements of temperature indicate that only by vertical migration could a species remain warm but not too hot throughout a 24-hour period. Grospietsch (1965) demonstrated that the analysis of the subfossil tests of rhizopods in peat can provide a valuable supplement to pollen analysis in the study of past climates.

Much can be learnt about the habitat distribution of testate rhizopods, not only in *Sphagnum* but also in other habitats such as the soil or the surface of mud in ponds, where some of the sphagnicolous species are also found. In *Sphagnum* one can look at the distribution of species (and of test size and form) in relation to the vertical horizons or to the water content of bog pools, lawns and hummocks.

Quantitative studies require no special apparatus other than a good microscope, a pair of scissors and a ruler. The estimation of absolute numbers of testate rhizopods is beset with technical and philosophical impediments, but it is possible to estimate the percentage composition of a fauna quite simply by counting the numbers of each species in a sample, of, say, 100 living animals. The results cannot quantify such phenomena as the virtual absence of testate rhizopods from the upper horizon in the drier regions of a moor, but, with appropriate reservations, the percentage composition of a fauna can tell one almost as much about it as estimates of absolute numbers.

It can be very rewarding to watch active living animals in *Sphagnum* squeezings that have been allowed to settle undisturbed for several hours in a dish under a binocular microscope. If the animals are seen in action such ideas as trophic relationships and the adaptation of form to habitat may emerge as practical realities instead of theoretical concepts.

Acknowledgements

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