AN ATLAS OF FRESHWATER TESTATE AMOEBAE

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Introduction

The term 'testate amoebae' is given to those amoebid protozoa (Protozoa: Sarcodina: Rhizopodea) in which the cytoplasm is enclosed within a discrete shell or test, and which extrude filose pseudopodia. Testate amoebae, also known as thecamoebae, are present in a wide range of moist and freshwater habitats from moss, soil, peat, and standing water to sewage-treatment works. They are most commonly found in any moist situation where there are mosses, even occurring above ground level on the barks of trees and on the roofs of buildings. This handbook is intended as a field and laboratory guide to the common British species. As an aid to identification details of the structure of the shell are provided together with brief reviews of the biology and ecology of these animals. A classification is also included. At present there are more than one hundred and fifty species recorded from the British Isles, of which about two-thirds are illustrated in this Atlas using scanning electron micrographs. The micrographs are shown at magnifications within the range of most optical microscopes and consequently will be of value to investigators who do not have access to electron microscopes.

The species illustrated in this handbook were collected from several localities in southern England, particularly Cranes Moor and Mately Bog in Hampshire. The majority of the specimens studied were wild material obtained from *Spagnum* mosses, others came from clonal cultures of several species which are maintained for study purposes in this laboratory. A number of these cultures have already been used for more detailed biological investigations (Hedley & Ogden, 1973, 1974*a*; Hedley *et al.*, 1974, 1977) and samples have been deposited at the Culture Centre of Algae and Protozoa, The Natural Environmental Research Council, Cambridge. Extensive use was also made of the collection of testate amoebae, many of which were identified by Penard (see below), available for reference in the Department of Zoology, British Museum (Natural History).

Monographs have been published on the Rhizopoda of North America by Leidy (1879), and of central Europe—particularly Switzerland—by Penard (1890, 1902). Mr James Cash initiated a similar work to cover the British fauna and five volumes dealing with British Rhizopoda and Heliozoa were published between 1905 and 1921 by the Ray Society, London. Following Cash's death in 1909, the three remaining volumes were completed by Mr G. H. Wailes and Cash's assistant, Mr J. Hopkinson. The works of Leidy, Penard and Cash *et al.*, contain many excellent descriptions and illustrations, the detail of which is remarkable considering that they were working close to the limit of the resolving power of the optical microscopes

available to them at that time. Since the majority of testate amoebae appear to be cosmopolitan, these monographs have become standard reference works. In this Atlas we have sought to complement the comprehensive bibliographies provided by Cash *et al.*, by listing only the more recent references to the literature.

With the development of the scanning electron microscope it is now possible to examine the surface features of testate amoebae, which range in size between 20 and 400 μm, in greater detail at both low and high magnifications with increased resolution and depth of field. Other studies using transmission electron microscopy on sectioned material provide additional information on the cellular organisation and structure of these protozoa. The addition of energy dispersive X-ray analytical equipment to these microscopes, allows qualitative elemental analyses to be made of the shell structures.

Specimens for examination by scanning electron microscopy are first cleaned individually by transference through distilled water using a single-hair brush. Next, each is placed on a small drop of Araldite on a cover slip previously cleaned with acetone and lint-free tissue. The prepared cover slip can then be mounted on a stub with either an electrically conductive paint (Silver Dag) or Araldite, and coated evenly with gold in a vacuum coating unit. The photomicrographs reproduced in this Atlas were obtained from an examination of these stubs using a Cambridge Stereoscan Mk II operating at 10 kV, and were recorded on Ilford HP4 film.

We wish to acknowledge the valuable assistance provided by Mrs N. J. Mordan during the initial stages of this work, and various colleagues who kindly collected samples.

Biology and Ecology

Shell

Shells of testate amoebae may be proteinaceous, agglutinate, siliceous or calcareous in composition, and normally consist of one chamber with a single aperture.

Proteinaceous shells

These shells are of two main types: those in which the shell wall is constructed of numerous alveoli or building blocks, as in some species of *Arcella* and *Centropyxis*, and those in which the shell wall is composed of an homogenous layer of material. The secretion and formation of the alveoli has been described for *Arcella vulgaris* var. *multinucleata* and *Centropyxis discoides* (Netzel, 1975*a*, *b*, *c*; 1976*a*). The daughter alveoli are formed in the cytoplasm of the parent prior to division. Then at the onset of division a pseudopodial sheet extends from the aperture of the parent to form an enclosed chamber, inside which the daughter alveoli are arranged to form a replica of the parent shell. When the daughter shell is complete the cytoplasmic sheet is withdrawn and the cell divides by binary fission.

Examination of fractured shells of *Arcella arenaria* and *A. discoides* has shown that each alveolus is surrounded either by a thick or thin wall, but apparently lacks contents. However, it has recently been demonstrated that alveoli of *Arcella* and *Centropyxis* often contain inorganic elements which may be used to strengthen the shell wall (Hedley *et al.*, 1976). For example, the alveoli of *Centropyxis hirsuta* are rich in amorphous manganese, whilst *Arcella* species have the alveolar contents enriched with iron. This inorganic material is not usually present in the alveoli of young animals, and in dried specimens the shell surface may have small pits or depressions. The pits or depressions are especially evident in specimens of *Arcella*, where the margins of the alveoli are often delimited by small pores (see page 35). The shell wall of *Arcella discoides* has been reported to contain several amino acids which are similar to those found in the organic cement of agglutinate marine foraminifera, and the term 'pseudochitin' is sometimes used to describe this material (Hedley, 1963; Moraczewski, 1971).

Information on the second type of proteinaceous shell, which has the appearance of a smooth continuous coat (see page 73) is based on two reports. The shell wall of *Hyalosphenia papilio* is apparently homogenous and composed of mucoprotein which appears uniformly electron dense in stained sections (Joyon & Charret, 1962). The shell of an unidentified species of *Difflugiella*, on the other hand, is composed of three layers only one of which is electron dense (Griffin, 1972).

Agglutinate shells

Agglutinate forms may be divided into two groups.

The first group contains most of the family Difflugiidae. These amoebae select quartz grains, whole diatoms or pieces of diatoms, from the environment and use them to construct a daughter shell, identical in size and shape to the parent. Some species appear superficially to have a shell composed of randomly arranged particles, however, close examination reveals that at least one area, usually the aperture, has a specific pattern of organisation. In *Difflugia corona*, for example, the particles are arranged in a tooth-like pattern around the aperture. *D. lanceolata* selects only flat faced particles to make its shell, whilst *D. bacillifera* appears to prefer diatom shells. At the onset of division in *Difflugia corona* the mass of siliceous particles which have been collected by the parent are arranged around a cytoplasmic extrusion (Jennings, 1937). As this cytoplasm extends the particles mix with a liquid secretion and cover the surface to produce the new shell. Initially the shell is soft but soon hardens. The fine structure of the cement or glue used by an allied species *Difflugia lobostoma* has been described by Eckert & McGee-Russell (1974) and appears similar to that of *Euglypha* (Hedley & Ogden, 1973, 1974*b*).

The second type of agglutinate shell occurs in the genera *Nebela* and *Heleopera*. It is generally agreed that these genera do not make their own shell plates but use those which are obtained following the ingestion and digestion of smaller siliceous testates, usually members of the superfamily Euglyphacea, on which they prey. Two sources of shell plates are available, the plates that are glued together forming the shell chamber, and the separate reserve plates stored in the cytoplasm of the vegetative animal. In *Nebela collaris* the shell plates obtained by ingestion are usually found in large numbers scattered throughout the cytoplasm (MacKinlay, 1936), unlike typical reserve plate formation where the plates congregate in the region of the nucleus. When *N. collaris* was cultured in the absence of other testate amoebae, Mackinlay observed that they produced daughter shells which were devoid of shell plates.

The pattern of shell plates is usually distinctive for different species of *Nebela* and *Heleopera*. *Nebela dentistoma*, for example, has its shell plates arranged so that they do not overlap, and a patterned structure is evident in the organic cement that joins them (see page 97). Chemical analysis of whole shells of *Nebela dentistoma, N. tincta, N. tubulosa* and *Heleopera rosea* has shown that they are composed mainly of inorganic calcium, potassium, silicon and iron. Since the shell plates themselves are siliceous, the other elements are probably constituents of the organic cement matrix, and the significant amounts of iron found in *Heleopera rosea* probably account for the colouration of the shell.

Siliceous shells

All members of the Euglyphacea make their own siliceous shells as do some species of the genera *Difflugia*, *Lesquereusia* and *Quadrullela*. The siliceous, oval or circular shell plates of the Euglyphidae are formed prior to cell division and are stored in the cytoplasm close to the nucleus of the vegetative adult (Hedley & Ogden, 1973,

1974*a*). As many as four different types of plates or spines can be produced by one species. At division, cytoplasm is extruded from the aperture of the parent and the reserve shell plates move from the parent's cytoplasm to a position around the cytoplasmic extrusion. The cytoplasmic extrusion is strengthened by a central core of microtubules, and the shell plates are held at the end of finger-like processes by adhesion plaques of concentrated microfilaments. The shell plates are first arranged in a regular sequence, often in longitudinal rows, later they assume the identical pattern to the parent and are fixed by organic cement (Hedley & Ogden, 1974*b*). Only a small amount of cement is usually required to hold the plates in position and maintain the specific shape, but more cement is present at junctions between shell plates and spines or other projections. *Lesquereusia* and *Quadrullela* undergo a similar process of division. In *Lesquereusia* the shell is made of siliceous rods, whilst in *Quadrullela* the plates are quadrangular. A few species of *Difflugia* also make their own siliceous elements. In *D. oviformis*, for example, siliceous particles called idiosomes are manoeuvered around a cytoplasmic extension at division until they are arranged to form a single layer which is identical to the parent shell. Division of the parent cytoplasm takes place when the daughter shell is complete (Netzel, 1972, 1976*b*, 1977).

In siliceous testate amoebae specific differences appear to be restricted to the shape and size of the siliceous elements and the structure of the organic cement. The Euglyphacea and *Quadrullela* have siliceous elements which either overlap or are packed close together, and the organic cement is seen only in those species which have an organic collar around the aperture. In *Lesquereusia* and *Difflugia oviformis* on the other hand the cement is found at the interstices of the siliceous elements where it is often arranged in a distinctive pattern (see page 87).

Calcareous shells

Only two species, *Paraquadrula irregularis* and *Cryptodifflugia oviformis* are reported as having calcareous shells. *Paraquadrula irregularis*, has quadrangular shell plates (Penard, 1903) and divides in a similar manner to the siliceous forms (Deflandre, 1953). The shell of *Cryptodifflugia oviformis* has been described as having a smooth outer surface and a wall made up of two uniform layers, a thin organic outer layer and a thick inner layer of amorphous calcium phosphate (Hedley *et al.*, 1977). It was suggested that the organic layer is produced at the onset of division to form an identical daughter shell, and that the calcareous layer forms later inside this organic layer.

Cytoplasm

The cytoplasm usually fills the chamber in smaller testate amoebae such as *Euglypha* (Fig. 1) and *Trinema*, whereas in larger species of *Nebela* and *Difflugia* it only partially fills the chamber and thin cytoplasmic strands attach it to the shell wall. The following information is based mainly on studies of proteinaceous, calcareous and siliceous amoebae. Reports relating to the cytoplasm of agglutinate species is sparse,

since their thick shells composed of quartz grains and diatom frustules are often opaque, and impose practical difficulties for both observation and sectioning.

A plasmalemma surrounds the cytoplasm. Pellicular microtubules or microfilaments, which may function as a cytoskeletal structure, sometimes lie beneath the plasmalemma. Ovoid or spherical mitochondria with tubular cristae and dense granular matrices, are distributed throughout the cytoplasm. The nucleus, which is normally spherical, is surrounded by two unit membranes with nuclear pores. The nuclear matrix is finely granular with small scattered concentrations of chromatin. The nucleolus is of variable shape, usually situated centrally in the nucleus, and stains densely (Fig. 1). The outer nuclear membrane is continuous with cisternae of the granular endoplasmic reticulum which forms a compact mass around the nucleus. This region appears more heavily stained than the surrounding cytoplasm because of the high concentration of ribosomes. One or more Golgi complexes are found in the perinuclear region, usually bordering the dense endoplasmic reticulum. In addition to the established role of packing secretory products, the Golgi bodies are believed to be involved in the formation of proteinaceous alveoli, organic cement and siliceous shell plates.

Contractile vacuoles occur close to the plasmalemma and discharge into the shell cavity. These vacuoles are often surrounded by numerous vesicles which are associated with the lumen of the vacuole. The fusion of these vesicles with the vacuole causes it to dilate slowly—'diastole', this is followed by the rapid collapse of the vacuole—'systole' as it discharges its contents. Microbodies or peroxisomes may also be present in the cytoplasm; each is enclosed in a single unit membrane and has a dense granular matrix containing tubular or lattice-like elements. The microbodies secrete the oxidative enzyme catalase, as well as other enzymes, and it is thought that they are ancillary sites for carbohydrate oxidation and therefore involved with energy production (Hruban & Rechcigl, 1969). Food vacuoles are formed by a process known as phagocytosis, when cytoplasm flows around and engulfs prey and food particles. After digestion and absorption of soluble materials, any residue is discharged from the vacuoles through the surface membranes. Food vacuoles usually occur near the aperture.

Other cytoplasmic vacuoles and vesicles are sometimes present and may be distinctive of a particular species, genus or larger group of amoebae. For example, in two species with siliceous shells, *Euglypha rotunda* and *Trinema lineare*, there are large electron-dense vacuoles situated anterior to the endoplasmic reticulum, vesicles containing reserve shell plates in the peripheral cytoplasm anterior to the nucleus, and vesicles containing organic cement scattered throughout the cytoplasm (Hedley & Ogden, 1973, 1974*a*). Netzel described (1975*b*, *c*; 1976*a*) electron-dense membrane bound granules in *Arcella vulgaris* and *Centropyxis discoides*, which he suggested may be used in the construction of proteinaceous shells. A storage area for acid mucopolysaccharide material has been described in the calcareous species *Cryptodifflugia oviformis* by Hedley *et al.* (1977), as well as large electron-dense inclusions of calcium occurring in the mitochondrial membranes.

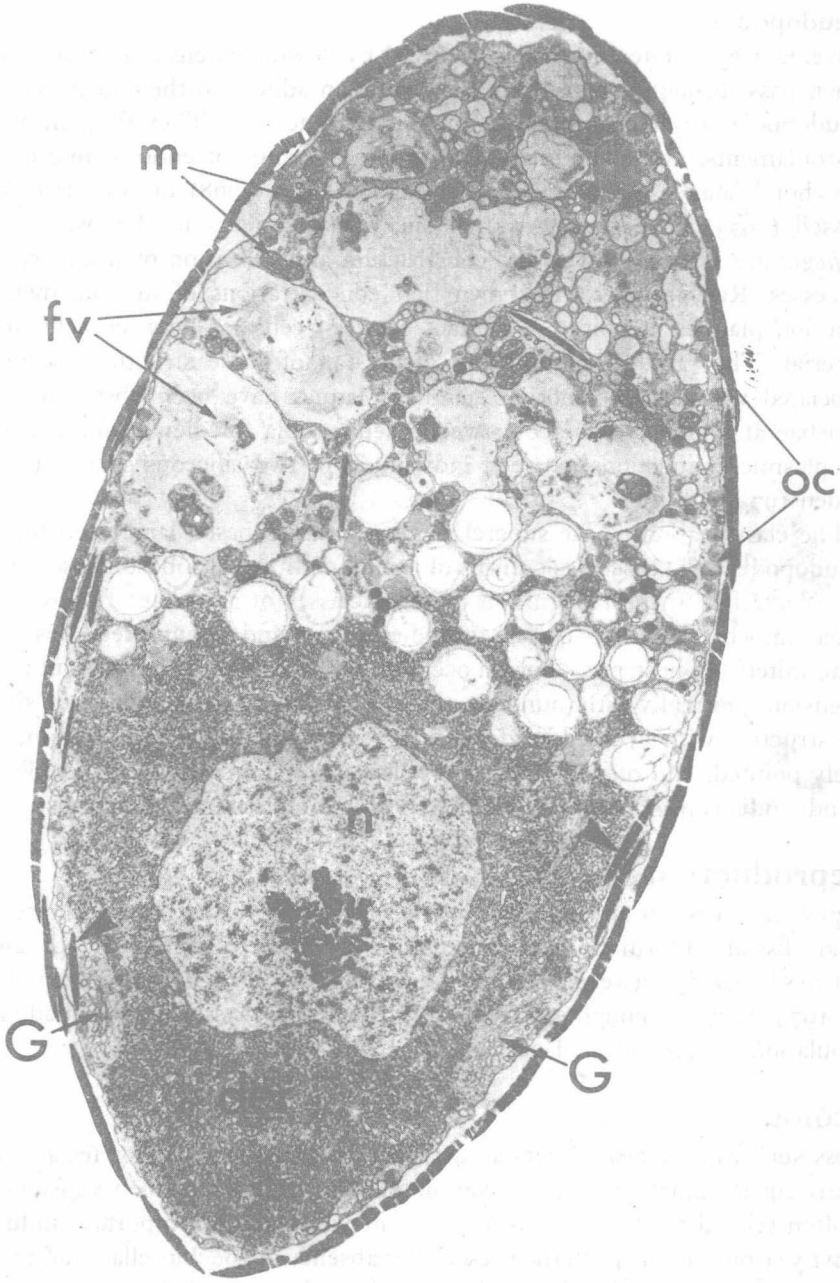

Fig. 1 Longitudinal section of the siliceous testate amoeba, *Euglypha rotunda*, showing the position of the nucleus (n) lying in the region of dense endoplasmic reticulum (der); Golgi complexes (G); mitochondria (m) and food vacuoles (fv). Note the reserve shell plates (large arrows) in the cytoplasm and the peripheral vesicles containing organic cement (oc).

Pseudopodia

Movement by testate amoebae is achieved by flowing extensions of the cytoplasm which pass through the shell aperture and can adhere to the substratum. These pseudopodia are diverse in shape and mode of activity. They frequently contain microfilaments, and sometimes microtubules, strands of endoplasmic reticulum, mitochondria and small vesicles. Wohlman & Allen (1968) and Eckert & McGee-Russell (1973) have suggested that the microfilaments in the pseudopodia of *Difflugia* are associated with the construction and extension of these cytoplasmic processes. Recent work has shown that concentrations of microfilaments form adhesion plaques at points of contact between cells, or between cells and inert material. The rapid formation and dispersion of these structures seems to be associated with cell locomotion. Similar plaques have been observed in testate amoebae at points of contact between pseudopodia (Hedley *et al.*, 1977) and in cytoplasmic connections between individuals of two siliceous species (Hedley & Ogden 1973, 1974*a*).

The classification of the superclass Rhizopoda is based largely on the type of pseudopodia. The three basic forms of pseudopodium are lobose, filose, reticulose, these have led to the recognition of three classes of amoebae: Lobosia—typical naked amoebae, Filosia—typical testate amoebae, and Granuloreticulosa—typical foraminifera. Lobose pseudopodia occur either as a single or a few stout trunk-like extensions, normally with rounded ends (Fig. 2), but may also appear as a single fan-like structure with a ruffled border. Filose pseudopodia are relatively thin, straight, finely pointed, and one extension may have several smaller branches. Reticulose pseudopodia consist of a network or web of fine interconnected strands.

Reproduction

Reproduction is, so far as is known, by replication of the parent during asexual binary fission to form an identical daughter-cell. The doubling time of laboratory cultures is usually between two to four days (Hedley & Ogden, 1973, 1974*a*; Hedley *et al.*, 1974, 1977), although estimates of six to eleven days have been made for wild populations (Heal, 1964*a*; Lousier, 1974).

Ecology

Moss such as *Sphagnum* offers a particularly suitable habitat for testate amoebae (Heal, 1962). Zonation is quite a common feature of testate amoebae distribution, it is often related to habitat moisture content which has an important influence on activity (Lousier, 1974), to the presence or absence of zoochlorellae, and in the case of agglutinate species to the availability of particles for shell construction (Heal, 1962; Meisterfeld, 1977).

The distribution of testate amoebae in soil seems to be determined largely by the size of the pore spaces and the thickness of the soil water film, although they are usually more numerous in soils having a high organic rather than a high mineral content (Stout & Heal, 1967). A vertical distribution is present in most soil and *Spagnum* habitats, which is correlated to some extent with shell shape. The larger

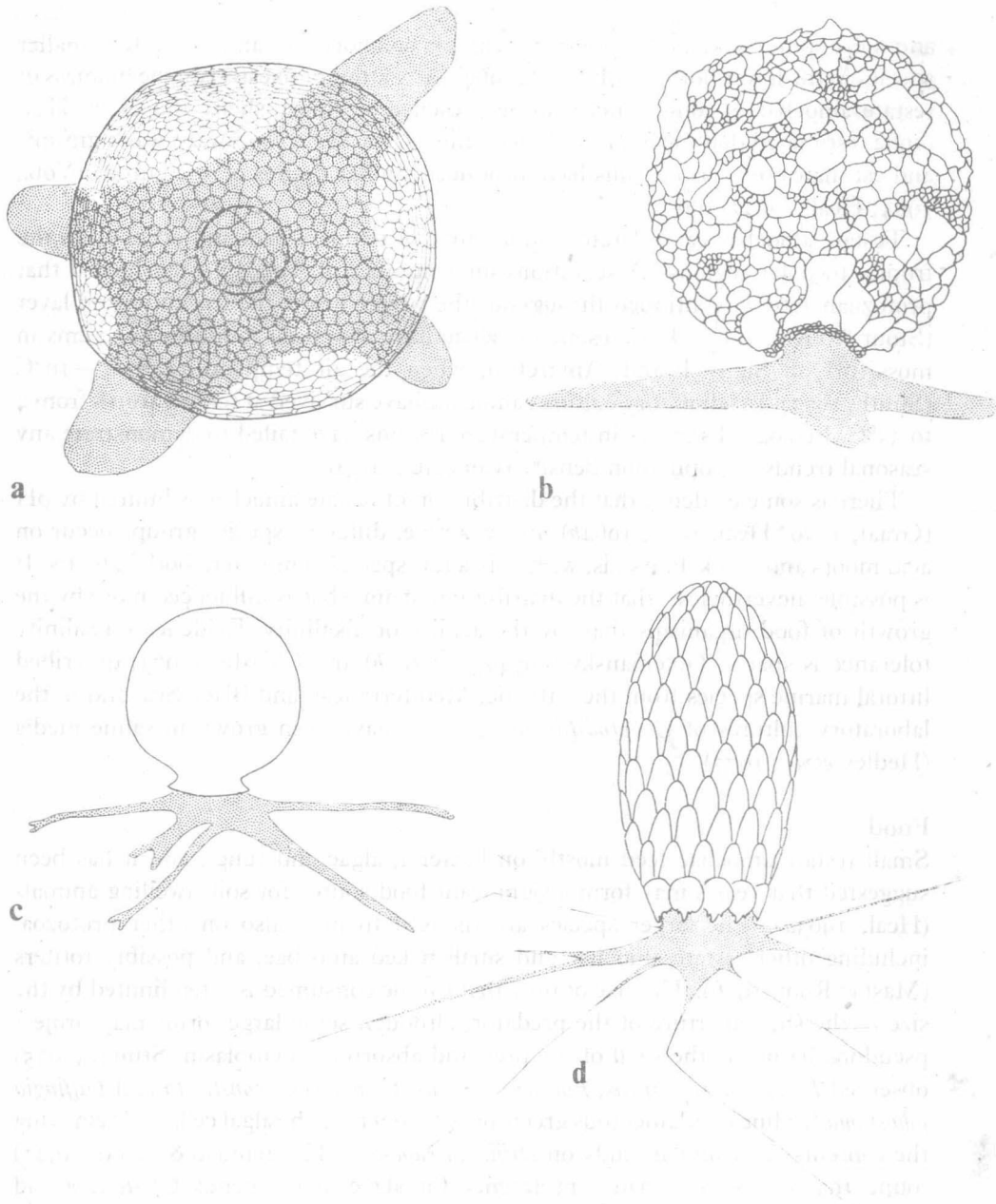

Fig. 2 Diagram illustrating the form of pseudopodia associated with different types of shell: (a) *Arcella vulgaris* with a proteinaceous shell, usually has about four lobose pseudopodia—but these may sometimes fuse to form a single fan-like pseudopodium with a ruffled edge (b) *Difflugia gramen* has an agglutinate shell and usually one or two large lobose pseudopods (c) *Cryptodifflugia oviformis* has a calcareous shell and the pseudopodia are recognised as being lobose, although, they appear to represent a transitional stage between lobose and filose structure (d) *Euglypha rotunda* with a siliceous shell shows a typical arrangement of filose pseudopodia.

and more spiney species are found in the upper soil horizons, and the flatter, smaller species in the lower horizons (Bonnet, 1964). Any attempt to estimate the biomass of testate amoebae is complicated by the presence of empty shells and cysts. Heal (1962) estimated that the biomass of live animals in a *Sphagnum* sward was 1 gm/m², and estimates for various soils have produced similar figures of 1–2 gm/m² (Volz, 1964; Heal, 1964*b*, 1965).

Testate amoebae can tolerate a wide range of temperatures and occur from the tropics to polar regions. Observations on a number of Russian soils showed that protozoan activity continued throughout the winter below the frozen topsoil layer (Stout & Heal, 1967). Live testate amoebae have also been found below 3 cms in moss-turf on Signy Island, Antarctica, when the air temperature was −10°C (Smith, 1973). In laboratory cultures amoebae have survived at temperatures from 4 to 35°C. Ecological surveys in temperature regions have failed to demonstrate any seasonal trends in population density (Couteaux, 1976).

There is some evidence that the distribution of testate amoebae is limited by pH (Graaf, 1956; Heal, 1961, 1964*b*). For example, different species groups occur on acid moors and in alkaline soils, with only a few species common to both habitats. It is possible, nevertheless, that the distribution of amoebae is influenced more by the growth of food organisms than by the acidity or alkalinity. Evidence on salinity tolerance is sparse, Golemansky (1974*a*, 1976*a*, *b*) and Chardez (1973) described littoral marine species from the Atlantic, Mediterranean and Black Sea, and in the laboratory cultures of *Cryptodifflugia oviformis* have been grown in saline media (Hedley *et al.*, 1977).

Food

Small testate amoebae feed mostly on bacteria, algae and fungi, and it has been suggested that yeasts may form a significant food source for soil-dwelling animals (Heal, 1963*a*). The larger species are thought to prey also on other protozoa, including other testate amoebae and small naked amoebae, and possibly rotifers (Mast & Root, 1916). The size of prey that can be consumed is often limited by the size of the shell aperture of the predator, although some large forms may project pseudopodia inside the shell of the prey and absorb the cytoplasm. Stump (1935) observed *Lesquereusia spiralis*, *Pontigulasia vas*, *Centropyxis constricta* and *Difflugia lobostoma* feeding on filamentous green algae by opening the algal cells and removing the contents. In a similar study on *Difflugia rubescens*, Hoogenraad & Groot (1941) found that this species had a preference for algae of the genus *Closterium* and described the way in which the testate punctured the cell wall and ingested the contents.

Cysts

Temporary or resistant cysts are formed at certain times, usually as a protection against adverse environmental conditions such as desiccation, exhaustion of food supplies or anaerobiosis. The cyst is contained within a cyst-membrane and usually lies against the shell wall in the aboral region, often with part of the membrane

forming a seal across the middle of the shell. In *Arcella*, and a few other genera, the aperture is sealed by a proteinaceous membrane, while some agglutinate species seal the chamber with a plug of siliceous particles. During encystment there is a reduction of the cytoplasmic volume, the number of organelles, and in siliceous species the reserve shell plates are discarded.

Classification

The classification adopted here is basically that proposed by Loeblich and Tappan (1964). In this, as in other recent classifications Deflandre (1953), Loeblich and Tappan (1961), two main criteria are used to divide the Superclass Rhizopoda; these are the cytoplasmic form of the pseudopodia and the structure of the shell. Division into classes is based on the characters of the pseudopodia, whilst the orders are separated on the presence or absence of a protective covering. Further divisions into superfamilies are based on the detailed structure of the shell. The few changes that are proposed here have been achieved within the framework of previously published names, and no new names are included. For the purposes of this study only those animals having a rigid shell have been considered, therefore the families Cochliopodiidae Taranek, 1882 and Microcoryciidae de Saedeleer, 1934 have been omitted.

A diagnosis based on the structure of the shell is given below for each family and genus that have been referred to collectively as testate amoebae:

Subphylum **SARCODINA** Hertwig and Lesser, 1874

Superclass **RHIZOPODEA** von Siebold, 1845
Locomotion associated with formation of lobopodia, filopodia or reticulopodia, or with protoplasmic flow without production of discrete pseudopodia.

Class **LOBOSIA** Carpenter, Parker and Jones, 1862
Pseudopodia lobose, or rarely filose but produced from a broader hyaline lobe, not anastomosing.

Order **ARCELLINIDA** Kent, 1880
With a shell or rigid external membrane, having a definite aperture for extrusion of lobose pseudopodia.

Superfamily **ARCELLACEA** Ehrenberg, 1843
Pseudopodia fingerlike.

Family **ARCELLIDAE** Ehrenberg, 1843. Shell circular of ovoid; composed of proteinaceous material, surface either smooth or pitted; aperture central, circular.

Genus *Arcella* Ehrenberg, 1832. Shell colourless, yellow or brown; circular or ovoid; in lateral view varying from plano-convex to hemispherical; surface either smooth or punctated, but may be moulded to have angular facets which sometimes develop into spines or prominences; wall composed of numerous alveoli made of a proteinaceous material, arranged in one or more layers; aperture central, circular, with a small collar, usually invaginated and occasionally surrounded by pores. . . . p. 24

Family **CENTROPYXIDAE** Jung, 1942. Shell circular, hemispherical or ovoid; usually laterally compressed at anterior margin; composed of proteinaceous material often with agglutinated mineral particles; aperture sub-terminal with recurved margin, circular or oval.

Genus *Centropyxis* Stein, 1859. Shell colourless, yellow or brown; circular, hemispherical or ovoid; in lateral view rounded posteriorly and tapering towards the anterior edge, which often has a recurved margin, conical spines sometimes present at lateral margins; surface either punctated or rough; wall composed of either numerous alveoli arranged in layers or agglutinated mineral particles; aperture sub-terminal or occasionally central, circular or oval and invaginated. . . . p. 46

Family **PLAGIOPYXIDAE** Bonnet, 1959. Shell circular or ovoid, bilaterally symmetrical; composed of agglutinated mineral particles; aperture sub-terminal elongate, usually with overhanging anterior lip.

Genus *Plagiopyxis* Penard, 1910. Shell grey, yellow or brown; circular or ovoid; composed of agglutinated mineral particles; aperture sub-terminal, elongated slit extending for about one third circumference of shell. . . . not illustrated

Genus *Bullinularia* (Penard, 1907). Shell, dark brown; circular or ovoid; composed of agglutinated mineral particles; aperture sub-terminal, elongated slit with lower lip depressed, upper lip incurved and perforated by rows of pores. . . . p. 64

Family **TRIGONOPYXIDAE** Loeblich and Tappin, 1964. Shell circular or hemispherical, radially symmetrical; composed of agglutinated mineral particles; aperture central.

Genus *Trigonopyxis* Penard, 1912. Shell brown; circular or hemispherical; composed of agglutinated mineral particles; aperture central, invaginated and triangular. . . . p. 66

Genus *Cyclopyxis* Deflandre, 1929. Shell brown; circular or hemispherical; composed of agglutinated mineral particles; aperture central, invaginated, circular. . . . p. 68