Progress in Protistology, Vol. 2, 69–212
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Soil Protozoa: Fundamental Problems, Ecological Significance, Adaptations in Ciliates and Testaceans, Bioindicators, and Guide to the Literature[1]

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[1]This study was supported by Fonds zur Förderung der wissenschaftlichen Forschung, Projekte Nr. P 5226 und P 5889 and Forschungsinstitut Gastein-Tauernregion. The helpful comments of some colleagues (S. Bamforth, H. Bick, T. Dale, W. Schönborn), and the technical assistance of Mrs K. Bernatzky are acknowledged. Particular thanks are due to Dr David J. Patterson (University of Bristol, England) and to Dr John R. Haslett, an ecologist at Salzburg University, who constructively criticized the entire work and corrected the English.

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ABSTRACT. A 'soil protozoon' is a single-celled eukaryotic organism that lives in the mineral substrate and associated organic matter in which terrestrial vegetation takes root. Research in most groups of soil protozoa is hindered by the lack of appropriate methods for the estimation of numbers of individuals and species, as well as by the poor taxonomic knowledge of many ecologists. Only direct counting methods give reliable estimations of numbers of individuals. A 'non-flooded petri dish method' is described for estimating the species richness of the soil ciliates. The concept of 'ciliatostasis' is introduced to explain the phenomenon that excystment, and growth, of ciliates in many natural and cultivated soils is much more limited than would be expected from their behaviour *in vitro*. Soil protozoa respire about 10% of the total carbon input, thus forming a significant proportion in the energy cycle of the soil. Their potential for biological control of soil-borne bacterial and fungal diseases is emphasized. The morphological and physiological adaptations, and the evolutionary and adaptive trends in soil ciliates and testate amoebae are described qualitatively and quantitatively. It is shown that the adaptations produced communities which can be sharply separated from those occurring in freshwater and marine sand. About 50% of the species of soil ciliates and testaceans may be considered to be the result of speciations that have occurred in the soil itself. It is questionable from which freshwater biotope (lake 'Aufwuchs', pools, etc.) the majority of the soil protozoa arose. All reliable data suggest a non-cosmopolitan distribution of soil testate amoebae and ciliates. Soil protozoa can be used as bioindicators in natural and human-influenced ecosystems. Over 100 papers relating to this subject are reviewed. They show that it is often possible to relate the occurrence and distribution of certain soil protozoa to certain biotopes and/or soil types. Fire, deforestation, removal of the top soil, soil compaction, pesticides, and partial sterilization of the soil often cause a strong depression of the protozoan activity and pronounced changes in their community structure. Fertilization and liming of the soil tend to increase numbers and biomass of the protozoa. A taxonomic guide to the soil protozoa, intensified methodological research, investigations on the protozoa in agricultural soils, and well designed experimental microcosm and field studies are pressing requirements. Many conflicting results seem to be caused by the misidentification of species and/or inappropriate counting methods.

I. INTRODUCTION

The occurrence of protozoa in the soil has been well established since the pioneering work of Ehrenberg (1838). But, more detailed investigations commenced only at the turn of the century (e.g., Cutler, 1920; Francé, 1921; Goodey, 1911, 1915a, b; Koch,

1915, 1916; Russell & Hutchinson, 1909). Since that time, many important articles and reviews about soil protozoa have appeared, but most written by general soil scientists, microbiologists, or soil protozoologists whose main interest was ecology (e.g., Bamforth, 1973, 1980; Biczók, 1979; Brodsky, 1935; Cutler *et al.*, 1922; Darbyshire, 1975; Franz, 1975b; Grandori & Grandori, 1934; Kühnelt, 1950; Nikolyuk, 1956, 1965a; Sandon, 1927; Singh, 1960, 1963, 1964; Smith, 1978; Stout & Heal, 1967; Stout *et al.*, 1982; Yakimoff & Zérèn, 1924). There are a few overviews about naked and testate amoebae compiled mainly by taxonomic protozoologists (Bonnet, 1964, 1973b; Chardez, 1965a, 1967, 1968; Chardez & Lambert, 1981; Decloitre & Cailleux, 1980; Page, 1976; Pussard, 1967). Not a single review has been prepared by a ciliate or flagellate specialist. This, and the frustrating taxonomic situation in all groups of soil protozoa, has influenced the entire field and perpetuated many taxonomic and ecological errors and misconceptions. A major part of this paper concentrates on the ciliates. The older literature on testate amoebae is excellently covered by Schönborn (1966a) and Bonnet (1964). Particular interest is paid to the German and East-European literature which has been too often neglected by Anglo-American reviewers. There is little recent work on the taxonomy and ecology of soil flagellates and naked amoebae, which is surprising because these forms are said to occur in great numbers in soils (Pussard, 1967). The most comprehensive taxonomic guides are: Sandon (1927), Grandori & Grandori (1934), and Lepşi (1965). These are outdated and their replacement presents a challenge to the new generation of soil protozoologists. As concerns the naked amoebae, I refer the reader to the excellent guides of Lepşi (1960), Page (1976), and Lee *et al.* (1985).

A further major concern of this review is to highlight the considerable potential of the soil protozoa as bioindicators. Their significant contribution to the standing crop of heterotrophs and to production in many soils around the world means that changes occurring in their community structure in stressed areas should no longer be neglected. General ecologists need to give more consideration to protozoa in their research programs.

II. SOME FUNDAMENTAL PROBLEMS

This section is devoted to some of the basic problems of soil protozoology and to the 'concept of ciliatostasis', which hopefully will influence future research. The thoughts and evidence presented here have greatly influenced the entire review.

A. *What Is a Soil Protozoon?*

The definition of soil as 'the mineral substrate in which the vegetation takes root, including the dead organic material which is found both in and upon the mineral substrate' (Van der Drift, quoted in Kevan, 1962) will be used in this review. This is appropriate because most protozoologists include in the term 'soil protozoa' not only the protozoa occurring within the mineral soil but also those inhabiting the litter. Comparisons with freshwater and marine sand protozoa are discussed in sections IV.C,E.

Also it may not be possible to distinguish between soil and moss protozoa, as many workers do! The existence of a true moss fauna has been shown fairly well for the testate amoebae (Bonnet, 1973a; Schönborn, 1966a). Schönborn (1962a) considered that only the rather rare genera *Microcorycia, Diplochlamys, Parmulina*, and *Capsellina* are true or autochthonous (= indigenous) moss organisms. The excellent study of Wenzel (1953) is often cited as proof of an autochthonous ciliate moss fauna.

Closer inspection of his sampling method ('the pieces of moss were sampled together with a more or less (max 2 cm) thick zone of soil') indicates that he worked with mixed material. Concerning contaminated moss samples, Horváth (1950) wrote, 'A great many of the moss-dwellers, however, were demonstrated by pouring water on collected moss, letting the 'raw' culture thus produced stand for a while and then describing the animals present in the culture as moss-dwellers. But with this method it is not in the least certain that these ciliates really live in the moss, for there is no question but that, in collecting earth mosses, for example, bits of earth also get into the culture and with them the cysts of soil-dwelling ciliates.' Gellért (1956) also stressed this difficulty. He found only a few ciliates in the water between the moss leaves. The scarcity of protozoa on the external surfaces of living plants (Bamforth, 1973; Mueller & Mueller, 1970) supports the view that authors who reported on a high species diversity in moss (e.g., Bovee, 1979; Fantham & Porter, 1946; Kahl, 1930, 1931, 1932, 1935; Sudzuki, 1964; Wenzel, 1953) used samples contaminated with soil.

From personal observations, I am convinced of the existence of a genuine ciliate moss fauna, but its exact composition and the differentiation from the soil community must be examined further. Particularly, future workers must discriminate between the green and the dead parts of the moss, and between the moss and the underlying litter or soil.

B. *Methodological Inconveniences*

There are many recent reviews of the methods used in soil protozoology (e.g., Alabouvette *et al.*, 1981a; Bamforth, 1979; Darbyshire, 1973; Geltzer, 1962, 1980; Heal, 1970, 1971; Stout & Heal, 1967; Schönborn, 1986; Wallwork, 1976). I shall confine my comments here to a few points of more general importance which have been largely ignored.

1. *Estimation of individual abundance.* Most authors agree that direct methods of investigation are useful for testate amoebae but inappropriate for ciliates, flagellates, naked amoebae, and algae, as these are hidden by the soil particles (Coûteaux, 1967, 1975; Foissner, 1983a; Jones & Mollison, 1948). Regarding the latter groups, the culture techniques (CT) of Cutler (1920) and Singh (1946, 1955) are widely used and said to be most satisfactory (Burges, 1958; Heal, 1971; Stout & Heal, 1967; Stout *et al.*, 1982). With these methods, Datta & Mangat (1975) and Formisano (1957), for instance, obtained 53 000 and 12 000 active ciliates g^{-1} of wet soil, respectively. In contrast, more than 50% of 280 soil samples investigated with a direct counting method yielded none or rather few active ciliates (Table 1). The highest value found was 623 active ciliates g^{-1} dry mass of soil.

With this background, some recovery experiments were performed using the direct counting method (Fig. 1). Despite objections of Alabouvette *et al.* (1981b), the recovery method is the only reliable way to test the fitness of a counting method. My experiments show that in watered soil suspensions the recovery rate for ciliates is 55–100% (mean 76%); for testate amoebae, 30–100% (mean 60%); for flagellates and diatoms, about 50%; and for small immobile algae and naked amoebae, less than 10% (Fig. 1). As far as I am aware, only Cutler (1920) and Singh (1946) tested their methods in a similar manner. Singh (1946) found 63–72% (mean 68%) recovery of inoculated cysts of *Naegleria* sp. Cutler (1920) and Ramsay & Ball (1983) obtained similar values for ciliates, flagellates, naked amoebae, and soil algae. Bunt & Tchan (1955) reported nearly 100% recovery with their method. Unfortunately, they did not indicate the amount of soil used. The data suggest that direct methods are not as

Table 1. Abundances of active ciliates in 280 freshly collected samples of alpine and lowland soils in Austria. (from Foissner, 1981a, 1985a, unpubl.; Berger *et al.* 1985a)

	Individuals g^{-1} dry mass of soil[1]							
	0	%	1–20	%	21–100	%	101–623	%
Number of samples	165	59	15	5	62	22	38	14
Average number of individuals	0		10		44		231	
Average soil moisture (%)	32		34		32		34	

[1]Estimated by the direct counting method described in the explanation to Fig. 1. Numbers g^{-1} dry mass of soil based on the inspection of 0.2–0.4 g wet soil.

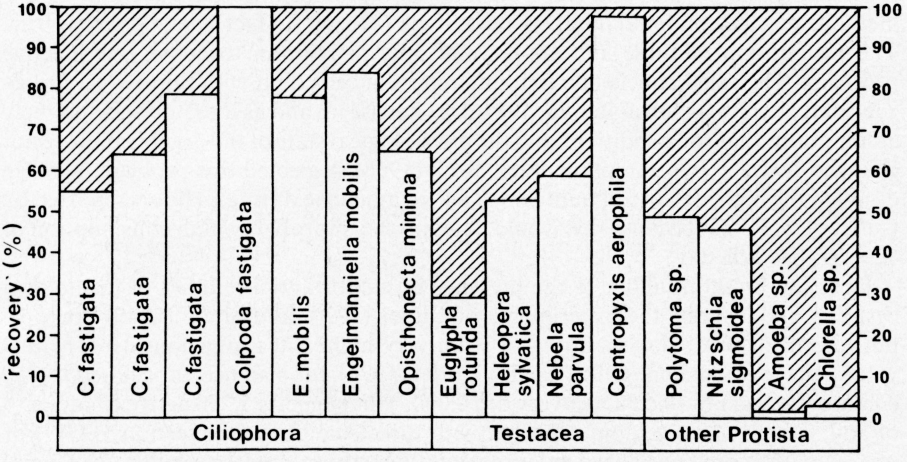


Fig. 1. 'Recovery' of various species of protista in soil suspensions made from 0.05 g dry soil with 3 ml tap water, to which were added a known number of the species indicated. Each suspension was dispersed on 10 slides and counted at a magnification of 100 : 1. Some experiments were repeated several times (*Colpoda fastigata, Engelmanniella mobilis*) to estimate the variation. (from Foissner, 1983a)

unsuitable as stated by Singh (1946), Stout & Heal (1967) and other authors, in relation to ciliates and the larger testate amoebae. However, many smaller testaceans are lost with such methods. This may explain why the membrane filter technique of Coûteaux (1967, 1975) yields much higher counts than watered soil suspensions (Lousier & Parkinson, 1981b). On the other hand, it is obvious from the data obtained with the membrane filter method that some of the rare autochthonous soil testacean species which frequently occur in low numbers (5–20 individuals g^{-1} dry mass of soil) are lost. This is not surprising because only 5–30 mg soil are examined, compared to 100–200 mg in other direct methods. Unfortunately, the rare species are often fairly large, and the loss of one individual of *Centropyxis oomorpha* is equivalent to 40 individuals of *Trinema lineare* with respect to biomass. This could explain why Lousier & Parkinson (1984) calculated a fairly low annual mean biomass in spite of the relatively high annual mean density (Table 4).

The CT methods yield a rough estimation of the active *and* inactive (cystic) proto-

zoa present in soil. The two states are usually distinguished by treating part of the sample with 2% HCl overnight. After removing the acid and washing with NaCl solution, counting continues as normal. The number from the acid-treated part of the sample (i.e., cysts) is subtracted from the total number of organisms to give the number of active protozoa (Bamforth, 1979; Singh, 1946). The estimation of *active protozoa* is therefore *indirect* and depends on the assumption that all cysts survive the acid treatment and that all cysts will excyst. A simple example demonstrates how the results depend on the recovery of the cysts. Assume 200 active and 800 cystic protozoa in a soil sample. If, for instance, the HCl treatment and the other procedures involved inactivate 400 cysts, 600 active protozoa will be calculated, which is an overestimation of 300%!

These peculiarities of the CT methods are important. Although unnoticed by many authors, they have been recognized recently by Foissner (1983a) and Pussard & Delay (1985). Singh (1946) and Elliott & Coleman (1977), for instance, assumed that the CT methods produce minimal numbers for active protozoa. In fact, the opposite is true. The assumption of these authors is valid only in relation to active *and* inactive protozoa. The usual conclusion that differences in cell count with time reflect protozoan activity (Rogerson & Berger, 1981c) is likewise invalid as it requires the unlikely assumptions that soil conditions and the physiological state of the organisms have not changed between two sampling dates. Beck (1968) suspected this problem, too. He doubted the high increase of numbers of naked amoebae during 24 hours reported by Cutler *et al.* (1922) because this would demand the improbably high consumption of 52×10^9 bacteria day^{-1}.

Does the literature indicate the presence of a substantial number of inactivated cysts? If one inspects the experiments of Cutler (1920) and Singh (1946), the proportion of inactivated cysts does not seem very high. But if one considers the real values, the relations change drastically. Cutler (1920), for instance, inoculated 15,250 ciliate cysts and obtained a recovery of 10,000. This suggests 5,250 active ciliates g^{-1} of soil, a high value seldom reported with direct methods (see section II.C). For species with more specialized requirements than those used by Cutler (1920) and Singh (1946) the recovery is certainly lower. The widely overlooked paper of Bodenheimer & Reich (1933) demonstrates clearly that the HCl-treatment sometimes inactivates nearly all of the cysts. Very recently, Pussard & Delay (1985) showed this again for some species of naked amoebae. Rather high inactivation rates were also reported by Crump (1950) and by Bunt & Tchan (1955). Ramsay & Ball (1983) tested the CT methods for soil algae and did not find a significant correlation between the numbers calculated with these techniques and those estimated using the chlorophyll *a* method.

Another disadvantage of the CT methods is the effect of the totally artificial milieu (e.g., agar plates with a very restricted bacterial flora) on excystment (Dixon, 1937; Heal, 1964; Koch, 1915; Martin & Lewin, 1915; Stout, 1958; Yakimoff & Zérèn, 1924). Dixon's (1937) paper provides impressive examples of discrepancies in results caused by artificial culture media: for example, soil extract agar yielded 371,000 protozoa g^{-1} of soil and 12 species, whereas peptone agar yielded only 1,111 protozoa g^{-1} of soil and six species. Bamforth (1969) also recognized the problem, stating, 'Only a few of the many ciliate species found in a qualitative culture of a soil or litter appear in dilution samples for quantitative estimation.'

There is some indirect evidence for rather high numbers of active flagellates and naked amoebae in the soil. Sherman (1914) and Martin & Lewin (1915) found high abundances of these protozoa using direct counting methods.

Alabouvette *et al.* (1981b) inoculated 1 amoeba g^{-1} in a sterilized *Fusarium*-enriched soil and counted 25,000 individuals g^{-1} with the CT method after 14 days. This indicates a fairly high rate of reproduction. Rogerson & Berger (1981c) implanted perforated tubes containing sterilized soil in an undisturbed soil. Within one week the CT counts for the naked amoebae and flagellates reached 1,781 and 7,541 cells g^{-1}, respectively. This may indicate rapid reproduction and/or fast migration of the protozoa under field conditions. These data must be treated cautiously, because soils in microcosm experiments or disturbed soils react quite differently compared with undisturbed field soils. Such differences will be discussed in section II.C.

The above considerations shed doubt on the reliability and appropriateness of data obtained using CT methods, particularly concerning the number of active protozoa. Stout *et al.* (1982) have expressed similar doubts. We can be sure that a high number of protozoan cysts are present in many soils, that there is a rather high abundance of active testaceans, and a fairly low abundance of active ciliates. Despite the high numbers of soil flagellates and naked amoebae reported (e.g., by Clarholm, 1981, 1984, 1985; Cutler *et al.*, 1922; Meisterfeld, 1981, 1986; Pussard, 1967), the relative importance of these groups may have been overestimated, as many may be present as cysts (Brzezińska-Dudziak, 1954; Feest, 1987; Goodey, 1911).

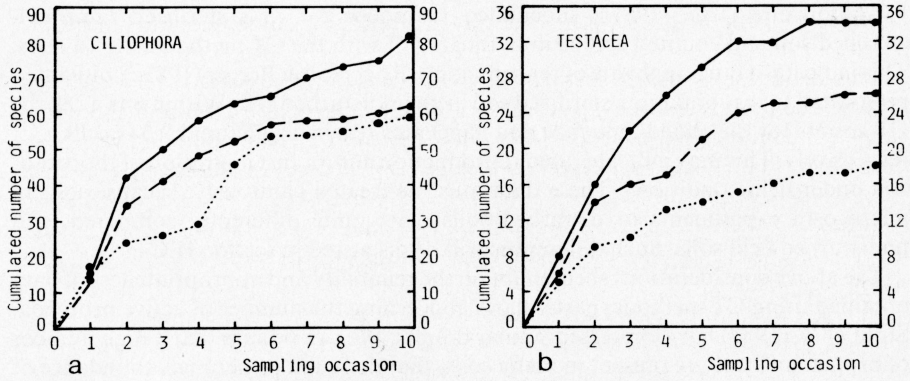
In view of the doubts surrounding the methods for counting numbers of individuals, all statements relating to sizes of populations in this review need to be interpreted with caution! The most reliable values are those that are based on direct counting techniques.

2. *Estimating the number of species.* Many methods have been recommended for the estimation of the species richness of soil protozoa. The best method for testate amoebae is the careful inspection of watered soil suspensions and the flotation of empty tests by gas bubbles (Décloitre, 1960; Schönborn, 1986).

Estimation of species richness in the other groups of soil protozoa is much more difficult, because these cannot be directly extracted so successfully from the soil. Therefore, enumeration involving various culture techniques have been suggested. In recent times, the method of Stout (1958) is frequently used: 1–10 g of soil is added to one side of a petri dish (10 cm diameter) the bottom of which is covered with 2% non-nutrient agar. To this, 20 ml of sterile distilled water is added. The culture is examined several times during one or more months. The protozoa can be observed in the soil-free part of the petri dish. Other methods use nutrient agar and/or various liquid culture media, such as diluted soil extract, hay infusion, and autoclaved sewage (Sandon, 1927; Shibuya, 1927; Varga, 1934; Viswanath & Pillai, 1977a; Yakimoff & Zérèn, 1924). Unfortunately, these techniques produce a temporary pond milieu which is artificial for most of the protozoa, and many species will not grow (Pussard, 1967).

A simpler and perhaps more effective method was described by Varga (1959), Starr (1973), and later by Foissner (1981a, 1985a). This 'non-flooded petri dish method' requires 10–50 g of a fresh or air-dried soil or litter sample to be placed in a petri dish (10–15 cm diameter) and saturated but not flooded with distilled water. A fauna of ciliates, flagellates, and naked amoebae, often unexpectedly rich, will develop after a few days. Usually, inspection of the cultures on days 4, 6, 10, 14, and 20 is sufficient. Later inspections add but few new species, due to the effects of ciliatostasis.

Several points influence the outcome of the method: (a) air-dried soil yields often more individuals and species, perhaps due to reduced microbiostasis (Section II.C and table 2); (b) the sample should contain much litter and plant debris and must be



Figs 2a,b. Cumulative totals of soil ciliate (a) and soil testacean (b) species from 10 sampling occasions over 27 months at three sites in the Tullnerfeld near Vienna (Austria). Ciliates were investigated with the 'non-flooded petri dish method', testate amoebae from a watered soil suspension (cf. Fig. 1). ———— beech forest; — — — — — xerothermic uncultivated grass land; . . . . . wheat field. (original)

spread over the bottom of the petri dish in at least a 1 cm thick layer; (c) the soil must not be flooded. Water should be added to the sample until 5–20 ml will drain off when the petri dish is tilted and the soil is gently pressed with a finger. This run-off contains the protozoa and can be used for further preparations, such as silver staining.

No systematic comparisons with other techniques are known. So many new species of soil ciliates have been discovered by myself with this method that it may be argued that it is more effective than other more frequently used techniques. The main reason for this is presumably that my samples (up to 50 g) are much larger than some used in earlier techniques. Repeated investigations of some soils showed that 2–5 samples distributed over one year produce approximately 50–80% of the species found in 10 samples investigated over two years (Fig. 2a). Thus, the method is not perfect and workers should be encouraged to look for a better alternative. In this context, the polyurethane foam method introduced to soil protozoology by Sudzuki (1978) should be mentioned.

The situation for the testate amoebae investigated in watered soil suspensions is similar to that for the ciliates (Fig. 2b).

3. *Horizontal distribution.* There are some data which suggest that soil protozoa have an aggregated (non-random, clumped) distribution (Brzezińska-Dudziak, 1954; Gellért, 1957; Stout, 1962). Although this could influence ecological results very much, there is not a single study devoted to this important question (but see Feest, 1987). However, most soil protozoologists are aware of the problem and use bulked samples of 5–20 separate cores from an area of approximately 1–20 m^2 or along a transect (Coûteaux, 1976d; Datta & Mangat, 1975; Foissner *et al.*, 1986; Meisterfeld, 1986; Schönborn, 1986; Singh, 1946, 1961; Singh & Crump, 1953; Stout, 1962). Of course, this cannot substitute for an analysis, which is badly needed!

C. *Ciliatostasis—a New Concept*

The hypothesis: The term 'ciliatostasis' refers to the phenomenon that excystation and growth of ciliates in evolved natural and cultivated soils is much less than might

be expected from their behaviour under similar conditions of temperature, moisture, pH etc. *in vitro*.

This definition is nearly identical to that given for 'fungistatis' by Lockwood (1977). The term is restricted to designating the phenomenon itself and should not carry any connotations as to causality. For this, appropriate modifying words like 'microbial ciliatostasis' or 'fungal ciliatostasis' can be used. In a more general sense, 'ciliatostasis' can be included in the term 'microbiostasis' which embraces, for instance, soil bacteriostasis and soil actinostasis (Ho & Ko, 1982). Soil microbiostasis may be a powerful means of maintaining an equilibrium between the different kinds of soil organisms.

This concept is introduced to circumscribe and partly to explain some well known but generally ignored or little understood field and laboratory data about soil ciliates. It probably does not apply to the testate amoebae, which grow well in litters *and* evolved soils (e.g., Foissner *et al.*, 1986; Meisterfeld, 1980). As concerns the naked amoebae and the flagellates, our knowledge about their real abundance in evolved soils is too uncertain (see preceding section) to determine the extent to which this concept applies to them, too. But, Menapace *et al.* (1975) reported on a quicker 'peak germination' of naked amoebal cysts in glucose-enriched soil microcosms and Mordkovitch (1977) found a strong increase in the number of naked amoebae during the decomposition of root residues. Such phenomena are typical for organisms which are influenced by soil microbiostasis.

The evidence: To clarify ideas on the concept and to show additional pathways for its verification, it is appropriate to repeat the generalizations of Lockwood (1977) for fungistasis and to compare them with equivalent results from studies on ciliates.

(a) 'Nearly all natural soils are fungistatic with the exception of deep subsoils where microbial populations are low.' Active ciliates are usually rare in a wide range of evolved natural soils, even under the high moisture conditions typical for many Austrian soils (Table 1). Similar low values have been reported by many authors, for instance, by Goodey (1911, 1915b), Koch (1916), Francé (1921), Aléxeieff (cited by Sandon, 1926), Koffman (1934), Heinis (1959), Szabó *et al.* (1964), and Mueller & Mueller (1970).

There are a few, but important, exceptions to this 'rule': Brunberg Nielsen (1968) reported, with a direct counting method, up to 28 503 active ciliates g^{-1} dry mass of leaf litter in a Danish beech forest; and Lehle, Funke & Foissner (unpubl.), Petz, Foissner & Adam (unpubl.), and Schönborn (pers. comm.) counted with direct methods up to 1000 active ciliates g^{-1} dry mass in coniferous litters. Very recently, we found also rather high numbers (up to 3000 individuals g^{-1} dry mass) of active ciliates in deciduous litters. Reinvestigation of the uppermost (0–1 cm, 1–3 cm, 3–8 cm) layers of cultivated soils (meadows) confirmed the earlier results of the absence of active ciliates, probably due to the lack of litter. These observations suggest that ciliatostasis is restricted to the humus and mineral zone of the soil, that is, to evolved soils and that ciliates must have an important role in litter decomposition.

The low numbers of active ciliates in evolved and cultivated soils contrast sharply with the high numbers of cysts present in them as evidenced by the large numbers of species and individuals appearing in air-dried and remoistened soils (Tables 2, 14), and by the results obtained from culture methods (e.g., Bamforth, 1971, 1984; Darbyshire & Greaves, 1967; Foissner, 1981a; Foissner *et al.*, 1986). Most of these genuine soil species seem to be active only for short periods because I could not encounter them in the fresh samples. Many of them have been found recently (unpubl. observations) in coniferous and deciduous litters, and Chardez (1967) has compiled

Table 2. Ciliatostasis in the top soil (0–5 cm) of a grassland and a coniferous forest

Habitat[1]	Day	Natural soil moistened to maximal saturation[2]		Air-dried soil rewetted to maximal saturation		Natural soil amended with 1% glucose and moist. to max. sat.	
		Individuals g^{-1} dry mass[3]	Number of species[4]	Individuals g^{-1} dry mass[3]	Number of species[4]	Individuals g^{-1} dry mass[3]	Number of species[4]
Grassland	2	21		5429		0	
(pH 5.5)	6	43		104		0	
	20	36		50		107	
	50	0	15	140	13	36	2
Coniferous	2	53		2447		728	
forest	6	926		840		1549	
(pH 4.0)	20	93		202		295	
	50	9	12	23	13	14	9

[1]100 g of a mixed sample of 10 borings were used in all experiments.
[2]No active ciliates were found in the natural, freshly collected soils. Litter was removed!
[3]0.4 g wet mass of soil were investigated by the direct method of Foissner (1983a).
[4]Total number of species of all days. The rather low values indicate that the optimal sample size has been not reached with the 0.4 g soil investigated.

a list of 95 species that have been found in fresh samples with direct methods of investigation.

(b) 'Fungistasis is frequently annulled by addition of energy-containing nutrients to the soil or to the propagules placed on a carrier after removal from soil.' Unfortunately, the effect of enriching soils with specific nutrients has not been investigated for ciliates. Complex nutrient sources have been frequently used, for instance by Koch (1915) and Waksman (1916), who found an increased number of ciliates and other protozoa in blood enriched soils. Viswanath & Pillai (1977a) reported extremely high abundances of ciliates when soil was added to autoclaved sewage or to a nutrient-rich 'agricultural medium.' Pena-Cabriales & Alexander (1983) found a marked increase in the number of protozoa in soil microcosms which were enriched with alfalfa grass residues. Preliminary experiments undertaken by myself using glucose-enriched soils, showed a substantial increase in the number of individuals but fewer species as compared with the non-enriched control (Table 2). Remoistening of air-dried soil also dramatically increased the number of individuals (Table 2). This has also been shown by Sherman (1914), Waksman (1916, 1937), Stout (1955a), Biczók (1959), Szabó *et al.* (1964), Darbyshire (1976), Elliott & Coleman (1977), Buitkamp (1979), and Foissner (1981a). In fact, the dramatic changes of the ciliate fauna observed in air-dried and remoistened soil samples, and their high abundance in litters, stimulated my formulation of the 'ciliatostasis' concept. Lockwood (1977) and Ho & Ko (1985) stated, 'Usually, complex material such as plant residues are most effective in annulling fungistasis.' It is clear that air-drying and rewetting stimulates organic breakdown, and causes an 'eutrophication' of the soil by decomposition of plant biomass (roots, etc.) and the liberation of carbohydrates and amino acids (Beck, 1968; Domsch *et al.*, 1983). Another similarity between fungistasis and ciliatostasis is the 'peak germination' of the spores and cysts. This is less with continually moist soils than rewetted

soils (Fantham & Paterson, 1924; Goodey, 1911; Roth & Griffin, 1980). This is also evident from the data presented in Table 2.

(c) 'Fungistasis normally requires the presence of living microorganisms; partial or complete sterilization of the soil by heat, volatile fumigants, or gamma radiation annuls the effect, but fungistasis may be restored to sterilized soil by reinoculation with microorganisms, more or less non-specifically and even including those apparently incapable of producing antibiotics.' Rather similar but inexact data have been obtained for ciliates. Stout (1955b) found that partial steam sterilization decreased the number of protozoan species, delayed the development of the fauna, but favoured the growth of the surviving ciliate species, especially in the treated topsoil. He observed, 'After 11 days of cultivation, these ciliates (*Colpoda inflata* and *Oxytricha pellionella*) were present in very great numbers which have never been paralleled by any other soil culture in my experience.' He speculated the reason to be a thermolabile toxic factor which is destroyed by the steam sterilization. In fact, with this statement, he anticipated the present concept! Comparable results were reported by Sherman (1914), by Singh & Crump (1953; *cf.* Table 34), and by Biczók (1955b, 1979) for protozoa in general and naked amoebae and ciliates in particular. Radu *et al.* (1974) found that low dosages of insecticides depress numbers of flagellates and naked amoebae but increase the abundance of the ciliates. Unfortunately, neither Stout (1955b) nor Radu *et al.* (1974) followed the further history of their experiments. Thus, it is impossible to find out if ciliatostasis was restored or not. There are, however, other studies which show the restoration of ciliatostasis in air-dried or sterilized and rewetted soils. Gellért (1957) and Biczók (1956, 1959) found that the ciliates in microcosms reach a peak during the first two weeks but then sharply decrease in spite of the unchanged culture conditions. This is also evident from the results of the experiments shown in Table 2.

(d) 'The propagules of most fungal species exhibit fungistasis in natural soils, though some are unaffected.' As already mentioned, the great variety of species of ciliates found in air-dried and remoistened soils are often very rare in fresh samples of soil. Exceptions are *Colpoda* spp., which are thus perhaps less affected by soil ciliatostasis.

The causes: The observations listed above are usually explained by changes in the bacterial flora (Singh & Crump, 1953), by changed environmental conditions (Foissner, 1981a), by increased soil moisture (Darbyshire, 1976), or by decreased competition (Radu *et al.*, 1974). The data of Tables 1 and 2, however, show no evidence for a correlation between the number of active ciliates and the soil moisture, though such a relationship might exist in soils under restricted moisture conditions (Darbyshire, 1976; Szabó *et al.*, 1964). The enriched, and perhaps changed, bacterial fauna in the remoistened microcosms may partly explain the increased abundance of active ciliates. But a correlation between the number of bacteria and protozoa in soil is uncertain (Stout & Heal, 1967), and perhaps restricted to microcosm experiments. Therefore, other factors may be involved. These are likely to be antiprotozoal substances produced by bacteria, fungi, actinomycetes, and plant roots (Beck, 1968; Biczók, 1955a, 1959; Darbyshire, 1972; Darbyshire & Greaves, 1973; Dive *et al.*, 1978, 1984; Geltzer, 1967, 1969; Heal & Felton, 1970; Krizková *et al.*, 1979; Petz *et al.*, 1985; Singh, 1942b, 1945; Zaher *et al.*, 1953), or by other protozoa. These substances can be destroyed by heat and other agents (Datta & Kaur, 1978; Singh, 1945), so offering a possible explanation for increased growth of protozoa in sterilized microcosms. *Colpoda*, a common soil ciliate, shows a greater resistance to mycotoxins than freshwater species such as *Paramecium* and *Stylonychia* (Geltzer, 1967, 1969).

This may reflect some adaptation of *Colpoda* to soil fungal ciliatostasis. *Colpoda* also secretes unknown substances which destroy some species of fungi (Brodsky, 1941; Nikolyuk, 1965b). The metabolites of some actinomycetes are more toxic to flagellates and ciliates than to bacteria (Zaher *et al.*, 1953).

The causal mechanism of fungistasis and soil microbiostasis in general is still being discussed (Ho & Ko, 1982; Roth & Griffin, 1980). Lockwood (1978) favoured the nutrient-deficiency hypothesis in which the level of available nutrients in soil is insufficient to support germination of nutrient-dependent propagules, except in nutrient-rich microsites. Inhibitory substances, where present, are most likely superimposed upon, and secondary to, a more pervasive fungistasis derived from chronic substrate deficiency. This explanation could apply to ciliatostasis, too, because the phenomena are so similar in both groups. Martin (1971) independently proposed the same to explain the pattern of distribution of testate amoebae. Kuserk (1980) showed that another group of soil protists in nature, the cellular slime moulds, are also food-limited.

The results presented and reviewed in this and the preceding section stress the contribution of microcosms to our knowledge of soil protozoa. But, in interpreting the results, we should keep in mind Meiklejohn's (1955) remark, 'The great dilemma in soil microbiology is how to obtain a true picture of what is really happening in the soil in the field.'

III. ECOLOGICAL SIGNIFICANCE

The excellent review of Stout & Heal (1967) was one of the first to demonstrate the importance of the protozoa in the soil ecosystem. More recent literature concerning the significance of the soil protozoa in regulating the bacterial populations and in contributing to nutrient mineralization, plant growth, and earthworm nutrition has been compiled and reviewed by Nikolyuk (1965a), Satchell (1967), Nikolyuk & Tapilskaja (1969), Biczók (1979), Stout (1979, 1980), Geltzer *et al.* (1980a), Finlay & Ochsenbein-Gattlen (1982), Clarholm (1984), Flack & Hartenstein (1984), and Ingham *et al.* (1985). Here, I will confine my discussion to a selection of more recent ecosystem studies, paying particular attention to soil protozoa as a potential means of controlling soil-borne plant diseases.

A. *Standing Crop and Respiration*

From the data of Ryan (1977), Persson *et al.* (1980), Davis (1981), and Grimm (1983), one can calculate that the microflora (bacteria and fungi) account for 91% (81–96%) of the heterotropic respiration of the soil. Only 9% of the total comes from the 'animals' and 69% of the 'animal' respiration is due to the protozoa, although their contribution to the standing crop biomass is 'only' approximately 30% (Fig. 3). These are mean values calculated from the few ecosystem studies which included protozoa (Table 3). This proportion of the biomass is significant and disproves Stout's (1980) conclusion 'that the protozoan biomass is in all cases minimal.' In this area, the studies of Volz (1951, 1967) are pioneering but too incomplete to draw reliable conclusions. Some of my own estimations (not included here) confirm protozoal importance, but in earthworm-rich soils the ratio of the protozoa to the total biomass is considerably lower than stated above (Bachelier, 1963; Meisterfeld, 1986). In most of the investigations mentioned in Table 3, only one or two groups of protozoa have been considered and the total dry mass may have been underestimated.

In spite of their high numbers, the total volume of soil organisms (microflora

Table 3. The contribution of the protozoa to the soil community

Site[1]	PROTOZOA			'WORMS'[2]			ARTHROPODS		
	Dry biomass $mg\,m^{-2}$	%	Respiration %	Dry biomass $mg\,m^{-2}$	%	Respiration %	Dry biomass $mg\,m^{-2}$	%	Respiration %
A	139	44	n.d.[3]	8	2	n.d.	170	54	n.d.
B	20	2	n.d.	394	45	n.d.	469	53	n.d.
C	87	6	n.d.	594	38	n.d.	869	56	n.d.
D	409	16	n.d.	1399	55	n.d.	751	29	n.d.
E	1242	36	n.d.	1287	38	n.d.	877	26	n.d.
F	185	3	n.d.	5202	85	n.d.	728	12	n.d.
G	n.d.	n.d.	39	n.d.	n.d.	27	n.d.	n.d.	34
H	1240	78	96	56	4	1	284	18	3
I	1660	84	98	96	5	1	219	11	1
J	3000	53	n.d.	2459	44	n.d.	173	3	n.d.
K	69	2	n.d.	2370	53	n.d.	2000	45	n.d.
L	1000	23	n.d.	2199	52	n.d.	1058	25	n.d.
M	410	39	75	447	43	13	182	18	12
N	200	12	39	605	35	34	922	53	27

[1]A–F: 6 sites in the Austrian Central Alps, from Foissner (1985a). A: poorly developed rendzina with cushion plants; about 2500 m NN. B: alpine pseudogley in a snow filled pit; about 2300 m NN. C: alpine mat on alpine pseudogley; about 2300 m NN. D: little grazed alpine pasture on alpine pseudogley; about 1800 m NN. E: isolated alder stand on alpine pseudogley; about 1800 m NN. F: alpine pasture on alpine brown earth; about 1900 m NN. Only testaceans and ciliates were investigated.
G: Beech forest near Sollingen, FRG, from Grimm (1983). Only testaceans were investigated.
H, I: 2 sites in the maritime Antarctic, Signy Island, South Orkney Islands, from Davis (1981). H: dry moss turf community. I: wet moss carpet community. Only naked amoebae and colourless zooflagellates were investigated.
J: Cultivated land at Turew, Poland, from Ryszkowski (1979). All protozoa were investigated.
K: Mixed prairie on lacustrine clay at Matador, Canada, from Coupland & van Dyne (1979). All protozoa were investigated (testaceans, however, may be excluded).
L: Mean of 4 habitats in a coastal tundra at Barrow, Alaska, from Bunnell *et al.* (1975). Values for the diptera are from MacLean (1980). For the protozoa, a biomass of 0.05 to 0.15 $g\,m^{-2}$ is given for the upper 1 cm. Assuming a well colonized depth of 10 cm, the standing crop may be estimated to be about 1000 $mg\,m^{-2}$.
M: Arctic meadow, Truelove Lowland, Devon Island, Canada, from Ryan (1977) and supplemented by the 9% standing crop of the nematodes mentioned in Procter (1977). All protozoa were 'provisionally' investigated.
N: Coniferous forest in Central Sweden, from Persson *et al.* (1980). Only naked amoebae, colourless zooflagellates, and ciliates were investigated.
[2]'Worms' include Nematoda, rotifers, Enchytraeidae, Lumbricidae.
[3]Not determined.

included!) amounts to only 2300 $cm^3\,m^{-2}$; supposing a colonized depth of 15 cm, soil volume is 150 000 $cm^3\,m^{-2}$ with an available pore space of 50% (Stöckli, 1946). An even lower value, about 500 $cm^3\,m^{-2}$, may be calculated from Fig. 3 of Bachelier (1963).

One of the most disappointing matters is the nearly complete lack of data on the dry mass of protozoa, particularly of soil protozoa. The estimated ratios (dry mass/wet mass) range from 0.05 (Foissner, 1985a), which is perhaps too low, to 0.59 (Gates *et al.*, 1982), which is very probably too high. Kalmus (1931) and Sinclair *et al.* (1981) found a biomass conversion ratio of about 0.1 in *Paramecium* and *Acanthamoeba polyphaga*.

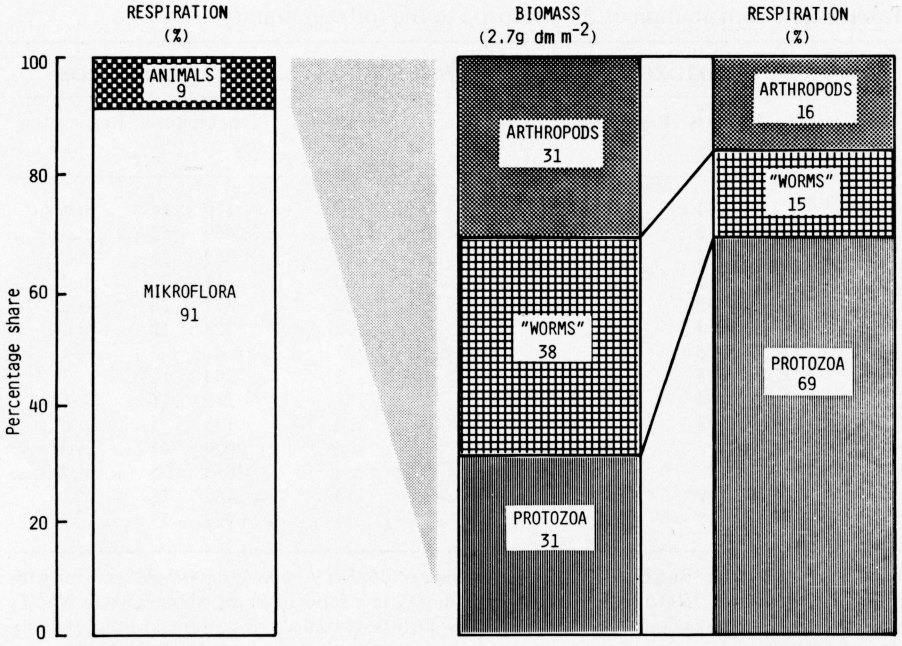


Fig. 3. Contribution of protozoa to the biomass and respiration of the soil animals. The graphs show the mean of 14 ecosystem studies from various sites of the world. Data from Table 3.

Another error is produced if the specific gravity of the soil, and not its bulk density, is used to calculate the standing crop m^{-2}. This is the cause of the high standing crop values of Pussard (1967) and Buitkamp (1979).

In spite of these and other deficiencies, the extraordinary contribution of the protozoa in the soil ecosystem becomes more and more obvious, especially in harsher climates of the world where earthworms are few or absent (Block, 1985; Davis, 1981).

B. *Annual Production*

Field studies of production of soil protozoa are mostly restricted to testate amoebae, the shells of which can be used to estimate their mortality (Schönborn, 1986). However, Heal (1967) and Stout & Heal (1967) calculated, from the daily counts of Cutler *et al.* (1922), that small naked amoebae and zooflagellates produce 50–300 times their standing crop within a year. Similar values were obtained by Lousier & Parkinson (1984) and Meisterfeld (1986) for testate amoebae of an aspen woodland soil and a beech forest soil, respectively (Table 4). The P/B (Production/Biomass) quotients of the naked amoebae (13) and zooflagellates (18) were considerably lower than the above figures (Meisterfeld, 1986). However, the production of these groups was probably underestimated, because the calculations did not include mortality.

The annual production of the testaceans has been investigated by Schönborn (1975, 1977, 1978, 1982a), Foissner & Adam (1981a), Lousier & Parkinson (1984), and Meisterfeld (1986). The values obtained by Schönborn (1975, 1977, 1978, 1982a) and Foissner & Adam (1981a) agree in their order of magnitude, whereas those of

Table 4. Comparison of population parameters for soil testaceans from different sites of the world

Parameter	Moss under beech forest[1] (moder)	Ash-maple forest[2] (mull)	Alpine rendzina[3] (moder)	Alpine mat[4] (moder)	Aspen woodland[5] (mor)	Beech forest[6] (mull)
Annual mean density ($\times 10^6$ m^{-2})	1.7	33.6	39.6	20.1	261	84
Annual mean biomass (mg m^{-2})	15.5	1033	2209	1165	723	1715
Number of generations (yr^{-1})	16.0	12.5	n.d.[7]	8	90	n.d.
Mortality rate (% day^{-1})	3.0	8.5	n.d.	n.d.	10.8	n.d.
Production numbers ($\times 10^6$ m^{-2})	145	940	29	118	90 930	358 000
Production biomass (g m^{-2})	0.11	25.9	1.4	5.4	206	73
Biomass turnover (P_B/B)	8.1	43.9	0.7	5	285	43

From: [1]Schönborn (1977); [2]Schönborn (1982a); [3]Foissner & Adam (1981a); [4]Foissner & Adam (1981a); [5]Lousier & Parkinson (1984); [6]Meisterfeld (1986); [7]Not determined.

Lousier & Parkinson (1984) are considerably higher (Table 4). Besides site differences, a probable explanation is the high rate of shell disappearance, which they calculated from oven-dried and remoistened soil microcosms. As already mentioned, such treatment changes the soil milieu and accelerates the decomposition processes. Meisterfeld & Heisterbaum (1986), working with a very similar method, reported significantly lower, but still high, rates of shell disappearance. They found a loss of 40% after one week, whereas Lousier & Parkinson (1981a) calculated a loss of 74–95%. These results show higher rates of shell disappearance than those supposed by Schönborn (1975, 1978, 1982a) and Foissner & Adam (1981a). Thus, their production values are very probably too low. On the other hand, the mean value of 90 generations yr^{-1} calculated by Lousier & Parkinson (1984) seems rather high, if one considers the low reproductive rate of testaceans in general (Heal, 1964; Laybourn & Whymant, 1980; but see Meisterfeld, 1981) and the estimated 15 generations yr^{-1} of naked amoebae in a prairie soil (Elliott & Coleman, 1977).

In spite of these and other methodological problems, it is clear that the production of the testate amoebae is in the same order of magnitude as that of the earthworms. The annual live mass production of the latter ranges from 30–250 g m^{-2} (Syers & Springett, 1984). The production of Enchytraeidae was 10–13 times lower than that of the testaceans in an aspen woodland soil, where the testacean community respired approximately 6% of the total carbon input (Lousier & Parkinson, 1984). If we take into account the standing crop and production of other protozoa, which is perhaps lower (Section II.B), we may raise this percentage to approximately 10%. This fully agrees with the recent calculation of Meisterfeld (1986) and is supported by Cowling (1983). He found the contribution of *Corythion dubium* to the annual respiratory loss to be of the same order of magnitude as that of the total mesofaunal component (Rotifera, Nematoda, Tardigrada, Collembola, and Acari combined) in terrestrial moss communities of Signy Island in the maritime Antarctic.

As Lousier & Parkinson (1984), Schönborn (1978), and Meisterfeld (1986) have stressed, the protozoa in general have been largely ignored by soil biologists, and in production and energy cycle studies. Soil protozoologists are at least partly responsible for this themselves. There is a tendency to underestimate the significance of the

group because workers appear sometimes to be unaware of the contribution of the other animals or fail to relate their results to that contribution (e.g., Darbyshire, 1975; Foissner & Adam, 1981a, corrected in Foissner, 1985a; Stout, 1980; Volz, 1971). The summary presented here clearly indicates the importance of the protozoa in the soil community.

C. *Potential for Biological Pest Control*

Some soil protozoa feed selectively on certain bacteria and fungi (Heal & Felton, 1970; Nikolyuk, 1969; Petz *et al.*, 1985; Severtzova, 1928; Singh, 1964). This suggests a potential for biological control of soil-borne bacterial and fungal plant diseases (Alabouvette *et al.*, 1981b; Anderson & Patrick, 1980; Chakraborty & Old, 1986; Petz *et al.*, 1986; Singh, 1960).

There are two main pathways of biological pest control by protozoa: through competition, and through direct effects either from certain metabolites or by predation. Most of the data concern the latter possibility.

Food competition between the bacteriophagous nematode *Mesodiplogaster* and an amoeboid protozoon was observed by Sohlenius (1968). When cultured with this amoeba, *Mesodiplogaster* did not reach as high a density as when it was cultured alone. However, this observation was not confirmed by Elliott *et al.* (1980), who found that *Mesodiplogaster*, which feeds on bacteria as well as amoebae, grows best in the presence of amoebae.

Hino (1935) first suggested the use of soil protozoa as biological pest control agents. He observed that potatoes remained healthy in the presence of soil protozoa, although *Bacillus aroideae*, a causal bacterium of vegetable soft rot, had been added to the cultures. In the absence of protozoa, the plants wilted in a few days. Later, Brodsky (1941) observed a suppression of the plant pathogenic fungus *Verticillium dahliae* by metabolic products of the ciliate *Colpoda*. In a large field experiment, Brodsky (1941) inoculated active cultures of *Colpoda* into a cotton field. This reduced the infection rate with *V. dahliae* by 7%–11%, and increased the yield by 30%. Similar results were reported by Nikolyuk (1965a,b). Spores and microsclerotia of *V. dahliae* did not germinate and the mycelia were lysed in the presence of *Colpoda steinii* (= *Paracolpoda steinii*), *C. cucullus*, or *Amoeba albida*. Some of the suppressive effects were probably due to bacteria attached to the protozoa. Nikolyuk (1965b) showed that ciliates would reduce cotton seed infection by *Rhizoctonia solani*. The results of Brodsky (1941) and Nikolyuk (1965a,b) were confirmed and extended by Mavljanova (1966) and Nikolyuk *et al.* (1980). They showed, for instance, that irradiated ciliates were less effective (Table 5).

Weber *et al.* (1952) found that plant pathogenic nematodes were attacked by the giant amoeba *Theratromyxa weberi*. They suggested a possible role of this organism in controlling potato root eelworm and other nematode pests. A direct inoculation approach, however, was unsuccessful (Van der Laan, cited in Old & Patrick, 1979). Recently, research has been focused again on these giant amoebae because several authors found that they attack hyphae, spores, and microsclerotia of a wide range of non-pathogenic and pathogenic fungi, including *Gaeumannomyces graminis* var. *tritici*, the cause of the take-all disease of wheat. The literature on this subject has been excellently reviewed by Old & Patrick (1979), Chakraborty & Warcup (1983), and Old & Chakraborty (1986). Several fungal diseases have been controlled in pot experiments by the addition of cysts or active vampyrellid amoebae to the soil. Practical application is difficult, however, because of the poor selectivity and the rather low reproduction rate of the amoebae. The quickly reproducing ciliates of the family

Table 5. Effect of the ciliate *Colpoda maupasi* on the infection of cotton seed with *Rhizoctonia solani* 30 days after sowing (from Mavljanova, 1966)

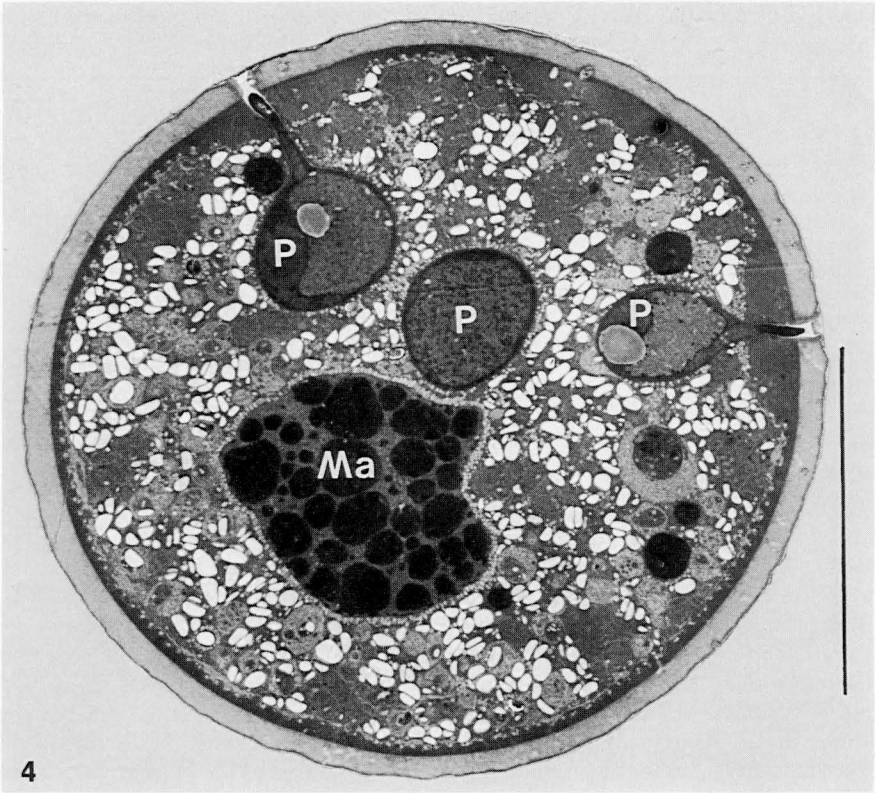
Experiment	Germination capacity (%)	Stem length (cm)
1. Seeds sown in non-infected soil	100.0	15.5
2. Seeds sown in *R. solani* infected soil	18.5	13.7
3. Seeds pretreated with *Azotobacter* and sown in *R. solani* infected soil[1]	11.2	13.8
4. Seeds pretreated with *C. maupasi* and sown in *R. solani* infected soil[1]	74.0	16.0
5. Seeds pretreated with γ-irradiated (1 kr) *C. maupasi* and sown in *R. solani* infected soil	33.3	16.9
6. As 5; dose 5 kr	51.9	17.3
7. As 5; dose 10 kr	55.5	15.1

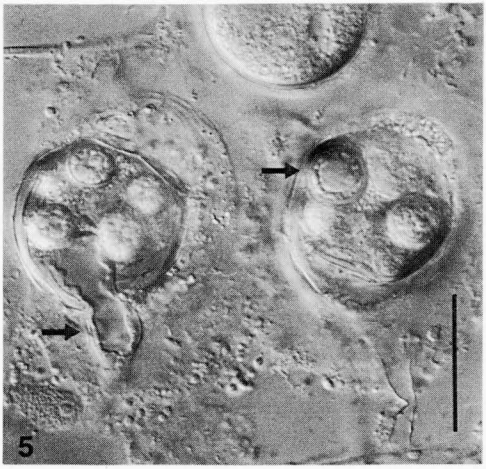
[1]Seeds were pretreated with actively growing cultures of *Azotobacter chroococum* or *Colpoda maupasi* for seven hours.

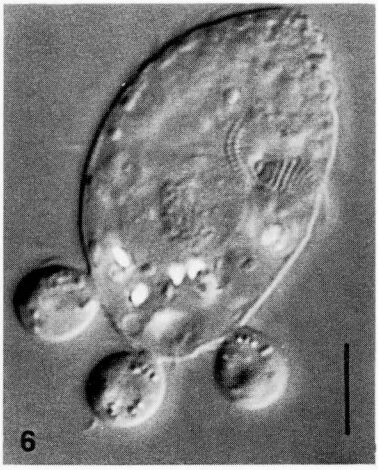
Grossglockneridae, which feed exclusively on the contents of fungal and yeast hyphae and spores, seem to be more promising (see Section IV.E). Petz *et al.* (1985) tested 12 species of fungi as food for *Grossglockneria acuta*. Only three of them, *Mucor mucedo*, *Aspergillus* sp., and a mucoracean, supported reproduction of the ciliate. Repeated inoculation of *G. acuta* into cultures of *Verticillum* sp. and *Penicillium* sp. caused rapid encystment or death. Furthermore, if *Penicillium* hyphae contaminated the cultures (e.g., *Mucor mucedo*) growth of *G. acuta* was considerably depressed. I believe that this is due to the production of toxic substances by the fungi and not to an inability of the ciliate to attack hyphal walls.

Another argument for the use of free-living protozoa as pest control agents is that most of them are not pathogenic to plants and man. There are some exceptions: phloem-restricted flagellates are associated with at least three economically important diseases of cultivated plants, marchitez of oil palm, hartrot of coconut, and phloem necrosis of coffee (Dollet, 1985). It is likely that active or cystic stages of these pathogens are transmitted by insects and may be found in soil, too. McLennan (1930) observed an amoeba, *Leptomyxa reticulata* var. *humuli*, associated with a disease of hops; and Tuzet & Rouquerol (1961, 1962) observed a parasitic amoeba in rice roots. Darbyshire & Greaves (1971) found *Acanthamoeba palestinensis* in the epidermis and outer cortex of pea roots experimentally infected with *Pseudomonas* sp. The amoebae apparently followed the bacterial invasion, as no amoebae were found inside pea roots when *Pseudomonas* was absent (Darbyshire & Greaves, 1973). Although *A. palestinensis* readily ingested *Pseudomonas*, it was unable to reduce the root damage. The inability of the protozoa to reduce bacterial density in soil and liquid below the rather high level of ca. 10^5–10^6 g^{-1} (Danso *et al.*, 1975; Fenchel, 1980; Habte & Alexander, 1975, 1977, 1978a,b), together with their sensitivity to bacterial toxins (Darbyshire, 1972; Heal & Felton, 1970; Singh, 1942b) and to root exudates (Biczók, 1979), are serious restrictions for their employment as biological pest control agents.

Many soil protozoa are themselves attacked by parasites which could also limit their use as such agents. Foissner, W. & Foissner, I. (1984), for instance, found a curious ectoparasitic flagellate, *Spiromonas gonderi*, which attacked *Colpoda* spp. and which caused a strong depression of these ciliates in a soil microcosm (Fig. 6).







Figs 4–6. Resting cysts of the soil ciliate *Kahliella simplex* parasitized by the zoosporic fungus *Ciliomyces spectabilis*. Fig. 4. TEM-picture of an early infection stage. Ma = macronucleus of the ciliate, P = parasites. Scale bar = 18 µm. Fig. 5. Late infection stage. The bottom arrow points to vegetative hypha of the fungus leaving the ciliate cyst. The upper arrow denotes a developing oospore. Scale bar = 30 µm (from Foissner & Foissner, 1986a). Fig. 6. Trophont of *Paracolpoda steinii* parasitized by three individuals of the flagellate *Spiromonas gonderi*. Scale bar = 10 µm. (from Foissner & Foissner, 1984)

Some fungi parasitize soil amoebae (e.g., Dayal & Srivastava, 1979), soil testaceans (Chardez, 1965b; Drechsler, 1936, 1937, 1939, 1947, 1959, 1961; Figs 77, 78), and soil ciliates (Figs 4, 5). Of the cysts of *Kahliella simplex* in culture, 90% were parasitized by *Ciliomyces spectabilis* (Foissner, I. & Foissner, W., 1986a,b). On the other hand, Purrini (1981) suggested that the population density of the forest soil fauna is regulated by various protozoan parasites (e.g., sporozoa). Exact data, however, were not provided.

Wolff (1909) drew attention to the potential importance of protozoa as pest vectors, via undigested expelled spores and cysts. Indeed, Heal 1963 (cited in Heal & Felton, 1970) found that spores of many different kinds of fungi were ingested and carried some distance by amoebal trophozoites but were expelled as viable propagules. Likewise, the conidia of *Cochliobolus sativus* were ingested but not digested by giant soil amoebae (Chakraborty & Old, 1982).

The known facts suggest some biological pest control potential of the soil protozoa (see also Old & Chakraborty, 1986). Unfortunately, the whole field is so understudied that its potential and limitations cannot be judged seriously.

IV. ADAPTATIONS BY CILIATES AND TESTACEANS

The heterogeneous physical and biological properties of the natural world has caused the organisms living in it to evolve a wide variety of characters which may be interpreted as 'adaptations' to their respective environments. The adaptations often appear to be more pronounced the more stable and, in geological terms, the more long-lived the habitat is. In principle, competition has led to a greater degree of niche segregation. The soil is a very special environment for free-living protozoa. Three factors are most important for their existence and activity: the structure of the porous space, the astatic water supply, and intraspecific and interspecific interactions.

Many adaptations to environments have been reported for freshwater, soil and marine sand protozoa, particularly for certain ciliates and testate amoebae. However, only for the testate amoebae have some of them been corroborated by quantitative methods. It seems reasonable to discuss the adaptations of soil protozoa in relation to those of freshwater protozoa, because it is presumed that many of them originated from this biotope (Section IV.C). Furthermore, it is of interest to compare the adaptations in soil protozoa with those in marine sand protozoa, because the latter habitat has a similar physical environment in respect of the porosity of the substrate and could have been the source of some protozoa in coastal soils.

For a treatment of the general morphology of the protozoa, the reader may turn to the excellent textbooks of Grospietsch (1965), Schönborn (1966a), Page (1976), Corliss (1979), Ogden & Hedley (1980), Hausmann *et al.* (1985), and Lee *et al.* (1985). Some general information on the morphological organization of the ciliates and testate amoebae is given in the explanation to the figures in this review.

A. *Adaptations by Ciliates*

1. *Morphological adaptations.* There is a generally accepted view that one of the most evident adaptations of soil ciliates is their small size (Brodsky, 1935; Stout & Heal, 1967; Szabó *et al.*, 1959). Mean body length, mean body width, and mean biomass are significantly smaller in soil ciliates than in ciliates from freshwater and marine sand (Table 6). The small size, and volume, is achieved either by an overall reduction in size (as in *Nivaliella plana, Stammeridium kahli, Microdiaphanosoma arcuata, Orthokreyella schiffmanni, Bardeliella pulchra, Pseudoplatyophrya nana,*

Table 6. A comparative description of the known ciliate communities of freshwater, soil, and marine sand

Character	Freshwater[1]	Soil[2]	Marine sand[3]
Mean biomass (mg) of 10^6 individuals[4]	1076 (n = 200)[5]	98 (n = 238)	872 (n = 200)
Mean body length (μm)	162 (n = 200)	110 (n = 238)	424 (n = 200)
Mean body width (μm)	56 (n = 200)	36 (n = 238)	54 (n = 200)
% Colpodea[6]	5 (n = 422)	18 (n = 238)	0 (n = 292)
% Hypotrichida	11 (n = 422)	37 (n = 238)	20 (n = 292)
% Peritrichida	21 (n = 422)	3 (n = 238)	0.3 (n = 292)
% cyst forming species	≤80	>95	<2
% species with reduced ciliature[7]	41 (n = 182)	53 (n = 229)	53 (n = 200)
% species with nodulated macronucleus[8]	8 (n = 200)	25 (n = 238)	43 (n = 200)
Ploidy of macronucleus	generally high	generally high	often low
Body form	often cylindrical	often flattened, elongated, worm-like	often flattened, elongated, worm-like
Caudal prolongation	uncommon	common	very common
'Cephalization'	unknown	unknown	known
Contractility	generally low	generally low	generally high
Fragility	generally low	generally low	generally high
Cytological peculiarities	cytoplasm seldom strongly vacuolated	cytoplasm seldom strongly vacuolated	cytoplasm often strongly vacuolated; skeletal rodlets
Movement	thigmotactic creepers common only in the Aufwuchs; sessile forms common	thigmotactic creepers common; sessile forms nearly absent	thigmotactic creepers common; sessile forms nearly absent
Nutrition	great majority of common species are bacteriovorous, or macrophagous	great majority of autochthonous species are bacteriovorous, predaceous, or mycophagous	great majority of autochthonous species are macrophagous (predaceous)
Symbiotic bacteria on the body surface of species within the sulfide system	present	unknown	present
Number of species	about 4000	about 300	about 600
Abundance[9] range m^{-2}	$5 \times 10^4 - 5 \times 10^6$	$0 - 4 \times 10^6$	$5 \times 10^6 - 3 \times 10^7$

[1,2,3]Data for freshwater species is based chiefly on the monographs of Bick (1972), Dragesco (1970), and Foissner (1983b, 1984a,c,d); that of the soil species is based on Table 14; and that of the marine sand ciliates is based on the monographs of Fauré-Fremiet (1950) and Dragesco (1960, 1963a,b).

[4]Mean biomass $= \frac{Bx + By + Bn}{n} \times 10^6$. Biomasses of single species were calculated as described in the footnote of Table 14. Rough estimations.

[5]n refers to the number of species considered.

[6]The percentages of Colpodea, Hypotrichida, and Peritrichida in freshwater are based on the faunal list of Foissner (1980b), who studied stagnant alpine pools; and on the list of indicators of saprobity of Sládeček (1973). Percentages referring to soil and marine sand ciliates are based on the above cited studies. Systematics of the Colpodea according to Foissner (1985c).

[7]Peritrichida and Suctorida are excluded because of their high degree of specialization. Calculated from the same data set as used for 'mean biomass'.

P. terricola; Figs 7–18, 126–130), or by a reduction of body width (e.g., *Hemisincirra filiformis, H. muelleri, Engelmanniella mobilis, Amphisiella acuta, Protospathidium bonneti, Phialina binucleata*; Figs 19–33). These variations in body size and shape seem reasonable if one considers that the space available between the soil particles is restricted. The issue remains open to question because some marine sand ciliates also living in small spaces are large; but such ciliates are a remarkable exception among the otherwise small inhabitants of this special biotope, inclusive of the testate amoebae which are generally small (Ax, 1966; Chardez, 1984; Dragesco, 1960, 1962; Fauré-Fremiet, 1950; Golemansky, 1978). No explanation is available at present (Ax, 1966; Dragesco, 1962). Some of the differences could be due to the fact that sand ciliates occupy pores that are water-filled at all times, whereas soil ciliates are often limited to a water film and must tolerate even complete desiccation.

The literature includes statements that individuals from soil populations are smaller than individuals of the same species from freshwater (e.g., Fantham, 1929; Kevan, 1962; Koffman, 1934; Kühnelt, 1950). The original reference(s) were not available to me however, my own measurements clearly indicate that the sizes of the soil and freshwater populations of the same species are similar (Table 7). If this is indeed the case, it is possible that the claim of differences may result from species misidentifications, which are often gross. For example, from his figures, we can see that Koffman (1926) misidentified *Chilodon cucullus* (really a *Pseudochilodonopsis* sp.), *Colpidium colpoda* (*Pseudocyrtolophosis* sp.), and *Blepharisma lateritia* (a hypotrich)! A further example is *Cyclidium glaucoma*, which is reported in many papers (including my own!) as being frequent in many soils of the world. Freshwater populations of this species have been carefully redescribed by Didier & Wilbert (1981). This led me to re-study my own slides and it became clear that my *Cyclidium glaucoma* was a different species, one already described by Kahl (1931) as *Cyclidium muscicola* (Figs 104, 105). Other examples can be found in the paper of Reinhard *et al.* (1967), who also claim that the soil specimens are smaller in size than those from freshwater populations. Examination of their species list shows many taxonomic errors, thus rendering their claim meaningless.

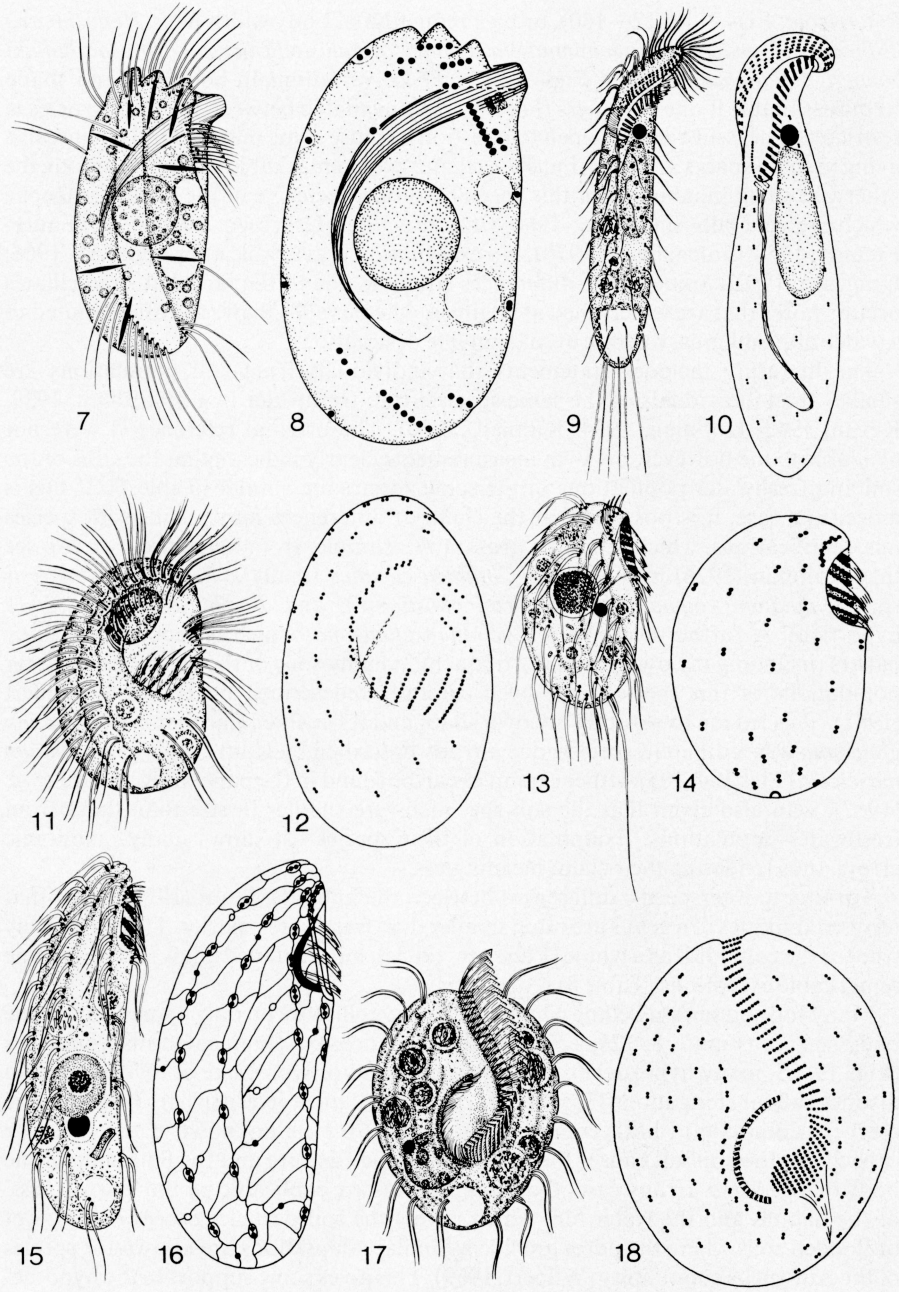
Turning to interspecific differences between the habitats, Stout (1952) noted that terrestrial species of a genus are often smaller than freshwater species. This is certainly true for the colpodids as a whole (Foissner, 1985c), but a detailed analysis shows some remarkable exceptions (Table 8).

Many soil and sand-dwelling ciliate species have ciliature on only a small part of the body surface (Figs 7, 8, 126, 127, 130, all hypotrichs), a fragmented macronucleus (Figs 19, 23, many hypotrichs), and a flattened and/or worm like body often with a distinct caudal elongation (Figs 19, 24, 26, 28, 143, most hypotrichs). Thigmotactic creepers dominate in both communities (Table 6). It is unknown if the adhesive capacity of the animals causes the reduction of the ciliature and the flattening of the body or *vice versa*. In any case, these adaptations are explicable by the 'narrowness' of the habitat and the water film which covers the soil particles except in very wet or flooded soils where the pores are filled. Similar adaptations are known for species of the Aufwuchs community (Wilbert, 1969). This gives some support to the hypothesis of Schönborn (1962b, 1966a) that the protozoa invaded the soil via the Aufwuchs.

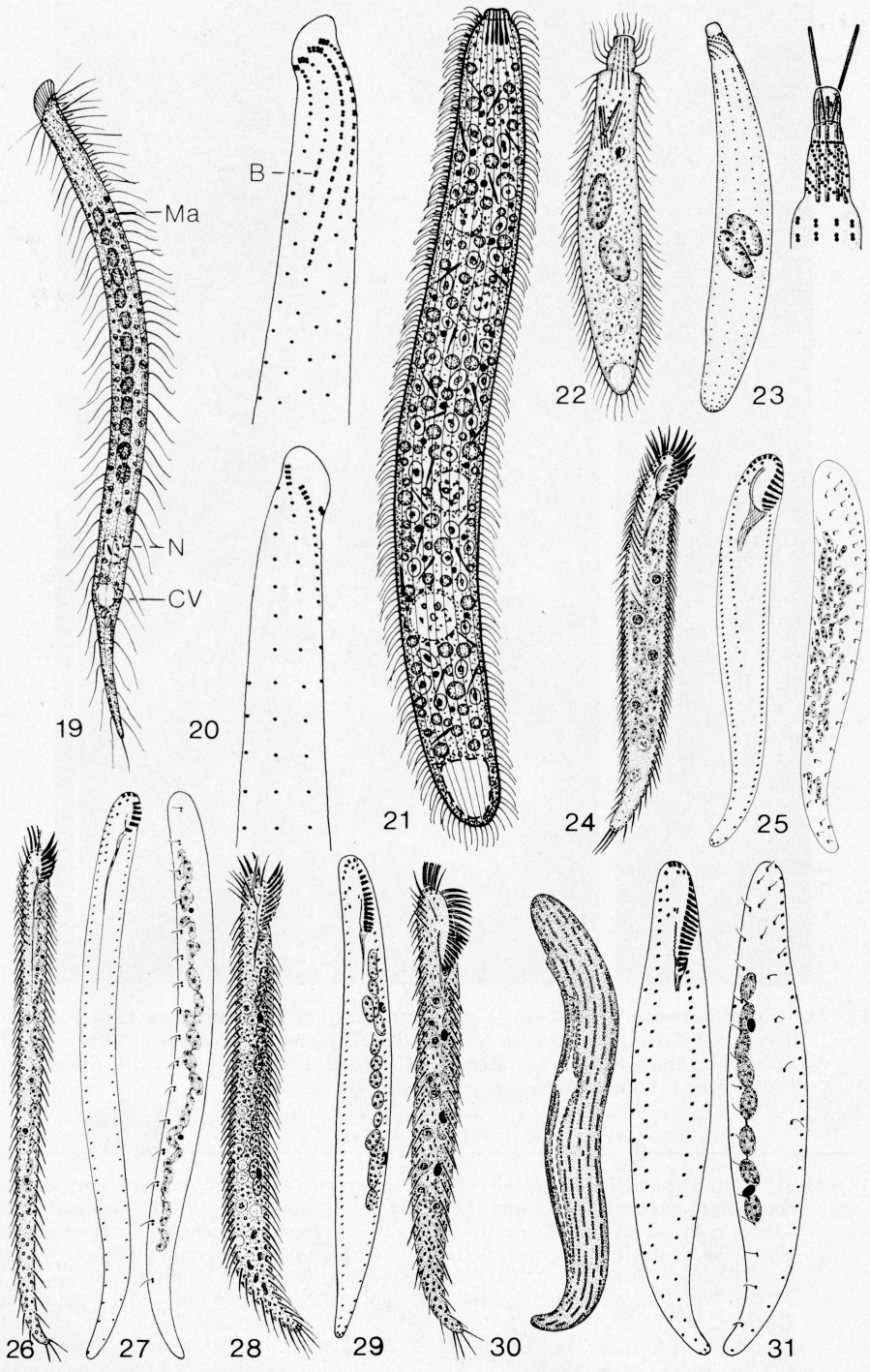
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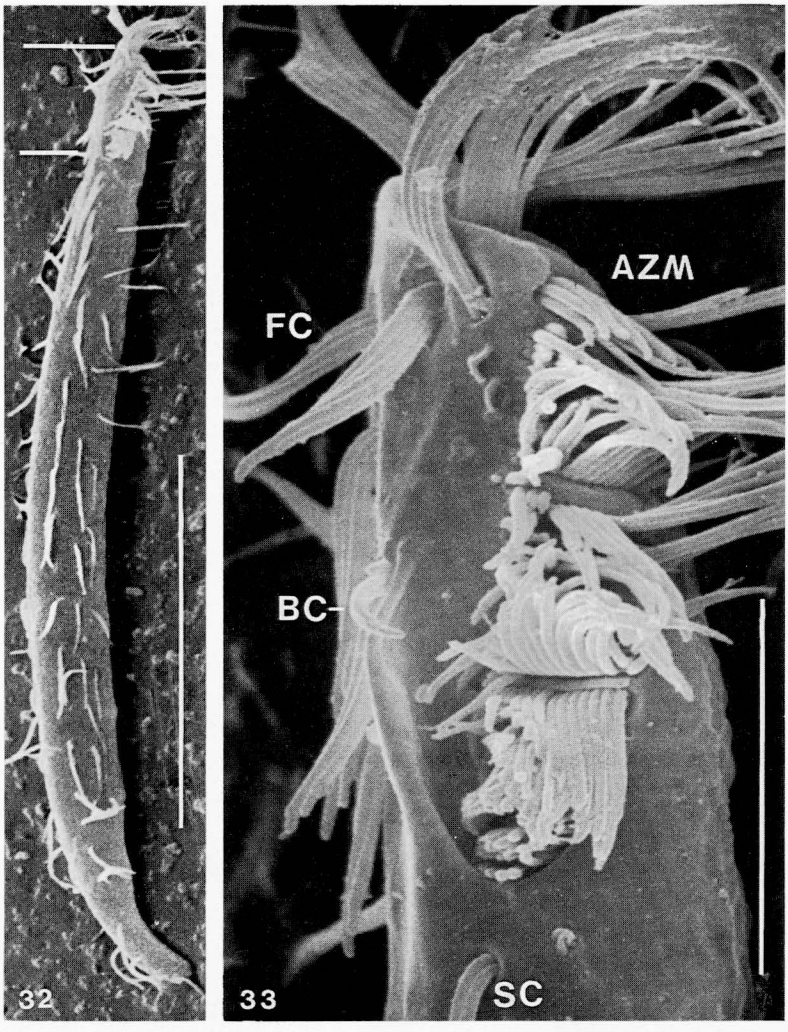
[8]Only species with more than two nodules have been considered as having a nodulated macronucleus. Two nodules are 'normal' for many groups (e.g., hypotrichs). Calculated from the same data set as used for 'mean biomass'.

[9]These are only a few, perhaps not representative, examples from mesosaprobic rivers (Schönborn, 1981, 1982b), alpine grassland soils (Foissner, 1981a), and marine sand (Fenchel, 1969).



Figs 7–18. Some very small autochthonous soil ciliates. Each species was drawn from specimens *in vivo* and after silver impregnation. Figs 7, 8. *Stammeridium kahli*, right side, 19 µm and 16 µm (from Foissner, 1985d). Figs 9, 10. *Metopus hasei*, ventrum, 90 µm and 65 µm (from Foissner, 1981b). Figs 11, 12. *Orthokreyella schiffmanni*, ventrum, 15 µm and 11 µm (from Foissner, 1984a). Figs 13, 14. *Microdiaphanosoma arcuata*, right side, 19 µm and 10 µm (from Foissner, 1981b). Figs 15, 16. *Pseudocyrtolophosis alpestris*, right side, 23 µm and 18 µm (from Foissner, 1980a). Figs 17, 18. *Bardeliella pulchra*, ventrum, 32 µm and 22 µm. (from Foissner, 1984a)


Ma
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Figs 32, 33. SEM-pictures of *Engelmanniella mobilis*, ventrum. Fig. 32. General view; the lines denote the very small oral area. Scale bar = 77 µm. Fig. 33. Detail of the oral area. AZM = adoral zone of membranelles, BC = buccal cirrus, FC = frontal cirri, SC = somatic cirri. Scale bar = 11 µm. (from Foissner & Simonsberger, unpublished)

Figs 19–31. Worm-like autochthonous soil ciliates. Each species, except *Enchelyodon terrenus*, was drawn from specimens *in vivo* and after silver impregnation. Figs 19, 20. *Protospathidium bonneti*, right and left side, 125 µm. B = brush, CV = contractile vacuole, Ma = macronucleus, N = food vacuole (from Foissner, 1981c). Fig. 21. *Enchelyodon terrenus*, right side, 300 µm (from Foissner, 1984a). Figs 22, 23. *Phialina binucleata*, 98 µm and 75 µm (from Berger *et al.*, 1984b). Figs 24, 25. *Amphisiella acuta*, ventrum and dorsum, 150 µm and 115 µm (from Foissner, 1982). Figs 26, 27. *Hemisincirra filiformis*, ventrum and dorsum, 212 µm and 130 µm (from Foissner, 1982). Figs 28, 29. *Hemisincirra muelleri*, ventrum, 186 µm and 103 µm (from Foissner, 1985e). Figs 30, 31. *Engelmanniella mobilis*, ventrum and dorsum, 223 µm, 172 µm, and 122 µm; cf. also Figs 32, 33. (from Foissner, 1982)

Table 7. Body lengths and widths of some ciliate species from freshwater and soil populations

Species[1]	Freshwater population		Soil population	
	Length	Width	Length	Width
Chilodonella uncinata	32.9 (±6.4)	20.2 (±4.5)	35.7 (±6.8)	23.4 (±4.3)
Trachelophyllum apiculatum	107.5 (±7.0)	14.1 (±0.7)	117.9 (±16.8)	25.6 (±5.3)
Spathidium anguilla	112.8 (±20.6)	17.3 (±3.6)	119.9 (±15.4)	14.5 (±2.3)
Cyrtolophosis mucicola	21.0 (±3.1)	8.7 (±1.0)	23.0 (±2.9)	10.1 (±1.3)
Cinetochilum margaritaceum	20.1 (±2.9)	13.8 (±2.0)	16.5 (±1.5)	11.2 (±1.4)
Histriculus muscorum	76.0 (±8.0)	41.9 (±5.3)	79.0 (±10.2)	39.6 (±4.9)
Urosomoida agiliformis	65.0 (±10.9)	18.9 (±3.5)	56.2 (±9.8)	17.0 (±2.2)

[1]Measurements (arithmetic mean and standard deviation; in μm) based on 15–20 protargol silver stained specimens. Most data are original, some are from Foissner (1982, 1984a) and Augustin, Foissner & Adam (unpubl.).

Table 8. Comparison of the sizes of some randomly selected soil and freshwater ciliate species of the same genus

Soil[1]	Length in μm ($\bar{x}$)	Freshwater[1]	Length in μm ($\bar{x}$)
Spathidium s. l. (20 species)[2]	156	*Spathidium s. l.* (20 species)[2]	132
Tachysoma spp. (6 species)	107	*Tachysoma* spp. (6 species)	85
Dileptus spp. (4 species)	121	*Dileptus* spp. (4 species)	437
Colpoda cucullus	62	*Colpoda variabilis*	77
henneguyi	81	*ovinucleata*	100
Bryometopus pseudochilodon	65	*Bryometopus chlorelligerus*	85
sphagni	124	*magnus*	155
Phialina terricola	72	*Phialina vermicularis*	50
binucleata	76	*vertens*	72
Frontonia terricola	87	*Frontonia acuminata*	100
depressa	97	*leucas*	350
Euplotes finki	60	*Euplotes affinis*	55
muscorum	60	*patella*	115
Chilophrya terricola	40	*Chilophrya utahensis*	50
Trithigmostoma bavariense	94	*Trithigmostoma cucullulus*	140
Average length:	87	Average length:	134

[1]The comparison is based mainly on the data of Kahl (1930, 1931, 1932), Foissner (1980a, 1981c, 1982, 1984a), and Hemberger (1985).
[2]Includes *Protospathidium, Spathidium, Arcuospathidium, Epispathidium.*

The high proportion of species with a fragmented macronucleus which occur in soil and marine sand is difficult to explain. It may be an adaptation among the often very fragile psammolittoral species to allow better survival following maceration by moving sand (Borror, 1968). However, in soil such a mechanical damage is not common.

The marine sand-dwelling ciliates possess some structural peculiarities which are not shared by the freshwater or soil species (Table 6). These are the reduced ploidy of the macronucleus (Karyorelictida), narrowing of the anterior end (cephalization), pronounced contractility and often fragility, and occurrence of skeletal rods. Hartwig

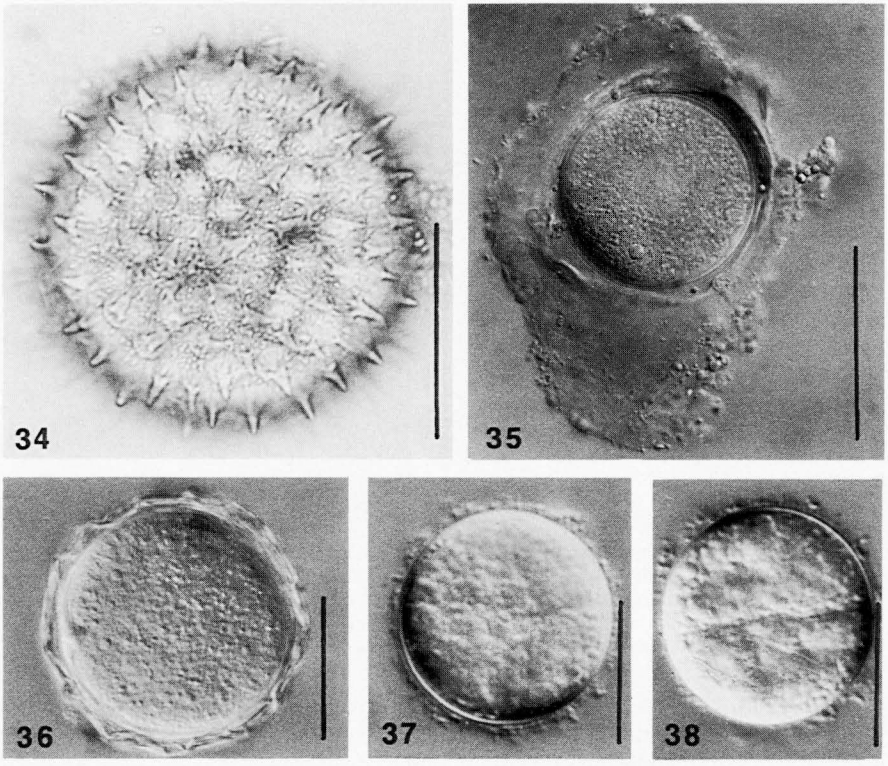
(1973) found a higher proportion of forms with skeletal rods in the splash zone of the littoral region, indicating a strengthening function of these structures.

Anaerobic conditions exist in many soils from time to time (Franz, 1981). Such biotopes in freshwater and marine sand have a special sapropelic ciliate fauna; for example, including many species of the family Metopidae (Fenchel, 1969; Jankowski, 1964). One would expect a similar fauna in anaerobic soils. There is, however, no evidence for this, perhaps indicating that the soil has been invaded much later by ciliates than have freshwater sites. The few species of *Metopus* (Figs 9, 10) which have been found in soil (Table 14) seem not to be confined to any particular soil type. Indeed, sometimes they become frequent in well aerated petri dish cultures. Some preliminary experiments exposing alpine gleyic soils to anaerobic conditions showed no development of ciliates, with exception of a few *Colpoda*. Well growing cultures die when they are exposed to such conditions. The ability of freshwater and marine sand ciliates to conquer the sulphide system may be linked to the presence of special endosymbiotic and ectosymbiotic bacteria (Fenchel, 1969; Fenchel *et al.*, 1977; Liebmann, 1937; Van Bruggen *et al.*, 1984). No such symbionts are known in association with soil ciliates.

The peculiarities of the habitat have, in turn, produced soil ciliate communities with peculiar characteristics. One way of describing the community is in terms of the distribution of species among higher taxonomic categories (e.g., peritrichs, hypotrichs). Using this method, Foissner (1981a) showed that suctoria and peritrichs are poorly represented in all terrestrial ciliate communities investigated. The Kinetofragminophora ($\approx$ holotrichs) and the Polyhymenophora (heterotrichs and hypotrichs) are much more common. The data in Table 6 are based on more samples (Table 14) and confirm the earlier findings. Thus, the motile life type is favoured against the sessile one. Of the known species of soil ciliates, 37% are creeping hypotrichs. The porous space structure of the soil and the film-like distribution of the water have perhaps been responsible for a selective pressure toward this form of ciliate. One of the most notable characteristics of the soil ciliate community is the high proportion of Colpodea, which has not been reported from marine sand nor from freshwater biotopes (Foissner, 1985c). This may be explained by their *r*-selected life strategy (Section IV. A.2).

Thus the ciliates found in freshwater, soil, and marine sand biotopes may be considered as three unique communities, contrary to the claim of Stout (1963) that they are very similar.

2. *Physiological adaptations.* *(a) Cysts:* One of the greatest differences between soil and marine sand-dwelling (or even most freshwater) ciliates is the universal ability of the former of producing temporary and protective resting cysts (Tables 6, 14). The cysts can withstand unfavourable environmental conditions. For example, many species survive for decades in air-dried soils (Berz, 1936; Goodey, 1915a; Lepşi, 1948; Nowikoff, 1923), though some do not recover after prolonged drying (Varga, 1961). The physiological and structural details of the cysts have been excellently reviewed by Pussard (1967) and Corliss & Esser (1974). Some examples are provided in Figures 34–38. Most marine sand ciliates are unable to produce these survival stages (Borror, 1968; Fenchel, 1969). In contrast, nearly all of the species listed in Table 14 have been isolated from air-dried and remoistened soil samples, indicating that desiccation resistant cysts can be produced. Some freshwater ciliates, such as *Paramecium, Colpidium*, and most species of the *Tetrahymena pyriformis* complex, are unable to make resting cysts (Corliss & Esser, 1974). In large part, this may be explained by

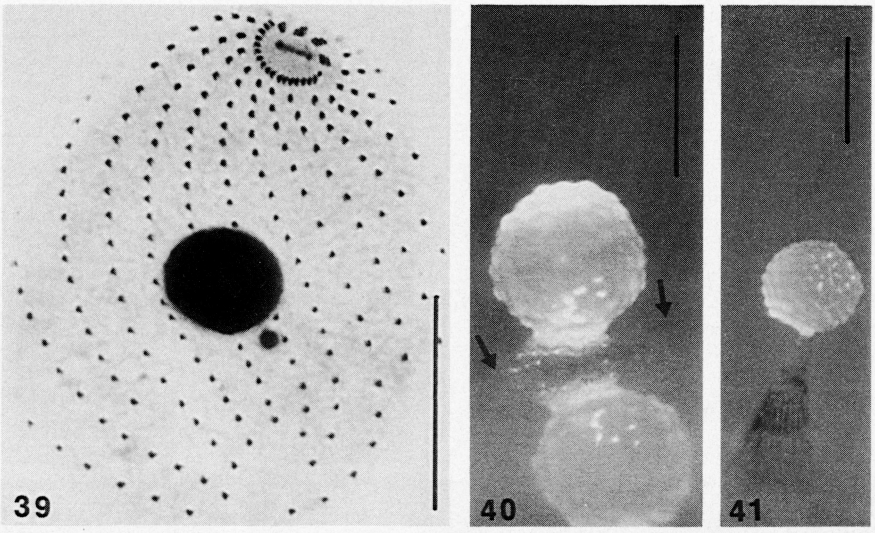


Figs 34–38. Cysts of soil ciliates under the light microscope. Fig. 34. *Enchelydium polynucleatum*. Scale bar = 30 µm. Fig. 35. *Kahliella simplex*. Note the voluminous mucuous envelope. Scale bar = 40 µm. Fig. 36. *Gastrostyla steini*. Scale bar = 27 µm. Fig. 37. Resting cyst of *Grossglockneria acuta*. Scale bar = 17 µm. Fig. 38. Division cyst of *Grossglockneria acuta*. Scale bar = 23 µm. (Fig. 34 from Foissner, 1984a; others are originals)

the water supply, which is constant in the marine environment, rather variable in many freshwater biotopes, and extremely astatic in most soils. One may speculate that protozoa evolved cysts mainly to resist drying and that other cyst functions, like reproduction and digestion, appeared later.

The remark of Gellért (1955, 1956), that ciliates which live in the thin humus layer under epilithic lichens and mosses possess a more active contractile vacuole due to the low and astatic ionic strength of the rain water, also needs further investigation. In apparent support of this, Schönborn (1968a) observed a shorter interval of the contractile vacuole in soil populations of *Corythion pulchellum* than in those from *Sphagnum* (60 s *versus* 120 s) but vacuolar output was not measured.

A spectacular adaptation, which is probably also related to astatic water conditions, is exhibited by the epiphytic genus *Sorogena* (Olive & Blanton, 1980). This colpodid ciliate (Bardele *et al.*, 1985) feeds on epiphytic and soil species of the genus *Colpoda*. It multiplies rapidly, aggregates, encysts, and produces noncellular stalked aerial sori which look very similar to those of cellular slime moulds (Figs 39–41). The sorogenesis requires alternate light and dark conditions, just as in the pink heteroloboseid slime mould *Acrasis rosea*.



Figs 39–41. *Sorogena stoianovitchae*. Fig. 39. Infraciliature of a trophic individual after silver carbonate impregnation. Scale bar = 26 µm. Figs 40, 41. Developing and mature sorocarp which is composed of hundreds of ciliate cysts. The stalked sorocarp is raised above the water level (arrows; 'reflection' in Fig. 40). Scale bars = 90 µm (Fig. 40) and 100 µm (Fig. 41). (Fig. 39 from Bardele, Foissner and Blanton, unpublished; others are originals)

(b) Anabiosis: Anabiosis (cryptobiosis, anhydrobiosis) is the property of organisms to resist drying without marked morphological changes, such as the production of a special cyst or membrane. It is common in some groups of soil and moss animals, such as rotifers, tardigrades, and nematodes, but it seems to be very restricted or even absent among soil protozoa. Watson (1943) reported that *Balantiophorus minutus* (= *Paracolpoda steinii*) survived without the formation of a cyst, when the free water completely disappeared from the agar culture surface. In this condition the body of the ciliate was shrivelled and flattened and showed no signs of life. On the addition of water, the cilia commenced beating, and within one hour the cell regained its normal form and activity. These observations are not fully convincing, however, because it is possible that some water remained in the agar used by Watson (1943). Huang (1984) found that another species, *Tetrahymena pyriformis*, remained active and did not lose its cilia in soft (0.75%) agar. In this viscous environment, the ciliates did not swim but moved like naked amoebae by changing their shape. True anabiosis occurs, perhaps, in the genus *Thecamoeba,* which is widespread in terrestrial biotopes. The organisms assume a disk-like shape under dry conditions, but do not produce a cyst wall (Page, 1976). This has yet to be verified experimentally.

Interestingly enough, a well documented case of anabiosis is known for the freshwater suctorian *Heliophrya erhardi* (Dragesco *et al.*, 1955).

(c) Food: The food spectrum of most soil ciliates is unknown. The lists in Table 14 are certainly incomplete, but approximately 50% of the 250 species prey on other ciliates, zooflagellates, and/or naked and shelled amoebae. This is in rough agreement with the results of Gellért (1957), but contrasts with the widely accepted view that most soil ciliates are bacterivorous (e.g., Brunberg Nielsen, 1968; Laminger, 1980; Nikolyuk, 1965b, 1969). This belief probably results from the use of a wide variety of selective culture methods which favour bacterivores. However, the colpodids, a

quantitatively important group, is predominantly comprised of bacterivorous species. They may skim off the dense bacterial standing crop provided by many soils. The rarer predators have often escaped the attention of ecologists and protozoologists.

Species specialized to eat fungi have been reported nearly exclusively from soil where there is a frequently high abundance of this food type (Petz *et al.*, 1985; Sections III.C and IV.E).

Many of the ciliates found in marine sands feed on diatoms, bacteria, and phytoflagellates (Fenchel, 1969), but the majority of the typical species prey on other protozoa or small metazoa (Dragesco, 1962).

The high share of predatory species in the soil ciliate community may be part of a feedback system involving stimulation of the production of the prey. This demands more detailed investigation of the widely neglected prey-predator relationships among the soil protozoa.

(d) Temperature: There is an increasing body of evidence for temperature adaptations in soil ciliates. Buitkamp (1979) studied the growth ranges of temperature for soil ciliates from tropical and temperate zones. In his microcosms, most ciliate species developed best near the highest mean annual temperature, in the region of 20°C for species from Bonn (FRG) and 25–30°C for those from an African savannah. Buitkamp (1979) also tested the temperature range in which selected species reproduced. The results show that local races are adapted to the temperature conditions of their environment (Table 9). Field data and laboratory experiments of Petz *et al.* (1985) support this suggestion. They found that the autochthonous soil ciliate *Grossglockneria acuta* is adapted to low soil temperatures, with highest numbers occurring at 4.5°C. The incidence and numbers of this species were higher in alpine soils than in lowland ones (Tables 10, 11). The most pronounced population growth occurred between 10°C and 21°C, which is near the highest mean monthly temperature (16.7°C) of the natural habitat of the population investigated.

(e) Carbon dioxide: Soil protozoa must be able to tolerate the high levels of CO_2 present in the soil air and soil water. Stout (1952, 1956) observed that *Colpoda* spp. and some other soil ciliates survive, but do not reproduce, for a long time under anaerobic conditions and high CO_2 levels. This is supported by results of Nikolyuk & Mavlajnova (1971). They found a high activity of glycolytic enzymes in *Colpoda maupasi*, which is typical for anaerobic organisms. Nikolyuk & Mavlajnova (1971) interpreted this as being an adaptation to occasional anaerobic conditions in soil. Datta (1979) found that the atmospheric level of CO_2 (0.03%) was essential for the excystment process of some soil amoebae. A slight increase in the CO_2 level (0.5–0.8%) enhanced excystment, but a further increase in CO_2 inhibited it.

(f) r/K-selection: Related to the question of temperature preferences and CO_2 adaptation, there is some evidence which suggests that the colpodids are particularly abundant in unpredictable and extreme habitats, such as leaves, lichens, and alpine soils (Bamforth, 1973; Foissner, 1979a, 1981a, 1986c; Mueller & Mueller, 1970). Recently, Lüftenegger *et al.* (1985) investigated the hypothesis that the colpodids of such habitats are more *r*-selected than rarer Polyhymenophora (heterotrichs, oligotrichs, hypotrichs). They undertook a large field census in an 'unpredictable' alpine region, and one in a more 'predictable' lowland area. The results indicated a higher C/P ratio (ratio of Colpodea to Polyhymenophora) in the unpredictable area, thus corroborating the theory (Fig. 42). In laboratory experiments, the colpodids *Colpoda aspera* and *Grossglockneria acuta* were less sensitive to changes in temperature and exhibited a more rapid increase in numbers and higher final numbers than did the polyhymenophorans *Blepharisma undulans* and *Gonostomum affine* (Table 11). The

Table 9. Temperature spectra (5–40°C) for some soil ciliates from different regions of the world (from Buitkamp, 1979)

Species[1]	Temperate zone (FRG)		Tropical zone (Africa)		
	Pasture	Mixed forest	Burned savannah	Unburned savannah	Gallery forest
Colpoda inflata	5–35	10–30	15–35	15–30	20–40
Paracolpoda steinii	10–40	5–30	15–35	20–30	15–35
Cyrtolophosis elongata	10–35	10–25	20–35	20–35	20–30
Cyrtolophosis mucicola	20–25	10–25	25–35	20–35	20–40
Gonostomum affine	10–35	5–30	15–40	25–30	20–35
Hemisincirra kahli	20	10–30	20–35	20–35	20–35

[1]Nomenclature adapted to that of Table 14.

Table 10. Comparison of frequency and numbers of *Grossglockneria acuta* in 24 alpine and 70 lowland samples (from Petz *et al.*, 1985)

Sites[1]	pH	Frequency (%)[2]	Number of positive samples[3]	Number of individuals[4]
Alpine	3–5	83	12	28.0
Lowland	7–8	44	6	6.4

[1]8 alpine sites were investigated three times a year. The seven lowland sites were analyzed 10 times during a period of three years (Foissner *et al.*, 1982c, 1985; Foissner & Peer, 1985).
[2]Determined according to the 'non flooded Petri dish method' described in section II.B.
[3]'Positive samples' means *G. acuta* has been found in countable numbers by Buitkamp's (1979) method.
[4]Numbers are given as means ($\bar{x}$) of individuals g^{-1} dry mass of soil and were estimated by the method of Buitkamp (1979).

Table 11. Body size, shortest generation time, and maximal density of some soil ciliates in laboratory cultures at different temperatures (means of three replicates) (from Lüftenegger *et al.*, 1985)

Species	Size ($\bar{x}$) (n = 10)[2]	Shortest generation time (h)				Maximal individual density (ml^{-1})			
		5°C	10°C	21°C	30°C	5°C	10°C	21°C	30°C
Colpoda aspera	28 × 18	19.2	14.2	9.6	4.1	35 700	37 500	29 500	5840
Grossglockneria acuta[1]	40 × 16	35.8	18.2	4.8	3.8	12 900	1500	3200	3900
Blepharisma undulans	170 × 51	11.5	11.5	8.9	7.2	120	1200	9300	4200
Gonostomum affine	64 × 16	Death	13.4	10.6	Death	0	2300	3800	0

[1]From Petz *et al.* (1985).
[2]Measurements from protargol silver impregnated specimens.

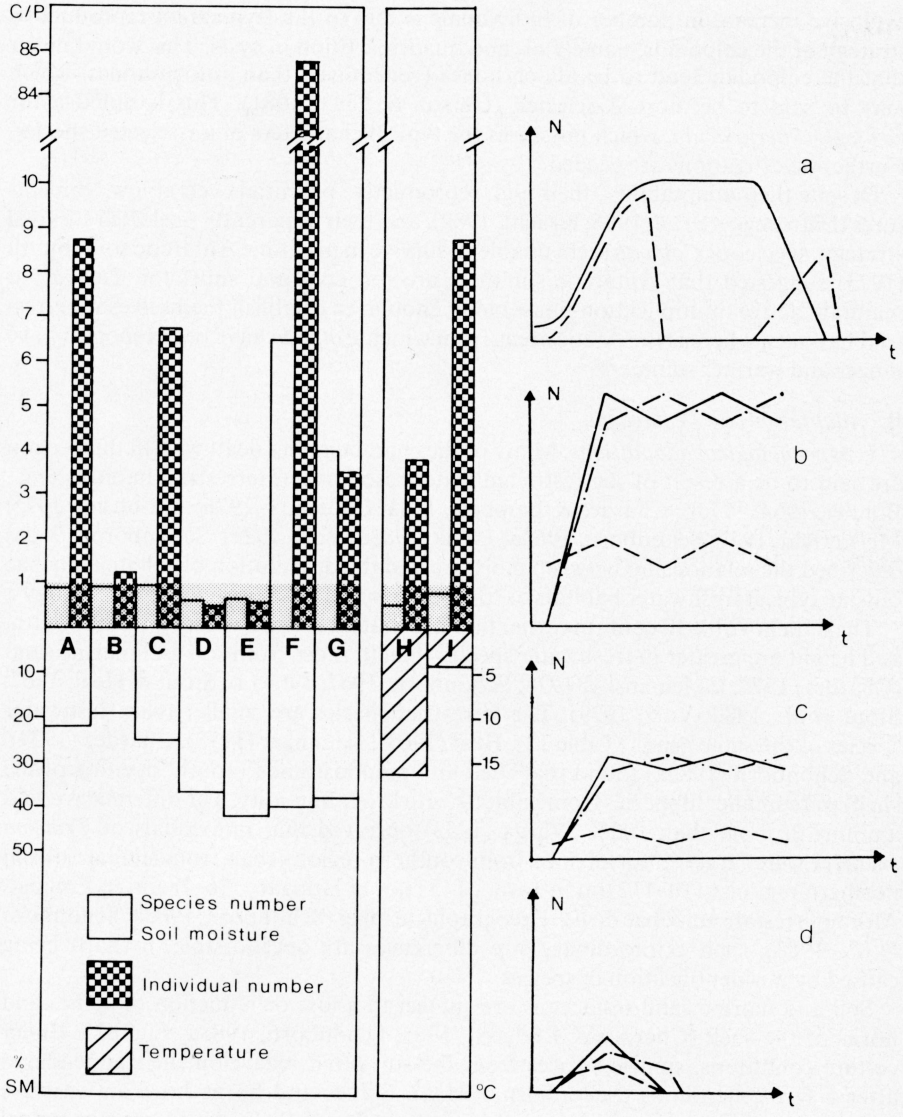


Fig. 42 (left). Ratio of colpodid to polyhymenophoran ciliates (C/P) from different sites and climates. A–E. Sites—Tullnerfeld, 'comparatively predictable', A–C are more 'extreme' than D and E, because they are subject to unpredictable desiccation. F,G. Alpine sites—Grossglockner region, 'comparatively unpredictable'. H. Sites A–E combined. I. 5 alpine sites—Stubnerkogl. Values < 1 indicate dominance of polyhymenophoran species (stippled band). SM = soil moisture (from Lüftenegger *et al.*, 1985). Fig. 42 (right). Relationships between production, mortality, and abundance (PMA-Types) in soil testacean communities (schematic). a. Optimal type (high abundance, low production and mortality). b. Productive type (high abundance, production and mortality). c. Retardative type (low abundance, high production and mortality). d. Sporadic type c low abundance and production, high mortality).——— production; ——·—— mortality; — — — — abundance; N = number of individuals (abundance); t = time. (from Schönborn, 1983b)

explosive increase in number of individuals is due to the (typical *r*-) reproductive strategy of the colpodids, namely bi- and quadripartition in cysts. This would mean that the colpodids tend to be allochthones (generalists) than autochthones, which may be said to be more *K*-selected (Gerson & Chet, 1981). This is unlikely for *Grossglockneria acuta*, which possesses the typical characters of a *r*-selected species. Further investigations are needed.

Despite their adaptability, their high reproductive potential even at low temperatures (Lüftenegger *et al.*, 1985; Kracht, 1982), and their apparently *r*-selected survival strategy, species of *Colpoda* seem unable to survive in maritime Antarctic soils. Smith (1973) suggested that Antarctic summers are too cool and short for *Colpoda* to maintain active multiplication phases long enough to establish themselves in terrestrial habitats, whereas the Arctic areas from which *Colpoda* have been reported have longer and warmer summers.

B. *Adaptations by Testaceans*

1. *Morphological adaptations.* Many of the characteristics dealt with in this section are said to be a result of the restricted water resources of terrestrial habitats (e.g., Bonnet, 1964, 1973b; Chardez & Lambert, 1981; Coûteaux, 1976c,d; Lousier, 1975; Meisterfeld, 1977; Schönborn, 1962a, 1966a, 1983a; Volz, 1929). Schönborn (1962a) described the relationship between moisture and the distribution of testate amoebae outside typical freshwater habitats as 'the best assured finding in testacean ecology'.

The data in Table 12 confirm earlier findings that mean shell volume, length, width, and height are greater in freshwater species than in those from soil and marine sand (Chardez, 1972; Golemansky, 1978; Schönborn, 1967, 1968a,b; Stout & Heal, 1967; Stout *et al.*, 1982; Volz, 1929). The terrestrial species are smaller than freshwater species of the same genus (Table 13). Heal (1963), Laminger (1978), Chardez (1979), and Schönborn (1982a) found that shell and pseudostome ('mouth' opening of the shell) were smaller in species from habitats with lower humidity. The differences could amount to more than 100%. Varga (1953) observed that individuals of *Trinema enchelys* were larger in forest soils from southern regions than from similar soils in northern regions: 110–112 μm in Java, 51–53 μm in Hungary, 26–28 μm in Finland. Although testate amoebae do have geographical races (Schönborn, 1966b; Schönborn *et al.*, 1983), such extraordinary size differences are questionable, perhaps being caused by misidentification of species.

Soil and marine sand testaceans are subject to a loss or reduction of spines and horns of the shell (Chardez & Leclercq, 1963; Schönborn, 1983a; Fig. 82). Under culture conditions, spineless races from the soil often redevelop their appendages after a few generations (Schönborn, 1983a). Spines and horns have an adaptive advantage in the Aufwuchs where they anchor the shells in the filamentous algal framework and prevent passive transport. This could equally be the reason for the prominent lateral and caudal horns in some marine sand testaceans (Golemansky, 1978). Such appendages have little value in the thin water film which encloses the litter and soil particles, where anchorage is not possible. In fact, they would impede colonization by enlarging the size of the cell (Schönborn, 1968a,b).

Laterally compressed or wedge-shaped tests dominate in the litter, whereas high-vaulted forms are most frequent in the humus layer (Coûteaux, 1976d; Foissner & Adam, 1981a; Meisterfeld, 1980; Schönborn, 1966a; Stout *et al.*, 1982). This characteristic vertical distribution (Fig. 43) is likely to be caused by the distribution of the water; which is film-like in the litter, and pool-like in the humus layer. To the first group belong common genera such as *Assulina* (Fig. 55), *Euglypha* (Figs 48, 57),

Table 12. A comparative description of the known testacean communities of freshwater, soil, and marine sand

Character	Freshwater[1]	Soil[2]	Marine sand[3]
Mean shell volume (~ biomass in mg) of 10^6 individuals[4]	740 (309)[4] (n = 88)[5]	90 (n = 66)	13 (n = 50)
Mean body length (µm)	103 (n = 88)	72 (n = 66)	40 (n = 50)
Mean body width (µm)	78 (n = 88)	55 (n = 66)	21 (n = 50)
Mean body height (µm)	56 (n = 88)	32 (n = 66)	15 (n = 50)
% species with xenosomes	47 (n = 88)	53 (n = 66)	26 (n = 50)
% species with idiosomes or with a chitinous shell	53 (n = 88)	47 (n = 66)	74 (n = 50)
% species with spines or horns	15 (n = 88)	6 (n = 66)	10 (n = 50)
% species with laterally compressed shell	23 (n = 88)	20 (n = 66)	52 (n = 50)
% plagiostomy[6]	21	28	8
% cryptostomy[6]	1	17	0
% cotylostomy[6]	0	< 1	50
% acrostomy[6]	61	38	34
Number of species[7]	about 1200	about 310	about 70
Abundance[8] m^{-2}	$6 \times 10^6 / 2.6 \times 10^5$	73×10^6	4×10^6

[1,2,3]Data for freshwater species is based chiefly on the species list of three lakes given by Schönborn (1962b), that of the soil species is based on studies of Foissner & Adam (1981a), Foissner & Peer (1985), Foissner *et al.* (1985) and Foissner (unpubl.), and that of the marine sand testacea comes from the species descriptions of Golemansky (1970a,b,c, 1971, 1973, 1974, 1976, 1982), Chardez (1972, 1977), and Sudzuki (1979b).

[4]Mean biomass $= \frac{Bx + By + Bn}{n} \times 10^6$. Value in brackets excludes the two very voluminous species *Difflugia urceolata* and *D. lebes*.

[5]n refers to the number of species considered.

[6]From Bonnet (1975b). Terms are explained in Schönborn (1966a) and Bonnet (1975b).

[7]Compiled from the data given by Chardez (1965a), Chardez & Lambert (1981), and Decloitre & Cailleux (1980). 'Freshwater' includes *Sphagnum* and 'Soil' includes aerophilic mosses (about 50% occur in soils only).

[8]These are only a few, perhaps not representative, examples! Freshwater (Schönborn, 1968): first value for Aufwuchs, second for bottom sediment. Soil: mean of the values shown in table 4. Marine sand: calculated from the cm^{-3} values of Sudzuki (1979a) supposing a colonized depth of 20 cm (Golemansky, 1971; Hartwig, 1973).

Table 13. Mean shell length (µm) of soil and freshwater species of the genera *Euglypha* and *Centropyxis* (from Schönborn, 1983a)

Habitat	Soil S	Soil N	Soil Mean shell length ± SD	Freshwater and *Sphagnum* S	Freshwater and *Sphagnum* N	Freshwater and *Sphagnum* Mean shell length ± SD
Euglypha	6	100	47.5 ± 17.6	6	100	65.5 ± 31.0
Centropyxis	14	200	63.6 ± 22.3	7	120	150.3 ± 82.4

S = number of species, N = number of individuals, SD = standard deviation.

Trinema (Fig. 58), *Corythion* (Fig. 188q), *Nebela* (Fig. 188p), *Heleopera* (Fig. 65), and *Hyalosphenia* (Figs 51, 59). The second group is represented, for instance, by the widespread genera *Phryganella* (Figs 180, 181), *Cyclopyxis* (Figs 54, 69), *Centropyxis* (Figs 49, 53, 60, 61, 62, 67), *Plagiopyxis* (Figs 50, 71), *Pseudawerintzewia* (Figs 52, 63), *Tracheleuglypha* (Fig. 56), *Difflugia* (Figs 44, 45, 66), *Schoenbornia* (Fig. 68), *Difflugiella* (Fig. 47), and *Pseudodifflugia* (Fig. 46). Some doubts remain with this interpretation, because more than 50% of the shells of the marine sand testacea are flattened for unknown reasons (Golemansky, 1978; Table 12). One may suggest that this could prevent a species from being washed out by water movements, because flattening reduces the surface area.

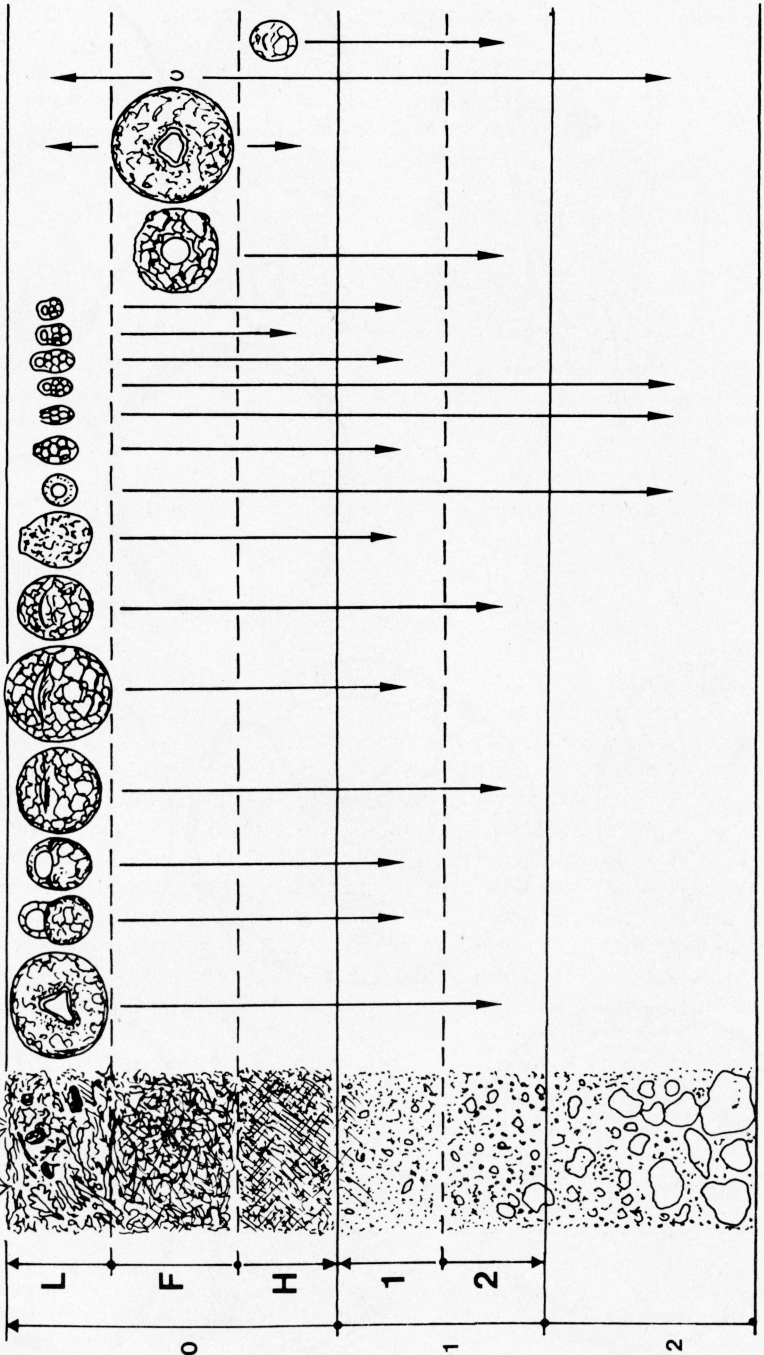
The greatest changes linked to colonization of the soil are expressed in the pseudostome. More common or autochthonous (true) soil testacea are globular with a flattened ventral side ('sole ventrale' of Bonnet, 1964) and have a plagiostomic, cryptostomic, microstomic, or invaginated shell opening (pseudostome). Some prominent representatives of these morphological types are shown in the Figures 55–71. A special mechanism to close the pseudostome is shown by *Difflugia lucida* and some related forms. They attach mineral particles around the pseudostome which seal off the entrance when the pseudopods are retracted (Figs 44, 45, 66).

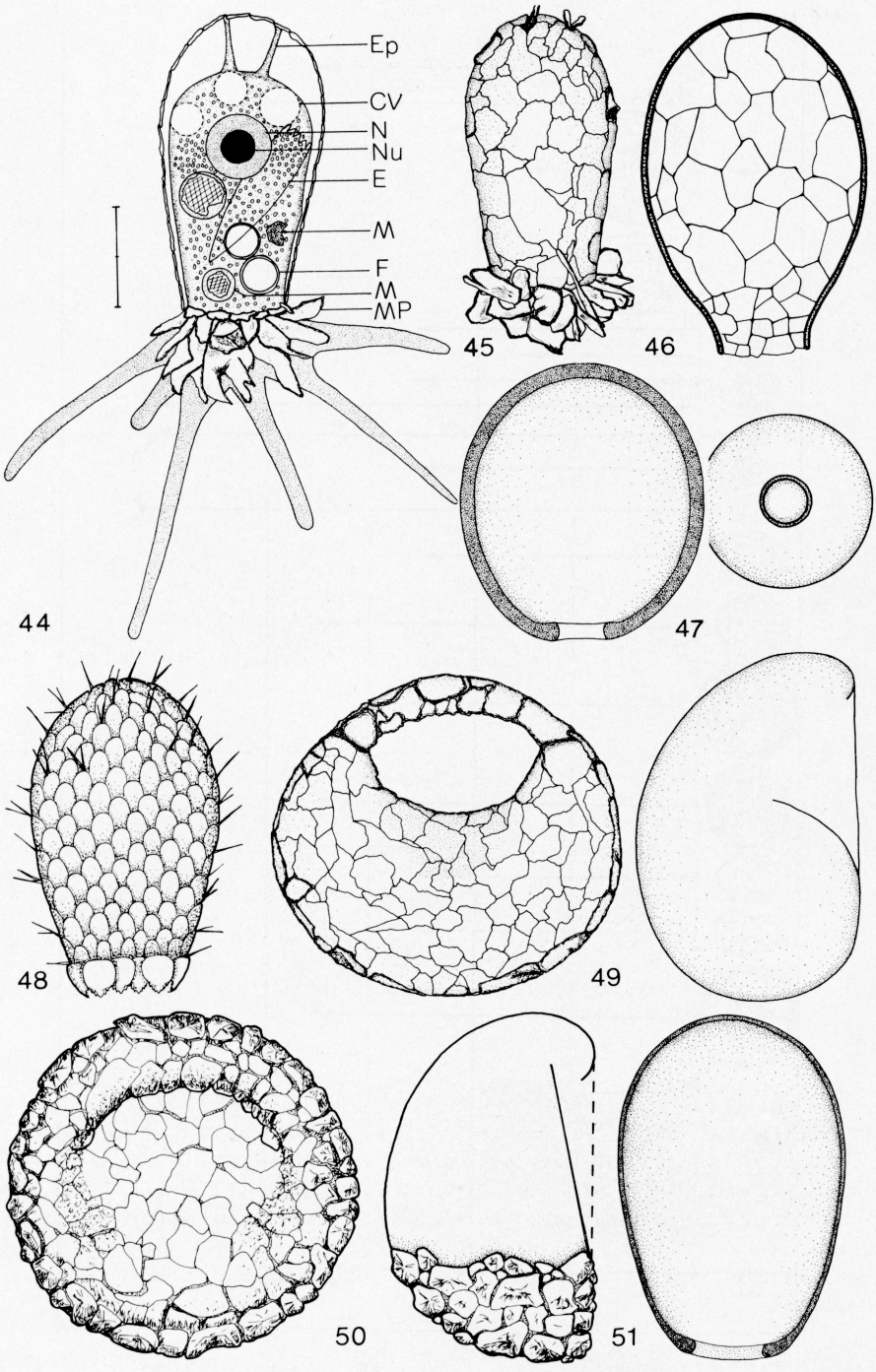
The reduced size of the pseudostome, the flattened ventral side, and the globular shape greatly reduce the cytoplasmic area which is exposed to air and desiccation. They are thus the strongest support for the hypothesis that moisture is the major factor affecting distribution and evolution of the testate amoebae. These adaptations hold the shell opening under the surface film of the water and protect the cytoplasm from surface tension. In marine sand testaceans there is often a kind of 'sole ventrale' (an enlarged peristomial collar) thought to aid in anchoring the organisms to the sand grains and to improve food-gathering (Chardez, 1972; Golemansky, 1978).

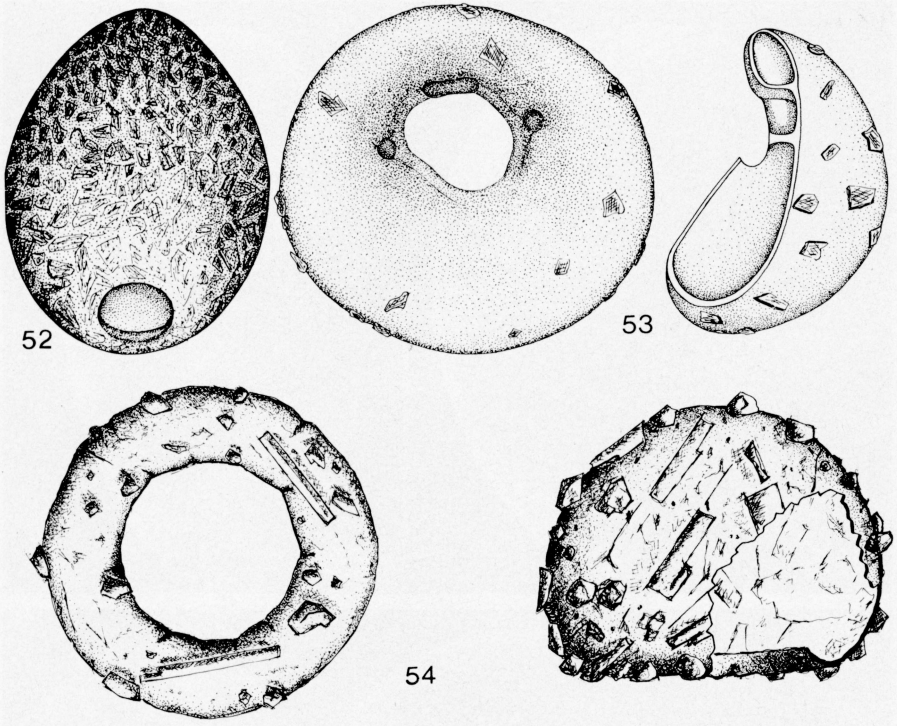
The testacean communities of freshwater, soil, and marine sand differ greatly in the proportion of plagiostomic, cryptostomic, cotylostomic, and acrostomic species (Table 12). Cryptostomy is nearly exclusive to soil testaceans (Bonnet, 1975b). Chardez & Lambert (1981) have summarized, diagrammatically, the occurrence and distribution of various morphotypes (Fig. 72). The soil community also contains the greatest proportion of species with shells composed of foreign particles (xenosomes, such as sand grains, etc.), whereas most marine species have rather flexible shells composed of pseudochitin or idiosomes (plates and other structures produced by the cell). The low weight of these shells is thought to facilitate movement among the sand grains. The adaptive value of the rather massive shells composed of xenosomes is unknown.

Although the above discussion has used limitations of water availability to explain the various morphologies, there may indeed be other causes. Martin (1971) asked the heretical question, 'Is moisture the limiting *and* determining or only the limiting factor?' After a careful discussion, he concludes that moisture is perhaps only the limiting ecological factor within which 'food' determines the presence or absence

Fig. 43. Vertical distribution of testaceans in a mixed woodland. Species from left to right: *Trigonopyxis arcula*, *Centropyxis aerophila*, *C. aerophila* var. *sphagnicola*, *Plagiopyxis callida*, *P. callida* var. *grandis*, *P. declivis*, *Nebela tincta*, *Phryganella acropodia*, *Tracheleuglypha acolla*, *Euglypha laevis*, *Trinema lineare*, *T. enchelys*, *T. complanatum*, *T. complanatum* var. *globulosa*, *Cyclopyxis kahli*, *Trigonopyxis arcula* var. *major*, *Difflugiella oviformis*, *Plagiopyxis minuta*. L = litter, F = fermentation layer, H = humus layer. (from Chardez, 1968)


L
F
H
1
2
A0
A1
A2

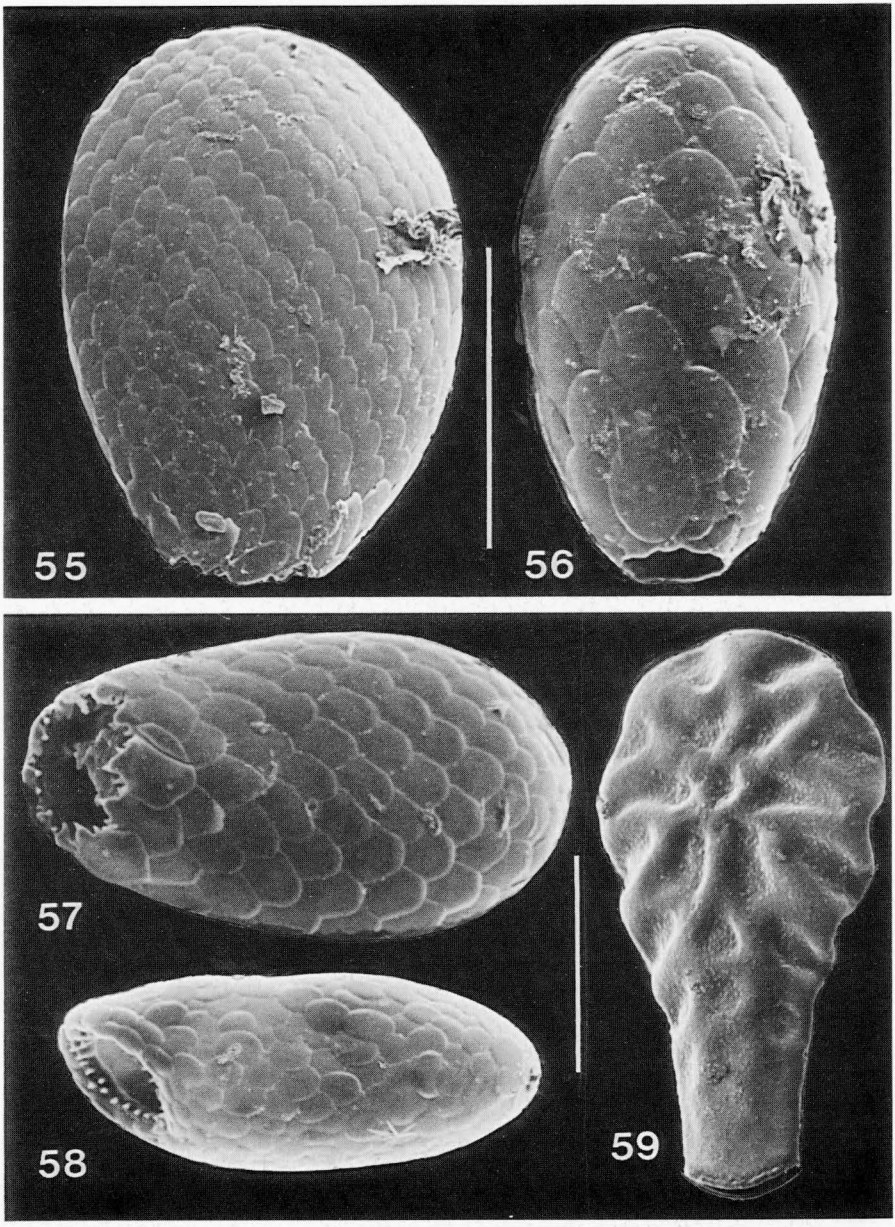

Ep
CV
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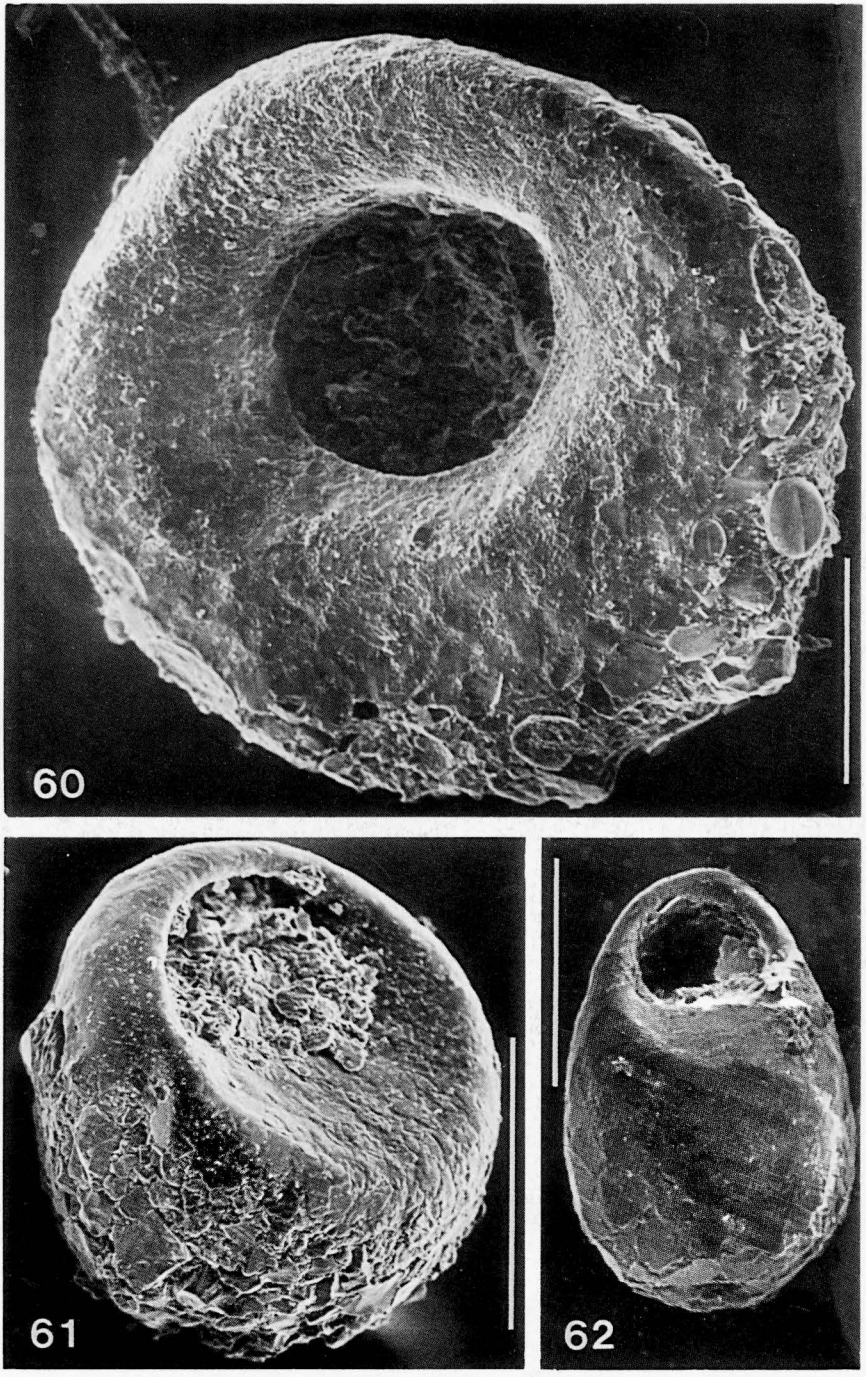
Figs 44–54. Some common soil and litter testaceans. Figs 44, 45. *Difflugia lucida,* lateral views. CV = contractile vacuoles, E = phagocytozed *Euglypha* sp., Ep = epipods, F = phagocytozed spore of a fungus, M = phagocytozed mineral particle, MP = mineral particles around the pseudostome, N = nucleus, Nu = nucleolus. Scale bar = 20 µm. Fig. 46. *Pseudodifflugia fascicularis*, lateral view, 33 µm. Fig. 47. *Cryptodifflugia oviformis*, lateral and ventral view, 15 µm. Fig. 48. *Euglypha strigosa*, lateral view, 75 µm. Fig. 49. *Centropyxis sphagnicola*, ventral and lateral views, 60 µm. Fig. 50. *Plagiopyxis declivis*, ventral and lateral views, 69 µm. Fig. 51. *Hyalosphenia subflava*, lateral view, 78 µm. Fig. 52. *Pseudawerintzewia orbistoma*, ventral view, 70 µm. Fig. 53. *Centropyxis laevigata*, ventral view and three-dimensional reconstruction, 78 µm and 87 µm, respectively. Fig. 54. *Cyclopyxis eurystoma*, ventral and lateral views, 56 µm. (Figs 52, 53 from Schönborn *et al.,* 1983; others from Petz, Lüftenegger, Foissner, Berger & Adam, unpublished)

of a given species. In fact, this possibility must be considered as an explanation for morphological adaptations, because the most spectacular adaptation in the soil ciliates, the feeding tentacle of the Grossglockneridae, is related only to food. Very probably, other agents, like pore size and genetic isolation, are involved in determining testacean distribution. Schönborn (1968b), for instance, found a positive correlation between particle size in lake sediments and the size of the testacean inhabitants.

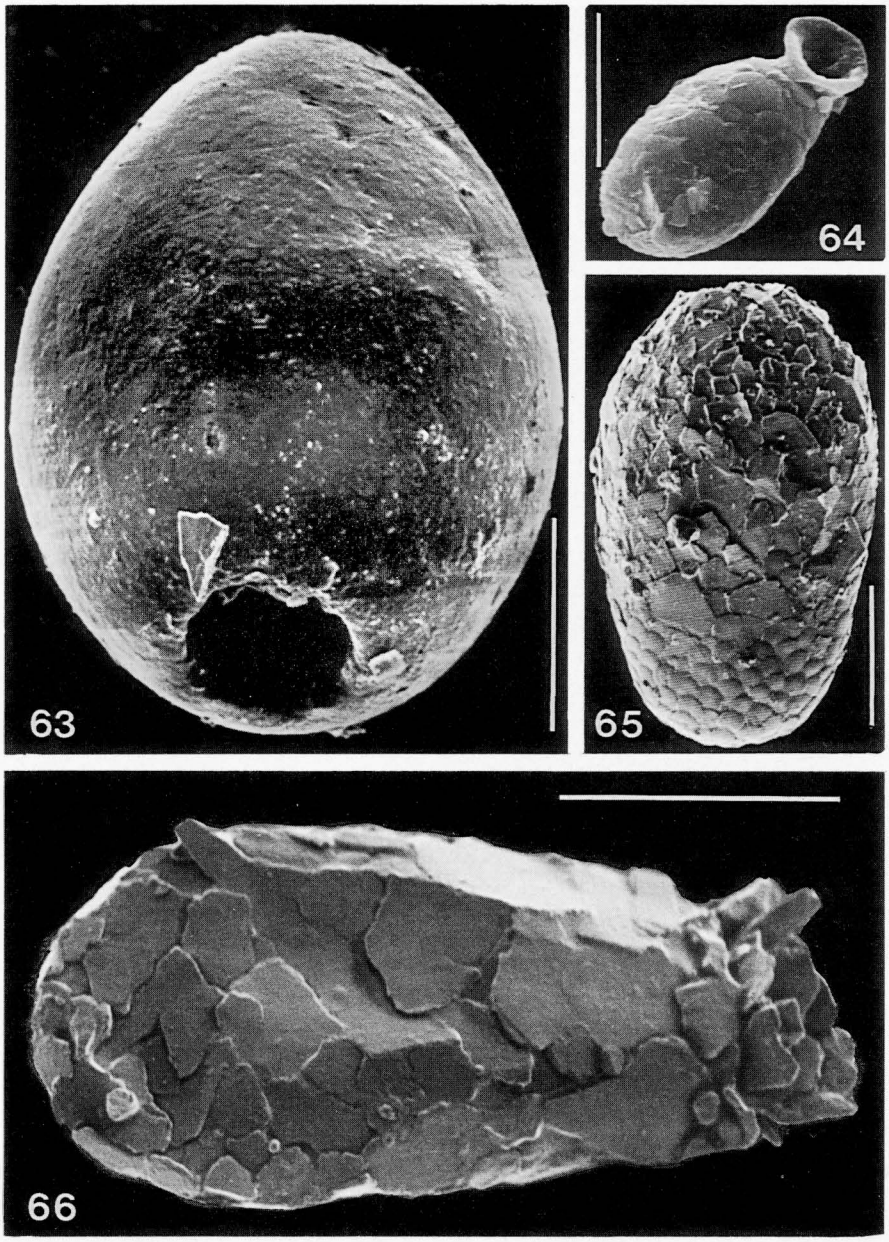
2. *Physiological adaptations.* (a) *Cysts:* Like ciliates, testate amoebae produce cysts under unfavourable environmental conditions (Bonnet, 1961c, 1963, 1964; Laminger & Sturn, 1984). Only some freshwater species, such as species of *Difflugia*, seem to be



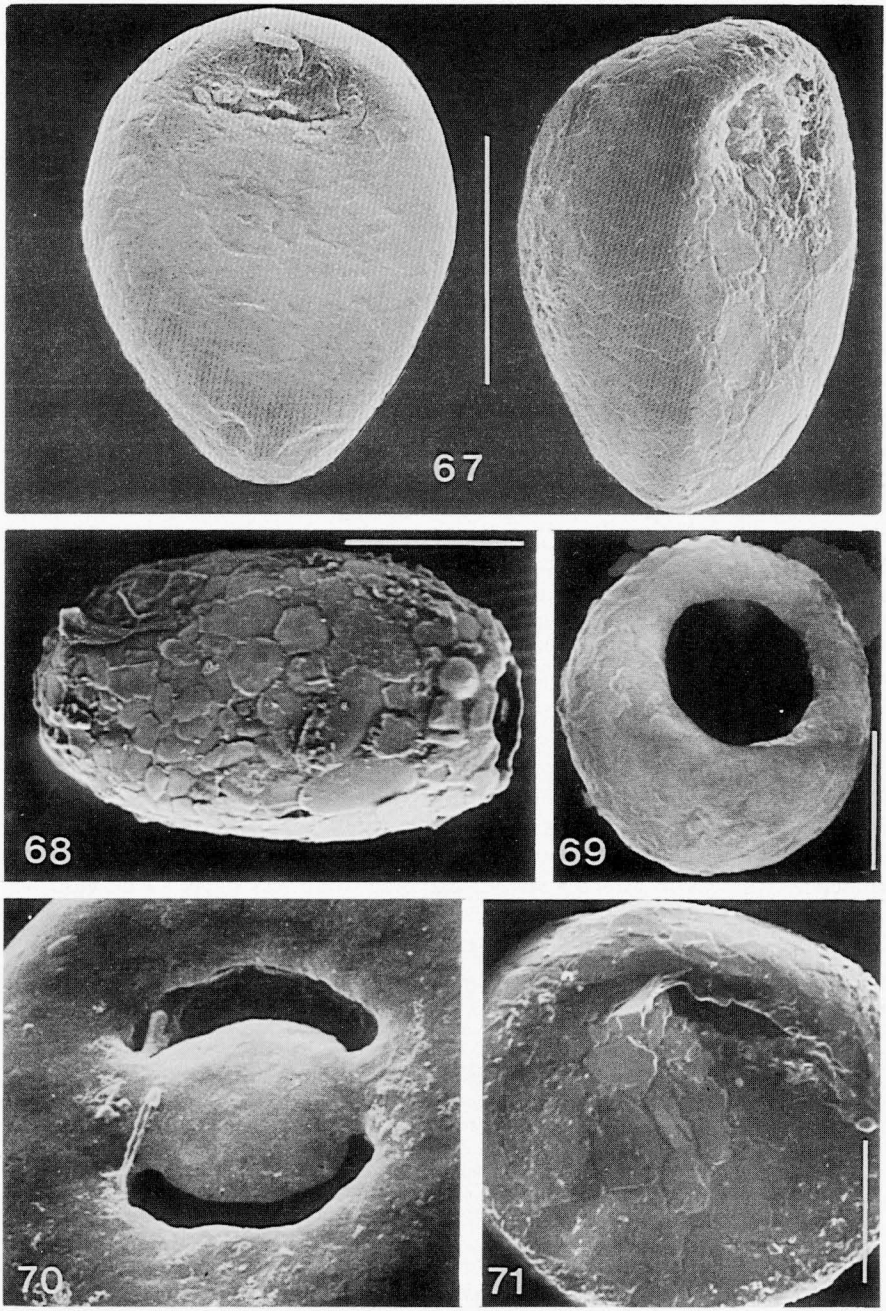
Figs 55–59. SEM-pictures of some soil and litter testaceans. Fig. 55. *Assulina seminulum*, lateral view. Scale bar = 40 µm. Fig. 56. *Tracheleuglypha acolla*, lateral view. Scale bar = 26 µm. Fig. 57. *Euglypha rotunda*, lateral view. Scale bar = 12 µm. Fig. 58. *Trinema lineare*, ventral view. Scale bar = 10 µm. Fig. 59. *Hyalosphenia elegans*, lateral view. Scale bar = 30 µm.



Figs 60–62. *Centropyxis laevigata*, ventral view. Scale bar = 24 μm. Fig. 61. *Centropyxis sphagnicola*, lateral view. Scale bar = 40 μm. Fig. 62. *Centropyxis constricta*, ventral view. Scale bar = 50 μm.



Figs 63–66. *Pseudawerintzewia orbistoma*, ventral view. Scale bar = 21 μm. Fig. 64. *Edaphonobiotus campascoides*, ventral view. Scale bar = 19 μm. Fig. 65. *Heleopera petricola*, lateral view. Scale bar = 20 μm. Fig. 66. *Difflugia lucida*, lateral view. Scale bar = 28 μm.



Figs 67–71. *Centropyxis oomorpha*, ventral and lateral views. Scale bar = 45 µm. Fig. 68. *Schoenbornia humicola*, lateral view. Scale bar = 10 µm. Fig. 69. *Cyclopyxis eurystoma*, ventral view. Scale bar = 22 µm. Fig. 70. *Distomatopyxis couillardi*, ventral view. Fig. 71. *Plagiopyxis minuta*, ventral view. Scale bar = 18 µm. (Figs 60, 63, 67 from Schönborn *et al.*, 1983; Fig. 64 from Wanner & Funke, 1986; Fig. 70 from Bonnet, 1975b; others from Petz, Lüftenegger, Foissner, Berger & Adam, unpublished)

incapable of doing this (Schönborn, 1966a). No cysts are known from marine sand testaceans. The resting cysts are produced within the tests and have a thick membrane decorated by spines or warts in some species (Figs 74, 75).

The 'precystic stage' is a special kind of short-term dormant form, comparable with the transitory cysts of the colpodid ciliates (Bonnet, 1964; Foissner & Didier, 1983). This stage was described earlier by Volz (1929) as the 'Kapselstadium.' It is characterized by a thin membrane, the epiphragm, which closes the opening of the shell and which is often externally coated with detritus (Figs 73, 76). During the formation of the epiphragm, the volume of the cytoplasm decreases through loss of water. Precystic cysts differ from resting cysts by their larger size, their thinner membrane, and their clearer cytoplasm, which moves from time to time. During 'excystment,' the epiphragm is lysed (e.g., in *Bullinularia*) or phagocytosed (e.g., in *Plagiopyxis*) (Bonnet, 1964).

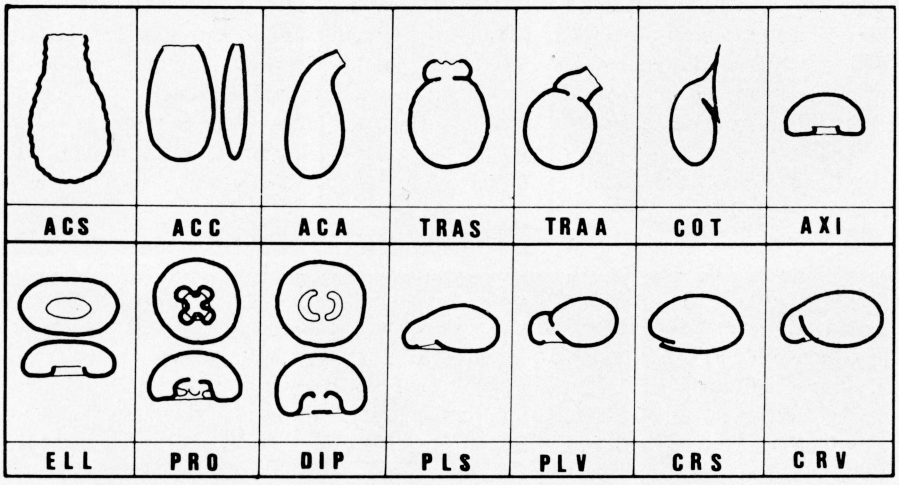
It is generally assumed that the precystic stage provides a means of 'dormancy' through short unfavourable periods, an adaptation to the often quickly changing soil environment. Bonnet (1964), however, observed periodic encystment and excystment even under fairly constant culture conditions, which suggests that other factors are also involved. Perhaps some endogenous rhythm exists, which would explain the regular short-term fluctuations (9 and 12 weeks) observed by Coûteaux (1976d) under field conditions. Even the more rapid fluctuations (2–16 days) of flagellate and ciliate numbers (Cutler *et al.*, 1922; Gellért, 1957) could be caused by such a phenomenon. It is, however, more likely that methodological shortcomings (Harmsen, 1940), meteorological influences (Section V. A.4) and/or microbiostasis (Section II. C) are responsible for these fluctuations.

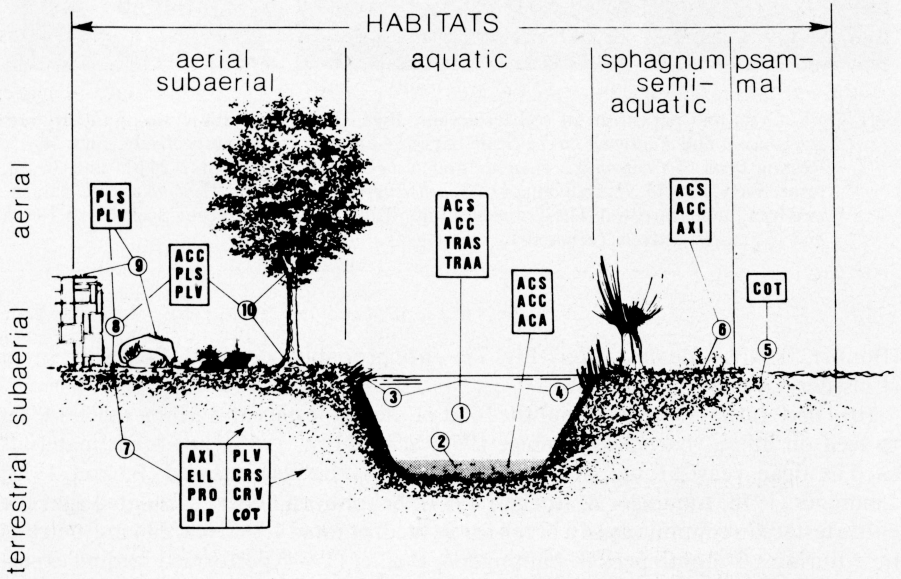
Young cysts of *Nebela dentistoma* need a longer time to reactivate than older ones (Laminger & Sturn, 1984). This observation is supported by the results of Varga (1933), but it is not a general phenomenon, because the experiments of Volz (1972) and Brunberg Nielsen (1968) show just the opposite for other testaceans, ciliates, nematodes, and rotifers. This is strengthened by the results of Crump (1950) who found excystment to be independent of the age of the cyst in one species of naked amoebae, whereas in another species the cysts were less likely to develop with increasing age.

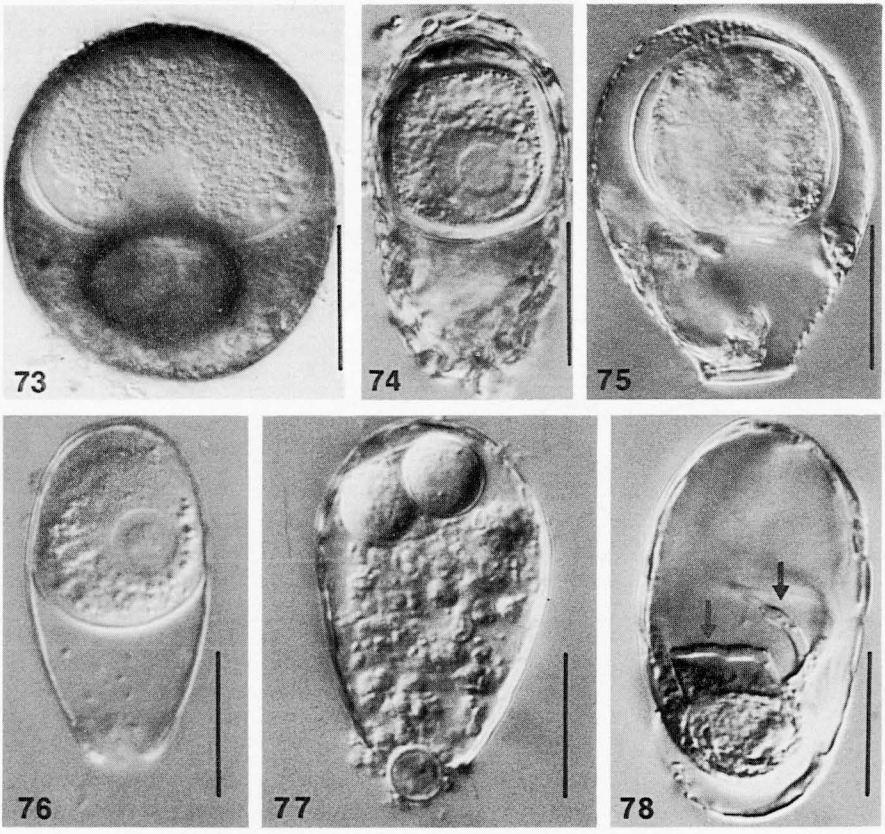
No reproductive or digestive cysts are known from soil testaceans. The 'cyclic cysts'—a stage in which the shell contains two or more small cyst-like globules

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Fig. 72. Morphological types of testacean shells and their occurrence in different kinds of biotopes. ACS = simple acrostomy, e.g., *Tracheleuglypha, Euglypha, Difflugia, Pseudawerintzewia, Schoenbornia* (see Figs 56, 57, 63, 66, 68); ACC = compressed acrostomy, e.g., *Assulina, Hyalosphenia, Heleopera* (see Figs 55, 59, 65); ACA = arched acrostomy, e.g., *Lamtoquadrula* (see Fig. 175); TRAS = simple trachelostomy, e.g., *Cucurbitella, Pontigulasia*; TRAA = arched trachelostomy, e.g., *Lecquereusia*; COT = cotylostomy, e.g., *Micropsammella, Edaphonobiotus* (see Figs 64, 170, 171); AXI = axial, e.g., *Cyclopyxis* (see Fig. 69); ELL = ellipsostomy, e.g., *Ellipsopyxella* (see Fig. 174); PRO = propylostomy, e.g., *Lamtopyxis* (see Fig. 166); DIP = diplostomy, e.g., *Distomatopyxis* (see Fig. 70); PLS = simple plagiostomy, e.g., *Centropyxis laevigata, C. oomorpha* (see Figs 60, 67); PLV = plagiostomy with visor, e.g., *Centropyxis sphagnicola, C. constricta, Trinema* (see Figs 58, 61, 62); CRS = simple cryptostomy, e.g., *Plagiopyxis minuta* (see Fig. 71); CRV = cryptostomy with visor, e.g., *Plagiopyxis callida, Paracentropyxis* (see Figs 164, 165, 197, 198). Types of biotopes: 1 = pelagic, 2 = benthic, 3 = floating plants, 4 = submerged plants, 5 = mesopsammon, 6 = *Sphagnum*, 7 = soil, 8 = epigeous mosses, 9 = epilithic mosses, 10 = epiphytic mosses. (after Chardez & Lambert, 1981)


ACS
ACC
ACA
TRAS
TRAA
COT
AXI
ELL
PRO
DIP
PLS
PLV
CRS
CRV


HABITATS
aerial
subaerial
aquatic
sphagnum
semi-
aquatic
psam-
mal
terrestrial
subaerial
aerial
PLS
PLV
ACC
PLS
PLV
ACS
ACC
TRAS
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AXI
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Figs 73–78. Cysts and parasitism of soil testaceans. Figs 73, 76. Precystic cysts of *Centropyxis sphagnicola* and *Euglypha laevis*. Scale bars = 24 µm and 16 µm, respectively. Figs 74, 75. Resting cysts of *Centropyxis elongata* and *Nebela tincta*. Scale bars = 24 µm and 36 µm, respectively. Figs 77, 78. Individuals of *Tracheleuglypha acolla* and *Trinema penardi* parasitized by a fungus (arrows). The globules in Fig. 77 are probably oospores. Scale bars = 19 µm and 25 µm, respectively. (originals)

(Bonnet, 1964; Coûteaux, 1976d; Fig. 77)—are probably oospores of parasitic fungi (Foissner & Foissner, 1986a,b).

(b) *Food:* Little is known about the food of the soil testaceans. Many species seem to feed on humus particles (Bonnet, 1964; Schönborn, 1965), but other materials such as algae, yeasts, fungi, protozoa, and bacteria are also ingested (Barron, 1978; Laminger, 1978; Laminger & Bucher, 1984). Schönborn (1965) calculated that the entire testacean community of a beech forest incorporated 1.8 ml (ca. 234 mg) detritus m^{-2} during a 3-month period. Laminger & Bucher (1984) performed feeding experiments which give some indication of food selection and nutritional specialization. They found that *Arcella arenaria* var. *sphagnicola*, *A. polypora*, and *Nebela dentistoma* were phytophagous, *Nebela collaris* and *Heleopera petricola* were more carnivorous, and *Quadrulella symmetrica* seemed to be polyphagous. The feeding rate

of these species depended on the prey density. At predator–prey ratios up to 1 : 100, the number of ingested prey organisms remained similar, whereas a ratio of 1 : 1000 drastically reduced the ingestion rate. This could have been caused either by metabolic products of the prey organism or too much tactile stress exerted on the amoebae by the prey (Laminger & Bucher, 1984). There may be some connection between these findings and the well known but still unexplained observation that most large autochthonous soil testaceans rarely extend their pseudopods (Bonnet, 1961c, 1963; Schönborn, 1966a).

Laminger (1978) observed relationships between soil moisture, shell size, and the kind of food ingested by *Trinema lineare*. Under low moisture conditions, the shells were often smaller (ca. 30 µm) and the amoebae ingested chiefly detritus particles. During periods with soil moisture near and above field capacity, the shells became larger (ca. 80 µm) and the amoebae grazed bacteria and even small *Euglypha laevis* and *Trinema lineare*.

Many soil testaceans probably feed on fungal hyphae and/or spores (Barron, 1978). The experiments of Coûteaux & Dévaux (1983) showed a greater abundance of *Phryganella acropodia* in fungi-enriched microcosms, whereas the number of *Plagiopyxis declivis* decreased under these conditions. Coûteaux & Dévaux (1983) were not able to observe the actual ingestion of hyphae, and thus supposed that the apparent increase in the number of protozoa could be an effect of the microcosm.

(c) *Temperature:* Smith & Headland (1983) studied the population ecology of *Phryganella acropodia* and *Corythion dubium* in soils of the sub-Antarctic island of South Georgia. They found high relative growth rates, of 4–7% day^{-1}, which they interpreted as an adaptation to 'switch on' rapidly and exploit successfully the periods during which temperatures are above 10°C. Such periods may be frequent, but their duration is never more than a few days. This ability may also explain the extraordinarily high abundance of these species in the soils of the South Orkney Islands (Heal, 1965).

(d) *r/K-selection:* The population ecology of the testate amoebae suggests that they are on the '*r*' side within the *r/K*-continuum (Jax, 1985; Lousier, 1982). In comparison with ciliates, flagellates, and naked amoebae, they might be considered as 'K' selected for their longer generation time and their preference for habitats, such as raw humus, with low decomposition capacity (Bamforth, 1980). Recently, Schönborn (1983b) studied the relationships among production, mortality, and abundance (PMA-types) in some representative soil testaceans (Fig. 42). He suggested that there are four PMA-types. (A) Optimal type, for instance *Trinema complanatum*; reproduction ceases as soon as a certain density is reached. Hence, there is a high abundance, a low production, and individuals are long-lived. (B) Productive type, for instance *Trinema enchelys* (Figs 213, 214); production, mortality, and abundance are high. (C) Retardative type, for instance *Euglypha ciliata*; production and mortality are relatively high, but abundance is low. (D) Sporadic type, for instance *Cyclopyxis kahli*; production and abundance are low, clones become extinct very quickly. There are transitions between these four types, such as, *Centropyxis plagiostoma* (Fig. 188a,b) which belongs to the B-C type. The optimal type is characteristic of autochthonous species, whereas the species also found in other habitats belong to the productive type. This would apply to *Phryganella acropodia* and *Corythion dubium*, described by Smith & Headland (1983) and discussed above. Lüftenegger *et al.* (1985) related the optimal type to *K*-selected, and the productive and the retarded types to *r*-selected species, which agrees with the hypothesis of Gerson & Chet (1981) that autochthones are more *K*-selected than allochthones.

C. *The Origin of the Soil Protozoa*

Early workers in soil protozoology noticed the apparent paucity of species of soil protozoa (e.g., Brodsky, 1935; Francé, 1921; Sandon, 1927; Tables 6, 12). Although recent studies have greatly enlarged the number of taxa, it seems unlikely that the number of species known from soil will ever exceed the number known from freshwater. This suggests that the soil is not their original environment.

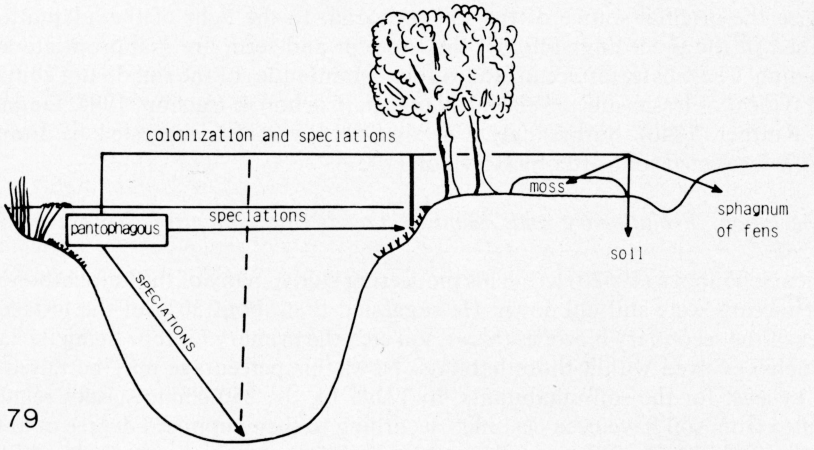
It is generally accepted that the soil fauna has evolved from freshwater immigrants (e.g., Bamforth, 1973; Gellért, 1957; Kühnelt, 1950; Martin, 1971; Schönborn, 1966a; Stout, 1984). Without taking into account the speciation which has occurred since that time, the soil protozoan community could be considered as an impoverished freshwater fauna (Ghilarov, 1978).

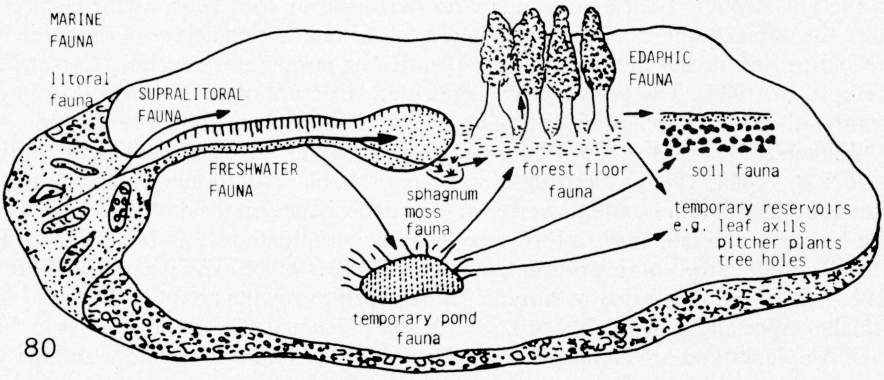
Which kind of freshwater biotope was the major source for the colonization of the soil? Schönborn (1962b, 1966a), working primarily with testate amoebae, suggested an origin from the lake Aufwuchs community (Fig. 79); whereas Sassuchin (1930), Biczók (1959), and Stout (1984), working with soil protozoa in general, suggested shallow temporary ponds and the moss and litter system (Fig. 80). Most of the marine sand testaceans are thought to be immigrants from freshwater and soil habitats (Golemansky, 1982). This is supported by the striking similarities which exist between some soil and marine sand testacean genera, such as between *Edaphonobiotus* and *Micropsammella* (Figs 168–171), and between *Lamtoquadrula* and *Pomoriella* (Bonnet, 1974a; Golemansky, 1970a; Golemansky & Coûteaux, 1982; Schönborn *et al.*, 1983). In contrast, the greater part of the psammal ciliates originated from marine source (Dragesco, 1960, 1962). Some interesting relict foraminiferans were discovered by Nikolyuk (1968) in the saline ground water of the Kara-Kum desert in Central Asia.

Schönborn (1962b, 1966a) based his evolutionary hypothesis on the similar appearances of testaceans from the Aufwuchs and litter. The testaceans of the Aufwuchs needed only relatively few new adaptations to become terriphilous because they had a number of features (e.g., flattened shells) which pre-adapted them for exploitation of soil niches. The strictly edaphic forms, the terribionts, evolved from these terriphilous species and have adapted to the special requirements of their habitat, for instance by cryptostomy, which has not been observed in lake testaceans. This attractive hypothesis probably does not apply to the soil ciliates, because the Cyrtophorida (Chilodonellidae, Dysteriidae, etc.), which are the most characteristic members of the Aufwuchs community, are poorly represented in the soil (Table 14).

Stout's (1984) hypothesis for a puddle source of soil protozoa was based on the observation that the soil protozoan fauna of a seasonally flooded grassland was composed of 20% edaphic cosmopolites (occurring in all soils, but not in freshwater), 35% aquatic-terrestrial, and 45% freshwater species. He considers the water-filled soil pores as 'a collection of miniature temporary pools.' If his species list is examined, ca. 30% of the forms were determined only to generic level and none of the 'typical' soil ciliate or soil testacean species were included. This suggests inappropriate methodology and/or poor taxonomy, so the evidence for this theory is weak.

It is true that soil and puddle ciliate faunas are similar in having a high incidence of colpodids, there being low numbers of attached species, and exhibiting ready recourse to encystment (Dingfelder, 1962). Yet, there is a very low species overlap between the two biotopes (Foissner, 1981a). The characteristic morphologies of soil and temporary pond ciliates are rather different (Dingfelder, 1962; Gelei, 1954; Foissner, 1980b, 1981a), and some colpodids perhaps entered the latter biotope via the soil (Foissner, 1985c; Fig. 86). Some prominent groups, like the nassulids and spirofilids, are nearly





Figs 79, 80. Suggested models for the origin of the terrestrial protozoa. For details see text. Pantophagous = polyphagous. (after Schönborn, 1966a, and Stout, 1984).

absent from edaphic habitats. Testaceans of temporary ponds are restricted to a few ubiquitous bottom forms.

The mosses and especially the litters are more likely candidates for the origin of the soil protozoa, at least for the ciliates, as suggested by the observations presented in section II.C. Litter is, however, slowly colonized by testate amoebae (Lousier, 1982; Lousier & Elliott, 1975) and a part of the soil *per definitionem* (Section II.A). Francé (1921) suggested that litters and mosses may have been colonized from soil and not *vice versa*.

Thus, in my opinion, it is not yet possible to identify from which freshwater biotope the majority of the soil protozoa originated. Very probably colonization of the soil occurred not only once for each major type of protozoon—but many times.

One further evolutionary hypothesis should be mentioned. Stout (1963) argued for very similar population structures of terrestrial and planktonic protozoan communities. He introduced the term 'terrestrial plankton,' with the idea that the plankton

could be the original source of the soil protozoa. In the light of the adaptations discussed in the preceding sections, this concept and term are inappropriate and misleading. The ciliate, testacean, and rotifer communities of the soil do not contain forms typical of freshwater or marine plankton (Cachon & Cachon, 1984; Donner, 1976; Ruttner, 1940). Surprisingly, this similarity was also suggested by Francé (1921), but rejected soon after by Nowikoff (1923).

D. *Speciation, Evolutionary and Adaptive Trends, and Adaptive Success in Soil Protozoa*

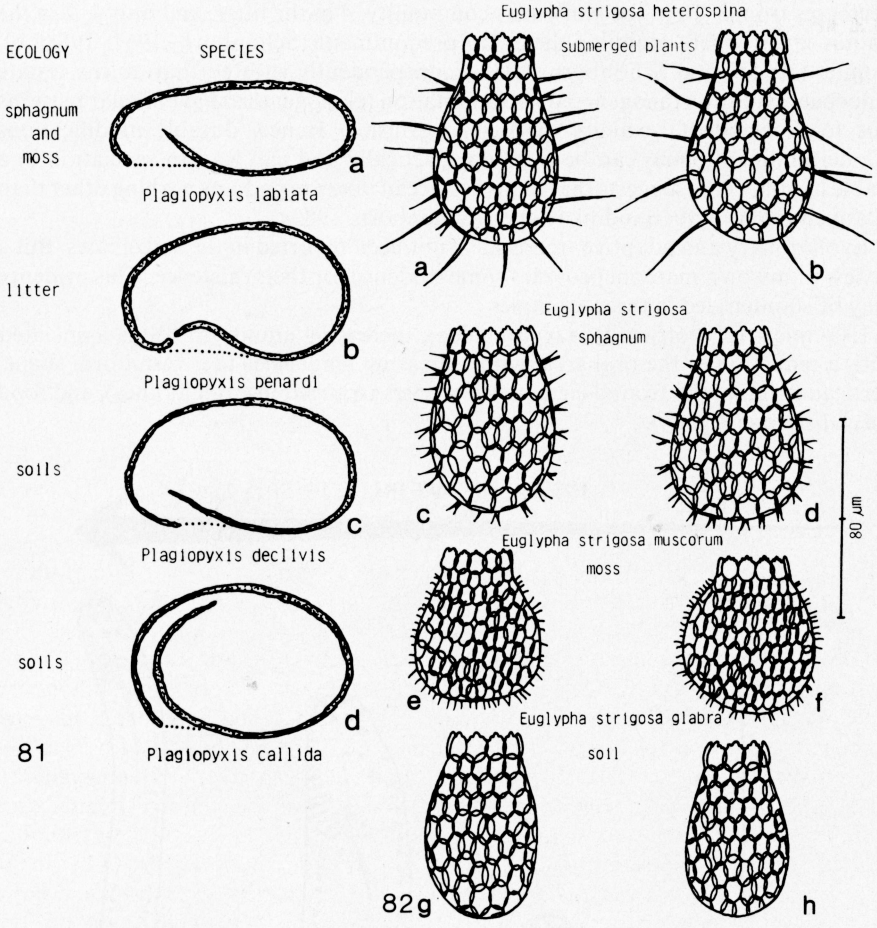
When Schönborn (1962b) wrote his pioneering study, many of the autochthonous soil testaceans were still unknown. He suggested that about 30% of the testacean species of the secondary biotopes (moss, soil etc.; the primary biotope being the lake Aufwuchs) evolved within those habitats. Now, this percentage may be raised to 50%, at least for the soil inhabitants. In Table 14, the 250 ciliate species reliably identified from soil have been classified according to their supposed degree of autochthonism: 61 (24%) of the species have also been found in freshwater habitats, 132 (53%) species are strongly associated with edaphic habitats, and 56 (22%) species have been classified as true (autochthonous) soil organisms. It is likely that most of the 132 'strongly associated' taxa are restricted to soil, too. Thus, we may expect, as in the testate amoebae, about 50% new species. Such a high degree of radiation is not surprising in the light of modern theories of population genetics (Carson & Templeton, 1984). The porous and fragmented structure of the soil can lead to a highly subdivided population structure which facilitates speciation and extinction.

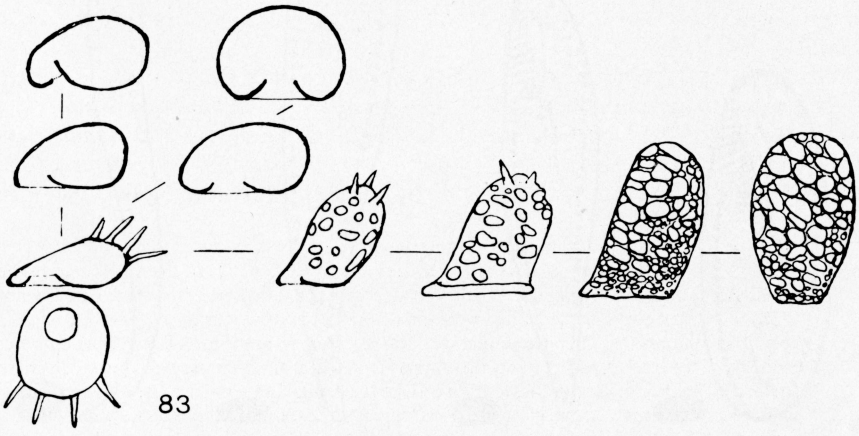
Bonnet & Thomas (1955), Thomas (1958), Bonnet (1975b), and Schönborn (1962a,b, 1966a, 1983a) discovered some remarkable evolutionary and adaptive trends in the testaceans, and have shown their dependence on the moisture regime of the biotope. The tendency to form plagiostomic, cryptostomic, and hemispherical shells is progressively more pronounced in those species which exhibit a preference for soil. This is well illustrated within the genus *Centropyxis*, the adaptive potential of which is especially high (Schönborn, 1983a). The presumed ancestral forms live in the lake Aufwuchs and are compressed. The terrestrial species became more and more cryptostomic and hemispherical, whereas the species which invaded the lake bottom became cylindrical and acrostomic (Fig. 83). The genus *Plagiopyxis* provides a second example (Fig. 81).

In each higher testacean taxon (family and above), test evolution tends to bilateral symmetry and to the differentiation of a vestibulum which is external in aquatic (e.g., *Centropyxis*; Figs 49, 53, 60, 62), and internal in strictly edaphic (e.g. *Distomatopyxis*; Figs 70, 163, 166), lineages. Plagiostomy apparently evolved by convergence in *Centropyxis* and *Trinema* (Bonnet, 1975b). The number of adaptive life forms

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Figs 81–83. Evolutionary and adaptive trends in testate amoebae. Fig. 81. In the genus *Plagiopyxis*, cryptostomy is more pronounced the more a species is associated with soils (after Thomas, 1958). Fig. 82. Adaptive trend in *Euglypha strigosa* from Aufwuchs to soil habitats. Note the loss of the spines and the size reduction with decreasing amounts of available space and moisture. Two individuals of a representative population are depicted each (after Chardez & Leclercq, 1963). Fig. 83. Evolutionary trends in the genus *Centropyxis*. The ancestral species, *Centropyxis aculeata*, which lives in the Aufwuchs, is flattened and has spines. The moss and soil species (vertical direction) became progressively more hemispherical and plagiostomic (*Centropyxis sphagnicola, C. sylvatica, Cyclopyxis*). The benthic species (horizontal direction) became progressively more acrostomic (*Centropyxis gibba, C. gibbosa, C. deflandri, Difflugia* sp.). (after Schönborn, 1983a)

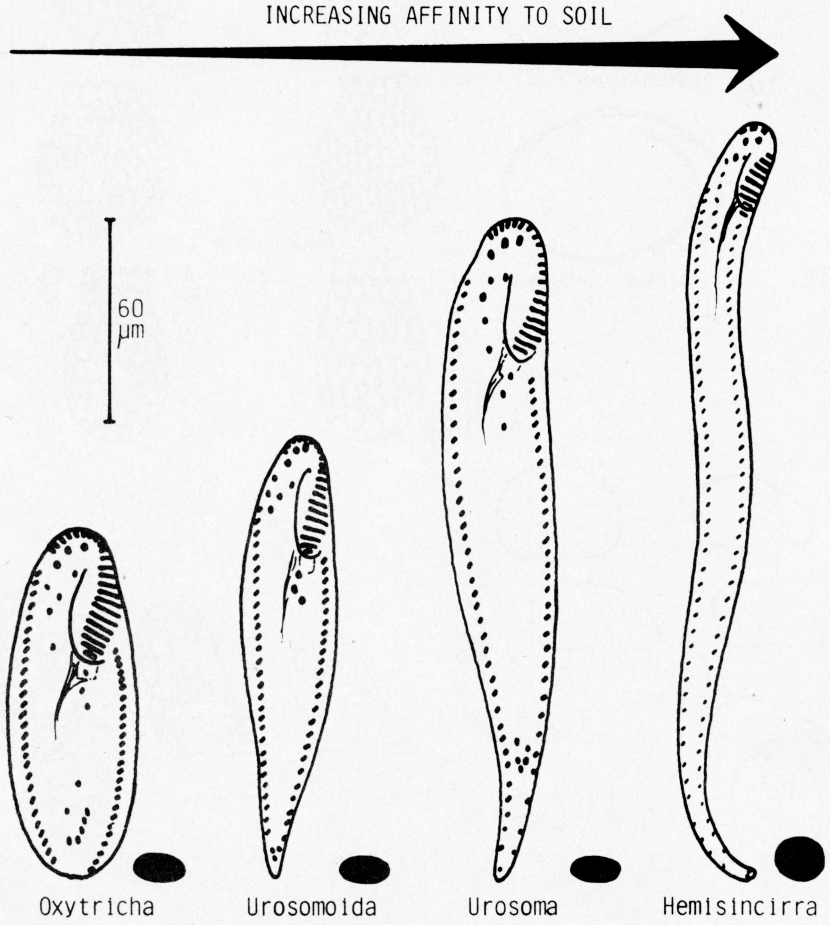

ECOLOGY
SPECIES
sphagnum and moss
Plagiopyxis labiata
a
litter
Plagiopyxis penardi
b
soils
Plagiopyxis declivis
c
soils
Plagiopyxis callida
d
81
Euglypha strigosa heterospina
submerged plants
a
b
Euglypha strigosa
sphagnum
c
d
80 µm
Euglypha strigosa muscorum
moss
e
f
Euglypha strigosa glabra
soil
82g
h


83

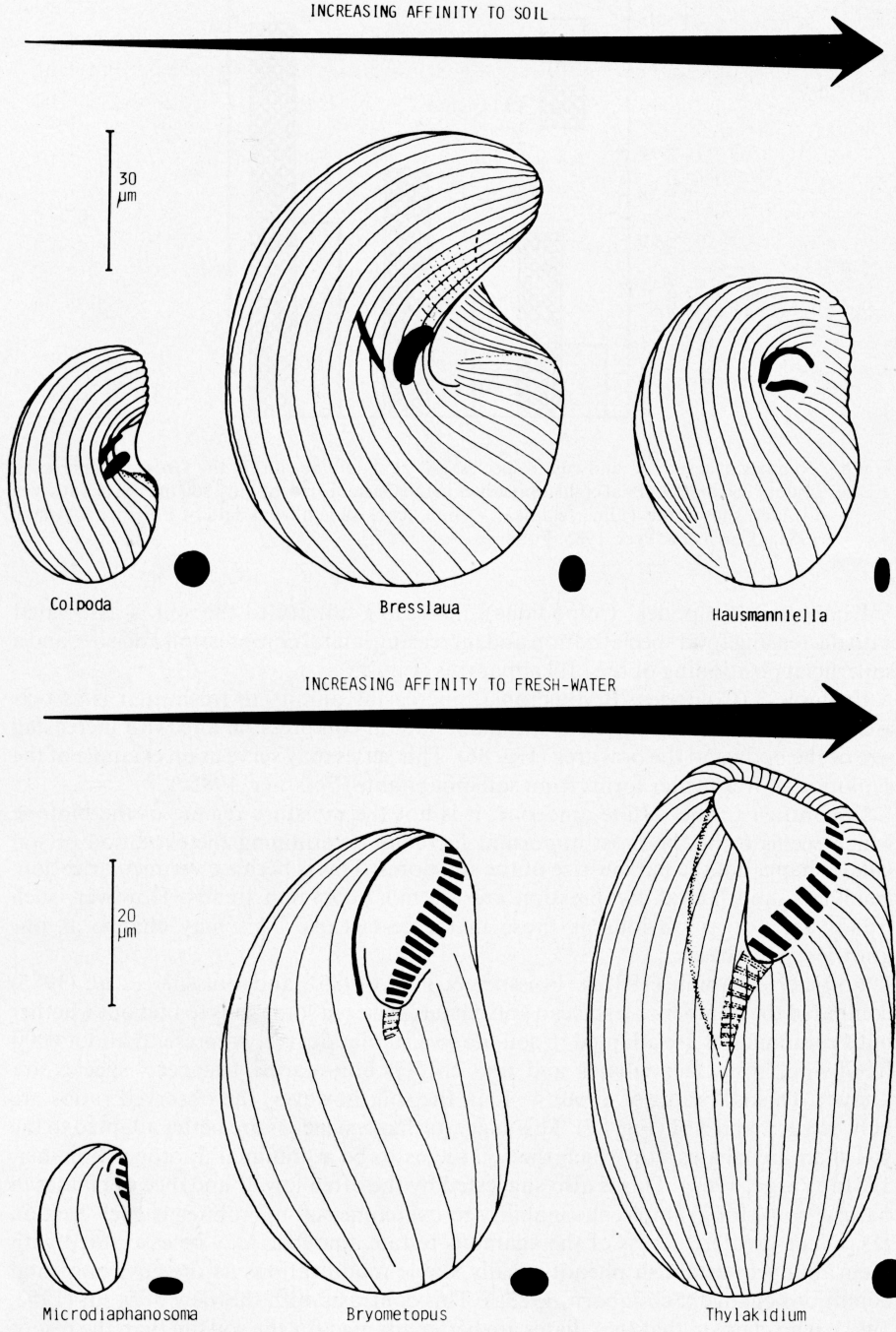
decreases from 8–10 in the Aufwuchs community, 4 in the litter, and only 1–2 in the humus layer, where globular shells are predominant (Schönborn, 1967, 1968a,b). Bonnet (1975b) and Schönborn (1983a) independently showed that, in the testate amoebae, evolution (anagenesis) and adaptation (cladogenesis) have similar patterns due to the lack of sexuality in these organisms. Hence, durable modifications (Dauermodifikationen) can be fixed epigenetically and can lead to speciation in a stable habitat. This suggests that many testacean taxa are perhaps nothing other than relatively stable Dauermodifikationen (Schönborn, 1983a).

Evolutionary and adaptive trends have not been reported in the soil ciliates. But a review of my own material provides some evidence for their existence. This evidence may be summarized in three examples.

Example 1 (Hypotrichida, Oxytrichidae): increasing affinity to soil is associated with a reduction of the oral area, with increasing tendencies to a vermiform shape, verticalization of the frontal cirral pattern (cirri arranged in straight lines), and food specialization (Fig. 84).



Figs 84–86. Evolutionary and adaptive trends in ciliates with regard to soil and freshwater habitats. At the bottom of each figure is shown the shape of the species in transverse section. (originals)


INCREASING AFFINITY TO SOIL
30 µm
Colpoda
Bresslaua
Hausmanniella
INCREASING AFFINITY TO FRESH-WATER
20 µm
Microdiaphanosoma
Bryometopus
Thylakidium

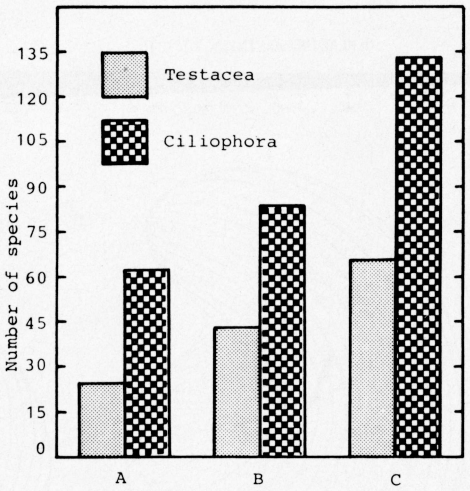


Fig. 87. Number of testacean and ciliate species: (A) at six alpine sites in the Grossglockner area, about 2260 m NN; (B) at eight alpine sites in the Gastein area, about 1860 m NN; (C) at seven lowland sites in the Tullnerfeld near Vienna. (constructed from data of Foissner & Adam, 1981a; Foissner & Peer, 1985; Foissner *et al.*, 1985)

Example 2 (Colpodea, Colpodidae): increasing affinity to the soil is associated with decreasing food specialization and increasing lateral compression and size, and a superficial positioning of the oral apparatus (Fig. 85).

Example 3 (Colpodea, Bryometopia): increasing affinity to freshwater is associated with reduced food specialization, and lateral compression and with increasing size of the body and the oral area (Fig. 86). This series may serve as an example of the evolution of freshwater forms from soil inhabitants (Foissner, 1985c).

In contrast to the testate amoebae, it is not the moisture regime of the biotope which seems to be the most important factor in determining the evolution of soil ciliate shape, but the narrow size of the soil pores. This is because vermicularization, smallness, and lateral compression are the most common trends. However, such trends are not as obvious as those in the testaceans. This may change as our knowledge increases.

Foissner & Adam (1981a), Foissner & Peer (1985), and Foissner *et al.* (1985) compared the number of testacean and ciliate species in some soils to find out whether both communities are adapted to soil life to a similar degree. At present, about 6000 free-living freshwater ciliates and about 1500 non-marine testacean species are known. This is a ratio of about 4 : 1. In the soil, however, the observed ratios are between 2 : 1 and 3 : 1 (Fig. 87). This suggests that testaceans are better adapted to the soil than are ciliates, for which the soil seems to be a 'minimal' biotope (Foissner, 1981a; Varga, 1960). This is also suggested by the often low abundance of ciliates in natural soils, for example, the inability to overcome soil microbiostasis (cf. Section II.C). The greater success of the agamous testate amoebae may be associated with their ability to establish phenotypically stable modifications as the environmental conditions change (Schönborn, 1983a). This contrasts with the view of Stout (1952, 1961), who claimed that the ciliates are better adapted for the soil life than the rest of the microfauna because the reduction of their species number after scrub burning was less pronounced than in the other groups. However, it may be argued that his species

Table 14. Taxonomic and ecological summary of recently described and redescribed soil ciliates[1]

Species[2]	Biomass of 10^6 indiv. (mg)[3]	Food[4]	Habitat type and notes on methodology[5]										Degree of autochthonism[6]
			a	b	c	d	e	f	g	h	i	j	
Acropisthium mutabile Perty, 1852	35	C	–	–	–	–	–	–	–	+	–	–	★
Amphisiella acuta Foissner, 1982	18	?	–	+	+	+	–	+	–	–	–	–	★★★
Amphisiella raptans Buitkamp & Wilbert, 1974	1280	C	–	–	–	–	–	–	–	–	–	+	★★★
Amphisiella terricola Gellért, 1955	100	C	–	–	–	+	–	–	–	+	–	–	★★★
Arcuospathidium cultriforme (Penard, 1922) Foissner, 1984	180	C	–	–	–	–	–	–	–	+	–	–	★★
Arcuospathidium lionotiforme (Kahl, 1930) Foissner, 1984	400	C	–	–	–	–	–	+	+	–	–	–	★★
Arcuospathidium muscorum (Dragesco & Dragesco-Kernéis, 1979) Foissner, 1984	87	C,H	+	+	+	+	+	+	+	+	–	–	★★
Arcuospathidium vermiforme Foissner, 1984	28	C?	–	–	–	–	+	–	–	+	–	–	★★★
Aspidisca cicada (Müller, 1786) Claparède & Lachmann, 1858	5	B	+	–	–	–	–	–	–	–	–	–	★
Aspidisca lynceus (Müller, 1773) Ehrenberg, 1830	6	B	+	–	–	–	–	–	–	–	–	–	★
Balantidioides bivacuolata Kahl, 1932	280	C	–	–	–	–	–	–	–	–	–	+	★★
Balantidioides corbifera (Fryd-Versavel & Tuffrau, 1978) Foissner, Adam & Foissner, 1982	360	C,G	–	–	–	–	–	–	–	–	–	+	★★
Balantidioides dragescoi Foissner, Adam & Foissner, 1982	135	C	–	–	+	–	–	–	–	–	–	–	★★
Bardeliella pulchra Foissner, 1984	8	B	–	–	–	–	–	–	–	–	–	+	★★★
Blepharisma bimicronucleata Villeneuve-Brachon, 1940	42	B	–	+	–	–	–	–	+	+	–	–	★
Blepharisma hyalinum Perty, 1849	11	B,H	+	+	–	+	–	+	+	–	+	–	★
Blepharisma steini Kahl, 1932	69	B	–	–	–	–	–	–	–	–	–	+	★
Blepharisma undulans Stein, 1867	225	B	–	–	–	–	+	–	–	–	–	–	★
Bresslaua insidiatrix Claff, Dewey & Kidder, 1941	192	C,F,G	–	–	–	–	–	–	–	–	–	+	★★
Bresslaua vorax Kahl, 1931	113	B,C,F,G,H	–	–	+	+	–	–	+	+	–	–	★★
Bryometopus atypicus Foissner, 1980	45	B,F,G	–	–	–	–	–	–	+	+	–	–	★
Bryometopus pseudochilodon Kahl, 1932	22	B	+	+	–	+	–	+	+	+	+	–	★★
Bryometopus sphagni (Penard, 1922) Kahl, 1932	198	C	–	+	–	–	–	–	–	–	+	–	★★
Bryophyllum loxophylliforme Kahl, 1931	252	C,R	–	+	–	–	–	–	–	–	–	–	★★
Bryophyllum tegularum Kahl, 1931	100	C,R	–	+	–	–	–	–	–	–	–	–	★★
Buitkampia angusta Foissner, 1985	3	B	–	–	–	–	–	–	–	–	–	+	★★
Chilodonella uncinata (Ehrenberg, 1838) Strand, 1928	13	B	+	–	+	+	+	+	+	+	–	–	★

Table 14. (*continued*)

Species[2]	Biomass of 10^6 indiv. (mg)[3]	Food[4]	Habitat type and notes on methodology[5]										Degree of autochthonism[6]
			a	b	c	d	e	f	g	h	i	j	
Chilodontopsis muscorum Kahl, 1931	15	?	−	+	−	−	−	−	−	−	+	−	★★
Chilophrya terricola Foissner, 1984	9	C?	−	+	−	−	−	−	−	−	−	−	★★
Chlamydonella alpestris Foissner, 1979	4	B,D	+	−	−	−	−	−	−	−	−	−	★
Cinetochilum margaritaceum (Ehrenberg, 1830) Perty, 1852	10	B	+	+	+	+	+	+	+	+	+	−	★
Cirrophrya haptica Gellért, 1950	25	B,G	−	−	−	−	−	−	−	−	−	+	★★★
Cirrophrya terricola Foissner, 1987	20	C	−	−	−	−	−	−	+	+	−	−	★★★
Colpoda acuta Buitkamp, 1977	4	B	−	−	−	−	−	−	−	−	−	+	★★
Colpoda aspera Kahl, 1926	6	B	+	+	+	+	+	+	+	+	+	−	★★
Colpoda augustini Foissner, 1987	20	B	−	−	−	−	−	−	−	−	−	+	★★★
Colpoda cavicola Kahl, 1935 (syn; *C. spiralis* Novotny *et al.*, 1977)	240	B	−	−	−	−	−	−	−	−	−	+	★★
Colpoda cucullus Müller, 1773	74	B,F	+	+	+	+	+	+	+	+	+	−	★★
Colpoda edaphoni Foissner, 1980	10	B	+	−	+	+	+	+	−	+	+	−	★★★
Colpoda elliotti Bradbury & Outka, 1967	5	B	−	−	+	−	−	−	+	+	−	−	★★
Colpoda fastigata Kahl, 1931	39	B	+	+	+	+	+	+	+	+	+	−	★★
Colpoda henneguyi Fabre-Domergue, 1889	122	B,H	+	+	+	+	+	+	+	+	+	−	★★
Colpoda inflata (Stokes, 1885) Kahl, 1931	40	B	+	+	+	+	+	+	+	+	+	−	★★
Colpodidium caudatum Wilbert, 1982	8	B	−	−	−	−	−	−	−	+	+	−	★★★
Cyclidium muscicola Kahl, 1931	1	B	+	+	+	+	+	+	+	+	+	−	★★
Cyclidium terricola Kahl, 1931	3	B	−	−	−	−	−	−	−	+	+	−	★★
Cyrtolophosis acuta Kahl, 1926	1	B	+	+	+	+	+	+	+	+	−	−	★
Cyrtolophosis elongata (Schewiakoff, 1892) Kahl, 1931	1	B	−	−	+	+	+	+	−	−	−	−	★
Cyrtolophosis mucicola Stokes, 1885	2	B	+	+	−	+	+	+	+	+	+	−	★
Dileptus alpinus Kahl, 1932	23	C	−	−	−	−	−	−	−	−	−	+	★★
Dileptus anguillula Kahl, 1931	15	C	+	+	+	+	−	+	+	−	−	−	★★
Dileptus gracilis Kahl, 1931	43	C	−	−	−	−	−	−	−	−	−	+	★★
Dileptus margaritifer (Ehrenberg, 1838) Wirnsberger, Foissner & Adam, 1984	170	C	−	−	+	−	+	−	−	−	−	−	★
Dileptus mucronatus Penard, 1922	456	C	−	−	−	−	−	−	−	−	−	+	★
Dileptus terrenus Foissner, 1981	226	C	+	−	−	−	−	+	+	+	−	−	★★
Dileptus visscheri Dragesco, 1963	64	C	−	+	−	−	−	−	−	−	−	−	★

Dimacrocaryon amphileptoides (Kahl, 1931) Jankowski, 1967	127	G,H,T	−	+	−	−	−	+	−	−	+	−	★★
Drepanomonas paucicilliata Foissner, 1987	1	B	−	−	−	−	−	−	−	−	+	−	★★
Drepanomonas revoluta Penard, 1922	1	B	+	+	+	+	+	+	+	+	+	−	★
Drepanomonas sphagni Kahl, 1931	1	B	+	+	−	−	−	+	+	+	−	−	★★
Enchelydium piliforme (Kahl, 1930) Foissner, 1984	88	C	−	−	+	−	−	−	−	−	−	−	★
Enchelydium polynucleatum Foissner, 1984	255	C	−	−	+	−	−	−	−	+	−	−	★★
Enchelydium terrenum Foissner, 1984	57	C	−	+	−	−	−	−	−	−	−	−	★★
Enchelyodon longinucleatus Foissner, 1984	63	C?	−	−	−	−	−	−	−	+	−	−	★★
Enchelyodon nodosa Berger, Foissner & Adam, 1984	367	C?	−	+	−	−	−	−	−	+	−	−	★★
Enchelyodon terrenus Foissner, 1984	132	C?	−	−	−	−	−	−	−	−	−	+	★★★
Enchelyotricha binucleata Foissner, 1987	16	C	−	−	−	−	−	−	−	+	−	−	★★
Enchelys multinucleata (Dragesco & Dragesco-Kernéïs, 1979) Berger, Foissner & Adam, 1984	141	C	−	+	−	−	−	−	+	+	−	−	★★
Enchelys terricola Foissner, 1987	99	C	−	−	−	−	−	−	−	+	−	−	★★
Enchelys vermiformis Foissner, 1987	50	C?	−	−	−	−	−	−	+	+	−	−	★★★
Engelmanniella mobilis (Engelmann, 1862) Foissner, 1982	34	B	−	−	+	+	+	+	−	+	−	−	★
Epispathidium amphoriforme (Greeff, 1888) Foissner, 1984	180	C	−	−	−	−	+	+	−	−	+	−	★★
Epispathidium ascendens (Wenzel, 1955) Foissner, 1987	64	C	−	−	−	−	−	−	+	+	−	−	★★
Epispathidium terricola Foissner, 1987	101	C	−	−	−	−	−	−	+	+	+	−	★★
Epispathidium papilliferum (Kahl, 1930) Foissner, 1984	135	C	−	−	−	−	−	−	−	−	−	+	★★
Epispathidium regium Foissner, 1984	360	C	−	+	−	−	−	−	−	−	−	−	★★
Eschaneustyla terricola Foissner, 1982	146	C,D,G,H	−	−	−	+	−	−	−	−	−	−	★★
Euplotes finki Foissner, 1982	17	B	+	+	−	−	−	−	−	−	−	−	★★
Euplotes muscicola Kahl, 1932	49	B	+	+	+	+	+	+	−	+	−	−	★★
Frontonia depressa (Stokes, 1886) Kahl, 1931	95	C,G,N	−	+	−	−	−	+	−	−	+	−	★
Frontonia terricola Foissner, 1987	192	C	−	−	−	−	−	−	+	+	−	−	★★
Fuscheria terricola Berger, Foissner & Adam, 1983	20	C	−	+	+	+	+	+	+	+	−	−	★★★
Gastrostyla dorsicirrata Foissner, 1982	96	C,H	+	+	−	−	−	−	+	+	−	−	★★
Gastrostyla steinii Engelmann, 1862	122	C	−	−	+	+	+	+	+	+	−	−	★
Gonostomum affine (Stein, 1859) Sterki, 1878	39	B	+	+	+	+	+	+	+	+	+	−	★★
Gonostomum franzi Foissner, 1982	30	B,F,S	+	+	+	−	+	−	+	−	−	−	★
Gonostomum kuehnelti Foissner, 1987	30	B,F	−	−	−	−	−	−	+	+	−	−	★★★
Grossglockneria acuta Foissner, 1980	5	H	+	+	+	+	+	+	+	+	+	−	★★★
Grossglockneria hyalina Foissner, 1985	4	H	−	−	+	+	+	−	+	+	−	−	★★★
Halteria grandinella (Müller, 1773) Dujardin, 1841	27	B	+	+	+	+	+	+	+	+	−	−	★
Haplocaulus terrenus Foissner, 1981	5	B	+	+	−	−	−	+	−	−	−	−	★★
Hausmanniella discoidea (Gellért, 1956) Foissner, 1984	67	C,G,H	+	+	−	−	−	−	−	−	+	−	★★★
Hemisincirra filiformis (Foissner, 1982) Foissner, 1984	5	?	−	−	+	+	+	+	+	+	−	−	★★★

Table 14. (*continued*)

Species[2]	Biomass of 10^6 indiv. (mg)[3]	Food[4]	Habitat type and notes on methodology[5]										Degree of autochthonism[6]
			a	b	c	d	e	f	g	h	i	j	
Hemisincirra gellerti (Foissner, 1982) Foissner, 1984	10	B	+	+	+	+	+	+	+	+	+	–	★★★
Hemisincirra gracilis (Foissner, 1982) Foissner, 1984	11	B?,H	–	+	+	+	+	+	+	+	+	–	★★★
Hemisincirra heterocirrata Hemberger, 1985	26	?	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra inquieta Hemberger, 1985	7	B	–	–	–	–	–	–	–	–	+	–	★★★
Hemisincirra interrupta (Foissner, 1982) Foissner, 1984	8	?	+	+	–	–	–	–	–	–	–	–	★★★
Hemisincirra kahli (Buitkamp, 1977) Hemberger, 1985	8	B	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra livida Berger & Foissner, 1987	24	B	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra muelleri Foissner, 1986	11	B	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra octonucleata Hemberger, 1985	24	?	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra polynucleata Foissner, 1984	30	?	–	–	–	+	–	–	–	+	–	–	★★★
Hemisincirra pori Wilbert, 1986	19	B,G	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra quadrinucleata Hemberger, 1985	26	?	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra similis (Foissner, 1982) Foissner, 1984	32	B?	–	–	+	–	–	–	–	–	–	–	★★★
Hemisincirra vermiculare Hemberger, 1985	24	?	–	–	–	–	–	–	–	–	–	+	★★★
Hemisincirra viridis (Foissner, 1982) Foissner, 1984	33	B	–	–	–	–	+	–	–	–	–	–	★★★
Histriculus cavicola (Kahl, 1935) Berger & Foissner, 1987	540	C,N	–	–	–	–	–	–	+	–	–	–	★★
Histriculus muscorum (Kahl, 1932) Corliss, 1960	72	B,C,F,N	+	+	+	+	+	+	+	+	+	–	★
Histriculus similis f. *tricirrata* Buitkamp, 1977	234	B,E	–	–	–	–	–	–	–	–	–	+	★★
Holosticha adami Foissner, 1982	66	C,D,R,S,T	+	+	–	–	–	–	+	–	–	–	★★
Holosticha distyla Buitkamp, 1977	136	F,T	–	–	–	–	–	–	–	–	–	+	★★
Holosticha multistilata Kahl, 1928	109	C,D,E,F,T	+	–	+	+	+	+	–	+	+	–	★
Holosticha muscorum (Kahl, 1932) Foissner, 1982	360	C,D,T	–	–	+	+	–	–	–	–	–	–	★
Holosticha sigmoidea Foissner, 1982	38	B,H	+	+	+	+	+	+	+	+	+	–	★★
Holosticha sylvatica Foissner, 1982	181	?	–	+	–	–	–	+	–	–	–	–	★★
Holosticha tetracirrata Buitkamp & Wilbert, 1974	39	B,C,D,G,H	+	–	–	+	+	+	+	+	–	–	★★
Homalogastra setosa Kahl, 1926	1	B	+	+	+	+	+	+	+	+	+	–	★
Kahliella bacilliformis (Gelei, 1954) Corliss, 1960	47	B,G	–	–	–	–	–	–	–	–	–	+	★
Kahliella simplex (Horváth, 1934) Corliss, 1960	157	B,D,F,H	–	–	–	–	–	–	+	+	–	–	★★
Kahlilembus fusiformis (Kahl, 1926) Grolière & Coûteaux, 1984	1	B	–	–	–	+	+	+	+	–	+	–	★★
Keronopsis algivora (Gellért, 1942) nov. comb.	64	G	–	–	–	–	+	–	–	–	–	–	★★

Keronopsis muscicola (Kahl, 1932) Hemberger & Wilbert, 1982	210	G	−	+	−	−	−	−	−	−	−	★★
Keronopsis wetzeli Wenzel, 1953	90	C,G	−	−	−	−	−	−	−	−	+	★★
Lagynophrya geleii Foissner, 1981	25	C?	+	−	−	−	−	−	−	−	−	★★
Lagynophrya trichocystis Foissner, 1981	3	C?	+	+	−	−	−	−	−	−	−	★★
Lamtostyla edaphoni Berger & Foissner, 1987	11	B	−	−	−	−	−	−	−	−	+	★★
Lamtostyla lamottei Buitkamp, 1977	26	C,D	−	−	−	−	−	−	−	−	+	★★
Lamtostyla perisincirra (Hemberger, 1985) Berger & Foissner, 1987	7	?	−	+	−	−	−	−	−	−	−	★★★
Leptopharynx costatus Mermod, 1914	5	B	+	+	+	+	+	+	+	+	−	★
Litonotus spp.	12	C	−	+	−	+	+	+	−	−	−	−	?
Metopus hasei Sondheim, 1929	14	B	+	−	−	−	+	−	+	+	−	−	★★
Metopus rectus (Kahl, 1932) Foissner, 1980	72	B	−	−	−	−	+	−	−	−	−	−	★
Microdiaphanosoma arcuata (Grandori & Grandori, 1934) Wenzel, 1953	0.5	B	+	+	−	+	+	+	−	−	+	−	★★★
Microthorax simulans (Kahl, 1926) Kahl, 1931	0.7	B	+	+	−	−	+	+	−	−	+	−	★★
Mycterothrix tuamotuensis (Balbiani, 1887) Kahl, 1931	20	B	−	−	−	−	−	−	−	−	−	+	★★★
Nassula picta Greeff, 1888	224	E	−	+	+	−	−	−	+	−	−	−	★
Nivaliella plana Foissner, 1980	0.5	H	+	+	+	+	+	+	+	+	+	−	★★★
Odontochlamys alpestris Foissner, 1981	10	B,F	+	+	−	+	−	−	−	+	−	−	★★
Odontochlamys gouraudi Certes, 1891	13	B	−	−	−	−	−	+	−	−	+	−	★
Opercularia arboricola (Biegel, 1954) Foissner, 1981	48	B	+	+	+	+	+	+	+	+	−	−	★★
Opisthonecta minima Foissner, 1975	143	B	−	−	−	−	+	−	−	−	−	−	★
Orthokreyella schiffmanni Foissner, 1984	0.2	B?	−	+	−	−	−	−	−	−	−	−	★★★
Oxytricha granulifera Foissner & Adam, 1983	72	B,F,H	−	+	+	+	+	+	+	+	−	−	★★
Oxytricha lanceolata Shibuya, 1930	70	B	−	−	−	−	−	−	+	+	−	−	★★
Oxytricha nauplia Berger & Foissner, 1987	26	F,G,H	−	−	−	−	−	−	−	−	−	+	★★
Oxytricha pseudosimilis Hemberger, 1985	180	?	−	−	−	−	−	−	−	−	−	+	★★
Oxytricha rubripuncta Berger & Foissner, 1987	200	B,C,D,G,T	−	−	−	−	−	−	−	−	−	+	★★
Oxytricha selvatica Hemberger, 1985	560	?	−	−	−	−	−	−	−	−	−	+	★★
Oxytricha setigera Stokes, 1891	8	B,F	+	+	+	+	+	+	+	+	+	−	★
Oxytricha siseris Vuxanovici, 1963	30	B?	−	−	+	+	−	−	−	−	−	−	★
Oxytricha tricirrata Buitkamp, 1977	56	C,N	−	−	−	−	−	−	−	−	−	+	★★
Papillorhabdos multinucleatus Foissner, 1984	44	C	−	−	−	−	−	−	+	−	−	−	★
Parabryophrya penardi (Kahl, 1931) Foissner, 1985	28	B	−	−	−	−	−	+	−	−	−	−	★★★
Paracolpoda steinii (Maupas, 1883) Lynn, 1975	5	B	+	+	+	+	+	+	+	+	+	−	★
Paraenchelys terricola Foissner, 1984	49	C	−	−	+	−	−	+	−	+	+	−	★★
Paraenchelys wenzeli Foissner, 1984	89	C?	−	−	−	−	−	−	−	−	−	+	★★
Parafurgasonia sorex (Penard, 1922) Foissner & Adam, 1981	56	G,H?,N	−	+	−	−	−	+	−	−	−	−	★★★
Paragastrostyla lanceolata Hemberger, 1985	120	?	−	−	−	−	−	−	−	−	−	+	★★
Parakahliella macrostoma (Foissner, 1982) Berger, Foissner & Adam, 1986	168	C,N	−	+	−	−	+	−	+	+	−	−	★★

Table 14. (*continued*)

Species[2]	Biomass of 10^6 indiv. (mg)[3]	Food[4]	Habitat type and notes on methodology[5]										Degree of autochthonism[6]
			a	b	c	d	e	f	g	h	i	j	
Parakahliella terricola (Buitkamp, 1977) Berger, Foissner & Adam, 1986	504	C	–	–	–	–	–	–	–	–	–	+	★★
Paraurostyla pulchra Buitkamp, 1977	300	C,D	–	–	–	–	–	–	–	–	–	+	★★
Paruroleptus muscorum (Kahl, 1932) Foissner, 1982	40	C,H,S	–	+	–	+	+	+	+	+	–	–	★★
Paruroleptus notabilis Foissner, 1982	32	F,H,T	+	–	+	–	–	–	–	–	–	–	★★
Pelagotrichidium tisiae (Gelei, 1929) Jankowski, 1978	396	C,D,F,H	–	–	–	+	–	–	–	–	–	–	★
Periholosticha acuminata Hemberger, 1985	56	?	–	–	–	–	–	–	–	–	–	+	★★
Periholosticha lanceolata Hemberger, 1985	30	?	–	–	–	–	–	–	–	–	–	+	★★
Phacodinium metchnicoffi (Certes, 1891) Kahl, 1932	280	B,C,G	–	+	–	–	–	+	–	–	–	–	★★★
Phialina binucleata Berger, Foissner & Adam, 1984	8	C	–	+	+	+	+	–	–	–	–	–	★★
Phialina terricola Foissner, 1984	5	C	–	–	+	+	–	–	+	+	–	–	★★
Plagiocampa difficilis Foissner, 1981	11	B,F	+	+	–	–	–	–	+	–	–	–	★★
Plagiocampa rouxi Kahl, 1926	7	B,G	–	–	+	+	+	+	–	–	–	–	★
Platyophrya macrostoma Foissner, 1980	1.5	B	+	+	+	+	+	+	+	+	–	–	★★
Platyophrya procera Foissner, 1980	5	B,C?,G,H	+	+	–	–	–	–	–	–	–	–	★
Platyophrya similis (Foissner, 1980) nov. comb.	180	G,F	+	+	–	–	–	–	+	–	+	–	★★
Platyophrya spumacola Kahl, 1927	40	B,C,F,G	–	–	+	+	+	+	+	+	+	–	★★
Platyophrya vorax Kahl, 1926	12	F,G	+	+	+	+	+	+	+	+	+	–	★
Platyophryides dragescoi Foissner, 1987	64	C	–	–	–	–	–	–	–	–	+	–	★★
Platyophryides lata (Kahl, 1930) Foissner, 1987	108	C	–	–	–	–	–	–	–	–	–	+	★★
Protospathidium bonneti (Buitkamp, 1977) Foissner, 1981	5	C	+	+	+	+	+	+	–	–	+	–	★★★
Protospathidium muscicola Dragesco & Dragesco-Kernéïs, 1979	7	F	–	–	–	–	–	–	–	–	–	+	★★
Protospathidium serpens (Kahl, 1930) Foissner, 1981	5	C?	+	+	+	+	+	+	+	+	–	–	★★
Pseudochilodonopsis mutabilis Foissner, 1981	8	B	+	+	+	+	+	+	+	+	+	–	★★
Pseudochilodonopsis polyvacuolata Foissner & Didier, 1981	30	B	–	–	–	–	+	+	–	–	–	–	★
Pseudocohnilembus putrinus (Kahl, 1928) Foissner & Wilbert, 1981	2	B	+	–	–	–	+	–	+	+	–	–	★
Pseudocyrtolophosis alpestris Foissner, 1980	2	B	+	+	+	+	+	+	+	+	+	–	★★
Pseudoholophrya terricola Berger, Foissner & Adam, 1984	32	C?	–	+	+	+	+	+	+	+	+	–	★★
Pseudokreyella terricola Foissner, 1985	3	B?	–	+	–	–	–	+	+	–	–	–	★★★
Pseudoplatyophrya nana (Kahl, 1926) Foissner, 1980	3	H	+	+	+	+	+	+	+	+	+	–	★★★
Pseudoplatyophrya terricola Foissner, 1985	3	H	+	+	+	+	+	+	+	+	+	–	★★★

Pseudouroleptus buitkampi (Foissner, 1982) Berger & Foissner, 1987	72	B,C,S	−	+	+	−	−	−	−	−	−	★★★
Pseudouroleptus caudatus Hemberger, 1985	375	?	−	−	−	−	−	−	−	−	+	★
Pseudouroleptus procerus Berger & Foissner, 1987	120	C,F,G,N	−	−	−	−	−	−	−	+	−	−	★★★
Pseudouroleptus terrestris Hemberger, 1985	330	?	−	−	−	−	−	−	−	−	−	+	★★
Pseudovorticella sphagni Foissner & Schiffmann, 1974	14	B	−	−	−	−	+	−	−	−	−	−	★
Sathrophilus muscorum (Kahl, 1931) Corliss, 1960	12	B	+	+	+	+	+	+	+	+	+	−	★★
Semiplatyophrya foissneri Wilbert, 1986	13	B	−	−	−	−	−	−	−	−	−	+	★★
Sorogena stoianovitchae Bradbury & Olive, 1980	54	C	−	−	−	−	−	−	−	−	−	+	★★
Spathidium anguilla Vuxanovici, 1962	25	C?	−	−	−	+	−	−	−	+	−	−	★★
Spathidium claviforme Kahl, 1930	31	C	−	−	−	−	+	−	+	+	−	−	★★
Spathidium lagyniforme Kahl, 1930	34	C?	−	−	+	−	−	−	−	−	−	−	★
Spathidium longicaudatum (Buitkamp & Wilbert, 1974) Buitkamp, 1977	18	C,N	+	+	+	+	+	+	+	+	−	−	★★★
Spathidium muscicola Kahl, 1930	84	C	−	+	+	+	+	+	+	+	−	−	★★
Spathidium procerum Kahl, 1930	15	C?	−	−	+	+	−	−	+	−	−	−	★★
Spathidium rusticanum Foissner, 1981	25	C?	+	−	−	−	−	−	−	−	−	−	★★
Spathidium scalpriforme Kahl, 1930	220	C?	−	−	+	−	−	−	−	−	−	−	★★
Spathidium spathula (Müller, 1773) Moody, 1912	45	C	+	+	+	−	−	+	+	+	+	−	★
Sphaerophrya terricola Foissner, 1986	8	C	+	−	+	+	−	−	−	+	−	−	★★
Stammeridium kahli (Wenzel, 1953) Wenzel, 1969	0.6	B	+	+	−	+	−	−	−	−	−	−	★★★
Steinia candens Kahl, 1932	150	B,C,F,N	+	+	+	+	+	−	+	+	−	−	★★
Steinia citrina Berger & Foissner, 1987	54	C,D,H,T	−	−	+	−	+	−	−	−	−	−	★★
Steinia muscorum Kahl, 1932	225	C,D,F,H	+	−	+	+	+	+	+	+	−	−	★★
Steinia platystoma (Ehrenberg, 1831) Kahl, 1932	480	C,F,G	−	−	−	−	−	−	−	−	−	+	★
Steinia quadrinucleata Dragesco & Njiné, 1971	81	C	−	−	−	−	−	−	+	+	−	−	★
Steinia tetracirrata Gellért, 1942	150	B,F	−	−	−	−	−	−	−	−	−	+	★★★
Steinia ultricirrata Berger & Foissner, 1987	77	C,D,F,H	−	−	−	−	−	−	−	−	−	+	★★
Strongylidium muscorum Kahl, 1932	192	C,F,H	−	−	+	−	+	−	−	−	−	−	★★
Strongylidium wilberti Foissner, 1982	152	T	−	−	+	−	+	−	+	−	−	−	★★
Stylonychia mytilus (Müller, 1773) Ehrenberg, 1830	70	B,C,G,Z	+	−	−	−	+	−	−	−	−	−	★
Tachysoma granulifera Berger & Foissner, 1987	26	F,G,H,N	−	−	−	−	−	−	−	−	−	+	★★★
Tachysoma humicola Gellért, 1957	9	B,T	−	−	−	−	−	−	−	−	−	+	★★★
Tachysoma hyalina Berger, Foissner & Adam, 1984	4	?	−	+	−	−	−	−	−	−	+	−	★★★
Tachysoma longa Hemberger, 1985	135	?	−	−	−	−	−	−	−	−	−	+	★★★
Tachysoma raptans Hemberger, 1985	150	?	−	−	−	−	−	−	−	−	−	+	★★★
Tachysoma terricola Hemberger, 1985	45	?	−	−	−	−	−	−	−	−	−	+	★★★
Telotrochidium cylindricum Foissner, 1978	66	B	+	+	−	−	−	−	+	+	−	−	★
Tetrahymena edaphoni Foissner, 1987	8	B	+	−	−	−	−	−	−	−	−	−	★★
Tetrahymena rostrata (Kahl, 1926) Corliss, 1952	12	B	+	+	+	+	+	+	+	+	+	−	★★

Table 14. (*continued*)

Species[2]	Biomass of 10^6 indiv. (mg)[3]	Food[4]	Habitat type and notes on methodology[5] a	b	c	d	e	f	g	h	i	j	Degree of autochthonism[6]
Tillina magna Gruber, 1879	2400	B,G	–	–	+	–	–	–	+	–	–	–	★
Trachelochaeta gonostomoida Hemberger, 1985	204	?	–	–	–	–	–	–	–	–	–	+	★★
Trachelophyllum apiculatum (Perty, 1852) Claparède & Lachmann, 1859	39	C	–	–	–	–	–	–	+	+	–	–	★
Trithigmostoma bavariensis (Kahl, 1931) Foissner, 1987	96	B	–	–	–	+	–	+	+	+	–	–	★★
Uroleptoides atypica Hemberger, 1985	184	?	–	–	–	–	–	–	–	–	–	+	★★
Uroleptoides binucleata Hemberger, 1985	412	?	–	–	–	–	–	–	–	–	–	+	★★
Uroleptoides caudata Hemberger, 1985	300	?	–	–	–	–	–	–	–	–	–	+	★★
Uroleptoides quadrinucleata Foissner, 1984	42	F,G,H	–	+	–	–	–	–	–	–	–	–	★★
Uroleptoides vitiphila Foissner, 1987	92	C,F	–	–	–	–	–	–	–	–	–	+	★★
Urosoma acuminata (Stokes, 1887) Kahl, 1932	73	D,H,G	–	–	+	+	+	–	+	+	–	–	★
Urosoma cienkowskii Kowalewski, 1882	34	B,C,F,H	–	–	+	–	+	–	–	–	–	–	★
Urosoma gigantea (Horváth, 1933) Kahl, 1935	270	B	–	–	–	–	–	–	–	–	–	+	★★
Urosoma macrostyla (Wrześniowski, 1870) Kahl, 1932	41	B	–	–	+	–	+	–	+	+	–	–	★
Urosomoida agilis (Engelmann, 1862) Hemberger, 1985	30	B,D,N,S,T	+	+	+	+	+	+	+	+	–	–	★
Urosomoida agiliformis Foissner, 1982	30	B,C	+	+	+	+	+	+	+	+	+	–	★★
Urosomoida dorsiincisura Foissner, 1982	38	B,C,N	–	+	+	+	+	+	–	–	–	–	★★
Urosomoida minima Hemberger, 1985	12	?	–	–	–	–	–	–	–	–	–	+	★★
Vorticella astyliformis Foissner, 1981	13	B,S	+	+	+	+	+	+	+	+	–	–	★★
Vorticella infusionum Dujardin, 1841	18	B	+	+	–	+	+	–	+	+	–	–	★
Vorticella similis Stokes, 1887	75	B	+	–	–	–	–	–	+	+	–	–	★
Woodruffia rostrata Kahl, 1931	126	C	–	–	–	–	–	–	–	–	–	+	★

Number of species[7]: 250

[1]Taxonomy is based on the accounts of Berger & Foissner, 1987; Berger *et al.*, 1983, 1984b, 1985b; Bradbury & Olive, 1980; Buitkamp, 1975, 1977a,b; Buitkamp & Wilbert, 1974; Dragesco, 1970; Dragesco & Dragesco-Kernéïs, 1979; Foissner, 1978, 1979b, 1980a,c, 1981b,c, 1982, 1983b, 1984a,b, 1985c,d, 1986a; Foissner & Adam, 1981b, 1983; Foissner & Didier, 1981, 1983; Foissner & Foissner, 1987; Foissner & Schubert, 1983; Foissner & Wilbert, 1981; Foissner *et al.*, 1982a,b; Fryd-Versavel & Tuffrau, 1978; Fryd-Versavel *et al.*, 1975; Grolière & Coûteaux, 1984; Hemberger, 1985; Hemberger & Wilbert, 1982; Lynn, 1976a–c; Lynn & Malcolm,

1983; Novotny *et al.*, 1977; Wilbert, 1982; Wilbert & Kahan, 1985. Only species that have been figured, correctly described, and determined with the aid of modern silver impregnation techniques, are included. True *Sphagnum*-species are excluded. As far as it concerns my papers, this summary supersedes my earlier species lists (Foissner, 1981a; Foissner & Peer, 1985; Foissner *et al.*, 1985).

[2]As an aid to taxonomists and ecologists, the author of the most recent taxonomic combination is also given.

[3]Rough estimation obtained by reducing the shape of the animals to simple geometric figures and assuming a specific gravity of 1.

[4]Food items were determined mainly by examination of the food vacuoles. B = bacteria, C = ciliates, D = diatoms, E = blue green algae, F = colourless flagellates, G = green algae (flagellates), H = hyphae and/or spores of fungi and yeasts, N = naked amoebae, R = rotifers, S = inorganic soil particles, 'detritus', T = testate amoebae.

[5]a: Twelve sites in the Austrian central alps (Hohe Tauern, Glockner area), sampled 1–10 times during 1–2 years. Acid (pH 3–6) alpine grasslands on alpine pseudogleys or alpine brown earths. Humus: moder and mull-like moder. Detailed description: Foissner (1981a).

b: Eleven sites in the Austrian central alps (Hohe Tauern, Gastein area), sampled three times during a year. Acid (pH 3–6) alpine grasslands and alder sites on alpine pseudogleys or alpine brown earths. Humus: Moder and mull-like moder. Detailed description: Berger *et al.* (1984b, 1985a, 1986); Foissner & Peer (1985).

c–f: Two wheat fields (c), two xerothermic uncultivated grassland sites (d), two humid lowland sites (e), and a beech forest (f) in the 'Tullnerfeld' near Vienna, sampled 10 times during 27 months. Alluvial soils and decalcified brown earth (beech forest) with near neutral reaction (pH 7). Humus: Mull (c), mull-like moder (d), mull (e), moder-like mull (f). Detailed description: Foissner *et al.* (1985).

g.h: Four cereal fields and six meadows near Salzburg, sampled four times in one year. Gleyic brown earths with near neutral reaction (pH 5.5–7.5). Humus: Mull. Detailed description: Foissner *et al.* (1986).

i: Two spruce forests (50–80 years old) near Ulm (FRG) sampled four times over eight months. Very acid (pH 2.8–4) brown earths. Humus: Raw humus and moder. Detailed description: Funke (1985).

j: Species described from terrestrial habitats other than those mentioned in a–i. These sites were either sampled only on one occasion or did not use appropriate methods and no full reliable species list is available for comparison. Most of these species are mentioned in the papers of Berger & Foissner (1987), Buitkamp (1977a, 1979), Foissner (1984a, 1986a), Hemberger (1985), and Wilbert & Kahan (1985).

[6]★ low, reliably recorded also from freshwater habitats; ★★ probably strong; includes most of the new species and many 'moss' inhabitants; ★★★ probably found exclusively in true terrestrial habitats (litter, soil, humus under moss etc.). Only species with special food requirements or very characteristic morphological adaptations have been classified to this level.

[7]Since this review was completed, some more species of soil ciliates have been described (Foissner, 1987a,b,e). Most of these are new species and genera, and have been found in soils of Austria, Germany, Denmark, Israel, Greece, Japan, Madeira, Kenya, the Cape Verde islands, and the Fiji islands. This increases the number of reliably recorded species of soil ciliates from 250 to 270. The species recorded, and their degree of autochthonism as indicated in footnote 6, are: *Bresslaua terricola* Foissner, 1987★★; *Enchelyodon tratzi* Foissner, 1987★★; *Erniella filiformis* Foissner, 1987★★★; *Hausmanniella patella* (Kahl, 1931) Foissner, 1984★★★; *Hemisincirra wenzeli* Foissner, 1987★★★; *Holosticha bergeri* Foissner, 1987★★★; *Holosticha stueberi* Foissner, 1987★★; *Holostichides chardezi* Foissner, 1987★★; *Ilsiella venusta* Foissner, 1987★★; *Kalometopia eurystoma* (Gellért, 1950) Foissner, 1985★★★; *Krasniggia auxiliaris* Foissner, 1987★★★;*Pattersoniella vitiphila* Foissner, 1987★★; *Platyophrya binucleata* Foissner, 1987★★★; *Pseudourostyla franzi* Foissner, 1987★★; *Rostrophryides africana* Foissner, 1987★★★; *Sagittaria hyalina* Foissner, Czapik & Wiackowski, 1981★; *Strongylidium granuliferum* Foissner, 1987★★; *Urosoma karini* Foissner, 1987★★; *Woodruffides metabolica* (Johnson & Larson, 1938) Foissner, 1987★★; *Woodruffides terricola* Foissner, 1987★★★.

list was too inaccurate to justify such a conclusion. The larger number of ciliate species in the cultures could be explained due to reduced ciliatostasis, as the fire may have supplemented the soil with energy-rich substances.

Poljansky & Cheissin (1965) and Bamforth (1981) speculated that many protozoa have bypassed terrestrial existence and taken their abode in the metazoan gut. Foissner & Foissner (1985) investigated the ultrastructure of the soil ciliate *Enchelydium polynucleatum* and found unexpected similarities with the buetschliids, a group of endocommensals in grass-feeding mammals. It is easy to imagine that the cysts were eaten by chance and developed in the bacteria-rich alimentary tract. Soil protozoa could be indeed the ancestors of some prominent endocommensal taxa, for example, the Archistomatida.

E. *Establishment of the Distinctiveness of the Soil Ciliate Community*

Since the study of the soil ciliates began, it has been constantly plagued by the misidentification of species and by a lack of communication between taxonomists and ecologists. If one looks at hundreds of species lists in faunistic and ecological papers, even recent ones (e.g., Bamforth, 1968, 1973, 1984; Chardez, 1967; Smith, 1978; Stout, 1984; Tomescu, 1980), one can gain the impression that the soil ciliate community is made up mainly of freshwater and moss species (e.g., Brodsky, 1935; Ghilarov, 1978; Kühnelt, 1950). Kevan (1962) and Viswanath & Pillai (1977a) have said that species of the genus *Colpidium* are among the most common and widely distributed soil protozoa. Until now no cysts have been reported from any species of this genus. I have thoroughly examined hundreds of soil samples without finding a single *Colpidium*. The same holds true for *Paramecium*, also often reported from soil, but likewise unable to make cysts. Bamforth (1973) reported *Trithigmostoma cucullulus* as being frequent in soil. I have never found it in my samples, but the related species *T. bavariensis*, known since Kahl (1930) to be typical for terrestrial habitats, occurs rather frequently (Table 14).

Workers (e.g., Lochhead, 1952; Pearce & Phillips, 1980) sometimes refer to the (methodologically) poor papers of Gray (1948, 1952) who stated that 'water ciliates are identical with those of the soil, one habitat being the source of the other.' Gray concluded this from a very inadequate 'species' list which shows that most species have been determined only to generic level. He also referred to experiments with cysts of *Colpidium*, extremely unlikely as this genus has no cysts. Many other scientists have also argued for a great similarity between the soil and the freshwater protozoan faunas (e.g., Bamforth, 1973; Fantham, 1929; Kühnelt, 1950; Martin & Lewin, 1915; Nicole, 1927; Stout, 1984). Unfortunately, all used very poor species lists.

One of the most curious consequences of low taxonomic standards adopted by many soil ecologists is the 'discovery' that nearly the same species of protozoa occur in soil, sewage, and activated sludge (e.g., Bamforth, 1973, 1980; Pillai & Subrahmanyan, 1946; Stout, 1952; Viswanath & Pillai, 1966). These authors, as well as Stout (1978, 1980), argued that the similarities of communities from the soil ecosystem, streams receiving sewage, and activated sludge were because all are rich in organic nutrients and because all have a large bacterial population. The species that make up the communities should be predominantly bacterivorous and tolerant of organic enrichment (polysaprobic and mesosaprobic). This is not the case for the ciliates and the testate amoebae, as is evidenced by the species lists in this paper (Table 14) and in Chardez & Lambert (1981). With the exception of a few ubiquitous forms, none of the typical inhabitants of sewage or heavily polluted rivers can be found in soil. Some 50% of the soil ciliate species feed on other protozoa. The similarity in

organic nutrient and supply of bacteria of the habitats is superficial because most of the soil organic matter is very stable (Cutler, 1927), and much of the soil bacterial flora is perhaps not available to the soil protozoa (Darbyshire, 1975; Heal & Felton, 1970). The ability of soil ciliates and testaceans to tolerate organic pollution is unknown. It is dubious if the saprobic systems of Kolkwitz & Marsson (1908, 1909) and Sládeček (1973) can be extended to the soil protozoa, as suggested by Grandori & Grandori (1934). According to Toom (1969), the saprobity of 26 soil algae is higher than the total saprobity of 299 non-soil algae. However, only 7.76% of the soil algal species have been classified as polysaprobic, and 26 species are barely enough on which to base such a conclusion.

It is only recently that the Wilbert school and I discovered a wealth of undescribed ciliates in soil, clearly indicating that all earlier faunistic reports are at best extremely incomplete, and probably incorrect. A similar situation existed with the testate amoebae until the pioneering studies of Thomas (1960), Bonnet & Thomas (1955, 1960), Bonnet (e.g., 1960, 1961a, 1974b, 1975a, 1976, 1979, 1980, 1981), and others (e.g., Coûteaux, 1978b; Coûteaux & Chardez, 1981; Schönborn, 1964a,b). Many faunistic and ecological results need to be reinterpreted and the remark of Stout *et al.* (1982) that 'the era of faunal lists and population estimates is now past' is simply untrue. Before we can fully understand the soil protozoan community, we must know which species constitute it. It is also time to correct statements such as that of Bamforth (1980): 'Terrestrial protozoa are ubiquitous limnetic species.' To overcome such shortcomings, I have compiled a list of the taxonomic findings of the past 10 years (Table 14). This list leaves no doubt as to the existence of many autochthonous soil ciliates and shows that the entire soil ciliate community has developed so separately from the freshwater one that it must have its own identity. The arguments for the distinctiveness of the soil ciliate community can be summarized as follows.

(a) Many genera and families are known from soil and moss only, indicating a long independent evolution. These genera are: *Balantidioides, Bardeliella* (Figs 17, 18), *Buitkampia, Cirrophrya, Colpodidium, Dimacrocaryon, Enchelyotricha, Grossglockneria* (Figs 131, 132), *Hausmanniella, Hemisincirra* (Figs 26–29, 143, 144, 149, 150), *Kahlilembus, Lamtostyla, Microdiaphanosoma* (Figs 13, 14), *Nivaliella* (Fig. 130), *Orthokreyella* (Figs 11, 12), *Parabryophrya, Parafurgasonia, Paragastrostyla, Parakahliella, Periholosticha, Phacodinium, Platyophryides, Protospathidium* (Figs 19, 20), *Pseudocyrtolophosis* (Figs 15, 16), *Pseudoholophrya* (Figs 92, 93), *Pseudokreyella, Pseudoplatyophrya* (Figs 126–129), *Pseudouroleptus, Semiplatyophrya, Sorogena* (Figs 39–41), *Stammeridium* (Figs 7, 8), and *Uroleptoides*. It is extremely unlikely that these genera would have been overlooked in the more extensively studied freshwaters, if they occurred there.

(b) The species similarity of the soil and the freshwater ciliate communities in the same geographical area is ca. 13% (Foissner, 1981a). Coppa (1921), Grandori (1934), Brodsky (1935), and Stout (1952) reported similarly low values. Foissner (1981a) provided the most careful analysis and showed significant differences in the community structure, for example, no characteristic species were common to both communities and the dominance relations were very different (Section IV.A.1).

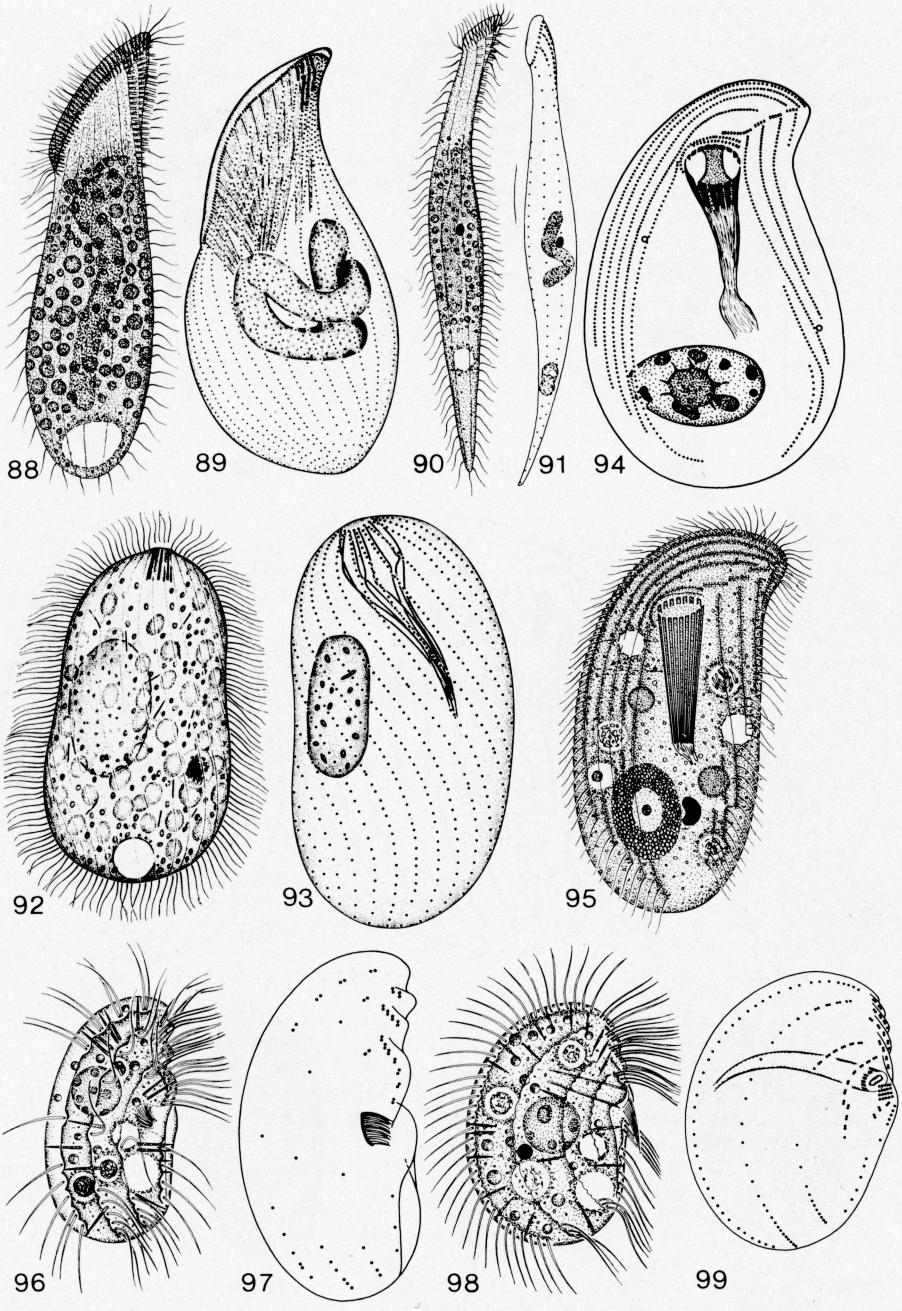
(c) The most frequent species are different in soil and freshwater communities. I have selected from Table 14 those 36 species that have been found in at least 8 out of the 9 site-groups investigated and they (except *Protospathidium serpens*; see Foissner, 1981c) are shown in Figures 15, 16, 88–153, 189, 190 to give ecologists some guidance in their identification. Only three (*Histriculus muscorum, Cinetochilum margaritaceum, Halteria grandinella*) of these 36 species are also common in freshwater habitats.

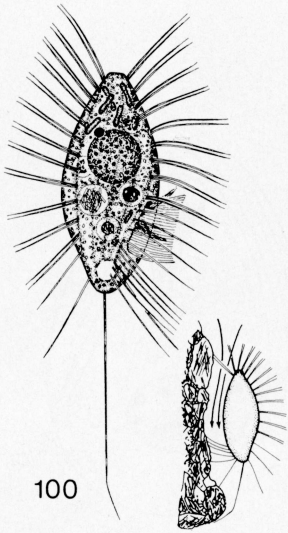
(d) One group restricted to soil, the Grossglocknerida, has developed a special oral apparatus which enables members to exploit the large supply of fungi and yeasts available in many soils (Foissner & Didier, 1983; Petz *et al.*, 1985). A small tentacle-like structure is used in breaking up and drawing the cytoplasm out of yeasts, hyphae, and spores of fungi (Figs 158–162). The method of attacking and feeding from the hyphae and spores is very similar to those described in testate amoebae (Barron, 1978; Chardez, 1985), the giant soil amoeba *Leptomyxa* (Anderson & Patrick, 1980) and some freshwater testaceans which feed on large algae (Schönborn, 1966a). It is perhaps a kind of 'myzocytosis' (Schnepf & Deichgräber, 1984).

This feeding strategy is a spectacular convergence found in very different groups of protozoa, and it deserves closer examination. The mechanism is unknown, but it would seem likely that holes in the fungal cell wall are produced enzymatically (Petz *et al.*, 1986). Chitinase and cellulase have been reported in some naked amoebae that also feed on yeasts (Tracey, 1955; Heal & Felton, 1970).

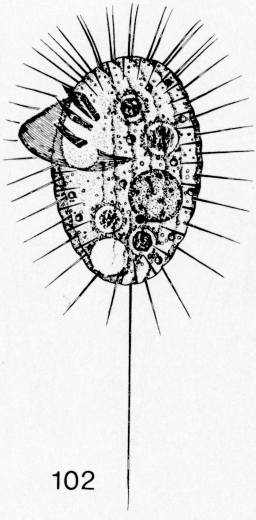
(e) Transfer experiments showed that freshwater and sewage plant protozoa survive badly in soil (Biczók, 1959; Brodsky, 1935; Lepşi, 1951; Stout, 1978).

Figs 88–153. Common species of soil ciliates. Most species are drawn from specimens *in vivo* and after silver impregnation. Figs 88, 89. *Arcuospathidium muscorum,* left side, 125 μm and 91 μm (from Foissner, 1981c and Berger *et al.*, 1983). Figs 90, 91. *Spathidium longicaudatum,* left side, 137 μm and 110 μm (from Foissner, 1981c). Figs 92, 93. *Pseudoholophrya terricola,* 70 μm and 55 μm (from Berger *et al.*, 1984b). Figs 94, 95. *Pseudochilodonopsis mutabilis,* ventrum, 42 μm and 40 μm (unpublished and from Foissner, 1981c). Figs 96, 97. *Drepanomonas revoluta,* right side, 25 μm and 21 μm (original). Figs 98, 99. *Leptopharynx costatus,* right side, 34 μm and 32 μm (original). Figs 100, 101. *Homalogastra setosa,* right side and ventrum, 31 μm and 22 μm (from Foissner *et al.*, 1982a). Figs 102, 103. *Sathrophilus muscorum,* ventrum, 35 μm and 24 μm (from Foissner *et al.*, 1982a). Figs 104, 105. *Cyclidium muscicola,* right side and ventrum, 17 μm and 15 μm (original). Figs 106, 107. *Cinetochilum margaritaceum,* ventrum, 30 μm (original and after Puytorac *et al.*, 1974). Figs 108, 109. *Tetrahymena rostrata,* right and left side, 70 μm and 57 μm (original). Figs 110, 111. *Colpoda aspera,* right side, 30 μm and 26 μm (from Foissner, 1980a). Fig. 112. *Paracolpoda steinii,* ventrum, 30 μm (from Foissner, 1980a). Figs 113, 114. *Colpoda inflata,* right side, 50 μm and 46 μm (from Foissner, 1980a). Figs 115, 116. *Colpoda cucullus,* right side, 54 μm and 56 μm (from Foissner, 1980a). Figs 117, 118. *Colpoda fastigata,* right side, 56 μm and 60 μm (from Foissner, 1980a). Figs 119, 120. *Colpoda henneguyi,* right side, 73 μm and 68 μm (from Foissner, 1980a). Figs 121, 122. *Platyophrya vorax,* right side, about 30–70 μm (from Foissner, 1980a). Figs 123, 124, 125. *Platyophrya macrostoma,* right and left side, ventrum, 30 μm (from Foissner, 1980a). Figs 126, 127. *Pseudoplatyophrya nana,* right and left side, 19 μm and 14 μm (from Foissner, 1980a; Foissner & Didier, 1983). Figs 128, 129. *Pseudoplatyophrya terricola,* right side and ventrum, 29 μm and 20 μm (from Foissner, 1985c). Fig. 130. *Nivaliella plana,* right side, 16 μm (from Foissner, 1980a). Figs 131, 132. *Grossglockneria acuta,* left and right side, 53 μm and 60 μm (from Petz *et al.*, 1985). Figs 133, 134, 135. *Opercularia arboricolum, in vivo,* contracted silver impregnated individual, silver impregnated swarmer, 53 μm, 27 μm, 32 μm. Gi = germinale kinety, Hi = haplokinety, Pi = polykinety, P_{1-3} = peniculi (from Foissner, 1981b). Figs 136, 137, 138. *Vorticella astyliformis,* freely moving, stalked, silver impregnated, 53 μm, 37 μm, 36 μm (from Foissner, 1981b). Figs 139, 140. *Gonostomum affine,* ventrum, 97 μm and 68 μm (from Foissner, 1982). Figs 141, 142. *Oxytricha setigera,* ventrum, 54 μm and 45 μm (from Foissner, 1982). Figs 143, 144. *Hemisincirra gracilis,* ventrum, 164 μm and 62 μm (from Foissner, 1982). Figs 145, 146. *Histriculus muscorum,* ventrum, 128 μm and 69 μm (from Foissner, 1982). Figs 147, 148. *Urosomoida agiliformis,* ventrum, 107 μm and 76 μm (from Foissner, 1982). Figs 149, 150. *Hemisincirra gellerti,* ventrum, 108 μm and 79 μm (from Foissner, 1982). Figs 151, 152. *Holosticha sigmoidea,* ventrum, 112 μm and 84 μm (from Foissner, 1982). Fig. 153. *Halteria grandinella,* ventrum, 30 μm. (original)

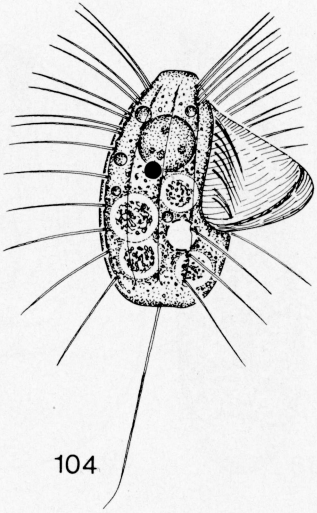

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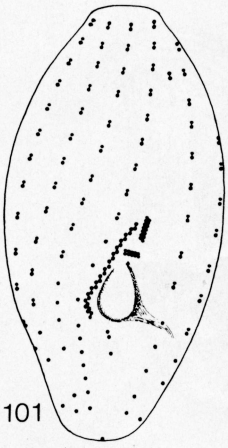
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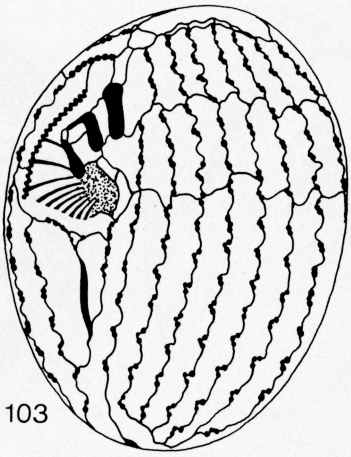
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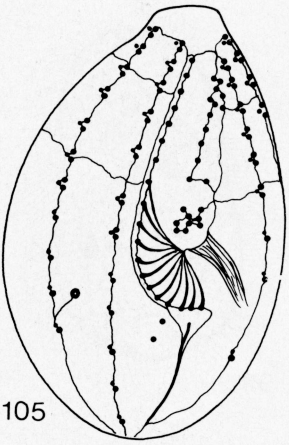
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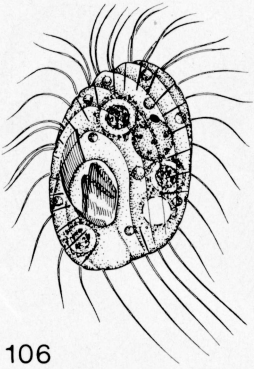
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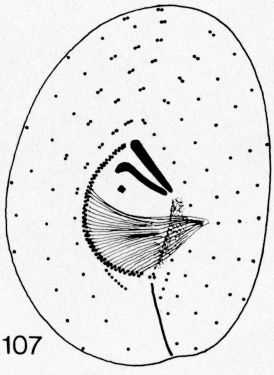
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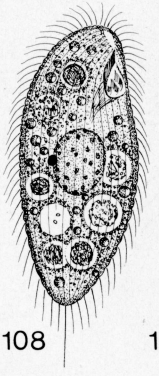
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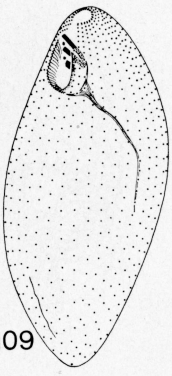
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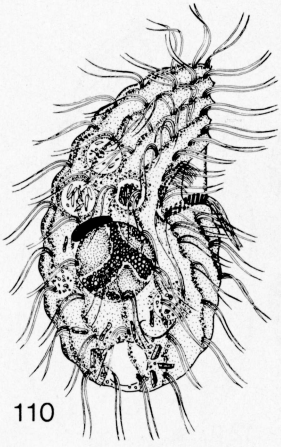
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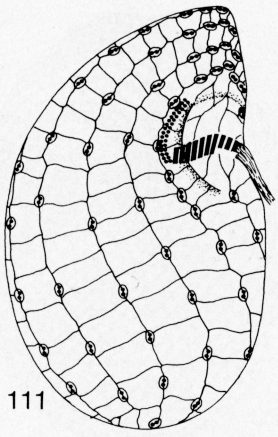
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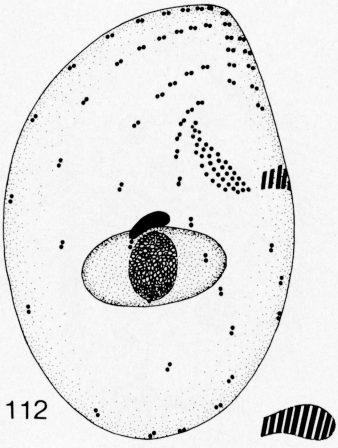
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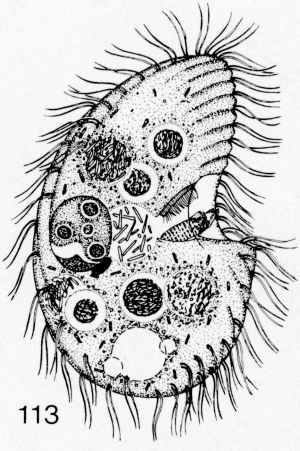
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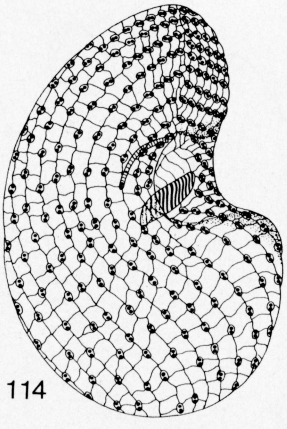
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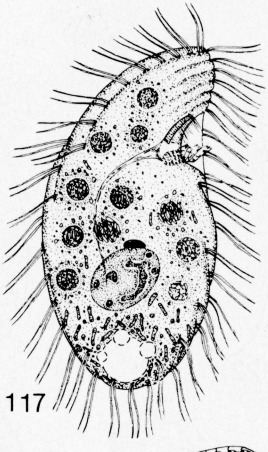
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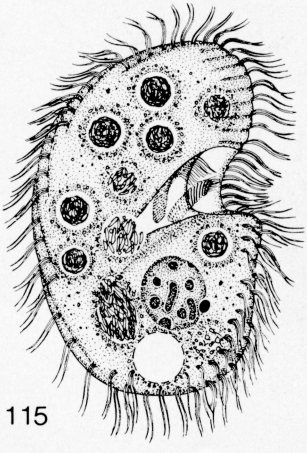
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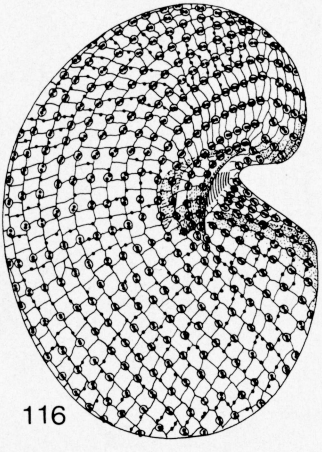
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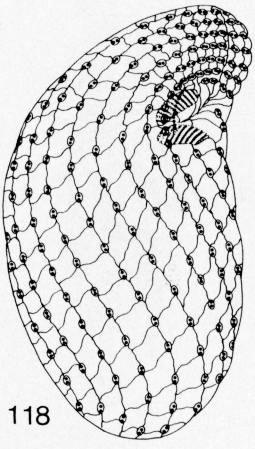
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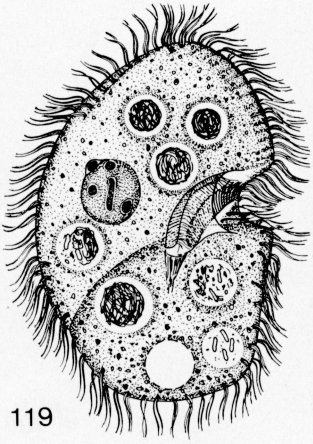
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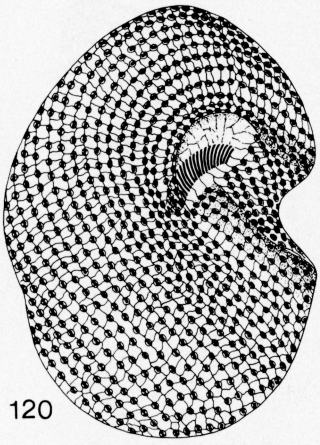
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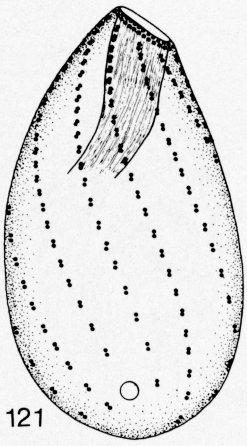
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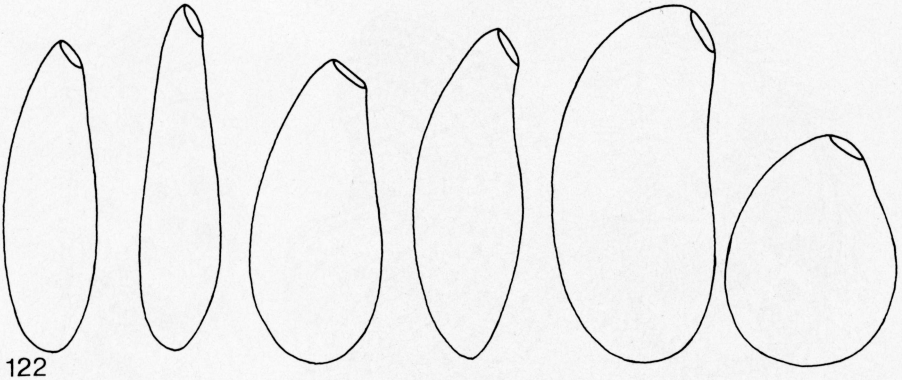
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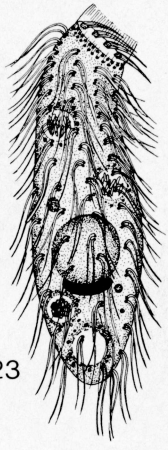
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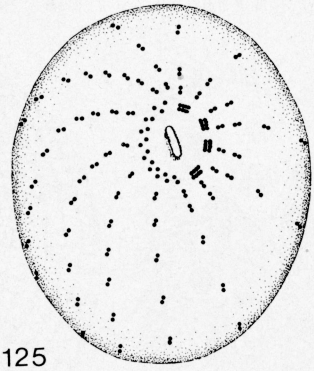
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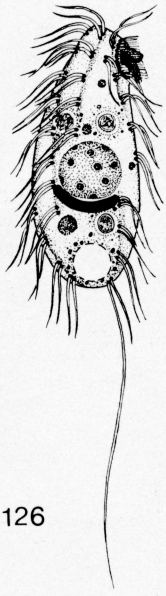
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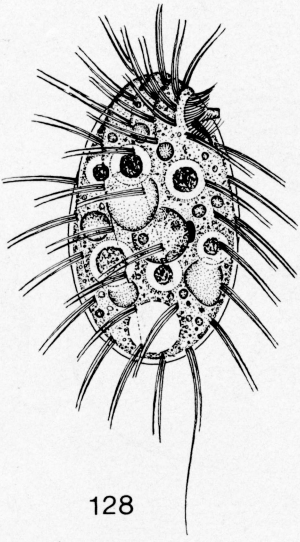
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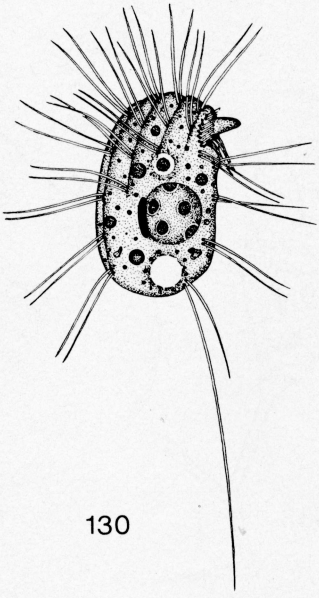
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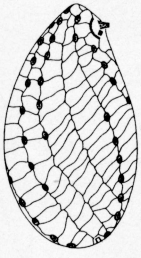
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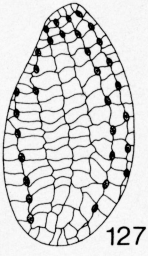


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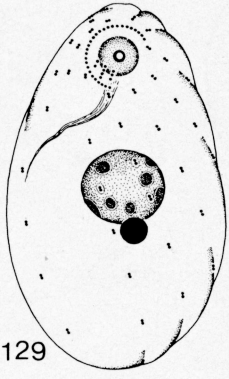


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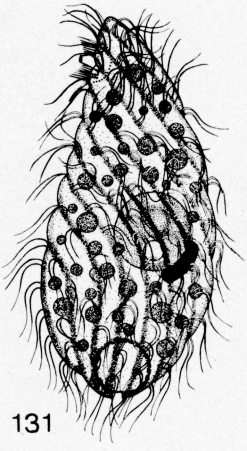




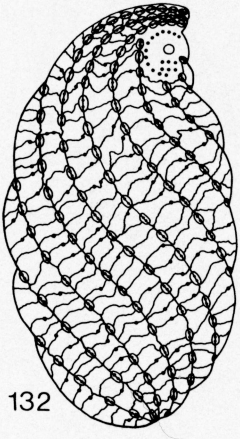
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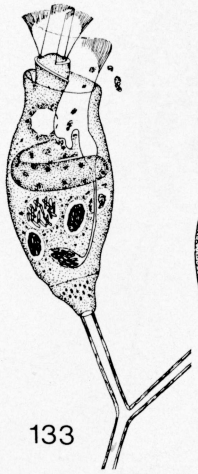
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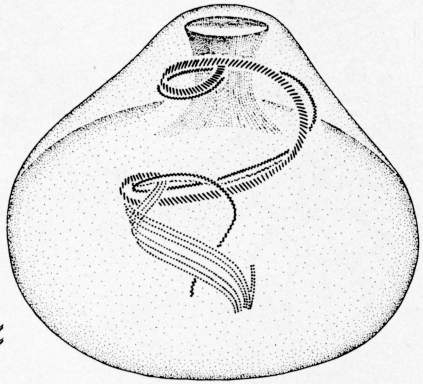
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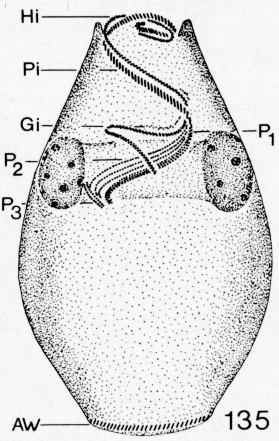
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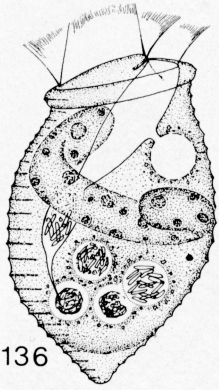
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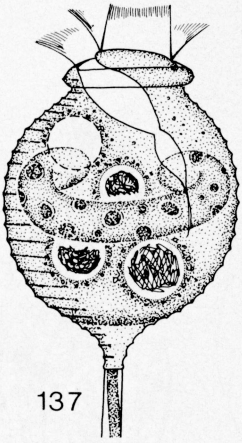
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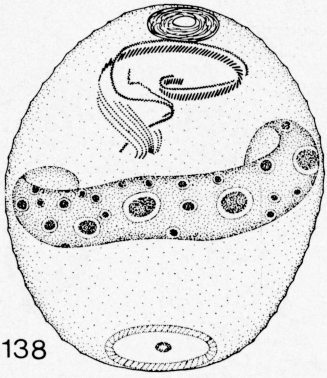
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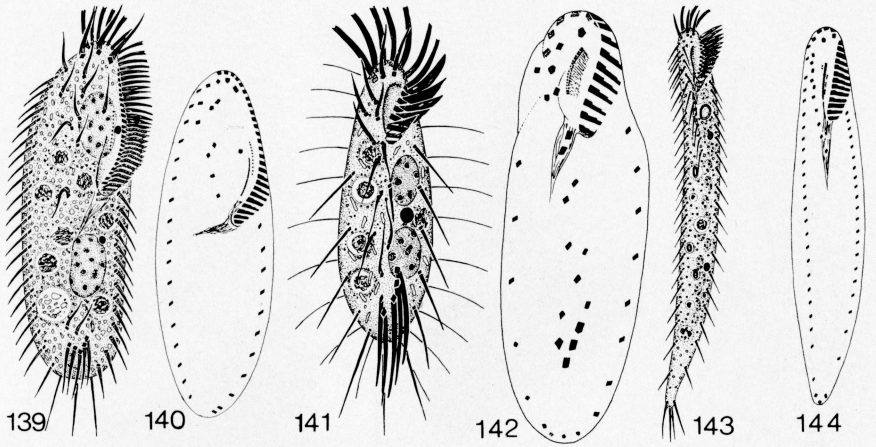
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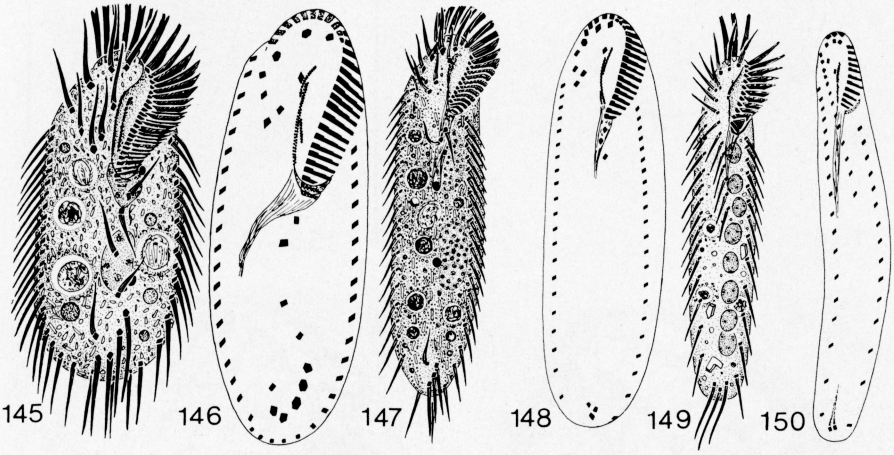


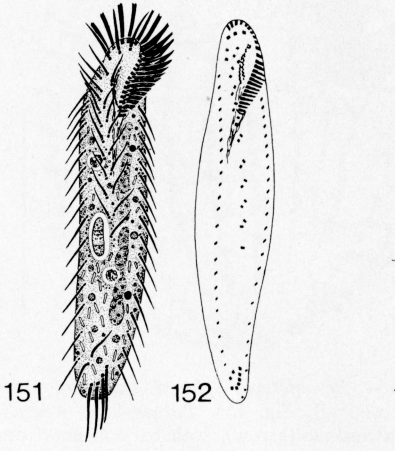
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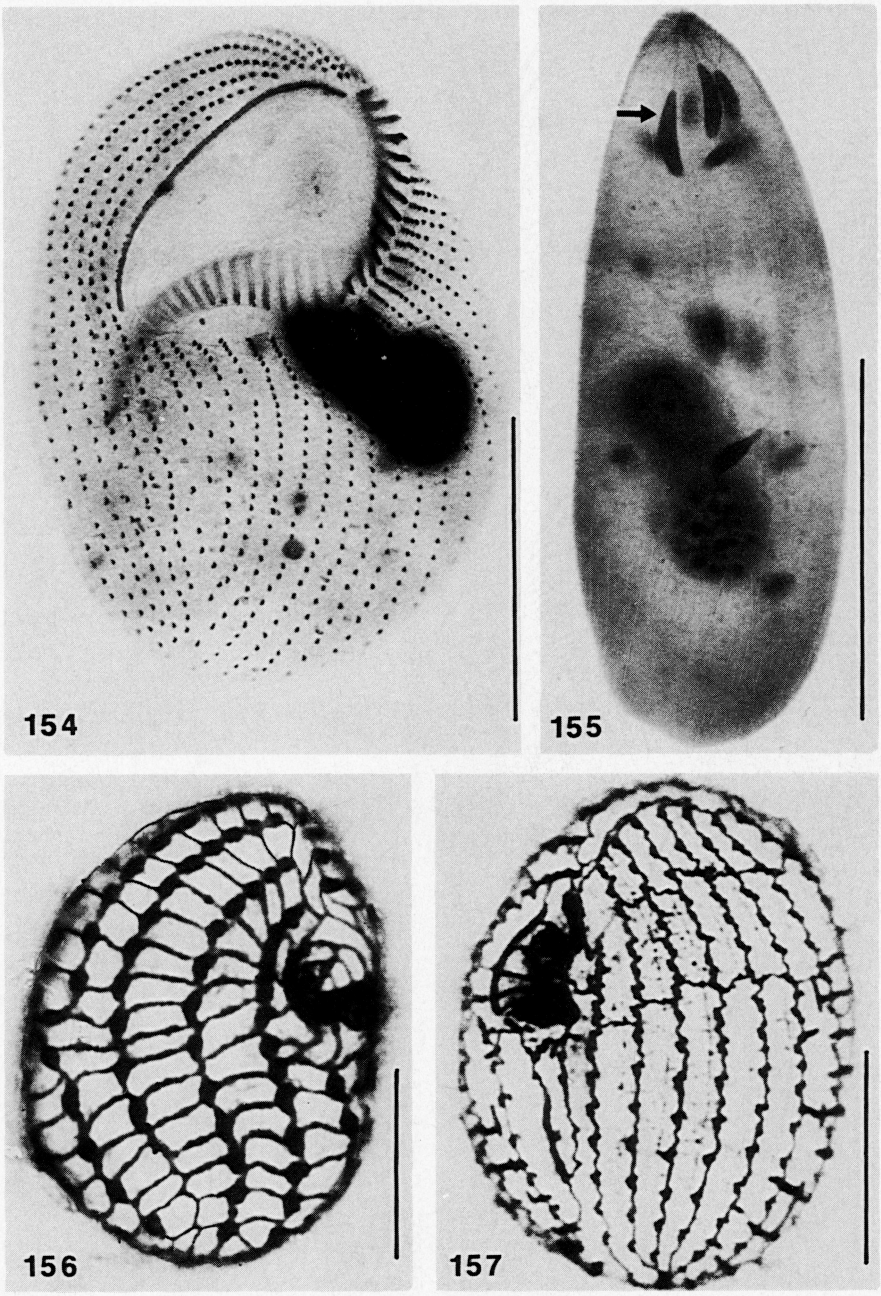


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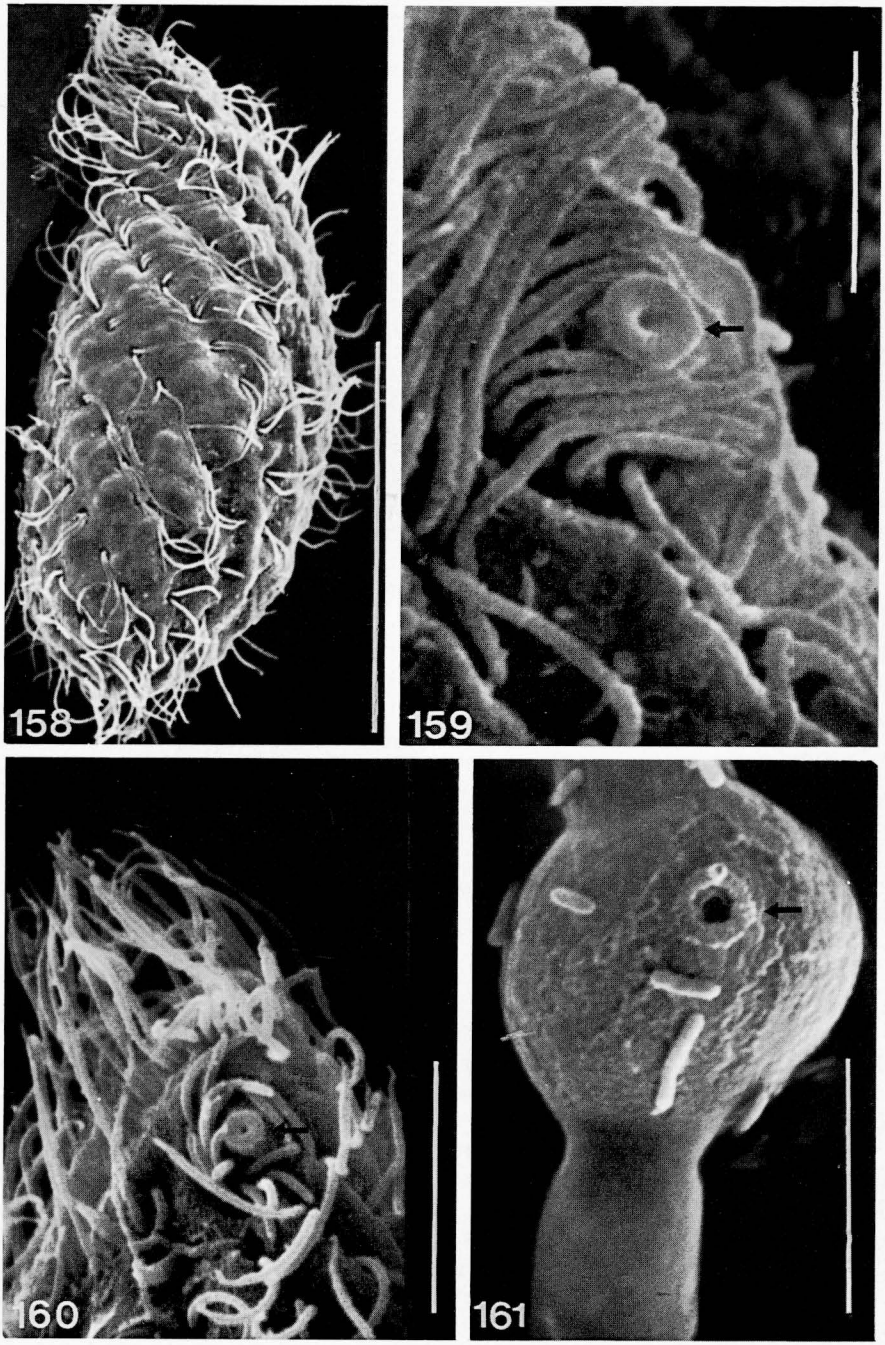

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Figs 154–157. Silver impregnated soil ciliates. Fig. 154. *Bryometopus sphagni,* ventrum, silver carbonate impregnation. Scale bar = 50 µm (original). Fig. 155. *Paraenchelys wenzeli,* protargol silver impregnation. Note the large extrusomes (arrow). Scale bar = 40 µm (from Foissner, 1984a). Fig. 156. *Paracolpoda steinii,* right side and ventrum, dry silver nitrate impregnation. Scale bar = 10 µm (from Foissner, 1974). Fig. 157. *Sathrophilus muscorum,* left side and ventrum, dry silver nitrate impregnation. Scale bar = 11 µm. (from Foissner *et al.*, 1982a)



Figs 158–161. SEM-pictures of *Grossglockneria acuta*. Fig. 158. Left side. Scale bar = 20 µm. Figs 159, 160. Oral area with the feeding tube (arrow). Scale bars = 2 µm and 4 µm. Fig. 161. Hypha of *Mucor mucedo* with a distinct hole (arrow) which is produced by the feeding tube of *G. acuta* (cf. Figs 159, 160). Scale bar = 4 µm. (from Petz *et al.*, 1986)

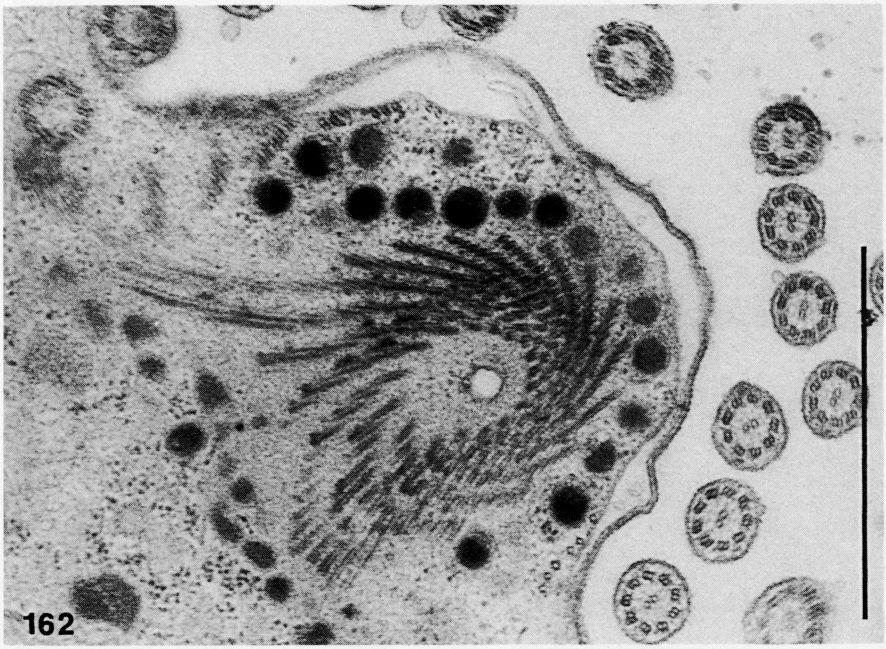


Fig. 162. TEM-picture of a transverse section of the feeding tube of *Grossglockneria acuta*. Note the microtubular lamellae which are surrounded by dark globules. These globules probably contain the enzymes used to break up the hyphae of the fungi. Scale bar = 1 μm. (from Petz *et al.*, 1986)

Unfortunately, these experiments were not very detailed and need to be repeated. Preliminary experiments by me have confirmed the very low survival, especially after desiccation of the soil (Table 15).

F. *Soil Protozoa: Cosmopolites and Ubiquists or of Restricted Distribution and Specialists?*

For the discussion of this controversial matter, I adopt the definitions of Smith (1978). Cosmopolites: occurring in all regions of the world, not necessarily in all types of habitat. Ubiquists: occurring in all types of habitat, not necessarily in all regions of the world.

Ecologists and systematists differ greatly in their view of cosmopolitism and ubiquitism in soil protozoa; and it is appropriate to cite some leaders to demonstrate this: 'It proved impossible, however, to correlate protozoan species distribution with particular geographical areas or major soil types or with most macroenvironmental factors. Soil protozoa were found to be ubiquitous; the same species occurred in arctic, temperate and tropical soils' (Darbyshire, 1975). Stout (1956) stated: 'Ciliates are of cosmopolitan distribution but are restricted to certain habitats solely by certain ecological factors. Similar habitats generally have similar faunas.' A very different view is held by Chardez & Lambert (1981) and Bonnet (1973b): 'Like in the beginning of protistology, many scientists even today resist in changing their belief in the cosmopolitan distribution of the soil and moss protozoa. Indeed, most species possess a

Table 15. Survival of freshwater ciliates in experimental soil microcosms

	Number of Species/% of survival[1]				
Day[2]	Control 1[3]	Control 2[4]	Control 3[5]	Experiment 1[6]	Experiment 2[7]
0	0	9/100	0	18/100	0
6	0	6/ 67	7/78	7/ 39	4/22
10	0	6/ 67	6/67	6/ 33	2/11
20	0	6/ 67	4/44	5/ 28	3/17

[1]Experimental design: Petri dishes (diameter 15 cm) were filled with 30 g of a mixed and sieved (2 mm) coniferous top soil.
[2]Time after adding the protozoa to the soil or after remoistening the air-dried soil to maximal saturation.
[3]Sterilized soil.
[4]Sterilized soil to which 30 ml of the normal soil protozoan community were added.
[5]Air-dried (2 weeks) and remoisted (distilled water) control 2.
[6]Sterilized soil to which 30 ml of a slightly concentrated protozoan community from an alpha-mesosaprobic river were added.
[7]Air-dried (2 weeks) and remoistened (distilled water) experiment 1.

world-wide distribution, if the environmental conditions are favourable. But in fact, they are not true cosmopolitans, especially the large species; there are many which are restricted to certain regions of the Earth (e.g., Distomatopyxidae).'

Hoogenraad & De Groot (1979), Cailleux (1978), Décloitre & Cailleux (1980), and Bonnet (1983) reviewed the literature and concluded that many testaceans are neither cosmopolitans nor ubiquists. As with plants and animals, there are at least two distinct geographical zones of distribution (Hoogenraad & De Groot, 1979): a northern zone, nearly identical to the geological Laurasia (North America, Europe, Asia) and a southern zone, identical to the geological Gondwana (South America, Africa, Australia, New Zealand, Antarctica). Décloitre & Cailleux (1980) compared cosmopolitism in plants and testate amoebae and found it to be greater for the testaceans than for the angiosperms and ferns. It is unexpectedly low even for the testaceans. Only 42% of the testacean families and only 6% of the testacean species have been reported from all continents (Table 16). Bonnet (1983) hypothesized that the equatorial winds act as a barrier for the distribution of cysts and that the few cysts which might drift to the northern hemisphere do not establish lasting populations. The simplicity of the thecamoebian communities in the European forest soils is explained by the instability (numerous marine transgressions, glacial devastation, etc.) of this region (Bonnet, 1983). However, some forms with a possibly restricted geographical distribution occur even in Europe, for instance the genus *Edaphonobiotus* Schönborn *et al.*, 1983 (Figs 64, 168, 169). Some typical species with restricted 'Laurasian' and 'Gondwanian' distribution are shown in Figures 163–177. As in many animals (Franz, 1975b; Procter, 1984), the species number of the protozoa decreases with increasing altitude, increasing geographical latitude, and with decreasing habitat size (Foissner, 1981a; Korganova, 1985; Smith, 1982).

Groups of soil protozoa other than testaceans have been poorly studied, and no firm conclusion about their biogeography can be made. The ciliates are certainly not ubiquitous, as indicated by the low similarity of populations from different habitats (Fig. 178). The list of soil ciliates (Table 14) also indicates a non-cosmopolitan

Table 16. Percentage (%) of cosmopolitan taxa in the angiosperms, pteridophytes, and testaceans (from Décloitre & Cailleux, 1980)

Region	Angiospermata		Pteridophyta	Thecamoebae		
	Genera	Families	Families	Species	Genera	Families
Cosmopolita sine Antarctica[1]	0.2	8.4	20	3.3	21	42
Cosmopolita cum Antarctica[1]	0.0	0.4	0	2.7	4.5	5
Number of taxa	235	503	48	1596	133	19

[1]In the paper of Décloitre & Cailleux (1980; Table III) these two lines are perhaps the wrong way round because cosmopolitanism cannot increase by including another region. Thus, I have changed the lines.

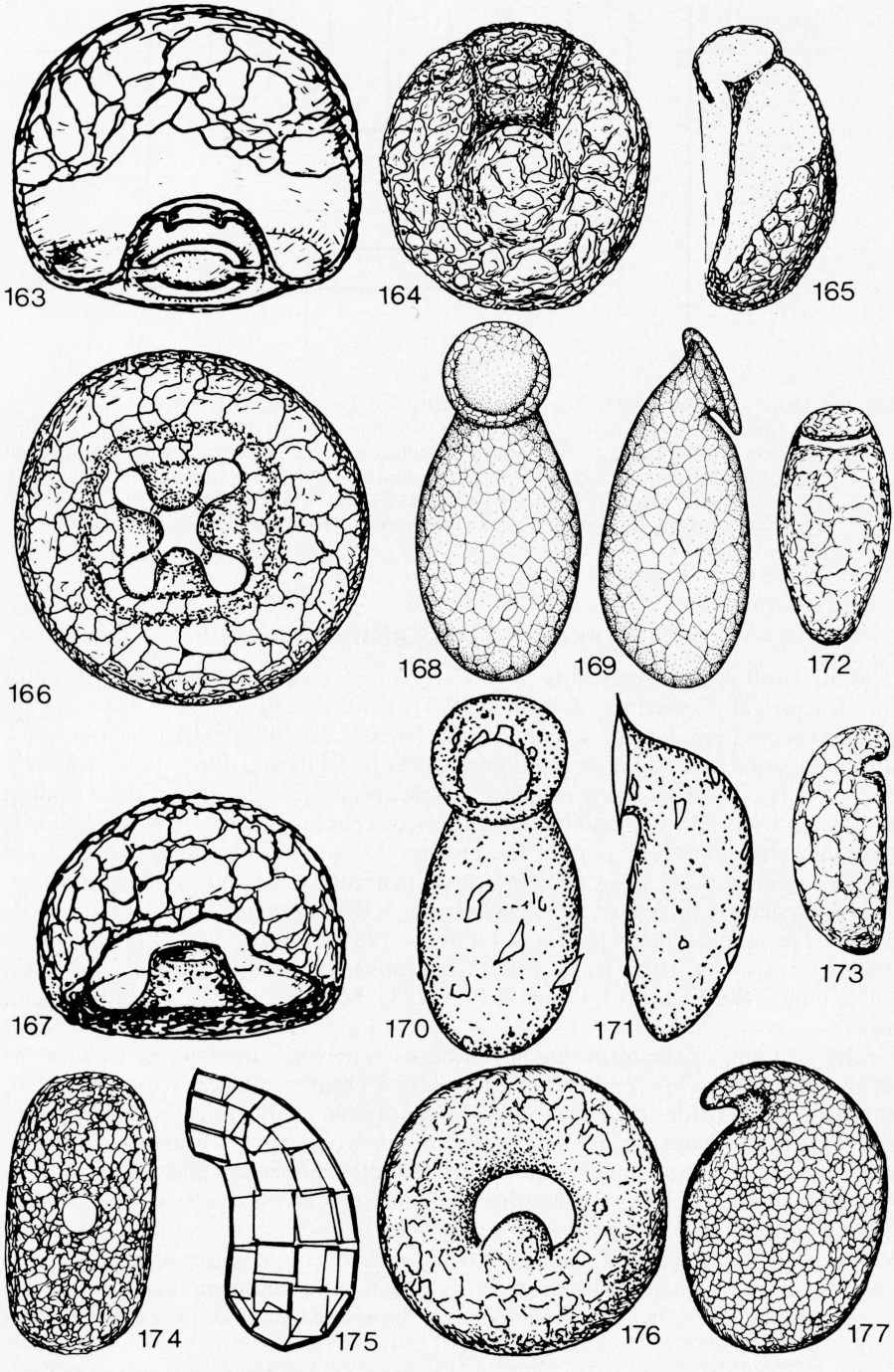
distribution. Unfortunately, no comparable studies are available for comparison from the southern hemisphere. However, many new hypotrichs have been described by Hemberger (1985) from Peruvian soils. Recently, I studied the ciliates of some soils from Kenya (Africa). They contain an exciting new wealth of ciliates, suggesting a distinct geographical zonation (Foissner, in preparation).

There is an increasing body of evidence for geographical zonation in freshwater and marine ciliates (Borror, 1980; Bamforth, 1981). Some of the species described by Dragesco (1970), Njiné (1979), and Dragesco & Dragesco-Kernéïs (1986) have been found only in Africa. Their large size makes it unlikely that they would have been overlooked in the northern hemisphere. Typical examples are *Paramecium africanum* Dragesco, 1970, *Neobursaridium gigas* Balech, 1941, and *Puytoraciella dibryophryis* Njiné, 1979. The sibling species of '*Tetrahymena pyriformis*' and '*Paramecium aurelia*' seem to be of restricted distribution, too (Sonneborn, 1975; Nanney & McCoy, 1976). In addition, physiological races exist (Section IV.A.2), as earlier suggested by Sandon (1924) who could not find a single species of autochthonous soil ciliate.

Rigorously controlled transfaunation experiments would be highly valuable for the resolution of many of the questions dealing with protist biogeography.

This section needs to be closed with an important directive. Statements about biogeography can be made with authority only if the taxonomic base is sound!

Figs 163–177. Autochthonous soil testaceans. Most have a restricted 'Laurasian' or 'Gondwanian' distribution. Fig. 163. *Distomatopyxis couillardi,* frequent in Gondwania, 125 µm (after Bonnet, 1983). Figs 164, 165. *Paracentropyxis mimetica* from Angola, ventral and lateral views, 40 µm (after Bonnet, 1960). Fig. 166. *Lamtopyxis callistoma* from Africa, 175 µm (after Bonnet, 1974b). Fig. 167. *Cyclopyxis puteus,* cosmopolitan, 145 µm (after Bonnet, 1975b). Figs 168, 169. *Edaphonobiotus campascoides* from Central Europe, ventral and lateral views, 39 µm. Perhaps a species with restricted 'Laurasian' distribution (from Schönborn *et al.,* 1983). Figs 170, 171. *Micropsammella retorta* from marine sand of the Polish coast, ventral and lateral views, 40 µm. Note the great similarity with *E. campascoides* (cf. Figs 168, 169) (after Golemansky, 1970a). Figs 172, 173. *Planhoogenraadia elegans* from Nepal and French-Guinea, ventral and lateral views, 61 µm (after Bonnet, 1979). Fig. 174. *Ellipsopyxella regularis* from Africa, ventral view, 90 µm (after Bonnet, 1975a). Fig. 175. *Lamtoquadrula deflandrei* from Africa, lateral view, 38 µm (after Bonnet, 1974a). Fig. 176. *Cornuapyxis lunaristoma* from French-Guinea, ventral view, about 140 µm (after Coûteaux & Chardez, 1981). Fig. 177. *Hoogenraadia humicola* from Africa, lateral view, 145 µm. (after Bonnet, 1976)


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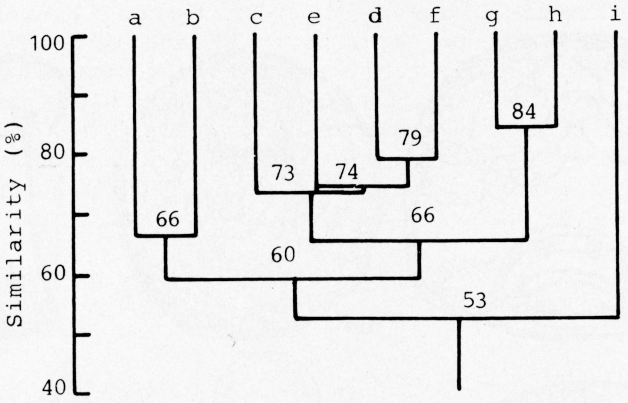


Fig. 178. Dendrogram of habitat discrimination (clustered species similarity index of Sørensen) by soil ciliates. a. 12 sites in the Austrian Alps (Glockner area); b. 11 sites in the Austrian Alps (Gastein area); c. 2 wheat fields (Austria, Tullnerfeld area); d. 2 xerothermic uncultivated grasslands (Austria, Tullnerfeld area); e. 2 humid lowland sites (Austria, Tullnerfeld area); f. 1 beech forest (Austria, Tullnerfeld area); g. 4 wheat fields (Austria, Salzburg area); h. 6 meadows (Austria, Salzburg area); i. 2 spruce forests (Germany, Ulm area). (original)

V. SOIL PROTOZOA AS BIOINDICATORS

The litter-soil system represents a 'sink' for many pollutants, including those of airborne origin (Grodziński & Yorks, 1981). Until recently, most of the work on pollutants has been done by soil physicists, chemists, microbiologists, and botanists, although some exceptions exist (Franz, 1975a,b; Ghilarov, 1965, 1978; Kühnelt, 1950; Wallwork, 1976). There can be no doubt about the high value of these fields in the description of natural and human influenced edaphic biotopes, but it is also true that they show only one part of the picture. There is an increasing trend to use animals, protozoa and algae, as bioindicators in natural and human influenced terrestrial ecosystems (e.g., Andre *et al.*, 1982; Berger & Rogerson, 1981; Berger *et al.*, 1986; Bick & Neumann, 1982; Chardez & Lambert, 1981; Clausen, 1984; Foissner *et al.*, 1982c; Gruschwitz, 1983; Karg, 1982; Korganova, 1978; Molodova, 1976; Nosek, 1982; Pipe & Shubert, 1984; Ponge & Prat, 1982; Schmidt, 1983; Syers & Springett, 1984).

The meaning of the term 'bioindication' is somewhat ambiguous. I adopt the definition of Bick (1982): bioindicators are, in a broad ecological sense, organisms that can be used for the detection and quantitative characterization of a certain environmental factor or of a complex of environmental factors. A different, narrower, definition confines bioindicators to human influences (Bick, 1982). A more discriminating classification is possible and sometimes necessary (Bick, 1982; Kneitz, 1983; Phillipson, 1983). Above all, it is important to discriminate between test organisms, monitor species, and characteristic species or communities of characteristic species; or, more generally, between physiological and phenomenological (presence/absence) indicators. In soil, protozoa have been used only as phenomenological indicators.

Traditionally, protozoa are used as indicators in freshwater ecosystems. Their value for estimating the degree of pollution of running and stagnant waters had been

recognized by Kolkwitz & Marsson (1908, 1909) at the turn of the century and was greatly improved in the fifties and sixties by Liebmann (1951), Bick (1972), and Sládeček (1973). It is surprising that protozoa have been seldom used for this purpose in terrestrial ecosystems, although many authors referred to this possibility (e.g., Bonnet, 1973b; Brodsky, 1935; Foissner, 1985b; Francé, 1921; Korganova, 1978; Nikolyuk *et al.*, 1980; Stout & Heal, 1967; Stout *et al.*, 1982). The best, but now rather dated, review on this matter is that of Viswanath & Pillai (1968). It is hoped that the present compilation will stimulate soil protozoologists and general ecologists to develop this field.

The recent literature which appeared after this review was written has been reviewed by Foissner (1987d).

A. *Indicators in Natural Ecosystems*

1. *Habitat and soil characterization.* It has been possible to link particular clusters of testate amoebae and ciliates with certain types of natural biotopes (Figs 178, 179; Bonnet, 1964, 1981; Coûteaux, 1976d; Geltzer *et al.*, 1980a; Louisier, 1975; Meisterfeld, 1980). Unfortunately, it is often impossible to endow these numerical results with a detailed ecological meaning, because our knowledge of the autecology and geographical distribution of the soil protozoa is too fragmentary. Only the testate amoebae are an exception in this respect, having been extensively studied by a variety of workers (e.g., Bonnet, 1964, 1984; Foissner & Peer, 1985).

In spite of this, several generalizations about protozoan communities from different soil types and biotopes are possible. The available data suggest, above all, an important role of humus and/or organic matter content in determining the abundance of individuals and number of species of the soil protozoa (Table 17; Bonnet, 1964; Crump, 1920; Datta & Mangat, 1974, 1975; Feller & Allison, 1920; Geltzer *et al.*, 1980a; Koch, 1915, 1916; Schnürer *et al.*, 1985; Schönborn, 1973; Smith, 1985). The exception of ciliate abundance is probably due to inappropriate culture methods (Table 17). Protozoa seem to be, potentially, good indicators of the humus status of the soil. 'Potentially' because further investigations are needed to show if other factors are involved, such as soil fertility, as suggested by Brodsky (1935), Gandori & Grandori (1934), and Stout (1975).

There is a further correlation—that between the soil protozoa and the moisture content of the soil. Stout (1984) and Bamforth (1984) classified the soil protozoa into three groups: edaphic, aquatic-terrestrial, and aquatic species (Section IV.C). The edaphic group dominates in well-drained and arid areas, whereas the aquatic group is more common in wet or flooded soils. The relation of edaphic and aquatic species may serve as an indicator of the moisture regime of the soil. This is certainly true for the testate amoebae (Schönborn, 1962a, 1966a) and for ciliates (Table 18). The differences, however, are fairly small, indicating again that most freshwater species are unable to survive in the soil (see Section IV.E).

An outstanding attempt to relate protozoan communities to soil types was undertaken by Bonnet (1961b, 1964). Using multifactorial methods, he compared the testacean communities in the Pyrenees and classified them in a similar manner to that used by phytosociologists for plant communities (Table 19). Bonnet (1964) found that, in skeletal and azonal soils, the fauna was related to the kind of parent material or parent rock, and consisted largely of Centropyxidae. In zonal and mature soils, the communities were independent of the parent material and were characterized by a high incidence of the Plagiopyxidae. *Phryganella* (Figs 180, 181) being the

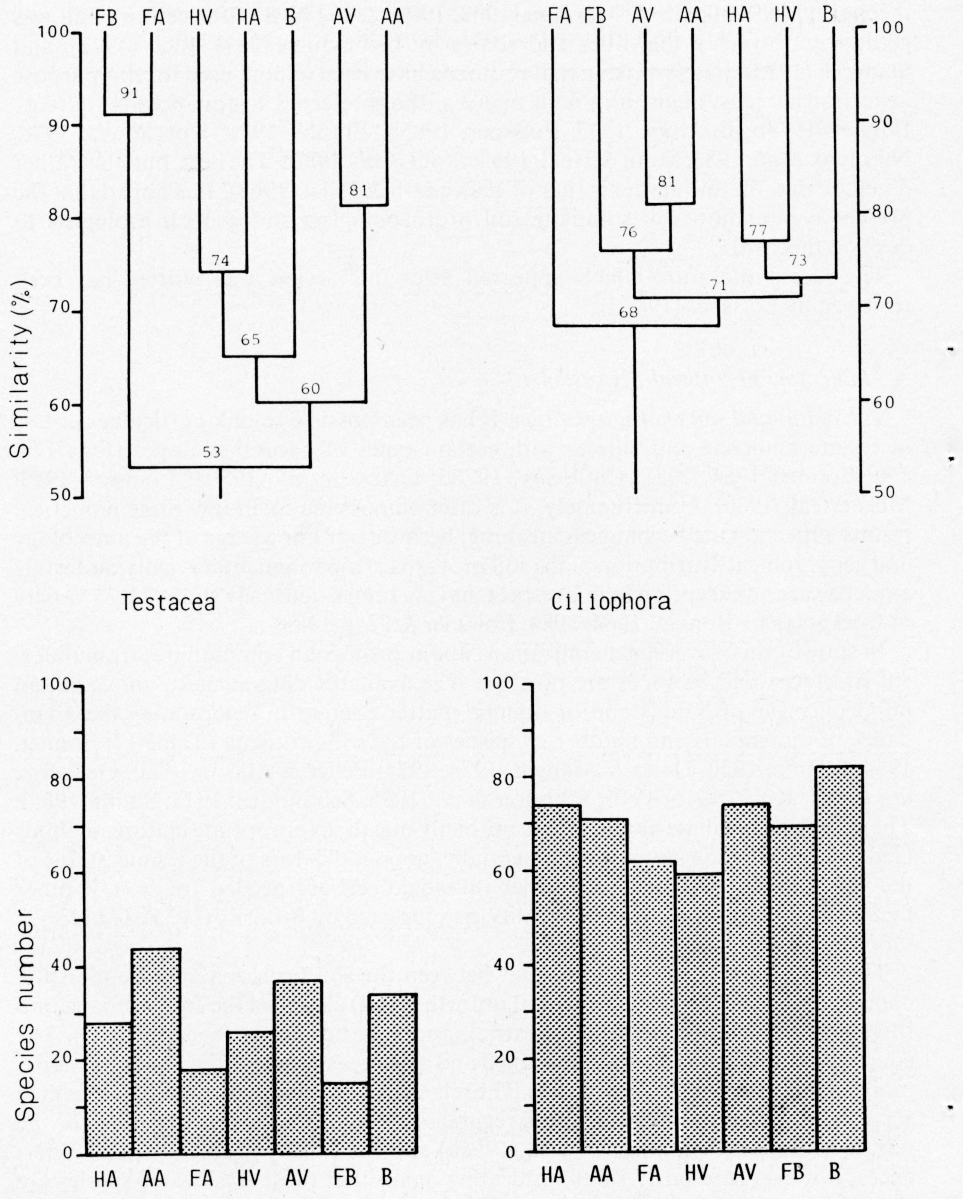


Fig. 179. Dendrogram of habitat discrimination (clustered species similarity index of Sørensen) by soil testaceans and ciliates. All sites were investigated 10 times during a period of 27 months (cf. Fig. 2) at 0–10 cm soil depth. They are located in the Tullnerfeld near Vienna (Austria). AA, AV = bottomlands; B = beech forest; FA, FB = wheat fields within the bottomlands AA and AV, respectively; HA, HV = xerothermic uncultivated grassland sites within the bottomlands AA and AV, respectively. (from Foissner *et al.*, 1985)

Table 17. Spearman rank correlation (R) between the numbers of species and numbers of individuals of protozoa and the humus content of the soil[1]

	R[1]	
	Individual numbers	Species numbers
Ciliophora	+0.2008 NS[2]	+0.7045 S
Testaceans	+0.7452 S	+0.9082 S
Number of habitats investigated	40	25

[1]Calculated from data of Foissner & Peer (1985), Peer & Foissner (1985), Foissner *et al.* (1982c, 1985), and Foissner (unpubl.).
[2]NS = non significant, S = significant at $P < 0.05$.

Table 18. Percentage (%) of soil ciliate species with high, medium, and low degrees of autochthonism in different habitat types (classification according to Table 14)

	Autochthonism (% of species present)		
Habitat	high	medium	low
Humid lowland sites (site 'e' Table 14)	21	41	38
Beech forest (site 'f' Table 14)	24	46	30
Cereal fields (site 'g' Table 14)	14	51	35

most common genus. Thus, this author named the entire soil testacean community Phryganelletea. Saline soils were characterized by the presence of *Centropyxis halophila* (Figs 182, 183). These findings have been confirmed by Foissner & Adam (1981a) and Foissner (1985a) who found similar communities in the Austrian Central Alps, indicating a broad range of application of this 'classification.' Detailed reviews of Bonnet's testacean communities have been published by Franz (1975b), Korganova (1978), and Laminger (1980).

The findings of Bonnet encouraged me to assess my own research on soil ciliates in a similar manner (Table 20). This classification is still very rough because of taxonomic and other problems. Also, many kinds of habitats have not yet been studied. However, some broad distinctions are recognizable. In agreement with Bamforth (1971) and others, the most widely distributed and characteristic soil ciliates are members of the genus *Colpoda*. Thus, I suggest the soil ciliate community may be referred to as 'Colpodetea'[2] (Figs 156, 184, 185). The only known exception are maritime Antarctic habitats where *Colpoda* is probably absent (Smith, 1973). Three eco-orders are distinguishable within this eco-class: the 'Grossglocknerietalia', the 'Hypotrichietalia', and the 'Pseudocohnilembetalia'. Species of the order Grossglocknerida (Figs 126–132, 158–160) are most frequent and dominant in

[2]The names of this and subsequent eco-taxa are not to be interpreted as formal taxonomic names, are not in competition with such names, and are not subject to nomenclatural rules.

Table 19. Ecological classification of testacean communities (from Lousier, 1975, after Bonnet, 1961b)

Class	Order	Alliance	Association
Soils in general Phryganelletea		Acid soils *Corythion dubii*	Soils with Saxicole vegetation and roots. — *Centropyxidetum deflandrianae*
			Skeletal soils — *Centropyxidetum vandeli*
	Azonal soils low in organic matter		Soils very low in organic matter — *Paraquadruleto-Hyalosphenietum insectae*
	Centropyxidetalia	Calcareous soils *Bullinularion gracilis*	Soils with accumulated organic matter — *Centropyxidetum plagiostomae*
			Decalcified clays — *Pseudawerintzewietum calcicolae*
			White rendzinas — *Geopyxelletum sylvicolae*
			Skeletal soils — *Arcelletum arenariae*
	Evolved soils rich in organic matter *Plagiopyxidetalia callidae*	Brown forest soils *Plagiopyxidion callidae*	Mor — *Plagiopyxidetum callidae*
			Mull — *Plagiopyxidetum penardi*
		Grassland soils *Tracheleuglyphion acollae*	Humic alpine soils — *Tracheleuglyphetum acollae*
			Calcareous grasslands — *T.a. centropyxidetosum elongatae*
	Saline soils	Saline soils	Saline greys — *Centropyxidetum halophilae*

soils with a low organic turnover, whereas a rich and diverse hypotrich ciliate fauna inhabits soils with high energy turnover. Members of the family Pseudocohnilembidae (Figs 186, 187) are fairly characteristic of saline soils (Nießen, 1984; unpublished observations of the author).

This conflicts with the widely accepted view that fast growing species, such as the small naked amoebae, flagellates, and ciliates, susceptible to rapid population fluctuations, dominate in soils with high energy turnover (e.g., warm temperate habitats), whereas larger amoebae, ciliates, and many testate amoebae prefer soils of relatively low productivity and with a low level of mineralization (e.g., coniferous litter) (Bamforth, 1971; Lousier, 1975; Stout, 1968). The most detailed study devoted to this question was performed by Bamforth (1971). He found that, in coniferous forests, testaceans were more than 10 times more abundant than ciliates and numbered 10 000–24 000 g^{-1} wet mass in litters and up to 8000 g^{-1} in soils. Ciliates numbered up to 1500 g^{-1}, but averaged less than 600 g^{-1} in litters and less than 300 g^{-1} in soils. In deciduous vegetation, ciliates approached, equalled, or exceeded testacea, and numbered 1000–5000 g^{-1} in litter while remaining about the same in soils. However, these results may be unreliable. They are based on culture methods only, and I am convinced that many ciliates, such as members of the family Grossglockneridae, from the coniferous forests could not develop under the culture conditions used by this author (Petz *et al.*, 1985). Furthermore, there is a growing body of evidence that

Table 20. Ecological classification of soil ciliate communities

Ecoclass: 'Colpodetea'	
Eco-order: *'Grossglocknerietalia'*	(fungi-rich mor and mor-like soils with strong accumulation of organic matter; e.g., coniferous forests, alpine mats)
Eco-order: '*Hypotrichietalia*'	(mull soils low or rich in organic matter; e.g., grasslands, arable land)
Eco-order: *'Pseudocohnilembetalia'*	(saline soils)

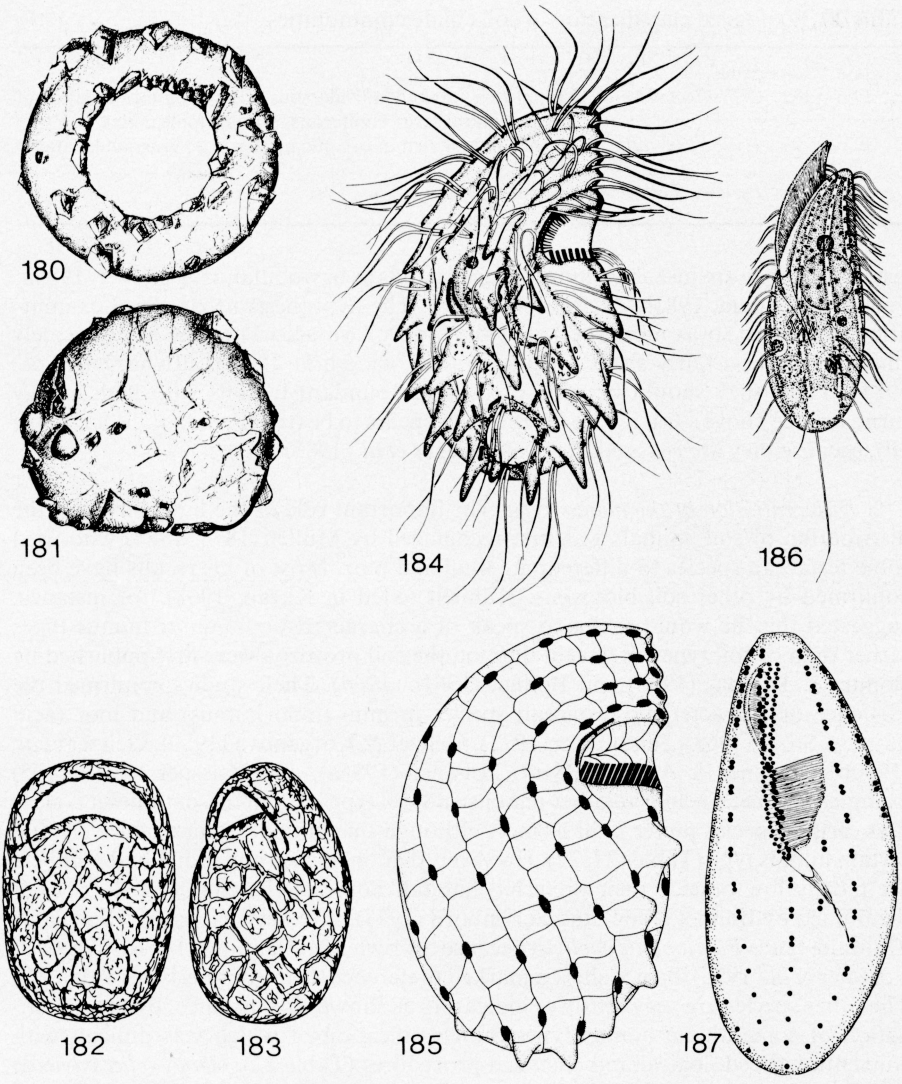
testate amoebae are just as abundant in grasslands as in woodlands (Foissner, 1985a; Foissner & Adam, 1981a; Meisterfeld, 1980). The hypothesis needs closer examination, the more so as most species of the family Grossglockneridae are extremely small and have a fairly short generation time, ca. 5 h at 21°C (Lüftenegger *et al.*, 1985). Thus, they should be widespread and abundant in soils with high energy turnover (see above). But in fact the reverse appears to be true (Petz *et al.*, 1985; Table 10), because they are *r*-strategists (Lüftenegger *et al.*, 1985).

2. *Differentiation of the humus type.* The important role of the humus type in the distribution of soil animals was first recognized by Müller (1878, 1884) who used some testacean species to differentiate mull and mor. Most of his results have been confirmed by other soil biologists. Kühnelt (cited in Kevan, 1962), for instance, suggested that he would prefer to speak of a characteristic fauna of humus types rather than of soil types. Relevant data on the soil protozoa were first published by Bonnet & Thomas (1960) and Bonnet (1961b, 1964). Their studies confirmed the existence of characteristic testacean species in mull (mild humus) and mor (acid humus). Stout (1968), Schönborn (1973), Geltzer & Korganova (1980), Geltzer *et al.* (1980b), Foissner & Adam (1981a), Foissner (1985a), and Foissner *et al.* (1985) extended Bonnet's results to other regions and soil types. From these studies it is clear that certain species prefer mull or mor, although they do not occur exclusively in a certain humus type (Tables 21, 22). However, their incidence and individual numbers are mostly low outside their preferred habitat. Some of the characteristic species mentioned by Bonnet (1964) and Schönborn (1973) have been excluded from Table 21, for instance *Plagiopyxis declivis*, because my own investigations (Foissner, 1985a; Foissner *et al.*, 1985) did not show a marked preference to any humus type (Table 22). The other species are very sensitive indicators as shown, for instance, by the investigation of some alpine humus types the classification of which was difficult with conventional pedological and chemical procedures (Table 22). *Geopyxella sylvicola* and *Paraquadrula* spp. indicate highly calcareous mull soils. To facilitate the use of these indicator species, I have depicted them in Figure 188.

This firm association of certain species with particular humus types may be responsible for the observation that, in terms of the testacean community, there is a greater similarity between corresponding soil layers of different sites than between different layers at the same site (Coûteaux, 1972; Meisterfeld, 1980).

Mor and mull are easily distinguishable also by the relation of full and empty tests ($\leqq 1:2$ in mull, 1 : 2 to 1 : 10 in moder, and $\geqq 1:10$ in mor) (Foissner, 1985a; Schönborn, 1973).

Recently, Foissner (1985a) and Foissner *et al.* (1985) suggested a similar system for the soil ciliates which is, however, still to be fully developed because only a few raw humus sites have been thoroughly investigated. Thus, the species listed in Table 21 and depicted in figures 189–194 are preliminary. However, I am sure that at least



Figs 180–187. Species characteristic of soil protozoan communities. Figs 180, 181. *Phryganella acropodia,* after which the Phryganelletea is named. Ventral and lateral views, 40 µm (from Petz, Lüftenegger, Foissner, Berger & Adam, unpublished). Figs 182, 183. *Centropyxis halophila.* This species is characteristic of saline soils. Ventral and lateral views, 70 µm (after Bonnet & Thomas, 1960). Figs 184, 185. *Colpoda elliotti,* a member of the 'type genus' of the Colpodetea. Right side, 28 µm and 26 µm (from Foissner & Schubert, 1983). Figs 186, 187. *Pseudocohnilembus putrinus.* Species of this genus occurs frequently in saline soils. Left side and ventrum, 32 µm and 22 µm. (from Foissner & Wilbert, 1981)

Frontonia depressa and *Bryometopus sphagni* (Figs 154, 191–194) are characteristic of acid humus, whereas *Urosoma* spp. (Fig. 84), *Colpoda elliotti* (Figs 184, 185), and especially *Urosomoida agilis* (Figs 189, 190) tend to be found in mild humus. The last-mentioned species also occurs infrequently and with low abundance in moder and mor.

Table 21. Species characteristic of the testacean and ciliate communities in mull and mor soils (compiled from Bonnet, 1964; Foissner, 1985a; Foissner *et al.*, 1985; Schönborn, 1973; Stout, 1968; and the data of Table 14)

	Testaceans		Ciliophora
Type of humus	Characteristic species	Ratio of full and empty shells	Characteristic species
Mull	*Centropyxis plagiostoma* *Centropyxis constricta* *Centropyxis elongata* *Plagiopyxis minuta* *Geopyxella sylvicola* *Paraquadrula* spp.	< 1 : 2–5	*Urosomoida agilis* *Urosoma* spp. *Hemisincirra filiformis* *Engelmanniella mobilis* *Grossglockneria hyalina* *Colpoda elliotti*
Moder and Mor	*Trigonopyxis arcula* *Plagiopyxis labiata* *Assulina* spp. *Corythion* spp. *Nebela* spp.	> 1 : 2–5	*Frontonia depressa* *Bryometopus sphagni* *Dimacrocaryon amphileptoides*

Table 22. Dominance (%) of testacean species characteristic of mull and mor (moder) in some alpine pseudogleys (from Foissner, 1985a)

Sites[1]	A	B	E	C	D
Type of humus	Mull-like moder			Moder	
C/N ratio	9.9	10.4	10.2	10.2	13.9
Plagiopyxis minuta	0.4	0.0	5.6	0.0	0.0
Centropyxis plagiostoma	0.4	0.0	2.3	0.0	0.0
Centropyxis elongata	1.8	6.0	0.9	0.4	0.0
Trigonopyxis arcula	0.0	0.0	0.0	1.1	1.6
Nebela parvula	0.0	0.0	0.0	0.0	1.9
Corythion spp.	0.0	0.0	0.5	1.4	1.3
Assulina spp.	1.3	1.7	0.0	2.2	4.5
Plagiopyxis declivis	22.2	14.8	17.9	12.7	7.2

[1]A: Grazed alpine pasture. B: Little grazed alpine pasture. C: Isolated alder stand. D: Alder stand mixed with dwarf shrubs and spruces. E: Heavily eutrophic alpine pasture (*Rumicetum alpini*).

3. *Truffle soils.* Bonnet (1974c, 1978) analyzed the testacean communities of 272 truffle (*Tuber melanosporum*) soils and compared them with 727 non-truffle calcareous soil samples using multivariate procedures. He found that the testacean communities of the truffle soils were rather poor in species and individuals and were dominated by acrostomic and plagiostomic morphotypes. Thus, his index of

'aerophily'[1] and the diversity were lower than in normal calcareous soils. A maximum 'truffle potential' was indicated by the combined occurrence of *Geopyxella sylvicola*, *Plagiopyxis oblonga*, and *Plagiopyxis callida* var. *pusilla* (Figs 195–200). The truffle potential decreased as the proportion of *Pseudawerintzewia calcicola* increased. The progressive replacement of *G. sylvicola* by *P. calcicola* indicates an evolution of the brown forest soil to a calcareous mull, which is an inappropriate environment for the growth of the mycelium of *Tuber melanosporum*.

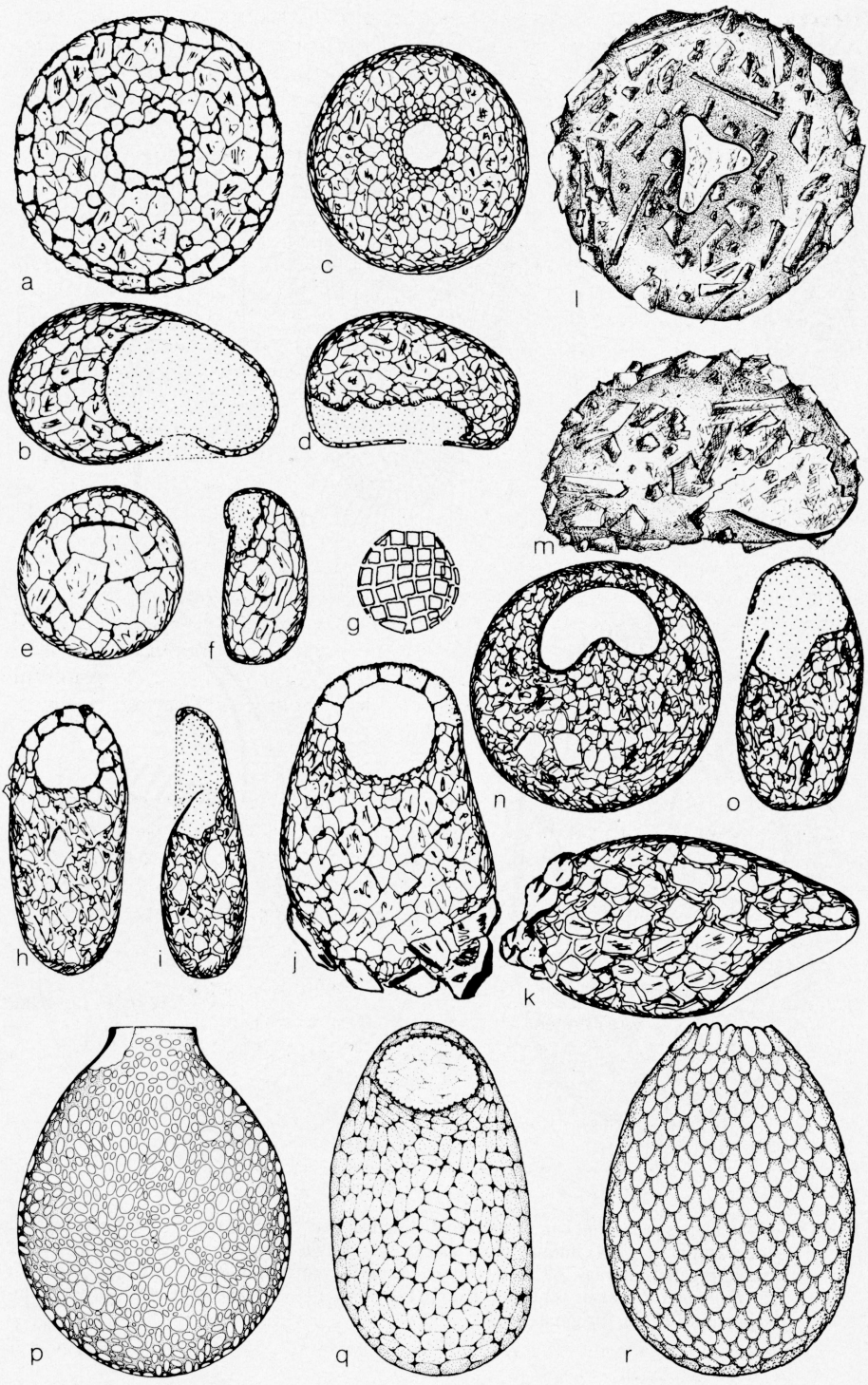
4. *Effects of weather-fronts*. Gelei & Szabados (1950) found a close relationship between the occurrence of algal 'water blooms' and advancing weather fronts. This observation was confirmed by Kiss (1959), who analyzed 112 'blooms' in stagnant waters over a period of 27 years and found them to be associated almost exclusively with cyclonal depressions and prefrontal weather conditions. He also cites an ancient Hungarian farmers' forecast for rain or rainy weather, when stagnant waters suddenly 'turn into blood' or become dark green. Likewise, under prefrontal weather conditions, Biczók (1956, 1979) noted a sudden increase in the number of individuals in protozoan cultures that were set up with the rhizosphere of wheat (Fig. 201). In addition, he observed that some species of ciliates (e.g., *Cyclidium glaucoma*) showed a more pronounced 'weather sensitivity' than others (e.g., *Chilodonella uncinata*).

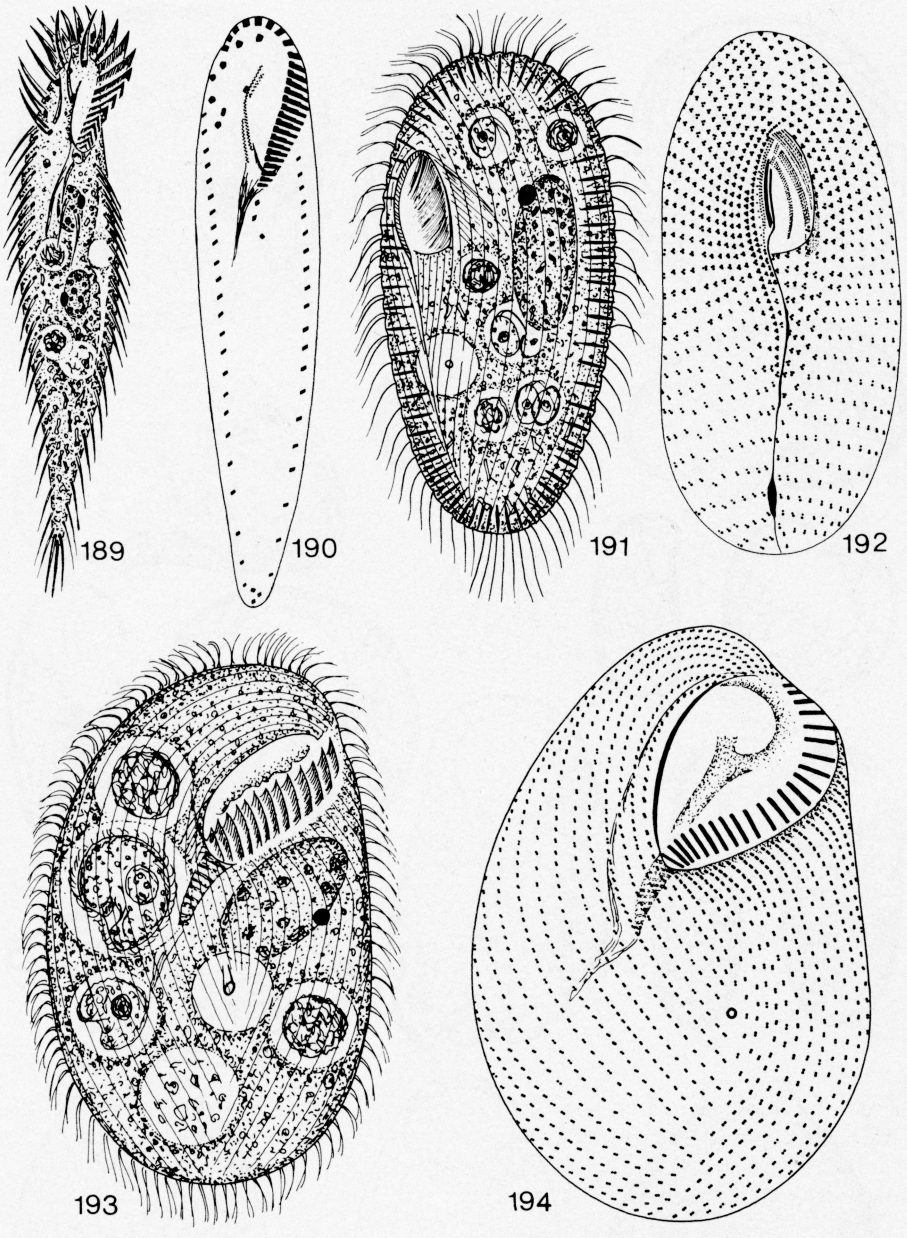
These observations would tend to suggest some relationship between weather conditions and the quantitative and qualitative changes of water and soil protozoan communities. More detailed experimental and field research is needed. It might well be that otherwise inexplicable fluctuations of protozoan communities under field conditions or in laboratory cultures are associated with specific meteorological conditions. However, other explanations, particularly methodological shortcomings, can not be excluded (Harmsen, 1940; Meiklejohn, 1957).

5. *Use in criminology*. Soil science is a powerful tool in modern criminology, but usually the physical and chemical composition, or plant residues such as pollen and leaves, are exploited. Lambert & Chardez (1978) reported on a case where soil testaceans became the 'key' for the conviction of a murderer. In 1977, a murdered girl was found in a forest. A man suspected as being the culprit was arrested; but he

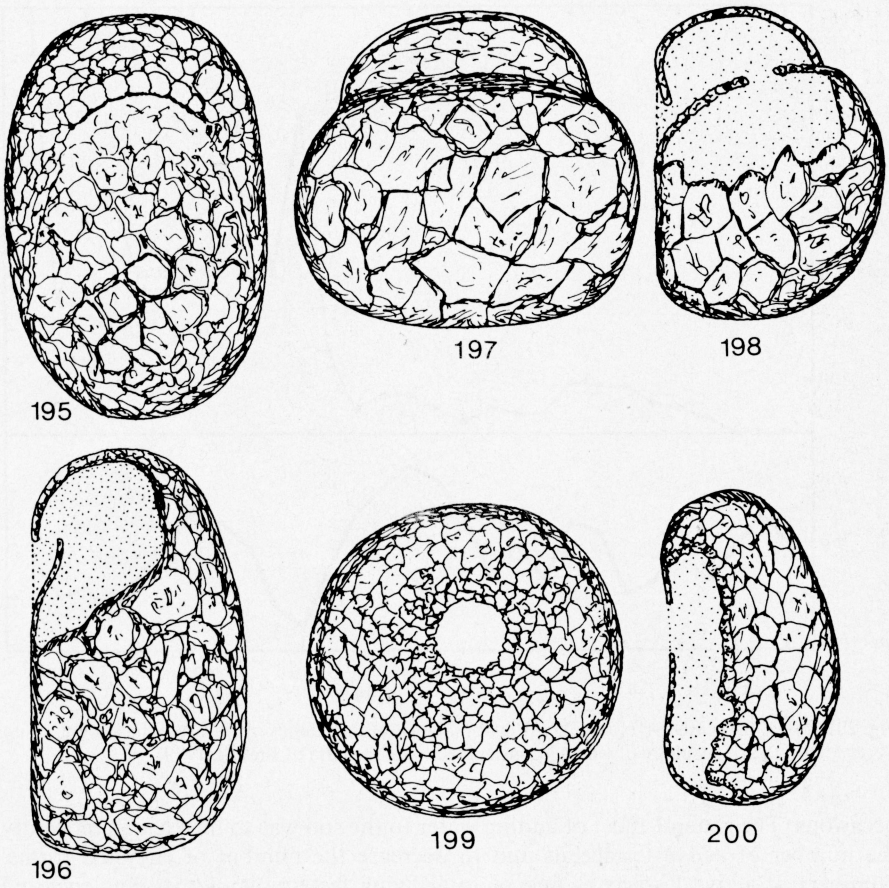
[1]Index of aerophily: $i = \frac{\text{plagiostomic species with visor} - \text{cryptostomic species}}{\text{plagiostomic species with visor} + \text{cryptostomic species}}$ The index takes the value +1 if the milieu is strictly 'aerial', and −1 if it is strictly 'edaphic'.

Fig. 188. Testacean species that can be used to distinguish between mild (mull; a–k) and acid (moder, mor; l–r) humus. a,b. *Centropyxis plagiostoma*, ventral and lateral views, 86 µm. c,d. *Geopyxella sylvicola*, ventral and lateral views, 73 µm. e,f. *Plagiopyxis minuta*, ventral and lateral views, 48 µm. g. *Paraquadrula discoidea*, lateral view, 29 µm. h,i. *Centropyxis elongata*, ventral and lateral views, 73 µm. j,k. *Centropyxis constricta*, ventral and lateral views, 130 µm. l,m. *Trigonopyxis arcula*, ventral and lateral views, 110 µm. n,o. *Plagiopyxis labiata*, ventral and lateral views, 83 µm. p. *Nebela parvula*, lateral view, 90 µm. q. *Corythion dubium*, ventral view, 46 µm. r. *Assulina seminulum*, lateral view, 90 µm. (a–i, n, o after Bonnet & Thomas, 1960; j, k after Deflandre, 1929; l, m, p–r from Petz, Lüftenegger, Foissner, Berger & Adam, unpublished)


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Figs 189–194. Ciliate species that can be used to distinguish between mild (mull; 189, 190) and acid (moder, mor; 191–194) humus. Each species was drawn from specimens *in vivo* and after silver impregnation. Figs 189, 190. *Urosomoida agilis,* ventrum, 140 µm and 87 µm. Figs 191, 192. *Frontonia depressa,* ventrum, 75 µm. Figs 193, 194. *Bryometopus sphagni,* ventrum, 100 µm and 105 µm. (originals)



Figs 195–200. Characteristic combination of testacean species in truffle soils. Figs 195, 196. *Plagiopyxis oblonga*, ventral and lateral views, 87 µm (after Bonnet & Thomas, 1960). Figs 197, 198. *Plagiopyxis callida* var. *pusilla*, dorsal and lateral views, 50 µm (after Bonnet, 1961a). Figs 199, 200. *Geopyxella sylvicola*, ventral and lateral views, 73 µm. (after Bonnett & Thomas, 1960)

asserted his innocence and disputed having been in this forest. The analysis of the testacean community in the soil traces on the shoes that he wore on the day of the murder showed striking similarities with the community at the site where the poor girl had been found. The man was convicted.

B. *Indicators in Human Influenced Ecosystems*

1. *Effects of irrigation.* Moisture is said to be the major factor in controlling the abundance and distribution of the soil protozoa (Sections IV.B.1 and V.A.1). Field and experimental evidence is weak and conflicting. Only the excellent papers of Lousier (1974a,b) provide us with reasonable data, at least for the testate amoebae (Table 23). He irrigated the soil-litter system of an aspen woodland during the seasonal dry period every three days with 3.78 l m^{-2}, and sampled the plots on three

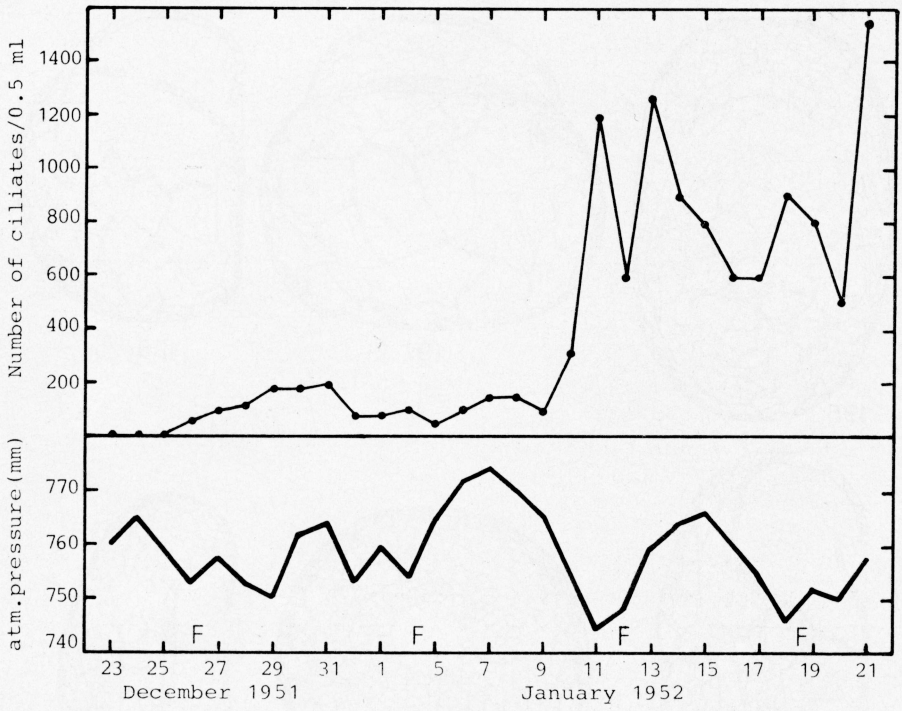


Fig. 201. Effect of weather-fronts (F) on the abundance of the ciliates in cultures which were set up with the rhizosphere of wheat. (constructed from the data of Biczók, 1979)

occasions. The general effect of adding water to the soil was to increase significantly the number of active testaceans and to decrease the number of encysted forms. Numbers of active testaceans and of total living testaceans (active plus encysted forms) showed significant, positive correlation with soil moisture content. At higher soil moisture levels, the larger (>60 μm) species present tended to have a larger proportion of living individuals as cysts than did the smaller forms which numerically dominated the population. Generation times were shorter and secondary production higher in the watered plots. These results support earlier field data reviewed by Bonnet (1964) and Schönborn (1966a).

For the other groups of soil protozoa, convincing experiments are still lacking and the data are contradictory. Crump (1920) and Cutler *et al.* (1922), working with their selective culture method, found no correlation between the daily rainfall and the fluctuations of the abundance of some species of flagellates and naked amoebae. This contrasts with results of Brodsky (1935) and Nikolyuk (1964, 1965a), who reported on a close correlation between total protozoa and soil moisture in irrigated and non-irrigated virgin and arable land. Detcheva (1972), also using a culture method, found that the total numbers of protozoa in the rhizosphere of irrigated and non-irrigated maize field plots were nearly the same (Table 32). The differences were that more ciliates and fewer naked amoebae were found in the irrigated plots. Similarly, Elliott & Coleman (1977) reported only a slight, statistically insignificant, increase of active and decrease of cystic individuals (mainly naked amoebae) in irrigated plots of a shortgrass prairie as compared with a non-irrigated control plot (Table 24). But,

Table 23. Comparison of standing crop, generation time, and secondary production between testacean populations in watered and unwatered plots in an aspen woodland soil (from Lousier, 1974b)

	Watered plots		Unwatered plots	
Horizon	A_0F	A_0H	A_0F	A_0H
Time period	$t_1 \rightarrow t_2$	$t_1 \rightarrow t_2$	$t_2 \rightarrow t_3$	$t_2 \rightarrow t_3$
Production numbers (a_2)[1] $a_2 = N_1 - N_0 + (T_1 - T_0)$	15 363	13 746	6367	4709
Intrinsic rate of increase (r) (individual/animal per day)	0.102	0.114	0.064	0.097
Generation times (T) (days)	6.8	6.1	10.9	7.2
Secondary production ($g\,m^{-2}$)	1.56	2.97	0.65	1.02
Standing crop numbers (g^{-1} dm)	1089	533	370	288
Standing crop biomass ($g\,m^{-2}$) (wet mass)	0.11	0.12	0.04	0.06

[1]All counts were made with the method of Coûteaux (1967).

Table 24. Effects of irrigation and fertilization on the soil protozoa and the net primary production of a Colorado shortgrass prairie (from Elliott & Coleman, 1977)

Date 1974[1]	Treatment[2]	Total precipitation (cm)[3]	% Soil water	Active protozoa[4]	$g\,CO_2$ $m^{-2}.day^{-1}$	Net primary production $g.m^{-2}.a$
27 June	C	3.49	3.8	16 869 g	9.4	60
27 June	F	3.49	3.0	14 125 hi	7.9	120
10 July	I	6.71	17.3	24 738 j	17.2	240
10 July	I+F	6.94	23.0	70 583 ghj	19.0	600
23 July	C	—	10.2	28 192 k	—	—
23 July	F	—	8.2	66 899 i	—	—
30 July	I	—	20.3	34 222 l	—	—
30 July	I+F	—	24.9	115 770 kl	—	—

[1]Start of the experiment, year 1970.
[2]Treatments: C = control; F = fertilized with 50 kg N . ha^{-1} . a only; I = irrigated to −0.3 to −0.8 bar of soil water tension during growing season; I + F = irrigated plus fertilized.
[3]Between sample dates 27 June–23 July and 10 July–30 July.
[4]Protozoan numbers g^{-1} dry soil were determined in the top 1 cm of mineral soil (overlaying litter included) by a modified culture method of Singh (1946) and Heal (1971). The letters denote significant differences (Turkey's Q test after $\log_{10}$ transformation of protozoan numbers; $P \leq 0.05$, $n = 5$).

they observed a significant increase in both fertilized *and* irrigated plots and in air-dried and remoistened microcosms. This agrees with the results published by Menapace *et al.* (1975), Clarholm (1981), and Bryant *et al.* (1982). Recently, Parker *et al.* (1984) tested the hypothesis that simulated rainfall would trigger higher levels of activity of soil protozoa under surface accumulation of litter in a desert soil. No significant differences occurred until day 6 of the experiment. On this day all protozoa in the dry plots were encysted while those in the wet plots were all trophic. Then, on day 24, they observed 100% cystic protozoa in the wet, litter-enriched plot. This they

explained by a decrease of the bacterial biomass. Protozoan numbers were independent of litter quantity and reached the maximum on day 18. On this day, the protozoa were most abundant in the non-irrigated plot.

Pot experiments also fail to show a clear relationship between soil moisture and active and cystic protozoa. Darbyshire & Greaves (1967) found many active amoebae and flagellates in a dry treatment pot with 1/4 water-holding capacity, whereas complete encystment of populations of amoebae and ciliates occurred sometimes in the moist soil with 3/4 water-holding capacity. From this they concluded that desiccation alone is not responsible for encystment of protozoa in the rhizosphere or in unplanted soil. This contrasts with earlier results of Cutler (1927), Cutler & Dixon (1927), Losina-Losinsky & Martinov (1930), and Volz (1972), who reported reduced abundances of protozoa below ca. 50% of the water-holding capacity of the soil. Volz (1972) concluded from his experiments that ciliates need at least a water film of 50 µm thickness to encyst, and field capacity of soil moisture to be active. This is unlikely, for most of the soil ciliates are much smaller and flatter than 50 µm. Darbyshire (1976) found a pF of 2.0–1.5 to be enough to provide successful and prolonged growth of ciliates (Fig. 202). This agrees with the results of Sherman (1914), Koch (1916), and Szabó *et al.* (1964). The last authors used a direct counting method and found a pronounced increase in ciliate growth when the moisture was raised from 30% to 40% (Fig. 203). My own field data on ciliates, based also on direct counting, show no clear relationship between abundance and soil moisture (Table 1). This is perhaps because the data did not give the 'history' of the moisture variation, and daily measurements and counts were not made. There was, for instance, sometimes a high moisture content, because the sample was taken a few hours after a heavy rain.

The results are conflicting and I am convinced that such differences are primarily caused by the unverifiable counts gained with selective culture methods and, to a lesser extent, by sampling problems and the artificial conditions in microcosms where such factors as ciliatostasis are normally not included in the interpretation of the results. Use of undisturbed irrigated field plots and a direct counting method (Fig. 1) would appear to offer the best way of collecting reliable data.

2. *Effects of fire and deforestation.* The first reports on the effects of fire on soil protozoa were published by Fantham & Paterson (1924), Rosa (1956), and Stout (1961), and deal only with the qualitative changes of the fauna. Fantham & Paterson (1924) burnt a small veld in South Africa and collected a sample from the surface to 15 cm depth on the following day. The water cultures from this sample yielded almost exactly double the number of protozoan species as that from the soil of a neighbouring unburnt control plot. Other preliminary experiments of these authors did not show such marked differences. Rosa (1956) investigated the micro-edaphon in the soil cover of slowly burning brown coal dumps. He found many species of protozoa and noted that algae colonized depleted areas as soon as the temperature had fallen below 52°C. Stout (1961) investigated the bacterial population and the microfauna of the litter and the topsoil of burnt and unburnt scrub areas in New Zealand over a period of five years (Fig. 204). Immediately after the burn, a ryegrass-clover pasture was sown. The fauna following the fire showed considerable instability associated with the physical, chemical, and pedological disequilibrium caused by the fire. For example, destruction of the upper litter and its conversion to ash raised the pH by two units. The rhizopods, especially the testate amoebae, were more severely affected than the ciliates. Only about two-third of the rhizopod and actinopod species were recorded.

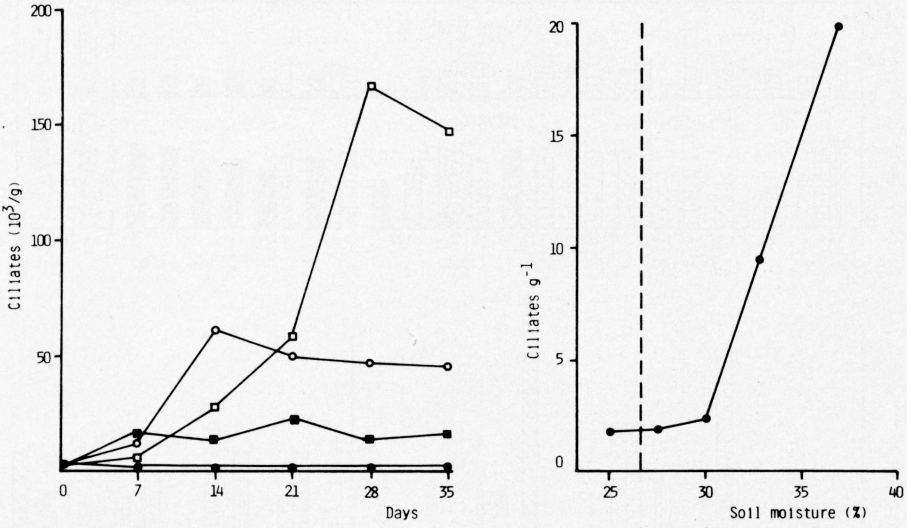
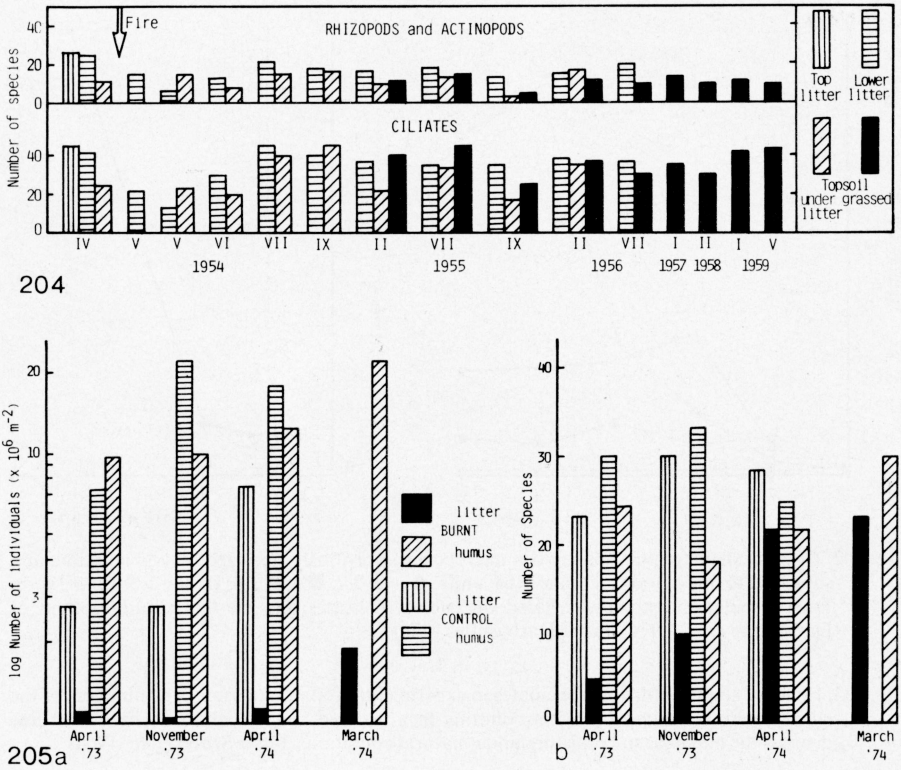


Fig. 202. *Colpoda steinii* populations in soil microcosms, previously sterilized by γ-irradiation, and subjected to one of four suctions, in pF units: ● – ● 2.7, ■ – ■ 2.0, ○ – ○ 1.5, □ – □ zero. Each population estimate is based on twelve replicates and on the culture method of Darbyshire *et al.* (1974). (after Darbyshire, 1976)

Fig. 203. Effect of soil moisture on the ciliates in experimental soil microcosms. The numbers of the ciliates were estimated by direct counting in a watered soil suspension. The dotted line denotes the maximal soil moisture under natural conditions. (after Szabó *et al.*, 1964)

The immediate effect of the fire was one of partial biological sterilization of the litter but there was considerable recovery reaching a climax within three months after the fire. There was subsequent adaptation of the fauna to the new ecological niches provided by the developing grassland topsoil. The litter fauna was depleted by the fire. In contrast, the topsoil fauna was enriched due to the incorporation of litter into the topsoil and the acquisition of the associated litter animals. Many species of rhizopods and ciliates, not initially recorded from the topsoil, were added to the fauna list. This could have been caused by a reduced ciliatostasis and the general changes which accompany the transition of a forest to grassland.

More detailed studies on the effects of fire and deforestation on the soil protozoa have been performed by Coûteaux (1976a,b, 1977, 1979) and Buitkamp (1977b, 1979). Coûteaux (1976a, 1977) found that the forest fire in a submediterranean region, dominated by pine and chestnut, totally destroyed the litter and mosses and their testacean faunas (Fig. 205). The recolonization of the new litter was slow; and even 12 months after the fire the density of individuals and species was very low. But species diversity, as measured with the Shannon-Weaver index, was high, indicating a rather unstructured community with an evolutionary potential to conquer the free niches. The recolonization of the new litter was from the humus layer, where the community was less affected. The drainage of water containing mineral salts from the litter ash modified the humus community, reducing the number of individuals and species and causing some changes in the community structure. The first litter colonizers were the strongly aerophilic *Corythion dubium* (Fig. 188q) and *Euglypha*



Figs 204, 205. Effect of scrub burning (Gorse—*Ulex europeaus* and Manuka—*Leptospermum scoparium*) on the protozoa of a New Zealand dark greyish brown heavy silt loam soil. The number of species was determined by inoculating 10 g of soil with 20 ml of distilled water on agar plates (after Stout, 1961). Figs 205a,b. Effect of fire on the individual and species number of the soil testaceans of a pine and chestnut forest in a submediterranean region. Numbers of individuals and species were estimated by the direct method of Coûteaux (1975). (compacted data from Coûteaux, 1976a, 1977)

ciliata. After six months, *Difflugia lucida* (Figs 44, 45, 66), *Centropyxis aerophila* var. *sphagnicola* (Fig. 61), *Corythion delamarei*, and *Trinema complanatum* appeared.

In another study, Coûteaux (1979) and Coûteaux & Chardez (1981) investigated fire and deforestation in some experimental areas in French Guiana (Table 25). The effects of the fire were similar to those described above. The testate amoebae were totally annihilated in the upper 0–3 cm soil layer. Even two years later, no recolonization could be detected. In the deeper zones the biomass increased. Deforestation caused a strong reduction of the numbers of testaceans, especially if the litter had been removed. Sixty-eight species occurred in the primary forest, 29 in the secondary forest, and only 13 species in the deforested area (Coûteaux & Chardez, 1981).

A third study was performed on two regularly burnt savannahs near Lamto (Ivory Coast) three months after the passage of the fire (Coûteaux, 1976b, 1978a). The general scarcity of organisms in these habitats was said to be reflected by the low individual density, biomass, production, and species richness of the testacean community. However, 51 species have been recorded, a number approaching the 68

species found in the 'rich' primary forest mentioned above. Unfortunately, Coûteaux (1976b, 1978a) did not compare the burnt area with unburnt and virgin controls. Buitkamp (1977b, 1979) investigated the ciliates in the same area (Table 26). Numbers of individuals and species were lowest in the unburnt savannah and highest in the burnt area, which confirms the early results of Fantham & Paterson (1924) and Stout (1961).

Conditions similar in some way to those due to fire are caused by volcanoes. Volcanic islands and volcanic tephra are also slowly colonized, probably because of lack of organic matter, very impoverished nutrients, etc. The first protozoan species appeared about one year after ash deposition (Holmberg & Pejler, 1974; Smith, 1985).

The results relating to fire effects are similar to those for higher soil animals (Franz, 1975b; Sohlenius, 1982). The litter and top soil protozoa, particularly the testate amoebae, are reduced or even annihilated. The ciliates are less depleted, especially in regularly burnt areas where their abundance and species richness increase. This may be due to a reduced ciliatostasis, because the fire enriches the soil with easily decomposed organic matter and the bacteria recover quickly (Stout, 1961). The recolonization rate of the testate amoebae is low and proceeds from the deeper soil layers and/or from the sods which survive the fire. This is in accordance with the results of Lousier (1982), who found that the first testaceans occurred in buried litter bags after only five months. The total colonization needed 60 months. Changes in the community structure can be ascribed to the raised temperature (which destroys the superficial soil layer, reduces and changes the food spectrum) and (also in deeper layers) to changes in the chemical milieu and the water regime.

3. *Effects of top soil removal.* Usually, protozoa are most abundant in the upper 0–10 cm of the soil (Foissner, 1981a; Foissner & Adam, 1980; Meisterfeld, 1980; Stout & Heal, 1967; Vergeiner *et al.*, 1982). Exceptions are known from extreme biotopes, such as desert soils in which the individual number was higher at 20–80 cm soil depth than at 0–20 cm (Brodsky & Yankowskaya, 1929).

When the topsoil layer has been removed, such as in the preparation and use of mountain ski slopes, a series of ecological changes takes place (Cernusca, 1978). Laminger *et al.* (1980), Foissner & Adam (1980), and Foissner *et al.* (1982c) studied the effects of such topsoil removal on the microfauna (Figs 206, 207). Five to seven years after smoothing the slopes, the abundance and biomass of testaceans and nematodes were still approximately 10 times lower in the center of the ski slopes than in the neighbouring alpine pastures. The decrease in the number of species was less pronounced (50%). At 5–10 cm soil depth, the abundance of the testaceans of the ski slopes was relatively greater than in the control plot. This might be an indication that the deeper members of the population escaped the mechanical (skiing) and chemical (ski wax, stabilization of the snow-cover by ammonium sulphate; see Berger *et al.*, 1984a, 1986) stresses. There were also pronounced changes in species composition. Shells composed of mineral particles (xenosomes) were more dominant in the stressed area than in the control plot (Fig. 207). This is comprehensible, because the other (non-xenosome bearing) species which normally dominate the litter (Schönborn, 1966a) which had been removed with the topsoil. A similar argument also accounts for the decreased abundance and biomass.

The ciliates, in contrast, showed no pronounced changes. This may be due to the pH, which was raised from the natural 3.5 to 7.6 by liming the ski slope (Foissner *et al.*, 1982c; Peer & Foissner, 1985). On a one-year old slope, which had not been limed, the decrease in the abundance and species richness of the ciliates was just as

Table 25. Effects of deforestation and fire on the number of soil testaceans in French Guiana (selected data from Coûteaux, 1979)

Site[1]	Soil depth (cm) 0–2		2–3		3–4		Total	
	I[2]	Bm[3]	I	Bm	I	Bm	I	Bm
Well drained forest soil	18	1.4	5	0.3	1	0.1	25	1.9
Poorly drained forest soil	11	1.0	6	0.2	5	0.6	22	1.9
Burnt deforested soil	0	0	0	0	6	1.1	6	1.1
Unburnt deforested soil without litter	6	0.1	4	0.2	0	0	10	0.4
Unburnt deforested soil with litter	13	0.5	5	0.5	4	0.7	21	1.7

[1]The investigations were performed with the direct counting method of Coûteaux (1975) about 1 year after the fire and the deforestation.
[2]Individuals mm^{-2}
[3]Biomass kg ha^{-1}

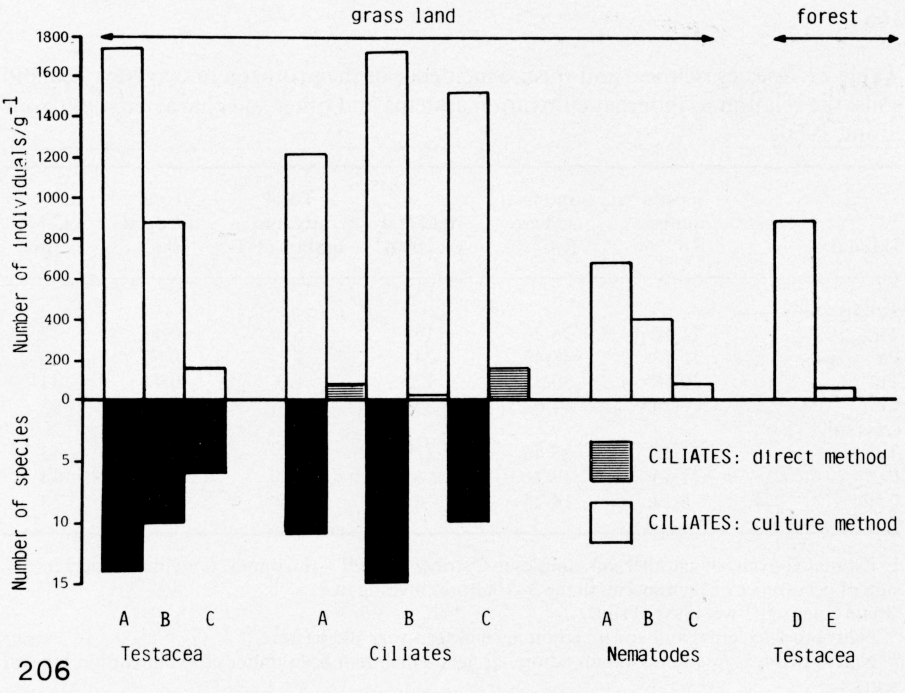
Table 26. Effects of deforestation and fire on the soil ciliates of a savannah near Lamto (Ivory Coast) (compiled from Buitkamp, 1977b, 1979)

Site	Number of species	Number of individuals at diff. temperatures[1] 15°C	20°C	25°C	30°C	35°C	40°C
Natural gallery woodland	22	64	926	961	1191	1291	1473
Unburnt savannah	19	0	546	844	373	385	0
Burnt savannah	33	36	2479	2935	2076	2978	4428

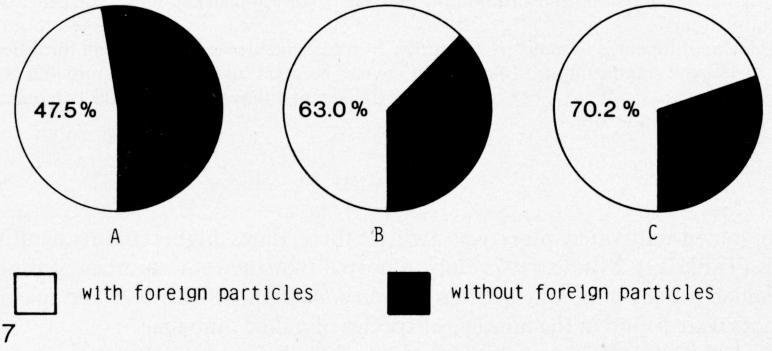
[1]Individuals g^{-1} dry mass of soil; estimated with the culture method of Buitkamp (1979).

dramatic as with the testaceans (Foissner & Adam, 1980). Foissner *et al.* (1982c) speculated that the unusual neutral pH perhaps allowed a higher decomposition and bacterial activity from which the ciliates benefited. However, Hofmann & Pfitscher (1982) found a reduced enzymatic activity and CO_2-release in the soils of ski slopes; pH was not measured.

4. *Effects of soil management.* (a) *Cultivation.* The protozoa and the microflora of the soil often occur with higher abundance and number of species in cultivated than in uncultivated soils or fallow lands (Beck, 1968; Datta & Mangat, 1974, 1975; Detcheva, 1965, 1972; Diercks, 1983; Fantham, 1929, 1931; Grandori & Grandori, 1934; Martyniuk & Wagner, 1978; Miteva, 1975a, 1975b; Nikolyuk, 1956, 1964; Stout, 1960; Sudzuki, 1979c). Stout (1960) and Datta & Mangat (1974, 1975) concluded that the protozoan populations of a given soil and vegetation complex are very stable. This stability is not disturbed even with a change of plant cover, provided that such changes do not cause marked differences in the soil organic cycle. Where cultivation or pasture establishment do result in increased soil fertility, the number and incidence of species increase (Table 27). Detcheva (1965, 1972) found that the number



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Fig. 206. Numbers of individuals and species of testaceans, ciliates, and nematodes in relatively undisturbed pasture soils and in soils of smoothed ski slopes in the Austrian Alps. The numbers of individuals (g^{-1} dry mass of soil for A, B, C; cm^{-3} for D, E) and species were determined by direct observation in a watered soil suspension. In addition, the culture method of Buitkamp (1979) was used for the ciliates. The graphs show the means of three (four for D, E) samples during the vegetation period. The differences between all sites are significant ($P \leqslant 0.05$) for testaceans and nematodes, but not for the ciliates ($P \geqslant 0.05$). The grassland sites A, B, C are located at the Schloßalm near Bad Hofgastein (Salzburg), about 1950 m NN; the forest sites (*Pinus cembra*) D, E are located at Obergurgl (Tyrol), about 2070 m NN. A = relatively undisturbed alpine pasture (control); B = marginal area of the ski slope, about 30 m to the west of site A; C = center of disturbance of the ski slope, about 50 m to the west of site B, smoothed about 5 years before the investigation was performed; D = undisturbed forest (control); E = ski slope near site D, smoothed about 7 years before the investigation was performed. (A, B, C, constructed from data of Foissner *et al.*, 1982c; D, E, constructed from the graphs of Laminger *et al.*, 1980)

Fig. 207. Average percentage (mean values of 3 samplings) of testacean shells with and without foreign particles used for shell building in (A) a relatively undisturbed alpine pasture, (B) a marginal area of a ski slope, and (C) in the center of disturbance of a smoothed ski slope. (from Foissner *et al.*, 1982c)

Table 27. Species richness and species incidence of the protozoa in two New Zealand soils: the relation to different cultivation systems and other soil characteristics (from Stout, 1960)

Habitat	Species number R/C[1,2]	Species incidence R/C[1,2]	Bacteria (× 1000)[3]	Total organic carbon (%)	Total nitrogen (%)	C/N ratio
Taupo soil						
Tu[4]	11/10[11]	36/26[11]	151	5.6	0.45	12
Pa[5]	15/18	48/49	245	7.2	0.69	10
Tu[6]	10/18	30/38	122	5.0	0.44	11
Cr[7]	16/20	44/62	349	5.9	0.47	13
Cass soil						
Tu[8]	12/18	25/46	129	3.1	0.23	13
Pa[9]	11/15	19/31	63	3.7	0.27	14
Cr[10]	8/14	14/25	67	3.0	0.23	13

[1,2]Estimated from 3–5 parallel soil samples in October 1955. R = rhizopods, C = ciliates, incidence = sum of occurrence of each species in the 3–5 cultures investigated.
[3]Plate counts g^{-1} wet mass of soil.
[4,5]Native tussock grassland and an adjoining eighteen-year-old pasture.
[6,7]Native tussock grassland and an adjoining field which had been under crop cultivation for two years.
[8,9,10]Native tussock grassland and an adjoining year-old pasture and an adjoining crop field in its first year of cultivation.
[11]No significant differences in numbers of species. In species incidence in Taupo soil the differences between species are significant at 0.1%. The differences between tussock and pasture and between tussock and crops are significant at 5%. There is no significant difference between the two tussocks or between the pasture and crops.

of protozoa in cultivated plots was two to three times higher than uncultivated controls (Table 32). Miteva (1975/76b) reported that the total number of protozoa was significantly lower in fallow lands than in soils planted with oats and maize. No differences were found in the number of species of naked amoebae.

Edwards & Lofty (1975) suggested that the overall effects of cultivation on the soil fauna is probably not very great (compare with Franz, 1975a,b). This seems to be supported by Nikolyuk's (1956), Stout's (1960), and my own investigations which do not show consistent differences in the number of individuals or species between grassland and grassland that had been under crop cultivation for many years. Only the abundance (culture method!) of the ciliates was constantly lower in arable land as compared with the adjoining grassland soil (Table 28).

Biczók (1952) however, found a decreased number of individuals of testaceans in continuously cultivated soils, though his statement was based on rhizosphere cultures and not on direct investigation of soil samples. It may indeed be that under the arid Hungarian climate, and under very intensive agriculture, such a reduction occurs. This is supported by my own (unpublished) observations.

Varga (1956, 1960) found that the strongly reduced microfauna in arable over-salted Szik-soils was substantially restored within 15 years in afforested areas. The protozoan fauna, however, was qualitatively and quantitatively poorer than those of old forests.

Table 28. Abundance and species richness of testate amoebae and ciliates in soils under different systems of cultivation

Site[1]	Testaceans[2]		Ciliates[3]	
	Individuals m^{-2} ($\times 10^6$)[4]	Total number of species recorded	Individuals m^{-2} ($\times 10^6$)[4]	Total number of species recorded
A_m Meadow	37.3	27	28.5	44
A_a Arable land	41.4	26	18.0	44
B_m Meadow	33.3	26	37.8	41
B_a Arable land	16.1	19	17.8	51
C_m Meadow	29.6	26	37.1	55
C_a Arable land	33.1	24	10.9	44

[1]A part of each of the meadows A_m, B_m, C_m had been turned to arable land A_a, B_a, C_a 10–15 years previously.
[2]Counted in a watered soil suspension.
[3]Estimated with a modified Buitkamp (1979) method.
[4]Arithmetic mean of 4 investigations of the top soil (0–5 cm) during the year 1984

Table 29. Abundance and species richness of the active protozoa in 0–5 cm soil depth of an alluvial soil under crop rotation (compiled from the graphs of Tomescu, 1978)

Crop	Individuals g^{-1} dry mass of soil[1]	Number of species[1]
Wheat	1300	12
Potato	2700	24
Lucerne	340	29

[1]Numbers were determined by a culture method and are the arithmetic mean of monthly estimations during the years 1972 (wheat) and 1973 (potato, lucerne). Testate amoebae were not investigated.

(b) *Ploughing*. Miteva (1975/76a) compared the soil protozoa under two regimes of autumn soil cultivation, namely: normal ploughing approximately 26 cm in depth; and surface cultivation at depth of about 8–10 cm. These two regimes did not essentially change either the species richness of the naked amoebae or the individual abundance of the ciliates, flagellates, and naked amoebae. The vertical distribution was different, being more even in the normally ploughed plots.

(c) *Crop rotation*. The influence of crop rotation on the composition of the protozoan fauna has been studied by Tomescu (1978). In a three-year rotation of wheat, potato, and lucerne, he found that the highest number of protozoa occurred in the potato culture, the lowest in the lucerne field (Table 29). Considering the low number of species recorded in this work, one must assume that Tomescu (1978) has overlooked many of them. Some ciliate species have obviously been misidentified (e.g., *Colpidium*).

(d) *Organic versus conventional farming*. Many popular books and newspapers often state that conventional agriculture is harmful to the soil life. Exact data on the

subject are rare and mostly confined to bacteria, fungi, earthworms, and the influence of different modes of fertilization on these organisms (Diercks, 1983; Franz, 1975b). However, 'fertilization' is only one of many components of organic farming methods (Bick, 1985; Cacek, 1984; Diercks, 1983).

Foissner *et al.* (1986) and Foissner (1986b) compared some biotic and abiotic soil parameters of organically and conventionally farmed wheat fields and meadows. The more general conclusions of these investigations are shown in Table 30 and may be summarized as follows: humus, numbers of species and organisms, and the enzymatic activities are slightly higher in the organically farmed plots, though differences are often not statistically significant, probably due to the low sample size.

These and other results (e.g., Cacek, 1984; Huber, 1985; Rühl, 1978) provide some support for the organic farming concept, because it increases the biological activity and conservation of the soil more than conventional agriculture. The higher activity and conservation are perhaps caused by the better humus management and by lesser soil compaction. The most prominent group, the earthworms, seem to be unaffected by conventional practices. This demonstrates the necessity of a widespread investigation program for such a sensitive problem with numerous ramifications.

5. *Effects of organic and mineral fertilizers.* Fertilization increases the abundance of most groups of soil organisms (Beck, 1968; Burges, 1958; Diercks, 1983; Franz, 1975a,b; Gams, 1967). The protozoa are no exception, as shown by field investigations (Allison, 1924; Berger *et al.*, 1986; Bhattacharya & Das, 1977; Bhattacharya *et al.*, 1977; Chardez *et al.*, 1972; Crump, 1920; Cutler, 1920; Detcheva, 1965, 1972; Dixon, 1937; Elliott & Coleman, 1977; Katznelson, 1946; Prasad & Jha, 1968; Rosa, 1962; Singh, 1949; Sudzuki, 1978, 1979c; Viswanath & Pillai, 1977b) and some laboratory experiments in which complex organic nutrients, such as blood, cow dung (Koch, 1916), mannitol, alfalfa grass residues (Pena-Cabriales & Alexander, 1983), and various kinds of leaf litter (Grandori & Grandori, 1934; Reinhard *et al.*, 1967; Varga, 1959) were added to soil microcosms. These studies show such a high degree of agreement that it is enough to consider in more detail only those with a clear experimental design and those concerning the testate amoebae. Very few reliable data are available on the effects of fertilizers on named species of protozoa and on their community structure in general. Some papers in this area (e.g., Viswanath & Pillai, 1977b) obviously contain serious misidentifications to the extent that they are best ignored.

The first extensive studies on the effects of organic and mineral fertilizers on the soil protozoa were performed by Cutler (1920), Crump (1920), Dixon (1937), and Singh (1949) at the Rothamsted (England) experimental plots. The most detailed investigation was made by the last author (Table 31). He found that the total numbers (active plus cystic) and the numbers of active amoebae in plots treated with complete minerals + ammonium sulphate or with farmyard manure were much higher than in the untreated plots. The complete minerals plot of Barnfield had a significantly lower total count of amoebae than the farmyard manured plot, although no significant difference existed between the counts of active amoebae. Neither difference between the complete minerals and the farmyard manure treated plots on Broadbalk was significant, with exception of one sampling occasion on which the farmyard manured plot had a significantly higher total number. No correlation was found between the percentage of organic carbon in the soils and the number of amoebae, indicating that the differences between the fertilized and the unfertilized soils may not be related to an increase in plant activity. This would also be reflected in root growth and root

Table 30. Comparison of the micro- and mesoedaphon and some abiotic factors in organically and conventionally farmed wheat fields and meadows. (from Foissner *et al.*, 1986)[1]

Parameter	Organic farming	Conventional farming	ANOVA[2]
TESTACEA[3]			
Individuals g^{-1} dry mass of soil	878	751	$0.25 < P > 0.1$
Biomass mg 1000 g^{-1} dry mass of soil	37.5	27.9	$P < 0.05$
Number of species	26	24	$P < 0.05$
Diversity (Shannon-Weaver; ln)	2.8	2.6	NT
Evenness	0.9	0.9	NT
Ratio of full and empty shells	1 : 1.3	1 : 1.5	NT
CILIOPHORA[4]			
Individuals (active) g^{-1} dry mass of soil	1.4	0.2	$P < 0.1$
Individuals g^{-1} dry mass of soil	1027	1285	$P > 0.1$
Biomass mg 1000 g^{-1} dry mass of soil	19.8	27.5	$P > 0.1$
Number of species	46	45	$P > 0.1$
Diversity (Shannon-Weaver; ln)	2.1	2.1	NT
Evenness	0.7	0.7	NT
NEMATODA[4]			
Individuals g^{-1} dry mass of soil	102	80	$P < 0.05$
LUMBRICIDAE[5]			
Individuals m^{-2}	174	181	$P > 0.1$
Biomass g m^{-2}	134	143	$P > 0.1$
Number of species	10	11	$P > 0.1$
MICROFLORA			
Catalase activity (ml O_2 g^{-1} dry mass)	3.6	3.1	$P < 0.05$
Urease activity (mg N g^{-1} dry mass of soil)	0.19	0.17	$P > 0.1$
Saccharase activity (mg C_6 g^{-1} dry mass)	0.54	0.58	$P > 0.1$
ABIOTIC FACTORS			
Soil moisture (% of dry mass)	31	31	NT
Humus (%)	7.5	6.5	$P > 0.1$
C/N ratio	7.7	7.8	NT
Bulk density (g cm^{-3})	0.86	0.89	NT

[1]The data (arithmetic means) are based on an investigation of two organically and two conventionally farmed wheat fields and on three organically and three conventionally farmed meadows. These 10 sites were examined four times during a year for testate amoebae, ciliates, nematodes, enzymatic activity, and soil moisture. The analysis of variance (ANOVA) is thus based on 40 samples. The earthworms and the abiotic factors were studied only once. Here, ANOVA is based on 10 samples only.

[2]A two-way analysis of variance was used. NT = not tested.

[3]All data derive from the investigation of 0.1 g soil (wet mass; bulked together from 10 thoroughly mixed soil cores) in a watered suspension (direct method).

[4]The abundance of active ciliates and nematodes were estimated in a watered suspension of 0.4 g soil (wet mass). All other data are based on a modified Buitkamp (1979) method.

[5]From formaldehyde extraction method as described in Satchell (1971).

exudates. The stimulating effect of root growth—the rhizosphere effect—has been well established for protozoa (Biczók, 1979; Darbyshire & Greaves, 1973; Stout & Heal, 1967). On the other hand, a relationship betwen the amount of organic matter and the number and kind of protozoan species present is also fairly well established (Smith, 1984; Bonnet, 1984) and could have contributed to the above findings. It is of

Table 31. The number of naked amoebae g^{-1} dry soil in untreated and treated plots at Barnfield near Rothamsted (compiled from Singh, 1949)

Parameter	Barnfield			Broadbalk		
Treatment	C[1]	O[2]	M[3]	C[1]	O[2]	M[3]
pH	7.2	7.0	7.1	8.1	7.7	7.9
% soil H_2O	14.0	18.8	15.2	14.3	18.1	15.5
% organic matter	0.8	2.5	0.8	1.1	2.6	1.2
Mean amoebae counts ($\times 10^3$)[4]						
Total	8	34	26	17	72	48
Active	5.3	28	23	10	52	40

[1,2,3]All plots have been treated in the same way since 1876. C = control; O = 14 tons of dung . 0.4 ha^{-1} . annum; M = 178 kg of superphosphate, 227 kg of potassium sulphate, 91 kg of sodium chloride, 91 kg of magnesium, 187 kg of ammonium sulphate and, at a second site, 178 kg of superphosphate, 102 kg of potassium sulphate, 51 kg of sodium sulphate, 51 kg of magnesium sulphate, 203 kg of ammonium sulphate . 0.4 ha^{-1} . annum, respectively.
[4]Estimated with the culture technique of Singh (1946). Means of nine and six sampling dates, respectively. Total numbers are significantly different at 10% level.

interest that the yield of mangolds and wheat in the untreated plots were about one-third those of either experimental plot, as were the numbers of amoebae. Crump (1920) and Cutler (1920) reported on similarly large differences in the numbers of flagellates and ciliates. They found, however, only insignificant differences in the number of the naked amoebae. Singh (1949) provided no explanation for these discrepancies; I suggest methodological shortcomings (see Dixon, 1937, and Section II.B).

These four studies show the stimulating effects of fertilizers on the soil protozoan community. The same is evident from the results of Detcheva (1965, 1972). She found an increase in the number of naked amoebae and ciliates in farmyard manured, and in superphosphate treated, plots as compared with the non-fertilized control. The zooflagellates showed no change (Table 32). A differential effect is supported by the results of Viswanath & Pillai (1977b). They observed a substantial increase in the abundance (culture method!) of the ciliated protozoa after superphosphate application. Viswanath & Pillai (1977b) found a positive correlation between the quantity of the fertilizer and the increase of protozoan numbers, whereas the bacterial population decreased at doses higher than 80 kg superphosphate ha^{-1} (Fig. 208). Thus, they suggested a selective stimulation of the ciliates by this fertilizer. Elliott & Coleman's (1977) field experiments suggest also a positive interaction among nitrogen, water, and soil protozoa. They counted more active protozoa, mainly naked amoebae, in nitrogen fertilized plots, especially when the mineral fertilizer was combined with irrigation (Table 24).

In contrast to these findings, Mavlyanova (1981) reported that, in a cotton field, mineral fertilizers (nitrogen 200 kg ha^{-1}, potassium 150 kg ha^{-1}) reduced the protozoan biomass by 25–30%, whereas a two-fold increase of their abundance and biomass was observed if microalgae (*Chlorella, Scenedesmus*) were used as organic fertilizers.

The results just reviewed deal with naked amoebae, flagellates, and ciliates and are based on selective culture methods with their associated shortcomings. The testate

Table 32. Effects of fertilization and irrigation on the number of soil protozoa in the rhizosphere of experimental maize field plots on a highly leached chernozem-smolnitsa (fertilizer experiments) and on a highly leached maroon forest soil (irrigation experiments) (from Detcheva, 1965, 1972)

	Numbers g^{-1} soil[1]						
Taxa	Super-phosphate	Farmyard manure	Non fertilized	Virgin control	Irrigated	Non irrigated	Virgin control
Flagellates	650 000	740 000	833 000	348 350	685 000	480 000	246 250
Naked amoebae	235 300	144 690	1295	25 190	175	166 730	129 690
Ciliates	12 360	11 265	2230	11 230	11 460	295	30
Total	897 660	895 955	837 025	384 770	696 635	647 025	375 970

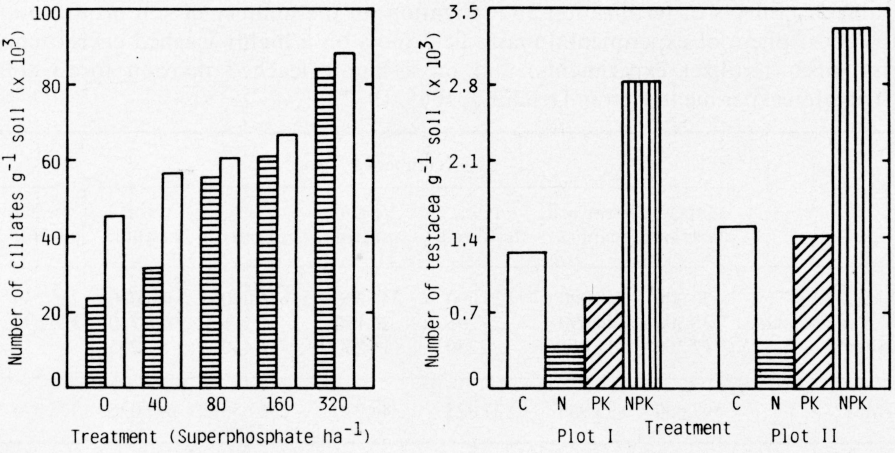
[1]The numbers were estimated by the method of Crump (1920) and are the means of three samples from spring, summer, and autumn.

Table 33. Species richness of the testate amoebae in the 0–4 cm depth soil layer of a fertilized Belgian forest (*Luzulo-Fagetum typicum*) (from Chardez *et al.*, 1972)

		Number and kind of species			
Plot[1]	Treatment	Terricolous	Muscicolous	Aquatic	Total
I	C	9	8	3	20
	N	8	5	1	14
	PK	11	2	3	16
	NPK	13	4	2	19
II	C	9	7	3	19
	N	8	0	2	10
	PK	11	2	3	16
	NPK	10	4	3	17

[1]Two identically treated plots, fertilized only once were investigated. The numbers show the mean of three sampling occasions during July 1967, three years after fertilization. C: control; N: 150 kg urea ha^{-1}; PK: 1000 kg potassium phosphate ha^{-1}; NPK: 325 kg urea and 1000 kg potassium phosphate ha^{-1}.

amoebae have attracted less interest, although these organisms could provide more reliable data because they can be counted with direct methods. The available studies are confined to the effects of a single application of fertilizers. Thus, the long-term effects are unknown. It seems that long-lasting cultivation and fertilization reduce the abundance and biomass of the testate amoebae, at least in the alpine meadow investigated by Vergeiner *et al.* (1982). Chardez *et al.* (1972) investigated changes in the soil testacean community of a deciduous forest three years after the application of some fertilizers (Fig. 209, Table 33). Urea decreased the numbers of individuals and species and biomass by two-thirds, whereas compound fertilizer doubled the individual

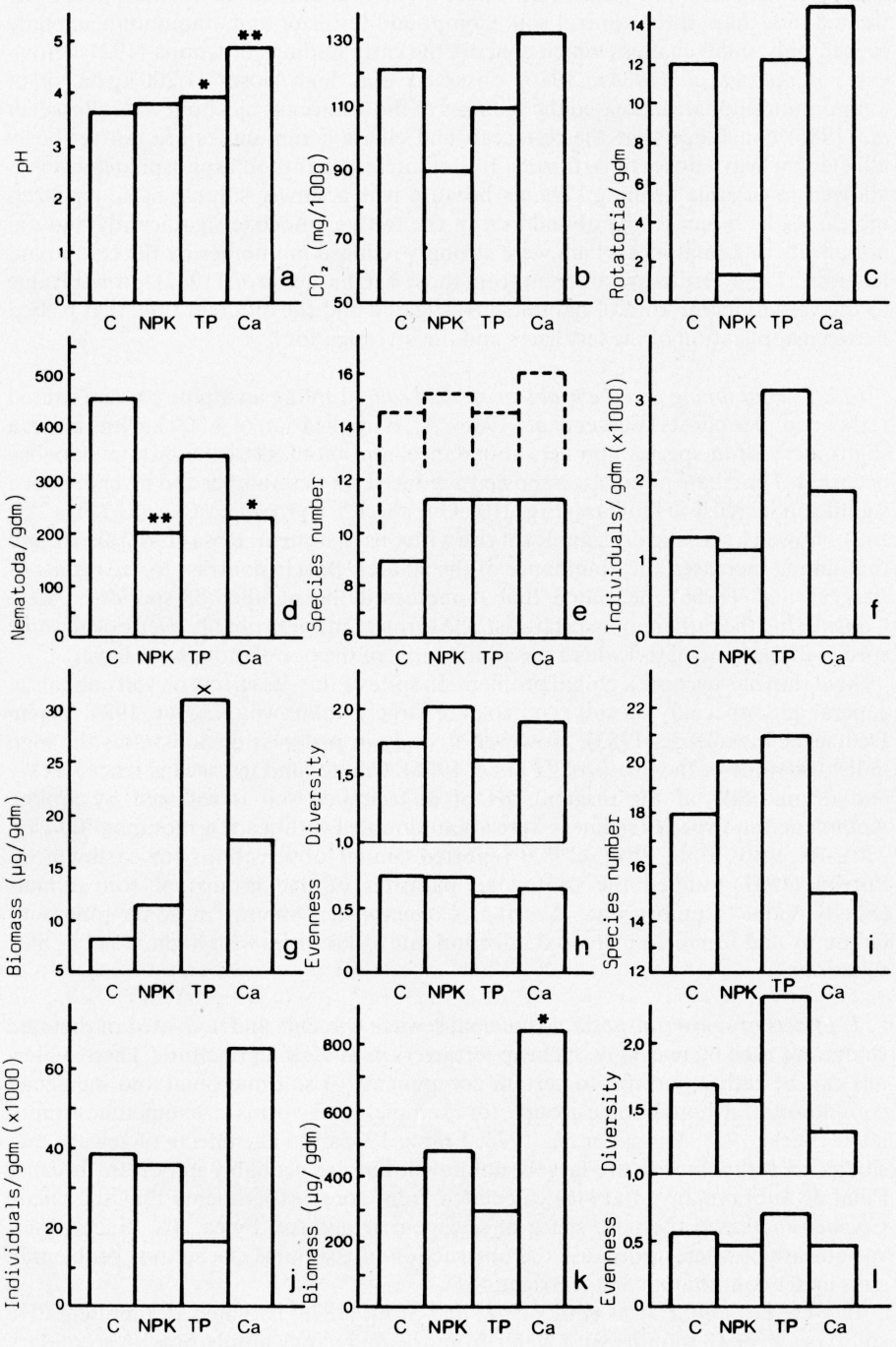


Figs 208, left; 209, right. Fig. 208. Abundance of the ciliates in a soil under ragi (*Eleusine coracana*) 9-2-7 variety, fertilized with different quantities of superphosphate (kg ha^{-1}) since 1967. Samples were collected in January 1969. Shaded: cultured in aerated autoclaved sewage. Unshaded: cultured in aerated 'agricultural medium'. For details of these methods see Viswanath & Pillai (1977a). (after Viswanath & Pillai, 1977b). Fig. 209. Abundance of the testate amoebae in the 0–4 cm depth soil layer of a Belgian forest (*Luzulo-Fagetum typicum*). Two identically treated (fertilized) plots were investigated. The graphs show the mean of 3 sampling occasions three years after fertilization. C = control; N = 150 kg urea ha^{-1}; PK = 1000 kg potassium phosphate ha^{-1}; NPK = 325 kg urea and 1000 kg potassium phosphate ha^{-1} (after Chardez *et al.*, 1972)

number and the biomass, but left the species number unchanged. Potassium phosphate caused only a slight decrease of individual and species numbers. All treatments reduced the number of the muscicolous species, such as *Assulina muscorum*, and favoured terricolous species like *Cyclopyxis eurystoma* and *Tracheleuglypha acolla*.

Berger *et al.* (1986) investigated the effects of some fertilizers on the microfauna of an alpine pasture using a randomized block design (Fig. 210). The blocks were treated with recommended maximum concentrations of compound fertilizer (NPK), thomasphosphate (14.5% P_2O_5, 45% CaO), and ammonium sulphate ($(NH_4)_2$ SO_2). The differences in the number of testacean and ciliate species were insignificant four months after the application of the fertilizers. Thomasphosphate markedly increased the biomass and the abundance of the testate amoebae, but decreased the abundance (culture method) and biomass of the ciliates. *Schoenbornia humicola* (Figs 68, 215)

Fig. 210. Means (n = 3) of the soil pH, the CO_2-release, and some animal community parameters in an alpine pasture on pseudogleyic brown earth, 4 months after application of compound fertilizer (600 kg NPK ha^{-1}), thomasphosphate (60 kg TP ha^{-1}), and lime (4000 kg $CaCO_3$ ha^{-1}). Testate amoebae, nematodes, and rotifers were counted in a watered soil suspension. The 'potential' abundance of the ciliates was estimated by a modified Buitkamp (1979) method. a. Soil pH; b. CO_2-release; c,d. Abundance of rotifers and nematodes; e,f,g,h. Species number (above, full and empty tests; below, full tests), abundance, biomass, and diversity and evenness of the testacean communities; i,j,k,l. Species number, abundance, biomass, and diversity and evenness of the ciliate communities. Randomized block design with a two-way analysis of variance: x, *, **, with $P \leqslant 0.10$, $P \leqslant 0.05$, or $P \leqslant 0.01$ different from the control (C). dm = dry mass of soil. (from Berger *et al.*, 1986)


pH
a
C NPK TP Ca
CO_2 (mg/100g)
b
Rotatoria/gdm
c
Nematoda/gdm
d
Species number
e
Individuals/gdm (x1000)
f
Biomass (µg/gdm)
g
Diversity
Evenness
h
Species number
i
Individuals/gdm (x1000)
j
Biomass (µg/gdm)
k
Diversity
Evenness
l

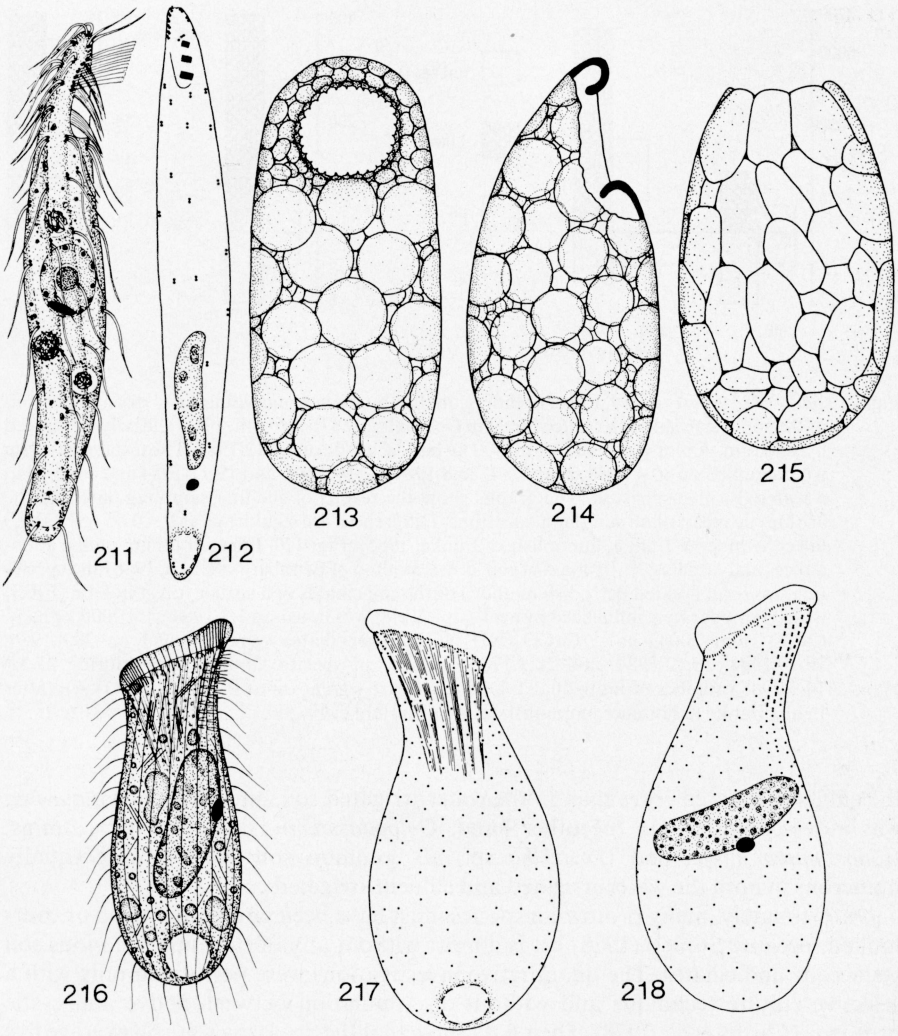
and *Trinema enchelys* (Figs 213, 214) were more abundant in the thomasphosphate-treated plot than in the control soil. Compound fertilizer and ammonium sulphate caused only small changes which concurs the early findings of Coppa (1921). However, Berger *et al.* (1984a, 1986) observed that high doses (1.200 kg ha^{-1}) of ammonium sulphate increased the biomass of the testaceans by about 30%. Berger *et al.* (1986) concluded that the testacean and ciliate communities are not seriously affected by heavy doses of fertilizers. It is of interest that thomasphosphate, which is allowed in organic farming systems because it is a slowly soluble basic fertilizer, increased the biomass and abundance of the testate amoebae significantly and did not affect the nematodes which were strongly reduced in number by the compound fertilizer. These results are different from those of Chardez *et al.* (1972), probably due to the very different kind of habitats investigated and the different time that passed between application of the fertilizers and the investigation.

6. *Effects of liming and the problem of 'acid rain'.* Liming an alpine pasture caused rather complex effects (Berger *et al.*, 1986). After application of 4.000 kg lime ha^{-1}, a slight increase in species number, abundance, and biomass of the testate amoebae occurred. The ciliate population showed a reduced species number and diversity but a significant increase in biomass (Fig. 210). One species, *Cyrtolophosis acutus* (Figs 211, 212), showed a statistically significant rise with this treatment. Rosa (1962) also found that liming increased the abundance of the ciliates. But, in contrast to the results of Berger *et al.* (1986), he stated that it increased the number of species as well. Considering the rather poor species list, the former author probably overlooked some species in the control soil where the abundances of the populations were lower.

Acid rain has become a global problem. In spite of this, its effects on soil animals in general and especially on soil protozoa are largely unknown (Hågvar, 1984; Verein Deutscher Ingenieure, 1983). However, a study in progress demonstrates the high indicator value of the protozoa (Funke, 1985). Ciliates and testaceans react quickly and dramatically if the original pH of an acidified soil is restored by liming. Abundance and species richness were about doubled within a few months (Figs 219, 220). Recently, Führ *et al.* (1985) reported similar observations for earthworms. Purrini (1981) studied the protozoan parasites of five groups of soil animals (Enchytreidae, Lumbricidae, Acarina, Collembola, Diptera) in some forests of Germany and found an increased infection rate at localities with higher load of SO_2 emissions.

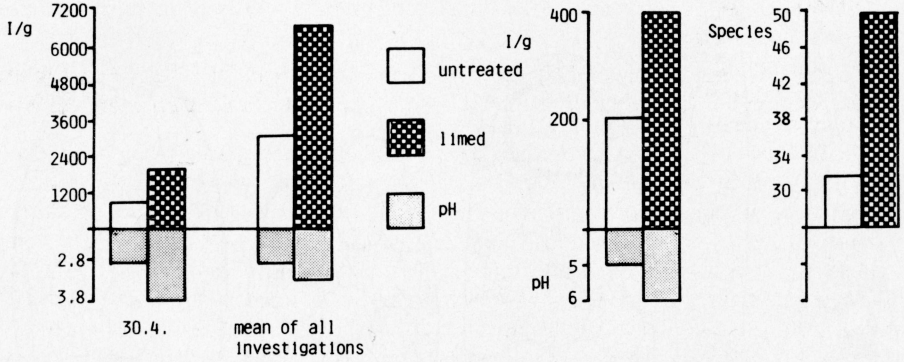
7. *Effects of sewage disposal.* Municipal sewage effluents and activated or digested sludge are used increasingly as cheap fertilizers in modern agriculture. These materials can be rather harmful to certain components of soil microbial and metazoan communities, although some groups, for example, earthworms, are sometimes stimulated (Beck, 1968; Dindal *et al.*, 1975; Franz, 1975a,b). The effects of sewage and sludge on soil protozoa are largely unknown, but are probably important because Pillai & Subrahmanyan (1946) calculated from some experiments that the ciliate *Colpoda* increased the pore space of sewage-irrigated soil by ca. 8%. Such observations are of interest, because the obstruction of the pores is a serious problem in soils under continuous sewage irrigation.

In New Zealand, Cairns *et al.* (1978) and Stout (1978) irrigated 10 representative soil types over 18 months with water from the municipal supply or with secondary effluent from a biological filtration plant. The soil properties that were measured were not affected and the soil microfauna was able to adapt to the altered moisture regime.



Figs 211–218. Some soil ciliates and testacea which showed a pronounced treatment effect in field and laboratory experiments. Ciliates were drawn from specimens *in vivo* and after silver impregnation. Figs 211, 212. *Cyrtolophosis acutus*, right side and ventrum, 44 µm and 47 µm (from Foissner, 1980a and original). Figs 213, 214. *Trinema enchelys*, ventral and lateral views, 50 µm (from Petz, Lüftenegger, Foissner, Berger & Adam, unpublished). Fig. 215. *Schoenbornia humicola*, lateral view, 35 µm (same source as Figs 213, 214). Figs 216, 217, 218. *Spathidium spathula*, left and right sides, 67 µm. (from Foissner, 1984a)

The macrofauna was suppressed by the persistently wet conditions (no earthworms were recovered). The fauna of the topsoils irrigated with tapwater consisted of typical soil species. The fauna of the effluent and the trickling filter was typical of those habitats, but few of these species persisted in the effluent-irrigated topsoils, which generally had a fauna similar to the topsoils irrigated with tapwater. Species such as *Trinema lineare*, *Enchelys* sp., *Colpoda inflata*, and *Uroleptus* sp. were less common in



Figs 219, left; 220, right. Fig. 219. Effect of liming on the abundance (individuals g^{-1} dry mass of soil) of the soil testaceans of a spruce forest in Ochsenhausen (near Ulm, FRG) heavily influenced by acid rain. A plot was limed with 2000 kg ha^{-1} $CaCO_3$ on 27.12.1983. The testate amoebae were sampled on 30.4.1984, 25.6.1984, 20.8.1984, 22.10.1984, and 19.12.1984 and counted in a watered soil suspension. The graphs show the results of the first sampling date and the arithmetic mean of all sampling occasions. Differences are significant at $P < 0.05$ (ANOVA) (after Wanner & Funke, unpublished; Funke, 1985). Fig. 220. Effect of liming on the abundance (individuals g^{-1} dry mass of soil; direct method of Brunberg-Nielsen, 1968) and species richness (non flooded petri dish method) of the soil ciliates of a spruce forest in Ulm (FRG) which is moderately influenced by acid rain. A plot was limed on 1.3.1984 with 2000 kg ha^{-1} $CaCO_3$ and 500 kg ha^{-1} $CaCO_3(NH_4NO_3)$. The ciliates were sampled on 20.8.1984, 20.10.1984, 20.12.1984, and 20.1.1985 (number of species) and 13 times during 23.3.–14.7.1985 (number of individuals). Differences are significant at $P < 0.05$ (ANOVA). (after Lehle, Funke & Foissner, unpublished; see also Funke, 1985)

the effluent-irrigated cores than in the water-irrigated soil, and *Cyclidium glaucoma* was more common. On the other hand, *Colpoda steinii, Leptopharynx costatus, Gonostomum affine*, and *Oxytricha* sp., all common soil species, were equally numerous in both the water-irrigated and effluent-irrigated cores.

Unfortunately, many protozoan species must have been poorly identified or overlooked, because Stout's (1978) list is almost without any of the autochthonous soil testaceans and ciliates. The quantitative investigations were performed only with a selective culture technique and without discrimination between active and cystic protozoa (Cairns *et al.*, 1978). Their data show that the protozoa were on average five times more abundant in the effluent-irrigated cores than in the tapwater-irrigated plots, although the numbers of bacteria, actinomycetes, and moulds were similar in both treatments.

Viswanath & Pillai (1974) found more protozoa in experimental soils of sand and betonite clay if they were enriched with organic materials. Raw sewage and refluxed sewage gave lower counts than activated sludge and (especially) sewage solids, which yielded values similar to those from cow dung and farmyard manure. But greater quantities of water stable aggregates of larger sizes ($\geqslant 2$ mm) were formed only in soil columns enriched with cow dung or straw powder and where the ciliate *Colpidium* sp. (very probably a misidentification) was abundant. This is strengthened by the above-mentioned results of Pillai & Subrahmanyan (1946).

Lüdeman & Kowalsky (1969) found many protozoa in the effluent of soil lysimeters irrigated with detergent containing mechanically purified sewage. They did not determine the exact number or the species composition.

8. *Effects of soil compaction.* Soil compaction is a slow poison of modern agriculture. It decreases the soil fertility and increases soil erosion (Cacek, 1984; Diercks, 1983; Scheffer & Schachtschabel, 1979). It is frequently caused by the use of heavy agricultural machines and by the reduced application of humus-producing substances such as organic manures.

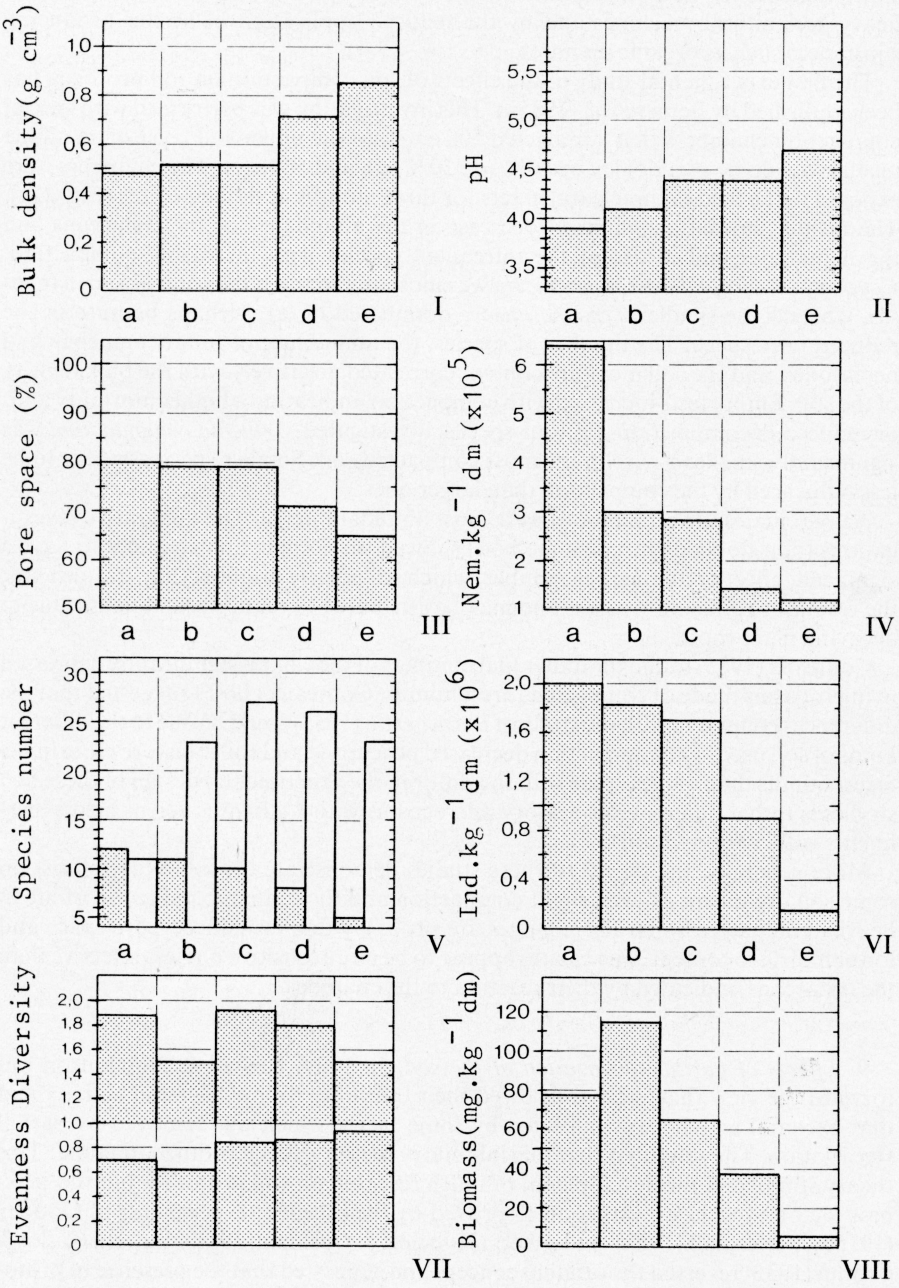
The first experimental study of the effects of soil compaction on soil protozoa has been published by Berger *et al.* (1985a). This investigation was performed with special compaction chambers that compacted 500 cm^{-3} of the upper soil layer of an alpine pasture on alpine pseudogley by 10% (c), 30% (d), and 50% (e). The chambers were exposed in the field in three parallel sets for three months at the same sites (Fig. 221). The results showed a significant decrease in the abundance of the testaceans and the nematodes and a loss of the infrequent species with increasing compaction. *Centropyxis aerophila* var. *sphagnicola* was most abundant in the control and in (c) to (d), whereas the smaller *Trinema lineare* dominated in (e), perhaps because of the reduced pore space. The number of species, the abundance of testate amoebae and nematodes, and the soil moisture content correlated negatively with the bulk density of the soil. Empty tests increased with compaction, indicating a higher mortality and/or reduced decomposition. Of four species investigated, *Trinema complanatum* was significantly smaller in size in the most compacted soil. Smaller species appear to be less influenced by the compaction than larger ones.

Active ciliates (direct method) were most abundant in (d). The qualitative investigations (non-flooded petri dish method) showed the compaction chamber to have a significant effect on the species number, which was nearly doubled (Fig. 221e). Thus, the results are difficult to assess and may be attributed to reduced ciliatostasis due to decaying plant roots.

Coûteaux (1985) found the individual numbers of the ciliates significantly depressed in microcosms made of compacted forest humus. Coûteaux (1985) suggested that the differences compared with the study of Berger *et al.* (1985) could be due to the different kinds of soil used. The compaction decreased pore space and soil moisture more in the forest humus than in the alpine soil. In addition, the experimental design of these two studies is rather different (laboratory microcosms with 4 g humus versus field experiments with 500 cm^{-3} soil).

More generally, the results of these studies demonstrate the inhibitory effects on some soil organisms of even slight compaction and the dramatic reduction of life in heavily compacted soils. The changes are probably due to reduced pore space and lower moisture content. The ciliates appear to be more sensitive but less selective than the testaceans, indicated by their reaction to the chamber.

9. *Effects of partial sterilization of the soil.* In 1909, Russell & Hutchinson put forward the view that 'sick' soils owed their infertility to low bacterial activity and that bacterial activity was inhibited by some factor which was removed by partial sterilization. They thought that this inhibitory factor was the protozoan fauna. This theory stimulated the development of much research on soil protozoa, but the 'sickness factor hypothesis' was soon disproved by the excellent experiments of Goodey (1915b), Sewertzoff (1925), and others (Kopeloff & Coleman, 1917). Indeed, Cutler & Crump (1935) reversed the original concept and suggested that the presence of protozoa in the soil keeps the bacteria at a level of maximum efficiency. This is supported by recent microcosm experiments (Clarholm, 1984, 1985; Habte & Alexander, 1977, 1978a,b).


Bulk density(g cm^{-3})
1,0
0,8
0,6
0,4
0,2
0
a b c d e
I
pH
5,5
5,0
4,5
4,0
3,5
a b c d e
II
Pore space (%)
100
90
80
70
60
50
a b c d e
III
Nem.kg^{-1}dm (x10^5)
6
5
4
3
2
1
a b c d e
IV
Species number
30
25
20
15
10
5
a b c d e
V
Ind.kg^{-1}dm (x10^6)
2,0
1,6
1,2
0,8
0,4
0
a b c d e
VI
Evenness Diversity
2,0
1,8
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
VII
Biomass(mg.kg^{-1}dm)
120
100
80
60
40
20
0
VIII

Russell & Hutchinson (1909) based their theory mainly on theoretical considerations, bacterial counts, and some microcosm experiments. More detailed investigations were performed only many years later. Singh & Crump (1953) steamed small plots of a Sitka spruce nursery for 20 min. In another experiment, they used 10% formalin in water at a rate of 5.7 l m^{-2} (Table 34). The first count, taken between 7 to 14 days after the treatment with steam or formalin, showed that all active amoebae were killed. The cystic forms were apparently undamaged. An immediate fall in bacterial numbers also occurred. After this, the number of both amoebae and the bacteria in the steamed plots rose very much higher than in the untreated plot. In the formalin-treated soil, the number of bacteria rose well above that in untreated soil but the numbers of active and cystic amoebae were generally much lower compared with the control soil. When formalin was applied once again to the same plot after a year, the population of amoebae was further decreased. This effect of formalin treatment on the numbers of amoebae was found to persist over a period of six months. Singh & Crump (1953) suggested that the unsuitable quality of bacterial food supply might be responsible for keeping the numbers of amoebae in check in the formalin-treated soil.

Very similar results were reported by Sewertzoff (1925) and by Stout (1955b). Stout (1955b) sterilized a green-house soil by steam injection to a depth of 46 cm. Samples were taken 100 days later from the topsoil (0–10 cm) and subsoil (51–61 cm) of both treated and untreated soil. The number of species in the treated topsoil was greatly reduced by the steaming; there being only six species compared with twenty-five in untreated topsoil. The treated subsoil, however, was little affected; twenty-one species were found as compared with twenty-two in untreated subsoil. The treatment delayed the development of the fauna, but favoured the growth of the surviving ciliate species, especially in the topsoil. Stout (1955b) suggested that the stimulated growth of the protozoa was due to the destruction of a thermolabile toxic factor that inhibits the development of protozoa. This view is supported by the concept of ciliatostasis.

10. *Effects of pesticides.* The literature on the side-effects of pesticides on soil microorganisms has been excellently reviewed by Lal & Saxena (1982) and Domsch *et al.* (1983). Field data on soil protozoa have not been fully considered. Lal & Saxena (1982) concluded from data with pure cultures under laboratory conditions that soil and water microorganisms accumulate agrochemicals fairly readily and concentrate them to many times their levels in the surrounding environment. Gregory *et al.* (1969) found that *Paramecium bursaria* and *P. multimicronucleatum* concentrated DDT and parathion 99 times and 964 times, respectively. Similar results have been reported for *Tetrahymena pyriformis* strain W which concentrated Mirex 193 times and Aroclor 60 times within seven days (Cooley *et al.*, 1972).

Fig. 221. Effects of soil compaction on the testacean, ciliate, and nematode communities and on some physical parameters of a pseudogleyic alpine soil. The graphs show the mean of three parallel experiments. Numbers of individuals and biomass were estimated in a watered soil suspension and are expressed in kg^{-1} dry mass (dm) of soil. The species numbers of the ciliates were estimated with the non-flooded petri dish method. a. Relatively undisturbed alpine pasture (control); b. Chamber effect (control; not compacted); c. 10% compacted; d. 30% compacted; e. 50% compacted. I. Bulk density of soil; II. pH of soil; III. Pore space of soil; IV. Individual numbers of the nematodes; V. Numbers of testacean (stippled) and ciliate (unstippled) species; VI. Individual numbers of the testaceans; VII. Diversity and evenness in the testacean communities; VIII. Biomasses of the testaceans. (after Berger *et al.*, 1985a)

Table 34. Numbers of amoebae and bacteria in untreated, formalin-treated, and steam-treated soils (from Singh & Crump, 1953)

Date	Numbers of amoebae g^{-1} wet soil[1]			Bacteria g^{-1} wet soil ($\times 10^6$)[2]	Soil water content (%)
	Total	Cystic	Active		
Untreated soil					
23.03.1950	12 200	979	11 221	3.30	12.4
20.04.1950	8570	3300	5270	10.75	12.6
4.05.1950	10 200	4670	5530	13.00	11.3
25.05.1950	15 800	6040	9760	—	—
8.06.1950	17 300	4670	12 630	11.90	8.5
6.07.1950	14 500	3600	10 900	10.40	11.2
31.07.1950	13 300	4280	9020	5.25	11.0
24.10.1950	17 300	4670	12 330	8.30	8.4
Formalin-treated soil (16.3.)					
23.03.1950	635	412	[3]	2.50	12.6
20.04.1950	1650	1390	[3]	27.55	12.1
4.05.1950	2770	1270	1500	13.75	11.7
25.05.1950	11 100	5540	5560	—	—
8.06.1950	8570	2770	5800	28.35	8.5
6.07.1950	7210	3020	4190	14.15	8.6
31.07.1950	11 100	5540	5560	7.00	10.9
24.10.1950	10 200	5540	4660	20.10	7.5
Steam-treated soil (10.3.)					
23.03.1950	693	126	567	5.00	13.9
20.04.1950	12 200	2540	9660	27.85	12.8
4.05.1950	20 500	5540	14 960	38.25	13.9
25.05.1950	54 000	12 200	41 800	—	—
8.06.1950	37 900	1960	35 940	42.55	8.8
6.07.1950	59 000	5540	53 460	18.00	10.0
31.07.1950	45 200	5540	39 660	8.30	13.1
24.10.1950	45 200	13 300	31 900	15.65	8.6

[1]The numbers were estimated by the culture technique of Singh (1946).
[2]Plate counts.
[3]Total and cystic not significantly different ($P \geqslant 0.05$).

The mode of action of pesticides on protozoa is not well understood. Recent studies have suggested the cell membrane to be the site of uptake (Dive *et al.*, 1984). An inhibition of DNA, RNA, and protein synthesis has also been observed (Saxena *et al.*, 1982, 1984; Lal & Saxena, 1980, 1982). The depression of the bacterial and fungal flora by most pesticides may indirectly influence protozoa under field conditions, as many of them feed on these organisms.

The first field experiments on the effects of pesticides on soil protozoa were performed by Smith & Wenzel (1947), Ilyin (1960), and Way & Scopes (1968). Smith & Wenzel (1947) found that 181 kg 0.4 ha^{-1} DDT had no effects on the soil protozoa. These results are doubtful because they used a selective culture method with three dilution levels only. With such a crude method, only very pronounced effects would be detectable. This interpretation is validated by the results of MacRae & Vinckx (1973), who found that the protozoa of a garden soil were strongly depressed by low

Table 35. Effects of DDT and Lindane upon the abundance of the protozoa in a garden soil (from MacRae & Vinckx, 1973)

	Protozoan numbers (active and cystic) ($\times 10^3$ g^{-1} soil)			
	Period of incubation (months)			
Treatment	0	1	2	3
Distilled water	493.2	400.2	93.4	70.8
DDT 5 ppm	246.6*	144.7*	11.7*	1.8*
DDT 50 ppm	162.7*	11.7*	0.8*	3.8*
Distilled water[1]	4.5	174.2	2.7	ND[2]
Lindane 5 ppm	1.4*	57.5*	2.2	ND
Lindane 50 ppm	1.4*	8.9*	3.6	ND

[1]The soil samples for each of the pesticide experiments were taken at different times of the year which may explain the very different number of protozoa in the controls. The culture method of Singh (1955) was used to estimate the abundances.
[2]ND = not determined. * = significantly different from control (distilled water) (P = 0.01).

doses of p,p'-DDT and Lindane, even three months after application (Table 35). The organo-phosphorus insecticide Phorate had no effects on protozoan numbers in a sandy loam soil at 10 ppm but depressed them significantly at a concentration of 250 ppm, which is sometimes reached at commercial application rates (Way & Scopes, 1968). These results are also of restricted value, because the treated plot was investigated only once, two months after application of the pesticide, and because the protozoa were extracted in Baermann funnels, which are probably inappropriate for this purpose.

More detailed experiments were performed by Radu *et al.* (1974) who studied the effects of three chloroderived insecticides (Duplitox, Aldrin, and Heptachlor) on the protozoa of a leached brown forest soil and a clay-sandy alluvial soil at application rates of 1, 2, and 4 kg ha^{-1} over a period of six months. All doses strongly depressed the abundance of the naked amoebae and the zooflagellates, whereas the ciliates showed a trend to increase at low doses (1 kg ha^{-1}), and to decrease at the higher application rates. No recovery was evident after six months. Similar results were reported by Thirumurthi & Lebrun (1978). The protozoa, mainly naked amoebae and flagellates, were found to be little affected by the insecticide Carbofuran at application rates of 1, 2, and 5 kg ha^{-1}. Ten and 15 kg ha^{-1} caused a rather marked decrease of the protozoa even after 90 days (Fig. 224). Experiments with air-dried and rewetted soil microcosms produced similar results.

Ilyin (1960) reported that field doses of the herbicide 2,4-D depressed the protozoa, which was confirmed by Deshmukh & Shrikhande (1974). They found that 2,4-D, NaTA, and Simazine at field doses, and at five times the field doses, significantly inhibited the protozoa of a red sandy clay loam in the first two weeks. Six weeks thereafter, the protozoan population fully recovered. Bladex had no effect. Low doses (0.1–1.0 ppm) of 2,4-D increased the growth of the common soil amoeba *Acanthamoeba castellani* under culture conditions (Prescott & Olson, 1972). Likewise, low doses of the dimethylamine salt of 2,4-D stimulated the growth of rooted macrophytes and the photosynthetic uptake of ^{14}C in natural phytoplankton assemblages (Boyle, 1980). Prescott & Olsen (1972) supposed that *Acanthamoeba castellani*

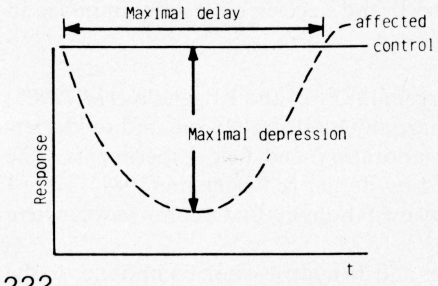
degrades 2,4-D and uses it as a carbon and/or energy source. This is supported by experiments of Pollero & Pollero (1978) who found this amoeba to be able to degrade DDT by 30% within three weeks.

Geltzer & Geptner (1976, 1980) reported that field doses (1.5 kg ha^{-1}) of the herbicides Diuron, Monuron, and Cotoran decreased the abundance of the entire soil protozoan population during the first 10 days. After 30 days the treated plot had a slightly higher individual number than the control (Fig. 226). The means of three estimations per year over a period of six years showed, with one exception, higher protozoan numbers in the experimental plots than in the control. Naked amoebae, flagellates, and ciliates contributed more or less equally to this increase. No pronounced changes in the species number and composition were found. This census recorded only a low number of species of ciliates, indicating perhaps a rather poor standard of the taxonomic investigation. *In vitro* experiments by the same authors showed that 150 mg l^{-1} Diuron shortened the LD_{50} of *Hartmanella rhysodes, Paramecium caudatum,* and *Euglena viridis.* Higher doses caused damage of the plasmamembrane and cell lysis. Very similar results were reported for the herbicides KOBEX and SGA by Miteva (1976). These agrochemicals inhibited the naked amoebae and flagellates only during the first weeks (Fig. 225). The ciliates and the species composition of the naked amoebae were not affected.

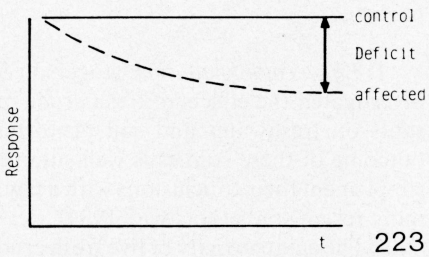
Field investigations on the side-effects of pesticides to soil protozoa appear rare as compared with the fairly large number of studies which have been undertaken with pure cultures over the last decade (e.g., Dive *et al.,* 1980, 1984; Lal & Saxena, 1980, 1982; Lord & Wright, 1985; Komala, 1984; Saxena *et al.,* 1982, 1984). In spite of this, some important conclusions may be drawn. (1) The general pattern of reaction of the soil protozoa to pesticide stress is the same as that of other organisms (Domsch *et al.,* 1983; Ottow, 1985; Figs 222, 223). (2) Many protozoan species seem to be just as sensitive to pesticides as other more commonly used test organisms (e.g., Dive *et al.,* 1980, 1984; Komala, 1984; Lord & Wright, 1985). (3) Insecticides are more toxic than herbicides. This is supported by studies with pure cultures (Dive *et al.,* 1980). In laboratory experiments, fungicides were most harmful, especially to ciliates (Dive *et al.,* 1980). No field investigations are available for comparison. (4) Domsch *et al.* (1983) introduced the '60 days rule' which means that side-effects (e.g., depression of the abundance) with delays of more than 60 days may be critical to the populations. Hence, one can discriminate between reversible and persistent responses (Figs 222, 223). If we apply this rule to the protozoa, it becomes clear that all insecticides tested are critical, whereas all herbicides show tolerable effects. Some of the newer herbicides seem to be extremely harmful to protozoa, at least in pure cultures (Lord & Wright, 1985). Soil algae are also seriously affected (Plumley & Davis, 1980; Zurek, 1981).

These conclusions show that the effects of pesticides on soil protozoa have been neglected and underestimated. Furthermore, recent approaches demonstrate very different sensitivities of species to pesticides, which can be used to prepare selective culture media (Pussard *et al.,* 1980). In spite of this, not a single reliable field study is available which has dealt with the 'effects on protozoa' at the species level. The testate amoebae have been totally neglected, regardless of their high ecological significance (Section III) and the reliable methods available for their abundance estimation. This is particularly frustrating in the light of recent studies which demonstrate more and more that the major portion of the pesticides and their metabolites is bound to the humus fraction of the soil (Khan, 1982), a main source of food for the testate amoebae (Section IV.B.2).

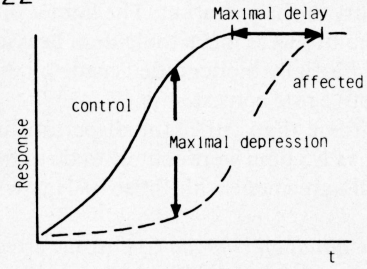
A recent paper by Laminger & Maschler (1986) describes interesting side effects

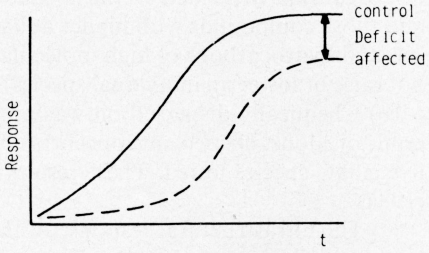


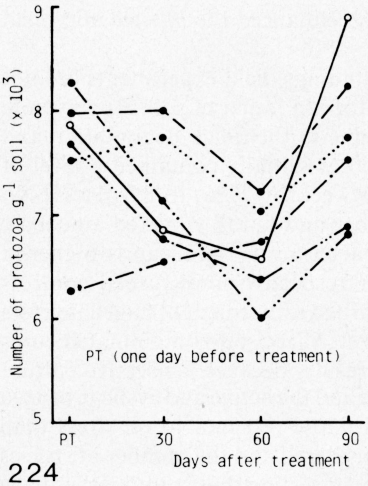
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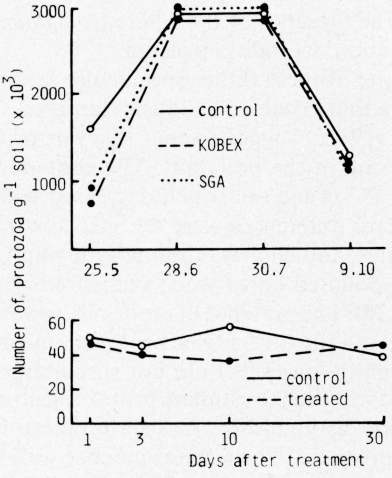
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Figs 222–226. Fig. 222. Principal types of reversible pesticide responses characterized by depression of microbial test parameters and delay periods for recovery (after Domsch *et al.*, 1983). Fig. 223. Principal types of persistent pesticide responses characterized by deficits at the end of the monitoring period (after Domsch *et al.*, 1983). Fig. 224. Effect of the insecticide carbofuran on the individual number of the soil protozoa ('overlay plaque' technique of Menapace *et al.*, 1975). ——— control; — — — 1 kg ha^{-1}; · · · · · 2 kg ha^{-1}; — · — · — 5 kg ha^{-1}; — ·· — ·· — 10 kg ha^{-1}; — ·· — ·· — 15 kg ha^{-1} (after Thirumurthi & Lebrun, 1978). Fig. 225. Effect of the herbicides KOBEX and SGA on the individual number of the soil protozoa (culture technique). The plots were treated on 7.5–8.5.1973 (constructed from data of Miteva, 1976). Fig. 226. Effect of the herbicide diuron on the individual number of the soil protozoa (culture technique). (after Geltzer & Geptner, 1976)

of some pesticides to soil protozoa in general and species of testate amoebae in particular.

11. *Effects of oil pollution.* Rogerson & Berger (1981a-c) and Rogerson *et al.* (1983) investigated the effects of fresh crude oils, partially biodegraded oil, and oil dispersants on freshwater and soil protozoa in laboratory and field experiments. The outcome of these studies is well summarized by Berger & Rogerson (1981). Here I supplement their conclusions with a few of my own thoughts and a comparison with a more recent study (Hartwig, 1984).

(a) The acute toxicity of five fresh crude oils and 36 hydrocarbon compounds to the test organisms depended on the aquaeous solubility of the pollutant. The lighter oils and those compounds with higher aquaeous solubility were more toxic than heavier oils and hydrocarbons of high molecular weight. Partially biodegraded crude oil did not raise or lower an individual species' reproductive rate consistently.

(b) Chemically dispersed oil was much more toxic than either the dispersant or crude oil alone. Dispersant concentrations as low as 1.5 ppm were acutely toxic to the five ciliate species tested. These results are in full agreement with those of Hartwig (1984).

(c) The ultrastructural response of the ciliate *Colpidium colpoda* to chronic stress with partially degraded crude oil was a dramatic increase in the number and size of lipid-hydrocarbon cytoplasmic vesicles as well as an increase in the number of cortical mucocysts.

(d) The presence of the ciliate *Colpidium colpoda* enhanced the *in vitro* microbial degradation of crude petroleum.

In spite of these rather spectacular laboratory findings, field experiments did not indicate that crude oil seriously damaged the protozoan fauna of soil. Rogerson & Berger (1981c) suggested that this was probably due to the quick degradation and weathering of the pollutant. The contaminated cores initially contained a level of 37.2 $\mu l\, g^{-1}$ crude oil, which decreased within one week by 77%, to 8.5 $\mu l\, g^{-1}$. No significant differences were detected for the number and kinds of naked amoebae, flagellates, and ciliates, although the number of bacteria was significantly higher in the oil-polluted cores when compared with their respective undisturbed controls (Table 36). The presence of crude oil, however, retarded excystment of flagellate cysts at 4°C; and the diversity of protozoa invading the sterilized, oil-contaminated cores was slightly lowered. I am not sure about these results because a selective culture method was used to estimate protozoan abundance and the active and cystic protozoa were not distinguished. Cysts are probably much more resistant to oil stress than active protozoa. The testate amoebae were not considered and the number of species recorded at all sampling occasions was rather low, suggesting that many species have been overlooked.

The results of Rogerson & Berger (1981c) contrast also with those of Hartwig (1984) who found a marked reduction in the number of ciliates, and some drastic changes in their community structure in a tidal sand flat which had been experimentally contaminated with crude oil. Of course, such differences in the effects of oil stress in soil and marine sand ciliates could be due to the different physical and chemical environment. Further studies are necessary.

Berger & Rogerson (1981) suggested that the increased storage of lipids in oil-stressed organisms may have practical application. Should a threshhold 'lipid' level be characterized for a protozoan or microinvertebrate community, this could conceivably form the basis of a quantitative assessment technique for *in situ* hydrocarbon

Table 36. Total number of flagellate, naked amoebal, and ciliate species as well as bacterial plate counts in crude oil contaminated soil cores (compiled from Rogerson & Berger, 1981c)

Treatment[1]	Sampling occasion (Nov. 1979–April 1980)								$\bar{x}$ of species number[2]	$\bar{x}$ of bacterial counts ($\times 10^6$)
	1	2	3	4	5	6	7	8		
A	31	35	30	28	17	18	22	23	25	9.4
B	24	31	27	26	25	17	20	23	24	9.8
C	26	24	19	25	28	16	19	21	22	21.6
D	13	16	19	23	20	11	12	16	16	40.1
E	15	15	20	15	13	14	12	10	14	58.4

[1]The sampling areas, except control (A), were delineated with plastic tubes.
A: Undisturbed soil collected randomly from within the study area.
B: Undisturbed soil enclosed within sunken tubes.
C: As treatment B, but initially contaminated with 250 ml Norman Wells crude oil.
D: Presterilized tubes packed with heat sterilized soil.
E: As treatment D, but contaminated with 250 ml crude oil.
[2]Species richness was studied by cultivating protozoa from 0.5 g of soil in Petri dishes containing a layer of 2% nonnutrient agar and 20 ml sterile distilled water. Amoebae were cultured on 1.5% Cerophyl-Prescott agar. First sampling occasion was 1 week after oil contamination. No exact data were given for the other sampling occasions.

stress. Furthermore, with the ability of hydrocarbons and lipids to sequester heavy metals and pesticides, the possibility of accumulation via these inclusions could be examined.

12. *Effects of radiation.* Some of the most common soil and moss ciliates, the spathidids and colpodids, show an unusual sensitivity to X-rays. The LD_{50} of a species of *Spathidium* is 46 kr (kiloroentgen) min^{-1}, whereas it ranges from 150 to 400 kr in many freshwater ciliates and in the soil amoeba '*Amoeba terrestris*' (Meissel & Sifrin; cited in Mavljanova, 1966; Wichterman, 1957; Williams, 1966). Williams (1962, 1966) irradiated *Spathidium spathula* (Figs 216–218) with 0 to 55 kr of X-rays and found numerous physiological (e.g., lengthened generation time) and morphological (e.g., enlargement of macronucleus) changes. The colpodids *Tillina* and *Colpoda* were less sensitive, but reduced survival was evident even at 25 kr (Bridgman & Kimball, 1954; Bridgman & King, 1962). Mavljanova (1966) observed a slightly increased division rate in *Colpoda maupasi* which had been irradiated with γ rays (1 to 10 kr), but its capacity to suppress the plant pathogenic fungi *Rhizoctonia solani* was markedly reduced (Table 5). *Azotobacter* mineralized 20–70% more nitrogen, and cotton seeds showed an increased germination rate in the presence of irradiated (0.5 to 10 kr) *Colpoda maupasi* (Table 5). Mavljanova (1966) suggested that these effects were due to a more rapid release of metabolites by the irradiated *Colpoda* which stimulated the growth of *Azotobacter* and cotton seeds.

The reasons for the high sensitivity of the spathidids and colpodids to radiation is unknown (Williams, 1966). In spite of this, it seems reasonable to use the morphological and physiological changes for bioindicative purposes. Unfortunately, field investigations of naturally and artificially polluted areas are nearly lacking. I could

find only one old report of Fantham (1929), who inspected some soils that were influenced by natural radioactive water. He found very few kinds and numbers of protozoa in these soils. Thus, Fantham (1929) suggested an inhibitory effect of radioactivity to the soil protozoa. Recently, the same has been reported for terrestrial arthropods and earthworms (Krivolutsky *et al.*, 1982).

VI. SUMMARY AND CONCLUSIONS

(1) A 'soil protozoon' is a single-celled eukaryotic organism that lives in the mineral substrate in which vegetation takes root and in and on which dead organic material is found. Much of the described 'moss fauna' probably includes soil protozoa, because samples have been contaminated with soil particles.

(2) Research in most groups of soil protozoa is greatly hindered by the lack of appropriate methods for the estimation of individual and species numbers, as well as by the poor taxonomic standards of many ecologists and systematists. The widely used culture methods for counting the individual numbers yield a rough estimation of the active *and* inactive (cystic) protozoa present in soil, but are inappropriate for a reliable estimation of the active protozoa alone. Direct counting techniques are suggested for the testate amoebae, ciliates, and flagellates. A 'non-flooded petri dish method' is described for the estimation of the species richness of the soil ciliates.

(3) The concept of 'ciliatostasis' is introduced to explain the phenomenon that excystation and growth of ciliates in evolved ('old') natural and cultivated soils are much more limited than would be expected from their behaviour *in vitro*. Evidence and possible causes are discussed. This concept may help to explain the often very low abundance of active ciliates in evolved natural soils, grasslands, and agricultural soils and their high abundance in litters. In contrast, testate amoebae are abundant in litters *and* evolved soils. Thus, these groups exploit different niches in the soil.

(4) Nine ecosystem studies that include the protozoa are reviewed. These investigations show that the microflora account for 91% of the heterotrophic respiration of the soil. Only 9% of the total comes from protozoa and animals, and two-thirds of that respiration is due to the protozoa, although their contribution to the animal standing crop biomass is only ca. 30%. Protozoa respire approximately 10% of the total carbon input. This proportion of the biomass and respiration is significant and represents a challenge for community ecologists who need to give greater recognition of the role of these minute but important organisms.

(5) Some soil protozoa feed selectively on certain bacteria and fungi and secrete metabolites that depress prey growth. This suggests a potential for biological control of soil-borne bacterial and fungal plant diseases. The whole field is so understudied that its potentials and limitations cannot be seriously estimated.

(6) The morphological and physiological adaptations of the soil ciliates and testaceans are described qualitatively and quantitatively and compared with those of similar organisms in freshwaters and marine sand. The most conspicuous environmental adaptations of the soil protozoa are their small size and their universal capability to produce protective resting cysts. These adaptations can be explained by the 'narrowness' of the soil pores and the limited and astatic water conditions of their biotope. The sizes of soil and freshwater populations of the same species are not significantly different. Terrestrial species of a genus are often smaller than the freshwater species. There is no evidence for a specific anaerobic (sapropelic) soil protozoan fauna or for anabiosis (cryptobiosis) of soil protozoa. Many soil protozoa are polyphagous, and approximately 50% of the known soil ciliates feed partly or exclusively

on other soil protozoa. Members of the ciliate family Grossglockneridae inhabit only soils and feed exclusively on fungi and yeasts. Many soil testaceans feed on humus (soil) particles. Other survival strategies of the soil protozoa include adaptation to the specific temperature conditions of their environment and *r*/*K*-selection.

(7) Many soil ciliates are thigmotactic creepers with a reduced ciliature, a flattened and/or worm-like body, and a fragmented macronucleus. These features have produced a soil ciliate community of unique structure, characterized by the high proportion of colpodids and hypotrichs and a strong under-representation of the peritrichs and suctorids, as compared with freshwater ciliate communities. The soil testacean community is characterized by having a high proportion of species with reduced pseudostome (opening of the shell) size, a flattened ventral side, and a globular shape.

(8) The published theories about the origin of the soil protozoa fail to explain all of the known facts. Hence, it is at present questionable from which freshwater biotope the major part of the soil protozoa arose. The term 'terrestrial plankton' is rejected.

(9) About 50% of the species of soil ciliates and testaceans may be considered the result of speciations which have occurred in the soil itself. Two hundred and fifty ciliate species reliably known from soil are listed, together with their biomass, distribution, and degree of association with the soil (autochthonism). In contrast to the testate amoebae, it is not the moisture regime of the biotope which seems to be the determining factor in soil ciliate evolution, but the narrow size of the soil pores and the film-like distribution of the water in the litter and soil. A worm-like shape, smallness, and lateral compression are the most obvious evolutionary and adaptive trends. The tendency of testate amoebae to form hemispherical shells and/or shells with a nearly closed opening (plagiostomy and cryptostomy) is more pronounced the greater is the affinity of the species to the soil. The agamous testaceans were more successful than the ciliates in exploiting the soil, probably due to their ability to establish phenotypically stable modifications if the environmental conditions change.

(10) The distinct existence of a soil ciliate community is evident from the following evidence. (a) Many species, genera, and families are known from soil and moss only, indicating a long lasting separate evolution. (b) The species similarity of the soil and freshwater ciliate communities of the same geographical region is very low. (c) The most frequent species in soil and freshwater ciliate communities are different. (d) Species of the Grossglocknerida, found only in soil, have developed a special oral apparatus which enables individuals to utilize the large supply of fungi available in many soils. (e) Transfer experiments show poor survival of freshwater and sewage plant protozoa in soil. Thus, claims of a great similarity between the ciliate faunas of soil, freshwater, sewage, and activated sludge are rejected. Such claims most probably arise from misidentification of species.

(11) All reliable faunistic data suggest a non-cosmopolitan distribution of the soil protozoa. There are at least two distinct geographical zones of distribution, a northern zone, nearly identical to the geological Laurasia, and a southern zone, nearly identical to the geological Gondwana.

(12) Soil protozoa can be used more as bioindicators in natural and human-influenced ecosystems. Changes in their community structure must be of value if one considers their significant contribution to the energy cycle of the soil. It is often possible to relate the occurrence and distribution of certain soil protozoa to certain biotopes and/or soil types. There are at least some clear correlations with soil evolution, type of humus, moisture, and amount of humus and/or organic matter present. The main humus types (mull and mor) can be distinguished by the presence of

certain (indicator) species of testate amoebae and ciliates. The soil ciliate community is referred to as the 'eco-class Colpodetea'. There are three 'eco-orders' within this class, the 'Grossglocknerietalia' (which characterizes soils with low organic turnover), the 'Hypotrichietalia' (which is characteristic for evolved soils with high energy turnover), and the 'Pseudocohnilembetalia', which characterizes saline soils. This classification agrees with that known from the testate amoebae.

(13) Nearly 100 papers have been published that deal with the soil protozoa in human-influenced ecosystems. Most relate to the naked amoebae and zooflagellates. In spite of current methodological problems and the paucity of well designed experimental studies, the following valuable conclusions may be drawn.

(a) Irrigation enhances the growth and production of the testate amoebae. The data for the other groups of soil protozoa are conflicting.

(b) Fire, deforestation, removal of the topsoil, soil compaction, and partial sterilization of the soil cause in most cases a strong reduction of the number of protozoa and pronounced changes in their community structure; either by direct annihilation or by making physical, chemical, and biological changes of the environment.

(c) The available data suggest that the overall effects of different soil cultivation techniques on the soil protozoa are not very great. Organic farming systems produce a higher standing crop of the testate amoebae as compared with conventionally farmed land.

(d) Fertilization (particularly organic and slowly dissolving basic mineral fertilizers) and liming tend to increase the abundance and biomass of the soil protozoa. Acid and quickly dissolving mineral fertilizers sometimes cause a slight depression of the standing crop and changes in the community structure of the soil protozoa. The abundance and species richness of the ciliates and testate amoebae are markedly depressed in strongly acidified soils, but are doubled within a few months if the original pH is restored by liming.

(e) The side-effects of pesticides on soil protozoa have been rather neglected and underestimated. All tested insecticides cause persistent responses, whereas herbicides show tolerable effects.

(f) A taxonomic guide to the soil protozoa, intensified methodological research, and investigations on the protozoa in agricultural soils are pressing requirements. In fact, many conflicting results seem to be caused by misidentification of species and/or inappropriate counting methods. Well-designed experimental microcosms and field studies would perhaps provide new enthusiasm and could help to solve some of the long-lasting problems of soil protozoology.

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No paper or book is included in this bibliography which has not been cited directly in one or more of the preceding chapters: 600 reports are included here, which is only about half of the available literature on soil protozoology. The fields which are most fully covered are the 'reliable' taxonomy of soil ciliates and the literature which concerns 'soil protozoa as bioindicators'. Two hundred and sixty other papers, especially those concerning the interactions between bacteria and protozoa in soil, are covered by the excellent guide of Finlay & Ochsenbein-Gattlen (1982). That and the present guide cover nearly all relevant literature on soil protozoa.

The bulk (77%) of the references below bear post-1960 dates. On the other hand, important monographs and classical papers of past decades are not excluded. Major

sources for the pre-1960 literature, in chronological order, are the reviews and monographs of Koch (1915), Kopeloff & Coleman (1917), Cutler *et al.* (1922), Koffman (1926, 1934), Sandon (1927), Volz (1929, 1951), Varga (1933), Grandori & Grandori (1934), Brodsky (1935), Waksman (1937), Nikolyuk (1956, 1965a), Singh (1960), Kevan (1962), Bonnet (1964), Schönborn (1966a), Viswanath & Pillai (1968), Pussard (1967), Stout & Heal (1967), Heal (1971), Darbyshire & Greaves (1973), Franz (1975b), Coûteaux (1976d), Smith (1978), Geltzer *et al.* (1980a,b), Foissner (1981a), and as already mentioned, Finlay & Ochsenbein-Gattlen (1982).

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