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The diversity and ecological significance of Protozoa

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The unicellular eukaryotes are currently grouped in the kingdom Protista, together with their multicellular relatives. The inclusion of protozoa, algae and water moulds in a single taxon has resulted in nomenclatural problems, academic homelessness, and a reduction in their teaching. There are around 40 000 described protozoan protist species. Protozoa are principally grazers of bacteria, increasing mineralization and making nutrients more available to other organisms; most are aquatic, but they are also widespread animal parasites and symbionts. Their biomass, role in food chains, roles as mutualists and pathogens, and value as biomonitors are reviewed. To assess the role of protozoa in ecosystems more accurately, the current poor taxonomic standards in ecological work on protozoa must be improved. The manpower to respond to existing and new challenges in the field is declining as protozoology disappears from university courses and this problem needs to be addressed.

Keywords: protozoa; protists; species numbers; pathogens; mutualists; biomass; food chains; biomonitors

Introduction: protozoa and protista

Protozoa are the most abundant animals on earth. There are some biologists who would disagree with this statement, not on the question of biomass, but on the question of animality. The definition of protozoa as unicellular eukaryote consumers has always raised eyebrows because some undoubted single-celled eukaryotes are both consumers and producers. What is more, some unicellular consumers are clearly related to groups of organisms which only contain producers or decomposers, or to organisms that are doubtfully unicellular. The current tendency is to mass together the primitive eukaryotes that are mainly unicellular into a kingdom of their own – the Protista (Corliss, 1984) or, to include these and their near multicellular relatives in a larger grouping – the Protoctista (Margulis *et al.*, 1990).

The blending of what were previously protozoa with algae and water moulds (Oomycota) into a single kingdom, has unfortunately precipitated several crises. The first is a series of high level taxonomic and nomenclatural problems (Corliss, 1984). Expansion of our knowledge of protist structure during the renaissance of descriptive cytology that centred around electron microscopy, plus the more recent flowering of interest in molecular phylogeny (especially that based on ribosomal RNA sequences), have provoked radical revision of our views on the evolutionary relationships of different protist groups. It is now clear that the genetic distances within traditional protist groups (e.g. the amoebae) are greater by far than the distances separating fungi, green plants and vertebrates (Schlegel, 1991). Corliss (1984) has proposed the division of the kingdom

Protista into 45 independent phyla. A further problem is what to call these phyla as many protist groups have in the past been given different names by botanists and zoologists.

A second crisis is one of 'academic homelessness' for the protists, especially those previously classed as protozoa. While most university courses in plant biology are happy to include the erstwhile algae, most zoologists are only too happy to exclude protozoa from courses on the animal kingdom, on the grounds that these organisms are no longer part of it. Microbiology has traditionally disowned the protists, despite their microscopic size, because they, and especially the heterotrophic ones, are difficult or impossible to grow in pure culture; their fastidious nutritional requirements and tediously long doubling times discourage all but the most stout hearted from trying.

The third, and most serious crisis is the effect of the first two on the teaching of protist biology, and particularly protist diversity, to future generations. It was possible to tackle protist diversity, even at first year university level when there were basically four protozoan phyla, but even in those universities which still afford the protists a home, how can the most motivated student be expected to cope with 45 phyla?

The outcome of these three crises could be a withering of interest, lack of recruitment, and possible extinction of authorities who know one protist from another. Yet much remains to be done. Our knowledge of protist diversity is still in its infancy as is our understanding of its significance. At present the protistologist has more cause to worry over the extinction of his own kind than over the conservation of protists!

The extent of biodiversity

In discussing the extent of diversity of protozoan protists in terms of numbers of described species, one has to bear in mind that the species concept, based on the gene pool in sexually-reproducing higher eukaryotes, has only limited relevance to protists because, in many flagellates and amoeboid protists, sexual processes appear to be clandestine, and mating rare – if it occurs at all. The much studied African trypanosomes clearly fall into this category (Vickerman, 1986) for, although evidence for diploidy, meiosis and syngamy in sleeping sickness trypanosomes is good, the relevant gamete stages have not yet been seen (Tait and Turner, 1990). The trypanosome causing Chagas' disease in humans, on the other hand, lacks a sexual process and has probably abandoned sex (Tibayrenc and Ayala, 1991). Many protists, parasitic forms in particular, display within a morphological species variants which differ in phenotypic characteristics other than form (e.g. host range, pathogenicity) linked to genotypic differences. These variants have been accorded their own specific names: amoebae of the genera *Naegleria* (De Jonckheere, 1987) and *Entamoeba* (Garfinkel *et al.*, 1989) provide examples, as also do the trypanosomes (Stevens and Godfrey, 1992). In the overtly sexual ciliates, the occurrence of sibling species is well-documented (Corliss and Daggett, 1983) and large genetic distances may separate the different gene pools ('syngens'), whose members are morphologically identical.

The approximate numbers of named species in the major protozoan protist phyla are given in Table 1. Not represented are groups with less than 500 species.

Among the Protozoa, whole phyla have been created for single organisms or small isolated groups which represent phylogenetic curiosities, e.g. Karyoblastea (1 sp.), Pseudociliata (4 spp.), Hemimastigophorea (1 sp.), Chlorachniophyta (2 spp.). Other

Table 1. Numbers of described extant species of protozoa[a,d]

Phylum	Number of species
Foraminifera[c]	10 000
Ciliophora	8 000
Actinopoda[c] (Heliozoa, radiolarians)	6 000
Sporozoa	5 000
Rhizopoda (including Heterolobosea)	2 500
Dinoflagellata[b] (including Syndinea)	2 000
Myxozoa	1 200
Euglenophyta[b]	1 000
Microsporidia	800
Polymastigota (Metamonadea, Parabasalia)	750
Eumycetozoa	700
Chrysophyta[b]	650
Xanthophyta[b]	650
Kinetoplastida	600
Haptophyta[b]	500

[a] Groups with more than 500 species only. Green, brown and red algae (included by some in Protista) have been excluded, as have diatoms. With the exception of Volvocales and Prasinophyta these algal groups were traditionally not included in the Protozoa.

[b] 'Algal' groups traditionally included among protozoa.

[c] Excluding the vast numbers of fossil species insofar as this is possible.

[d] See Corliss (1984) for sources of literature.

groups with more substantial but still modest numbers of species include the Plasmodiophorea (40 spp.), Heterolobosea (amoeboflagellates; 40 spp.), Xenophyophorea (10–12 spp.), Bicosoecida (30–40 spp.), Opalinata (200 spp.), Labyrinthomorpha (36 spp.) and Haplosporidia (25 sp.).

The above numbers, totalling over 40 000 species, represent a conservative estimate. Several groups of small heterotrophic flagellates have been excluded from consideration, for want of formal studies on their diversity, yet their importance as consumers in both terrestrial and aquatic environments is now undeniable (Patterson and Larsen, 1991). Such organisms include the *Cercomonadidae*, *Thaumatomonadidae*, *Amastigomonadidae*, *Phalansteriidae*, and a rabble of isolated genera of uncertain relation to any established taxonomic group. The small, naked amoebae, another important group of bacterial consumers, may have a diversity ten times that currently attributed to them and shortage of students of this diversity is a serious problem for ecologists.

The ecological significance of protozoa

Free-living protozoa occur in most aquatic habitats, freshwater or marine, in plankton, benthos and interstitial habitats. In addition they are widespread as parasites and symbionts of animals, and to a lesser extent of plants. Their principle ecological role is as grazers of bacteria, increasing mineralization of nutrients and thus making them more available to primary producers. Their role in nutrient recycling is out of proportion to their biomass. For a detailed treatment of protozoan ecology see Fenchel (1986).

Biomass

There are scattered estimates of 'protozoan' biomass in the literature, though these may not be very meaningful as it is not always obvious what is being referred to as protozoa. Bak and Niewland (1989) estimated that benthic protist biomass in the Wadden Sea ranges from 24.5–91.4 × 10^{-3} g cm^{-2} and is small compared with bacterial (10–15 g cm^{-2}, meiofaunal (0.45 g cm^{-2}) and macrofaunal (10 g cm^{-2}) standing crops. In soils, protozoa contribute about 30% to the standing crop biomass (cf. arthropods 31%, worms 38%), but nearly 70% of the total animal respiration (Foissner, 1987). Grant and Schwinghamer (1987), measuring the contribution of nanoflagellates to total community metabolism in sand-shelf sediments in Nova Scotia found nanoflagellate biomass averaged 16.1 × 10^{-3} g cm^{-2} over 25% of community biomass, and nearly 27% (148.5 μl) of O_2m^{-2} h^{-1} of total microbial and meiofaunal community respiration. At the other extreme, the giant (up to 2.5 cm across) fragile testate rhizopods known as xenophyophores and large komokiacean foraminiferans, which are suspension feeders in the oligotrophic ocean abyss and are 'calorific dwarfs'. Although they may comprise up to 97% of the total benthic biomass in the South Pacific (Vinogradova *et al.*, 1978), much of the Xenophyophore body mass is composed of elaborate skeletal structures and stercomata (faecal pellets), so their dry weight is not comparable to that of other animals. They have, moreover, slow growth rates and low metabolic requirements. Most protozoa have high weight-specific metabolic rates relative to larger organisms (Fenchel and Finlay, 1983).

Some of the most detailed studies on biomass with respect to specific protozoa have been conducted on the planktonic choanoflagellates, which may account for as much as 50% of the heterotrophic flagellate fauna in marine plankton samples. Identification of these organisms (especially the 70 species of Acanthoecidae which have complex siliceous skeletons) is easier than identification of most heterotrophic nanoflagellates and their biomass has been followed on a seasonal basis in Californian waters (Buck *et al.*, 1991). Choanoflagellate biomass was found to comprise approximately 12% total heterotrophic biomass and calculated to clear between 0.1 and 180% of the water column per day.

Food chains and nutrient recycling

Phagotrophic protozoa are capable of consuming large amounts of prey on a daily basis, often several times their own body weight. The smallest heterotrophic flagellates are perhaps surpassed only by the heterotrophic bacteria in the rate at which they can process food material. The fate of biomass ingested by phagotrophic protozoa is an area of active research in microbial ecology (Berninger *et al.*, 1991) especially in aquatic ecosystems. For further details see the symposium fronted by Graham (1991).

On average, 60% of the primary production of aquatic communities may enter microbial food webs (Cole *et al.*, 1988). In the so-called 'microbial loop' (Pomeroy, 1974), dissolved organic carbon released from primary producers, and at all stages along the consumer food chain, is utilized by heterotrophic bacteria. These bacteria are grazed by nanoflagellates (e.g. choanoflagellates, chrysophytes, kinetoplastids) which, in turn, fall prey to larger flagellates (e.g. euglenophytes, ebriids, dinoflagellates) actinopods or ciliates, which in turn are consumed by animal predators, thus re-entering the classical phytoplankton-zooplankton-fish food chain. Many planktonic protozoa are herbivorous, carnivorous or omnivorous and can ingest prey as large as, or even larger than, themselves (Patterson and Larsen, 1991). Grazing by protozoa directly on photosynthetic organisms is particularly important where small ($>5\ \mu m$) algae and cyanobacteria dominate the phytoplankton biomass. Larger food webs result in greater loss of energy as respiration than shorter ones (Berninger *et al.*, 1991).

Protozoa have relatively high gross growth efficiencies (values of 40–50% are common) but also release a significant fraction of their ingested nutrients in remineralized form as NH_4^+ or PO_4^{3-}. The weight specific nutrient excretion rates for small flagellates are among the highest encountered for eukaryotes (Caron and Goldman, 1990). For further discussion of protozoa in planktonic food webs, see Porter *et al.* (1985).

In the soil, also, protozoa are important in re-mineralization and return of nutrients to plants. Here too, protozoa are most active as bacterial grazers, especially the small amoebae, heterotrophic flagellates and ciliates. Ciliates form an important source of food for earthworms (Bamforth, 1975; Foissner, 1987). The rhizosphere around growing plant roots is particularly rich in protozoa because organic matter secreted as a carbohydrate-rich gel at root tips and disintegrating root surface cells provides a source of food for bacteria which are in turn grazed by protozoa. Ten to twenty per cent of the plant's net photosynthate may pass through its roots into the soil in this way.

Mutualisms

Apart from the vast numbers of protozoa (radiolarians, foraminiferans) or invertebrates (corals, sea anemones, giant clams) which harbour photosynthetic dinoflagellates as symbionts, other mutualistic relationships involve protozoa. Most celebrated are those between higher zooflagellates (Metamonadea, Parabasalia) and wood-eating insects – termites and certain roaches. The insect host relies upon the flagellate symbionts to produce the cellulase which allows it to survive a diet of wood; the mutualism here is obligatory (Cleveland, 1924; Martin, 1991).

More enigmatic is the role of ciliates (orders Trichostomatida and Entodiniomorphida) in the digestion of herbage by ruminant artiodactyls (in the stomach) and perissodactyls (in the caecum). Although defaunation (removal of the ciliate population) experiments suggest that the protozoa are not essential for digestion, there is evidence that they increase digestion of dietary protein, organic matter and fibre in the rumen, though net microbial synthesis and the flow of protein to the lower digestive tract may be reduced by their presence (Williams, 1991).

In recent years the fascinating mutualistic relations between protozoa and prokaryote symbionts have received increasing attention. It appears that some ciliates farm their appended bacteria, transporting them to favourable environments, and ingesting some of them to provide a source of food: a well documented example is the interstitial marine ciliate *Kentrophoros* which farms an H_2S utilizing photosynthetic sulphur bacterium (Fenchel and Finlay, 1989). Protozoa (especially ciliates) from anoxic habitats (e.g. aquatic sediments, sewage tanks and landfill sites) frequently harbour methanogenic bacteria (Fenchel and Finlay, 1991), providing the methanogens with substrates so that they reach much higher intracellular densities than they can achieve in the world outside. Such protozoa, therefore, play an important role in methanogenesis, as do the ruminant and termite symbionts mentioned above.

A surprising finding has been the ability of phagotrophic ciliates (tintinnids, oligotrichs) to take over the chloroplasts of their algal food as functioning organelles

(Stoecker *et al.*, 1987), and so become primary producers. As, at times, the biomass of ciliates is equivalent to the biomass of the larger zooplankton (Smetacek, 1981) such primary production is far from being insignificant. Protozoa have contributed much to our understanding of the evolution of organelles from symbionts, and new consortia of protozoa with other protists and prokaryotes are constantly being discovered.

Parasitism and pathogenicity

As parasites, protozoa are better known than their free-living counterparts, especially those causing disease in humans and domestic animals. Whole phyla (Sporozoa, Microsporidia, Myxozoa, Haplosporidia, Opalinata, Syndinea) are composed of parasitic forms while others (Parabasalia, Metamonadea) are predominantly parasites. The majority parasitize animals and give rise to no discernible disease; patent pathogenicity is the exception. Plants are rarely host to parasitic protozoa, but the Plasmodiophorea (causing disease in the roots of angiosperms) and kinetoplastids of the genus *Phytomonas*, provide exceptions. The latter are found as harmless inhabitants of latex of numerous dicotyledons but in the phloem seive tubes of coffee and coconut or oil palms they cause a fatal wilt (Dollet, 1984).

Major agents of disease in man are species of trypanosomes (causing sleeping sickness or Chagas' disease) and *Leishmania* (Kala azar, oriental sore, espundia) of the Kinetoplastida; *Giardia* and *Trichomonas* of the Metamonadea and Parabasalia; *Plasmodium* (malaria), *Toxoplasma* and *Cryptosporidium* of the Sporozoa; *Entamoeba* (amoebiasis), *Naegleria* (amoebic meningoencephalitis) and *Acanthamoeba* (amoebic encephalitis; keratitis of the cornea) of the Rhizopoda. In domestic animals trypanosomes, coccidians (Sporozoa) and piroplasms (Sporozoa) are important agents of disease (Kreier, 1977).

Protozoa are coming to light as agents of epidemic disease in food molluscs and crustaceans (e.g. the sporozoan *Bonhamia* in oysters and syndinean dinoflagellates in crustaceans; Myers, 1990).

Protozoa are abundant parasites of insects, including some pests, and their role in controlling insect populations is largely to be explored. However, the Microsporidia may prove of value in biological control of such pests, (Canning, 1982).

Biomonitoring

Protozoa have long been used as indicators of water quality; their optimal requirements for growth are met within certain concentration limits of oxygen, CO_2, NH_4^+, NO_3^- and other ions. Ciliates, in particular, have been used as indicators of dissolved oxygen content (Bick, 1972). For a discussion of biomonitoring see Phillipson (1983).

Protozoa have also been used as indicators in soil characterization and humus type differentiation and in human-influenced ecosystems (e.g. irrigation, fire, deforestation, top-soil removal, fertilizer or pesticide regimes, acid rain, sewage disposal, oil pollution). Testate amoebae have even found a use in criminology and gastronomy (detection of truffle soils!). Further details and references are given in Foissner (1987).

Climatic change

Free-living protozoa, such as bacterial grazers, are often assumed to be distributed widely on a geographical basis, but this assumption needs better evidence to support it. The effect of global warming on free-living protozoa is difficult to assess, but in the case of parasites a marked redistribution of hosts, especially insect vectors might be expected.

The contribution of protozoa to the generation of methane, an important greenhouse gas, has already been mentioned.

Concluding remarks

To assess the role of protozoa in natural ecosystems, we need better methods of estimating individual and species numbers and a better knowledge of the diversity of these organisms. The current poor taxonomic standards in ecological work on protozoa must be improved.

It is difficult to see who is going to do this, as funding is not available for training young people; grant provision for taxonomic research in protozoology is virtually non-existant. There is also the added difficulty of attracting recruits to the field, when protozoology is disappearing from university courses; the overwhelming chaos of current protozoan taxonomy does not help.

Undoubtedly new challenges will arise as environments change, protozoa previously insignificant in their known ecological context may suddenly become important in a new context. The AIDs pandemic has thrown into prominence previously obscure protozoan parasites; pollution may well do the same for free-living protozoa. Who will respond to these challenges? They should not go unanswered.

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