Protozoan Diversity and Biogeography

Secondary article

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Over 100 000 protozoa have been named. Many are associated with particular types of habitats and there is a growing view that many protozoa can be found in those habitats anywhere in the world.

The Ubiquity of Protozoa

Protozoa are often said to be ubiquitous. Probably, statements like these are intended to suggest that any aqueous habitat has the potential of harbouring one or more species of this arbitrary grouping of eukaryotic microorganisms. Hence, protozoa may be found in all ocean habitats, ice and snow, freshwater, plant fluids and animal juices, terrestrial and even endolithic habitats in which free water may be present at some time. As many protozoa may form cysts or can dry out (i.e. are cryptobiotic) and come back to life when rewetted, free water does not have to be present at all times for protozoa to be present.

Statements of ubiquity should not be taken to mean that the same species can be found in all habitats. As with larger organisms, most species have habitat preferences. The clearest examples are those protozoa that use other organisms as their habitats. Many of these parasites occur in only one species of host. Some major groups of protozoa occur only in marine habitats – these include the foraminifera, the Acantharea, Polycystinea and Phaeodarea (the latter three collectively referred to as the radiolaria). Other species tolerate a remarkably wide range of habitats (the flagellate *Rhynchomonas nasuta* has been found in oceanic and coastal marine habitats in northern and southern hemispheres, in polar, temperate and equatorial locations, in deep oceans and saturated salt, in freshwater, terrestrial ecosystems and in anoxic conditions). Generally, the majority of species prefer marine or freshwater habitats, oxic or anoxic conditions, and have certain food preferences. See also 'Adaptations', below.

The term 'protozoa' now has a number of meanings. The term does not meet contemporary criteria for definitions of taxa (i.e. the group is not guaranteed to be monophyletic or holophyletic). However, it can still be used in its traditional form – which is to refer to eukaryotes that are usually unicellular, are not plants or animals, and do not have chloroplasts (but may have symbiotic algae capable of photosynthesis). Traditionally they have been placed in one of several adaptive groups – the ciliates, amoebae, flagellates and sporozoa.

Habitat types

The habitats of protozoa have generally not been well characterized. A habitat is here considered as a physical locality that can be occupied by protozoa. Individual species occupy a habitat or niche that is defined by an unspecified number of protist-perceptible parameters. The greatest distinction among habitats is between those habitats that are other organisms (i.e. these habitats are occupied by parasites) and the habitats that are more easily defined by reference to the physical world and occupied by free-living protozoa. Even these two categories are not clear-cut. Some very common free-living organisms can be facultative parasites in humans; other organisms may be pathogenic at one stage of their life, but not at another.

Parasitism usually refers to an association that benefits one partner (the parasite) but harms the other partner (the host). Meeting the challenge of living in or on another organism, and resisting its defences, is expected to be achieved through the evolution of a variety of specializations. However, in some cases, the association seems to be entirely fortuitous. Amoebae of the genus *Naegleria* are common in soils and freshwaters, but some species have the capacity to infect humans, penetrating the central nervous system through the nose, and consuming the brain. It is, however, more usual for parasites to be well adapted to the biology of their host. They often have phases in their life cycles, which seem to serve particular objectives – such as multiplication, transmission between hosts or sexual interaction. Some suggest that for each species of animal (or plant) we should expect at least one species of parasitic protozoon. Of possible vertebrate hosts investigated, about 25% have been infected with protozoa, but most hosts may have many species actually or potentially living inside them. Although some parasites are associated with over 100 species of host animals, others are restricted to a single species of host. Rough estimates suggest that there may be as many as half a million species of parasitic protozoa, but only about 10 000 species of parasitic protozoa have been described.

Parasitic protozoa have successfully exploited, as hosts, vertebrate and invertebrate animals, algae, plants and indeed other protozoa. The results of the infection may be relatively innocuous – as is usually the case with infection of people by the widespread and water-borne flagellate *Giardia* or the sporozoon *Cryptosporidium*. Other protozoa have had an impact so great that they have moulded the social and economic destinies of countries. The trypanosomes which cause sleeping sickness (a blood disease) have determined how and where people live. Over 500 000 000 people are at risk each year of being infected with *Plasmodium* – the causative agent of malaria. With annual infections counted in millions, malaria remains the cause of more human deaths than any other infectious disorder.

Other protozoa have a more benign coexistence with other organisms. Many herbivores – such as cattle or termites – harbour communities of protozoa within their guts. Some protozoan endosymbionts, such as the opaline *Zelleriella antilliensis*, are known to accompany their host (the cane toad, *Bufo marinus*) throughout the range of its host, including those locations to which the host has been introduced in a misguided attempt to control pests of sugar cane. If forced to generalize, it is best to regard parasitic protozoa as occupying narrowly defined niches, and that their geographic distribution is determined by the range of their niche – their host.

The term ‘free-living’ means something slightly different when used in reference to protozoa than to bacteria. ‘Free-living’ bacteria are those that can swim freely, while ‘free-living’ protozoa are species that do not form an association with other species. Free-living protozoa are usually grouped for convenience into those that occur in marine habitats, those from freshwater habitats, those from soils, and those that are often regarded as ‘extreme’ because they are at the ‘extreme’ ends of the tolerance range of most species. Extreme habitats include black muds which are totally devoid of oxygen, or saturated salt solutions. Extreme habitats currently excite considerable interest as they may be analogous to the habitats in which life first evolved, and the organisms which occupy these habitats may have stories to tell us about what early life was like.

In the more normal range of habitats, the marine habitats are home to some types of protozoa not found elsewhere. The most obvious of these are the large marine amoebae (the foraminifera and the radiolaria), but also includes some members of other types of protozoa – the collar-flagellates (choanoflagellates) with siliceous loricas are only found in marine habitats while the naked species or ones with organic loricas are to be found in freshwater habitats as well; the oligotrich ciliates with loricas – the tintinnids – are also almost totally associated with marine habitats. For the majority of groups, representatives are to be found in freshwater and marine habitats. Terrestrial habitats are probably best considered as a special type of freshwater habitat. The thin layer of water which coats soil particles or fills the pores is an ion-rich freshwater, but the habitat is special because it is prone to drying up, because it may be flooded (leading to the loss of oxygen), and because the thin film of water may require physical adaptations to avoid damage from surface tension. Organisms that live here often have physical protection (the testate amoebae), or can easily form cysts, or like heterolobose amoebae, can transform quickly from amoebae to flagellates.

Adaptations

The occurrence of protozoa in any habitat is only made possible by having a morphology, physiology and life history that allow them to survive. Some facets of the life history or physiology have been rationalized by arguments that they ‘adapt’ organisms to their habitats. As an illustration, free-living protozoa, especially those from soils or ephemeral aquatic habitats (e.g. billabongs or other ponds), are at a high risk of desiccation. Although a few species are believed to be capable of completely drying out and surviving, most species will be killed by drought. Many soil dwelling protozoa can change into almost inactive forms that are surrounded by a desiccation-resistant wall – that is, they become encysted. Because some cells develop into cysts, so a population will survive drought, and indeed may be distributed widely in this form by wind. Not all cysts are desiccation resistant; others are produced under different conditions – such as the lack of food – but still secure the survival of the individual. The resilient spores that are included in the life history of many parasitic protozoa can be thought of as cysts which allow passage from one host to another.

Virtually every freshwater protozoon contains contractile vacuoles. By virtue of their nature (single cells that ingest particles of food), protozoa must have at least one part of their body surface that is naked. Consequently, water will be drawn into the cell by osmosis, and some devices must be present to offset this flux. The contractile vacuole is part of a volume regulatory homeostatic device, serving to accumulate fluid from the cytoplasm and periodically expel it from the cell.

The concept of adaptations has been extended to aspects of the sexual life history of ciliates. Ciliates have genders (mating types). After a bout of sexual activity (conjugation) there is a delay before ciliates can mate again, and this is followed by a sexually competent period. After this, ciliates decline into sexual senescence if conjugation does not occur within a critical period; many ciliates become unable to undergo any further sex. The number of genders varies from 2 to over 70, as the phases of the sexual competency require a specified number of fissions to take place and this may require periods from hours to weeks (or longer). Efforts have been made to rationalize these differences in the context of breeding strategies. Some species are said to seek strangers as mating partners in order to promote sexual diversity, others seem to be adapted to mate with close relatives and protect a genome that is successful.

Organs of motility are appropriate to the habitat occupied – flagella and cilia are used to assist in the movement of cells through aqueous habitats or in moving water so that protozoa may extract food from it whereas pseudopodia are usually of advantage to organisms that live within or against solid substrates. Protozoa have food preferences: some eat bacteria and other small particles in suspension, others ingest large lumps of food. Each food type requires a different design of the ingestion devices. Those species that eat suspended bacteria typically have some type of propellor which drives water and suspended food towards a capture device. Those that are predators must have various killing and/or harpooning structures – typically explosive 'extrusomes' around the mouth. Finally, those that eat large lumps of food must have strong jaws with which they can manipulate particles of food into their mouths.

Adaptations are not only morphological. Generally, the physiological tolerances of protozoa as a group are greater than the tolerances of animals or plants – but not quite as great as those of bacteria. Some individual species can live in a remarkably diverse array of habitats – the example of the flagellate *Rhynchomonas nasuta* is given above. Protozoa with broad physiological tolerances will tend not to perceive as many barriers as multicellular organisms to their distribution and may be expected to occupy more extensive habitats.

Abundance

The abundance of protozoa in natural habitats is spectacular. Heterotrophic flagellates are now regarded as the principal consumers of bacteria in aquatic habitats. Typically, flagellates may occur at concentrations of about 10^2–10^5 cells mL^{-1} and the total amount worldwide has been estimated to be in the region of about 10 000 000 tonnes. Amoebae are often found in terrestrial habitats and comparable numbers have been estimated for them. Where studies have been carried out, the contribution of protozoa to respiration in terrestrial habitats exceeds that of invertebrate animals. Larger protozoa are less abundant than smaller ones, ciliates of natural aquatic ecosystems tend to be one thousand times less abundant than the smaller flagellates, while the larger shelled amoebae and marine amoebae are almost as rare as small invertebrate animals.

In considering abundance, it is useful to consider concepts of weeds and specialists. Weeds are those organisms that are found in a very high proportion of samples. They are often organisms with catholic feeding tastes, frequently consuming bacteria in suspension or attached to the substrate. They have broad physiological tolerances, and high rates of growth. Among the flagellates, the weeds include species in the genera *Amastigomonas*, *Ancyromonas*, *Bodo*, *Cafeteria* and *Rhynchomonas*. Among the ciliates, *Tetrahymena*, *Colpidium*, *Cinetochilum*, *Euplotes*, *Aspidisca* and *Vorticella* contain species that comply well with the definition of weeds. The larger proportion of species (90%?) occur more rarely. The rarities make up the larger part of the diversity of protozoa, but the lesser part of abundance. Most surveys are relatively superficial and lead to catalogues of weeds. The value of such surveys is therefore questionable.

Biogeography, Cosmopolitanism and Endemism

The concepts of cosmopolitanism and endemism complement that of ubiquity. Biogeography is the discipline of recording and explaining the (large-scale) distribution of organisms in space. In its simplest form, biogeography involves statements about the patterns of geographical distribution. Explanations of the geographic distribution need to refer in part to evolutionary history (both evolutionary diversification which may have led to lineages diversifying in one area but not others, and dispersal by which species are distributed away from their sites of evolutionary origins). Dispersal tends to obscure evolutionary history. A second dimension which may influence large-scale patterns of distribution relates to ecophysiology, habitats and niches. Some species have a restricted distribution not because of their history, but because they appear to have preferences for certain types of habitats (dinoflagellates, radiolaria and foraminifera are all said to contain some species associated with warmer waters, and others associated with cooler conditions. Cosmopolitanism and endemism are concepts that are applied to the distribution of individual species. A cosmopolitan species is one that may be found in its preferred habitats anywhere in the world.

Some argue that individual species of protozoa have a worldwide distribution. The alternative view is that protozoa – like the majority of larger organisms – occupy geographically defined patches (i.e. show endemism). At the moment, the argument for a worldwide distribution is in the ascendancy, but must be interpreted with certain caveats.

Some case histories

Recently, efforts have been made to understand the distribution of free-living heterotrophic flagellates. Over half of the species have been reported from only one geographical location. At first glance, this is suggestive of endemism. Yet, endemism is difficult to prove. The vast bulk of studies have concentrated on habitats in northern Europe and northern America. There has been insufficient effort in many parts of the world to know with confidence that particular protozoa do not occur there. Many species may occur rarely, and will be infrequently encountered and so may not reported even if they occur. Weeds on the other hand tend to be known from worldwide locations – at least in habitats to which they are adapted and are commonly reported. The evidence for cosmopolitanism largely comes from reports of the weeds.

Many marine protozoa are not found in all water bodies, even though these are contiguous. Foraminifera, radiolaria, dinoflagellates or choanoflagellates are known to occur in regions characterized by certain environmental conditions. There are warm-water dinoflagellates and cold-water dinoflagellates; there are species of choanoflagellates from open oceans and others associated with inshore waters – just as much as some other species prefer anoxic sites or estuarine sites. However, some of the marine 'habitats' are large enough to be identifiable in geographic terms. This can confound issues of geographical distribution.

Causes of and questions about cosmopolitanism

Currently, the argument for cosmopolitanism is the prevailing one. Cosmopolitanism occurs when the processes of dispersal overwhelm the processes by which new species emerge. The emergence of new species is usually linked to the isolation of populations which are then liberated to develop a distinctive genetic identity – eventually becoming incompatible with the original population. However, with very high abundances the likelihood of local extinction is improbable. Similarly, protozoa can be carried in the air as cysts, they can be carried in water droplets on the surfaces of moving animals or by meteorological phenomena, and freshwater organisms may be able to move through ground water. Marine protozoa live in contiguous habitats which are unlikely to become isolated. Protozoa invade ponds which have been isolated within days of their creation. Similarly, protozoa exhibit greater ecophysiological tolerances than many larger organisms, again something that will ensure survival and capacity to recolonize vacated habitats. Overall, the sense is that high abundances and easy dispersal will work against the isolation of communities and to cosmopolitanism. Total diversity is a function of local diversity and numbers of niches; cosmopolitanism should mean fewer species.

There is an alternative view. Most of the statements above refer to species that are defined by morphological appearance. These are the morphospecies. Morphospecies in familiar genera of ciliates such as *Paramecium* or *Tetrahymena* are known to occur all over the world. Yet, careful morphological examination and molecular studies have shown that the species defined by their morphological appearance are usually comprised of a number of mutually exclusive interbreeding 'biological species'. In the case of ciliates, these biological species are called 'syngens'. Many of the syngens have a geographically limited distribution. This alerts us to the possibility that as more discriminating concepts of species are developed, so the concept of cosmopolitanism may give way to endemism.

The Diversity of Protozoa

Corliss (1982) estimated that there are about 115 000 species of extant protists of which three-quarters may be included within classifications of protozoa (**Table 1**).

May (1988) has sought to estimate the total number of organisms in the world. He pointed out that there is a relationship between size and numbers of species, such that with every 10-fold decrease in the size of organisms, there is

Table 1 Diversity of protozoa

Name of group	No. of species
Pelobiont amoebae and flagellates	200
Rhizopod amoebae	2500
Foraminiferan amoebae	37 500
Acrasid cellular slime moulds	26
Eumycetozoan slime moulds	550
Hyphochytriomycetes, parasitizing flagellates	25
Flagellates	300
Plasmodiophorids (endoparasitic slime moulds)	36
Labyrinthulid amoebae	36
Actinopod amoebae	7000
Euglenoid flagellates inclusive of some algae	1200
Kinetoplastid flagellates – mostly parasitic	550
Stephanopogon multiflagellated organism	4
Cryptomonad flagellates inclusive of some algae	200
Choanoflagellates	140
Chrysomonad flagellates including some algae	850
Proteromonad parasitic flagellates	10
Metamonad parasitic flagellates	2200
Opalinid parasitic flagellates	400
Apicomplexa (parasitic) sporozoa	4800
Microsporidia (parasitic) sporozoa	800
Haplosporidian (parasitic) sporozoa	30
Dinoflagellates – flagellates including some algae	4200
Ciliates	7500
Myxozoa – sporozoa, derived from Metazoa	875
Total	71 932

a 100-fold increase in the number of species. He noted, however, that there was a considerable shortfall of species in the microbial size range. He envisaged two reasons for this – the first being that there are very few small species. The alternative is that there is a great diversity, but this has not yet been reported because there are not very many taxonomists to describe them – as is suggested by the apparent revelation of considerable undescribed microbial diversity by molecular means.

There have been several recent attempts to assess the accuracy of our current sense of diversity of free-living protozoa – some directed at understanding the diversity of ciliates, and others at understanding the diversity of flagellates. Both approaches concluded that there is not an immense diversity of morphospecies out there. These studies suggest that Corliss' estimates of species numbers is in the right ballpark.

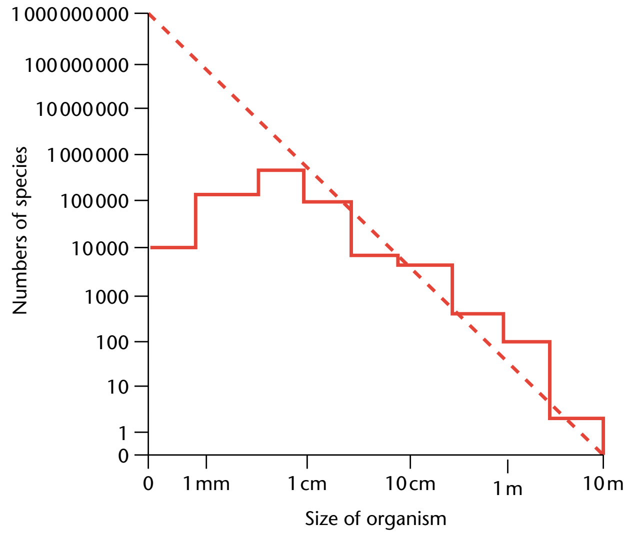

Figure 1 Numbers of species of organisms plotted against size – adapted from May 1988. The scale is the log of the numerical values. The dotted line projects the relationship that appears to exist for the larger organisms to the microorganisms.

Diversity and species concepts

The number of species recognized is very much a function of how one thinks of what a species might be. There are dozens of concepts, but the primary ones are the morphospecies concept and the biological species concept. The latter refers to that community of organisms which do or may interbreed. As many protozoa do not indulge in interbreeding, but reproduce by asexual means, the biological species concept has limited applicability. Morphospecies are distinguished from each other because in one or more aspects they differ (according to the protozoologist) from all other species. Most morphospecies generally seem to have a worldwide distribution. However, within well-studied morphospecies such as *Tetrahymena pyriformis* or *Paramecium aurelia*, there are sexually isolated populations that cannot interbreed and do have a geographically restricted distribution. Morphospecies typically contain more than one molecular identity (i.e. populations with different characteristics of proteins or of sequences of bases in selected parts of the genome). Again, in those cases where the 'molecular species' have been studied (in ciliate genera such as *Tetrahymena*, *Paramecium* or *Euplotes*, dinoflagellates such as *Crypthecodinium* or *Alexandrium*, or amoebae such as *Naegleria*) molecular species often have a more restricted geographic range than morphospecies.

The bottom line is that our concepts of geographic distribution are constrained by our species concepts. The use of more discriminating concepts would almost certainly lead to a stronger sense that protozoan species exhibit endemism.

What determines where species occur?

The primary factors that influence the local and global distributions of protozoa have yet to be resolved. At a local level, a few factors, such as salinity and the amount of oxygen or the reduction/oxidation capacity of the habitat, are principal agents determining the presence or absence of particular species. The abundance of those species is then determined by the available food and the recent history of the habitat such that the presence of preferred foods is also a primary determinant of local abundance.

At the global level, the physical characteristics of habitats come into play – as there are clearly warm- and cold-water communities of foraminifera, dinoflagellates and others. That said, the tendency for (morpho-)species to have a worldwide distribution is the result of a balance between those factors that tend to lead to the emergence of new species and those forces that tend to ensure genetic mixing which prevents new genetic identities becoming established. Speciation is accelerated by a variety of factors – but small isolated populations are likely to have a high rate of speciation. However, the abundance and small size of individuals will tend to prevent the isolation of populations. Because of the small size, protozoa can be easily carried from one place to another on rafts (rafts may include on the bodies of other organisms), or moved around by water currents, or indeed lifted into the air by storms. A site in which a species becomes extinguished can therefore be repopulated easily. Similarly, the physiological tolerances of protozoa ensure that many habitats are actually or potentially contiguous, and again inhibiting the emergence of local populations of endemism.

References

Corliss JO (1982) Numbers of species comprising the phyletic groups assignable to the kingdom protista. *Journal of Protozoology* **29**: 499.

May RM (1988) How many species are there on Earth? *Science* **241**: 1441–1449.

Further Reading

Adlard RD and O'Donoghue PJ (1998) Perspectives on the biodiversity of parasitic protozoa in Australia. *Australian Biologist* **11**: 121–132.

Allsopp D, Colwell RR, Hawksworth DL (eds) (1995) *Microbial Diversity and Ecosystem Function*. Oxford: CAB International.

Berninger U-G, Caron DA, Sanders RW and Finlay BJ (1991) Heterotrophic flagellates of planktonic communities, their characteristics and methods of study. In: Patterson DJ and Larsen J (eds) *The Biology of Free Living Heterotrophic Flagellates*, special vol. 45, pp. 39–56, Oxford: Clarendon.

Fenchel T (1987) *The Ecology of Protozoa*. Madison, WI: Science Tech.

Finlay BJ (1998) The global diversity of protozoa and other small species. *International Journal of Parasitology* **28**: 29–48.

Lee WJ and Patterson DJ (1998) Diversity and geographic distribution of free-living heterotrophic flagellates – analysis by PRIMER. *Protist* **149**: 229–243.

Patterson DJ (1994) Protozoa, evolution and systematics. In: Hausmann K and Hülsmann N (eds) *Progress in Protozoology, Proceedings of the IX International Congress of Protozoology*, pp. 1–14. Stuttgart, Germany: Gustav Fischer.

Patterson DJ (1999) The diversity of eukaryotes. *American Naturalist* **154**: S96–S124.

Patterson DJ and Larsen J (eds) (1991) *The Biology of Free-living Heterotrophic Flagellates*. Oxford: Clarendon Press.

Tyler PA (1996) Endemism in freshwater algae. *Hydrobiologia* **336**: 127–135.