
Review

Dispersal and Biogeography of Protists: Recent Advances

Wilhelm Foissner

Universität Salzburg, FB Organismische Biologie, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria

SUMMARY

This review summarizes recent progress in the debate on distribution of micro-organisms, especially protists. I present three fundamental evidences for restricted distribution of protists, viz., a study on global soil ciliate diversity which shows a “meaningful” distinction of Laurasian and Gondwanan ciliate communities; flagship and vicarious testate amoebae and ciliates which are too conspicuous to be overlooked in Europe, if they were there; and spore-forming cryptogams which show that minute sizes and high abundances do not habitually cause cosmopolitan distribution. Regional and local protist endemism and factors restricting the distribution of micro-organisms are discussed. The most misleading generalizations are a tendency to consider protists as a homogenous group with similar properties and high abundances. Actually, however, protists are highly diverse and most species have low or very low abundances, as obvious from frequency distributions which are

highly similar to those of flowering plants and animals. The data available are consistent with the “moderate endemism model” which suggests about 30% of morphological and/or genetical and/or ecological protist endemics.

INTRODUCTION

The reviews by Foissner (2006), Green and Bohannan (2006) and Martiny et al. (2006) show biogeographic patterns in micro-organisms, disproving the famous metaphor of Beijerinck (1913) and others “that, in micro-organisms, everything is everywhere, the environment selects”. These reviews demonstrate also the two basic research strategies used in biogeographical studies. While Foissner (2006) emphasizes morphological and distributional data, Green and Bohannan (2006) and Martiny et al. (2006) strengthen ecological and molecular studies.

At first glance it appears rather academic whether or not micro-organisms have biogeographies. However, the answer influences several basic theories in biology and ecology, for instance, species diversity and conservation and the influence of historical contingencies (e.g., split of Pangaea) on organ-

Tel: +43(0)662 8044 5615; Fax: +43(0)662 8044 5698

E-mail: Wilhelm.Foissner@sbg.ac.at

(Received: 18 November 2006)

ism distribution.

The cosmopolitan model, now driven mainly by Finlay et al. (1996, 2004), proposes that micro-organisms are ubiquitous and cosmopolitan because their small size and high abundance favour global dispersal and low allopatric speciation. Thus, they have low global but high local diversity as well as high migration and low extinction rates. Finlay et al. (1996, 2004) explain the lack of certain micro-organisms in certain areas as a result of uneven sampling effort and/or misidentification of species. The best demonstration of the cosmopolitan view is found in Finlay and Esteban (1998): "As protozoan species are probably globally ubiquitous, there is every reason to believe that all species of freshwater protozoa could eventually be discovered in one small pond". Such extreme opinion is hardly found in the more recent literature, where most data and authors support a view which I called the "moderate endemism model" (Foissner 1999, 2004, 2006; Foissner et al. 2002; Green and Bohannan 2006; Katz et al. 2005; Martiny et al. 2006; Scheckenbach et al. 2005). The moderate endemism model takes into account the great differences in morphology and ecology of micro-organisms by assuming that about 30% of them are historical (palaeoendemic; split of Pangaea), continental, regional, or local endemics. Further, it suggests that the high rates of local:global diversity are partially caused by our ignorance of the actual global species number needed for the calculation; that global diversity is high because the short generation times and low extinction rates foster diversification by various modes of speciation; and that micro-organisms are not ubiquitous but as precisely adapted as macro-organisms to the environment (Weisse 2004a, b; Weisse et al. 2001).

Although the two models produce pronounced differences, they agree in a fundamental matter, viz., the usually wide and even global distribution of many microbial species, likely due to their small size, the high abundance of euryoecious species,

and the old age. Hopefully, the ongoing research will show the reasons why part of them does not follow this pattern. This and some recent evidences for restricted distribution of protists will be reviewed in the present paper, emphasizing flagship species, community structures, and spore-forming cryptogams as ultimate proofs for protist endemism.

THREE FUNDAMENTAL EVIDENCES FOR PROTIST BIOGEOGRAPHIES

In this chapter, I summarize my most convincing evidences for protist biogeographies: (i) the distribution of soil ciliates, (ii) flagship and vicarious species, and (iii) spore-forming cryptogams. I am still convinced that protist biogeographies must be shown by distinct morphospecies, as in plants and animals, because gene analyses do not tell us how the organisms look like. Frequently, quite dissimilar taxa have highly similar gene sequences (difference 1 % or less in, e.g., the 18S rRNA) and vice versa, that is, genes often do not adequately represent the morphological diversity. Impressive examples are found in ciliates from tank bromeliads (Foissner et al. 2003) and in pond ciliates from Austria and Antarctica (Schmidt et al. 2007).

World soil ciliates

Foissner (1998) and Foissner et al. (2002) investigated ciliates in about 1000 soil samples from all biogeographical regions. Later, unpublished data were added and various statistical analyses were performed (Chao et al. 2006). The similarity cluster resulting from the distribution of the 1136 ciliate species found clearly shows the separation of Laurasia and Gondwana (Fig. 1). This provides convincing statistical support for the influence of historical events on the distribution of soil ciliates. The same has been shown for a flagellate flagship,

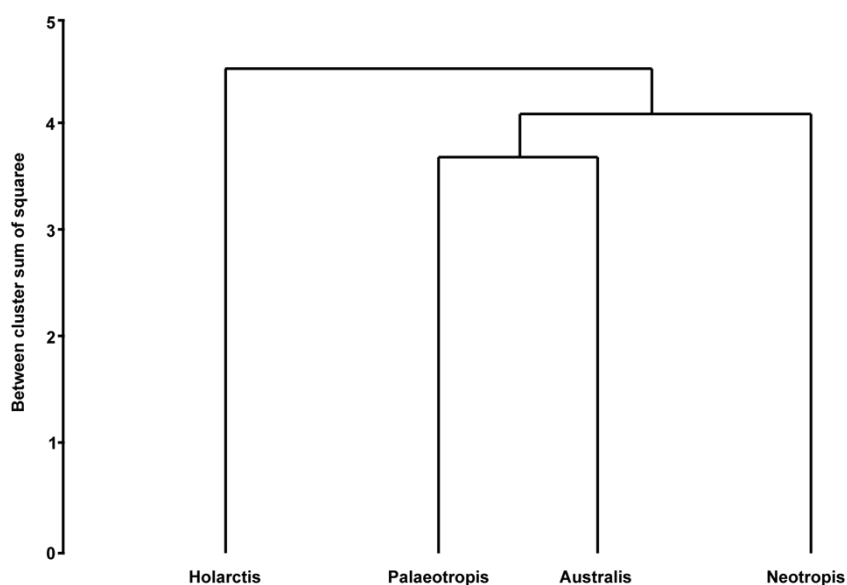


Figure 1. World soil ciliate species cluster based on the classic Jaccard dis-similarity index and Ward's error sum of squares method. From Chao et al. (2006).

viz., *Hemimastix amphikineta* which is fairly common in Gondwana (~ 50 records), while absent from Laurasia (Foissner 2006).

Flagship and vicarious species

Flagship species are the “ultimate” proof of protist endemism (Foissner 2006). However, Finlay et al. (2004) argue that flagship species “is a more-or-less convincing argument for large mammal species, but in case of protists, it evades the crucial question. In many cases we can confidently demonstrate that a large mammal species does not exist outside of its endemic range, but how are we to demonstrate that a protist species does not exist elsewhere in the biosphere? Using typical sampling methods, there is no practical means of doing so, and one is left wondering what the term ‘endemic protist’ actually means”. In my opinion, this argumentation does not hold for scientists working lifelong on a certain taxonomic

group, for instance, Penard, Kahl, Dragesco, Jung, Bonnet, Meisterfeld, and myself. Taxonomists see such species, simply because they stand out like elephants from the mass of other organisms. Further, if the existence of endemic protist species cannot be proven with the methods available, then the opposite is also impossible, showing that the argumentation of Finlay et al. (2004) is a *circulus vitiosus*. I have seen and documented about 2000 ciliate species from habitats globally during the past 40 years (Chao et al. 2006; Foissner 1993; Foissner and Xu 2006, 2007; Foissner et al. 1995, 1999, 2002; Kreutz and Foissner 2006). Most of them, I saw only a few times, and rather many I found only in a certain region.

I put together some of the most impressive protist flagship species previously (Foissner 2006). Since then, several new ones have been discovered or redescribed. They will be briefly discussed in the following paragraphs. Unfortunately, Australia is still almost a *tabula rasa* with respect to ciliates

and testate amoebae. It appears that quite a lot of the large-sized testate amoebae and ciliates are absent from this continent.

Testate amoebae

Testate amoebae provide the most convincing evidences for protists with restricted geographic distribution because the stable test and the rather low diversity fostered faunistic investigations. Foissner (2006) reviewed the biogeographic data, emphasizing species of the *Nebela* family, several of which are Gondwanan relicts, e.g., *Apodera vas* and *Certesella certesi*. Fortunately, testacean research has been increased in Asia, showing the existence of several Asian endemics belonging to the *Diffugia* family (Yang and Shen 2005; Yang et al. 2004, 2005). Many curious testate amoebae, including six new genera and two new families, were recently described from rivers in Western Azerbaijan (Snegovaya and Alekperov 2005). Unfortunately, river testaceans are poorly explored globally, making it impossible to estimate the geographic range of the Azerbaijan species.

Diffugia biwae Kawamura (1918) was originally described from Lake Biwa in Japan, and then has been considered as a local endemic for a long time (Ichise et al. 2004). However, recently it has been found in three lakes of China, viz., Mulan Lake, Poyang Lake, and Qiandao Lake (Yang and Shen 2005). These authors state: “*Diffugia biwae* is probably endemic to East Asia because it has such a large size (165–306 μm) that it would have been easily found in Europe and North America, if it were there”. Indeed, the distinct collar flare and the long aboral horn set apart *D. biwae* from all congeners (Fig. 2).

Diffugia tuberspinifera Hu et al. (1997), as redescribed by Yang et al. (2004), is a highly characteristic species as yet found only in a pond and in a lake of China (Figs 6, 7). It has a moderate size ($\sim 110 \mu\text{m}$), but the conspicuous spines, the

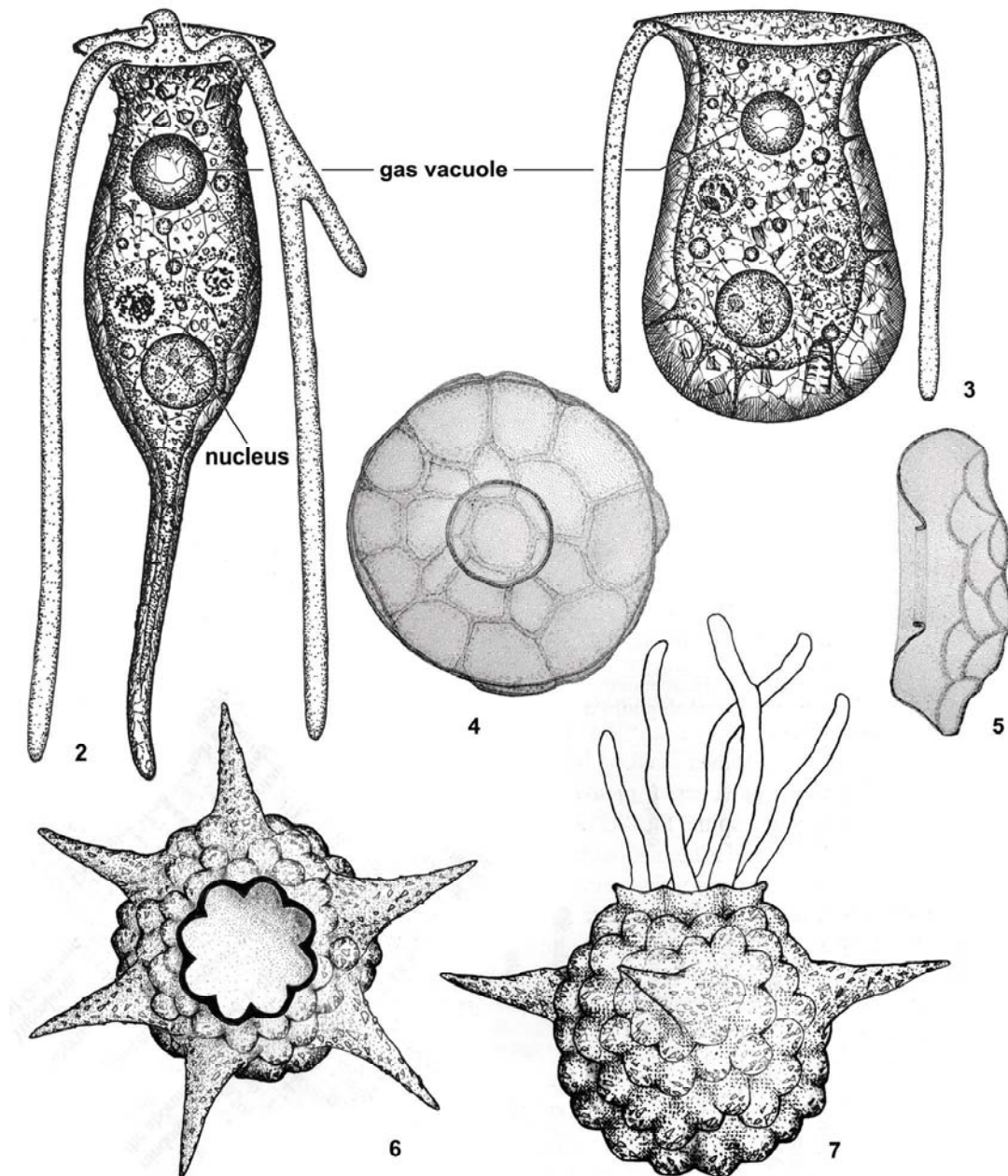
mulberry-shaped wall structure, and the crenate aperture margin make it unmistakable and easy to recognize. Interestingly, this species is abundant, emphasizing the proposed endemism.

Diffugia mulanensis Yang et al. (2005) is another flagship from the oligotrophic Lake Mulan in China. Like *D. tuberspinifera*, it is a middle-sized species ($\sim 110 \times 70 \mu\text{m}$), but the highly characteristic shape, viz., the widely projecting apertural collar makes it easily recognizable (Fig. 3). The authors suggest that “*D. mulanensis* might have a restricted geographical distribution with endemic areas located in East Asia, because it was not found in Europe and North America where numerous investigations of testate amoebae fauna have been made”.

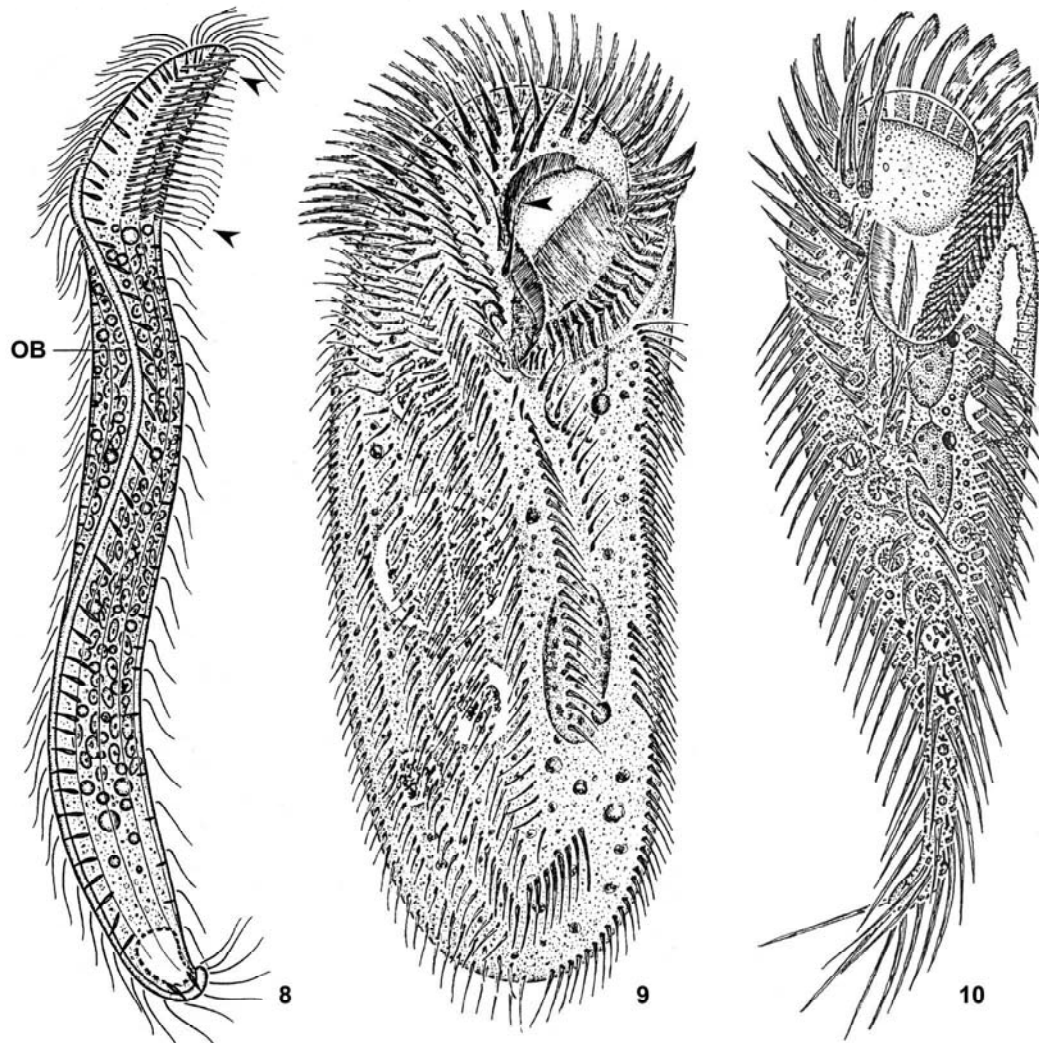
Two other testate amoebae with the capacity to become holarctic endemics are *Arcella formosa* and *Cyclopyxis acmodonta*, both described by Nicholls (2007) from a *Typha*-dominated wetland in Ontario, Canada. Both are $\geq 200 \mu\text{m}$ in size and differ by various morphological features from the congeners (Figs 4, 5). One of these species, viz., *A. formosa* occurs also in Germany (Meisterfeld, pers. comm.). In discussing the geographic distribution, Nicholls (2007) states: “Recognizing that many species of *Arcella* and *Cyclopyxis* were known to science nearly a century ago, if *A. formosa* and *C. acmodonta* were widespread in other habitats on other parts of the world, they should have been detected by others long ago”.

Ciliates

The richly structured ciliates offer good chance to define flagship species very sharply. Indeed, quite a lot are known, most defined by size and/or colour (Chao et al. 2006; Foissner 2006). Here, I report on three recently described species not contained in the studies just cited. Further examples are the vicarious species discussed in the next chapter.



Figures 2–7. Endemic Asian (2, 3, 6, 7) and Holarctic (4, 5) flagship testate amoebae. 2: *Diffflugia biwae*, average length 227 μm . Drawn from data of Yang and Shen (2005). 3: *Diffflugia mulanensis*, average length 109 μm . Drawn from data of Yang et al. (2005). 4, 5: *Arcella formosa*, ventral and lateral view, average diameter 192 μm . From Nicholls (2007). 6, 7: *Diffflugia tuberspinifera*, ventral and lateral view, average diameter 110 μm (without spines). From Yang et al. (2004).



Figures 8–10. Endemic haptorid (8) and stichotrichid (9, 10) flagship ciliates from Africa. 8: *Bryophyllum longisetum* has an average size of $180 \times 20 \mu\text{m}$ and as yet has been found only in soil from the Kilimanjaro Mountains, Central Africa. The arrowheads mark the up to $10 \mu\text{m}$ long bristles of dorsal brush row 3, i.e., one of the most conspicuous features of this species. OB – oral bulge. From Foissner and Lei (2004). 9: *Saudithrix terricola* occurs in soils of Saudi Arabia and China. It is a size flagship ($270 \times 100 \mu\text{m}$ on average) with a highly characteristic, sickle-shaped buccal lip (arrowhead) and ventral cirral pattern. From Berger et al. (2006). 10: *Rigidothrix goiseri* has an average size of $230 \times 70 \mu\text{m}$ and as yet has been found only in soil from the Niger floodplain, West Africa. It is a size and shape (tail!) flagship with a highly distinct organization of body (rigid) and cirral pattern (holostichid). From Foissner and Stoeck (2006).

My estimation that these species have restricted distribution is based on the investigation of over 1000 soil samples collected globally and on over 2000 limnetic samples from Austria and Germany. If these species would have been present in any other sample, I would have recognized them because all are 200 μm or larger.

Bryophyllum longisetum Foissner and Lei (2004) was discovered in soil from a cloud forest on the Kilimanjaro Mountains in Africa, about 2600 m above sea-level. The understory mainly consists of highly conspicuous, tree-like Ericaceae. Thus, this is a very special habitat, suggesting that *B. longisetum* could be a regional endemic. *Bryophyllum longisetum* is a vermiform species with an average size of 180 x 20 μm and a distinctly twisted oral bulge. The most conspicuous features are the vermiform body and the up to 10 μm long bristles of dorsal brush row 3 (Fig. 8). These and other features set widely apart *B. longisetum* from all members of the family Bryophyllidae.

Saudithrix terricola was discovered by Berger et al. (2006) in soil from a vegetable field in the surroundings of the town of Riyadh, Saudi Arabia. With an average size of 270 x 100 μm and a highly characteristic, sickle-shaped buccal lip and cirral pattern it is a flagship with respect to both, size and morphology (Fig. 9). Thus, it was referred to a new genus, *Saudithrix*. Very recently, I found *S. terricola* in soil from the floodplain of the Yangtze River in China, suggesting a palaeotropical distribution. Further, I discovered a second species in soil from the floodplain of the Chobe River in Botswana, Africa.

Rigidothrix goiseri Foissner and Stoeck (2006) was discovered in soil from the Niger floodplain near to the town of Timbuktu, Republic of Mali, West Africa. It has an average size of 230 x 70 μm and a distinct tail, making it easily recognizable (Fig. 10). This ciliate, which belongs to the stichotrichine spirotrichs (hypotrichs s.l.), has so many specific features that it was classified into a

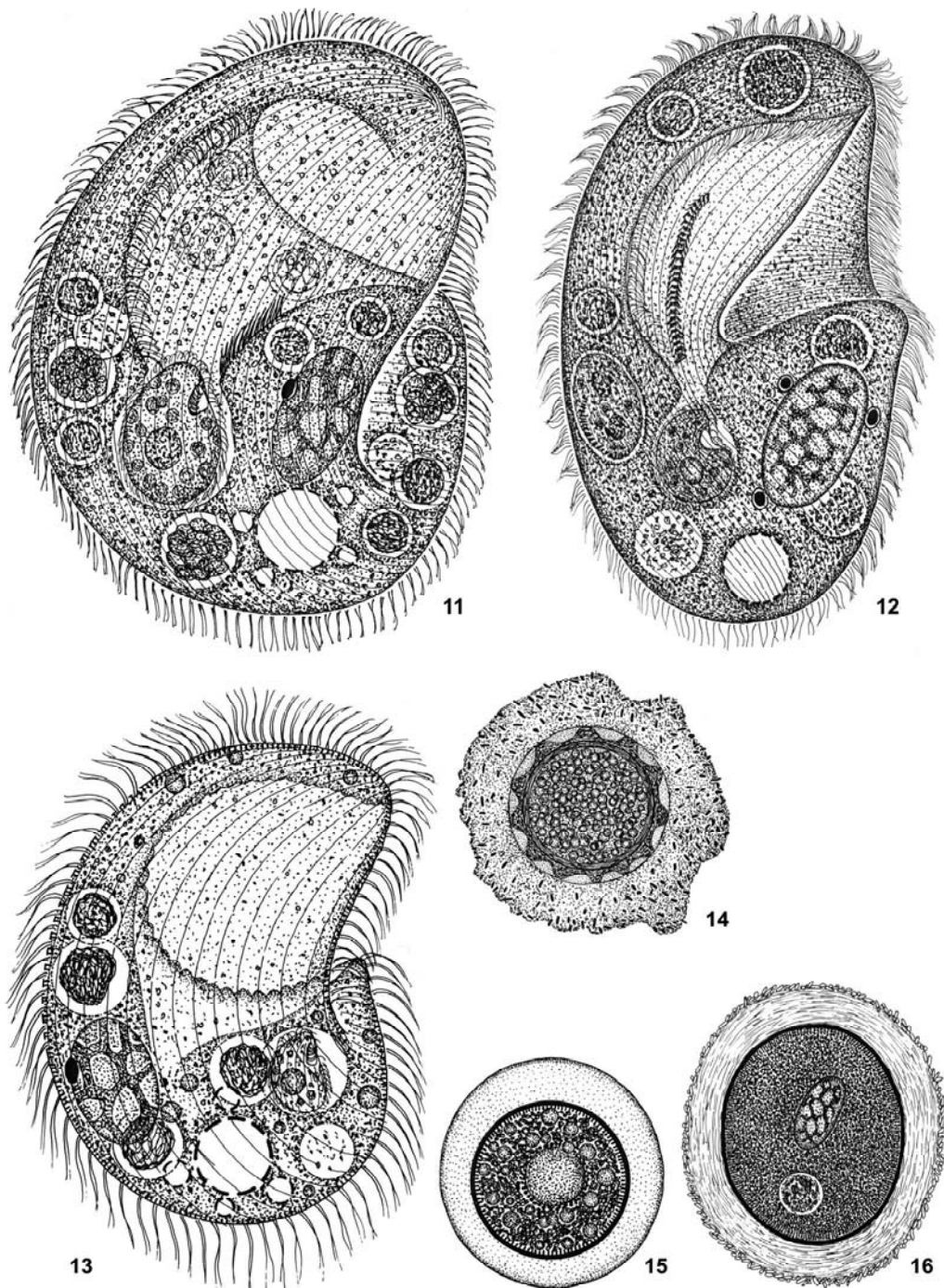
new genus and family, the Rigidotrichidae. Specifically, *R. goiseri* has a rigid body, while the cirral pattern is like that of flexible stichotrichs. Thus, *R. goiseri* breaks the flexibility-dogma in the classification of stichotrichine spirotrichs (Berger 1999).

Vicarious species

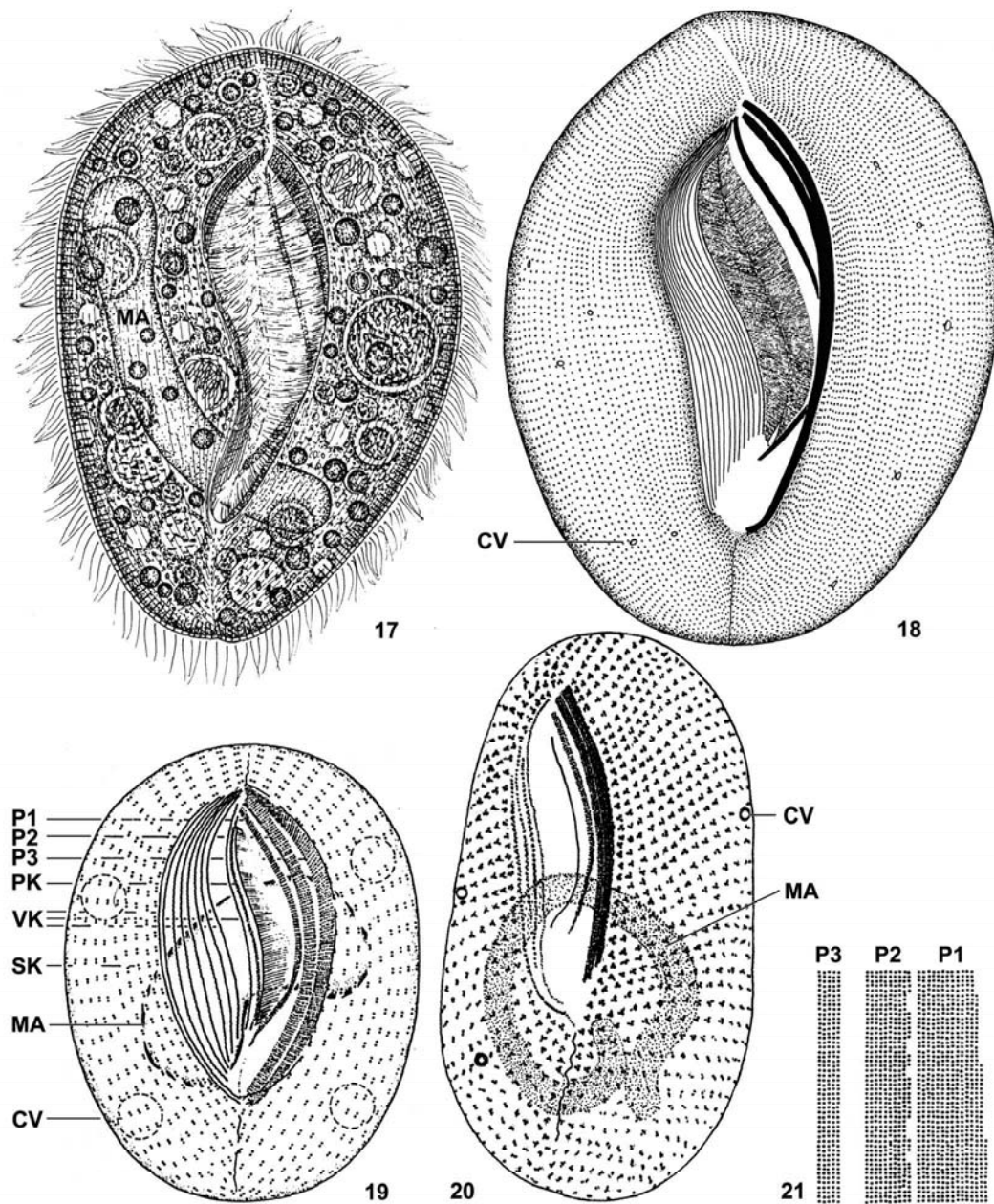
The vicarious model suggests that the components of major biota evolve together and are subject to parallel effects of geographical and climatic fluctuations, and that modern biogeographical distributions result from the division of ancestral biotas by the formation of natural barriers. In other words, vicariants are closely related taxa isolated geographically from one another by a vicariance event, e.g., continental drift (Lincoln et al. 1982). Thus, vicariant species verify by definition restricted geographical distribution.

In protists, the vicariance model has not yet applied, as far as I know, although some impressive examples occur in ciliates and testate amoebae, and likely also in other groups. Here, I shall show some examples from ciliates, while the Nebelidae provide firm evidence in testate amoebae. Likely, the examples mentioned are basically related to continental drift.

The first example is the genus *Kuehneltiella*, which belongs to the class Colpodea (Figs 11–16). Three species are known, all living in astatic, dry environments (Foissner 1993; Foissner et al. 2002). *Kuehneltiella terricola* (size 136 x 100 μm) lives in soil of arid hummock grassland near to the town of Alice Springs, Australia (Figs 11, 14); *K. namibiensis* (180 x 120 μm) was discovered in bark from a *Sterculia africana* tree in Namibia, West Africa (Figs 12, 16); and *K. muscicola* (84 x 63 μm) inhabits alpine mosses at the Austrian-German border in Tyrol (Figs 13, 15). These three species are highly similar, but differ in body size, details of the oral structures and, especially, in the



Figures 11–16. Vicarious species of the colpodid genus *Kuehneltiella*, right side views (11–13) and resting cysts (14–16) in vivo. They differ mainly in body size and resting cyst morphology. 11, 14: *Kuehneltiella terricola* occurs in dry Australian soils and has an average size of 136 x 100 μm . From Foissner (1993). 12, 16: *Kuehneltiella namibiensis*, which was discovered in bark of a tree in Namibia, West Africa, has an average size of 180 x 120 μm , i.e., is a size flagship. From Foissner et al. (2002). 13, 15: *Kuehneltiella muscicola* occurs in German mosses and has an average size of 84 x 63 μm . From Foissner (1993).



Figures 17–21. Vicarious species of the peniculine genus *Apofrontonia*, ventral views in vivo (17) and after silver impregnation to show the complex somatic and oral ciliary pattern (18–21). These species, which are flagships due to the big mouth, differ from each other mainly by morphometric features, such as body size and number of vestibular ciliary rows (Table 1). 17, 18, 21: *Apofrontonia lametschwandneri* occurs in mud from coastline puddles of Venezuela and has an average size of 180 x 120 μm . Figure 21 shows the complex structure of the adoral membranelles (peniculi, P1–P3) recognizable in Fig. 18 as long, black lines at the left mouth margin. From Foissner and Song (2002). 19: *Apofrontonia obtusa* was discovered in a pond of Germany and has an average size of 95 x 75 μm . It has only 4–5 contractile vacuoles (CV), while the congeners have 20 or more. From Song and Wilbert (1989). 20: *Apofrontonia dohrni* occurs in coastline puddles of Italy and has a size of 118 x 61 μm . From Fokin et al. (2006). CV – contractile vacuoles, MA – macronucleus, PK – paroral kinety, P1–P3 – peniculi (adoral membranelles), SK – somatic kineties, VK – vestibular kineties.

Table 1. Comparison of the vicarious species *Apofrontonia lametschwandneri* (*A. lamet.*), *A. dohrni* and *A. obtusa*, based on the original descriptions

Characteristics	<i>A. lamet.</i>	<i>A. dohrni</i>	<i>A. obtusa</i>
Cell size, μm (average of prepared specimens)	180 x 120	118 x 61	95 x 75
Ratio body length:body width	1.3–1.6	1.6–2.0	1.3–1.4
Ratio mouth length:body length	0.75	0.4–0.6	0.5–0.75
Somatic ciliary rows, average number	155	68	90
Vestibular ciliary rows, average number	13	4	9
Contractile vacuoles, average number	29	20	4–5
Habitat	coastline puddles	coastline puddles	freshwater pond
Country	Venezuela	Italy	Germany
Reference	Foissner & Song (2002)	Fokin et al. (2006)	Song & Wilbert (1989)

structure of the resting cyst (Figs 14–16).

The second example is the genus *Apofrontonia*, a relative of the widely known *Paramecium* (Figs 17–21, Table 1). The three species known are fairly similar, but live in slightly different habitats (saline coastline puddles vs. freshwater ponds) and in different geographic regions (Germany, Italy, Venezuela).

Spore-forming cryptogams

With all their theories and complex investigations, microbial biogeographers have forgotten a simple fact of paramount significance (Fig. 22): spores, the dispersal means of macrofungi, lichens, mosses, ferns and horsetails are in the size and abundance range of trophic and cystic protists, suggesting that dispersal is subjected to similar constraints in both groups (Foissner 2006); even some flowering plants, for instance, many orchids have seeds in the size of *Paramecium* (Fig. 22). Further, reproduction of cryptogams is about as simple as in protists, and the abundance of spores is extraordinary: a single *Agaricus campestris* re-

leases 1.6×10^{10} spores with a size of $7\text{--}10 \times 5\text{--}7 \mu\text{m}$ within six days (Webster 1983), which exceeds the abundance of ciliates in a m^2 of forest soil by several orders of magnitude (Meyer et al. 1989).

There is no doubt that many cryptogams have restricted ranges, in spite of their minute and abundant spores, although the areals are usually larger than those of flowering plants and animals, suggesting that minuteness and high abundance of the spores facilitate dispersal, as in micro-organisms (Finlay et al. 2004; Wilkinson 2001). On the other hand, cryptogams make clear that minute size and high abundance do not habitually cause cosmopolitan distribution. Other factors must be involved and will be discussed in the last chapter.

EVIDENCES FOR REGIONAL AND LOCAL PROTIST ENDEMISM

“The existence of endemic morphospecies appears unlikely, since rates of global transport of micro-organisms, although restricted, are too much higher than evolutionary speciation into morpho-

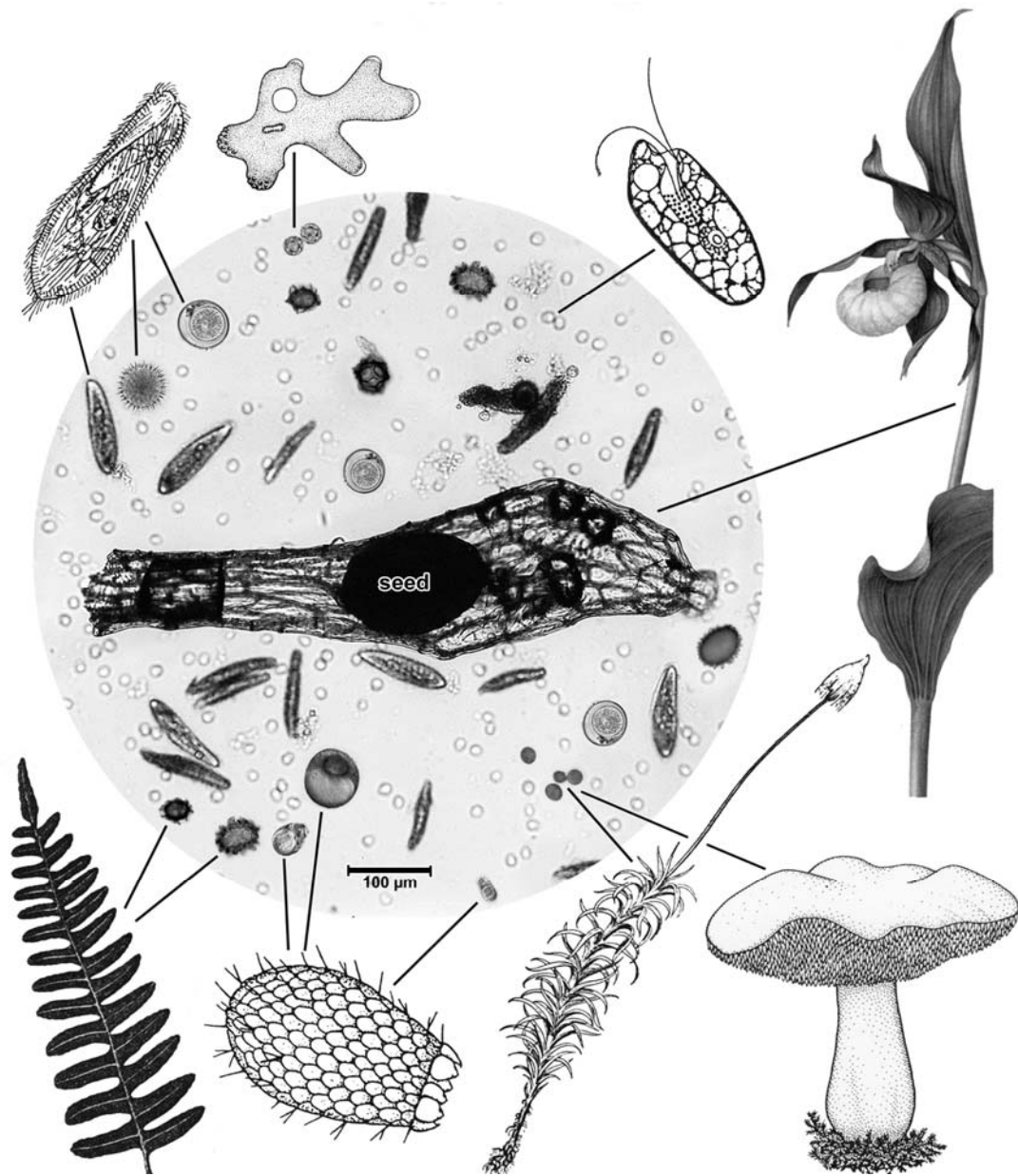


Figure 22. This figure compares, at about the same magnification, trophic and cystic protists (ciliates, flagellates, naked and testate amoebae) with spores of macrofungi (mushrooms), mosses, ferns, and the minute seed of an orchid (*Vanda caerulescens*). Obviously, all are of similar small size and very abundant, for instance, a single *Agaricus campestris* (mushroom) releases 1.6×10^{10} spores within six days (Webster 1983), which exceeds the abundance of ciliates in a m^2 of forest soil by several orders of magnitude (Meyer et al. 1989). While nobody denies that mushrooms, mosses, and ferns have biogeographies, protists are widely assumed to be cosmopolitan because their small size and high abundance (supposedly!) favour air dispersal, an opinion flawed by this figure. Further, protist cysts lack adaptations for air dispersal, while seeds of many flowering plants have such adaptations, including the orchid seed shown which has wings of large-sized, air-filled cells.

logically distinct organisms” (Boenigk et al. 2006). I disagree with such statements for a simple reason: when fish in postglacial and tropical lakes (e.g. Lake Malawi) can produce dozens of distinct species within 15 000 years (Mayr 1963; Schluter 1998), then this likely can occur also in protists, especially, when considering their short generation time and high diversity; further, many postglacial land plants and animals have reached an extent of divergence to be recognized as operational taxonomic units, i.e., morphologically distinguishable subspecies (Mayr 1963; Schluter 1998). Thus, this and similar generalizations by other authors, who assume slow morphological diversification of micro-organisms due to their (supposedly!) high rates of dispersal, would possibly apply only if allopatric speciation would be the sole speciation process. This, however, is not the case (Johnson and Gullberg 1998; Schluter 1998). In protists, local and regional endemism are difficult to prove due to their “invisibility” and the poor state of distribution science. None the less, there are some evidences which will be discussed in the following paragraphs.

In Lake Alatsee, a remote, alpine lake at the German-Austrian border, Stoeck et al. (2007) discovered an *Urocentrum turbo*-like ciliate, differing from the nominal and sole species of the genus by the lack of functional trichocysts. Trichocysts are a highly conspicuous feature, shaping the species’ ecology, physiology and morphology (Harumoto and Miyake 1991; Plattner 2002). Thus, the presence/absence of trichocysts has been widely used by taxonomists to distinguish species within genera. Using this feature, the Alatsee population of *Urocentrum* is a distinct species, although the 18rDNA and the ITS sequences are nearly identical to those of the nominal species.

A very similar case has been reported by Esteban et al. (2000). These authors found a highly distinct species of *Lembadion* in a remote crater-lake of an extinct volcano in Tasmania. Indeed, *L.*

curvatum has such a distinct shape that it can be considered as a flagship species which would have been recognized at least in Europe if it were there.

A further case concerns *Ophrydium versatile*, a peritrich ciliate widely distributed in Eurasia. It makes green (due to symbiotic algae) colonies up to 15 cm across (for a review, see Foissner et al. 1999). In some pre-alpine lakes of Austria occurs another *Ophrydium*, viz., *O. eutrophicum*, differing from *O. versatile* mainly by one distinct feature: it has a much longer adoral ciliary spiral causing a conspicuous cephalisation of the anterior (peristomial) end. All my efforts to find this species elsewhere failed. However, recently it has been reported from a Polish lake (Mieczan 2005). Unfortunately, the author did not respond to my request for material so that I could not check the identification.

A special case represents *Gonostomum albicarpaticum*, a stichotrich (hypotrich s.l.) ciliate recently described by Vd’ačný and Tirjaková (2006). It is only 70 x 22 µm in size, but conspicuous in having four macronucleus nodules, while all congeners possess two or eight nodules. A close relative, *G. affine* has two nodules and is one of the most common soil ciliates globally (Foissner et al. 2002). I never saw the quadrinucleate species in over 1000 soil samples, including many from the region (northern and eastern Austria) *G. albicarpaticum* occurs, suggesting that it could be a local or Carpathian endemic.

The last example comes from a study of Kreutz and Foissner (2006), who investigated and documented 656 species of bacteria, protists, and micro-metazoa occurring in a three hectare-sized moorland in southern Germany. This moorland formed after the last (Würm) ice-age, that is, about 15 000 years ago. Thus, a considerable diversity accumulated during this rather short period. On the other hand, some common species are lacking (e.g., the ciliate *Colpidium colpoda*, the euglenid *Phacus pleuronectes*, and rotifers of the genera

Proales and *Floscularia*) and many undescribed species were discovered. While a mass of undescribed species is comprehensible in amoebas, flagellates and ciliates, which are poorly researched, this is surprising in well-known groups, such as euglenids and chrysophytes. Thus, the authors state: "We must face the possibility that some of the undescribed species are regional or local endemics".

FACTORS LIMITING DISTRIBUTION OF MICRO-ORGANISMS

Most micro-organisms are very fragile in trophic conditions. Thus, it is reasonable to assume that dispersal occurs mainly via the more stable resting cysts. Certainly, there are exceptions, for instance, *Paramecium* which likely lacks a cystic stage, while *Tetrahymena pyriformis* GL, long considered as a cystless ciliate, can make resting cysts under certain conditions (Nilsson 2005). Dispersal by human activities, both in trophic (e.g. ballast water) and cystic form is a second, often forgotten main route (Foissner 2006). When one experiences the masses of European tourists visiting the Titicaca Lake, then it becomes understandable why we find holarctic protists all around the world. None the less, there are still protists with restricted occurrence, and we have to think about the reasons.

(i) Cyst viability is likely much more restricted than widely assumed. Foissner (2006) presented evidences that, e.g., cysts of soil ciliates from rain forests are very unstable, dying under dry conditions within a few months. Likewise, most cysts produced under laboratory conditions do not excyst, either because they are not viable or the right conditions are not found. Certainly, there are a lot of evidences that cysts are transported by air, but very few species have ever been identified, suggesting that most are not viable or need special

conditions to excyst.

(ii) Distinct geographic barriers, such as high mountains, large deserts, and specific water and wind currents. As endemics occur also in the sea (Foissner 2006), such barriers likely exist on land, too. Unfortunately, the barrier hypothesis is difficult to prove for the reasons discussed in the foregoing paragraph.

(iii) Speciation is an ongoing process. Thus, the communities present are a mixture of old and young species, and many of the latter had not yet time to spread globally and, especially, to establish viable populations.

OUTLOOK

Finlay et al. (1996, 2004) and Boenigk et al. (2006) argue that the high abundances and rates of global transport make the existence of endemic protist morphospecies unlikely. While this might apply for some euryoecious species, it is likely incorrect for the mass of micro-organisms most of which are rare or very rare, as in flowering plants and animals. This becomes obvious when frequency distributions or protist counts are studied. For instance, 200 of the 365 species of soil ciliates found in Namibia occurred at only one or two sites (Fig. 23). This has been emphasized also by Green and Bohannan (2006). Basically, the same problem exists with resting cysts. While some species easily encyst and excyst, the mass of species does not. Thus, we must learn to consider micro-organisms as highly individualized entities with very different properties. Then, there will be place also for endemic morphospecies.

ACKNOWLEDGEMENTS

The technical assistance of Kustos Peter Gruber, Mag. Birgit Peukert and Andreas Zankl is

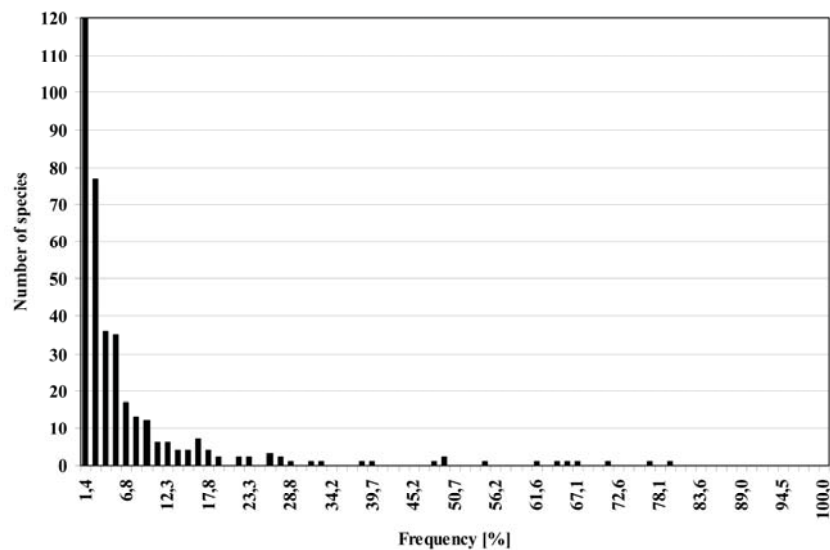


Figure 23. Frequencies of 365 ciliate species in 73 samples from terrestrial habitats of Namibia (from Foissner et al. 2002).

greatly acknowledged. I also gratefully acknowledge financial support by the Austrian Science Foundation (FWF-projects P-15017 and P-16796) and the Japanese Society of Protistologists who invited this review at occasion of a Plenary Lecture given during the annual meeting in Saga city.

REFERENCES

- Beijerinck, M. W. (1913) De infusies en de ontdekking der bacteriën. Jaarboek van de Koninklijke Akademie v. Wetenschappen. Müller, Amsterdam.
- Berger, H. (1999) Monograph of the Oxytrichidae (Ciliophora, Hypotrichia). Monographiae biol 78, i–xii, 1–1080.
- Berger, H., Al-Rasheid, K.A.S and Foissner, W. (2006) Morphology and cell division of *Saudithrix terricola* n. gen., n. sp., a large, stichotrich ciliate from Saudi Arabia. J Eukaryot Microbiol 53, 260–268.
- Boenigk, J., Pfandl, K., Garstecki, T., Harms, H., Novarino, G. and Chatzinotas, A. (2006) Evidence of geographic isolation and signs of endemism within a protistan morphospecies. Appl Environ Microbiol 72, 5159–5164.
- Chao, A., Li, P. C., Agatha, S. and Foissner, W. (2006) A statistical approach to estimate soil ciliate diversity and distribution based on data from five continents. Oikos 114, 479–493.
- Esteban, G. F., Finlay, B. J., Olmo, J. L. and Tyler, P. A. (2000) Ciliated protozoa from a volcanic crater-lake in Victoria, Australia. J Nat Hist 34, 159–189.
- Finlay, B. J. and Esteban, G. F. (1998) Freshwater protozoa: biodiversity and ecological function. Biodiv Conserv 7, 1163–1186.
- Finlay, B. J., Corliss, J. O., Esteban, G., Fenchel, T. (1996) Biodiversity at the microbial level: the number of free-living ciliates in the biosphere. Q Rev Biol 71, 221–237.
- Finlay, B. J., Esteban, G. F. and Fenchel, T. (2004) Protist diversity is different? Protist 155, 15–22.
- Foissner, W. (1993) Colpodea (Ciliophora). Protozoenfauna 4, i–x, 1–798.
- Foissner, W. (1998) An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. Europ J Protistol 34, 195–235.
- Foissner, W. (1999) Protist diversity: estimates of the near-imponderable. Protist 150, 363–368.
- Foissner, W. (2004) Ubiquity and cosmopolitanism of protists questioned. SILnews 43, 6–7.

- Foissner, W. (2006) Biogeography and dispersal of micro-organisms: a review emphasizing protists. *Acta Protozool* 45, 111–136.
- Foissner, W. and Lei, Y.-L. (2004) Morphology and ontogenesis of some soil spathidiids (Ciliophora, Haptoria). *Linzer biol Beitr* 36, 159–199.
- Foissner, W. and Song, W. (2002) *Apofrontonia lamet-schwandtneri* nov. gen., nov. spec., a new peniculine ciliate (Protozoa, Ciliophora) from Venezuela. *Europ J Protistol* 38, 223–234.
- Foissner, W. and Stoeck, T. (2006) *Rigidothrix goiseri* nov. gen., nov. spec. (Rigidotrichidae nov. fam.), a new “flagship” ciliate from the Niger floodplain breaks the flexibility-dogma in the classification of stichotrichine spirotrichs (Ciliophora, Spirotrichea). *Europ J Protistol* 42, 249–267.
- Foissner, W. and Xu, K. (2006) Monograph of the Spathidiida (Ciliophora, Haptoria). Volume I: Proto-spathidiidae, Arcuopathidiidae, Apertospathulidae. *Monographiae biol* 81, 1–485.
- Foissner, W. and Xu, K. (2007) Monograph of the Spathidiida (Ciliophora, Haptoria). Volume II: Spathidiidae and Pharyngospathidiidae. *Monographiae biol* (in preparation).
- Foissner, W., Berger, H., Blatterer, H. and Kohmann, F. (1995) Taxonomische und ökologische Revision der Ciliaten des Saprobiensystems – Band IV: Gymnostomatea, *Loxodes*, Suctorina. *Informationsberichte des Bayer Landesamtes für Wasserwirtschaft* 1/95, 1–540.
- Foissner, W., Berger, H. and Schaumburg, J. (1999) Identification and ecology of limnetic plankton ciliates. *Informationsberichte des Bayer Landesamtes für Wasserwirtschaft* 3/99, 1–793.
- Foissner, W., Agatha, S. and Berger, H. (2002) Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha Region and the Namib Desert. *Denisia* 5, 1–1459.
- Foissner, W., Strüder-Kypke, M., Van der Staay, G.W.M., Moon-Van der Staay, S.-Y. and Hackstein, J. H. P. (2003) Endemic ciliates (Protozoa, Ciliophora) from tank bromeliads: a combined morphological, molecular, and ecological study. *Europ J Protistol* 39, 365–372.
- Fokin, S., Andreoli I., Verni, F. and Petroni, G. (2006) *Apofrontonia dohrni* sp. n. and the phylogenetic relationships within Peniculia (Protista, Ciliophora, Oligohymenophorea). *Zool Scr* 35, 289–300.
- Green, J. and Bohannan, B. J. M. (2006) Spatial scaling of microbial biodiversity. *Trends in Ecol Evol* 21, 501–507.
- Harumoto, T. and Miyake, A. (1991) Defensive function of trichocysts in *Paramecium*. *J Exp Zool* 260, 84–92.
- Hu, D. L., Shen, Y. F., Gu, M. R. and Gong, X. J. (1997) New species and new records of protozoa from Wuling Mountains Area. Pp. 40–72 in D.-X. Song, ed. *Invertebrates of Wuling Mountains Area, Southwestern China*. Science Press, Beijing (in Chinese).
- Ichise, S., Morita, T., Wakabayashi, T., Kusuoka, Y. and Nishino, M. (2004) Disappearance and its past distribution of the endemic protista *Diffugia biwae* Kawamura, 1918 in Lake Biwa, Central Japan. *Rep Shiga Pref Inst Pub Hlth & Environ Sci* 39, 57–63 (in Japanese).
- Johnson, P. A. and Gullberg, U. (1998) Theory and models of sympatric speciation. Pp. 79–89 in D. J. Howard and S. H. Berlocher, eds. *Endless Forms*. Oxford Univ. Press, New York and Oxford.
- Katz, L. A., McManus, G. B., Snoeyenbos-West, L. O., Griffin, A., Pirog, K., Costas, B. and Foissner, W. (2005) Reframing the “everything is everywhere” debate: evidence for high gene flow and diversity in ciliate morphospecies. *Aquat Microb Ecol* 41, 55–65.
- Kawamura, T. (1918) *Japanese Freshwater Biology*. Syoukabou, Tokyo, Japan, pp. 113–115 (in Japanese).
- Kreutz, M. and Foissner, W. (2006) The Sphagnum ponds of Simmelried in Germany: a biodiversity hot-spot for microscopic organisms. *Protozool Monogr* 3, 1–267.
- Lincoln, R. J., Boxshall, G. A. and Clark, P. F. (1982) *A Dictionary of Ecology, Evolution and Systematics*. Cambridge Univ. Press, Cambridge and Sydney. 298 pp.
- Martiny, J. B. H., Bohannan, B. J. M., Brown, J. H., Colwell, R. K., Fuhrmann, J. A., Green, J. L., Horner-Devine, M. C., Kane, M., Krumins, J. A., Kuske, C. R., Morin, P. J., Naeem, S., Øvreås, L., Reysenbach, A.-L., Smith, V. H. and Staley, J. T. (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews* 4, 102–112.
- Mayr, E. (1963) *Artbegriff und Evolution*. Parey, Hamburg and Berlin. 617 pp.
- Meyer, E., Foissner, W. and Aescht, E. (1989) Vielfalt und Leistung der Tiere im Waldboden. *Öst Forstz* 3, 15–18.
- Mieczan, T. (2005) Periphytic ciliates in littoral zone of

- three lakes of different trophic status. *Pol J Ecol* 53, 489–502.
- Nicholls, K. H. (2007) *Cyclopyxis acmodonta* n. sp. and *Arcella formosa* n. sp.: two new species of testate rhizopods (Arcellinida, Protozoa) from remnant wetlands in Ontario, Canada. *Canadian Field-Naturalist* 119 (in press).
- Nilsson, J. R. (2005) Ethanol affects endocytosis and proliferation of *Tetrahymena pyriformis* GL and promotes encystment. *Acta Protozool* 44, 293–299.
- Plattner, H. (2002) My favorite cell – *Paramecium*. *BioEssays* 24, 649–658.
- Scheckenbach, F., Wylezich, C., Weitere, M., Hausmann, K. and Arndt, H. (2005) Molecular identity of strains of heterotrophic flagellates isolated from surface waters and deep-sea sediments of the South Atlantic based on SSU rDNA. *Aquat Microb Ecol* 38, 239–247.
- Schluter, D. (1998) Ecological causes of speciation. Pp. 114–129 in D. J. Howard and S. H. Berlocher, eds. *Endless Forms*. Oxford Univ. Press, New York and Oxford.
- Schmidt, S. L., Bernhard, D., Schlegel, M. and Foissner, W. (2007) Phylogeny of the Stichotrichia (Ciliophora; Spirotrichea) reconstructed with SSU rDNA gene sequences: discrepancies and accordances with morphological data. *J Eukaryot Microbiol* (in press).
- Snegovaya, N. and Alekperov, I. (2005) Fauna of testate amoebae of western Azerbaijan rivers. *Protistology* 4, 149–183.
- Song, W. and Wilbert, N. (1989) Taxonomische Untersuchungen an Aufwuchsciliaten (Protozoa, Ciliophora) im Poppelsdorfer Weiher, Bonn. *Lauterbornia* 3, 2–221.
- Stoeck, T., Bruemmer, F. and Foissner, W. (2007) Evidence for local ciliate endemism in an alpine anoxic lake. *Microb Ecol* (in press).
- Vd'ačný, P. and Tirjaková, E. (2006) A new soil hypotrich ciliate (Protozoa, Ciliophora) from Slovakia: *Gonostomum albicarpaticum* nov. spec. *Europ J Protistol* 42, 91–96.
- Webster, J. (1983) *Pilze. Eine Einführung*. Springer, Berlin, Heidelberg, New York.
- Weisse, T. (2004a) Pelagic microbes – protozoa and the microbial food web. Pp. 417–460 in P. O'Sullivan and C. R. Reynolds, eds. *The Lakes Handbook*, Vol I. Blackwell Science, Oxford.
- Weisse, T. (2004b) *Meseres corlissi*: a rare oligotrich ciliate adapted to warm water and temporary habitats. *Aquat Microb Ecol* 37, 75–83.
- Weisse, T., Karstens, N., Meyer, V. C. L., Janke, L., Lettner, S. and Teichgräber, K. (2001) Niche separation in common prostome freshwater ciliates: the effect of food and temperature. *Aquat Microb Ecol* 26, 167–179.
- Wilkinson, D. M. (2001) What is the upper size limit for cosmopolitan distribution in free-living microorganisms? *J Biogeogr* 28, 285–291.
- Yang, J. and Shen, Y. (2005) Morphology, biometry and distribution of *Diffugia biwae* Kawamura, 1918 (Protozoa: Rhizopoda). *Acta Protozool* 44: 103–111.
- Yang, J., Beyens, L., Shen, Y. and Feng, W. (2004) Redescription of *Diffugia tuberspinifera* Hu, Shen, Gu et Gong, 1997 (Protozoa: Rhizopoda: Arcellinida: Diffugiidae) from China. *Acta Protozool* 43, 281–289.
- Yang, J., Meisterfeld, R., Zhang, W. and Shen, Y. (2005) *Diffugia mulanensis* nov. spec., a freshwater testate amoeba from Lake Mulan, China. *Europ J Protistol* 41, 269–276.