

Biogeography and Dispersal of Micro-organisms: A Review Emphasizing Protists

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Summary. This review summarizes data on the biogeography and dispersal of bacteria, microfungi and selected protists, such as dinoflagellates, chrysophytes, testate amoebae, and ciliates. Furthermore, it introduces the restricted distribution and dispersal of mosses, ferns and macrofungi as arguments into the discussion on the postulated cosmopolitism and ubiquity of protists. Estimation of diversity and distribution of micro-organisms is greatly disturbed by undersampling, the scarcity of taxonomists, and the frequency of misidentifications. Thus, probably more than 50% of the actual diversity has not yet been described in many protist groups. Notwithstanding, it has been shown that a restricted geographic distribution of micro-organisms occurs in limnetic, marine, terrestrial, and fossil ecosystems. Similar as, in cryptogams and macrofungi about, 30% of the extant suprageneric taxa, described and undescribed, might be morphological and/or genetic and/or molecular endemics. At the present state of knowledge, micro-organism endemism can be proved/disproved mainly by flagship species, excluding sites (e.g., university ponds) prone to be contaminated by invaders. In future, genetic and molecular data will be increasingly helpful. The wide distribution of many micro-organisms has been attributed to their small size and their astronomical numbers. However, this interpretation is flawed by data from macrofungi, mosses and ferns, many of which occupy distinct areas, in spite of their minute and abundant means of dispersal (spores). Thus, I suggest historic events (split of Pangaea etc.), limited cyst viability and, especially, time as major factors for dispersal and provinciality of micro-organisms. Furthermore, the true number of species and their distribution can hardly be estimated by theories and statistics but require reliable investigations on the number of morphospecies in representative ecosystems. Generally, the doubts on Beijerinck's famous metaphor "in micro-organisms everything is everywhere" can be focussed on a simple question: If the world is teeming with cosmopolitan unicells, where is everybody?

Key words: cryptogam spores, cyst viability, flagship species, Gondwana, human dispersal, Laurasia, local vs. global diversity, protozoa, undersampling.

INTRODUCTION

A comprehensive review on biogeography and dispersal of micro-organisms does not exist so far. Consequently, the relevant literature is highly scattered, often vague, and burdened with numerous misidentifications

due to methodological shortcomings and flaws, patchy information, and, lastly, the widespread practice to use Holarctic identification literature to determine species from other regions (Foissner 1987, 1998; Lhotský 1998; Hoffmann 1999; Alongi *et al.* 2002). The view was developed that prokaryotes, unicellular eukaryotes and small multicellular organisms have a cosmopolitan distribution because of their minute sizes and their ability to form dormant stages (cysts, eggs, spores), which facilitate dispersal by air, dust, and migrating animals. As early as in 1913, this peaked in Beijerinck's famous

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metaphor “in micro-organisms, everything is everywhere, the environment selects”, which soon became a paradigm in microbial ecology. Part of this view is likely to have been caused by the intuitive feeling that such minute creatures must have simple ecologies. This assumption, however, could not be supported in many recent studies (Laybourn-Parry 1992, Weisse *et al.* 2001, Azovsky 2002, Hausmann *et al.* 2003, Weisse 2004).

In recent times, Beijerinck's metaphor has been emphasized in particular by Fenchel *et al.* (1997), Finlay (2002), and Azovsky (2000, 2002), who applied ecological methods and concepts on both original studies and literature data of heterotrophic protists, mainly ciliates. This approach tends to be flawed by the fact that more than half of the protist world is still undescribed, especially the rare species (World Conservation Monitoring Centre 1992, Foissner *et al.* 2002). Accordingly, concepts which work well with higher plants and animals must fail if applied to micro-organisms where the global diversity is largely unknown. Furthermore, it is well established that even intensive studies of a certain habitat provide only a small fraction of global protist diversity (Finlay and Maberly 2000, Foissner *et al.* 2002). Thus, the postulate of Finlay and Esteban (1998) that “all species of freshwater protozoa could eventually be discovered in one small pond” is unlikely to be ever confirmed experimentally or by classical ecological and morphological studies. It has been shown repeatedly that the carrying capacity of habitats for species is limited not only for multicellular organisms but also for protists (Foissner 1999b). Accordingly, local distribution patterns must exist. This is supported by the meta-analysis of Hillebrand *et al.* (2001), who showed a decreasing similarity of species composition with increasing geographic distance both in diatoms and ciliates.

Data which fail to support the “everything is everywhere” paradigm have largely been ignored in the past, although they convincingly demonstrate a rather restricted distribution of many “flagship” genera and species belonging to various groups of protists (Bonnet 1983, Dragesco and Dragesco-Kernéis 1986, Tyler 1996, Vyverman 1996, Foissner 1999b, Foissner *et al.* 2002). Refined morphological methods and more sophisticated techniques, such as electron microscopy and molecular analyses, increasingly support the taxonomists' view on the existence of provincial micro-organisms, including small metazoans (Ferris and Ferris 1985; Bayly 1995; Reid 1998; Lee 2000; Gómez *et al.* 2002; Segers 2001,

2003; Trontelj 2004), protists (Foissner *et al.* 2001, Kristiansen 2001, Pawlowski and Holzmann 2002, Schlegel and Meisterfeld 2003, Fokin *et al.* 2004, Pochon *et al.* 2004) and bacteria (Cho and Tiedje 2000, Papke and Ward 2004). On the other hand, it is obvious that small organisms *tend* to have broader geographic ranges than large ones. This can be attributed, however, also to their high phylogenetic age that gave them more time to disperse. Thus, I basically agree with the statement of Fenchel (1993): “... smaller organisms tend to have wider or even cosmopolitan distribution, a higher efficiency of dispersal, a lower rate of allopatric speciation and lower rates of local and global extinction than do larger organisms”. The more strict view that all micro-organisms are distributed globally, however, receives increasing criticism not only from protistologists, like me and Coleman (2002), but also from other disciplines, especially molecular ecologists (Zettler Amaral *et al.* 2002, López-García *et al.* 2003, Stoeck and Epstein 2003, Lachance 2004, Šlapeta *et al.* 2005).

Related to the distribution problem is that of species diversity. The cosmopolitan school argues that micro-organisms have low species richness because of the obvious lack of opportunities for allopatric speciation (Fenchel 1993, Wilkinson 2001, Finlay 2002). On the other hand, many micro-organisms are much older than the extant multicellular organisms giving them sufficient time for accumulating a high diversity, even if speciation rates are low! This interpretation is supported by bacteriologists (Cohan 2002) and mycologists (Hawksworth 2001), who envisage millions of species, nearly approaching May's (1986) famous correlation between body size and species numbers. The question of species richness has been addressed in my previous reviews, where I have provided evidence that, at least in ciliates, more than half of the free-living species have not been described yet (Foissner 1999b, Foissner *et al.* 2002). Notably, Aptroot (2001) has identified 200 species of ascomycetes associated with a single *Elaeocarpus* tree in Papua New Guinea, a figure which is similar to the numbers of species of soil nematodes per sampling site (Ettema 1998). Since some 160 ciliate species were found by Foissner (1999b) under 100 m² of beech forest soil, soil ciliates might be as diverse as nematodes and microfungi (World Conservation Monitoring Centre 1992, Hawksworth 2001, Foissner *et al.* 2002). This and the figures mentioned by the World Conservation Monitoring Centre (1992) should be kept in mind if one tries estimating the number of endemic taxa. Obviously, we

know mainly the common, euryoecious species, which usually have wider geographic ranges than the more demanding species.

The highly divergent views on microbial diversity and dispersal illustrate the need for a comprehensive review. The present paper is a first attempt at compiling the literature dealing with the geographic distribution of representative groups of unicellular organisms, from bacteria to ciliates. This review highlights an urgent need for more detailed research and emphasizes provinciality in limnetic, marine, terrestrial, and fossil microbial ecosystems. Furthermore, the distribution patterns of mosses, ferns and macrofungi are compared with the distribution of micro-organisms. The main dispersal forms, i.e. the spores, of these organisms are similar in size and abundance to large bacteria and small protists. Notwithstanding, many of these mosses, ferns and fungi exhibit pronounced endemism. This reinforces the assumption that also micro-organisms do have biogeographies, which remain to be unravelled.

Terminology

The terms endemic, endemism, endemicity, provinciality and restricted geographic distribution are used throughout the paper in the same, very general sense (see Anderson 1994 for a detailed discussion of this matter). The same applies to the term “ubiquity”, where I adopt the usual meaning, that is, the occurrence in a wide variety of habitats. Names of higher taxa, such as orders and classes, are usually vernacular, as outlined by Margulis *et al.* (1990). The authorities of the genera and species are omitted because they can be found in the literature cited.

Some basic considerations and major problems in estimating diversity and distribution of micro-organisms

“Everything is everywhere” is not falsifiable and thus a metaphor

Beijerinck’s statement cited above is widely considered as a scientific hypothesis. However, scientific hypotheses must be falsifiable (Popper 1962). This is not the case with Beijerinck’s statement testing of which would require the existence of at least two identical habitats in different biogeographical regions. Further, these habitats should have a representative size and age to allow the establishment of a micro-organism community such as found, for instance, in old ponds. Such

conditions do not exist in the real world, and it is unlikely that they can be created experimentally. It might be important to note that “similar” or “almost identical” would be insufficient because this could imply that differences in species composition are due to genuine differences in the habitats. Similar considerations were made also by Finlay *et al.* (2004).

The local vs. global diversity measure is futile unless the global diversity is known

The ratio of local:global diversity is an important measure in conservation biology because it indicates “hot spots” of biodiversity. It is derived from MacArthur’s and Wilson’s theory of island biogeography and based on the fact that the number of species increases with the size of the area under investigation. In protists, this measure was first used by Fenchel *et al.* (1997). They found that about 10% of the estimated global diversity of free-living ciliates (3000 species) could be detected in local samples. From this, they conclude that “everything is (almost) everywhere” (Fenchel *et al.* 1997) and that “all species of fresh-water protozoa could eventually be discovered in one small pond” (Finlay and Esteban 1998). At first glance, this conclusion appears reasonable because the ratios of local:global diversity in protozoa is much higher than those found in metazoan and plant communities (usually < 1%). However, it is obvious that this method must be seriously flawed if the global diversity is largely unknown, as is the case in protists. The following example may illustrate the problem for the about 800 described species of soil ciliates (Foissner 1998, 2000; Foissner *et al.* 2002). At least 270 of them have been reliably recorded from Germany (Foissner 2000). In 1987, when just 250 species of soil ciliates were known globally (Foissner 1987), nearly 100% of the global diversity occurred in Germany. Today, with some 800 described species of soil ciliates (Foissner *et al.* 2002), the percentage has dropped to 34%, and if the 500 hitherto undescribed species, which I have in my records (Foissner 1998), are added, the percentage would drop to about 23%. Finally, when the very conservative estimate of 2000 species of soil ciliates globally is used in our calculations (Foissner 1997b, Chao *et al.* 2006), the ratio of local: global diversity drops to 14%. This is, compared to higher organisms, still a high value. However, the assumed global diversity of 2000 species is likely to be an underestimate.

These simple calculations show that the local: global diversity measure is flawed, as long as the actual global

diversity of the group under consideration is unknown. Unfortunately, Fenchel and Finlay (2004) refuse such evidences and stick to their view that global diversity of free-living ciliates is sufficiently known to use the local:global diversity measure. However, global ciliate diversity is not known, but likely more near to 30,000 species (Foissner *et al.* 2002) than to the 3,000 species proposed by Finlay (2001). Potentially, the species-area curves used by Azovsky (2002) are also influenced by this phenomenon. He compares the total world macrofauna with just a small fraction of the protists, i.e. the free-living ciliates.

Taken together, both Beijerinck's original metaphor and its interpretation by Finlay and Esteban (1998) are flawed not only by ecological theory but also by the common knowledge that nobody has ever found all species of a certain taxonomic group (e.g., ciliates) in a single pond, lake, or area. For instance, only 256 ciliate taxa have been reported from Priest Pot, Finley's well-studied model pond (Finlay and Maberly 2000). Likewise, an estimated maximum of only 200 ciliate species occurs in a 100 m² area of beech forest (Foissner 1999b), that is, about 10% of the estimated global soil ciliate diversity (Foissner *et al.* 2002).

Undersampling: the key to understand diversity and distribution of micro-organisms

Micro-organisms are difficult to recognize because they are small and dormant for extended periods of time. Thus, various culture methods are required to make them "visible". Then, however, a very selective community may develop and many of the "rare" species may escape detection among the few highly abundant and ubiquitous species. Only if a variety of different culture methods has been applied and the samples were carefully inspected have these rare species a chance to be identified. It is well known that such "rare" species comprise more than 80% of the total species pool in most communities studied so far (Schwerdtfeger 1975, Foissner *et al.* 2002), and that far less than 10% of the environmental bacteria can be grown on the commonly used culture media (Cohan 2002). Accordingly, it is likely that we know the majority of the more common, euryoecious species of protists quite well, but that we are rather ignorant about the more than 90% uncultured species. The effect of undersampling becomes especially evident if samples are manipulated to create new niches (Fenchel *et al.* 1997) or if the same site is investigated repeatedly (Foissner *et al.* 2002): 13 sampling campaigns, distributed over a period of 17 months, were required to find

80% of the 160 ciliate species identified until now in just 100 m² of an Austrian beech forest soil.

These problems in recognizing protist diversity concern also the recognition of undescribed species which are notoriously undersampled and whose large proportion becomes evident only if many samples from a large area are analysed (Foissner 1997b, Foissner *et al.* 2002). While most individual samples provide only 1 to 3 (4-7%) new species, the samples collectively show that up to 50% of the species found are undescribed.

Undersampling is not only caused by the methodological problems discussed above, but also by misidentifications, which are quite common (Foissner 1987, 1998; Alongi *et al.* 2002); by neglecting the rare and very rare species, a quite usual practice; by classifying distinct, but undescribed species as malformed individuals of known species; and the strongly decreasing number of well educated alpha-taxonomists (Cotterill 1995). All these problems mean that the diversity of microbial communities is usually greatly underestimated and distribution data become skewed to the common, euryoecious and/or easy-to-identify species. Undersampling is even a serious problem in higher organisms, such as fish and mammals (Kodric-Brown and Brown 1993).

Flagship taxa: an "ultimate" proof of endemism

Species with conspicuous size, morphology and/or colour are called "flagship taxa". They are the elephants of the microscopic world. Tyler (1996) has summarized the reasons why such taxa have the greatest probability of real endemism: "Because they are so showy, or so novel, it is unlikely that such species would be overlooked if indeed they were widely distributed. If the Australian endemics occurred in Europe or North America then they would have been seen there, long ago".

Many more flagships are known from algae than from heterotrophic protists. In my opinion, this is simply because the latter found less attention in the past. Thus, it is relatively easy to discover new flagship species in ciliates, especially in Africa and South America and the marine environments (see below).

A brief review on restricted geographic distribution of bacteria and microfungi

Using data from recent molecular studies, Dykhuizen (1998) estimated that thirty grams of forest soil contain over half a million bacterial species, that there are 2,000 different bacterial communities, and possibly a trillion (!)

of bacterial species globally. More recent analyses tend to surpass these estimations (Gans *et al.* 2005)! Although such numbers depend highly on the species concept used, it is clear that the number of bacterial species is enormous. Modern bacterial species concepts even suggest that the named molecular species are more like genera than species (Cohan 2002).

Molecular techniques also provided evidence for a restricted geographical distribution of soil bacteria, such as *Pseudomonas* and *Rhizobium* on the basis of autofluorescence and multilocus enzyme electrophoresis (Cho and Tiedje 2000, Souza *et al.* 1992). Indeed, the most recent studies, using refined molecular methods, reveal biogeographies in various bacteria and endemism of genotypes at continental and local level (Borneman and Triplett 1997, Hagström *et al.* 2000, Madrid *et al.* 2001, Whitaker *et al.* 2003, Bavykin *et al.* 2004, Lawley *et al.* 2004, Papke and Ward 2004, Silva *et al.* 2005).

Lhotský (1998), who believes that there are only a few really cosmopolitan algal species, re-evaluated Komárek's studies on cyanobacteria: of 20 exclusively planktonic freshwater cyanophytes only 25% were cosmopolitan, 40% were tropical species, 5% were restricted to the neotropic region, and 15% were species known only from Cuba. Likewise, 50% of the chlorococcal algae have a restricted distribution. Potentially, temperature is a major factor controlling the distribution of the marine species of cyanobacteria (Hoffmann 1999).

About 120,000 fungal species have been described, but their global diversity has been estimated to be well above one million species (Hawksworth 2001). While it is textbook knowledge that most macrofungi occupy rather distinct areas, notwithstanding their dispersal by microscopical spores (see chapter on dispersal), the distribution of microfungi is much less clear because most are associated with particular host plants and animals as parasites or mutualists; therefore they have a distribution similar to those of their hosts (Hawksworth 2001). However, even "free-living" microfungi appear to occupy restricted areas, for instance, the soil and litter species belonging to the genus *Aspergillus* (Klich 2002). This is emphasized by data of Green and Bohannan (2006) for ascomycete fungi: using intergenic spacer analysis (ARISA), geographic distance was a more useful predictor for ascomycete fungi community than habitat across scales of 1 m to ~ 100 km. *Geosiphon pyriforme*, a coenocytic soil fungus living in endocytobiotic association with a cyanobacterium, *Nostoc punctiforme*, represents a remarkable case of local endemism. At the

hyphal tips, the fungus forms unicellular, multinucleated 1-2 mm bladders, which host the symbiotic cyanobacteria. Although this fungus is of almost macroscopic size and known since 1915, a region in the Spessart Mountains (Germany) is the only known natural habitat so far (Schuessler and Kluge 2000).

A brief review on restricted geographic distribution of autotrophic and heterotrophic protists

According to Taylor and Pollinger (1987), Tyler (1996), Vyverman (1996), and Coleman (1996, 2001), there is little doubt that both freshwater and marine algae do have biogeographies, although it is sometimes difficult to distinguish between patchy search results, restricted distributions, and genuine invasions into a certain region (see dispersal chapter). In addition to a large cluster of pantropical and temperate-montane species with representatives in all major taxonomic groups, there are large numbers of taxa endemic to each of the different tropical regions. Among the heterotrophic protists, which have been much less intensively studied so far, we can at least distinguish genera and species with a restricted Laurasian/Gondwanan distribution. However, I am convinced that increased research will reveal distribution patterns of heterotrophic protists that are basically similar to those found in algae.

Dinoflagellates (Figs 1; 3e, f)

Older data were extracted from the valuable reviews of Taylor and Pollinger (1987) and Pollinger (1987). Both freshwater and marine dinoflagellates show endemism in the strict sense of the word, i.e. are restricted to only one particular region, despite the potential continuity of all oceans and genuine man-made introductions into a given region.

It might be expected that the Polar Regions would host endemic species because of the great distance between north- and south polar regions. This is indeed the case, with roughly 80% endemism in each polar region. As with other groups, the Indo-West Pacific region possesses a variety of endemic species, most of which are neritic (Fig. 1). One such species is *Dinophysis miles*, a distinctively shaped, neritic dinophysoid "flagship" which occurs from the Western Indian Ocean and Red Sea to the Gulf of Tonkin. *Ceratium dens* (Fig. 3e) is another species with such a restricted distribution, which is difficult to understand in a region in which a strong inter-ocean flow exists that reverses seasonally

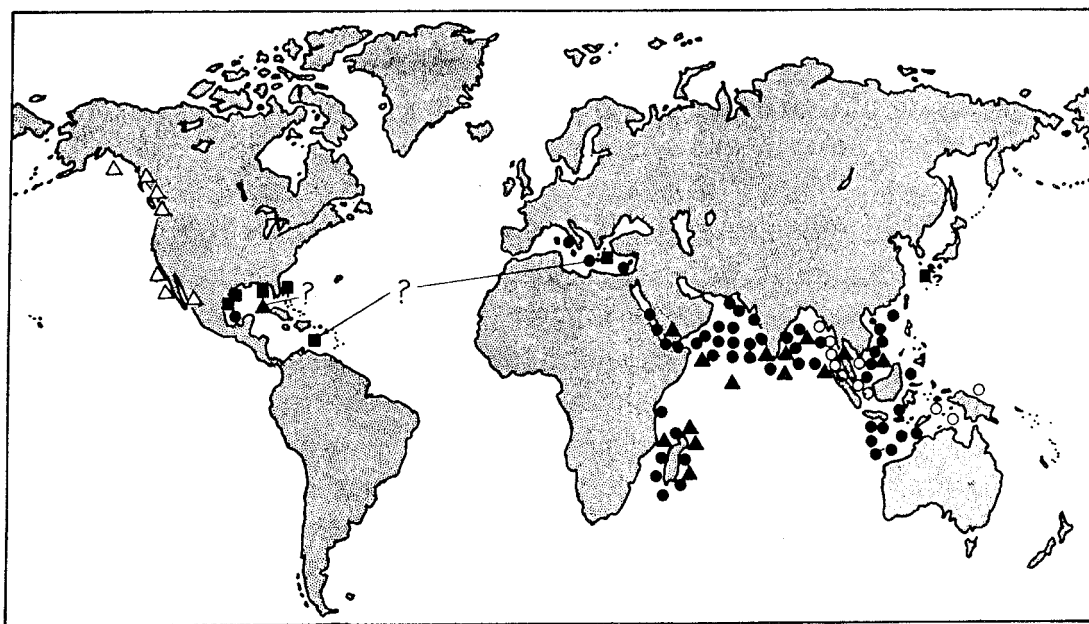


Fig. 1. Distribution of some endemic dinoflagellates (from Taylor and Pollinger 1987). *Dinophysis miles* (closed circle), *Dinophysis miles* var. *schröeteri* (open circle) and *Ceratium dens* (closed triangle) are Indo-west Pacific taxa; *Oxyphysis oxytoxoides* (open triangle) is a Pacific endemic, and *Ptychodiscus brevis* (square) is probably a Caribbean endemic.

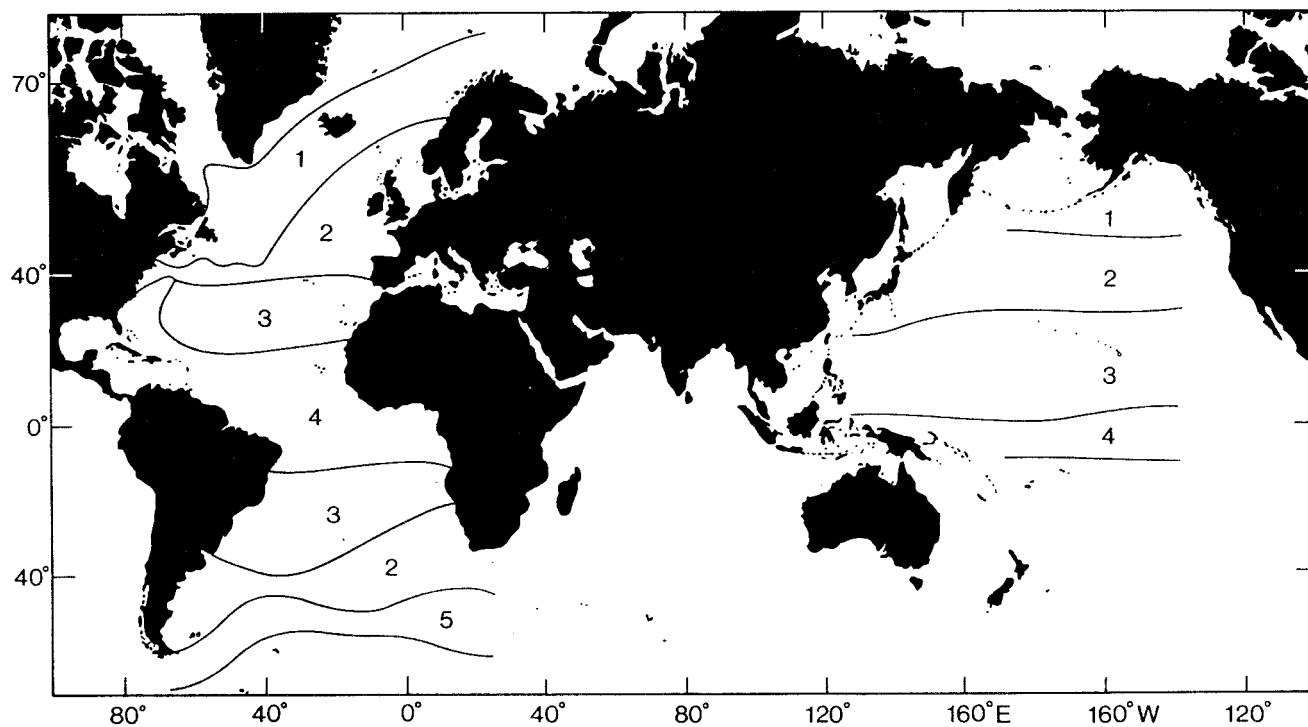
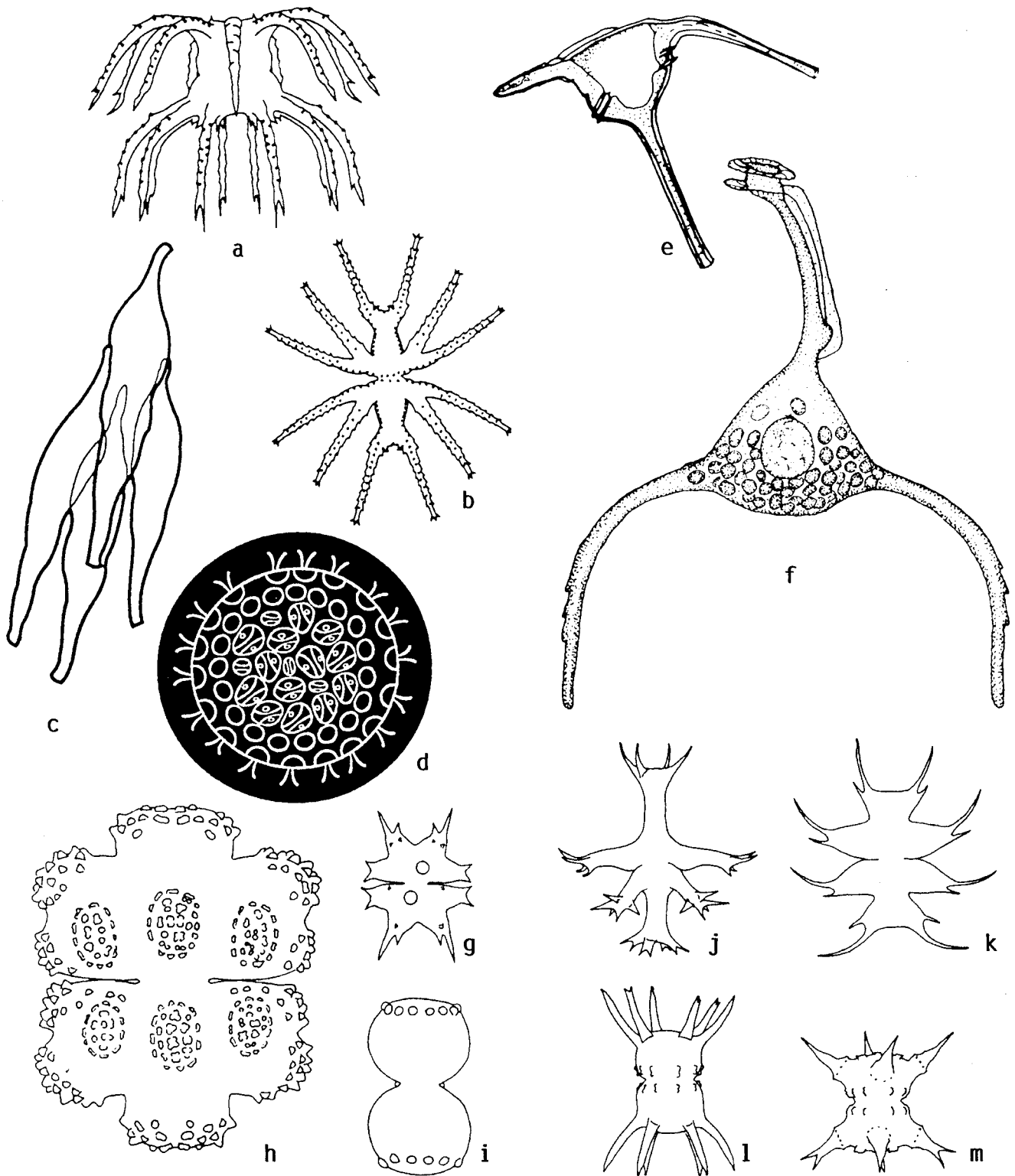


Fig. 2. Biogeographic coccolithophore zones from the Atlantic and Pacific Oceans (from Winter *et al.* 1994). 1 - Subarctic, 2 - Temperate (Transitional), 3 - Subtropical (Central), 4 - Tropical (Equatorial), 5 - Subantarctic. Similar distribution patterns are found in foraminifera.



Figs 3a-m. Some endemic algae, viz., desmids (a, b, g-m), dinoflagellates (e, f), and chrysophytes (c, d). **a-d** - Australian flagship endemites (from Tyler 1996): *Amscottia gulungulana*, *Micrasterias hardyi*, *Dinobryon unguentariaforme*, and *Tessellaria volvocina*; **e, f** - *Ceratium dens*, an Indo-west Pacific species, see also figure 1 (from Taylor 1987) and *Triposolenia intermedia*, a tropical marine species (from Dodge and Lee 1985); **g-i** - Neotropic desmids (from Coesel 1996): *Euastrum grandioratum*, *Euastrum foersteri*, and *Cosmarium redimitum*; **j-m** - Desmids from equatorial Africa (from Coesel 1996): *Allorgeia incredibilis*, *Micrasterias sudanensis*, *Staurostrum rhoskae*, and *Staurostrum fuellebornii* var. *evolutum*.

with the monsoons. Another species, *Ceratium egyptiacum* occurs only in the Suez Canal, the Red Sea and the south-eastern Mediterranean. Other species are restricted to the tropical Atlantic Ocean (e.g., *Gessnerium monilatum*, *Ptychodiscus brevis*) and the North Pacific, for instance, *Oxyphysis oxytoxoides* (Fig. 1).

Also, there is molecular evidence for provinciality and cryptic speciation in dinoflagellates. Montresor *et al.* (2003b) performed morphological and genetic investigations on several populations of the cosmopolitan marine species *Scrippsiella trochoidea*. They found that very similar morphs of *Scrippsiella trochoidea* exhibit genetic differences in the order of different species. Recently, Pochon *et al.* (2004) showed biogeographic partitioning and host specialization of the foraminiferan dinoflagellate symbiont *Symbiodinium*. They discovered a distinctive biogeographic break between the kinds of symbionts found in *Sorites* from the East Pacific and Caribbean. Garcia-Cuetos *et al.* (2005) suggest that the strong host-symbiont specificity observed in soritid foraminifera is a combined effect of a selective recognition mechanism, vertical transmission of symbionts, and biogeographical isolation.

In freshwater environments, the most striking examples for local endemism come from studies in the large, old lakes. Lake Baikal harbours four dinoflagellate species, three of which are endemic forms: *Gymnodinium baicalense*, *G. coeruleum* and *Peridinium baicalense*. In Japan, Lake Biwa contains endemic algae from various groups, and Lake Ohrid in the former Yugoslavia contains, *inter alia*, the endemic dinoflagellate *Cystodinium dominii*. A lot of endemic dinoflagellates occur also in Australia (Tyler 1996, Hallegraeff *et al.* 2004), and the very common "cosmopolitan" *Ceratium hirundinella* seems to be absent from Indonesia (Vyverman 1996), Venezuela, the Amazonian basin and the southern part of South America (Pollinger 1987).

Diatoms

The siliceous, highly structured frustules of the diatoms provide excellent possibilities for biogeographical research, especially when scanning electron microscopy is used. Diatoms show distinct global distribution patterns and even local endemism. For instance, 8% (30 taxa) of the diatom flora of Lake Tanganyika can be considered as regional endemics (Vyverman 1996). Kienel (2003) described a restricted distribution of a common planktonic species, viz., *Aulacoseira subarctica*. Probably, this provinciality is caused by a preference for low temperatures, low light intensities and high concentra-

tions of silicate and mineral nutrients. And recently, Shayler and Siver (2004) discovered several endemic diatoms and *Mallomonas* in a pond area of Florida, U.S.A. They suggest that such specific flora is related to the history of the ponds which suffered a transition from alkaline to very acidic conditions over the years. Thus, strong environmental changes could have promoted the evolution of locally adapted lines that eventually speciated. Another excellent example is represented by the genus *Actinella* which presently comprises 29 species, only two of which (*A. brasiliensis*, *A. punctata*) have a worldwide distribution (Sabbe *et al.* 2001). Nine *Actinella* species are endemic to Australasia, and there are even marked differences in the geographic distribution at smaller spatial scales: some species are only known from a few lakes (Sabbe *et al.* 2001).

Coccolithophores (Fig. 2)

Coccolithophores are marine, planktonic algae with highly structured, calcified scales. It is a relatively small group presently comprising about 200 species. Probably, their diversity is much higher because a number of novel species have been described recently. Biogeography of species is still rather incomplete because reliable identification requires an electron microscopical analysis. However, the gross distribution patterns are well established and described here, using the excellent reviews of Brand (1994), Winter *et al.* (1994) and Roth (1994).

Coccolithophores, like most phytoplankton and microzooplankton, can be classified according their occurrence in five major latitudinal zones: Subarctic, Temperate (or Transitional), Subtropical (or Central), Tropical (or Equatorial) and Subantarctic (Fig. 2). Distinct species assemblages occur in each of these zones, which are, in most cases, similar to those in the corresponding zones of the other hemisphere. Exceptions are found in the Subarctic-Subantarctic zones, which host similar genera but few "bipolar" species.

The fossil records reveal a distinct provinciality of many coccolithophore species in the Cretaceous and Tertiary periods (Green *et al.* 1990). Moreover, the biogeographic distribution of individual coccolithophore species changes over geological times, obviously in response to changing environmental conditions and the global distribution of the water masses. For instance, the subpolar *Coccolithus pelagicus* expanded its range towards the equator during the last glacial peak, while several tropical species (e.g., *Calcidiscus leptoporus*, *Syracosphaera pulchra*) exhibited markedly reduced biogeographic ranges closer to the equator during this

period (Brand 1994). Similar changes were observed in the various fossil freshwater and marine algal communities (Coleman 1996, Adey and Steneck 2001).

Chrysophytes (Figs 3c, d)

The biogeographic data dealing with the silica-scaled chrysophytes were excellently summarized by Kristiansen (2001) and Kristiansen and Funch Lind (2005): "It is now evident from electron-microscopical examinations of samples from lakes and ponds all over the world that the silica-scaled chrysophytes show distinct distribution patterns. Differences in ecological requirements determine local occurrence, and on a global basis several distribution types can be established. Best known in this respect is the genus *Mallomonas* with 172 described taxa. Of these, 31 taxa are cosmopolitan or widely distributed, 59 taxa have a northern temperate-subarctic-arctic distribution, of these 22 are endemic. A total of 17 taxa have a bipolar distribution. Eighteen taxa are restricted to the tropics, seven of which are endemics. Seventeen taxa have scattered distributions with scant occurrence. Including the already mentioned species, altogether 69 taxa must be deemed endemic, although several of them may lose this status after further investigations. The genus *Synura* apparently has a similar biogeography. The very small species of *Paraphysomonas* and *Spiniferomonas* have been argued to be cosmopolitan, although there are so far no satisfactory investigations (see Foissner *et al.* 2002 for detailed discussion).

Desmids (Figs 3a, b, g-m)

These fancy organisms have attracted many professionals and amateurs. Many desmids are obviously cosmopolitan, while others have a restricted Laurasian/Gondwanan distribution, for instance, the "northern" *Micrasteria crenata* and the "southern" *M. alata* from Amazonia (Bremer 2002). Today, 10 regions with well known desmid floras can be distinguished, with a most pronounced endemism in the Indo-Malaysian/Northern Australian region, in tropical America, and equatorial Africa (Coesel 1996; Fig. 3a, b, g-m). It is likely that endemism is much more common in this group than previously assumed. In an extensive literature search, Vyverman (1996) found that among the more than 2680 desmids recorded from the Indo-Malaysian/Northern Australian region, about 800 (31%) have never been found elsewhere, and 4% of the desmids of Papua New Guinea can be considered as paleotropical taxa. Sometimes, related species show distinct or partially overlap-

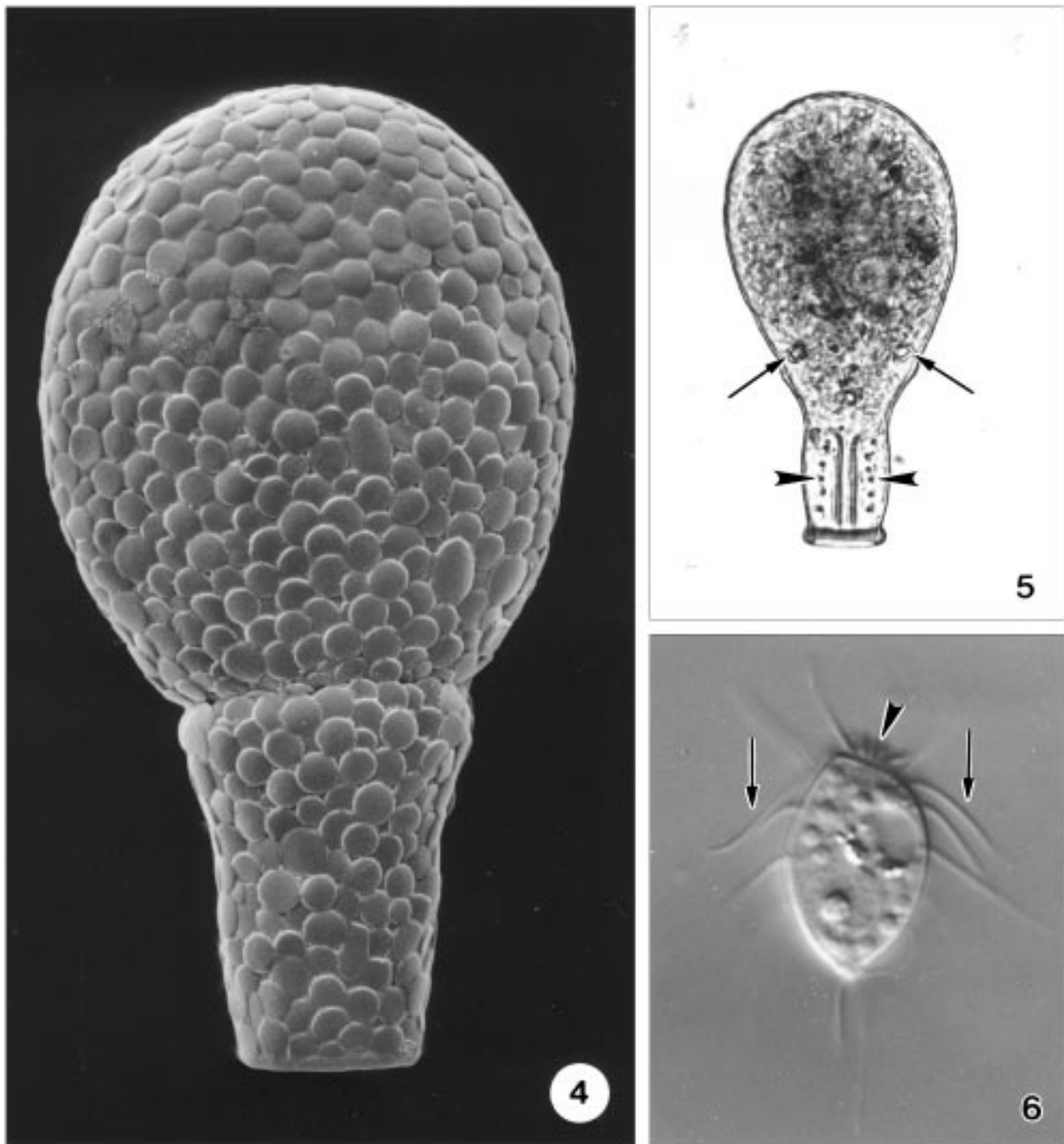
ping geographic distributions. For instance, *M. cruxmelitensis* has its main occurrence in temperate regions, while *M. radians* has a pantropical distribution. Similar distribution patterns are known, *inter alia*, also from diatoms and dinoflagellates (Vyverman 1996): in some tropical lakes, the genus *Surirella* is abundant in the plankton, while most temperate species of this genus are benthic; and the dinoflagellate genus *Peridinium* seems to replace the genus *Ceratium* forwards the equator (see above).

Naked amoebae, heliozoa, and heterotrophic flagellates (Fig. 6)

Naked amoebae are difficult to identify. Thus, reliable faunistic data are scarce. Nonetheless, there is some evidence for a restricted distribution of several species (Page 1976, 1991) and molecular varieties (Smirnov *et al.* 2002). *Naegleria italica*, for instance, could not be found elsewhere than in Italy during a worldwide search (Jonckheere 2002). Likewise, a study of amoebae from lens cases in Korea found that ~ 88% of these were potential keratitis pathogens, with distribution of isolates reflecting geographic regions of the country (Schuster and Visvesvara 2004). Cavender *et al.* (2002) reported evidences that the assemblage of dictyostelid slime moulds from New Zealand is quite distinctive and reflects the isolation of this land mass; five of the thirteen species found were undescribed.

The available data on Heliozoa were reviewed by Siemensma (1991). About 100 species are known globally, but many novel species have been described in the eighties suggesting that many more might be discovered in future research. A reliable identification often requires scanning electron microscopy (SEM); the lack of SEM analysis might have flawed many of the older data. The few studies which used SEM in the past discovered not only many new species but also suggest that some might have a restricted Laurasian/Gondwanan distribution.

For the free-living, heterotrophic flagellates, Lee and Patterson (1998) favour a model in which there are relatively few species most of which have cosmopolitan distribution. On the other hand, the structure of their data highly resembles those reported by Foissner (1997b) for soil ciliates: there are few new species in the individual samples, but many if one adds together data from several samples from larger areas. Thus, Foissner (1999b) concluded that free-living flagellate diversity is probably also larger than presently assumed. This appears to be confirmed by recent electron microscopical and molecu-



Figs 4-6. Gondwanan testate amoebae (4, 5) in the scanning electron and bright field microscope, and a Gondwanan heterotrophic flagellate (6) in the interference contrast microscope (originals). **4** - *Apodera vas* is an eye-catching species with a length of about 170 μm and a characteristic shell shape; **5** - An even more distinct “flagship” is *Certesella certesi*, which is about 130 μm long and has highly characteristic teeth (arrowheads) at both sides of the neck and two pores on each side (arrows); **6** - Although *Hemimastix amphikineta* is only about 20 μm long, it is a “flagship” flagellate because it has two highly characteristic flagella rows (arrows) making it looking like a small ciliate. Arrowhead marks mouth entrance.

lar work that discovered a great variety of undescribed taxa (Zoological Record, Moon-van der Staay *et al.* 2001, Scheckenbach *et al.* 2005).

There is at least one soil flagellate, *Hemimastix amphikineta*, with a distinct biogeography. This highly characteristic organism (Fig. 6) has been found in about 50 out of 300 soil samples from Gondwanaland (South America, Africa, Australia) and the transition zone of Gondwana and Laurasia (Central America, Malaysia), but never in Laurasia (mainly Europe and about 60 samples from North America), even not in a recent study of soils from twelve natural forest stands in Austria, where I specifically looked for this organism (Foissner *et al.* 2005).

Foraminifera

Extant and fossil foraminifera have distinct biogeographies at large scale (Fig. 2), controlled mainly by temperature, water currents, and food availability (Bé 1977, Kemle-von Mücke and Hemleben 1999, Kucera and Darling 2002, Groves *et al.* 2003). A considerable number of species appears to have a restricted distribution (Bé 1977). However this endemism might be less pronounced in the deep sea species (Gooday 1999).

Recently, molecular investigations revealed not only a considerable cryptic diversity in foraminifera, but also highlighted the endemic character of the allogromiid foraminifera from Explorers Cove, Antarctica (Kucera and Darling 2002, Pawlowski and Holzmann 2002). Notably, none of the sequences derived from non-Antarctic species clusters with the Antarctic ribotypes. This and other data support the hypothesis that the morphological resemblance between foraminiferal taxa from the northern and southern hemispheres is due to convergence rather than evidence for a common origin (Pawlowski *et al.* 2002). However, very recent data suggest another mechanism for the “bipolar cosmopolitan” *Neoglobobulimina pachyderma* (Darling *et al.* 2004). Fossil and molecular data demonstrate a stepwise progression of diversification starting with the allopatric isolation of Atlantic Arctic and Antarctic populations after the onset of the Northern Hemisphere’s glaciation. Similar genetic divergence has also been reported between a bipolar planktonic dinoflagellate from the high polar water mass and Antarctic Sea ice (Montresor *et al.* 2003a).

Many foraminifera occupy wide geographic ranges (Bé 1977). However, these potentially cosmopolitan morphospecies exhibit a high genetic diversity. For in-

stance, the highly variable and cosmopolitan *Globobulimina truncatulinoidea* consists of four different rRNA lineages, which should be considered as distinct species: lineages 1 and 2 occur mainly in subtropical waters, lineage 3 is abundant only in the Subantarctic Convergence, and lineage 4 inhabits subantarctic waters (Vargas *et al.* 2001).

Testate amoebae (Figs 4, 5, 7; 8a-v)

Among the heterotrophic protists, testate amoebae provide the most convincing evidence for a restricted geographic distribution of many genera and species. Most of these endemics are “flagships” with a large size (> 100 µm) and distinct morphology, for instance, *Apodera vas* (Fig. 4), which is quite common in Gondwanan areas but absent from the northern hemisphere. Meisterfeld (2002b) summarizes this quite concisely: “Testate amoebae are found world-wide, but they are neither cosmopolitan nor ubiquitous. Several species, mainly from the Nebelidae, Distomatopyxidae, and Lamtopyxidae have a restricted geographical distribution, which is certainly not a result of uneven sampling effort”. Briefly, there are distinct differences in the Laurasian and Gondwanan testacean faunas and, in addition, between the temperate and tropical regions (Hoogenraad and de Groot 1979, Bonnet 1983, Bobrov 2001). Furthermore, molecular investigations showed that some of the common, cosmopolitan “species” are genetically highly diverse; they consist of several ribospecies which, subsequently, could be distinguished also morphologically (Vargas *et al.* 2001, Wylezich *et al.* 2002).

The following compilation, based on the authoritative reviews of Meisterfeld (2002a, b), shows that a restricted distribution is not an exceptional phenomenon in testate amoebae. Certainly, the knowledge is still incomplete for many genera and species because reliable biogeographical data are rare. It seems possible that some of the interstitial marine testacean genera and species also have a restricted distribution. The genera *Heteroglyphia* (Fig. 8q), *Lamtopyxis* (Fig. 8m), *Lamtoquadrula* (Figs 8b, c), *Moghrebina* (Figs 8f, g), *Paracentropyxis* (Fig. 8n), *Pentagonia* (Figs 8h, i), and *Pseudonebela* (Fig. 8d) occur only in (mostly tropical) Africa. *Alocodera*, *Ampullataria* (Fig. 8v), *Certesella* (Fig. 5), *Cornuapixis* (Fig. 8o), *Oopyxis* (Fig. 8l), *Pileolus* (Fig. 8r), and *Suidifflugia* occur only in Central and South America. *Wailesella*, *Deharvengia* (Fig. 8u), and *Playfairina* occur only in Indonesia and Australia. *Microquadrula* (Fig. 8a) appears to be a

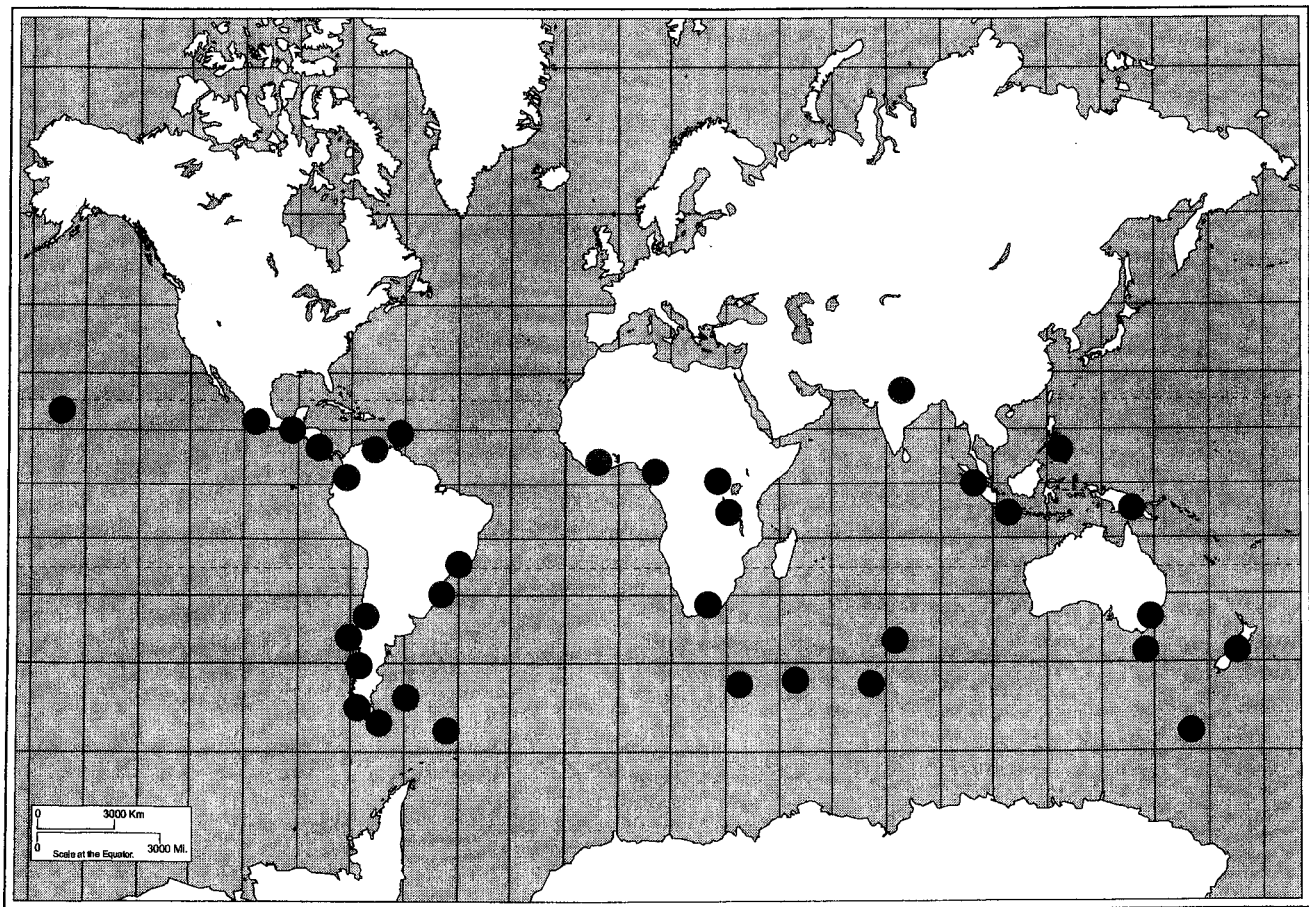


Fig. 7. Recorded occurrences of *Nebela* (*Apodera*) *vas*, a Gondwanan testate amoebae (cp. Figure 4). From Smith and Wilkinson (2005). This compilation disproves the statement of Finlay *et al.* (2004) that *N. vas* occurs in the Holarctic.

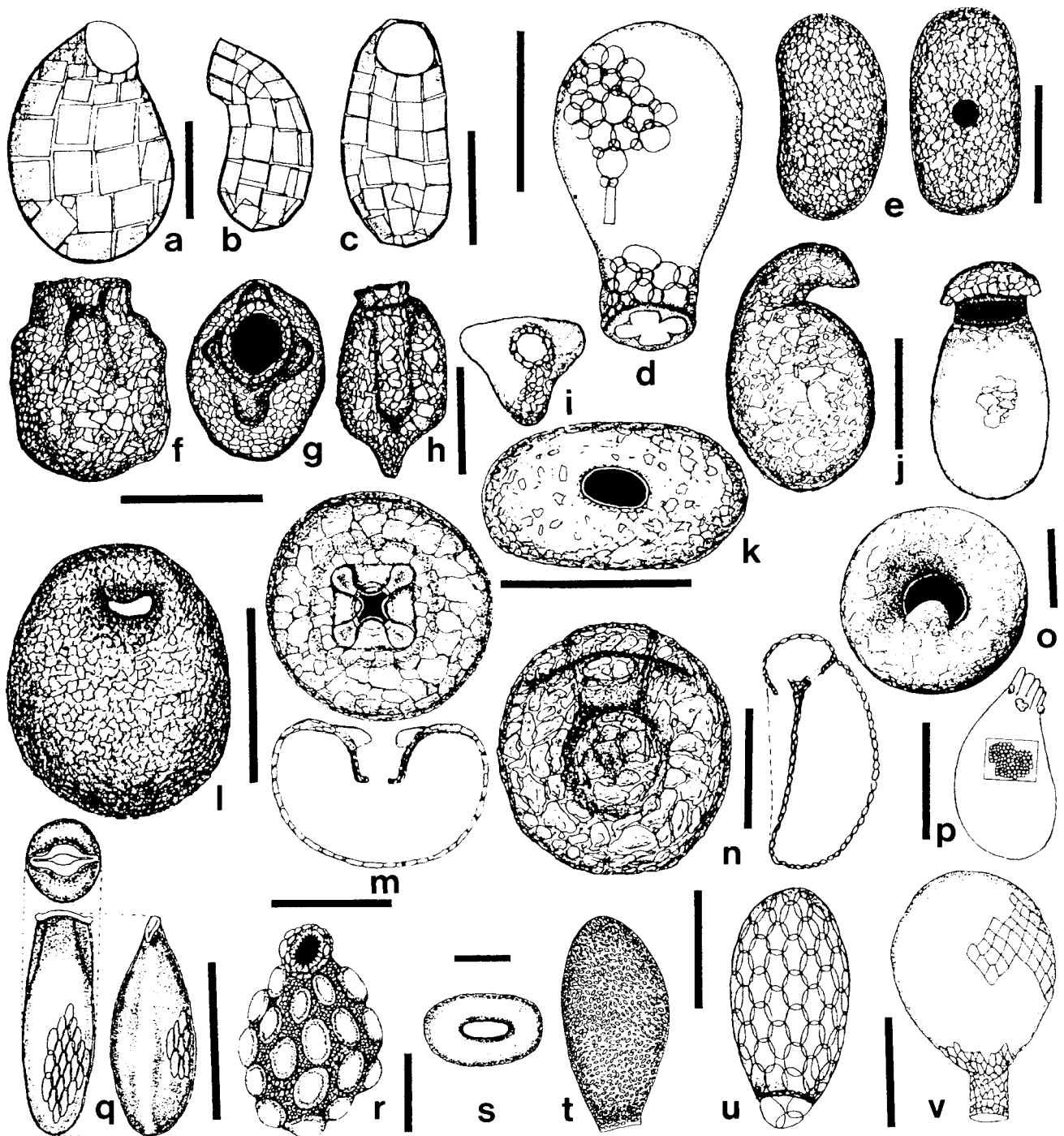
Cuban endemic, and *Feuerbornia* (Fig. 8p) has been reported only from South America and New Zealand. *Jungia* and *Ellipsopyxis* (Fig. 8k) are restricted to Indonesia, Africa and South America. *Hoogenraadia* (Fig. 8j) occurs in Africa and East Asia. *Ellipsopyxella* (Fig. 8e) appears to be restricted to Africa and South America. *Distomatopyxis* occurs in North and Central America, East Asia and Spain. *Matsakision* (Figs 8s, t) is probably a Laurasian endemic.

Recently, Finlay *et al.* (2004) claimed that *Apodera* (formerly *Nebela*) *vas*, a Gondwanan flagship species (Fig. 4), might be a misidentified *Pontigulasia* and thus occurs in the Holarctic. This claim is based on very old literature from around 1900, which contains some misidentifications, and, of course, cannot take into account the more recent contributions of acknowledged taxonomists, such as Bonnet, Grospietsch, Meisterfeld

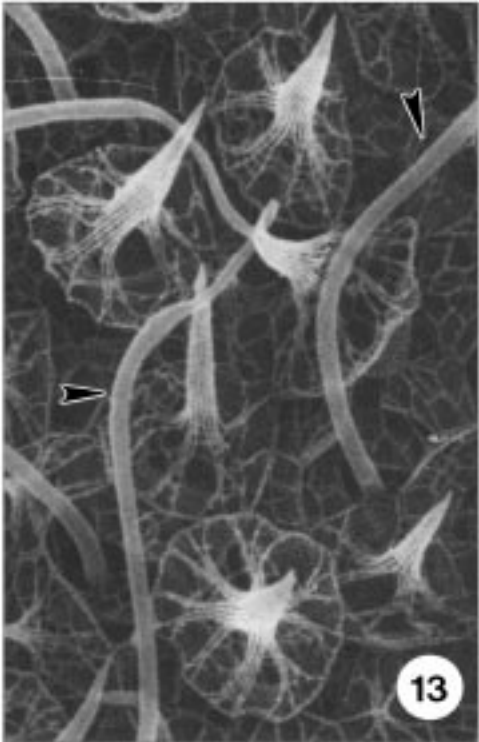
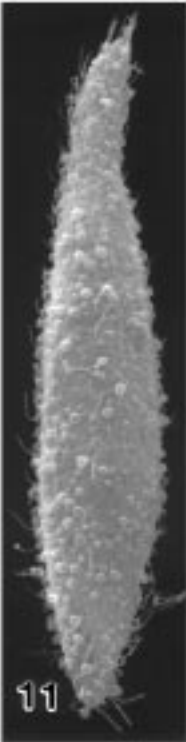
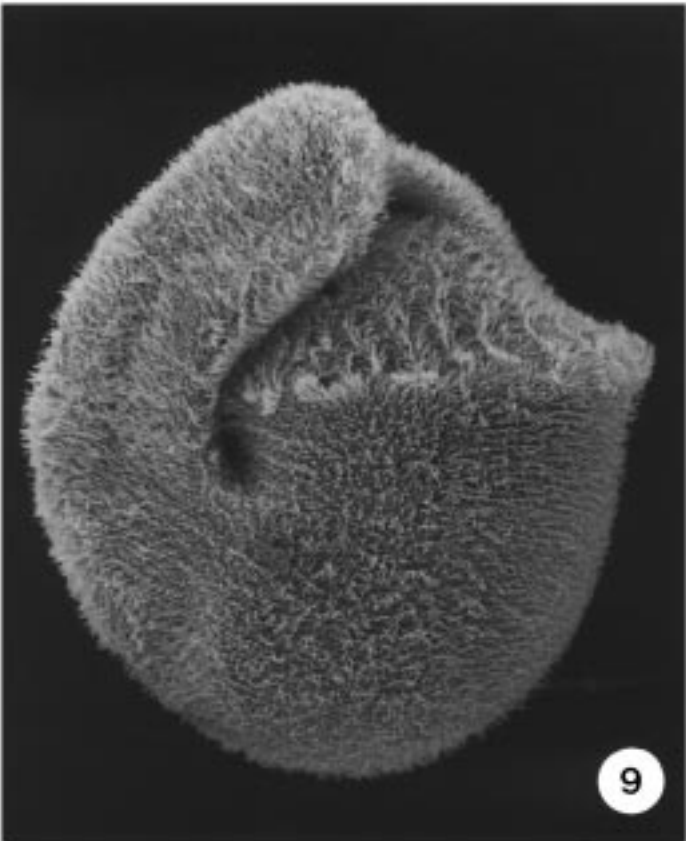
and Golemansky. Smith and Wilkinson (2005) carefully reviewed the literature on the occurrence of *A. vas* (Fig. 7). According to this compilation, *A. vas* has never been found in the Holarctic despite the presence of many suitable habitats. Thus, Smith and Wilkinson (2005) suggest that the patterns of atmospheric circulation do not enable cysts to be carried from Nepal across high montane Tibet, or from Mexico across the desert states of USA, to reach suitable habitats further north. Lastly, also the distinct distribution of other Gondwanan flagship nebeliids, such as *Certesella certesi* (Fig. 5) and *Alocodera cockayni* is beyond any doubt.

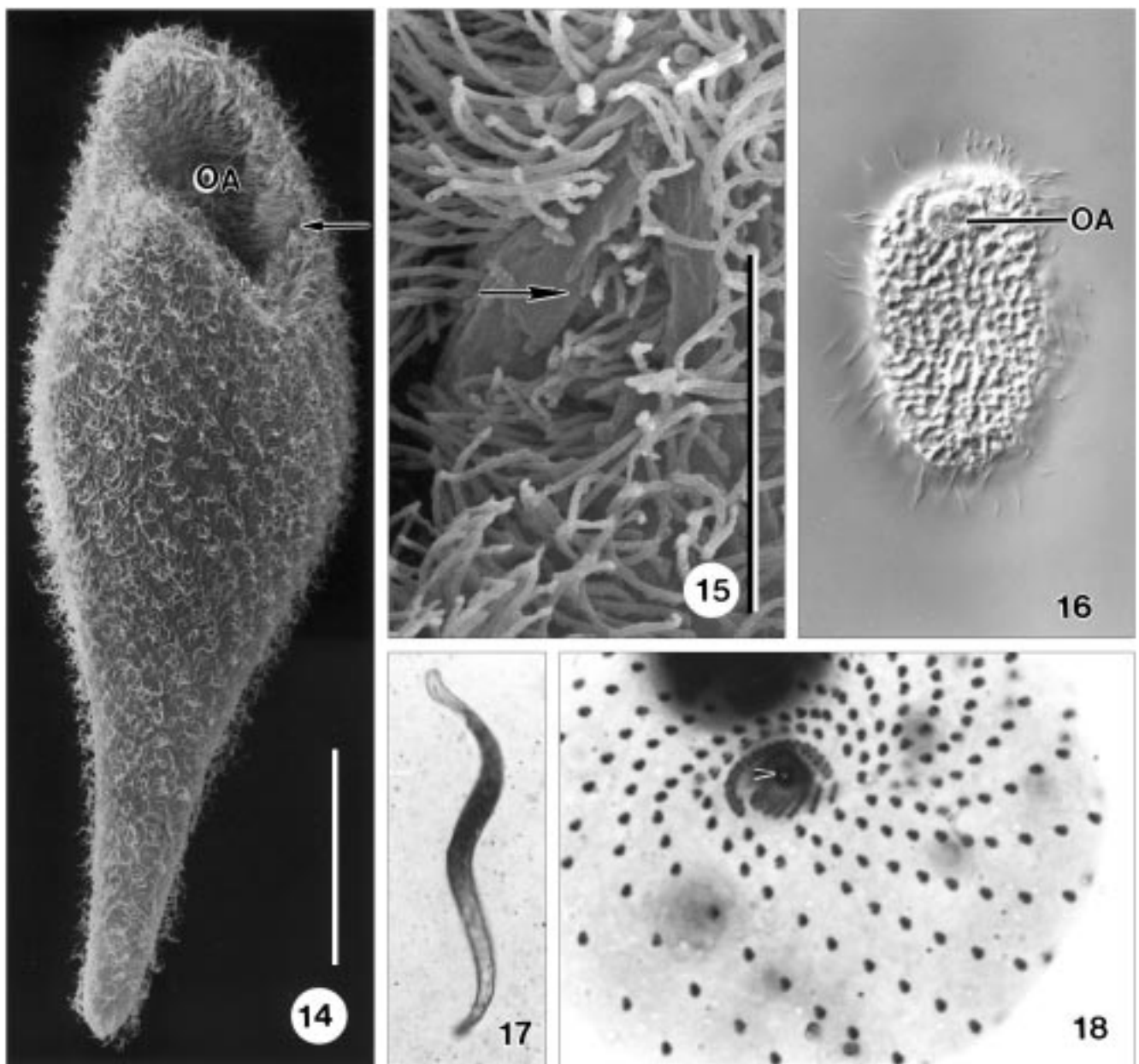
Ciliates (Figs 9-21a-h)

Ciliates exhibit a broad spectrum of distinct morphologies (Corliss 1979), but rather complicated methods (various silver impregnation techniques, scanning elec-



Figs 8a-v. Some endemic testate amoebae genera (compiled from Meisterfeld 2002a, b). Further genera, see figures 4 and 5. African endemics: *Lamtoquadrula* (b, c), *Pseudonebela* (d), *Moghrebica* (f, g), *Pentagonia* (h, i), *Lamtopyxis* (m), *Paracentropyxis* (n), *Heteroglyphia* (q). Central and South American endemics: *Oopyxis* (l), *Cornuapyxis* (o), *Pileolus* (r), *Ampullataria* (v). Indonesian endemic: *Deharvengia* (u). Cuban endemic: *Microquadrula* (a). Laurasian endemic: *Matsakision* (s, t). *Ellipsopyxella* (e) occurs in Africa and South America; *Hoogenraadia* (j) occurs in Africa and East Asia; *Feuerbornia* (p) occurs in South America and New Zealand; *Ellipsopyxis* (k) occurs in Asia, Africa and South America. Scale bars: 10 μ m (q-u), 20 μ m (b, c, n), 50 μ m (d-q, v), 100 μ m (f, g, m).





Figs 14-18. Endemic ciliates in the light (16-18) and scanning electron (14, 15) microscope. **14, 15** - a still undescribed tetrahymenid ciliate from bromelian tanks in the Dominican Republic (from Foissner *et al.* 2003). This species reaches a length of 800 μm and is thus a size "flagship" which would have been recognized in Europe, if it were there. The bromelian ciliate represents a new genus and family because it has many peculiarities, for instance, possesses a large, functional oral apparatus (OA) and a minute, likely functionless original mouth (arrows) with partially reduced adoral membranelles. Scale bars: 50 μm and 10 μm ; **16, 18** - *Fungiphrya strobli* has been found only on the Table Mountain of the Republic of South Africa (from Foissner 1999a). This small (about 50 μm) ciliate is highly characteristic because the oral apparatus (OA) possesses a minute feeding tube used to penetrate fungal hyphae and spores; **17** - *Circinella arenicola* is a worm-like hypotrichous ciliate which reaches a length of 600 μm (from Foissner 1994). Among 1000 soil samples investigated, it occurred only in an inland sand dune of Utah, USA, although many similar habitats were investigated in Namibia (Southwest Africa) and Australia.

Figs 9-13. Endemic soil ciliates in the scanning electron microscope (from Foissner 1993, 2005). **9** - *Bresslauides discoideus* is a massive, up to 600 μm -sized "flagship" occurring only in Laurasia and the transition zone to Gondwana (Fig. 19). With its large, table-like mouth, it can feed even on rotifers; **10** - *Cosmocolpoda naschbergeri*, although being only up to 70 μm long, is also eye-catching because it has highly characteristic ridges. The arrow marks the small mouth entrance. Among 1000 soil samples investigated, this species occurred only in a single sample from the Caribbean coast of Costa Rica, Central America; thus it is possibly a regional endemic; **11-13** - *Sleighophrys pustulata* (11, 12) and *Luporinophrys micelae* (13) are rod-shaped, about 200 μm long Venezuelan flagships with highly characteristic epicortical scales (12, 13), which are 5-12 μm high and thus easily recognizable also in the light microscope.

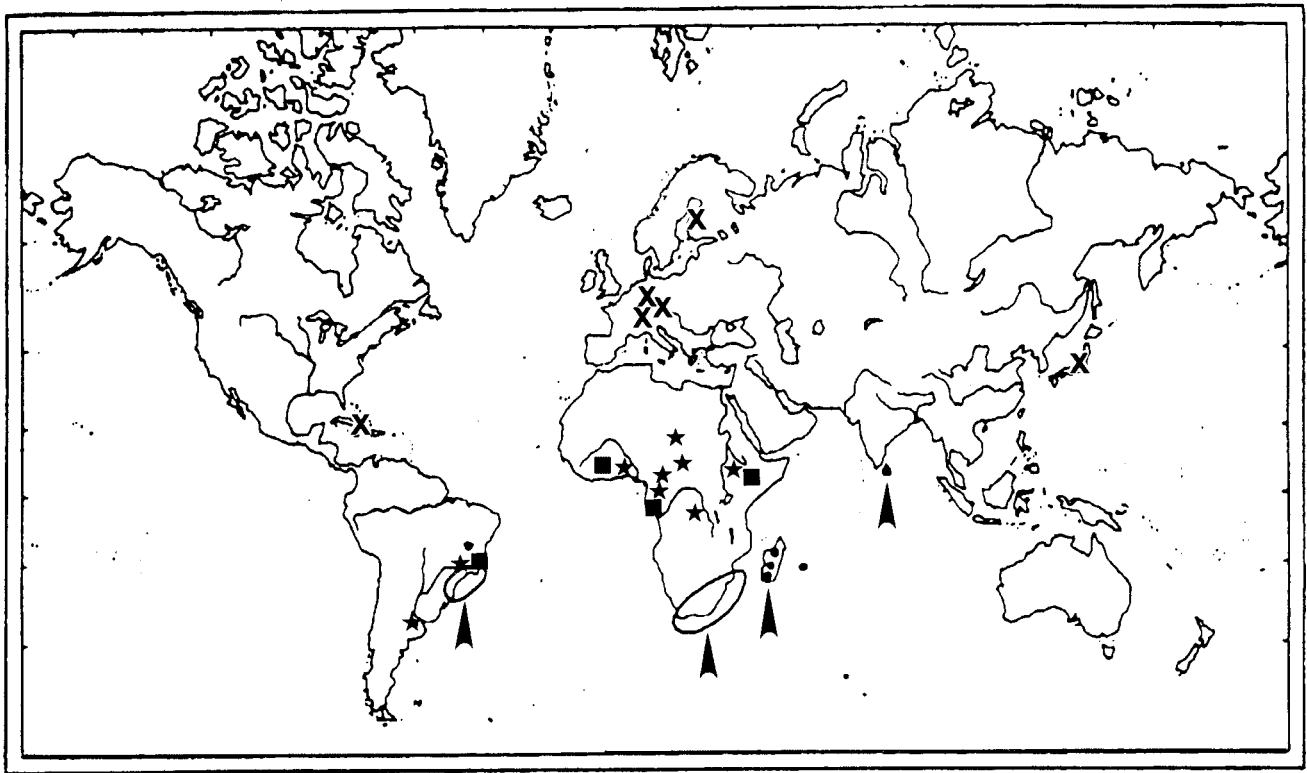


Fig. 19. Gondwanan areas of the moss *Campylopus twaitesii* (arrowed dots and ellipses; from Frahm 2001) and the ciliates *Neobursaridium gigas* (asterisk) and *Frontonia vesiculosa* (square); after data from Dragesco and Dragesco-Kernéis (1986). *Bresslauides discoideus* (x), in contrast, is a Laurusian ciliate so far found only in Europe, Japan, and in mud from tank bromeliads of the Dominican Republic (based on Foissner 1993 and more recent, unpublished data).

tron microscopy) are required to distinguish the huge amount of genera and species (Foissner *et al.* 2002). Therefore, parts of the old faunistic literature, mainly based on live observation, might be inconclusive or even misleading.

Genetic and molecular biogeographic studies are still sparse in ciliates, but those available show that ciliate diversity is larger by at least one order of magnitude than anticipated by morphologists and ecologists (Dini and Nyberg 1993, Hackstein 1997, Nanney *et al.* 1998, Foissner *et al.* 2001, López-García *et al.* 2003, Katz *et al.* 2005, Šlapeta *et al.* 2005). Obviously, most ciliate morphospecies consist of multiple, microscopically indistinguishable species whose distinct molecular distances indicate continuous speciation over long periods of time. The fact that several sibling species are often found in the same sample indicates that they might occupy different ecological (micro)-niches (Nanney 2004). Significant evidence for these conclusions comes from studies on

Paramecium, *Tetrahymena* and *Euplotes*, the “pets” of the ciliatologists.

The *Tetrahymena pyriformis* complex presently consists of 25 species. Some are cosmopolitan or near cosmopolitan (e.g., *T. cosmopolitanis*), while others are highly restricted in their distribution. For instance, *T. thermophila*, which has been collected hundreds of times in eastern North America, has never been found outside this region (Nanney *et al.* 1998, Nanney 2004). Likewise, *Paramecium novaurelia*, a member of the *P. aurelia* complex, has never been collected outside of Europe, where it is the most widespread species of the complex (Przyboś and Fokin 2000, Fokin *et al.* 2004). Another example is *P. schewiakoffi* which is confined to Asia, as shown by Fokin *et al.* (2004) in a combined morphological and molecular approach. Basically, the same pattern is recognizable in *Euplotes*. For instance, *Euplotes octocarinatus*, which is quite common in ponds of North America, has never been found in central

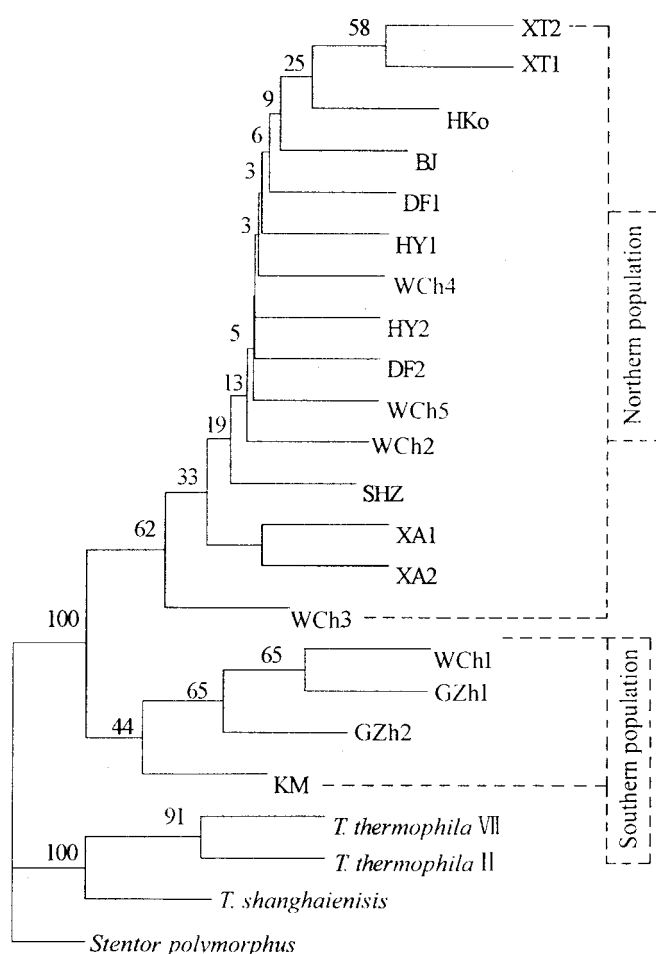


Fig. 20. Neighbour-joining tree of 19 populations of *Carchesium polypinum* (from Miao *et al.* 2004). The tree is based on 18S-ITS1-5.8S ribosomal DNA and shows a well-supported separation of the *Carchesium* populations found in northern and southern China.

Europe, as mentioned by Heckmann (pers. inform.), a recognized specialist for this species. Provinciality is also known for the common “cosmopolite” *Stylonychia mytilus*, which now consists of four reproductively isolated species three of which can be separated also morphologically, albeit by sophisticated features such as the dorsal bristle pattern and micronucleus size (Gupta *et al.* 2001, Shi and Ammermann 2004). While *S. mytilus* and *S. lemnae* are probably cosmopolites, *S. ammermanni* and *S. harbinensis* are restricted to India and China.

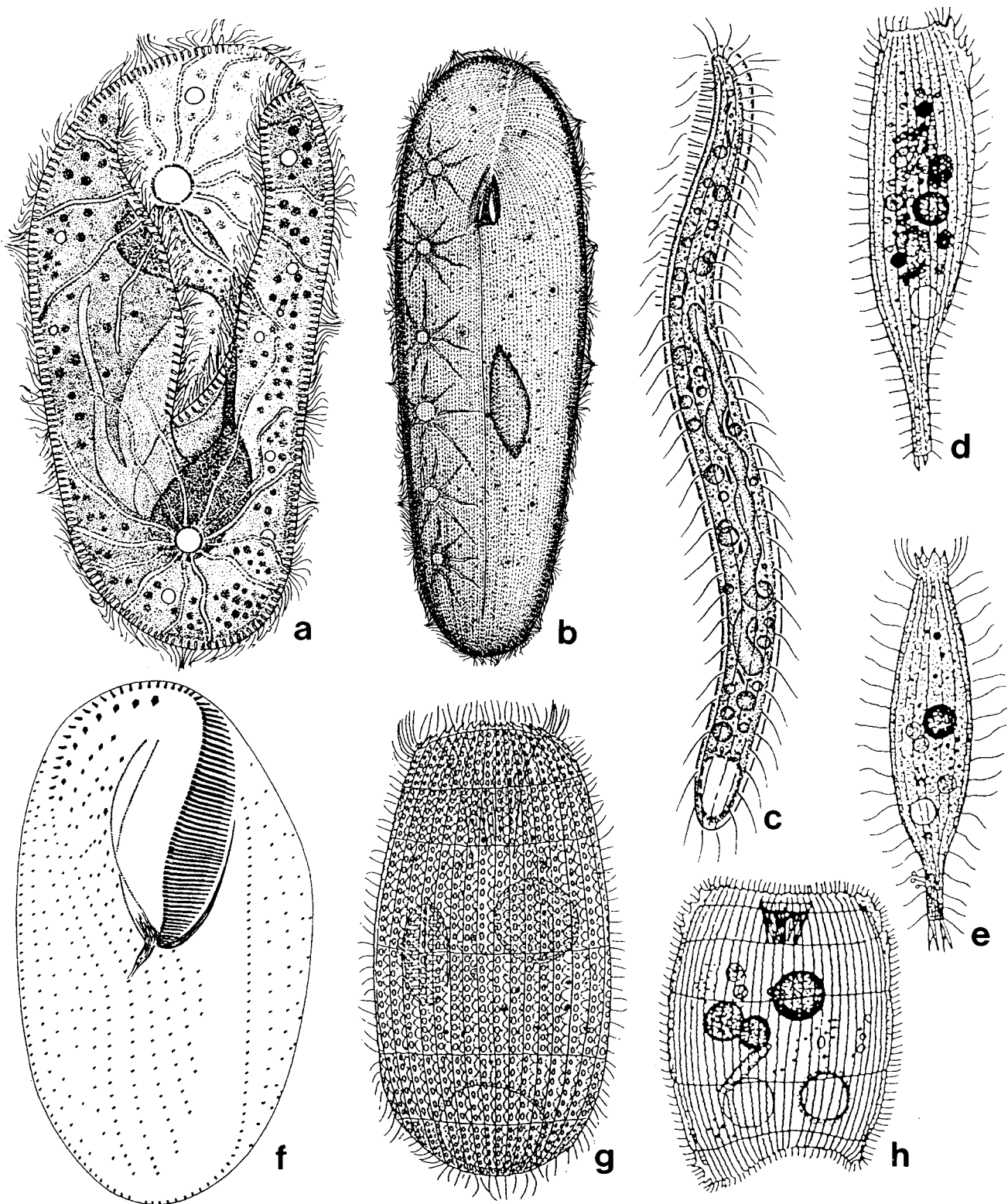
Speciation as a consequence of geographical barriers has been highlighted in an excellent study by Miao *et al.* (2004). They investigated the abundant cosmopolitan ciliate *Carchesium polypinum* in China (Fig. 20). The 18S-ITS1 rDNA sequences separated the 19 popula-

tions analysed in this study into a northern and a southern phylogroup, basically matching those found in fish. Within the large northern territory, some fine-scaled differences were found.

This brief overview shows that the genetic and molecular data argue consistently for a geographically restricted distribution of ciliate species, both at a global scale (Gondwanan/Laurasian distribution, Nanney *et al.* 1998, Pucciarelli *et al.* 2003) and at the continental level (Nanney *et al.* 1998, Foissner *et al.* 2001, Droste *et al.* 2003, Fokin *et al.* 2004, Katz *et al.* 2005) and local level (Nanney *et al.* 1998, Przyboś and Fokin 2000, Snoeyenbos-West *et al.* 2002). This is strongly supported by field data discussed in the following paragraphs.

There is solid morphological evidence that a number of “flagship” families, genera and species have a restricted global distribution. These eye-catching species, which approach a size of about 1 mm would have been found in Europe, if they were there. Well-known examples are *Neobursaridium gigas* (Fig. 21a) and *Frontonia vesiculosa* (Fig. 21b), which occur only in South America and Africa (Fig. 19); and *Loxodes rex*, an endemic of tropical Africa (Dragesco and Dragesco-Kernéis 1986; a recent record from Bangkok is doubtful, see Foissner *et al.* 2002). *Neobursaridium gigas* is a stenothermic ciliate well adapted to the tropics, which has its highest growth rates at temperatures between 71.6°F and 78.8°F (Dragesco 1968). Other excellent examples are the Colepidae from Lake Baikal (Figs 21d, e, h). These ciliates have distinct body shapes and highly structured calcareous scales which make a misidentification unlikely. Interestingly, a potentially endemic colepid genus was discovered in Lake Tanganyika (Fig. 21g).

Impressive examples for recently described flagship species are three heterotrichs from very different habitats and two holotrichs (haptorids) from Venezuela. The first is *Stentor araucanus*, an up to 300 µm long, blue-green planktonic ciliate, which is frequent in South American lakes (Foissner and Wölfl 1994). The second is *Maristentor dinoferus*, an up to 1 mm long, purple, *Stentor*-like ciliate, which is common on the coral reefs of Guam, Mariana Islands, in the Pacific Ocean (Lobban *et al.* 2002). Finally, *Heterostentor coeruleus*, a 200–300 µm long, bluish ciliate was discovered in the littoral of Potter Cove, King George Island, Antarctica (Song and Wilbert 2002). The two haptorids from astatic grassland ponds at the north coast of Venezuela are each about 200 µm in size and have complex, up to 12 µm high



Figs 21a-h. Eye-catching ciliates with restricted biogeographic distribution. **a, b** - *Neobursaridium gigas* and *Frontonia vesiculosa* are up to 1 mm long freshwater ciliates occurring only in South America and tropical Africa (from Dragesco and Dragesco-Kernéis 1986; see also figure 19); **c** - *Apobryophyllum vermiforme*, a 200 µm long species from ephemeral habitats in Namibia (from Foissner *et al.* 2002); **d, e, g, h** - endemic Colepidae from Lake Baikal (**d, e, h**; from Obolkina 1995) and Lake Tanganyika (**g**; from Dragesco and Dragesco-Kernéis 1991). These species, each representing a distinct genus, are real “flagships”, although being only 100-150 µm long, because they have highly characteristic body shapes and/or calcareous plates in the cortex; **f** - *Gigantothrix herzogi*, an up to 400 µm long, stichotrichine soil ciliate from Kenya (from Foissner 1999c).

scales easily recognizable with the light microscope (Figs 11-13, Foissner 2005). Each of these species is a flagship with distinct morphology, considerable size and/or conspicuous colour. If they would be ubiquitous they could not have been overlooked, at least in Europe. These five flagship ciliates demonstrate that even common - in their region - and abundant species were unknown until recently, demonstrating our ignorance of free-living ciliate diversity.

Recently, Foissner (2003) and Foissner *et al.* (2003) opened the door to another large ecosystem, viz., the endemic ciliate fauna in the tanks of bromeliads, with species reaching a length of up to 800 μm (Figs 14, 15). Bromeliads occur mainly in Central and South America and their tanks, which are formed by the coalescing leaf axils, form minute ponds. Altogether the tanks form a specific ecosystem whose extensive compartmentalization obviously fosters speciation. Thus, an impressive mixture of cosmopolitan (e.g., *Leptopharynx costatus*) and endemic (e.g., *Bromeliophrya brasiliensis*) ciliates occur in the tanks, often representing new genera and families. One of the new families, which are represented by three new genera and four novel species, is an excellent example for the evolution of ciliate genera and species due to a long-lasting spatial separation from the main gene pool, since these species are closely related to *Glaucoma scintillans*, a widely distributed species in "ordinary" limnetic habitats. The differences between the endemic and the ubiquitous species became obvious only through a combined morphological, molecular, and ecological approach (Foissner *et al.* 2003). A similar situation is found in certain metazoans. Packer and Taylor (1997), for instance, suggest that the presence of morphologically unrecognized species may be more common among widespread, easily identified "species" than it is generally assumed.

Detailed faunistic data are available from soil ciliates (Foissner 1998). Of 643 species identified in 1000 samples collected worldwide, 44% have been found so far only in one biogeographic region. Potentially, further investigations will show that one or the other (or even many) of these species occur also in other areas of the world (Foissner *et al.* 2002). On the other hand, such studies will invariably reveal a large number of novel species, which trivially, have not been described previously in other environments (Foissner *et al.* 2002, 2005). Thus, it is unlikely that the percentage of species with restricted distribution will decrease significantly even after intensified sampling. As these figures are based on 1000 samples, it is very likely that there exist many endemic

Table 1. Number of ciliate species in rainforest litter and soil from Borneo and Malaysia.

Sample no.	Time elapsed since collection	Species number
Fresh samples		
1	< 10h	32
2	< 10h	29
3	~ 12 h	32
4	~ 12 h	28
5	< 10h	28
6	< 10h	12
7	< 10h	19
8	< 10h	22
		\bar{X} 25
Air dried and stored up to 9 months ^a		
9	~ 6 m	36
10	~ 6 m	34
11	~ 5 m	29
12	~ 5 m	50
13	~ 5 m	35
14	~ 5 m	12
15	~ 9 m	15
		\bar{X} 30
Air-dried and stored 9-65 months ^a		
16	~ 59 m	12
17	~ 65 m	7
18	~ 65 m	4
19	~ 25 m	7
20	~ 41 m	2
		\bar{X} 6.4
Air-dried and stored 82 months ^a		
21	82 m	4
22	82 m	3
23	82 m	1
24	82 m	1
25	82 m	0
		\bar{X} 1.8

^a Investigated with the non-flooded Petri dish method for four weeks (Foissner *et al.* 2002).

soil ciliates, which await their discovery, similar to the situation in soil testate amoebae (Bonnet 1983). Some of the supposed endemics are shown in Figures 9, 10, 16-18, 21c, f. All of them have large size and/or a very distinct morphology, for instance, *Circinella arenicola*, which was discovered in an inland sand dune of Utah, USA (Fig. 17). This species, which is highly conspicuous due to its size (up to 600 μm), did not occur in the plethora of sand dune samples from the Namib Desert (Foissner *et al.* 2002) and Australia (Foissner, unpubl.), although all these habitats look quite similar. It is likely that *Fungiphrya strobli* is another example of local endemism: although it is a small species (~ 50 μm), it is very distinct because it is an obligate mycophage with a

very special oral apparatus (Figs 16, 18). Among the 1000 soil samples investigated so far, *F. strobli* occurred only in one sample from the Table Mountain in the Republic of South Africa. This area is well known for its numerous endemic plants, which characterize it as a distinct phytogeographical region (Sitte *et al.* 1991).

The high number of endemites in soil is not surprising because soil is a highly compartmentalized ecosystem with unfathomed niches for minute protists. Each plant species may provide specific niches by providing specific root exudates and particular microenvironments. Thus, it is difficult to believe that the fractal structure of soil limits ecological niches, and, consequently, protistan species diversity, as postulated by Finlay and Fenchel (2001). Furthermore, it has been shown that self-similarity leads to a distribution of species-abundance which deviates considerably from the commonly assumed log-normal distribution and predicts considerably more rare species than the latter (Harte *et al.* 1999). Exactly this has been observed in the above-mentioned 1000 soil samples: a very limited number (~50) of common (frequent) species is opposed to a very high number (> 700) of rare species (Foissner *et al.* 2002).

Very recently, Chao *et al.* (2006) used improved statistical tools to estimate global soil ciliate diversity and distribution based on 359 samples from five continents. The “abundance-based coverage estimation” model provided a global soil ciliate diversity of at least 1900 species which is consistent with the findings of Foissner (1997b), who used a probability-based method. Further, Chao *et al.* (2006) provided evidences for a distinct separation of the Laurasian and the Gondwanan soil ciliate biota, and thus for the influence of historical events on the distribution of micro-organisms.

Dispersal

Cysts and passive dispersal

Many micro-organisms, especially those living in terrestrial and limnetic habitats, can produce dormant stages named spores, stomatocysts, resting cysts, or cysts (my preferred general term), depending on the group of organisms investigated and personal taste. Cysts are generally assumed to be the major dispersal vehicle of unicellular organisms, since they remain viable under various harsh influences (e.g., drought and cold) for a long period of time (for reviews, see Corliss and Esser 1974 and Foissner 1987).

However, the biogeographical discussion ignored that cysts have very different properties, depending on the region and habitat in which they have been produced. While ciliate and flagellate cysts formed in extreme habitats withstand desiccation, drought and frost for years (Foissner 1996, Foissner *et al.* 2002) or even decennia (Foissner 1987), most of those produced in rainforest soil are viable for only a few months (Foissner 1997a and Table 1). Likewise, cysts from cultivated cells are often much “weaker” than those from environmental specimens, and frequently species lose the ability to produce cysts at all on prolonged laboratory cultivation (Corliss and Esser 1974; Foissner 1987, 1997a). This makes sense. Soil (and, of course, laboratory cultures) from evergreen rainforests is slightly wet most of the time due to the frequent rainfalls and the high air humidity. Thus, most protists are probably permanently active and hardly forced to produce desiccation-resistant dormant stages (Foissner 1997a). Accordingly, these species have little chance to disperse via cysts over large areas. This and the lack of glaciation might be the main reasons that endemics are more frequent in tropical than temperate regions.

It is widely assumed that trophic cells and cysts of micro-organisms are dispersed by wind and animals, especially migrating birds. There are many investigations supporting this view (some cited in Corliss and Esser 1974 and Foissner 1987). Unfortunately, cysts often could be reactivated only partially and most organisms were not identified to species level. But it appears that mainly common ubiquists are found, emphasizing the restricted cyst viability reported above.

However, not all cosmopolitan protists can produce cysts. Well known examples are the ciliate complexes *Paramecium aurelia* and *Tetrahymena pyriformis*, some of whose sibling species appear to have a restricted distribution (Elliott 1973, Nanney and McCoy 1976, Sonneborn 1975). This indicates that time is a crucial factor for becoming a cosmopolite, as discussed below.

Dispersal by human activities

Biogeographic changes due to human activities have been largely ignored in the discussion of distribution of protists and small metazoans, although a number of examples are well known for a long time. For example, several tropical and indopacific species of foraminifera entered the Mediterranean Sea via the Suez Canal (Lesseps’ immigrants) and tropical aquaria. Moreover, it is likely that certain toxic dinoflagellates spread by human activities (Hallegraeff and Bolch 1992). In roti-

fers, many of which have a similar size as ciliates, *Brachionus havanaensis* and *Keratella americana* have been introduced to southeast Asia by human activities (Segers 2001).

Shipping (ballast water), the transport of goods, and the construction of canals are three major reasons for the artificial dispersal of protists. Millions of tons of water and many thousands of tons of soil are transported across the world each year. Hallegraeff and Bolch (1992) and Hülsmann and Galil (2002) suppose that since the introduction of water as ballast in the middle of the 19th century, many protists may have spread globally, unheeded by protozoologists. The diatoms *Odontella sinensis* and *Coscinodiscus wailesii* entered the North Sea and the Baltic Sea rather recently, together with their parasites (Kühn 1997, Hülsmann and Galil 2002). Likewise, *Lagenophrys cochinesis*, an ectosymbiotic ciliate of wood-boring, marine isopods, has probably been transported from New Zealand to California in wooden ship hulls rather recently (Clamp 2003), while the coccolithophore *Emiliania huxleyi* invaded the Black Sea about 1500 years ago (Winter *et al.* 1994). Elliott (1973) proposed that a species of the *Tetrahymena pyriformis* complex entered the Pacific Islands when man migrated westward from South and perhaps Central America. The same might have happened more recently with *Paramecium quadecaurelia*, a member of the *P. aurelia* sibling species complex. This species, which was known only from Australia, was recently reported from a pond of the city of Windhoek, the capital of Namibia, Africa (Przyboś *et al.* 2003). Dispersal by ship's ballast water might also be responsible for the occurrence of four euryhaline psammobiontic (obligate sand-dwelling) testate amoeba species in the Great Lakes, Canada (Nicholls and MacIsaac 2004).

Another impressive example is the appearance of *Hydrodictyon* in New Zealand where this very distinctive alga had never been seen before. It was found in a pond belonging to a hatchery supplying fish and aquatic plants to aquarists. Obviously, *Hydrodictyon* had been imported together with fish or aquatic plants from East Asia (Kristiansen 1996).

Spores of macrofungi, mosses and ferns show that small size and high numbers do not necessarily cause cosmopolitan distribution

It is a matter of fact that, at the morphospecies level, higher plants and animals usually have a more restricted distribution than micro-organisms. The reasons are unclear and difficult to exploit experimentally, but small size

and high numbers are assumed to play a major role (Fenchel 1993, Finlay *et al.* 1996, Finlay 2002). A more differentiated view is held by Kristiansen (2000), who concisely summarized the hypotheses on micro-organism dispersal and biogeography: "Round remarked that the occurrence of so many freshwater algae throughout the world is a reflection of ease of transport - yet for the majority there is no information on transport mechanisms. Dispersal may thus be successful only rarely and under especially favourable circumstances; still the dispersal mechanisms will work if only there is time enough. This has been expressed by Gislen 'Wherever a biotope suitable for a certain organism exists, that organism will appear there as soon as sufficient time has elapsed to allow it to be transported to and to settle in that locality'. This adds a time dimension to Beijerinck's statement that, in micro-organisms, everything is everywhere, the environment only selects. Thus, time is a crucial factor. This means that we can consider the distribution of a species as a momentary picture based on: Age of the species - Available dispersal vectors - Adaptations for dispersal - Suitable available localities - and Sufficient time. In a cosmopolitan species, all these parameters are in optimum".

Basically, I agree with all these statements and hypotheses, but they are incomplete because they do not explain why mosses, ferns and macrofungi have indisputable biogeographies, although their main dispersal means (spores) are in the size of large bacteria or small protists and are produced in gigantic numbers (Tryon and Tryon 1982, Webster 1983, Carlile and Watkinson 1994, Kramer *et al.* 1995, Schwantes 1996, Frahm 2001). Even some groups of flowering plants have seeds in the size of middle-sized *Paramecia* (100-300 µm), for instance, many species of the families Pyrolaceae, Orobanchaceae and Orchidaceae (Sitte *et al.* 1991; Foissner, unpubl.), and the Orchidaceae comprise more than 20,000 species! Further, many seeds of higher plants have highly effective morphological adaptations for air dispersal, but are not cosmopolites, although many of these "exotics" grow well in our home gardens. Morphological adaptations for air dispersal are unknown in cysts and spores of micro-organisms, suggesting that this kind of distribution never played a major role.

Mosses, ferns and macrofungi, altogether well above 40,000 species, have distinct biogeographies, although their spores are in the size of those of small protists, that is, have a usual range of 10-50 µm and are produced in astronomical numbers, for instance, a single *Agaricus campestris* releases 1.6×10^{10} spores in six days

(Webster 1983), which exceeds the abundance of ciliates in a m² of forest soil by several orders of magnitude (Meyer *et al.* 1989). This fact has been completely ignored by protist and general ecologists (Fenchel 1993; Azovsky 2000, 2002; Wilkinson 2001; Finlay 2002; Hillebrand 2002). In my opinion, it is impossible to explain their restricted distribution by more complex ecologies and/or biologies (e.g., sex) because these are found also in micro-organisms (Weisse *et al.* 2001, Hausmann *et al.* 2003). Even the mycotrophic orchids are no exception, if one assumes global distribution of micro-organisms (Finlay 2002). The same has been observed in freshwater invertebrates, where potential and actual dispersal rates differ greatly (Bohonak and Jenkins 2003). Although nobody will deny that micro-organisms, macrofungi, mosses, and ferns usually have larger areals than flowering plants and higher animals, the minute size of the dispersal stages does not cause global distribution. This casts strong shadow on the hypothesis of Wilkinson (2001) that organisms with a size of less than 100–150 µm are generally cosmopolitan because their low mass facilitates air distribution. As a consequence, the hypotheses that micro-organisms are distributed globally and have low species richness because of lack of opportunities for allopatric speciation (Fenchel 1993, Finlay 2002, Wilkinson 2001) are also doubtful. Thus, I favour the more differentiated view of Kristiansen (2000), cited above.

Conclusions: Not everything is everywhere

A rapidly increasing number of studies, ranging from bacteria to small metazoans, are beginning to challenge Beijerinck's "everything is everywhere" metaphor and its contemporary variants. The data available suggest that micro-organisms have distribution patterns similar to those known from higher plants and animals, and that these patterns reflect historical (Gondwanan/Laurasian), ecological (tropical/temperate), and continental/local conditions. However, the biogeographical patterns of protists are usually less distinct than those of multicellular organisms because (i) they appear to occupy wider ranges, (ii) reliable distribution data are rare for most groups, and (iii) at least half of their diversity is still undescribed, especially that of the rare species which tend to have more restricted distributions than the common euryoecious species. Notwithstanding these limitations by a lack of data, it is realistic to assume that at

least 30% of the protists are endemic (in the broadest sense).

Further research is necessary to assess to what degree historic, biological, climatic and habitat factors have contributed in creating the distribution patterns of micro-organisms. However, most specialists would agree on the following reasons:

(i) Historic (separation of Pangaea into Gondwana and Laurasia) and/or more recent (continental) geographic isolation were pivotal in limnetic and terrestrial ecosystems (Elliott, 1973; Bonnet 1983; Ferris and Ferris 1985; Najt and Weiner 1996; Reid 1998; Foissner 1999b; Kristiansen 2001; Foissner *et al.* 2002; Meisterfeld 2002a, b; Pawlowski and Holzmann 2002; Pucciarelli *et al.* 2003), while water current systems, temperature, and food played a major role in marine environments (Taylor and Pollinger 1987, Brand 1994, Roth 1994, Winter *et al.* 1994, Kemle-von Mücke and Hemleben 1999). More recently, artificial dispersal of micro-organisms by human activities increasingly masks the genuine distribution patterns.

(ii) Age of the species, that is, sufficient time to disperse. As many micro-organisms are much older than higher plants and animals (Cohan 2002, Arber 2004), this explains their usually wider distribution.

(iii) Limited cyst viability could be responsible for the restricted distribution of certain micro-organisms at large scale. At smaller scales, protected dispersal stages (cysts) explain the fast local distribution of euryoecious species, experimentally shown by Wanner and Dunger (2002) and others.

Lastly, we must take into account the 300 years and numerous taxonomists that were required to describe the world's mammals and higher plants, and even these lists are not yet complete (Cotterill 2005). Scientific protistology is just 150 years old and has attracted few taxonomists. Thus, it is not surprising that the majority of the protists is still undescribed, especially if their cryptic diversity due to developmental homeostasis is taken into account (Dini and Nyberg 1993, Nanney *et al.* 1998, López-García *et al.* 2003, Šlapeta *et al.* 2005). Thus, I agree with Nanney (2004): "We are all blind men trying to describe a monstrous elephant of ecological and evolutionary diversity".

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