

Diversity and geographic distribution of ciliates (Protista: Ciliophora)

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Abstract About 4,500 free-living ciliate morphospecies have been described, applying an average synonymy rate of 20%. We estimate that 83–89% of the ciliate diversity is still undescribed, using the following probabilities: detailed habitat studies suggest that the described number of morphospecies must be doubled: 4,500 → 9,000; this figure has to be increased by about 50% due to species with similar interphase morphology but different resting cysts: 9,000 → 13,500; the genetic and molecular data suggest that this value must be doubled or trebled: 13,500 → 27,000 to 40,000 free-living, biological ciliate species. The knowledge on geographic distribution of ciliates heavily depends on flagship species and statistical analyses because reliable faunistic studies are rare and molecular data are still in its infancy. We present a list of 52 ciliate flagship species as a testable hypothesis, i.e., the hypothesis of restricted distribution of certain ciliate species must be refused when a considerable number of them is found in all or most biogeographic regions. Flagship species and statistical analyses consistently show Gondwanan and Laurasian ciliate communities, suggesting that the split of Pangaea deeply influenced ciliate distribution and rare species play a key role in geographic differentiation. However, there is also substantial evidence for continental, regional, and local endemism of free-living ciliates. The molecular studies usually show a high level of genetic diversity underlying ciliate morphospecies, suggesting that morphologic and molecular evolution may be decoupled in many ciliate species. Molecular studies on ciliate biogeography are at variance, possibly because most are still focusing on single molecular markers. In sum, the data indicate that

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ciliate biogeography is similar to that of plants and animals, but with an increased proportion of cosmopolites, favouring the moderate endemicity model.

Keywords Actual and estimated diversity · Cyst species · Flagship species · Floodplains · Genetic and molecular diversity · Gondwana · Laurasia · Moderate endemicity model · Pangaea

Introduction

Ciliates are unicellular, heterokaryotic organisms having a macronucleus and a micronucleus of distinctly different size and function within the same cytoplasm (Raikov 1972). The macronucleus, which is usually highly polyploid (except of the curious Karyorelictea, where it is diploid and does not divide) and divides amitotically during asexual reproduction, controls mainly somatic functions, such as RNA synthesis and ontogenesis. The diploid micronucleus is active mainly during sexual reproduction, called conjugation (Raikov 1972; Corliss 1979).

Ciliates are found in a great variety of habitats and many live on or inside of various animals, for instance, the commensalic rumen ciliates and the special species which colonize the surface of crustaceans and water beetles; some are even true parasites, for instance, *Balantidium*, which infects humans, and *Ichtyophthirius*, which causes severe disease in fish. Thus, it is not surprising that ciliates have a lot of highly specific morphologies, making species very distinct, especially since we have methods to reveal cilia and their basal bodies very selectively by scanning electron microscopy and various methods of silver impregnation (for a review, see Foissner 1991).

The distinctness of morphospecies and the comparatively large size (most between 50 μm and 200 μm) causing ciliates to lead a major role in the discussion on protist diversity and distribution (for reviews, see Finlay et al. 1996, 2004 and Foissner 1999b, 2006). Indeed, the often large ($\geq 200 \mu\text{m}$) flagship species have dozens of distinct features, making them easily recognizable and unmistakable (Foissner 2007). Thus, both schools on protist diversity developed on ciliates, viz., the cosmopolitan model of Finlay et al. (1996) and the moderate endemicity model of Foissner (1999b, 2004b).

The present contribution deals with free-living species because these are independent of host distribution. Further, more and better data are available than on host-bound species. Likely, less than 10% of the commensalic and parasitic ciliates have been described because most potential host species have never been investigated, except of the rumen ciliates (Foissner 1999b).

Diversity

Described diversity of free-living ciliates

An index of described ciliate species is not available. Thus, the following figures are rough estimates. Corliss (2000) suggested a total of 8,000 described ciliate morphospecies, of which about 200 are fossil tintinnids and 2,600 are commensals s.l., leaving about 5,200 extant free-living species. Since that, about 400 new species have been described, about half each in individual papers and in monographs (Song and Wang 1999; Foissner et al.

2002; Foissner and Xu 2006). Thus, we arrive at about 5,600 described free-living ciliate species.

Not all described species are valid, i.e., some are junior synonyms. Five recent monographs estimated the following synonymy rates: class Colpodea (Foissner 1993a): 22%; family Oxytrichidae (Berger 1999): 33%; suborder Urostyloidea (Berger 2006): 30%; spathidiids (Foissner and Xu 2006): 3%; aloriccate Oligotrichea (Agatha, pers. comm): 10%. This gives an average synonymy rate of 20%, which is close to the 19% generic synonymy calculated by Aesch (2001). Applying this figure to the total estimate reported above, we arrive at about 4,500 valid, free-living ciliate species. Note that Berger (1999, 2006) miscalculated synonymy rates, not using the total number of species (valid and synonymous species) but only the valid ones.

Undescribed diversity of free-living ciliates

For a concise overview, we calculate the number of undescribed, free-living ciliate species ahead, providing the evidences in the following paragraphs. Applying the biological morphospecies concept, some crude calculations can be performed. The habitat studies suggest that we must at least double the described number of morphospecies: 4,500 → 9,000. This figure has to be increased by at least 50% due to the cyst species: 9,000 → 13,500. The genetic and molecular data suggest multiplying this figure by 5, at least. However, many of the “cyst species” and “ecological species” might be “genetic” and/or “molecular” species. Thus, we use conservative multipliers of 2 and 3: 13 500 → 27,000 to 40,000 free-living, biological ciliate species, that is, 83–89% of the ciliate diversity are still undiscovered.

Habitat studies. Combining classical and modern methods, a few researchers have discovered hundreds of new ciliate morphospecies during the past 15 years, suggesting that most ciliate diversity is still unknown (Foissner 1993a, b; Petz et al. 1995; Song and Wang 1999; Foissner et al. 2002; Foissner and Xu 2006). We shall briefly discuss some recent studies, showing that our ignorance is global and concerns all main habitats (see also Cotterill et al. this issue).

The Sphagnum ponds of Simmelried in Germany (Kreutz and Foissner 2006). The Simmelried is a three hectare-sized moorland which formed after the last ice-age, that is, about 15,000 years ago. There were about 700 species of bacteria, protists, and micro-metazoa which likely represent about two thirds of the morphospecies present. Many undescribed species were discovered, viz., at least 40 ciliates, 40 amoeboid organisms, and about 20 flagellates.

A statistical approach to estimate soil ciliate diversity and distribution (Chao et al. 2006). A total of 359 soil samples from Africa, Asia, Australia, South America, and Europe were investigated for ciliate diversity, using the monograph of Foissner et al. (2002) as a starting point. A total of 964 species were recorded, of which 320 were undescribed. The frequency distribution of species over samples was used for regional and global diversity estimation, applying the abundance-based coverage estimation (ACE) model. A consistent finding over all five continents was that at least half of the species diversity is still undiscovered, with a minimum of 1,928 species and a 95% confidence interval of 1600–2427 species (Table 1). This is consistent with the findings of Foissner (1997) who used a probability-based method.

Floodplain soils (Table 2). The results of Foissner (1997), Kreutz and Foissner (2006), and Chao et al. (2006) are sustained and surpassed by our data from floodplain soils, a

Table 1 Regional and global soil ciliate species diversity (from Chao et al. 2006)

Region	Subregion	Estimate of minimum species diversity	95% confidence interval	Percentage of unseen species (%)
Africa		900	(757, 1134)	41
	Kenya	217	(180, 285)	37
	Namibia	830	(685, 1078)	41
Asia		463	(319, 844)	50
Australia		865	(703, 1148)	44
Europe		706	(575, 937)	43
	Austria	446	(367, 601)	36
	Germany	552	(384, 971)	51
South America		638	(477, 971)	49
	Costa Rica	576	(377, 1100)	55
	Amazon	317	(254, 426)	46
Global		1928	(1600, 2427)	50

Table 2 Diversity and structure of floodplain soil ciliate communities

Floodplains	Total number of species	Freshwater species ^a	New or supposedly new species ^b
Danube River, Austria (2 samples from close sites)	86	28 (33%)	8 (10%)
Bukaos River, Namibia (1 sample)	90	22 (24%)	17 (19%)
Matjulu River, Krueger National Park, South Africa (1 sample)	79	32 (41%)	17 (22%)
Chobe River, Botswana (1 sample)	98	27 (27%)	26 (26%)
Niger River, Mali (2 samples from close sites)	79	20 (25%)	11 (14%)
Rio Corobici, Cost Rica (1 sample)	87	14 (16%)	5 (6%)
Amazon River, Brazil (2 samples from close sites)	112	27 (24%)	23 (21%)
Murray River, Australia (2 samples from close sites, year 1997)	110	35 (32%)	25 (23%)
Murray River, Australia (1 sample taken in year 2006 from same site as in year 1997)	79	31 (39%)	15 (19%)

^a Proportion for all described soil ciliates (643 species, Foissner 1998): 16%

^b Overlap of new species: <5%

generally highly diverse type of ecosystem which was never investigated for protist diversity. In 13 samples from nine sites, 137 undescribed species were discovered, that is, on average 11 new species/sample (Table 2). Considering that these few samples are a glimpse when compared to the earth's floodplain diversity, there must be thousands of undescribed ciliates in floodplain soils. Thus, the above mentioned estimates of Foissner (1997) and Chao et al. (2006) are likely too conservative, possibly applying mainly to ordinary soil.

Tank bromeliads (Foissner et al. 2003). In a combined morphological, molecular, and ecological approach, Foissner et al. (2003) discovered an endemic ciliate fauna in tank bromeliads, with species reaching a length of 800 μm (Figs. 2, 3). 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, above-ground ecosystem whose extensive compartmentalization obviously fosters speciation. As yet, we discovered about 50 undescribed ciliates in less than 100 samples mainly from Central America. Considering that there are about 3,000 bromelia species, many of which live in very specific habitats (e.g., Tepuis), their tanks likely contain hundreds of undescribed ciliate species.

Marine habitats. During the past 15 years, Weibo Song and his colleagues discovered about 150 undescribed, free-living and parasitic ciliate species at a single locality in China, viz., the coast near to the town of Qingdao (Song and Wang 1999; Song et al. 2003; and many individual papers, e.g., Xu et al. 2006). This matches data from Petz et al. (1995) and Dragesco (1999). Petz et al. (1995) found 46 ciliate species, of which 17 were undescribed, in Antarctic sea ice during a single cruise in the eastern Weddell Sea. Dragesco and Foissner discovered about 20 new species in the interstitial of two localities on the French coast (see Dragesco 1999 for a literature overview). Altogether, about 200 new marine ciliates have been described during the past 15 years by a few researchers, showing that the marine ciliates are as poorly known as those from freshwater and soil.

Cyst species. Most ciliates can survive adverse environmental conditions by forming a dormant stage, the so-called resting cyst. Foissner (1993a), Foissner et al. (2002) and Xu and Foissner (2005) showed that several morphologically highly similar species have different resting cysts. For instance, four very similar populations of *Epispathidium amphoriforme*, a common moss and soil ciliate, have different resting cysts, suggesting classification as different species (Foissner, unpublished). Likely, “cyst species” will increase the number of free-living ciliate species by 50% and play an important role in biogeography. Cyst morphology is increasingly used to distinguish species also in other protists. For instance, Jonckheere and Brown (2005) isolated the amoebaflagellate *Naegleria* from freshwater of Peru. Although there was little sequence difference between the new isolate and *N. pussardi* and both populations grew at 40°C, their cysts were very different and were thus used to define the new species *N. angularis*.

Genetic and molecular studies. Genetic and molecular evidences suggest that ciliates are greatly underclassified, by at least an order of magnitude, and perhaps by two orders of magnitude (Nanney et al. 1998). Dini and Nyberg (1993) reviewed the mating types of 24 species, of which 19 turned out to be a complex of morphologically highly similar taxa composed of up to 16 biological species. On average, the 24 species each consist of five biological species that do not interbreed. Taking this figure as a rough measure, the 4,500 described, valid ciliate morphospecies likely represent 22,500 biological species!

The genetic data are increasingly sustained by molecular investigations, not only in *Paramecium* (Strüder-Kypke et al. 2000; Barth et al. 2006; Hori et al. 2006) and *Tetrahymena* (Lynn and Strüder-Kypke 2006), the pets of the ciliatologists, but also in other species, such as *Carchesium polypinum* (Miao et al. 2004; Zhang et al. 2006), *Halteria grandinella* (Katz et al. 2005), *Strombidium oculatum* (Katz et al. 2005), *Stylonychia lemnae* (Schmidt et al. 2006), and *Cyclidium glaucoma* (Finlay et al. 2006). These studies consistently show a high genetic diversity underlying ciliate morphospecies that likely will be described as distinct species in the near future (Fig. 1); indeed, this has begun in both ciliates (Foissner and Berger 1999) and heterotrophic flagellates (Hausmann et al. 2006).

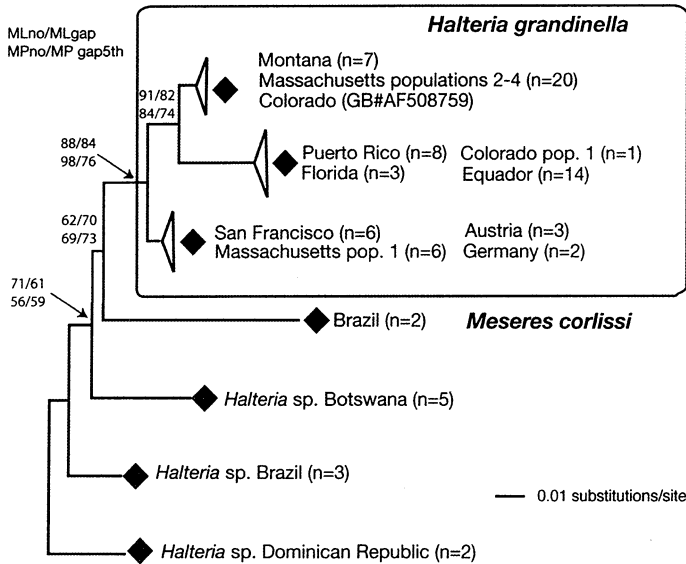


Fig. 1 *Halteria grandinella* is a very common, cosmopolitan ciliate. However, populations from different sites differ significantly in the ITS nucleotides, which even include a related species, *Meseres corlissi*. Morphologically, most populations are very similar. The figure shows a maximum-likelihood analysis of the ITS sequences. Bootstrap values are shown at nodes: upper values are maximum-likelihood with gaps removed (MLno), and maximum likelihood with gaps included (MLgap); lower values are maximum parsimony with gaps excluded (MPno), and maximum parsimony gaps treated as 5th character (MPgap5th). From Katz et al. (2005)

In only a few cases have widely-sampled isolates of ciliate morphospecies been shown to lack substantial genetic diversity, for instance, *Laboea strobila* (Katz et al. 2005).

Although most molecular studies to date have focused on only a single marker, one multimarker study of two *Paramecium* morphospecies revealed substantially different levels of variation between nuclear-encoded ITS sequences and mitochondrial cytochrome oxidase I (COI) sequences (Barth et al. 2006). Populations of *Paramecium caudatum* sampled from several sites in Europe plus a single site in China and Australia are identical at the ITS locus but show two distinct clusters for COI (Europe and China + Australia). Similarly, isolates of *Paramecium multimicronucleatum* fall into two ITS clusters but four divergent COI clusters, though there is no clear geographical pattern. Barth et al. (2006) discuss possible explanations for the observed patterns including elevated rates of mitochondrial sequence evolution compared to nuclear sequences and cryptic speciation.

The consistently high genetic diversity underlying many ciliate morphospecies suggests that morphological and molecular evolution may be decoupled in many ciliate species. Under such a scenario, morphospecies may often represent multiple genetically-isolated populations. At the same time, different morphotypes of some ciliates such as tintinnids have been shown to share identical sequences at the ITS locus (Snoeyenbos-West et al. 2002), and ecotypic variation in morphology has been demonstrated experimentally in this clade (Laval-Peuto 1981). Elucidation of the relative rates of morphological and molecular evolution in ciliates requires further analyses of multiple markers from broadly sampled morphospecies.

Ecological studies. Clonal cultures of ciliates usually reveal pronounced differences in many ecophysiological parameters, such as cell volume, growth rate, and production (for a review, see Weisse 2004). A numerical model suggests that differences in growth rates by 10% may significantly alter the clonal composition in the course of a ciliate peak (Weisse and Rammer 2006). Thus, Weisse and Rammer (2006) agree with Nanney et al. (1998) that the functional diversity of ciliates is considerably larger than it is obvious at the morphospecies level; further, they emphasize that the morphospecies concept grossly underestimates the number of species, the number of niches, and the complexity of ecosystems.

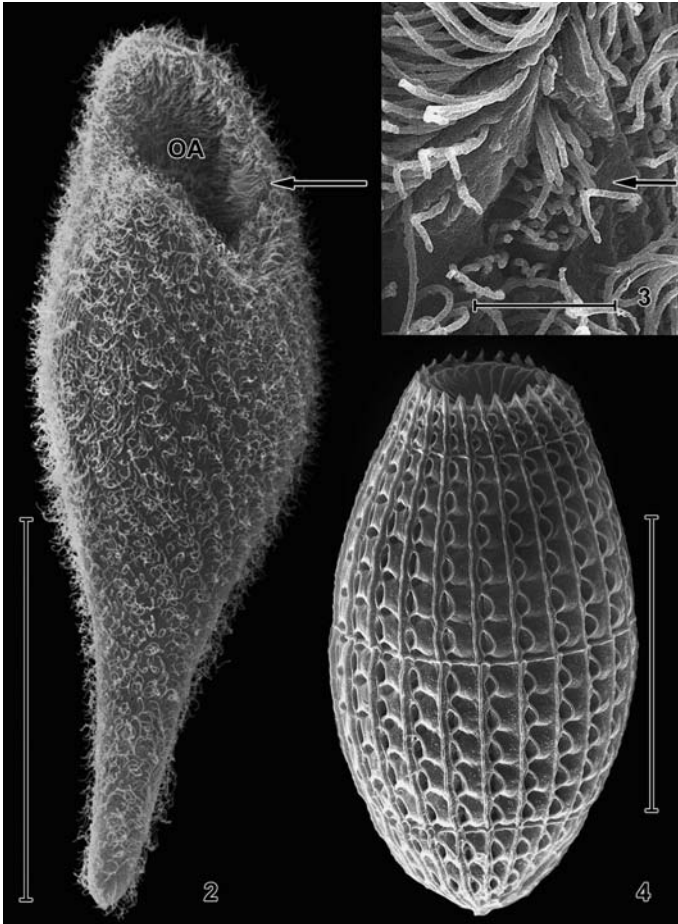
Unfortunately, the morphospecies concept is the only one which works in practice. Certainly, the biological species concept is preferable, but it is a matter of fact that more than 90% of the described species were never tested for mating, both in protists and animals; the same applies to ecological populations and clones. Thus, new ideas are needed to reconcile ecological, molecular and morphological diversity.

Geographic distribution

Flagship species

Ciliates have complex morphologies which can be clearly revealed by several methods, especially silver impregnation and scanning electron microscopy (Figs. 2–4). Thus, it is not surprising that we have sound evidences for a restricted distribution of many species. Here, for the first time, we provide a list of supposed endemics (Table 3), containing so-called flagship species which are, according to Tyler (1996) and Foissner (2006), the “ultimate proof” for protist endemism. Flagships are so showy, or so novel, making it unlikely that they would be overlooked if indeed they were widely distributed. We emphasize that the species listed in Table 3 are just a selection; they could be easily doubled! However, some doubt remains because (i) flagships could be too rare to be met in even detailed studies and (ii) reliable distribution data are rare, even for conspicuous species. For instance, *Puytoraciella dibryophrys*, an about 250 µm long colpodid described in 1979 from a temporary pond in West Africa (Foissner 1993a), has been recently found in a similar habitat of North America (Bill Bourland, personal communication). Further, we usually cannot decide whether such species are local, regional or continental endemics because large regions of the world never have been carefully investigated for ciliates (Cotteril et al., this issue). In the sense of Popper (1962), this list represents a testable hypothesis, i.e., the hypothesis of restricted distribution of certain ciliate species must be refused when a considerable number of them is found in all or most biogeographic regions.

Most of the species listed in Table 3 are likely historical (split of Pangaea) or continental endemics, for instance, *Neobursaridium gigas* and *Frontonia vesiculosa*. Others are regional or local endemics, for instance, the colepids of the ancient lakes (Lake Baikal, Lake Biwa, Lake Tanganyika). However, regional and local endemics are found not only at these famous places but also in more ordinary biotopes, as reviewed by Foissner (2007). Very recently, Stoeck et al. (2007) discovered such a species in a remote alpine lake in Germany. This ciliate is highly similar to the likely cosmopolitan *Urocentrum turbo*, both morphologically and in various molecular characteristics, but lost the ability to produce functional trichocysts. A similar case has been reported by Esteban et al. (2000), who discovered a very distinct *Lembadion* in a remote lake of Tasmania. Another example is the study by Kreutz and Foissner (2006) who found 250 ciliate species, of which 40 were



Figs. 2–4 Two undescribed ciliate flagship species in the scanning electron microscope. **2, 3:** A new, tetrahymenid ciliate from tank bromeliads. This up to 800 μm long ciliate has a functionless, minute primary oral apparatus (arrows) and a large secondary mouth (OA) used to capture large prey, e.g., rotifers. Scale bars 100 μm and 5 μm . From Foissner et al. (2003). **4:** A new colepid flagship from lake Biwa, a 4 million years old freshwater lake in Japan. This ciliate is about 80 μm long in vivo and armed with calcified plates. It is related to the widely distributed *Coleps hirtus*, but lacks the posterior spines and is genetically different by 7%. Scale bar 30 μm . From Foissner, Kusuoka and Shimano (submitted)

likely undescribed, in postglacial moorland ponds. Obviously, a considerable diversity accumulated over 15,000 years, emphasizing the great distribution capacity of microorganisms. On the other hand, some common species were lacking, for instance, the ciliate *Colpidium colpoda*, the euglenid *Phacus pleuronectes*, and rotifers of the genera *Proales* and *Floscularia*.

While a mass of undescribed species is comprehensible in amoebae, heterotrophic flagellates and ciliates, which are poorly researched, this is surprising in well-known groups, such as euglenids and chrysophytes. Thus, the authors concluded that some of the undescribed species might be regional or local endemics.

Table 3 Ciliate flagship species with very likely restricted geographic distribution

Species	Habitats	Geographic distribution ^a	References ^b
<i>Apofrontonia dohrni</i>	Mud from coastline puddles	Europe, Italy	Foissner (2007)
<i>Apofrontonia lametschwandneri</i>	Mud from coastline puddles	South America, Venezuela	Foissner (2007)
<i>Apofrontonia obtusa</i>	Freshwater pond	Europe, Germany	Foissner (2007)
<i>Baikalocoleps quadratus</i>	Sand of open littoral	Russia, Lake Baikal	Obolkin (1995)
<i>Bresslauides australis</i>	Forest soil	Australia	Foissner (1993a)
<i>Bresslauides discoideus</i>	Soil and moss	Europe, Japan, Central America	Foissner (2006)
<i>Bromeliophrya brasiliensis</i>	Bromelian tanks	South America, Brazil	Foissner (2003)
<i>Bryophyllum longisetum</i>	Soil	Tropical Africa, Kilimanjaro	Foissner (2007)
<i>Circinella arenicola</i>	Sand dunes	USA, Utah	Foissner (1994)
<i>Condylostomides etoschensis</i>	Swamp soil	Africa (Namibia, Benin)	Foissner et al. (2002)
<i>Corticocolpoda kaneshbergi</i>	Tree bark	Hawaii	Foissner (1993b)
<i>Cosmocolpoda naschbergi</i>	Coastal soil	Central America	Foissner (1993a)
<i>Cyrtohymena (Cyrtohymenides) aspoeki</i>	Floodplain soil	Austria	Foissner (2004a)
<i>Eschaneustyla lugeri</i>	Rainforest soil	Fiji Islands	Foissner et al. (2002)
<i>Etoschothrix terricola</i>	Swamp soil	Africa, Namibia (Etosha Pan)	Foissner et al. (2002)
<i>Frontonia vesiculosa</i>	Freshwater	Tropical Africa, South America	Dragesco and Dragesco-Kernéis (1986)
<i>Fungiphrya strobli</i>	Pond mud	South Africa, Table mountain	Foissner (1999a)
<i>Heterostentor coeruleus</i>	Marine littoral	Antarctica	Song and Wilbert (2002)
<i>Holosticha foissneri</i>	Sea ice	Antarctica (Weddell Sea)	Petz et al. (1995)
<i>Jaroschia sumptuosa</i>	Tree bark	Australia, rainforest near Cairns	Foissner (1993a)
<i>Kentrophyllum antarcticum</i>	Sea ice	Antarctica (Weddell Sea)	Petz et al. (1995)
<i>Koimia affinis</i>	Sand of open littoral	Russia, Lake Baikal	Obolkin (1995)
<i>Koimia arcuata</i>	Sand of open littoral	Russia, Lake Baikal	Obolkin (1995)
<i>Koimia heterolobata</i>	Sand of open littoral	Russia, Lake Baikal	Obolkin (1995)

Table 3 continued

Species	Habitats	Geographic distribution ^a	References ^b
<i>Krassniggia auxiliaris</i>	Rainforest soil	Africa (Kenya) and Australia	Foissner (1993a)
<i>Kuehneliella muscicola</i>	Moss	Germany	Foissner (1993a)
<i>Kuehneliella namibiensis</i>	Tree bark	Africa, Namibia	Foissner et al. (2002)
<i>Kuehneliella terricola</i>	Grassland soil	Australia	Foissner (1993a)
<i>Levicoleps biwae</i>	Littoral	Japan, Lake Biwa	Foissner et al. (submitted)
<i>Loxoccephalus foissneri</i>	Freshwater pools	Tropical Africa, Lake Tanganyika	Dragesco and Dragesco-Kernéis (1991)
<i>Loxodes rex</i>	Freshwater	Tropical Africa, possibly Thailand	Foissner et al. (2002)
<i>Luporinophrys micelae</i>	Soil from coastline puddles	South America, Venezuela	Foissner (2005)
<i>Macrocoleps aculeatus</i>	Sand of open littoral	Russia, Lake Baikal	Obolkina (1995)
<i>Macrocoleps caudatus</i>	Sand of open littoral	Russia, Lake Baikal	Obolkina (1995)
<i>Maristentor dinoferus</i>	Coral reefs	Pacific Ocean	Lobban et al. (2002)
<i>Maryna namibiensis namibiensis</i>	Ephemeral pool	Africa, Namibia	Foissner et al. (2002)
<i>Maryna n. costaricensis</i>	Ephemeral pool	Central America	Foissner et al. (2002)
<i>Neobursaridium gigas</i>	Freshwater	Tropical Africa, South America	Dragesco and Dragesco-Kernéis (1986)
<i>Neokeronopsis aureus</i>	Floodplain soil	South Africa, Krueger National Park	Foissner and Stoeck (submitted)
<i>Neokeronopsis spectabilis</i>	Freshwater	Europe, China	Foissner and Stoeck (submitted)
<i>Notoccephalus parvulus</i>	Marine	Antarctica (Weddell Sea)	Petz et al. (1995)
<i>Onychodromus quadricornutus</i>	Freshwater	China, India	Berger (1999)
<i>Planicoleps psammophilus</i>	Littoral sand	Tropical Africa, Lake Tanganyika	Dragesco and Dragesco-Kernéis (1991)
<i>Protospathidium namibicola</i>	Dune sand	Africa, Namibia (Namib Desert)	Foissner et al. (2002)
<i>Rigidolothrix goiseri</i>	Floodplain soil	Tropical Africa, Niger River	Foissner and Stoeck (2006)
<i>Rostrophrya regis</i>	Ephemeral pool	Tropical Africa, Cameroun	Foissner (1993a)
<i>Saundithrix terricola</i>	Field and floodplain soil	Saudi Arabia, China	Berger et al. (2006)
<i>Sleighophrys pustulata</i>	Soil from coastline puddles	South America, Venezuela	Foissner (2005)

Table 3 continued

Species	Habitats	Geographic distribution ^a	References ^b
<i>Stentor araucanus</i>	Lake plankton	South America	Foissner and Wölfl (1994)
<i>Supraspathidium armatum</i>	Swamp soil	Africa, Namibia (Etosha Pan)	Foissner et al. (2002)
<i>Tiarinella gracilis</i>	Sand of open littoral	Russia, Lake Baikal	Oboolkina (1995)
<i>Vermioxytricha arenicola</i>	Sand dunes	Africa (Tunisia, Namib desert)	Foissner et al. (2002)

Note that this list contains (i) only a small selection of especially conspicuous species, (ii) includes only such flagships which have been described or redescribed with modern methods, and (iii) refers only to free-living ciliates, that is, excludes the many conspicuous species living on or inside certain hosts, e.g., on water beetles or in the digestive tract of metazoans

^a Gives the area and/or the locality a certain species has been found. Considering our ignorance of ciliate diversity and distribution, it is likely that the range is often larger. However, we consider it as unlikely that one of these species crosses the ancient Gondwanan-Laurasian border. For instance, *Stentor araucanus*, as yet found only in various lakes of South America (Foissner and Wölfl 1994) may occur also in Australia, but not in the Holarctic

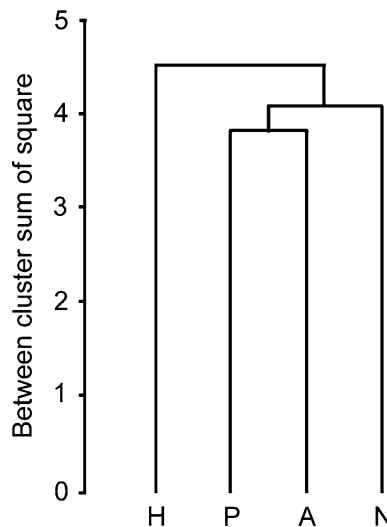
^b For space constraints, often only reviews or monographs are cited

Last but not least, vicarious species should be mentioned, as discussed by Foissner (2007), using as examples species of the genera *Kuehneliella* and *Apofrontonia* (Table 3). Very recently, we found other impressive examples. The first are species of the genus *Neokeronopsis*. *Neokeronopsis spectabilis* was described in the thirties of the past century and is a 300–400 μm long size-flagship, as yet found only in central Europe and China with altogether only eight records (Berger 2006). Foissner and Stoeck (submitted) discovered a new *Neokeronopsis* species in floodplain soil from South Africa. It differs from *N. spectabilis* not only in many morphological features but also in ontogenetical details, suggesting it as a representative of a distinct subgenus. The second example is the recently described *Saudithrix terricola* from field soil of Saudi Arabia (Berger et al. 2006). When the paper was in press, we found this conspicuous ciliate in soil from the Yangtse river floodplain in China, and some weeks later, Foissner discovered a new *Saudithrix* species in soil from the Chobe river floodplain in Botswana, tropical Africa. These and similar observations strongly formed Foissner's view that not everything is everywhere, both in higher and lower (micro) organisms.

Statistical studies

Large, reliable data sets on the geographic distribution of ciliates are, unfortunately, available only for terrestrial biota. Foissner (1998) and Foissner et al. (2002) investigated ciliates in over 1,000 soil samples from all biogeographic regions. Later, unpublished data were added and the whole data set analysed with new statistic tools (Chao et al. 2006). The similarity cluster resulting from the distribution of the 1,136 ciliate species clearly shows not only the separation of Laurasian from Gondwanan soil ciliate biota, but also differences within the Gondwanan sites (Fig. 5). This provides convincing statistical support for the influence of historic events on the distribution of soil ciliates, viz., the split of Pangaea and continental drift. A further study showed that geographic differentiation is related to the rare species which thus would play a key role in future studies (Chao et al. in preparation).

Fig. 5 World soil ciliate species cluster based on the classic Jaccard dis-similarity index and Ward's error sum of squares. From Chao et al. (2006). A—Australis, AR—Archinotis, H—Holarctis, N—Neotropis, P—Palaeotropis



Considering the rarity of such data, we analysed the occurrence of the free-living (= freshwater, marine, and soil) species contained in the monographs and revisions of Foissner (1993a) and Berger (1999). This resulted in clusters very similar to that obtained from soil ciliates (Figs. 5–7), and suggests that the conclusions drawn above are valid for ciliates as a group.

The results of Foissner (1998), Foissner et al. (2002) and Chao et al. (2006) match the conclusions of Hillebrand et al. (2001), Green et al. (2004) and Telford et al. (2006) that similarity in species composition of various microbial assemblages generally exhibits a decreasing trend as distance increases, implying the absence of ubiquity and the existence of geographic differences.

Another possibility to test distribution patterns offers the neutral model, as shown by Řezáčová and Neustupa (2007). We used this and a modified model to calculate the probability of restricted southern or northern distribution for some proposed endemics. The

Fig. 6 The Colpodea similarity (Jaccard) cluster is based on 194 species revised/described in Foissner (1993a, 1998) and Foissner et al. (2002). Further, 25 undescribed species from sites globally are included. Thus, it is based on 219 well defined species. A—Australis, AR—Archinotis, H—Holarctis, N—Neotropis, P—Palaeotropis

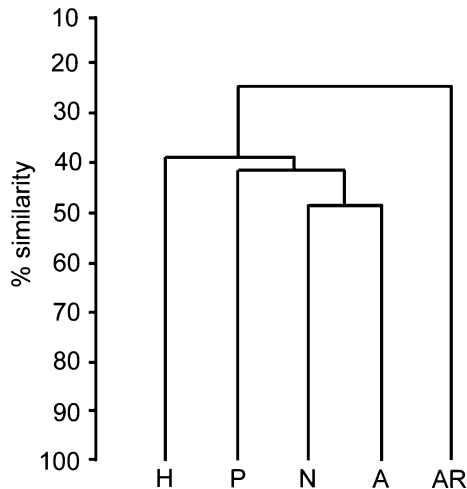


Fig. 7 The oxytrichid similarity (Jaccard) cluster is based on 191 species revised/described in Foissner (1998), Berger (1999) and Foissner et al. (2002, 2005). A—Australis, AR—Archinotis, H—Holarctis, N—Neotropis, P—Palaeotropis

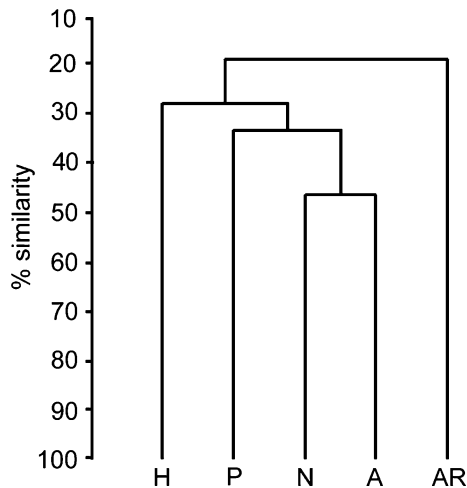


Table 4 Distribution of some proposed endemics according to the neutral model, using the formula of Řezáčová and Neustupa (2007)

Species	Group	Number of samples and occurrence ^a	Probability of restricted southern or northern occurrence
<i>Nebela (Apodera) vas</i>	Testate amoeba	100/80/220/0	0.000
<i>Hemimastix amphikineta</i>	Flagellate	350/42/400/0	0.000
<i>Bresslauides discoideus</i>	Ciliate	350/0/400/10	0.002
<i>Rigidothrix goiseri</i>	Ciliate	200/1/800/0	0.200
<i>Neobursaridium gigas</i>	Ciliate	150/6/1000/0	0.000

^a The four numbers are: southern samples, positive southern samples, northern samples, positive northern samples. For calculation of probability, see Řezáčová and Neustupa (2007). The numbers are based on original investigations (e.g., Chao et al. 2006; Foissner 1998, 2006; Foissner et al. 2002) and critical evaluation of literature data from many sources

Table 5 Distribution of the species shown in Table 4, using a formula that considers missing reports due to undersampling

Species	D = {A, Z, x} ^a	Posterior probabilities ^c for		
		Hypothesis 1	Hypothesis 2	Hypothesis 3 ^b
<i>Nebela (Apodera) vas</i>	320/100/80	0.000	0.270	0.730
<i>Hemimastix amphikineta</i>	750/350/42	0.000	0.270	0.730
<i>Bresslauides discoideus</i>	750/400/10	0.001	0.269	0.729
<i>Rigidothrix goiseri</i>	1000/200/1	0.127	0.235	0.638
<i>Neobursaridium gigas</i>	1150/150/6	0.000	0.269	0.731

^a The three numbers describe: A, the number of all independent reports worldwide; Z, the number of independent reports from a particular region, e.g., the northern hemisphere; x, the number of independent reports of a particular species

^b Hypothesis 1 (H1): neutral dispersal model, i.e., individuals of a species are randomly distributed worldwide, implying the chance finding this species is the same in the northern and southern hemisphere. Hypothesis 2 (H2): the species occurs worldwide, but the chance finding it in the northern hemisphere is different from that in the southern hemisphere, i.e., missing in southern reports due to undersampling. Hypothesis 3 (H3): the species occurs only in the northern or southern hemisphere

^cThe posterior probabilities (P) for each hypothesis are calculated with Bayer's theorem:

$$P(H1|D) = \frac{P(D|H1) \cdot P(H1)}{P(D|H1) \cdot P(H1) + P(D|H2) \cdot P(H2) + P(D|H3) \cdot P(H3)} \quad P(H2|D) = \frac{P(D|H2) \cdot P(H2)}{P(D|H1) \cdot P(H1) + P(D|H2) \cdot P(H2) + P(D|H3) \cdot P(H3)}$$

$$P(H3|D) = \frac{P(D|H3) \cdot P(H3)}{P(D|H1) \cdot P(H1) + P(D|H2) \cdot P(H2) + P(D|H3) \cdot P(H3)}$$

results confirm restricted distribution for all species with a probability of >95% (Tables 4, 5). The modified formula shows that undersampling plays a minor role if sample numbers are as high as in our examples (Table 5).

Molecular studies

Molecular biogeography of ciliates has just begun, and many studies to date have focused on only a single molecular marker from relatively limited geographical samples. Katz et al. (2005) found evidence of restricted southern and northern hemisphere ITS haplotypes in

the cosmopolitan morphospecies *Halteria grandinella* (Fig. 1). Similarly, Schmidt et al (2006) characterized a single nucleotide polymorphism in the SSU-rDNA gene between Eurasian and North American isolates of *Stylonychia lemnae*.

Speciation as a consequence of geographic barriers has been proposed in studies of the freshwater species *Carchesium polypinum* (Miao et al. 2004) and *Halteria grandinella* as well as the tide pool species *Strombidium oculatum* (Fig. 1). The study by Miao et al. (2004) investigated the cosmopolitan ciliate *Carchesium polypinum* in China. The 18S-ITS1-5.8S rDNA separated the 19 populations analyzed into a northern and a southern phylogroup, basically matching those found in the fish fauna. More recent multilocus analysis of this taxon using inter-simple sequence repeat (ISSR) fingerprinting reveals little evidence of isolation by distance in local contemporary populations (Zhang et al. 2006). Similarly, Katz et al. (2005) argue that past geographic isolation explains the high level of genetic diversity underlying morphospecies found in habitats that are unstable over evolutionary time periods (e.g., tide pools).

For a few ciliate morphospecies, evidence has been found of high gene flow for at least some haplotypes, though these studies have also largely focused on only a single genetic marker. For example, identical haplotypes of *Strombidium oculatum* and *Laboea strobila* have been found on either side of the Atlantic Ocean (Katz et al. 2005). Similarly, there was no evidence of geographic patterns for haplotypes of *Cyclidium glaucoma*, despite the high genetic diversity underlying this morphospecies (Finlay et al. 2006). Identical (or nearly identical) haplotypes are also widespread in the freshwater species *Paramecium multimicronucleatum* and *P. caudatum* (Barth et al. 2006).

Culture-independent sampling can reveal additional insights into the biogeography of microbes. While ciliates have been sampled in numerous eukaryotic-specific surveys of microbial diversity, we are aware of only one study that focuses explicitly on ciliates (Doherty et al. submitted). These authors used primers specific for oligotrich and choreotrich ciliates to look at diversity from three Northwestern Atlantic sites sampled each in fall and spring. The bulk of haplotypes found were rare, being represented by less than two sequences in a survey of over 600 clones. Moreover, while the level of diversity was similar in all six samples, the membership within the communities varied by site and time. A few haplotypes were common to most sites, including haplotypes identical to a published sequence for *Pelagostrobilidium neptuni* and *Strombidium biarmatum*, both originally sampled from Italy (Agatha et al. 2005). Yet, the bulk of the SSU-rDNA sequences in this study had no match to sequences available from GenBank. Clearly, substantially more ciliate-specific studies are needed to assess the diversity and biogeography of uncultured ciliates.

A related emerging controversy centers on the effective population size of ciliates. Effective population size reflects the evolutionary history of populations and can be measured by the level of standing neutral variation within a species. If a strictly cosmopolitan hypothesis is true such that census population sizes are large and relatively stable over time, then one might expect ciliate populations to contain high levels of neutral variation as has been argued for *Tetrahymena thermophila* (Gerber et al. 2002; Lynch and Conery 2003) and for several species of *Paramecium* (Snoko et al. 2006). Reanalysis of the *SerH* locus used in the *Tetrahymena* studies revealed that this protein-coding gene is likely under balancing selection and therefore not a good marker for effective population size (Katz et al. 2006). In contrast, little to no silent site variation was found in an overlapping sample of natural isolates of *T. thermophila*, indicating that at least this ciliate has a low effective population size (Katz et al. 2006). This observation is consistent with the limited geographic distribution of *T. thermophila* (Foissner 2006).

Data on *Paramecium* isolates are more controversial. Observations of high levels of diversity in nuclear and mitochondrial protein coding genes from several species have been used as evidence of high effective population sizes in *Paramecium* (Snoko et al. 2006). Similarly, Barth et al. (2006) see high levels of diversity within two *Paramecium* species and recognize that, in addition to a large effective population size, alternative explanations for the observed data include undescribed syngens within this genus. Finally, Zufall et al. (2006) have demonstrated that ciliates have elevated rates of protein evolution when compared to other eukaryotes and suggest that these elevated rates may obscure estimates of effective population size from analysis of silent site variation.

Rather than two alternative explanations for the biogeography of ciliates (endemism versus cosmopolitanism), we argue that there are likely numerous patterns of distribution in ciliate morphospecies. For example, a moderate endemism model indicates that two thirds of protists are expected to be distributed globally (Foissner 2006). Moreover, there are likely complex interactions between levels of current gene flow and genetic diversity underlying morphospecies as some of them are likely subject to low gene flow and low genetic diversity, e.g., *T. thermophila* (Katz et al. 2006); some morphospecies may have high gene flow and high genetic diversity, e.g., *P. multimicronucleatum* and *P. caudatum* (Barth et al. 2006), as well as *H. grandinella* and *S. oculatum* (Katz et al. 2005) and *Cyclidium glaucoma* (Finlay et al. 2006); while still others may have high gene flow and low genetic diversity, e.g., *Laboea strobila* (Katz et al. 2005).

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