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Global soil ciliate (Protozoa, Ciliophora) diversity: a probability-based approach using large sample collections from Africa, Australia and Antarctica

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Large sample collections from Africa (92 samples), Australia (157) and Antarctica (90) were investigated for soil ciliates using the non-flooded Petri dish method, which re-activates the ciliates' resting cysts from air-dried samples. Species were determined from life and by silver impregnation. The African samples were the richest, containing 507 species (240 undescribed, = 47%), followed by the Australian (361 species, 154 = 43% undescribed) and the Antarctic (95 species, 14 = 15% undescribed) samples. The percentage of new species/sample was consistently low, viz. 4–8% on average, indicating that new species were considerably undersampled relative to described ones, very probably due to methodological shortcomings, i.e. usually only cysts of the more euryoecious species could be reactivated. Thus, a probability theory-based statistical approach was applied to the data sets to compensate for the underestimated number of undescribed species. This procedure indicated that, depending on the region, 70–80% of the soil ciliates are still unknown and global soil ciliate diversity amounts to at least 1330–2000 species. Several indicators, especially the constant rate at which new species have been found during a 20-year period of intensive research, suggest that this estimate is conservative.

Keywords: soil protozoa; soil ciliates; global diversity; Africa; Australia; Antarctica.

Introduction

There is general agreement that microorganisms, including the smaller fungi, algae and protozoa, as well as bacteria and viruses, present the greatest challenge to any serious attempt at assessing the overall scale of global species richness (Vickerman, 1992; World Conservation Monitoring Centre, 1992; O'Donnell *et al.*, 1994). About 40 000 extant protozoan species have been described (Vickerman, 1992), including 8000 ciliates (Corliss, 1984) of which about 600 were originally discovered in terrestrial habitats (Foissner, 1997).

Reliable field studies on global protozoan diversity are lacking for any habitat and region. However, new protozoa are being described at a rather constant rate of about 360 species/year (World Conservation Monitoring Centre, 1992), and Finlay *et al.* (1996) tried to estimate global diversity of free-living ciliates by an extensive literature evaluation. They concluded that the majority of ciliates in the more frequently studied habitats, such as rivers and ponds, have probably already been discovered and may number close to 3000 species. However, they also emphasized that an accurate picture of ciliate diversity on a global scale requires substantial taxonomic revisions, together with the investigation and description of new forms from previously unexplored habitats.

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Terrestrial protozoan diversity has been underestimated for a long time owing to superficial taxonomy. The view prevailed that soil protozoa were common invaders from freshwater habitats (for review, see Foissner, 1987). It was only rather recently that some scientists recognized that soils are inhabited by a rich and highly specific protozoan fauna (Foissner, 1987, 1997). Since 1980, I have thus concentrated my research activities on sampling and analysing ciliates from terrestrial habitats worldwide. About 700 new species were discovered whose full description will require years of work, though some have already been described (for reviews, see Foissner 1987, 1997).

These large sample collections provided an excellent means for calculation and speculation regarding global soil ciliate diversity, using the probability theory-based approach proposed by Hodkinson and Hodkinson (1993). The main result of this analysis was that at least 70–80% of the soil ciliates are still undiscovered. Possibly, this is true also in other habitats, including those addressed by Finlay *et al.* (1996), who did not take into account that most studies they analysed were cursory, i.e. did not investigate species richness in detail. In fact, many descriptions were based on occasional observations. 'Directed' studies, i.e. detailed investigations of certain ciliate groups and/or habitats by recognized specialists, often almost doubled the species known (e.g. Hadži, 1951; Biegel, 1954; Dragesco, 1960; Jankowski, 1973; Foissner, 1980, 1993; Song and Wilbert, 1989).

Materials and methods

Areas and sampling

Samples were collected in tropical (Kenya) and subtropical (Namibia, Republic of South Africa) Africa, Australia and Tasmania, Antarctica (including two islands in the southern oceans), and, for comparison only, in Europe. Details about the areas are provided in Table 1 and in the respective results section. Generally, collections were made from a variety of biotopes covering most principal soil and vegetation types of the respective region.

The material collected usually included mineral top soil (0–5 cm depth) with fine plant roots, the humic layer, and the deciduous and/or grass litter from the soil surface. Furthermore, many samples contained some terrestrial mosses with adhering soil and/or bark from trees. All these habitats are referred to as 'terrestrial', as opposed to freshwater, because they contain, although in varying amounts, true humic and mineral soil (Foissner, 1987). Usually, about 10 small subsamples were taken from an area of about 100 m^2 and mixed to a composite sample. All samples were air-dried for at least 1 month and then sealed in plastic bags. Such samples can be stored for years without any significant loss of species (Foissner, 1987, and unpublished results).

Sample processing and faunistic methods

All collections were analysed with the non-flooded Petri dish method as described in Foissner (1987). Briefly, this simple method involves placing 10–50 g terrestrial material in a Petri dish (10–15 cm in diameter) and saturating but not flooding it with distilled water. Such cultures were analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21 and 28.

Identification of species was according to the literature cited in Foissner (1987, 1997). Most of the species found were either new or had been described or re-described by my students and myself. Thus, determinations were done mainly on live specimens using a high-power oil-immersion objective and differential interference contrast microscopy. However, all 'difficult', new or supposedly new, species were treated with the silver staining techniques described in Foissner (1991). Usually, these methods yield permanent slides which have been or will be deposited in the Oberösterreichische Landesmuseum in Linz (LI).

Species concept

The species concept, of course, influences the number of species found and/or recognized as 'undescribed' (Luckow, 1995; McDade, 1995). I usually apply the phylogenetic species concept as defined by Nixon and Wheeler (1990): 'A species is the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)'. Basically, this is a morphospecies concept which is, according to Ehrendorfer (1984) and Finlay *et al.* (1996), as valid as any, and probably more pragmatic than any other; see Ehrendorfer (1984), Luckow (1995) and McDade (1995) for detailed discussions.

I do not consider myself a splitter, i.e. I classify new species as such only when populations can be separated from their nearest relatives by at least one distinct (non-morphometric) morphological character. For examples, see Blatterer and Foissner (1988) and Foissner (1993).

Data arrangement and statistics

Most of the taxonomic and faunistic data upon which the present paper is based have not yet been published, the colpodids being a paradigmatic exception (Foissner, 1993, 1997) because the full description of hundreds of new species is very time-consuming. On the other hand, the calculation of the percentage of undescribed species strongly depends on the number of described species (Table 3). Thus, I had to select a 'starting point', i.e. a certain date as concerns this number. Pragmatically, I chose the year 1987 when the last comprehensive review on soil ciliates was published and many of the more common forms, especially from Europe, were accurately determined and described (Foissner, 1987). See section on global soil ciliate diversity for details.

For statistics, each sample collection was considered as a unique entity. Thus, a new species found, for instance, in both Africa and Australia, was classified as 'undescribed' in each of the data sets.

The sample collections were tested for differential capture rates between undescribed and previously described species using the probability theory-based method suggested by Hodkinson and Hodkinson (1993). Briefly, this technique requires that the sample collections be split in two equal sets, A and B, each containing a set of described (d) and undescribed (u) species. For the present purpose this was achieved by allocating the samples in such a way that both subsets contained a similar number of undescribed species. Taking the two subsets together we can recognize a combined total of described species (n_d) and undescribed species (n_u) that are found in either sample. We can also recognize a number of described (w_d) and undescribed species (w_u) common to both samples and these can be expressed as proportions (p_d and p_u) of the respective totals (n_d and n_u). Further, the number of described and undescribed species restricted to sample A (y_d and y_u) or B alone (z_d and z_u) can be listed.

If described and undescribed species were sampled equally efficiently, then we would expect that p_d would equal p_u. Provided that A and B sample equivalently from the total population, then the difference (d) between p_d and p_u, which can be tested for statistical significance using the χ^2 test for contingency tables, represents a measure of the differential rate of capture of described versus undescribed species. Therefore, if $p_d > p_u$ then described species are captured more efficiently than undescribed species, and vice versa.

Results

Overview

Table 1 provides the main characteristics of the soil ciliate faunas investigated. In all regions, except for Antarctica, about one-half of the species recorded were undescribed. The highest percentage (54%) of new species were found in Europe. However, these data are not fully comparable to those from the other regions because they include sites investigated between 1980 and 1987, i.e. when the soil ciliate fauna was still poorly known. Furthermore, about one-third of the samples were investigated with a slightly different method and studied 3–10 times within 1–2 years. In spite of this, the data prove that Europe is not an exception.

The most remarkable observation was the low percentage (4–7%) of undescribed species/sample as compared with the high percentage (15–54%) of undescribed species in all samples. This may indicate a high degree of undersampling of undescribed species relative to described ones. Thus, the data were tested for differential capture rates between described and undescribed species, as described in the method section; this provided the following area calculations.

Area calculations

Africa. A few of the taxonomic results, mainly colpodids, have been published (Foissner, 1988, 1993). The samples include collections mainly from Kenya, Namibia and the Republic of South Africa, spanning a wide range of habitats, including the Namib desert, a coastal rain forest near Mombasa, and strongly saline soils from the Etosha Pan.

Table 1. Data summary on diversity of soil ciliates in Europe, Africa, Australia and Antarctica

Characteristics	Europe[a] (99 samples)	Africa (92 samples)	Australia (157 samples)	Antarctica (90 samples)
Total number of species[b]	345	507	361	95
Species/sample (mean)	26	35	23	4
Undescribed species	185	240	154	14
Undescribed species (%)	54	47	43	15
Undescribed species/sample (mean)	1.9[c]	2.6	1.0	0.2
Undescribed species/sample (%)	7.2	7.5	4.4	3.9

[a] For comparison only because, in about half the samples, the investigation method and data collection are not directly comparable with those used in the other regions. See results section for details.

[b] Each sample collection was considered as a unique entity. Thus, a new species found, for instance, in both Africa and Australia, was classified as 'undescribed' in each of the data sets.

[c] Sample size (n) = 52.

Many of the African samples were extremely rich, and total species number was markedly greater than in the other sample collectives (Table 1). For instance, 12 samples from the centre and periphery of the Etosha Pan contained 153 species, 53 of which were undescribed (Foissner, 1995).

Sub-sets A and B sampled equivalently from the total population, and undescribed species were less likely to be sampled than described ones; thus the number of undescribed species increases from 240 to 240 × 4.3 = 1032, yielding a grand total of 1299 (Table 3).

Species	Number in one sub-set only		Number in both sub-sets	
	A	B	A and B	Total
Described	y_d (46)	z_d (77)	w_d (144)	n_d (267)
Undescribed	y_u (88)	z_u (122)	w_u (30)	n_u (240)

$p_d/p_u = 4.32$; χ^2 (that A and B sample equally from total) = 0.412 ($P > 0.5$); χ^2 (that described and undescribed species are equally likely to be sampled) = 96.4 ($P < 0.01$).

Australia. A few of the taxonomic results have been published (Blatterer and Foissner, 1988; Foissner, 1988, 1993). The samples include collections from Australia and Tasmania spanning a wide range of habitats, including the central desert, swamps in the Northern Territory, and rain forests near Cairns (Australia) and in the Mt Field National Park (Tasmania).

Of the 361 species recorded 154 were undescribed (Table 1). Surprisingly, all rain-forest samples were very poor, often containing less than 20 species, some were even ‘empty’. The reason for this is very likely a methodological failure (Foissner, 1998). Thus, mean species number/sample and percentage of new species/sample were rather low (Table 1).

Species	Number in one sub-set only		Number in both sub-sets	
	A	B	A and B	Total
Described	y_d (34)	z_d (62)	w_d (111)	n_d (207)
Undescribed	y_u (51)	z_u (76)	w_u (27)	n_u (154)

$p_d/p_u = 3.1$; χ^2 (that A and B sample equally from total) = 0.295 ($P > 0.5$); χ^2 (that described and undescribed species are equally likely to be sampled) = 48.8 ($P < 0.01$).

Sub-sets A and B sampled equivalently from the total population, and undescribed species were less likely to be sampled than described ones; thus, the number of undescribed species increases from 154 to 154 × 3.1 = 477, yielding a grand total of 684 (Table 3).

Antarctica and southern oceans. All data have already been published (Ryan *et al*., 1989; Foissner, 1993, 1996a, b). Sixty-three samples were from the maritime and continental Antarctic, following a cline from 60°–78°S, i.e. of increasing climatic severity (Ryan *et al*., 1989; Foissner, 1993, 1996a). Twenty-seven samples were from Gough Island and Marion Island, two small volcanic elevations in the South Atlantic and southern Indian Ocean (Foissner, 1996b).

Only 95 species were found in the 90 samples investigated (Table 1). The sample mean (four species) and the number of new species (14) were also low, indicating that euryoecious colonizers predominate in these harsh environments (Table 1). This is sustained by the high proportion of colpodids, most of which very probably have an r-selected survival strategy (Smith, 1973; Foissner, 1987); accordingly, spirotrichs, which are more k- than r-selected, are underrepresented (Table 2).

As in the other regions, sub-sets A and B sampled equivalently from the total population, and undescribed species were less likely to be sampled than described ones; thus, the number of undescribed species would increase from 14 to $14 \times 2.43 = 34$, yielding a grand species total of 115 (Table 3).

Species	Number in one sub-set only A	B	Number in both sub-sets A and B	Total
Described	y_d (18)	z_d (21)	w_d (42)	n_d (81)
Undescribed	y_u (7)	z_u (4)	w_u (3)	n_u (14)

$p_d/p_u = 2.43$; χ^2 (that A and B sample equally from total) $= 0.604$ ($P > 0.5$); χ^2 (that described and undescribed species are equally likely to be sampled) $= 4.5$ ($P < 0.05$).

Discussion and interpretation

Undersampling of undescribed species

It was clearly shown that the number of undescribed relative to described species in the samples is a gross under-representation of the real situation in the areas investigated. This requires statistical correction of the proportion of undescribed species found and is thus rather vague. In this context, it is worth considering the complementarity of sub-sets A and B in the main data sets (Africa and Australia) in a little more detail. In our notation, complementarity (c) is defined by $c = 1 - p$, where a value of zero indicates identity, and a value of one (or 100%) complete distinctness of the species lists in the sub-sets A and B. In both data sets, the sub-sets show extremely high complementarity (> 80%) for undescribed species, but also for described species complementarity is not low (about 50%). Two factors may be involved here. First, our data may indicate that many soil ciliate species show restricted geographical or ecological ranges. The second factor is undersampling, where many of the rare species are missed.

The extent of endemism in free-living ciliates, to which soil protozoa belong, is difficult to rate because comprehensive, reliable faunistic data are very rare. Usually, they are considered to be cosmopolitan, especially by ecologists (e.g. Stout, 1956; Finlay *et al.*, 1996). I do not entirely share this view because there is good evidence that some species, especially testate amoebae, have a restricted Laurasian or Gondwanian distribution (Bonnet, 1964; Foissner, 1987); however, I agree that the percentage of endemics is low. This is also indicated by the rather limited genetic differentiation found among 15 isolates from three continents of a common soil ciliate, *Colpoda inflata* (Bowers and Pratt, 1995). On the other hand, we cannot exclude that the rarer species, many of which we certainly do not yet know, are geographical and/or ecological (habitat) endemits, especially as concerns soil protozoa, where global distribution is probably more difficult than in limnetic habitats, and isolation due to extensive microhabitat formation is extremely pronounced. However, all these problems have not yet been investigated in detail and thus cannot be seriously addressed. Moreover, even my investigations on soil ciliates are much too incomplete for a conclusive figure. I shall thus concentrate the further discussion on undersampling of undescribed species, for which definite evidence is available.

Soil protozoa can survive adverse periods (drought, food shortage etc.) by forming a dormant stage, the so-called resting cyst (Corliss and Esser, 1974). As in bacteria (Hawksworth and Colwell, 1992), many or most of the dormant individuals remain in this inactive, protective stage for long periods because the standing crop number of active soil protozoa, especially of ciliates, is usually much lower than the cystic portion (Foissner, 1987; Berthold and Palzenberger, 1995). No method for re-activating most or all resting cysts is known. The non-flooded Petri dish method used in this study, although being probably the most efficient technique available (Foissner, 1987), very probably also re-activates only a small proportion. Repeated investigation of some sites showed that only 10–20% of the species found at 10 sampling occasions were recorded in the first sample (Fig. 1). Thus, the real number of species, described and undescribed, in the samples investigated for the present study, must be much higher. It is reasonable to assume that, usually, only the euryoecious species become re-activated, whereas those having more specialized demands will mostly remain in the dormant stage or not reproduce to detectable numbers. There is convincing evidence for this hypothesis, viz. the great disproportionality between the percentage of undescribed species/sample (4–7%) and the total number of undescribed species found in large sample collections (15–54%, Table 1). Further evidence is represented by, for instance, the mycophagous soil ciliates, which

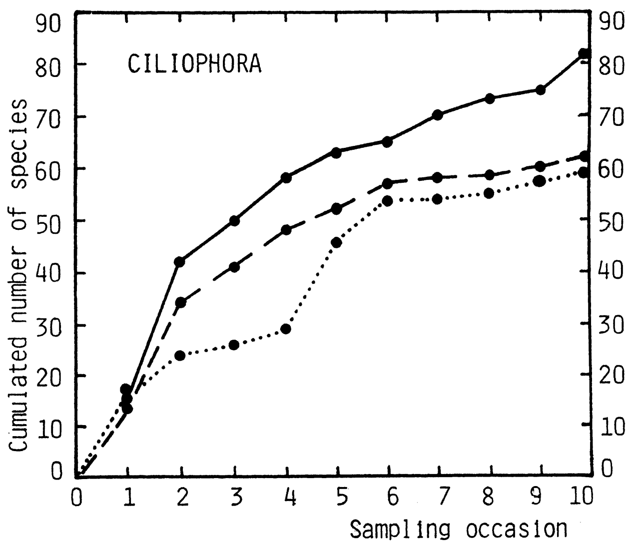

Figure 1. Cumulative total of soil ciliate species (described and undescribed) from 10 sampling occasions over 27 months at three sites in the Tullnerfeld near Vienna (Austria). Ciliates were re-activated from dried samples with the non-flooded Petri-dish method. —— (beach forest), ---- (xerothermic uncultivated grassland), ······ (wheat field). From Foissner (1987).

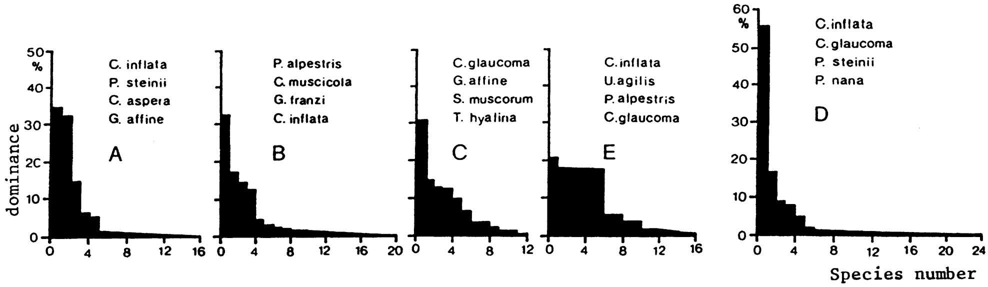

Figure 2. Dominance structure of soil ciliates at five sites (A–D) in the Austrian Central Alps near Gastein. Abundances were estimated using Buitkamp's (1979) culture method. Dominant species: *Colpoda aspera*, *Colpoda inflata*, *Cyclidium glaucoma*, *Cyrtolophosis mucicola*, *Gonostomum affine*, *Gonostomum franzi*, *Paracolpoda steinii*, *Pseudocyrtolophosis alpestris*, *Pseudoplatyophrya nana*, *Sathrophilus muscorum*, *Tachysoma hyalina*, *Urosomoida agilis*. From Foissner (1985).

remained undiscovered for a long time although being very common and abundant, because they did not grow with the conventional culture methods (Foissner, 1987). Undersampling of the autochthonous species has been well-documented in testate amoebae which do not grow with the available culture methods (Bonnet, 1964), and I have never found one of these particular species growing in my cultures for soil ciliates.

A second line of evidence for undersampling of undescribed species comes from the dominance structure of soil ciliate communities. As common in many animal and plant assemblages, only few and mostly euryoecious species account for 50–80% of the individuals, i.e. most species have low or very low abundances and are thus difficult to detect (Fig. 2). In fact, many of the new soil ciliates I have found belong to the low-abundance

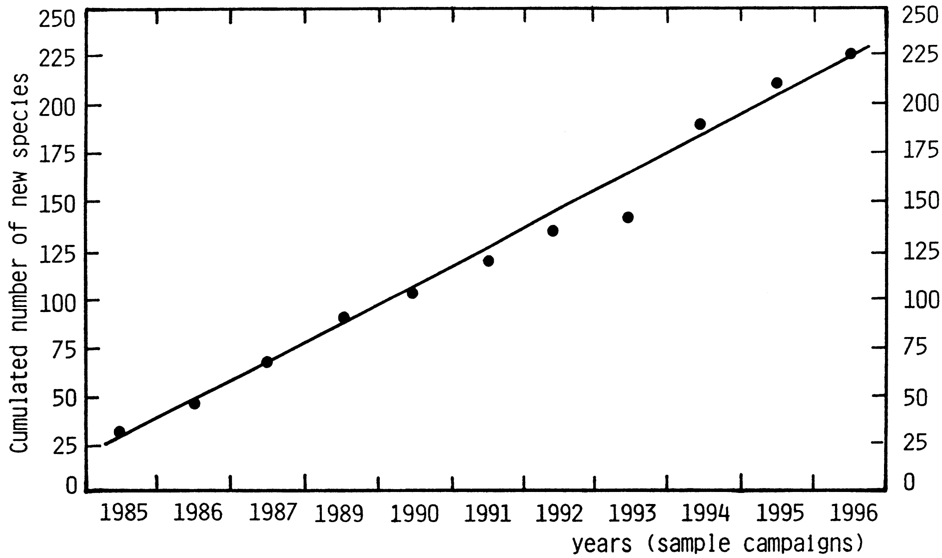

Figure 3. Cumulative total of undescribed soil ciliate species found in 20 arbitrarily selected samples each from the years 1985–1996. Ciliates were re-activated from dried samples with the non-flooded Petri dish method.

category and were active only for a few days. Thus, their detection was more a matter of chance than of science, and permanent silver slides prepared from a whole sample usually contain, in very low numbers, some or even rather many described and undescribed species not recognized during the routine procedure (Blatterer and Foissner, 1988).

The final but probably most important evidence for our ignorance on the real soil ciliate diversity is shown in Fig. 3. When I commenced studying soil ciliates 20 years ago and recognized the huge number of undescribed species, I hoped that, if I worked hard and described most of them, there would come a time where most samples contained only described species. However, this optimistic view was soon overtaken by reality. The number of undescribed species found in 20 arbitrarily selected samples each for the period 1985–1996 shows a completely steady rate, indicating that the real number of soil ciliates must be very high (Fig. 3).

Global soil ciliate diversity

In calculating global soil ciliate diversity not only the species concept used and undersampling of undescribed species, as discussed above, have to be taken into account, but also the representativeness of the faunas found, the number of known soil ciliates, and the synonymy rate (Hodkinson and Casson, 1991; Hodkinson and Hodkinson, 1993; Solow *et al*., 1995).

Table 2 shows that soil ciliate communities, as compared to a representative freshwater assemblage, have a distinctly higher percentage of colpodids (3 versus 23%) and spirotrichs (30 versus 40%), while hymenostomes (14 versus 4%), peritrichs (17 versus 5%) and suctorians (6 versus 2%) are markedly underrepresented. These differences have been correlated with morphological and ecological peculiarities of the respective groups (Foissner, 1987). The faunas investigated in this study matched the general pattern very well, indicating that they contained a representative subset of the world soil ciliate fauna (Table 2). The similar situation in all sample collections, including Europe (Table 1), further suggests that the results are not peculiar to a certain geographical region.

Table 2. Comparison (%) of the taxonomic composition of the faunas investigated with the world list of soil ciliates and a representative freshwater ciliate assemblage

	Soil				
Groups	Africa	Australia	Antarctica	World list[a]	Freshwater[b]
Spirotrichs[c]	39.3	40.5	25.8	40.0	30.3
Gymnostomes[d]	26.2	26.2	15.8	18.2	14.2
Colpodids[e]	16.4	18.2	27.4	23.0	3.0
Cyrtophorids[f]	6.5	6.1	9.5	6.6	9.7
Hymenostomes	3.9	3.6	7.4	4.0	14.3
Peritrichs	3.2	2.2	3.2	4.8	16.7
Suctorians	3.1	1.4	1.1	1.6	6.3
Prostomatids	1.4	1.9	0.0	1.8	5.7

[a] From Foissner (1987, 1997).
[b] From Table 3 in Foissner *et al.* (1995).
[c] Include hypotrichs, heterotrichs, oligotrichs.
[d] Include haptorids and pleurostomes.
[e] Include taxa mentioned in Foissner (1993).
[f] Hypostomata sensu Corliss (1979).

Table 3. Calculation of global soil ciliate diversity using 400 described species

Parameters	Africa	Australia	Antarctica
Number of undescribed species found	240	154	14
Multiplier for undersampling of undescribed species	4.3	3.1	2.4
Corrected number of undescribed species	1032	477	34
Undescribed species (%)	80	74	70
Estimated global diversity (~)	2000	1540	1330

The number of soil ciliates described till 1987, when the present study commenced, was calculated from the compilations by Foissner (1987, 1997). In 1987 Foissner collated 270 well-described species, while the 1997 list contains all species originally described from terrestrial habitats, regardless of whether or not they have been confirmed. Using these compilations, the number of soil ciliates known in 1987 can be estimated to be close to 450 species. Foissner (1997) also estimated a synonymy rate of about 8%. Thus, about 400 species of soil ciliates were known in 1987.

Using a number of 400 described species and the multipliers calculated for undersampling of undescribed species one arrives, depending on area, at a global soil ciliate diversity of between 1330 and 2000 species (Table 3). Unfortunately, it is difficult to say how reliable this estimate is (Gaston, 1991; May, 1992). However, the estimate is very probably conservative, considering the methodological shortcomings discussed above, and the constant rate at which one finds new species, even after a 20-year period of intensive research (Fig. 3). Furthermore, the total amount of soil investigated so far is, seen on a global scale, negligibly small, i.e. less than 1000 kg, and large areas, like Asia and South America, were never investigated in detail. At present, about 600 soil ciliate species are known, together with some 500 new species not yet described (Foissner, 1997). Thus, about 50% of the species diversity estimated in the present study is known.

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