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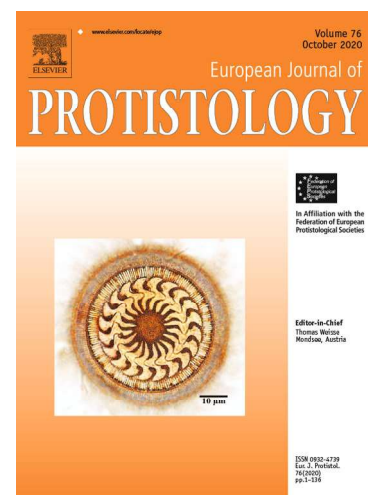
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A Reassessment of Testate Amoebae Diversity in Tierra del Fuego Peatlands: Implications for Large Scale Inferences

Luciana Burdman^{a,b,c}, Gabriela Mataloni^a, Edward A.D. Mitchell^{b,d}, Enrique Lara^{b,e}

a Laboratorio de Biodiversidad, Limnología y Biología de la Conservación, Instituto de Investigación e Ingeniería Ambiental (IIIA CONICET-UNSAM). Campus Miguelete, Universidad Nacional de San Martín. 25 de Mayo y Francia, 1650 San Martín, Provincia de Buenos Aires, Argentina

b Laboratory of Soil Biodiversity, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

c Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, Missouri, USA

d Jardin Botanique de Neuchâtel, Neuchâtel, Switzerland

e Department of Mycology, Real Jardín Botánico, CSIC. Plaza de Murillo 2, 28014 Madrid, Spain

Corresponding authors

L. Burdman, Center for Conservation and Sustainable Development, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, USA.

e-mail: lburdman@mobot.org

E. Lara, Department of Mycology, Real Jardín Botánico, CSIC. Plaza de Murillo 2, 28014 Madrid, Spain.

e-mail: enrique.lara@rjb.csic.es

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Abstract

Testate amoebae are a diverse group of shelled protists frequently used as model organisms in microbial biogeography. Relatively few species have been reported for the Southern Hemisphere, however, it remains unclear whether this lower diversity is real or an artifact of under-sampling or misidentifications, which would reduce their potential to address macroecological questions. We evaluated testate amoebae diversity from the full range of habitats occurring within two Tierra del Fuego peatlands and compared it with the reported diversity for the area and from the Northern Hemisphere peatlands. We recorded 87 species, of which 69 are new for the region and 45 of them probably new to science and likely to have restricted geographical distributions. Combined with previous studies, the total diversity of testate amoebae only from Tierra del Fuego peatlands now reaches 119, as compared with 183 reported from all Northern Hemisphere peatlands. Our results demonstrate that the number of Gondwanian and Neotropical endemic testate amoeba may be substantially higher than currently known. Previous reports of Holarctic taxa in Tierra del Fuego may result from forcing the identification of morphotypes to the descriptions in the most common literature (force-fitting) South American species into species common in literature from other regions.

Keywords

Arcellinida; biogeography; distribution; endemism; Euglyphida; Gondwana; Neotropics; peat bogs

Introduction

Understanding global biodiversity patterns requires taxonomy and biodiversity inventories of comparable quality and coverage depth at the global and regional scales. Both of these conditions are best fulfilled for larger organisms while data are more limited for microbial taxa (Decaëns, 2010; Wilkinson, 1998). Nevertheless, an increasing number of studies have aimed to compile existing data on various groups of unicellular and multicellular microscopic organisms, including nematodes (e.g. van den Hoogen et al. 2019), rotifers (Fontaneto et al., 2008), fungi (Tedersoo and Lindahl, 2016), bacteria (Delgado-Baquerizo et al., 2018), protists or microorganisms in general (Bass et al., 2007), ciliates (Azovsky and Mazei, 2013; Foissner, 1997), flagellates (Azovsky et al., 2020, 2016) and testate amoebae (Fernández et al., 2016, 2015). Still it is clear that the intensity of research effort on both taxonomy and biogeography is very unevenly distributed across the globe and this potentially undermines any efforts to infer general patterns from existing data (Mazei et al., 2017). As filling this important research gap is a daunting task, a useful approach is to focus on comparable ecosystem types or biomes that occur in distant regions, ideally in both hemispheres (Bahl et al., 2011; Sharifian et al., 2020).

One such example is *Sphagnum*-dominated peatlands, which are common in the boreal regions and in some austral regions such as Tierra del Fuego. Our focus here is on testate amoebae, a group of shell-producing protozoa, which are common and diverse in soils and freshwater habitats and have been best studied in such peatlands. Testate amoebae are considered as valuable bioindicators for environmental conditions, due to their narrow ecological tolerance and the fact that their diversity can be predicted from current and past climatic conditions as well as soil characteristics (Fernández et al., 2017; Lara et al., 2016; Singer et al., 2019). Moreover, due to the long-term persistence of their shells in the environment they are commonly used as

proxies in palaeoecological studies of lakes and peatlands (Amesbury et al., 2016; Mitchell et al., 2008). They also include clear examples for endemism in microbial biogeography (Heger et al., 2011; Qin et al., 2016). Therefore, knowing the geographical distribution of testate amoebae is fundamental for assessing the geographical range within which models - that are typically developed for a given region - are valid.

Testate amoebae are a polyphyletic group distributed within three major eukaryotic lineages, Amoebozoa (Arcellinida, characterized by blunt pseudopodia), Rhizaria (Euglyphida and Tectofilosida, with thread-like pseudopodia) and Stramenopiles (Amphitremida; thread-like pseudopodia and double aperture) (Kosakyan et al., 2016). Generally, their diversity evaluation is based on microscopic observations; species are defined mostly by the overall shape, size and composition of their test (shell). Their global diversity is currently estimated to ca. 2000 taxa (Meisterfeld, 2002a, 2002b), but recent molecular studies revealing the existence of cryptic species suggest that their true diversity is much higher (Kosakyan et al., 2012). Such closely-related cryptic species were also shown to have diverging ecologies (Singer et al., 2018) and distribution (Singer et al., 2019). However, until a vast barcoding effort is achieved to expand the testate amoeba molecular database combined with the development of protocols adapted to these particular organisms, morphological identification of taxa remains the only option available to study their diversity. This approach has proven to be accurate for past and present bioindication (Mitchell et al., 2008; Swindles et al., 2019). Indeed, morphological diversity can be considered as a good proxy for specific diversity (Kosakyan et al., 2012) and even genus-level identification was shown to be significantly correlated to species-level diversity (Wilkinson and Davis, 2000).

Most studies on testate amoebae have focused on boreal *Sphagnum*-dominated peatlands, where they are known to be highly diverse and functionally important; they can constitute half of

the microbial biomass and are considered as the top microbial predators (Gilbert et al., 1998a, 1998b; Jassey et al., 2012; Mitchell et al., 2008). Amesbury et al. (2016) compiled a dataset from 31 studies in 18 boreal countries, building a list of 183 species and varieties, similar numbers are expected for other widely studied Northern Hemisphere countries such as China and Canada (Smith and Wilkinson, 2007). As *Sphagnum*-dominated peatlands are also found in the Southern Hemisphere under comparable climates, it is possible to directly compare the diversity of testate amoebae of both hemispheres and thus to test if geographical distance has an impact on diversity or taxonomic composition.

Only few testate amoeba species have been documented from Southern Hemisphere *Sphagnum*-dominated peatlands (e.g. 44 from Galápagos; Fournier et al. 2016; 34 from New Zealand; Mckeown et al., 2021; 21 from Malvinas/Falkland Islands; Mauquoy et al., 2020). Tierra del Fuego is located in southern South America (Fig. 1), encompasses the southernmost extensive area of peatland development (Lindsay et al., 1988) and is therefore an ideal region to conduct comparative studies of *Sphagnum*-dominated peatland biodiversity between the Northern and Southern Hemispheres. In the Big Island of Tierra del Fuego, Vucetich (1974) reported 30 species in *Sphagnum* peatlands located near Ushuaia. More recently, van Bellen et al. (2014) reported 32 species from five peatlands in the same region. As only 12 species were common to the two studies it is likely that the impoverished austral fauna is an artefact of under-sampling and more work is needed to assess the true diversity of testate amoebae in peatlands of this region. Moreover, these studies focused exclusively on the *Sphagnum* matrix, and peatland pools have been overlooked. Contrary to the common belief that testate amoebae only occur in the water column by resuspension of benthos and detached from surrounding macrophytes,

planktonic communities have been well documented in lakes and rivers (Lansac-Tôha et al., 2009; Mucio Alves et al., 2008; Velho et al., 2003).

Among the relatively few diversity studies in the Southern Hemisphere, a recent systematic analysis of testate amoeba diversity and distribution in Chile has revealed the existence of a high diversity (352 taxa) including 24 novel taxa. This study performed a detailed examination of latitudinal diversity patterns and testing macroecological hypotheses (Fernández et al., 2016, 2015). Although very detailed in the geographical coverage of samples, this study did not pursue an in-depth exploration of the diversity within any given ecosystem type. Addressing such a question would require a detailed study of the main microhabitats within single ecosystem type, as was done for example in the Russian taiga wherein 80 taxa were observed, while the next highest diversity reported in less systematic previous studies was 65 (Tsyganov et al., 2015). It is therefore likely to still find ca. 1/3 more diversity by enhancing the coverage of environmental heterogeneity in a rather well-studied biome even using only morphological approaches.

In this work, we aimed at re-evaluating the diversity of Southern Hemisphere testate amoebae in *Sphagnum*-dominated peatlands by surveying all landscape elements and microhabitats along a transect crossing the dome-shape microtopography of two peat bogs. We hypothesized that the testate amoeba diversity from Tierra del Fuego peatlands was formerly underestimated by sampling only the *Sphagnum* bryosphere. Given that the vast majority of the species known today were found in *Sphagnum* lawns, we predicted that richness would be higher there than in the pools, while amongst the latter, vegetated pools would host richer assemblages than clear water ones, on account of their higher substrate diversity. In addition, species richness in the water column of pools would be lower than that of substrate-associated assemblages.

Materials and methods

Study sites and sampling

Rancho Hambre and Andorra are two *Sphagnum magellanicum*-dominated peat bogs located in Tierra del Fuego, Argentina. Rancho Hambre peat bog (RH) is located in the Tierra Mayor Valley Natural Reserve and its area is approximately 41.3 ha. It is located among the southernmost ridges of the Andes at 32 km from Ushuaia City. Andorra peat bog (AN) is in a relatively narrow NW-SE oriented valley near the Beagle Channel at 32 km from RH and 7 km from Ushuaia City; its total area is ca. 55 ha, (Fig. 1). Both have been classified as ombrotrophic dome-shaped peat bogs (Roig and Roig, 2004). The landscape of these peat bogs is composed of a terrestrial matrix dominated by the peat-forming moss *Sphagnum magellanicum*, containing patches of both clear and vegetated pools (Fig. 1 A-E).

While the *Sphagnum*-matrix only includes the *S. magellanicum* bryosphere as a micro-habitat for microbial communities, separate micro-habitats can be distinguished in the pools: the water column, sediments and bryosphere from different moss species. *Sphagnum magellanicum* is present in the margins of all pools, as it constitutes the peat bog matrix, whereas *S. fimbriatum* and *S. anioniauncinata* can also be present. The *Sphagnum*-matrix presents more terrestrial characteristics as compared to the pools (lower pH and higher conductivity), holding lower diversity of algal communities and distinctive bacterial composition (Mataloni, 1999; Oloo et al., 2016). Meanwhile, the physical and chemical characteristics of the pools are mainly dictated by their minero-ombrotrophic status and their degree of development toward terrestrial conditions. These vary both among and within peat bogs (González Garraza et al., 2019, 2012) and drive the

structure of phytoplanktonic and periphytic desmids (González Garraza et al., 2019) and planktonic communities in general (Lara et al., 2015; Quiroga et al., 2013).

In order to retrieve as much diversity as possible, our sampling design covered the full range of habitats occurring within the two peat bogs. Along a transect perpendicular to the dome-shape of each peat bog (Fig. 1 A-B), we randomly selected sites of each landscape element: five clear pools (CP), four vegetated pools (VP) and four *Sphagnum*-matrix sites (SM). At each of the 18 pool sites [(5 + 4) x 2], we collected samples from all present micro-habitats, while in the case of SM the only micro-habitat present was the *S. magellanicum* bryosphere. The total number of samples was 75, collected in November-December 2016, during austral summer.

Plankton samples of ca. 50 L of water were concentrated by means of a 20 µm pore diameter plankton net and fixed with 2% formaldehyde. Composite benthic samples were taken with a large sterile pipette and fixed in 2% formaldehyde. For moss-associated communities, we separately collected the top 5 centimeters of three to five stems of each moss species that were submerged in the pools, and fixed with 4% formaldehyde. The micro-organisms were separated from the mosses by shaking with distilled water and filtering through a 1-mm mesh handheld sieve (Booth et al, 2011 modified). The filtrate was collected and fixed with 2% formaldehyde.

Laboratory procedures

All samples were observed with an optic microscope Olympus CX 41 equipped with a digital camera Infinity (Lumenera Scientific, Canada). For each sample, slides were analyzed systematically in the search of new morphotypes until the diversity was saturated (curves not shown). Taxonomic identifications were based on a vast range of literature, most importantly Vucetich (1975, 1974, 1973), Lena and Cachi (1972), Lena and Zaidenweg (1975), Zapata

(2005), Zapata et al. (2007), Tsyganov et al. (2016), Fernández and Zapata (2011), Fernández et al. (2015); we also used the excellent website on amoeboid protist systematics maintained by Ferry Siemensma (<http://www.arcella.nl>; updated version on Feb, 2019). When discriminating species, we applied a criterion of morphological discontinuity; species were considered different when the length or the width of the shell or the aperture varied by more than 10% between the most resembling specimens, without any intermediate state. This approach can be regarded as conservative, given that variation between individuals from a single species should fall below that range, even when showing considerable phenotypic plasticity (Mulot et al., 2017; Singer et al., 2015).

Statistical analyses and data compilation

In order to assess if our sampling design was successful to retrieve the total richness of each peat bog, we estimated this value based on the asymptotes of the species accumulation curves using. In addition, non-parametric estimators of richness Chao2, ICE and Jackknife2 were calculated (Chao *et al.*, 2009; Lee & Chao, 1994). All numerical analyses were performed using R-studio (packages Biodiversity R and vegan) (R Core Team, 2017).

For analysing the geographical distribution of the diversity, species were classified into one of four categories (1) cosmopolitan taxa, such as *Assulina muscorum*, *Nebela collaris*, *Centropyxis aerophila*, *Heleopera petricola*, *Padaungiella lageniformis*, *Trinema lineare*, *etc.* (Vucetich, 1973; 1974; Hoogenraad, 1979; Smith et al, 2008, Fernandez et al., 2015); (2) taxa distributed Southwards from the Cancer Tropic desert belt (= "Gondwanian taxa") like *Apodera vas*, *Alocodera cockayni*, *Certesella certesiand C. martiali* (Smith et al., 2008); (3) likely

endemics to South America such as *Certesella australis* (Vucetich, 1973) and (4) unknown distribution (Table 1).

In order to compare the diversity found in Tierra del Fuego peatlands with a broadly studied Northern Hemisphere region, the European dataset of Amesbury et al. (2016) was used. This compiled list of species derived from 1799 samples from 113 sites in 18 European countries: Poland, Switzerland, Sweden, Russia, France, Finland, Netherlands, United Kingdom, Greece, Scotland, Northern Ireland and England, as well as one sample from Turkey and one from Israel. This dataset was built by compiling taxonomic lists of ecological studies and some degree of taxonomical errors are expected. However, it is sufficiently robust for the purpose of diversity comparison between hemispheres. To avoid overestimation of differences between Southern and Northern Hemispheres, morphotypes corresponding to the same species were grouped together.

Results

A total of 87 species belonging to 30 genera were identified. The species accumulation curves reached the asymptote for both peat bogs when all samples were included (i. e. 38 samples for RH and 37 for AN; Fig. 2). Total richness of RH was 83 and the estimators indicated that between 3 and 14 more species could occur. For AN, the total richness was 49 and between 2 and 10 species more were estimated.

Forty-five (51.7%) of the species found in this study are probably new for science. This proportion is constant among landscape elements and microhabitats (Table 2). However, the number of species in clear and vegetated pools is twice that of the *Sphagnum* matrix.

The total richness more than doubled that of previous records for the region. This is the first record for 69 species for Tierra del Fuego, with only 18 species in common with previous studies. Of the 119 species known to date from Tierra del Fuego peatlands, 61 (51.3%) are cosmopolitan (17 Cercozoa, 40 Amoebozoa and four Stramenopile, Table 1), while 8 (6.7%, including *Apodera vas*, *Alocodera cockayni*, *Certesella certesi*, and *Certesella martiali*) have been only reported from locations south of the Tropic of Cancer and five (4.2%, *Certesella australis*, *Sphenoderia ovoidea* and *Trigonopyxis microstoma*) only from South America. The distribution of the 45 (37.8%) newly reported species cannot be identified yet. Remarkably, this is the second record for three species only known so far from other locations in the Southern Hemisphere: *Amphitrema paparoensis* described from New Zealand, *Amphitrema congolense*, from the Republic of Congo and *Hoogenraadia sylvatica* from the Buenos Aires Province in Argentina (Fig 3).

While 183 species were listed from 1799 samples from European peatlands, only 41 are in common with the 116 species recorded in 225 samples from Tierra del Fuego. Thus, 142 (78%) of European species and 75 (63%) of Tierra del Fuego species were exclusive to their respective region.

Discussion

Our goal was to reassess if the diversity of testate amoebae differed between the Southern Hemisphere and the Northern Hemisphere by focusing on *Sphagnum* peatlands, a well-defined ecosystem extensively surveyed for testate amoebae in the Northern Hemisphere. Our study revealed a large number of morphotypes that do not correspond to any previously described

species, thus suggesting the potential magnitude of the diversity with restricted distributions in the Southern Hemisphere.

Southern Hemisphere testate amoebae are less studied than their Northern counterparts, with the possible exception of Chile (Fernández et al., 2015). This remains also true for peatlands, which is the best studied ecosystem type overall. We therefore expected to find many new species in Tierra del Fuego bogs. In this work, we analysed 75 samples from only two peatlands while Vucetich (1974) and van Bellen et al. (2014) studied, respectively, three and five peatlands; 125 samples were examined in van Bellen et al. (2014). Still, we observed that 69 (79.3%) out of 87 species were novel for the region and 45 (51.7%) were undescribed (Table 2). We attribute this high novelty primarily to our sampling design that aimed to cover all possible habitats within these peatland ecosystems and was indeed effective to retrieve virtually all the diversity, independently from the total richness at each site (83 taxa for RH and 49 for AN). By contrast, ecologically oriented studies designed to build transfer functions for paleohydrological reconstruction typically include mostly or only *Sphagnum* mosses from wet (pools, hollows) to drier (lawns, hummocks) microsites (e. g. Lamentowicz and Mitchell 2005; Swindles et al. 2014; van Bellen et al. 2014; Zhang et al. 2018). Pools, typically the richest environments in our study are typically only marginally studied (i.e. only *Sphagnum* samples but not plankton and benthos).

Bog pools located only a few meters apart can present different physical and chemical conditions such as pH, conductivity and nutrients concentrations (González Garraza et al., 2012). Testate amoeba communities are known to vary in relation to such environmental conditions (Ju et al., 2014; Mitchell et al., 2000) and these patterns may be explained, at least partly, by the impact of such environmental heterogeneity on potential food resources, such as bacteria, fungi, algae and other micro-eukaryotes (González Garraza et al., 2019; Oloo et al., 2016; Quiroga et

al., 2015). Meanwhile, only a few studies have covered the diversity in the different landscape elements that are pools and moss matrix, in which communities are also affected by metacommunity processes (e. g. mass effect, patch dynamics or species sorting; Leibold et al. 2004).

In forests soils, testate amoebae species richness at regional level (γ) was mainly determined by turnover (β -diversity) above in-site richness (α -diversity), suggesting that diversity patterns below the landscape level are strongly regulated by environmental conditions at local scales (Tsyganov et al., 2015). This suggests that testate amoeba species richness at the landscape level will only be detected by sampling designs covering the full range of biotopes present. To the contrary, designs covering only a few ecosystem types will miss a part of the diversity. In line with this, as surveys in the Northern Hemisphere focus mostly on *Sphagnum*-associated communities, it is not impossible that an unknown diversity is yet to be discovered in these systems too. Our study thus suggests that this habitat should be studied more intensively also in the Northern Hemisphere peatlands.

Within pools, different micro-habitats hold species with distinct adaptations for locomotion and hunting. An example of this is described for some *Netzelia* species (earlier classified as *Diffugia*), presenting gas vacuoles for flotation in plankton (Meisterfeld, 1991; Štěpánek and Jiří, 1958). The existence of planktonic testate amoebae has been previously reported in Brazilian rivers and lakes (Lansac-Tôha et al., 2009; Mucio Alves et al., 2008; Velho et al., 2003). Here, contrary to our hypothesis, taxonomic richness was higher in both the sediments and the water column than in the bryosphere (Table 2). This shows that pools are not simply sinks in which living amoebae or empty shells accumulate but are a habitat with their own specific communities.

Moreover, testate amoebae richness differed between the three mosses associations, suggesting that the host moss have an influence on microbial communities as shown for rainforest mosses differing in architecture and likely hydrological dynamics (Acosta-Mercado et al., 2012). Although there are no studies to our knowledge dealing with associations of testate amoebae with different macrophytes, the mechanical conditions such as the physical support offered by the different mosses could affect the periphytic communities. Vickery (2006) suggested that differences in leaf arrangement could explain the differences in testate amoeba community richness between *Sphagnum capillifolium* and *S. papillosum* bryospheres. Altogether, these results show the importance of considering all micro-niches when setting species checklists for particular regions. In addition, the comparison of our results with previous studies shows that it is indispensable to include the full range of micro-habitats and to describe clearly the habitats studied. Only so will it be possible to compare studies accurately and to assess patterns of testate amoeba diversity and ecology to address bioindication and microbial biogeography at broader scales.

Patagonia is considered as a protist endemism hotspot (Fernández et al., 2015; Vucetich, 1974; Woelfl, 2006). Indeed, a similar trend in distribution types was observed for peatland diatoms. Nearly half (49.5%) of the observed morphotypes could not be assigned to any species and 22 of them were described as new taxa (Casa, 2020; Casa et al., 2018, 2017a, 2017b). However, given the above-mentioned uncertainty, it is clearly impossible to determine if testate amoeba species richness from Tierra del Fuego peatlands is indeed higher as compared to other regions or if the large number of species recorded simply results from our sampling protocol.

Comparison of diversity in Tierra del Fuego and European peatlands

The 116 species now reported from 225 samples from two Tierra del Fuego peatlands, including 75 species exclusive to the region is remarkably high compared to the total of 183 species reported from 1799 samples distributed throughout Europe. Furthermore, 60% (142) of these European species were not found in Tierra del Fuego bogs.

However, these numbers should be taken with caution. Indeed, we believe that identification may in many cases suffer from force-fitting (i. e. forcing the identification of morphotypes to the descriptions in the most common literature) which overestimates the geographical range of many species and underestimates local endemism. This is particularly evident in Euglyphida, for which scanning electronic microscopic imaging is often needed to observe diagnostic traits (Chatelain et al., 2013; Tsyganov et al., 2017).

Furthermore, taxonomic uncertainties are a major issue in testate amoebae biogeography (Heger et al., 2009). Indeed, there is a lack of consensus on species validity, ancient literature is often difficult to access and no curated list of valid species exists. The genus *Amphitrema* illustrates this well: while *A. wrightianum* is frequently reported in the literature, *A. paparoensis*, described from New Zealand (van Oye, 1956), is similar in morphology, but can be differentiated by its test with scattered particles on the surface. Therefore, previous studies in the region could have misidentified the less known *A. paparoensis*. Likewise, *A. congolense* (van Oye, 1958) presents a similar general morphology, but the pseudostomes are difficult to observe, as they are surrounded by large particles (Fig. 3 A-C). This species has not been cited since its original description and its existence has likely remained ignored in later works. Furthermore, the validity of these taxa has not been assessed by detailed molecular and morphological studies. Similar cases may exist in other genera, e. g. *Diffflugia*, *Centropyxis*, *Heleopera* and *Pseudodifflugia*.

The high morphological variability observed for some testate amoebae (Krashevskaya et al., 2020; Luketa, 2017, 2015) calls for combined morphological and molecular studies. However, at least some of the observed morphological diversity may result phenotypic plasticity as demonstrated by experimental studies (Mulot et al., 2017; Wanner, 1999). However, until a vast effort to document the molecular diversity based on environmental DNA or an in-depth revision of their taxonomy combining molecular and morphological approaches is completed (e. g. Kosakyan et al. 2015; Singer et al. 2019), species morphology remains the best proxy for specific diversity (Kosakyan et al., 2012).

Biogeographical considerations

Cosmopolitan species accounted for half of the testate amoeba diversity known for Tierra del Fuego peatlands (Table 2). A typical example is *Assulina muscorum* which has been recorded in identical ecosystems around the world. This species is supposed to be good a disperser and has a wide ecological tolerance which would explain its broad geographical range with only limited genetical diversity (Lara et al., 2011). However, even apparently clear examples of cosmopolitan distribution may be misleading. For example, several *Euglypha* species of presumably global distribution have been previously recorded in Andorra bog by van Bellen et al. (2014), including *E. rotunda*, *E. strigosa* and *E. tuberculata*. Van Bellen and co-workers based the identification of species only on overall shell size. This is common practice in palaeoecological studies where shells are often not very well preserved (Amesbury et al., 2016). We also found three species similar to the former ones in the same peat bog, for which the shape of the anterior thickening of apertural plates and its denticulation -a trait used to discriminate among *Euglypha* species (Tsyganov et al., 2017)- did not correspond with the original description of any known species.

The three species –named here *Euglypha* sp. 1, 2 and 3- we observed are thus different from the “cosmopolitan” *E. rotunda*, *E. strigosa* and *E. tuberculata*, and could potentially represent endemic forms. Therefore, for biogeographic studies and diversity inventories it is important to work at the finest taxonomic level possible to detect patterns of spatial distribution (Singer et al., 2019). This may, unfortunately mean that much of the published ecological studies are of limited use for such purpose, despite their value in other respects.

As in previous studies, we also species *Apodera vas*, *Alocodera cockayni*, *Certesella certesi* and *Certesella martiali* which are all known to be restricted to regions South of the Tropic of Cancer. Additionally, *Amphitrema paparoensis*, *Amphitrema congolense* and *Hoogenraadia sylvatica* are recorded here for the first time since their descriptions from Southern Hemisphere locations. These species are probably not found north of the Cancer tropic desert belt (Smith et al., 2008), but while not being cosmopolitan, if the morphotypes we identified indeed correspond to these taxa, their geographical distribution would be immense. Indeed, even though *H. sylvatica* has been only reported to date from Argentina, the absolute distance between records locations *terra typica* exceeds 2000 km, while *A. congolense* was described from 10000 km away. Zapata and Fernández (2008) reported considerable morphological variability within *A. vas*, suggesting the existence of several species. If true some of these at least may have more restricted geographical distributions.

Some species are morphologically clearly distinct and can be securely considered as endemic to the Southern cone of South America. The best example is *Certesella australis* is, which, to our knowledge, is restricted to this region and it has been suggested that climatic conditions may limit its extension northwards (Fernández et al., 2016). Many other species from the American continent may also have such restricted distribution, but the scarcity of studies and

specialists in the region makes it impossible to assess this at present (Mazei et al., 2017). An atmospheric circulation modelling study showed that the dispersal potential of free-living microbes is clearly related to their size (Wilkinson et al., 2012). In line with this, a barcode sequence of *Sphenoderia valdiviana*, a small euglyphid species described from South-Central Chile (Chatelain et al., 2013), was later found in the Dominican Republic, at high elevation i.e. 2240 m.a.s.l. (Lara et al., 2016). Nevertheless, this, together with the high number of undescribed morphotypes found in our samples (Table 2), suggests that the number of South American endemic species is likely to be substantially higher than currently known.

This study allowed us to expand the number of testate amoeba species in Tierra del Fuego peatlands from 50 to 119. This number is considerably higher than the richness known for entire under-sampled countries such as Peru, Colombia, Ecuador or Mexico (Bobrov and Krasilnikov, 2011; Escobar et al., 2005; Haman and Kohl, 1994; Krashevskaya et al., 2007). It is obviously impossible for the diversity of testate amoebae in a single ecosystem type of Tierra del Fuego to be higher than in any of these countries. The data from the better-sampled Chile is here informative. A total of 314 species have been recorded considering all types of ecosystems, 10% of which were endemic to Chile (Fernández et al., 2015). However, species accumulation curves for this country did not reach saturation, suggesting the existence of many more species. Furthermore, these authors made predictions on the magnitude of local diversity, estimating the richness of Chilean Tierra del Fuego to about 25 species (Fernández et al., 2016); an estimate way below values we actually found in the two studied peatlands. This supports our primary statement that biodiversity inventories extended to the widest possible variety of microhabitats are needed to understand (testate amoebae) global biodiversity patterns.

Conclusions

The detailed analysis of testate amoebae from a broad range of micro-habitats in two peatlands of Tierra del Fuego revealed the existence of a high diversity, including a number of previously undocumented morphotypes, many of which likely represent new species probably endemic to the Tierra del Fuego region. The diversity of testate amoebae in Southern South America and much of the Southern Hemisphere and tropics remains poorly documented. Previous level of knowledge was sufficient to build inference models for paleoecology at regional level, but much more work is needed to describe the full diversity and understand the geographical distribution as well as the ecological preferences of species. This would best be done in a concerted way by applying a standard sampling design worldwide and with a common taxonomic framework based on combined morphological and molecular analyses.

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Figures and tables

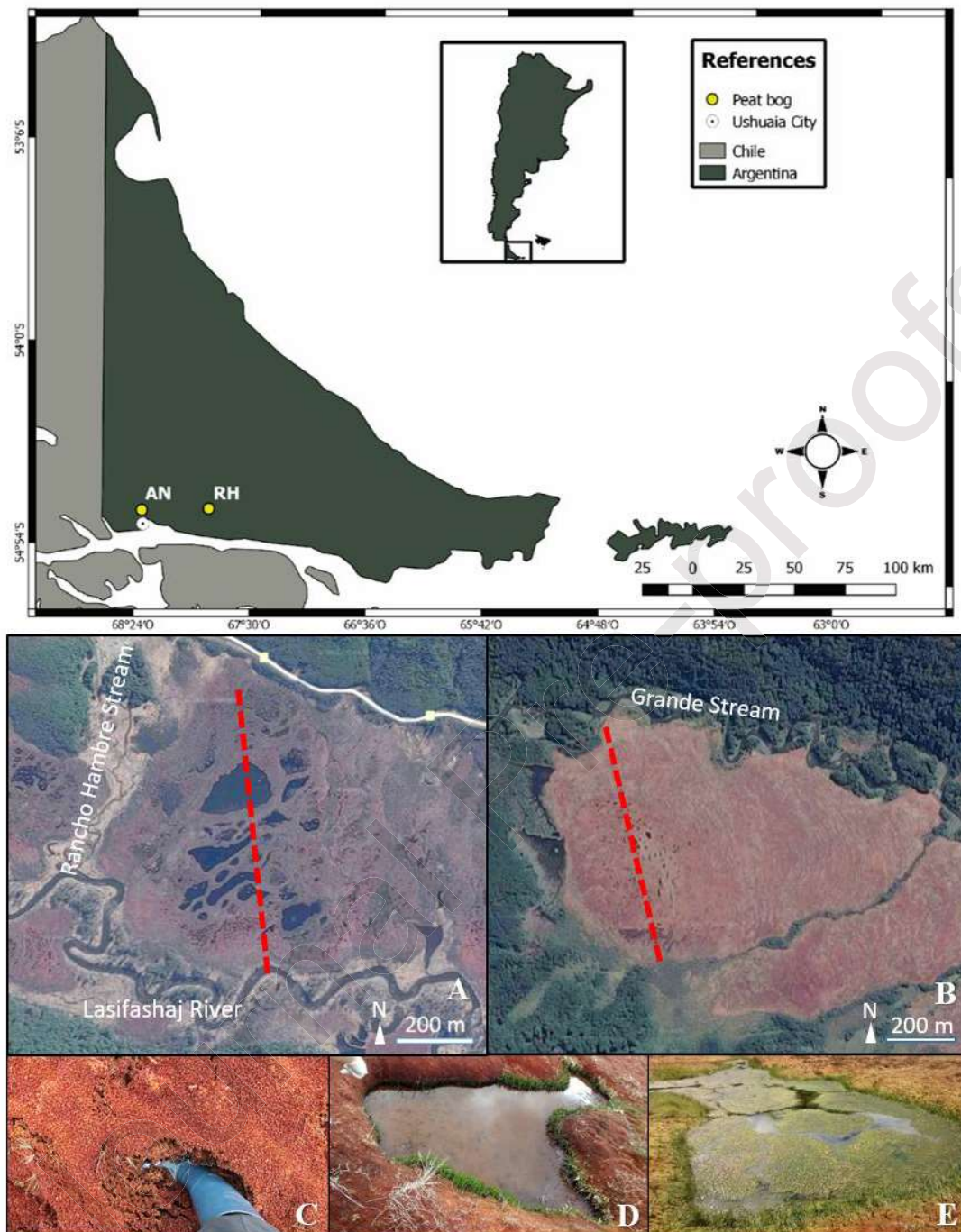


Fig 1. Location of Rancho Hambre (RH), Andorra (AN) in Tierra del Fuego Province, Argentina (top). Satellite view of RH (A) and AN (B) with sampled transects (---). Landscape elements detailed: matrix of *S. magellanicum* (C), clear pool (D) and vegetated pool (E).

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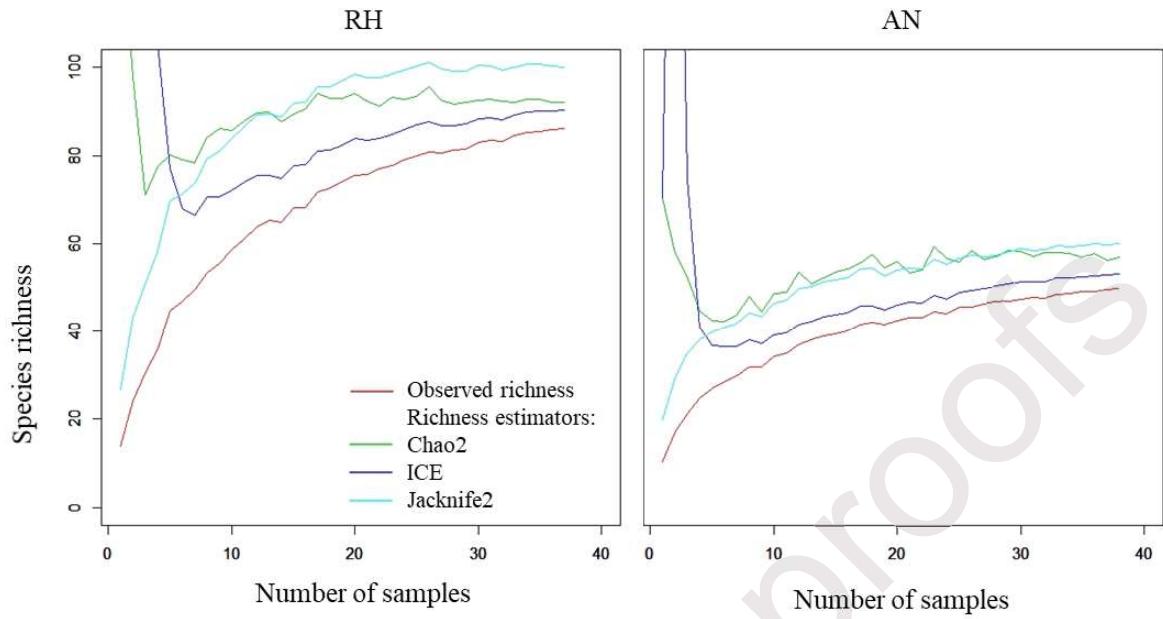


Fig 2. Species accumulation curves (Observed richness) and richness estimators (Chao2, ICE and Jackknife2).

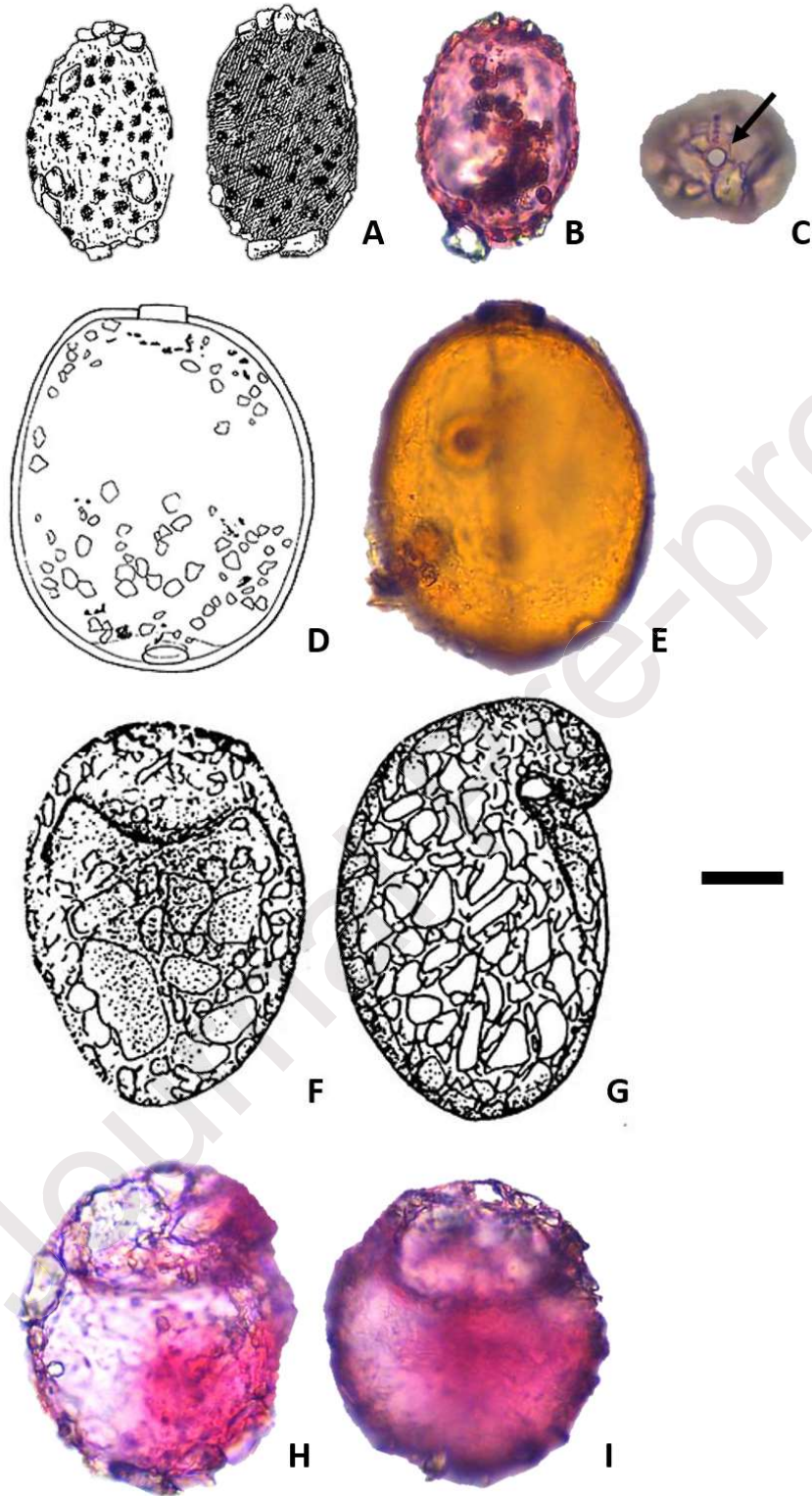


Fig 3. Species that are recorded for the first time since their description (specimens stained with Rose Bengal): *Amphitrema congolese* after Van Oye (1958) showing the characteristic mineral grains around the pseudostomes (A), *A. congolense* from Tierra del Fuego general appearance (B) and detail of one of the pseudostomes (C), *Amphitrema paparoensis* after Van Oye (1956) (D), *A. paparoensis* from Tierra del Fuego not stained showing characteristic brownish color and scattered mineral grains on the test surface (E), *Hoogenraadia sylvatica* after Vucetich (1973) ventral (F) and lateral view (G), *H. sylvatica* from Tierra del Fuego ventral view (H) and detail of the pseudostome (I). Scale bar = 20 μm

Table 1. List of species and species registered in peatlands from Tierra del Fuego (Argentina) in this and previous studies (+) and their geographical distribution (•).

	Vucetich (1974)	van Bellen <i>et al.</i> (2014)	Present study	Cosmopolitan	Only registered in South of the Tropic of Cancer	Only registered in South America	Unknown, probably new species for science
Testate amoebae species registered for peatlands in Argentinean Tierra del Fuego							
Amphitremitida							
<i>Amphitrema congolense</i> van Oye, 1958			+		•		
<i>Amphitrema paparoensis</i> van Oye, 1956			+		•		
<i>Amphitrema</i> sp.			+				•
<i>Amphitrema stenostoma</i> Nusslin, 1884		+		•			
<i>Amphitrema wrightianum</i> Archer, 1869		+	+	•			
<i>Archerella flavum</i> (Archer, 1877) Loeblich et Tappan, 1961	+			•			
Amebozoa							
<i>Alocodera cockayni</i> (Penard, 1910) Jung, 1942	+	+	+		•		
<i>Apodera vas</i> (Certes, 1889) Loeblich et Tappan, 1961	+	+	+		•		
<i>Arcella hemisphaerica</i> Perty, 1852	+		+	•			
<i>Arcella</i> sp. 1			+				•
<i>Arcella</i> sp. 2			+				•
<i>Argygnia caudata</i> Leidy, 1879	+				•		
<i>Argygnia dentistoma</i> var. <i>hesperia</i> (Penard, 1902) Wailes, 1913	+			•			
<i>Argygnia dentistoma</i> var. <i>oblonga</i> (Penard, 1902) Gauthier-Lievre, 1958	+			•			
<i>Argygnia similis</i> (Vucetich, 1973)	+					•	

<i>Centropyxis aculeata</i> (Ehrenberg, 1832) Stein, 1859			+	•			
<i>Centropyxis aerophila</i> Deflandre, 1929			+	•			
<i>Centropyxis cassis</i> (Wallich, 1864) Deflandre, 1929		+	+	•			
<i>Centropyxis</i> cf. <i>discooides</i> morphotype 1 Penard, 1902			+	•			
<i>Centropyxis</i> cf. <i>discooides</i> morphotype 2 Penard, 1902			+	•			
<i>Centropyxis platystoma</i> (Penard, 1890) Deflandre, 1929	+	+	+	•			
<i>Centropyxis</i> sp. 1			+				•
<i>Centropyxis</i> sp. 2			+				•
<i>Certesella australis</i> Vucetich, 1973	+		+			•	
<i>Certesella certesi</i> (Penard, 1911) Loeblich et Tappan, 1961	+	+	+		•		
<i>Certesella martiali</i> (Certes, 1889) Loeblich et Tappan, 1961	+	+	+		•		
<i>Cryptodifflugia oviformis</i> Penard, 1902			+	•			
<i>Cryptodifflugia</i> sp.			+				•
<i>Cyclopyxis arcelloides</i> type (Penard, 1902) Deflandre, 1929 <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			
<i>Cyclopyxis eurystoma</i> Deflandre, 1929			+	•			
<i>Cyclopyxis</i> sp. 1			+				•
<i>Cyclopyxis</i> sp. 2			+				•
<i>Cyclopyxis</i> sp. 3			+				•
<i>Difflugia acuminata</i> Ehrenberg, 1838	+			•			
<i>Difflugia bacillifera</i> Penard, 1890			+	•			
<i>Difflugia echinulata</i> Pénard, 1911	+			•			
<i>Difflugia</i> cf. <i>elegans</i> morphotype 1 Penard, 1890			+	•			
<i>Difflugia</i> cf. <i>elegans</i> morphotype 2 Penard, 1890			+	•			
<i>Difflugia globulosa</i> type (Dujardin, 1837) Penard, 1902 <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			
<i>Difflugia lanceolata</i> Penard, 1890		+		•			
<i>Difflugia</i> cf. <i>lucida</i> Penard, 1890		+	+	•			
<i>Difflugia oblonga</i> Ehrenberg, 1838	+			•			
<i>Difflugia pulex</i> Penard, 1890		+	+	•			
<i>Difflugia rubescens</i> Penard, 1891		+		•			
<i>Difflugia pristis</i> type Penard, 1902 <i>sensu</i> van Bellen <i>et al.</i> , 2014		+		•			

<i>Diffflugia</i> cf. <i>pyriformis</i> morphotype 1 Perty, 1852			+	•			
<i>Diffflugia</i> cf. <i>pyriformis</i> morphotype 2 Perty, 1852			+	•			
<i>Diffflugia</i> sp. 1			+				•
<i>Diffflugia</i> sp. 2			+				•
<i>Diffflugia</i> sp. 3			+				•
<i>Diffflugia</i> sp. 4			+				•
<i>Diffflugia</i> sp. 5			+				•
<i>Diffflugia</i> sp. 6			+				•
<i>Diffflugia</i> sp. 7			+				•
<i>Diffflugia</i> sp. 8			+				•
cf. <i>Diffflugia</i> sp. 9			+				•
<i>Heleopera petricola</i> Leidy, 1879	+	+	+	•			
<i>Heleopera rosea</i> Penard, 1890			+	•			
<i>Heleopera sphagni</i> Leidy, 1874	+	+		•			
<i>Heleopera</i> cf. <i>sylvatica</i> Penard, 1890	+	+	+	•			
<i>Heleopera</i> sp. 1			+				•
<i>Heleopera</i> sp. 2			+				•
<i>Heleopera</i> sp. 3			+				•
<i>Heleopera</i> sp. 4			+				•
<i>Hoogenraadia sylvatica</i> Vucetich, 1973			+		•		
<i>Lesquereusia spiralis</i> (Ehrenberg, 1840)			+	•			
<i>Microchlamys</i> sp.			+				•
<i>Nebela collaris-bohemica</i> type <i>sensu</i> van Bellen <i>et al.</i> , 2014		+		•			
<i>Nebela lageniformis</i> var. <i>cordiformis</i> Heinis, 1914	+			•			
<i>Netzelia</i> sp. 1			+				•
<i>Netzelia</i> sp. 2			+				•
<i>Netzelia</i> sp. 3			+				•
<i>Padaungiella lageniformis</i> (Penard, 1890) Lara et Todorov, 2012			+	•			
<i>Padaungiella walesi</i> (Deflandre, 1936) Lara et Todorov, 2012	+	+		•			
<i>Padaungiella</i> sp. 1			+				•

<i>Padaungiella</i> sp. 2			+				•
<i>Phryganella acropodia</i> type (Hertwig et Lesser, 1874) Hopkinson, 1909 <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			
<i>Phryganella</i> sp.			+				•
<i>Pontigulasia bigibbosa</i> Penard, 1902	+			•			
<i>Pontigulasia compressa</i> Carter, 1864	+			•			
<i>Pontigulasia contusa</i> Jung, 1942	+					•	
<i>Pontigulasia</i> sp.			+				•
<i>Pyxidicula operculata</i> (Agardh, 1827) Ehrenberg, 1838			+	•			
<i>Pyxidicula</i> cf. <i>patens</i> morphotype 1 Claparède et Lachman, 1858			+	•			
<i>Pyxidicula</i> cf. <i>patens</i> morphotype 2 Claparède et Lachman, 1858			+	•			
“ <i>Trigonocyrrillium</i> ” sp.			+				•
<i>Trigonopyxis microstoma</i> Hoogenraad et de Groot, 1948	+	+	+			•	
Cercozoa							
<i>Assulina muscorum</i> Greeff, 1888	+	+	+	•			
<i>Assulina seminulum</i> (Ehrenberg, 1848) Leidy, 1879	+	+	+	•			
<i>Corythion dubium</i> Taranek, 1871	+			•			
<i>Corythion</i> sp. 1			+				•
<i>Corythion</i> sp. 2			+				•
<i>Corythion</i> - <i>Trinema</i> type <i>sensu</i> van Bellen <i>et al.</i> (2014)		+					
<i>Diaphoropodon mobile</i> Archer 1869			+	•			
<i>Euglypha ciliata</i> (Ehrenberg, 1848) Leidy, 1878	+			•			
<i>Euglypha cristata</i> Leidy, 1874	+			•			
<i>Euglypha rotunda</i> type (Ehrenberg, 1845) <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			
<i>Euglypha</i> sp. 1			+				•
<i>Euglypha</i> sp. 2			+				•
<i>Euglypha</i> sp. 3			+				•
<i>Euglypha strigosa</i> (Ehrenberg, 1848)	+			•			
<i>Euglypha strigosa</i> type (Ehrenberg, 1848) <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			
<i>Euglypha tuberculata</i> type (Ehrenberg, 1848) <i>sensu</i> van Bellen <i>et al.</i> (2014)		+		•			

cf. <i>Frenzelina</i> sp.			+				•
<i>Nadinella</i> sp. 1			+				•
<i>Nadinella</i> sp. 2			+				•
<i>Pseudodifflugia</i> cf. <i>klarae</i> Kiss et Török, 2009			+	•			
<i>Pseudodifflugia fascicularis</i> Penard, 1902		+		•			
<i>Pseudodifflugia</i> sp. 1			+				•
<i>Pseudodifflugia</i> sp. 2			+				•
<i>Pseudodifflugia fulva</i> (Archer, 1869) Penard, 1902		+		•			
<i>Schwabia</i> sp.			+				•
<i>Sphenoderia lenta</i> Schlumberger, 1845		+		•			
<i>Sphenoderia ovoidea</i> Jung, 1942			+			•	
<i>Trinema</i> cf. <i>enchelys</i> (Ehrenberg, 1838)			+	•			
<i>Trinema lineare</i> Penard, 1890		+	+	•			
<i>Trinema penardi</i> Thomas et Chardez, 1958			+	•			
Unknown species 1			+				•
Unknown species 2			+				•
Unknown species 3			+				•
Total	30	32	87	61	8	5	45

Table 2. Global distribution of species registered in Tierra del Fuego peatlands to date and only by our study, per landscape element and per micro-habitat. Average number of species per landscape element and per micro-habitat and number of replicates for each. SD: standard deviation.

	Total species	Number of replicates	Average number of species per landscape element/micro-habitat (SD)	Cosmopolitan taxa (% , SD)	Only registered South of the Tropic of Cancer (% , SD)	Only registered in South American (% , SD)	Unknown distribution, probably new for science (% , SD)
Tierra del Fuego peatlands (past and present study)				51,00	6,70	4,20	38,00
Per sample (present study)		75	11,79 (6,41)	36,65 (16,62)	11,20 (9,17)	6,45 (5,65)	45,70 (15,81)
Clear pools	76	10	28,70 (12,94)	36,46 (11,73)	10,56 (5,84)	5,21 (2,50)	47,77 (10,48)
Vegetated pools	53	8	24,62 (6,43)	32,29 (7,28)	15,44 (3,49)	6,89 (2,66)	45,39 (3,21)
<i>Sphagnum</i> -matrix	18	8	10,87 (2,16)	30,73 (6,07)	6,11 (6,77)	11,15 (3,78)	52,01 (5,70)
Water column	21	18	15,17 (7,65)	33,18 (12,80)	12,03 (8,38)	7,64 (5,90)	47,15 (16,73)
Sediments	28	14	15,36 (7,70)	33,26 (14,65)	10,59 (8,14)	6,63 (6,02)	49,51 (9,34)
<i>Sphagnum magellanicum</i>	21	26	9,58 (3,74)	41,05 (16,70)	10,35 (10,13)	5,46 (5,10)	43,15 (15,14)
<i>Sphagnum fimbriatum</i>	7	9	6,68 (2,53)	43,57 (25,50)	13,57 (12,30)	3,48 (5,25)	39,38 (24,18)
<i>Sanionia uncinata</i>	16	8	10,75 (4,23)	36,08 (14,36)	6,97 (4,85)	4,07 (6,32)	52,88 (12,08)

Supporting information

A Reassessment of Testate Amoebae Diversity and Taxonomic Identity in Tierra del Fuego Peatlands: Implications for Large Scale Inferences by Luciana Burdman, Gabriela Mataloni, Edward A.D. Mitchell, Enrique Lara

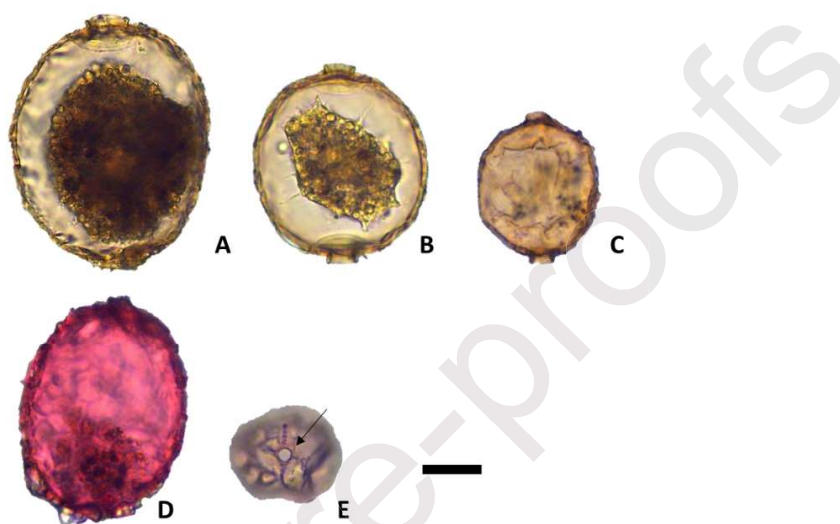


Fig. S1. (A) *Amphitrema papparoensis*, (B) *Amphitrema wrightianum*, (C) *Amphitrema* sp. 1, (D) *Amphitrema congolense* lateral view, (E) *Amphitrema congolense* detail of the pseudostome. Scale bar: 20 μm .

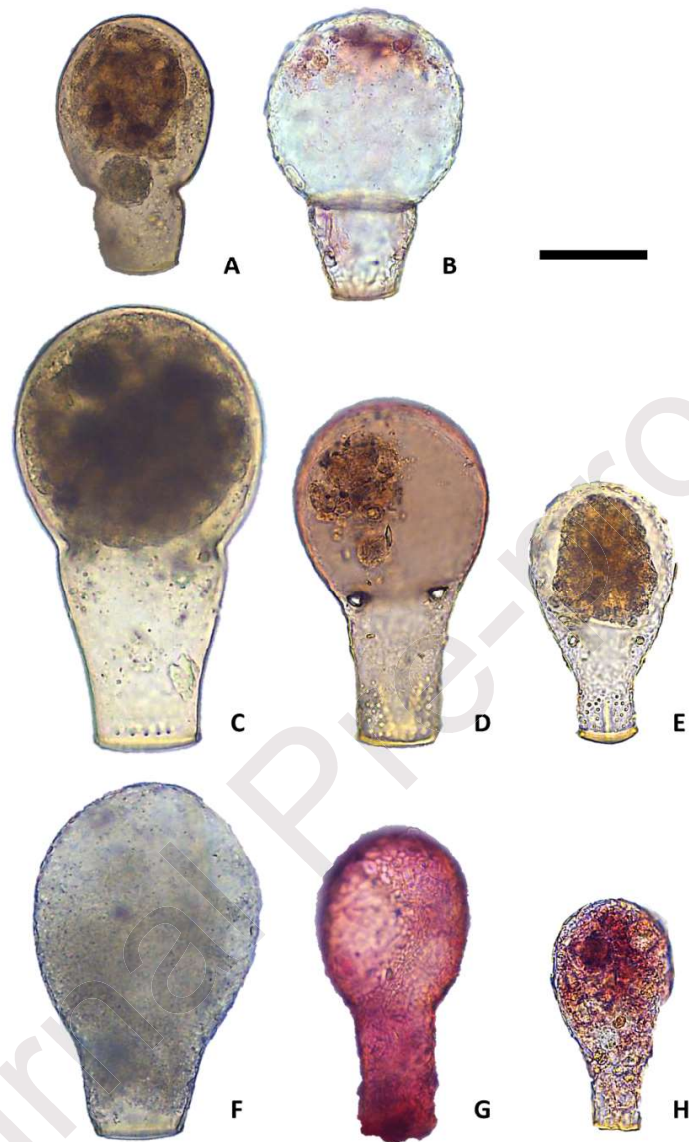


Fig. S2. (A) *Alocodera cockayni*, (B) *Apodera vas*, (C) *Certesella australis*, (D) *Certesella martiali*, (E) *Certesella certesi*, (F) *Padaungiella* sp. 1, (G) *Padaungiella lageniformis*, (H) *Padaungiella* sp. 2. Scale bar: 50 μm .

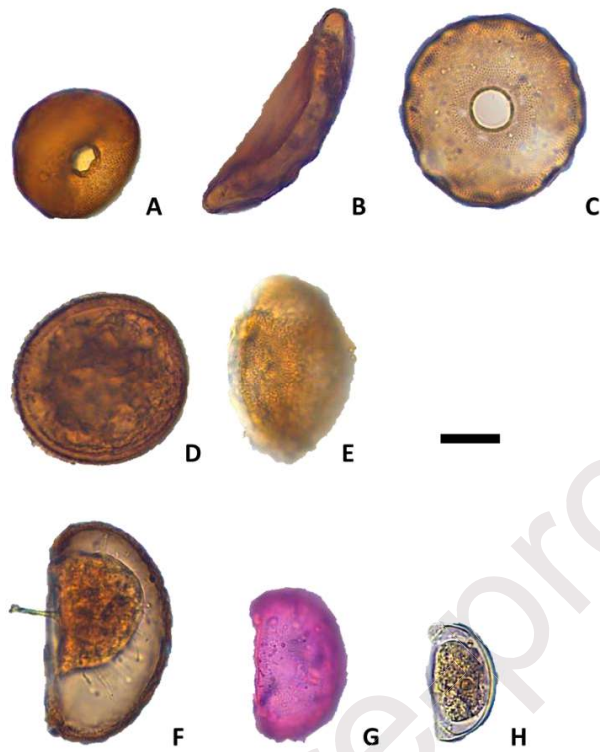


Fig. S3. (A) *Arcella hemisphaerica*, (B) *Arcella* sp. 1, (C) *Arcella* sp. 2, (D) *Microchlamys* sp. pseudostome view, (E) *Microchlamys* sp. lateral view, (F) *Pyxidicula* cf. *patens* morpho 1, (G) *Pyxidicula* cf. *patens* morpho 2, (H) *Pyxidicula operculata*. Scale bar: 20 μ m.

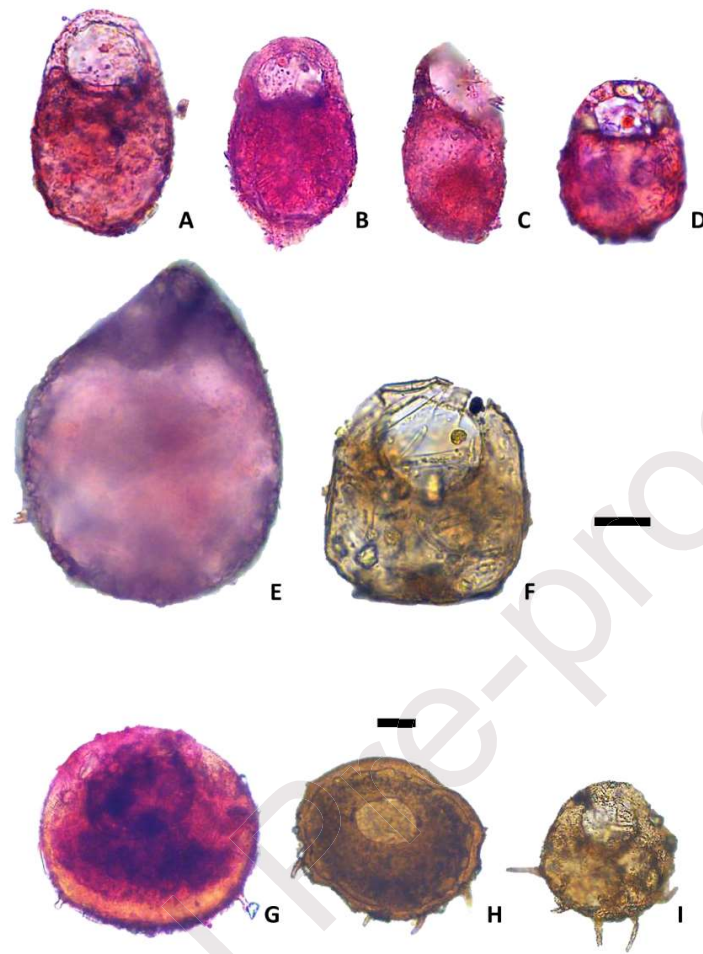


Fig. S4. (A) *Centropyxis* sp. 1, (B) *Centropyxis platystoma*, (C) *Centropyxis* sp. 2, (D) *Centropyxis aerophila*, (E) *Centropyxis* sp. 3, (F) *Centropyxis cassis*, (G) *Centropyxis* cf. *discoides* morpho 1, (H) *Centropyxis* cf. *discoides* morpho 2, (I) *Centropyxis aculeata*. Scale bars: 20 μ m.

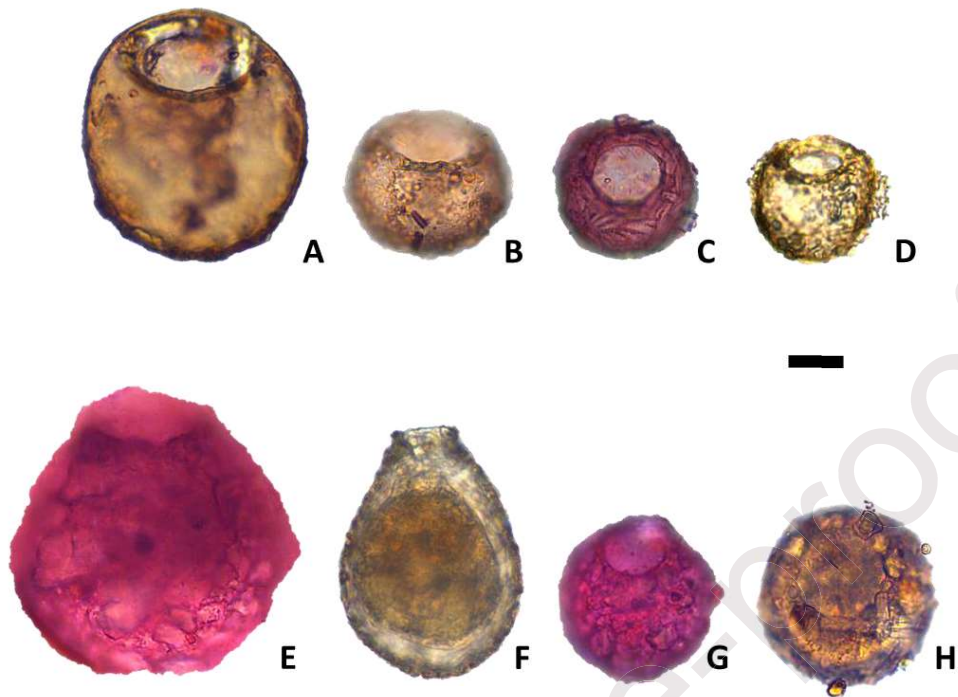


Fig. S5. (A) *Cyclopyxis* sp. 1, (B) *Cyclopyxis* sp. 2, (C) *Cyclopyxis eurystoma*, (D) *Cyclopyxis* sp. 3, (E) *Netzelia* sp. 2, (F) *Netzelia* sp. 3, (G) *Netzelia* sp. 1, (H) *Phryganella* sp. Scale bar: 20 μm .

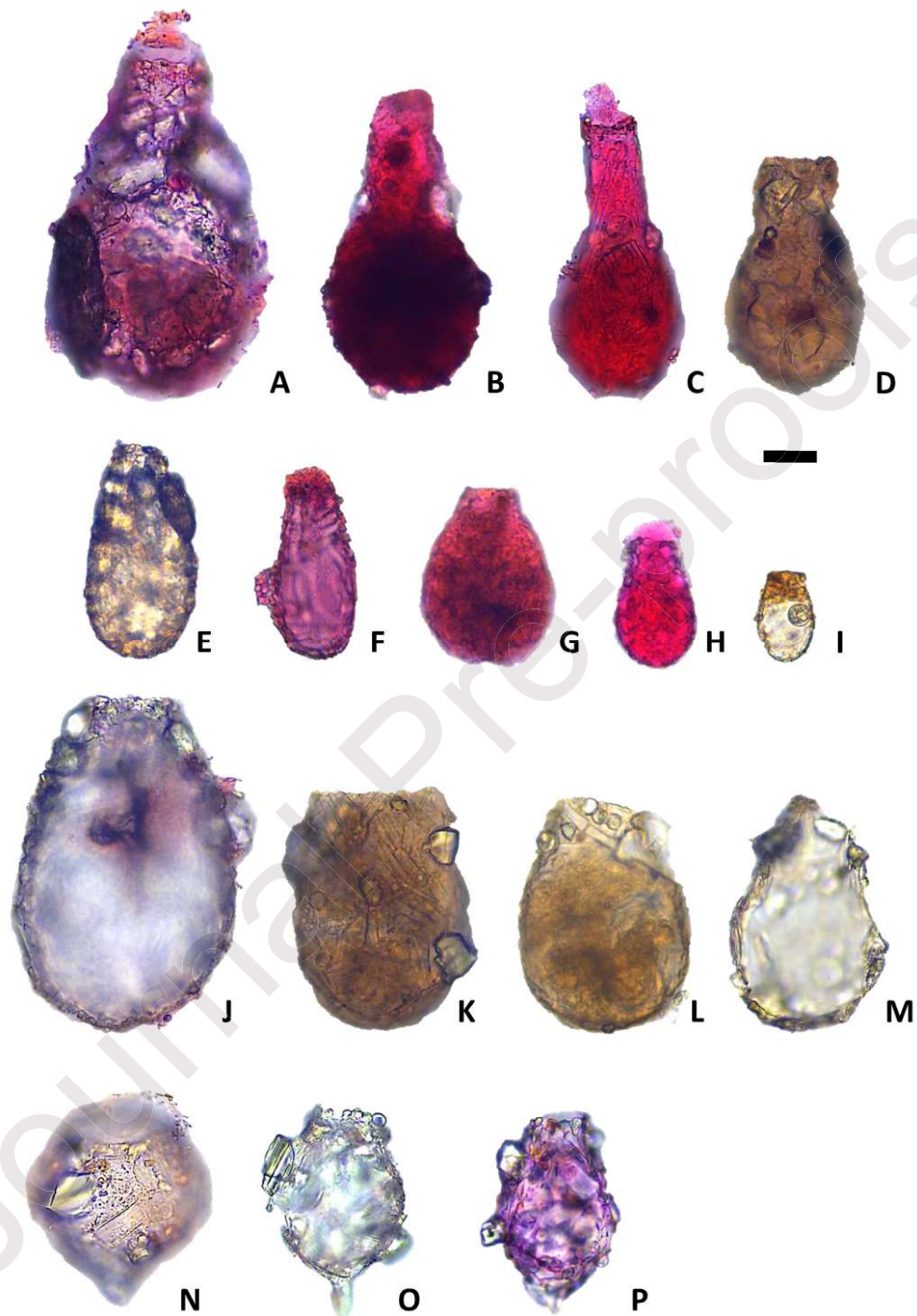


Fig. S6. (A) *Diffugia* cf. *pyriformis* morpho 1, (B) *Diffugia* cf. *pyriformis* morpho 2, (C) *Diffugia bacillifera*, (D) *Diffugia* sp. 1, (E) *Diffugia* sp. 2, (F) *Diffugia* sp. 3, (G) cf. *Diffugia* sp. 4, (H) *Diffugia* cf. *lucida*, (I) *Diffugia pulex*, (J) *Diffugia* sp. 5, (K) *Diffugia* sp. 6, (L) *Diffugia* sp. 7, (M) *Diffugia* sp. 8, (N) *Diffugia* sp. 9, (O) *Diffugia* cf. *elegans* morpho 1, (P) *Diffugia* cf. *elegans* morpho 2. Scale bar: 20 μ m.

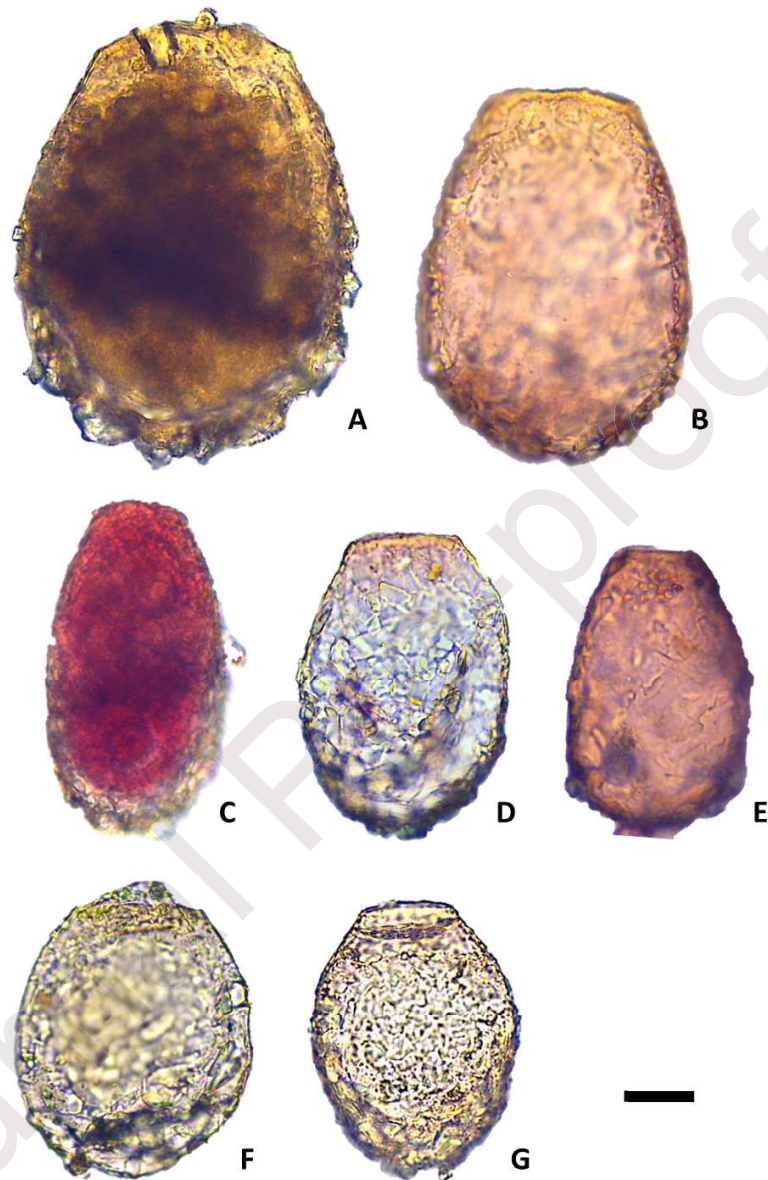


Fig. S7. (A) *Heleopera* sp. 1, (B) *Heleopera rosea*, (C) *Heleopera petricola*, (D) *Heleopera* cf. *sylvatica*, (E) *Heleopera* sp. 2, (F) *Heleopera* sp. 3, (G) *Heleopera* sp. 4. Scale bar: 20 μm .

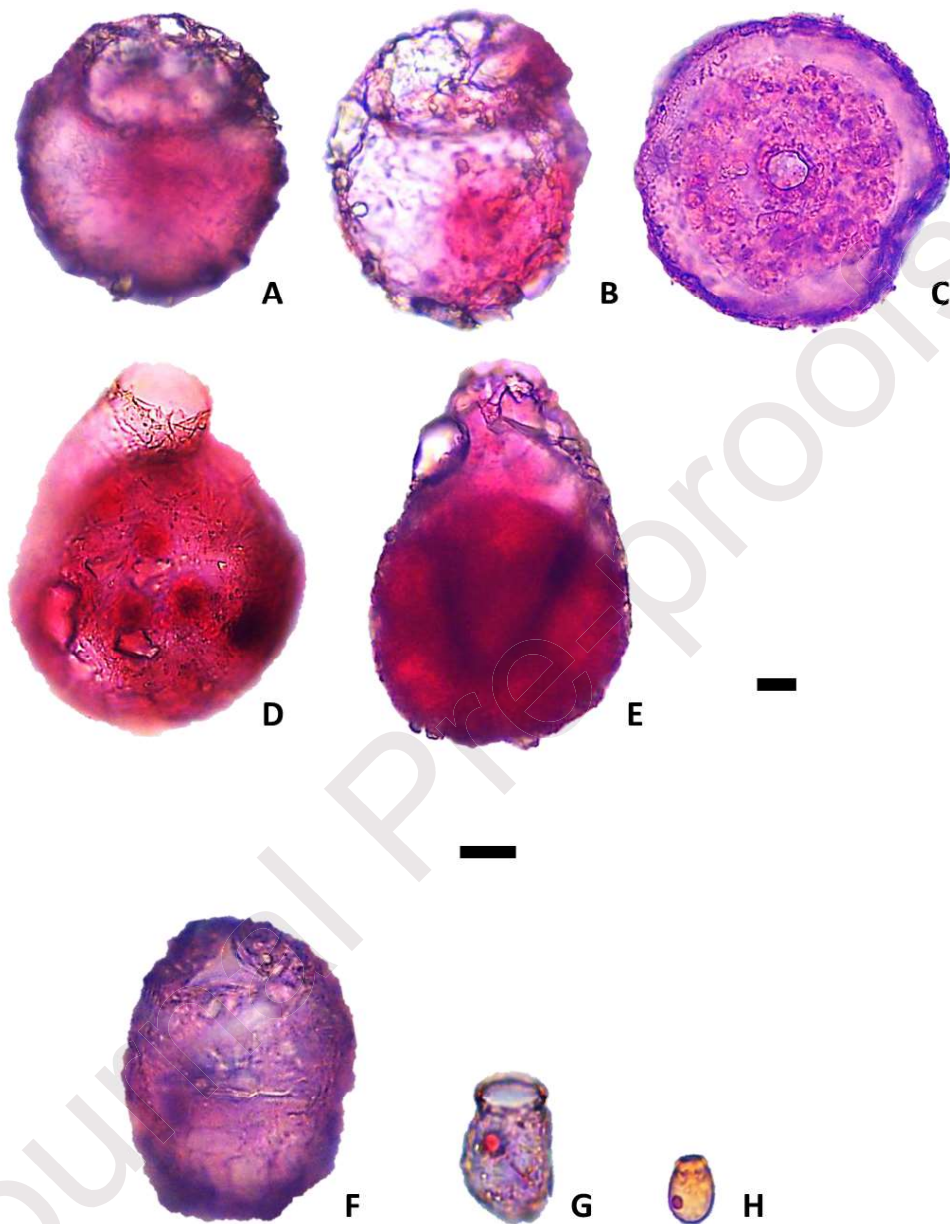


Fig. S8. (A) *Hoogenraadia sylvatica* pseudostome view, (B) *Hoogenraadia sylvatica* lateral view, (C) *Trigonopyxis microstoma*, (D) *Lesquereusia spiralis*, (E) *Pontigulasia* sp., (F) *'Trigonocyrrillium'* sp., (G) *Cryptodifflugia* sp., (H) *Cryptodifflugia oviformis*. Scale bar: 10 μ m.

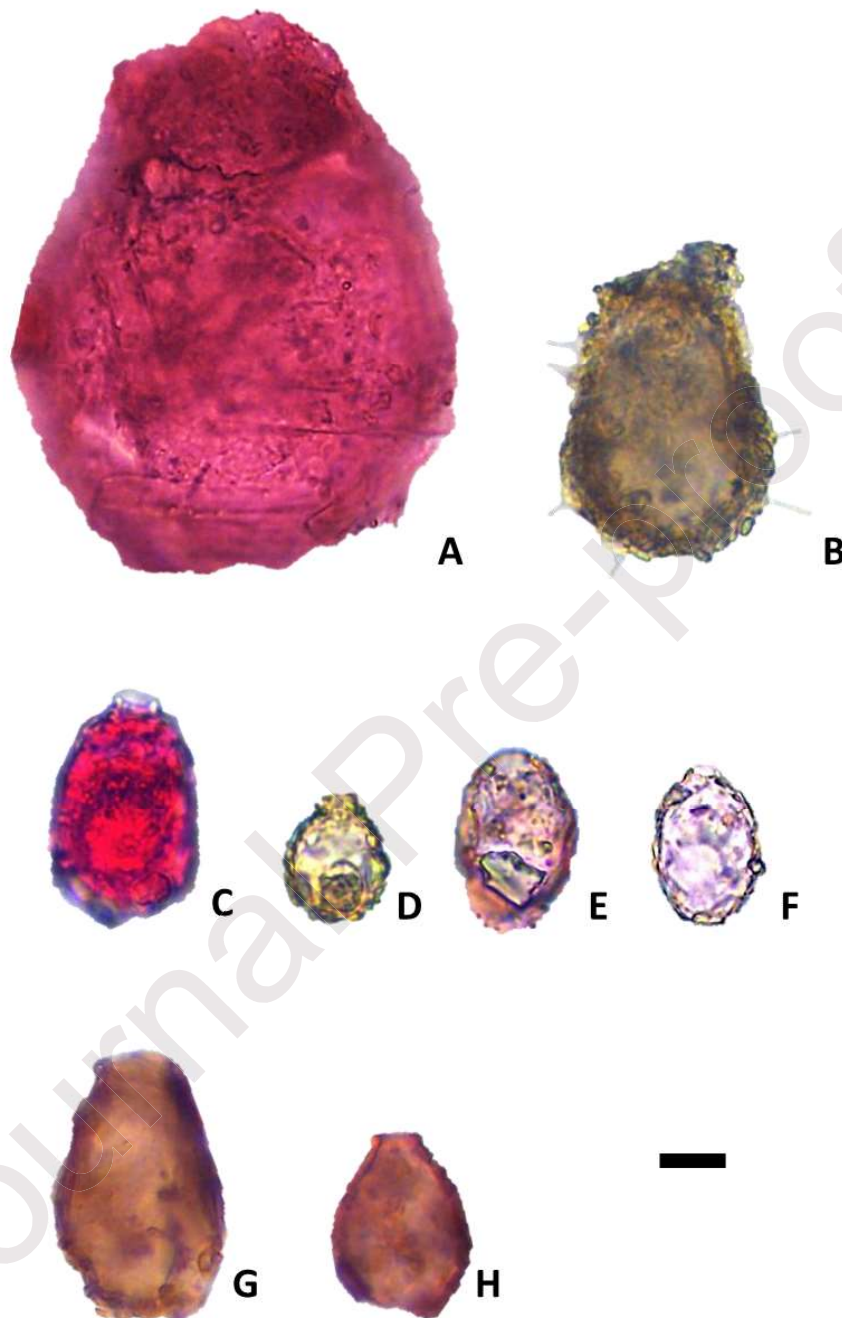


Fig. S9. (A) *Schwabia* sp., (B) *Diaphoropodon mobile*, (C) *Nadinella* sp. 1, (D) *Nadinella* sp. 2, (E) cf. *Frenzelina* sp., (F) *Pseudodifflugia* cf. *klarae*, (G) *Pseudodifflugia* sp. 1, (H) *Pseudodifflugia* sp. 2. Scale bar: 10 μ m.

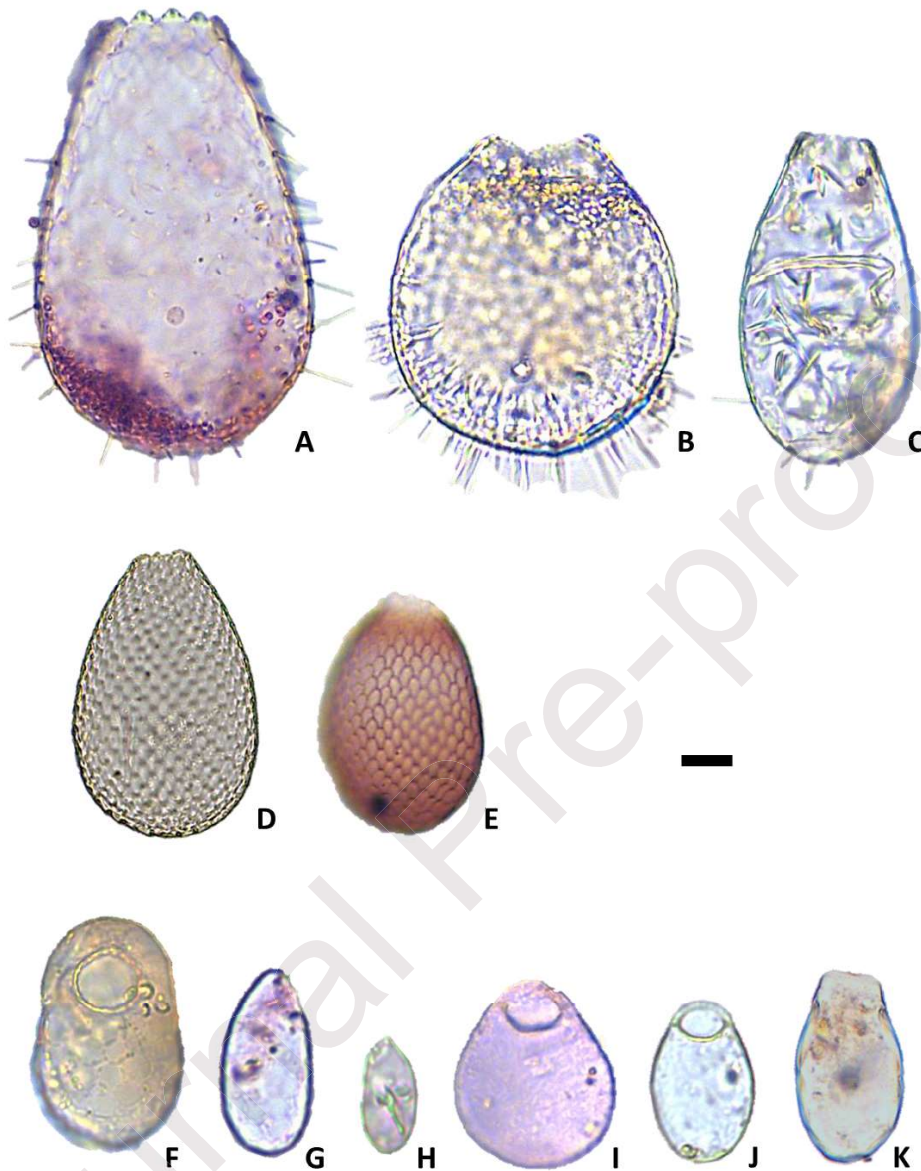


Fig. S10. (A) *Euglypha* sp. 1, (B) *Euglypha* sp. 2, (C) *Euglypha* sp. 3, (D) *Assulina seminulum*, (E) *Assulina muscorum*, (F) *Trinema penardi*, (G) *Trinema* cf. *enchelys*, (H) *Trinema lineare*, (I) *Corythion* sp. 1, (J) *Corythion* sp. 2, (K) *Sphenoderia ovoidea*. Scale bar: 10 μ m.

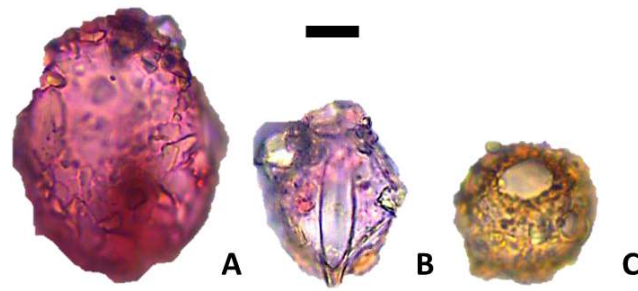


Fig. S11. (A) Incertae sedis 1, (B) Incertae sedis 2, (C) Incertae sedis 3. Scale bar: 10 μm .

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Credit authorship contribution statement

Luciana Burdman: Data collection, Analyses, Writing - original draft.

Gabriela Mataloni: Resources, Conceptualization, Data collection, Writing - review & editing.

Edward A.D. Mitchell: Resources, Analyses, Writing - review & editing.

Enrique Lara: Analyses, Writing - original draft, Supervision.

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