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A brief history of testate amoebae research and introducing the International Society for Testate Amoeba Research (ISTAR)

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INTRODUCTION

Research on testate amoebae goes back to the early 19th century, more precisely the year 1815 when Leclerc (or Le Clerc) described the genus *Diffugia*, which he presented as a “new type of amorphous polyp” (Leclerc 1815). Since then the pace of publication was uneven but some very significant early works such as the seminal works of Leidy, Penard, and Cash, Hopkinson and Wailes paved the way to future research (Cash et al. 1905–1921; Leidy 1879; Penard 1890; Penard 1902; Penard 1911). These early studies focused on describing the diversity of testate amoebae but also included discussions (or speculations) about their geographical distribution and ecology. The lives and scientific careers of Leidy and Penard were nicely described by Corliss who had the privilege of meeting Penard towards the end of his long life (Corliss 2001).

Identification of testate amoebae is relatively easy for some species but more challenging for others. In recent decades, some useful taxonomic monographs and identification guides greatly helped researchers in the often-difficult challenge of identifying some taxa. Meisterfeld (2002a, 2002b) published two well illustrated chapters in the illustrated guide to the protozoa. Tzyganov and Mazei (2006) compiled most original descriptions in a monograph, unfortunately published in Russian but still useful for the completeness of the compilation. They later published a useful key to the genera (Tsyganov et al. 2016). Mazei in collaboration with Warren did a great service to the community by revising the large and complex genus *Diffugia* in a series of three papers (Mazei and Warren 2012; Mazei and Warren 2014; Mazei and Warren 2015). An especially useful resource is the website arcella.nl created by Ferry Siemensma and regularly updated. This has become for many an essential resource. Todorov and Bankov (2019) recently also published a very nicely illustrated guide to *Sphagnum*-dwelling testate amoebae in Bulgaria. And the long-awaited monograph on hyalospheniid testate amoebae by Anush Kosakyan

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and colleagues was just released (Kosakyan et al. 2025). This monograph is freely available on the publisher's website.

From these early works onwards, peatlands have been a favoured hunting ground for testate amoeba specialists. Indeed, there is no better way to start studying testate amoebae than to squeeze a few drops of water from a wet moss, ideally *Sphagnum*, and put it under the microscope. The result may look like Fig. 1.

HISTORY OF RESEARCH ON TESTATE AMOEBAE AS (PALEO)BIOINDICATORS

The detailed study of the ecology and bioindication of testate amoebae in peatlands as well as their use as palaeoecological indicators was established in Germany in the first part of the 20th century (Dubois and Dubois 1943; Grospietsch 1953; Harnisch 1924; Harnisch 1925; Harnisch 1927; Harnisch 1929; Harnisch 1937; Harnisch 1948; Jung 1936; Schönborn 1962; Schönborn 1963; Schönborn, 1965; Steinecke 1914; Steinecke 1929; Steinecke 1934). This led to the

description of communities along the water table depth gradient as well as the recognition of the vertical distribution of species along the mosses (Fig. 2).

Jung (1936) developed a very practical semi-quantitative moisture scale to help testate amoeba ecologists characterise the sampling places. The use of this scale is illustrated in Figure 2.

COMMUNITY ECOLOGY AND APPLICATION OF THE PHYTOSOCIOLOGICAL CLASSIFICATION SYSTEM TO DESCRIBE TESTATE AMOEBEA COMMUNITIES

The phytosociological classification system initially developed by plant community ecologists (Braun-Blanquet 1928) was used by Schönborn (1963) to describe peatland testate amoeba communities, as illustrated in Figure 3. Bonnet (1964) used the same system to describe edaphic testate amoeba communities (Fig. 4) and matched different compositions of testate

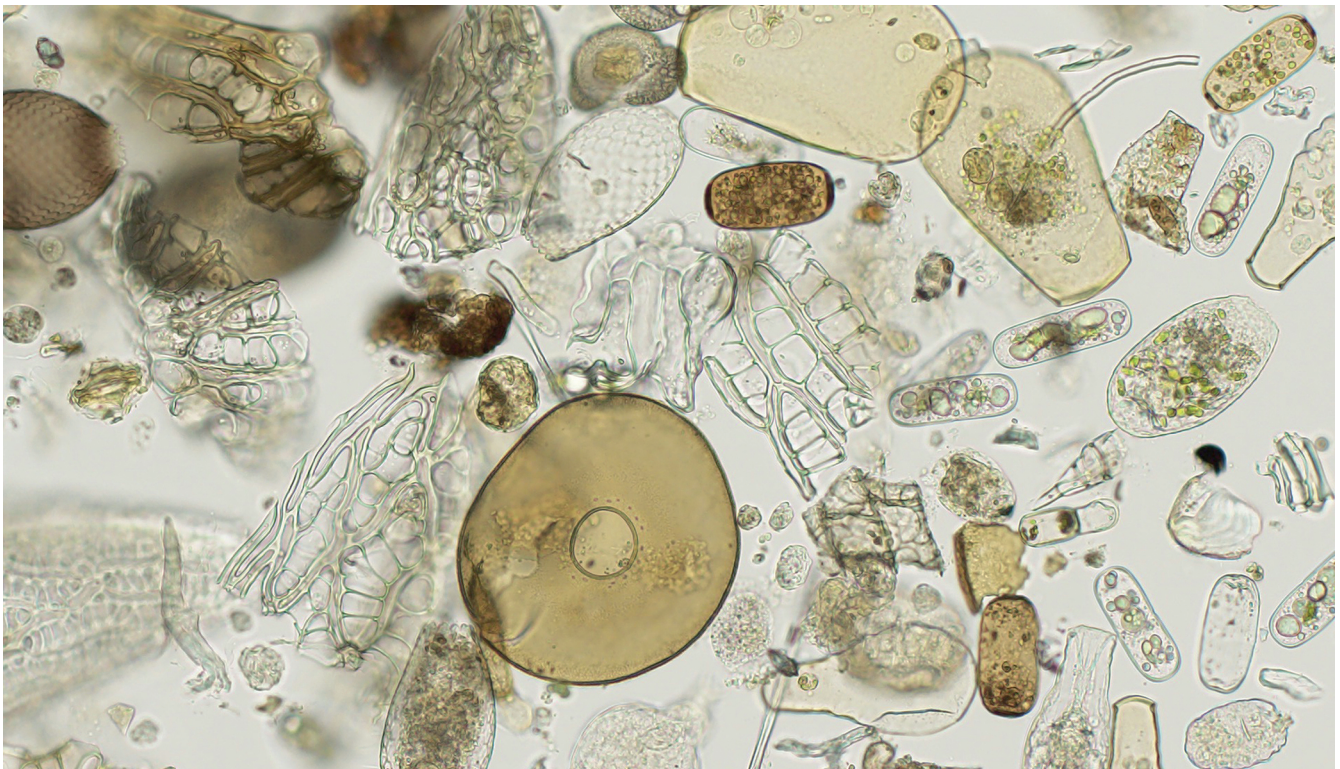


Fig. 1. An abundant and diverse assemblage of testate amoebae and other microorganisms extracted from a *Sphagnum* moss sample. *Galeri-pora artocrea*, *Hyalosphenia papilio*, *H. elegans*, *Euglypha compressa*, *Archerella flavum*, *Assulina seminulum*, with bdelloid rotifers, desmids (green algae), conifer pollen, and fragments of *Sphagnum* leaves.



Fig. 2. Top: The Trogenmoos bog in the Swiss Pre-Alps (canton Bern) and illustration of four characteristic species for the hydrological gradient from bog pools to hummocks: (*Heleopera sphagni*, *Hyalosphenia papilio*, *Bullinularia indica*, *Trigonopyxis arcula*), images: E. Mitchell (the landscape image is flipped left to right to match the bottom illustration). Bottom illustration of the horizontal patterns of testate amoeba along the moisture gradient (Schönborn, 1962). The roman numbers refer to the semi-quantitative moisture scale of Jung:

- I: Submerged,
- II: Floating, partly submerged and partly at the surface,
- III: Very wet – Water drips without pressure,
- IV: Wet – Water drips with slight pressure, V: Semi-wet – Water drips with moderate pressure,
- VI: Moist – Only little water drips by strong pressure,
- VII: Half-dry – Only a few drops can be extracted by strong pressure,
- VIII: Dry – No water drips even with strong pressure) (Jung 1936).

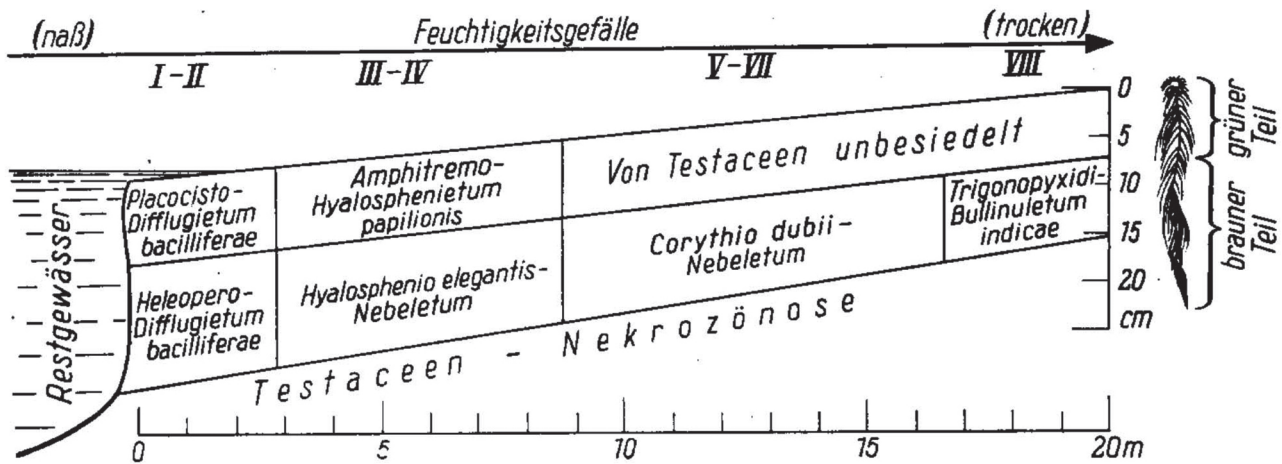


Fig. 3. Illustration by Schönborn of the horizontal and vertical patterns of testate amoeba communities in *Sphagnum* mosses along the pool to hummock gradient (Schönborn 1963). The names of communities are inspired from the phytosociological classification system in which the scientific name of its most characteristic species is used as namesake, changing the ending of the generic name to “-etum” and treating the specific epithet as adjective (Braun-Blanquet 1928). In this example for each association two taxa are used to create the name (e.g. *Placocista* sp. and *Difflugia bacillifera*).

amoeba communities to different habitats and soil types that had evolved over time from shallow mineral-dominated soils through to deep organic soils with several soil horizons (Fig. 5). He also noted an interesting correlation between the community structure of testate amoebae and the potential production of truffles (Bonnet 1974; Bonnet 1977b; Bonnet 1979).

BIOGEOGRAPHY

With increasing records of testate amoebae from different parts of the World, the question of their distribution patterns became a possible research topic. The idea that testate amoebae had a cosmopolitan distribution was first expressed by Penard in his 1902 monograph on the testate amoebae from the Lake Geneva basin (Penard 1902). Penard considered the question of the cosmopolitan distribution of testate amoebae established following the works of Ehrenberg and Schewiakoff. Penard cited the short contribution of Schewiakoff (Schewiakoff 1893) but did not refer to any specific publication by Ehrenberg. Penard personally observed 92 % of all known species in the region covered by his book over a period of only two years. He found new species until the last week of his work and therefore

he concluded that it would be likely that his list was incomplete, and that more species could be found in the region. He therefore concluded that testate amoebae were mostly cosmopolitan. He listed the 19 species that to his knowledge he had not found in the region. As he predicted, at least two were soon after found in Switzerland by Heinis: *Porosia bigibbosa*, formerly *Nebela bigibbosa* and *Placocista spinosa* (Heinis 1910). Penard also speculated that many new species remained to be discovered. Nevertheless, his list of species already contained good examples of non-cosmopolitan testate amoebae (e.g. *Nebela caudata*, *N. hippocrepis*, *N. ansata*, and *Sphenoderia macrolepis*, the former three now respectively *Argynnia caudata*, *Cortnutheca equicalceus* and *C. ansata*). *Argynnia caudata* is frequently found in moss samples from the Southern Hemisphere and inter-tropical region and subtropical islands (Bamforth 2015; Souto et al. 2021; Vucetich 1974). *Cortnutheca equicalceus* is known from the East coast of the United States (Leidy 1879), with records from Europe considered doubtful and a record from Korea attributed to a new species (*C. jiuhuensis*) and a record from Nepal likely also corresponding to another, currently undescribed, species (Qin et al. 2016). *Cortnutheca ansata* is known only from the East coast of the United States and Canada (Heger, Booth et al.

2011). *Sphenoderia macrolepis* was also never reported in Europe but has been reported from several regions in the Southern Hemisphere and inter-tropical zone (Bamforth 2015; Fernández et al. 2015; Hoogenraad and De Groot 1940). A key species missing in Penard's list was *Apodera vas* (then *Nebela vas*) which had been described three years prior to the publication of the monograph (Certes 1889).

In his PhD monograph, Decloître compiled the existing data on the diversity of testate amoeba genera in different parts of the World (Decloître 1953). He focused on the ten most diverse genera, accounting for 514 species out of a total of ca. 800 species in his global database. He then tallied the known species richness in different regions of the world (Table 1). The first observation is that for all the top 10 most diverse genera except one, the highest number of species known at the time had been reported for Western Europe (specifically: England, Switzerland, France, Germany and Italy) where two thirds of all species known for the ten most diverse genera of testate amoebae had been reported while other regions range between 18 % and

36.5 %. This clearly illustrates the much higher sampling effort in western Europe. This sampling bias persists today. When comparing the other regions some stand out with a relatively high diversity for some genera (e.g. *Nebela* s.l. in North America, *Arcella* and *Centropyxis* in tropical Africa). However, Decloître was understandably cautious about any interpretation of these patterns. He pointed out that the samples were collected in different habitats, but the range of habitats sampled was the choice of each researcher and did not follow a strict protocol such as stratified random that would give more robust results. Such an approach has to this day not been done and a global well-coordinated effort would certainly be extremely timely. This is something the ISTAR could and should be leading!

Bonnet (1964) observed that the characteristic communities of well-developed soils were similar from southern France to North Africa and even Angola and Argentina (Bonnet 1964). He noted that this observation was at odds with the well-documented endemism of soil animals. He attributed this broad distribution to the combination of small size and

Table 1. Compilation of testate amoeba species richness data by Decloître (1953).

Genus	Nb sp	Percentage of 10 most diverse genera observed in different regions of the World								
		Global %	Global	Western Europe*	North America	Neotropics	Temperate S America	Australia	Java & Sumatra	Tropical Africa
<i>Arcella</i>	90	11	18	10	5	3	1	4	1	6
<i>Centropyxis</i>	60	8	12	5	3	2	3	1	3	7
<i>Diffugia</i>	140	18	27	25	8	2.5	5	6.5	3	5
<i>Euglypha</i>	60	8	12	6	6	3	3	4	2	4
<i>Heleopera</i>	14	2	3	2	2	1	1.5	0	1	0
<i>Hyalosphenia</i>	13	2	3	2	1	0.5	0.5	0	0.5	1
<i>Lesquereusia</i>	15	2	3	2	0.5	0.5	0.5	1	0	1
<i>Nebela</i> (s.l.)	100	13	19	12	10	5	6	2.5	6	2
<i>Sphenoderia</i>	12	2	2	1	0.5	0	0.5	2	1	0.5
<i>Trinema</i>	10	1	2	1	0.5	1	0.5	0.5	0.5	1
Total top 10 genera	514	64	100	66	36.5	18.5	21.5	21.5	18	27.5
Global total (estimated)	800									

* Countries included: England, Switzerland, France, Germany, Italy.

Hiérarchie des groupements			
CLASSE	ORDRE	ALLIANCE	ASSOCIATION
Phryganellatea	Centropyxidetalia (sols peu évolués, souvent squelettiques)	<i>Centropyxidion globulosae</i>	I. <i>Arcelletum arenariae</i> . II. <i>Diplochlamydetum timidae</i> . XI. <i>Plagiopyxidatum intermediae</i> .
		<i>Assulinion muscorum</i> ..	III. <i>Assulinetum muscorum</i> . IV. <i>Nebeletum</i> . V. <i>Centropyxidatum vandeli</i> . VI. <i>Corythietum dubii aerophilae</i> .
		<i>Plagiopyxidion labiatae</i> .	VII. <i>Plagiopyxidatum labiatae</i> .
		<i>Centropyxidion deflandrianae minimae</i> ...	XIX. <i>Centropyxidatum deflandrianae minimae</i> . XX. <i>Plagiopyxidatum intermediae cyrtostomae</i> . XXII. <i>Phryganelletum paradoxae</i> .
		<i>Centropyxidion constrictae minimae</i>	XVIII. <i>Centropyxidatum plagiostomae</i> . XXI. <i>Hyalosphenietum insectae</i> .
		<i>Tracheleuglyphion acollae</i>	VIII. <i>Centropyxidatum aerophilae sphagnicolae</i> . IX. <i>Tracheleuglyphetum acollae</i> . X. <i>Trinemetum</i> .
		<i>Diffugiellion oviformis</i> .	XII. <i>Euglyphetum</i> . XIV. <i>Plagiopyxidatum penardi</i> .
		<i>Pseudodiffugion gracilis terricolae</i>	XIII. <i>Euglyphetum cuspidatae</i> . XV. <i>Corythietum delamarei</i> . XVI. <i>Plagiopyxidatum bathys-tomae</i> .
		<i>Bullinutarion gracilis</i> ..	XVII. <i>Heleoperetum petricolae humicolae</i> . XXV. <i>Schwabietum terricolae thomasi</i> .
		<i>Plagiopyxidion oblongae</i>	XXIII. <i>Geopyxelletum sylvicolae</i> . XXIV. <i>Pseudawerintzewietum calcicolae</i> .
	Plagiopyxidetalia (sols évolués, riches en matière organique) ..	<i>Centropyxidion halophilae</i>	XXVI. <i>Centropyxidatum halophilae</i> .

Fig. 4. Louis Bonnet's classification system of soil testate amoeba communities (Bonnet 1964).

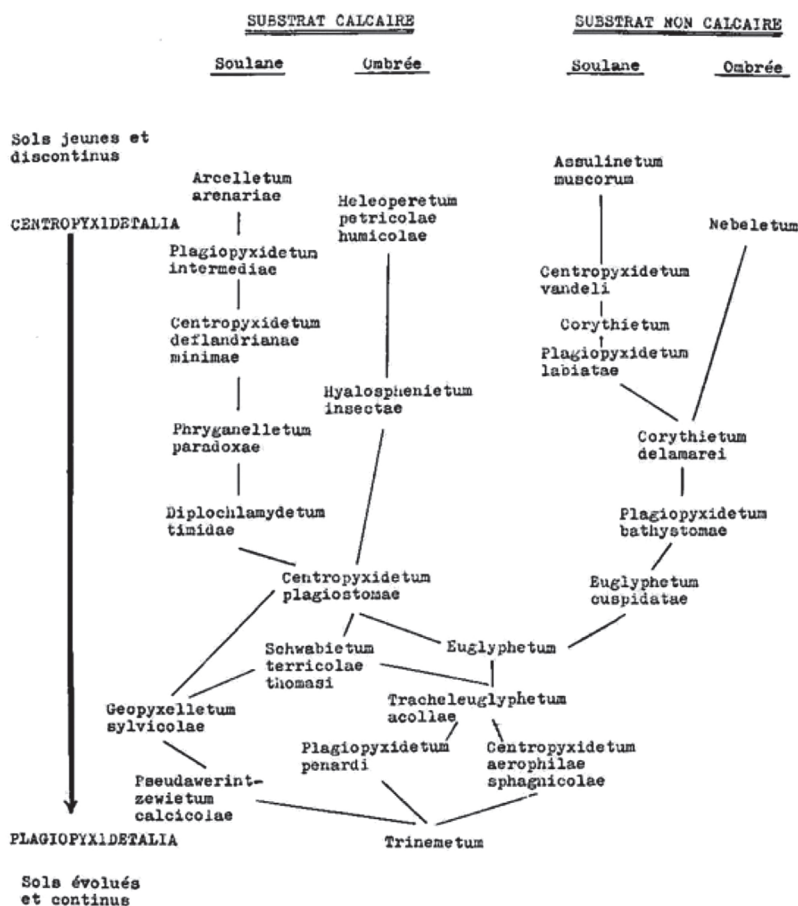


Fig. 5. Succession of testate amoeba communities associated to the development of soil described from the French Pyrenees region (Bonnet 1964). “Soulane” refers to south-facing slopes, while “ombrée” refers to north-facing slopes. In young, patchy soils communities are clearly distinct between calcareous and non-calcareous soils and between south- and north-facing slopes. As soils develop and become more continuous, the testate amoeba communities become gradually more similar.

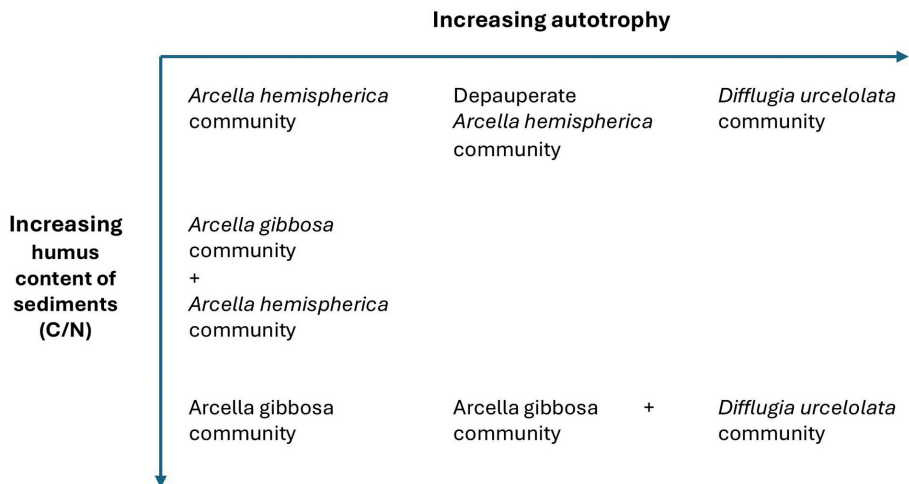


Fig. 6. Schönborn’s classification of lake testate amoeba communities according to lake humus content (C/N ratio) and autotrophy gradients (redrawn and translated) (Schönborn 1966).

capacity to produce very resistant cysts that made it possible for soil testate amoebae to be passively transported over long distances (Bonnet 1961). This was also the argument in favour of the cosmopolitan distribution of free-living protists (Finlay et al. 2001, Finlay et al. 2004; Finlay and Fenchel, 2004). He later speculated that dispersal could be made easier by shifts to drier periods in the tropics leading to the expansion of savannas at the expense of closed forests much less favourable to the passive transport of soil protist (Bonnet 1977a).

The question of cosmopolitanism vs endemism of soil protists became a highly contentious topic towards the end of the 20th century and testate amoebae emerged as a key model group in this debate (Foissner 1999a; Foissner 2004; Foissner 2006; Heger et al. 2009; Heger, Lara et al. 2011; Smith et al. 2008). Biogeography became a dynamic research topic with new insights from atmospheric circulation modelling (Wilkinson et al. 2012), climatic niche modelling and comparison of realised and predicted (potential) distribution of species (Bruni et al. 2024), and phylogeography (Heger et al. 2013; Lara et al. 2011; Lara et al. 2016; Singer et al. 2019).

TESTATE AMOEBA STUDIES IN LAKES AND RIVERS

Testate amoebae are also common in lakes and rivers and a considerable body of literature exists on these habitats (Schwind et al. 2016). As for soils, testate amoebae have long been recognised as valuable bioindicators in aquatic habitats (Nasser et al. 2016; Patterson et al. 2019; Roe and Patterson 2014; Semensatto et al. 2023; Wojewódka-Przybył et al. 2022). For example a classification system was developed by Schönborn (1966) for lakes and such data opened the door for the use of testate amoebae as indicators for a range of environmental factors from temperature to anthropogenic pollution in palaeolimnological studies (Kauppila et al. 2006; Kihlman and Kauppila 2012; Lorencova 2009; McCarthy et al. 1995; Nasser et al. 2020; Ndayishimiye et al. 2019; Patterson and Kumar 2002; Roe et al. 2010; Wall et al. 2010). Testate amoebae were also shown to be valuable indicators in estuarine environments, especially when combined with other groups such as tintinids (ciliates) or foraminifera (Camacho et al. 2015; Charman et al. 1998; Roe et al. 2002).

RECENT DYNAMICS IN THE COMMUNITY OF TESTATE AMOEBA RESEARCHERS AND ISTA MEETINGS

Research on testate amoebae has considerably expanded in recent decades (Fig. 7). It seems that we are currently living a new golden era for research on these charismatic and fascinating organisms. Based on the Scopus data base, and using the keywords indicated in the caption of Fig. 7, the number of publications on testate amoebae was very low before 1973, then oscillated between 10 and 30 until 1995, then between 30 and 50 until 2006 after which 60 or more publications were listed annually with a peak at over 100 in 2015. Although these numbers are certainly partly wrong because some publications may be missing in Scopus or did not match the keywords the trend is most likely correct. These numbers are higher than those shown by Kosakyan et al. (2016), but this can be explained by the fact that I used many keywords while they used only “testate amoebae.” Still the trend is similar except that the increase seems to have stopped in the last few years.

The diversity of topics also reflects the dynamism of the community. Historically a large proportion of testate amoeba publications were palaeoecological studies in which testate amoebae were “only” used as proxies. Most often this was for reconstructing past water table depth and to a lesser degree pH from peat records (Charman 2001; Mitchell et al. 2008; Kuuri-Riutta et al. 2022), and changes in trophic or pollution from lake sediments (Ndayishimiye et al. 2020; Patterson et al. 2012; Patterson et al. 2015; Qin et al. 2021). Estuarine sediments were also used to infer past sea-level changes (Charman et al. 1998; Charman et al. 2010; Roe et al. 2013; Whittle et al. 2022).

Other popular topics include functional aspects such as population dynamics (Schönborn 1986; Schönborn 1992), interactions with other organisms (Vohník et al. 2011), and the role of testate amoebae in biogeochemical cycling (Anderson 2008; Aoki et al. 2007; Puppe et al. 2014; Schröter et al. 2003; Sommer et al. 2013; Meisterfeld 1987; Meisterfeld 1989; Wilkinson 2008). Testate amoeba population dynamics and community structure in relation to environmental conditions (including experimentally modified) were especially studied in forest ecosystems, in several cases in relation to other groups of soil organisms, and with a fair amount of work done in tropical forests (Aesch et al. 1992; Krashevskaya 2008; Krashevskaya et al.

2010; Krashevskaya, Krashevskaya, Sandmann et al. 2012; Krashevskaya et al. 2014; Krashevskaya et al. 2017; Lousier 1974a; Lousier 1974b; Lousier 1982; Lousier 1984a; Lousier 1984b; Lousier 1984c; Lousier 1985; Lousier and Parkinson 1984; Maraun et al. 2012; Mazei and Belyakova 2011; Mazei and Chernyshov 2011; Mazei et al. 2012; Mazei et al. 2020; Meisterfeld 1982; Meisterfeld 1986; Rakhleeva et al. 2011; Scheu et al. 2010; Todorov and Golemansky 2014; Tsyganov et al. 2015; Tsyganov et al. 2022; Wanner 1991).

Cultivating testate amoebae was achieved by several colleagues who were able to quantify population growth (Medioli et al. 1987; Porfírio-Sousa et al. 2017; Ribeiro et al. 2019; Wanner 1999; Wanner and Meisterfeld 1994; Wanner et al. 1997; Wanner et al. 2016) and experiment on the effect of culture condition on morphology. This also led to using testate amoebae in ecotoxicology (Amacker et al. 2018; Nguyen-Viet et al. 2008). The common use of testate amoebae as bioindicators (Foissner 1999b) also led to their use as forensic indicators, either as trace indicators (Lambert and Chardez 1978; Swindles and Ruffell 2009) or to estimate the postmortem interval (Szelez et al. 2014; Wanner et al. 2018).

The above-mentioned lists only show a small fraction of the range of possibilities and clearly demonstrates that the study of testate amoebae is currently a very dynamic field. This is also attested by the number of young researchers, MSc and PhD students as well as post-docs, and the fact that several of these young scientists, including several of my former students, have been appointed to permanent positions which allows them to train the next generation of students.

In 2006 Louis Beyens and his team organised an international symposium on testate amoebae. In doing so, he revived a tradition of informal meetings focusing solely on testate amoebae that had started in the late 1970'. The community responded very well to this invitation and for many of us it was the first opportunity to meet. This symposium was an excellent stimulation for new collaborations, and it was clear to all of us that this should be repeated. Since then, meetings were held at first every three years: ISTA-5, in 2009 co-organised by Daniel Gilbert, me and our teams in Montbéliard, France and ISTA-6, co-organised by Jun Yang, Satoshi Shimano and their teams in 2012 in Xiamen, China. During ISTA-6 it was decided that ISTA meetings should be held every two years and that they should alternate between Europe and other continents to reflect

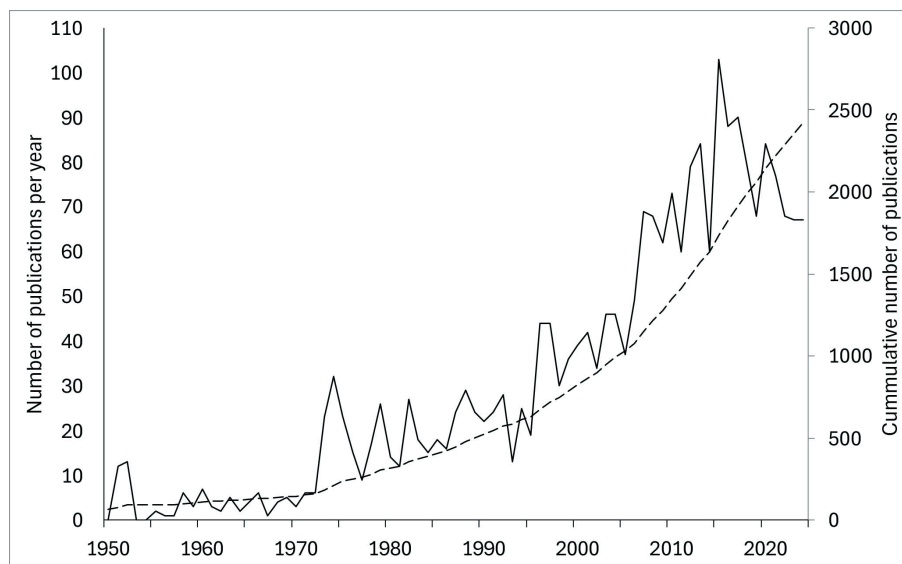


Fig. 7. Number of publications per year and cumulative number of papers listed on Scopus until 2024 (search done on 17.01.2025, data for 2025 excluded) using the keywords: “thecamoebien” OR “testaceen” OR “testate amoeba” OR “testate ameba” OR testacean OR “shelled amoeba” OR “shelled ameba” OR rhizopod* OR arcella* OR euglyph* OR amphitrema OR arcella OR archerella OR argynnia OR asulina OR bullinularia OR campascus OR centropyxis OR corythion OR cryptodiffugia OR cyclopyxis OR cyphoderia OR diffugia OR euglypha OR galeripora OR gibbocarina OR heleopera OR hyalosphenia OR lagenodiffugia OR lesquereusia OR longinebela OR nebela OR padaungiella OR paraquadrula OR phryganella OR physochila OR placocista OR plagiopyxis OR planocarina OR pseudodiffugia OR quadrulella OR sphenoderia OR tracheleuglypha OR trigonopyxis OR trinema).

the fact that most active researchers in this field were based in Europe but that it was important to offer scientists, including students, opportunities to attend meetings in their respective regions also. Holding the meetings every two years maximises the chances for PhD students to attend at least one meeting during their thesis. The subsequent meetings were then held ISTA-7, organised by Mariusz Lamentowicz and team in 2014 in Poznan, Poland, ISTA-8, organised by Daniel Lahr and team in 2016 in Ilhabela, Brazil, ISTA-9 organised by Helen Roe & team in 2018, in Belfast, UK. ISTA-10 was supposed to be held in Niagara, Canada in 2020, but was postponed due to the Covid-19 Pandemic. In 2021 my group organised an online meeting which we called ISTA 9 ¾. ISTA-10 finally took place in 2023, organised by Enrique Lara and team in Madrid, Spain. ISTA 11 is now planned for June 2025, organised by Tim Patterson, Francine McCarthy & teams in Niagara, Canada.

Participants to ISTA (International Symposium on Testate Amoebae) meetings have several times discussed about the option of creating an official society. As we were a rather small and friendly group this did not seem necessary. We have however reached a point where this makes sense and it is our goal to establish ISTAR, the International Society for Testate Amoebae Research as a formal society at the 2025 ISTA in Canada.

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