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Testate amoebae and their role in the reconstruction of the Holocene palaeoenvironments in Romania

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Abstract. Testate amoebae are unicellular organisms that have been intensely studied in the last century due to their high sensitivity to ecological, hydrological and palaeoenvironmental factors. They are ubiquitous in wet environments, such as lakes or peatlands, being suitable for providing information from these natural archives about the Holocene palaeohydrological conditions. In the present paper we tried to synthetize their applicability in the Romanian peatlands and wetlands based on previous studies and to analyze their potential for future research.

Key words. Testate amoebae, peatlands, palaeoenvironment, palaeohydrology, palaeoecology, Holocene.

Introduction

Testate amoebae (TA), also referred to in the past as thecamoebians (Medioli & Scott 1983), arcellaceans (Patterson et al. 1985) or rhizopods (Harnisch 1948, Tolonen 1986), are unicellular organisms belonging to Subkingdom Protozoa, phylum Sarcomastigophora (Honigberg & Balamuth 1963). In the past 100 years, worldwide, they have been used as indicators of palaeoenvironmental conditions in peatlands (Tolonen et al. 1992, Charman 2001, Lamentowicz et al. 2020) or even in lake sediments (Ellison 1995, Patterson et al. 2002, Marcisz et al. 2020).

As these organisms are ubiquitous in peatlands, the interest in studying the relationship between TA assemblages and environmental factors such as pH, water table fluctuations or surface moisture increased, providing quantitative reconstructions of these variables (Charman & Warner 1997, Lamentowicz et al. 2010).

Although worldwide there are numerous studies of this kind, the number of quantitative reconstructions of the depth to water-table (DWT) (Schnitchen et al. 2006, Feurdean et al. 2015, Diaconu et al. 2017, 2019, Longman et al. 2017, Ruskal et al. 2020) or pH (Diaconu et al. 2017) in Romania are few, even though in 1960 Emil Pop counted and described 436 peatlands in Romania, out of which 171 are eutrophic and 265 oligotrophic (Pop 1960), suggesting therefore that there is great potential for palaeoenvironmental reconstructions lying in these areas.

Testate amoebae and their sensitivity to hydrological changes

The biology of testate amoebae was broadly studied and described by Sleigh (1989) and Patterson & Hedley (1992). The study of fossil TA began over 100 years ago (Lindberg 1899, Steinecke 1927) and has been of great interest ever since.

TA are unicellular protists that live in wet environments (peatlands, soils, lakes, rivers), with their size ranging preponderantly between 20-200 μm. They build their shell from siliceous, calcareous or proteinaceous material, or they agglutinate organic or minerogenic material from their surroundings and form a test. These tests have a wide variety of morphologies and shapes and are a key in identifying the organisms to a species level. TA are well preserved especially in peat sediments (Warner, 1990), and they were mostly studied from Quaternary (especially Holocene) onwards (Mitchell et al., 2008).

The response of the TA assemblages to ecological changes in peatlands has been established for almost a century (Harnisch 1925, Jung 1936) and has been extensively studied ever since. The focus of recent or present studies of fossil amoebae is the relationship between them and peat hydrology, as water availability is controlling the occurrence and abundance of different species, for the living space of TA is the water film on the host substrate (Charman 2007). To quantitatively reconstruct the depth to water-table (DWT) levels in peatlands, in the past decades many studies quantified the TA-water availability relationships (Charman & Warner 1997, Lamentowicz & Mitchell 2016) and several transfer functions were developed (Charman et al. 2007, Amesbury et al. 2016).

One of the most useful natural archives for the reconstruction of water availability, soil moisture or DWT values are ombrotrophic peat bogs. Their importance lies in the fact that their only source of water is from precipitation (rainwater and snowmelt), and their water balance is controlled primarily by precipitation and evapotranspiration (Lindsey 1995). Three main advantages of peat bogs, compared to other archives, identified by Chambers et al. (2012), are: (i) their widespread distribution around the globe and therefore their accessibility; (ii) they almost exclusively contain autochthonous organic matter and can be well-dated, leading to high-resolution chronologies, and (iii) they have a strong atmospheric signal, as they are isolated from groundwater.

Such peat bogs can be found primarily in the mountainous regions of Romania, along the Carpathian Mountains. Some of them have already been included in palaeohydrological studies, with peat accumulation starting from the Late Glacial - Holocene transition (i.e., Ic Ponor, 1050 m a.s.l., (Ruskal et al. 2020), Mohoș peat bog, 1050 m a.s.l. (Longman et al. 2017) and during the Late and Mid-Holocene (i.e., Tăul Muced, 1360 m a.s.l. (Diaconu et al. 2017), Fenyvestető, 1340 m a.s.l. (Schnitchen et al. 2006).

How to use testate amoebae in the reconstruction of Holocene palaeoenvironments: Ic Ponor case study

There are several steps to follow for the analysis of testate amoebae, which include: i. subsampling of the peat cores, laboratory treatment and analyzing each sample to ii. determine the relative abundance of the testate amoebae communities and reconstruct the water table levels, followed by the iii. interpretation of the results and comparison with other proxies from the same area or with other testate amoebae studies and water table depth reconstructions. In the following section, we will describe the points mentioned above by means of a case study from Ic Ponor peat bog (Fig. 1).

The reconstruction of the DWT fluctuations and the palaeohydrological conditions has already been published and described in detail (Ruskal et al. 2020), the aims of that study being (a) the determination of the development phases of the peat using peat physical properties, (b) the interpretation of the ecological trends of fossil TA communities and the quantitative reconstruction of the DWT, (c) the identification of the relationship between local hydrological conditions and vegetation response, and (d) the assessment of the correlation between the past local, regional and European climate conditions. We will focus mainly on aim (b), emphasizing the usefulness of testate amoebae in palaeoenvironmental studies.

Fig. 1. Localization of the Ic Ponor peat bog (NW Romania)

I. Analyzing the testate amoebae samples

Similarly to other proxies used on peat sediments, the testate amoebae analysis starts with the sampling process. For this analysis, 1 cm^3 subsamples are taken from the peat cores and are prepared by the standard protocol (Charman et al. 2000), being boiled for approximately 10 minutes until the samples are disintegrated and then sieved through a 300 μm mesh. The remains are centrifuged for 10 minutes at 3000 rpm and afterwards are stored in glycerol. After the samples' preparation, we analyze them under a biological microscope at 400x magnification, counting at least 150 specimens per sample and identifying them to species level using the available scientific literature (Mazei & Tsyganov 2006, Charman 2007).

At Ic Ponor peat bog a total of 20 TA species were identified in 85 analyzed samples. The most frequent and significant taxa are: *Alabasta militaris*, *Assulina seminulum, Assulina muscorum, Arcella catinus, Archerella flavum, Cyclopyxis arcelloides, Difflugia pulex, Heleopera sylvatica, Hyalosphenia papilio, Nebela tincta,* and *Trigonopyxis arcula* (Fig. 2) (Ruskal et al. 2020).

The chronology of the peat sequence was established by 8 AMS radiocarbon measurements. After converting the C^{14} ages in cal yr. BP (calibrated years before the present) using the Intcal13 database (Reimer et al. 2013), we found that the peat started to accumulate at around 12,700 cal yr. BP. A depositional hiatus occurs after 6220 cal yr. BP, and the recent peat re-began accumulating in the past 100 years (Ruskal et al. 2020).

II. Results: creating the testate amoebae diagram and reconstructing the depth to water table (DWT)

The following step in TA analysis is creating a testate amoebae diagram for the visualization of the results using specific software such as C2 (Juggins 2007). The TA diagram (Fig. 3) helps us observe changes in the testate amoebae communities and percentage fluctuations for each species. TA zones (TAZ) are being statistically determined by a classical clustering analysis, which at the Ic Ponor sequence was conducted using PAST software (Hammer et al. 2001). Based on the ecological preferences of certain species, we could identify time periods described by wetter or drier conditions, but to get a clearer idea about the past hydrological conditions, we quantitatively reconstructed the DWT levels using a pan-European testate amoebae-based transfer function (Amesbury et al. 2016) (Fig. 3).

Throughout the Ic Ponor sequence, the DWT values fluctuated between 11.9 and 25.5 cm, recording an altogether drier phase between 12,000 and 7600 cal yr. BP, and a wetter phase between 7600 and 6200 cal yr. BP. During this timeframe, four TAZ, described below, were delimited, TAZ-2 being divided into two subzones (a, b) (Ruskal et al. 2020).

During TAZ-1 the most abundant species were *Cryptodifflugia oviformis* and *Difflugia pulex,* both species being indicators of relatively drier conditions (Charman 2007, Amesbury 2016). The DWT values were high (23-25 cm), also indicating drier conditions.

TAZ-2a is characterized by the dominance of *Cryptodifflugia oviformis,* while during TAZ-2b *Difflugia pulex* dominates. The reconstructed DWT values were the highest in TAZ-2a (25.5 cm), indicating the driest phase recorded, but had a decreasing trend during TAZ-2b, suggesting a wetting phase.

During TAZ-3 *Difflugia pulex* dominated the TA associations, but *Archerella flavum* and *Hyalosphenia papilio* have notable presence, both being generally associated with wet conditions (Charman 2007, Amesbury 2016). The DWT values decreased significantly, also recording the wettest phase with a water table level of 11.9 cm.

TAZ-4 is still dominated by *Difflugia pulex,* suggesting drier conditions, but *Archerella flavum* also has a significant presence, suggesting short, but wetter phases. The DWT levels are oscillating, being higher in the periods dominated by *Difflugia pulex* and lower in those dominated by *Archerella flavum*.

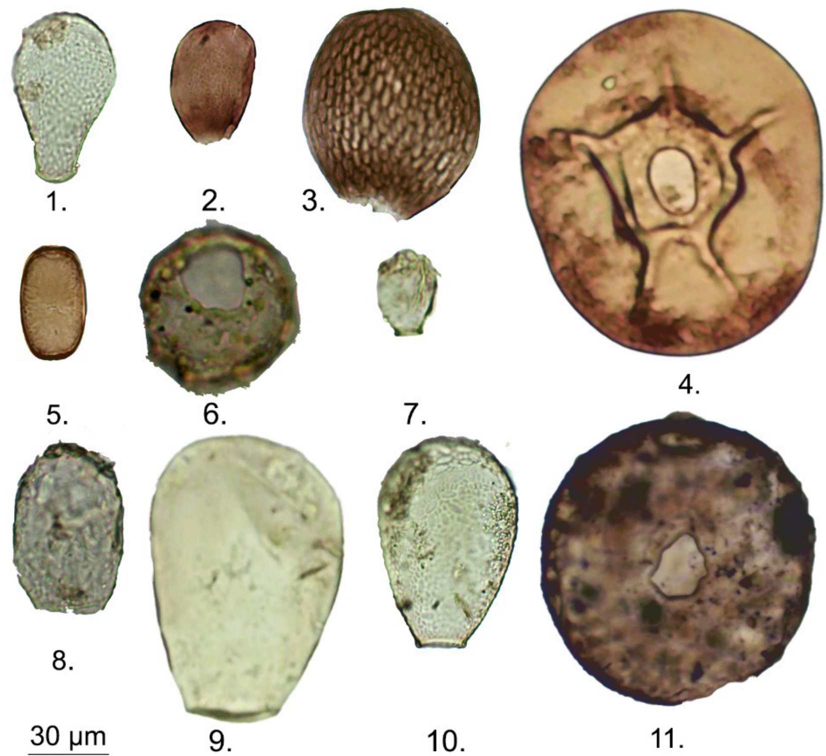

Fig. 2. Most abundant TA species at Ic Ponor sequence: 1. *Alabasta militaris*, 2. *Assulina seminulum,* 3. *Assulina muscorum,* 4. *Arcella catinus,* 5. *Archerella flavum,* 6. *Cyclopyxis arcelloides,* 7. *Difflugia pulex,* 8. *Heleopera sylvatica,* 9. *Hyalosphenia papilio,* 10. *Nebela tincta,* 11. *Trigonopyxis arcula.*

III. Interpretation of the results and correlation with other proxies

By determining the TA relative abundance and by reconstructing the DWT values, we were able to obtain an idea about the past hydrological conditions, thus we divided the sequence into two main phases, a drier one (TAZ-1, TAZ-2a, b) and a wetter one (TAZ-3, TAZ-4).

However, in order to gain a better and broader understanding of the environmental conditions during the Early and Mid-Holocene (12,000-6200 cal yr. BP), we correlated our TA results with other proxies and analyses from the Ic Ponor peat bog (Fig. 4). These include peat physical properties (loss on ignition, magnetic susceptibility), microcharcoal concentration (Ruskal et al. 2020), and pollen analysis (Grindean et al. 2015).

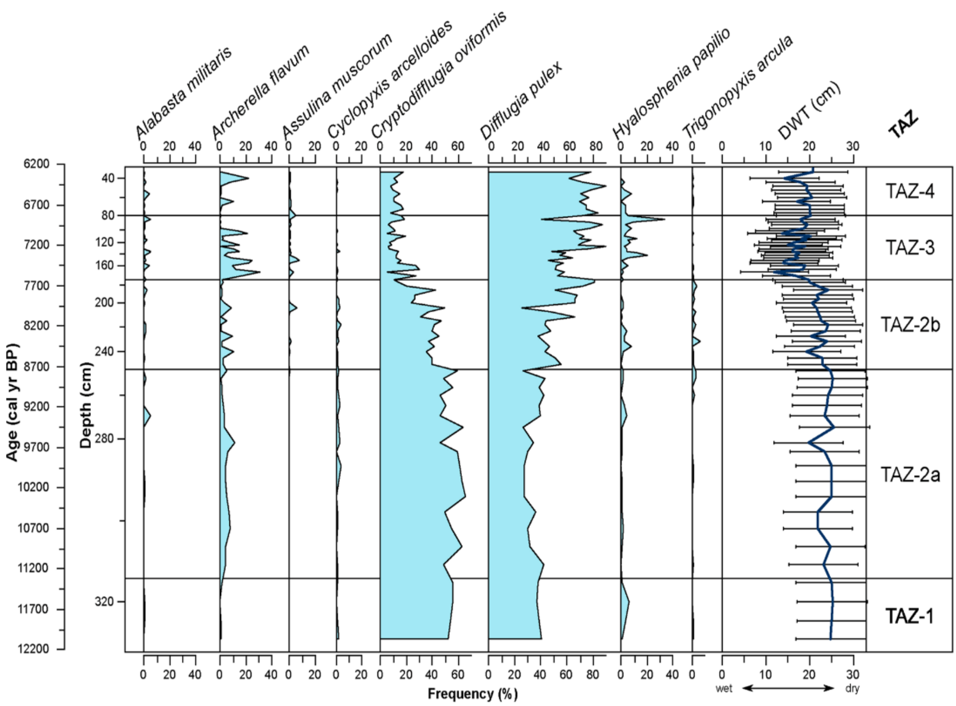

Fig. 3. Relative abundance of the most abundant TA species from the Ic Ponor peat sequence, reconstruction of depth to water table (DWT); TAZ - testate amoebae zones (after Ruskal et al. 2020, modified).

The lithology of the 340 cm long core sequence from Ic Ponor consists of a grey sandy-clayey layer at the bottom part (340-337 cm), followed by a clayey peat layer (337-310 cm). The following 280 cm consists of brown peat, but between 31 and 28 a clayey layer occurs. The top part of the sequence is made up of undecomposed and fresh *Sphagnum* peat (Ruskal et al. 2020). The clayey layer confirms the hiatus that was intercepted by the radiocarbon dating as well.

The loss on ignition and magnetic susceptibility results also confirm the previously described evolution phases of the Ic Ponor sequence (Fig. 4). The minerogenic content (MC) and magnetic susceptibility (MS) values were higher at the bottom part (the sandy-clayey layer), between 12,700 and 12,000 cal yr. BP, when Ic Ponor evolved into an ombrotrophic peat bog from a lacustrine phase. The ombrotrophic peatland phase is confirmed by the high organic matter (OM) and low MS values during the Early and Mid-Holocene (12,000-6220 cal yr. BP) (Ruskal et al. 2020).

The pollen analysis gives us insight on the past vegetation dynamics and thus about palaeoclimate conditions as well. Combined with TA analysis, we can assess how the local hydrological changes are reflected in the regional vegetation dynamics. Throughout most the drier phase of the peat bog development (12,000-7600 cal yr. BP), the surrounding vegetation cover was characterized by open forests of pine, gradually replaced by spruce, and a variety of early successional trees (e.g., birch, hazel) which probably colonized vast areas where other woody species could not develop due to drier soil conditions. Notable abundances of herbaceous species such as *Artemisia* (sagebrush), Poaceae (grass) and chenopods also support the drier palaeohydrological conditions. Wetter conditions, as indicated by higher DWT values (7600-6200 cal yr. BP) coincide with the expansion and development of dense spruce forests in the area, as this tree species prefers moist acidic soils.

The microcharcoal analysis enables us to reconstruct the past regional fire activity (Whitlock & Larsen 2001). At the Ic Ponor peat bog, the high microcharcoal concentrations (associated with large fires of high intensity) correlate with drier phases, as indicated by the high DWT values (Fig. 4).

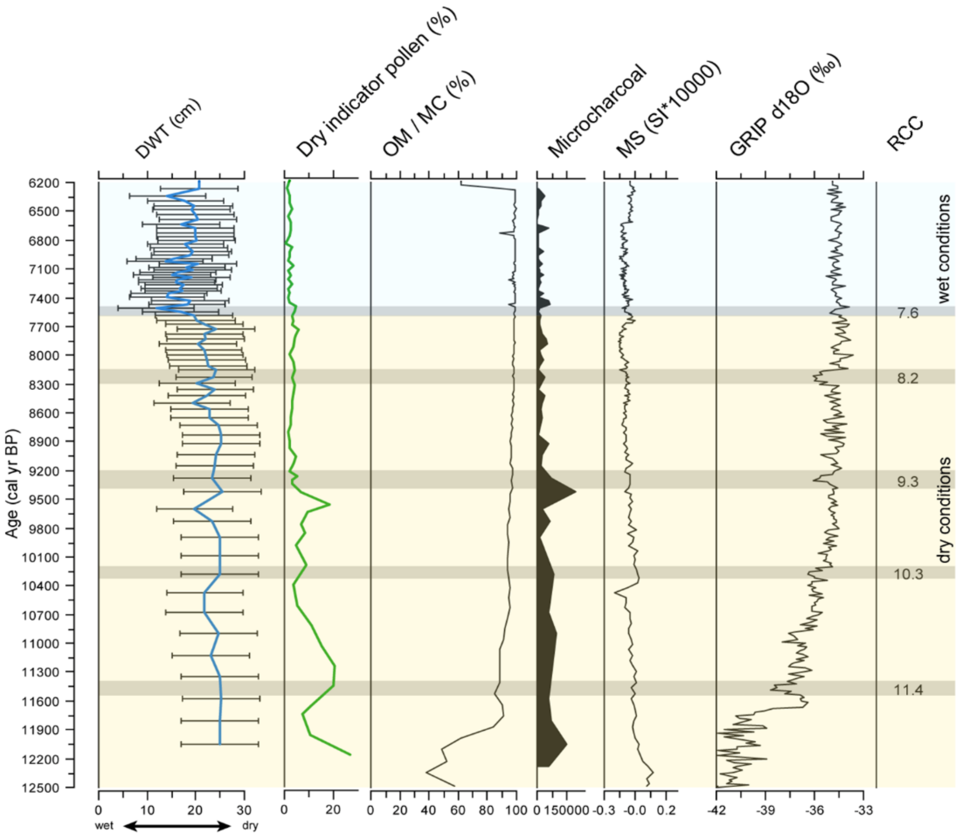

Fig. 4. Correlation of the inferred variables from the Ic Ponor sequence: depth to water table (DWT), dry conditions indicator pollen (Artemisia, Poaceae, chenopods) (Grindean et al. 2015), organic material (OM) and minerogenic content (MC) ratio, microcharcoal concentration and magnetic susceptibility (MS) (Ruskal et al. 2020) and δ^{18}O from the GRIP ice-core record (Vinther et al. 2006); RCC - rapid climate change events (after Ruskal et. 2020, modified).

The local response of several large-scale rapid climate change events (RCC) was also highlighted by our palaeohydrological results (Fig. 4). These include the cooling event between 11,400 and 11,300 cal yr. BP recorded in the Greenland Ice Core (Blockley et al. 2014), a dry event at Ic Ponor with DWT values of 25 cm, the “10.3 ka” cooling event (Bjorck et al. 2001), also dry in the studied area, with DWT values 21-24 cm, and the “9.3 ka”, “8.2 ka” and “7.6 ka” cold events (Magny and Bégeot 2004) with slightly wetter local conditions, with DWT values of 20-23 cm (Ruskal et al. 2020).

Conclusions

As proven by countless studies conducted around the globe, testate amoebae are a very suitable proxy for the reconstructions of the Holocene palaeohydrologic conditions. However, in order to get a broader image about past conditions, the addition of other proxies (i.e., lithology, loss on ignition, humification, pollen, or others) is necessary. Romania is rich in natural archives such as ombrotrophic peatlands which provide a high potential for palaeoclimatic and palaeoenvironmental studies, therefore a high amount of work and research in this field could and should be undertaken.

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