

RICCIA SPORES IN QUATERNARY DEPOSITS; FOSSIL EVIDENCE FROM POLISH SEQUENCES

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Abstract:

The manuscript presents fossil records of *Riccia* spores in the Quaternary deposits. They are rarely reported and identified to the species level during routine pollen analysis. In the available sequences 5 species, including *R. cavernosa*, *R. beyrichiana*, *R. sorocarpa*, *R. crinita* and *R. bifurca* were noted. The occurrence of spores in fossil records proves the existence of temporary wet habitats characteristic both for natural environments (e.g. temporary dry lake shores or peat bogs) as well as habitats resulting from human activity, e.g. microhabitats in crops and pastures or trench walls. The spores recorded in sequences present an opportunity for discussion of their potential use as proxies in palaeoenvironmental reconstructions.

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Key words: *Riccia*, spores, Quaternary deposits, Poland.

Manuscript received 23 January 2023, accepted 13 March 2023

INTRODUCTION

Spores of liverworts (*Marchantiophyta*), as well as closely related hornworts (*Marchantiophyta*) are rarely reported in palynological sequences from the Pleistocene and the Holocene. This is limited to the occasional identification at the genus level of such taxa as *Riccia*, *Fossombronia*, *Anthoceros* and *Phaecoceros* (Mamakowa, 1989; Ralska-Jasiewiczowa *et al.*, 1998; Granoszewski, 2003; Lopez-Saez *et al.*, 2019) (Fig. 1). The genus *Riccia* includes hepatics with small bifurcated rosettes about 1–2 cm in diameter and branches with embedded sporophyte capsule producing very big spores. The most frequent species are characterized by spores easy to identify. However we must bear in mind that taxonomic value of some species is questioned (Schumacker and Vaňa, 2005). Fortunately, they are rarely reported from the communities.

In Central Europe *Riccia* occupies seasonally wet habitats: on the arable fields, lake shores drying in the late summer, trench walls, etc. The preservation of the spores in the lake deposits and somewhat different individual preferences of particular species creates the possibility to use them to the palaeoenvironmental reconstruction.

In Poland 11 species of *Riccia* producing spores are reported. They are: *R. cavernosa*, *R. huebeneriana*, *R. canaliculata*, *R. duplex*, *R. crinita*, *R. ciliifera*, *R. bifurca*, *R. beyrichiana*, *R. glauca*, *R. warnstorffii*, *R. sorocarpa* (Schu-

macker and Vaňa, 2005). *R. ciliata* (Rejment-Grochowska, 1966; Koła and Turzańska, 1995) noted in our country is probably conspecific with *R. crinita* (Hugonnot, 2010). *R. fluitans* is propagated vegetatively in Poland and spores of *R. rhenana* are unknown. Pollen analysis of modern arable soils collected in the Mazovian Lowland as well as in the adjacent regions shows that *R. sorocarpa*, *R. crinita*, *R. bifurca* and rarely *R. warnstorffii* and *R. cavernosa* are the only species noted in the spectra.

The specimens of *Riccia* occur usually in the field plant communities (order *Radiolion linoidis*), overgrowing together with the member of class *Isoëto-Nanojuncetea* on wet and exposed soil (furrows, shores of puddles, renovated shores of small trenches or cattle footprints). They appear in late summer and early autumn on bottoms of drained ponds and oxbow lakes (*Elatini–Eleocharition ovatae* association, Popiela, 1997). They are differential species of the class *Isoëto-Nanojuncetea* (*R. bifurca*) of the order *Cyperetalia fusci* (*R. glauca*) and of the alliance *Elatini–Eleocharition ovatae–R. canaliculata*, *R. cavernosa* and *R. crinita* (Popiela, 1997).

The feature of *Riccia*, as well as other bryophytes, is a very quick regeneration after disturbances in the environment (e.g. ploughing fields, removal of soil). This ability results from adaptation of their life cycle to any ground disturbances and also from regenerative strategies, possibilities for the long-term survival in a form of “a prop-

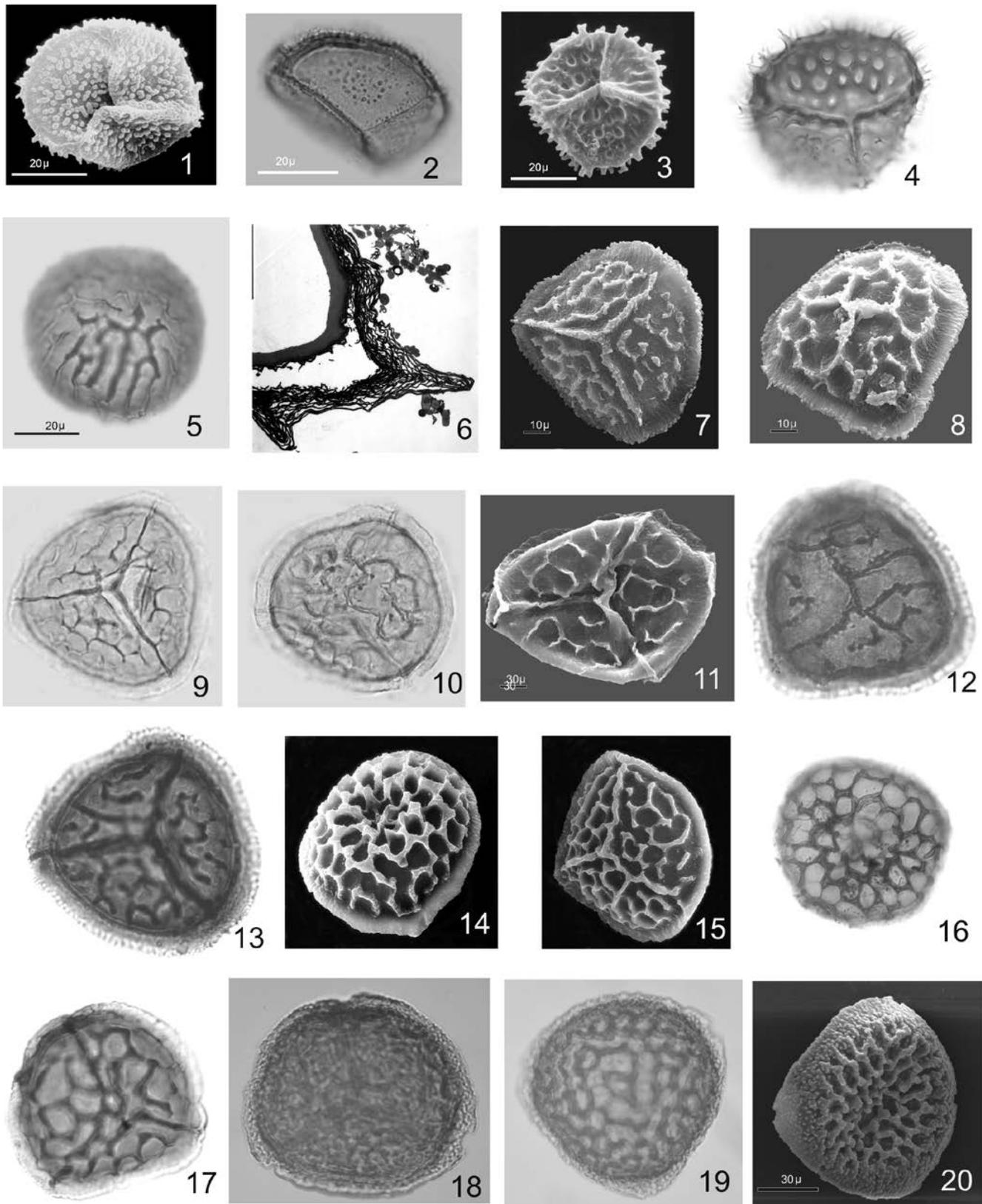


Fig. 1. 1-2 – SEM and LM of the *Phaeoceros* spore, 3-4 – SEM and LM of *Anthoceros* spore, 5 – spore of *Fossombronina*, LM; 6-13 – *Riccia cavernosa*: 6 – TEM of a spore ridges formed by lamellar layers, x6000, 7 – SEM proximal side, 8 – SEM, distal side (recent), 9 – LM, proximal face, 10 – distal face, 11 – SEM, proximal face (Holsteinian, Wilczyn site), 12 – LM, distal side, 13 – proximal side (recent); 14-17 – *Riccia bifurca*: 14 – SEM distal side, 15 – proximal side, 16 – LM distal side, 17 – proximal side (recent); 18-20 – *Riccia beyrichiana*, 18 – LM proximal side, spore without reticulum, 19 – LM distal side, 20 – SEM distal side (recent, Kosmy Pruszkki n. Ciecchamów).

agule bank” (Andriušaitytė and Jukonienė, 2013). There have been also reported from the locations where spores of *Riccia* from herbarium germinated after several years (Szweykowski and Mendelak, 1964).

Recently in Poland, most *Riccia* species are eliminated from agricultural fields and even common species are rarely noted. Our observations suggest that there are different reasons of this disappearance – a use of crop protection agents, progressive droughts, ploughing just after harvest period resulting in a removal of young specimens from the field, expansion of mono-cultures and finally extensive grazing fruiting in a lack of suitable habitats.

MATERIAL AND METHODS

Examined fossil spores were isolated from the Pleistocene and the Holocene lacustrine and peat bog sequences in the Mazovian and the Podlasie Region in mid-eastern Poland. In this area modern reference material (spores) of *Riccia* species was also collected. For light microscopy (LM) and scanning electron microscopy (SEM) modern spores of hepatics were treated similarly as pollen grains in palynological procedures, i.e. KOH, HF and finally, acetolysis (Erdtman, 1960). For transmission electron microscopy (TEM) collected spores of *Riccia cavernosa* were treated with hot HF (24 hours), then acetolyzed and finally, they were embedded in Spurr’s low viscosity resin using standard TEM procedures (Spurr, 1969).

SPORE MORPHOLOGY AND STRUCTURE OF WALL

Spores of *Riccia* species recorded in Poland are usually large, from 50 µm to even 150 µm depending on the species. *R. beyrichiana* has large spores of about 120 µm. The size of the remaining species is commonly from 65 µm to 90 µm and this is not an effective tool to identify the fossil spores. Spores from the Pleistocene deposits noted in this examination, *R. beyrichiana* and *R. cavernosa*, are characterized by slightly smaller size than in modern species.

The sculpture of the spores shows to a certain extent intraspecific variation and it is differently shaped on proximal and distal faces. The sculpture of the proximal side is more diverse than of the distal one. It is characterized by the presence of reticulum, irregularly developed muri or more or less protruding elevation in a variety of shapes (verrucae, spines, pila, gemmae etc.). Trilete mark (lesure) may be clearly defined or it is barely visible. Spores of some species are devoid of scar of attachment. In the equatorial area, a wing is present or spore is wingless. In some species, in the corners of the equator apparent pores may appear. On a distal side, reticulum is present. The number of its lumina is useful in identification of the species.

In the case of *Riccia* spores, analysis of the exine structure is possible only if using TEM procedures. During routine pollen analysis this time-consuming examination

is ignored. However, features of structure seem to be important in systematics, allowing delimitation of a group of species or even of particular species. The wall of crystalwort spore (*R. cavernosa*) is built of multiple layers, often being grouped in weakly outlined packages (Steinkamp, 1979; Thaithong, 1982), e.g. structure wall of *R. cavernosa* (Fig. 1).

From the evolutionary point of view, spores of *Riccia* show two primitive features. The first one is the multilayered wall resembling this in cryptospores from the Lower Palaeozoic and the second one, a production of fused permanent tetrads observed in some African species (Perold, 1996). The last feature is also noted very early in the fossil records (Jansonius and McGregor, 2002).

PROVISIONAL KEY TO THE RICCIA SPORES OF THE TAXA NOTED IN POLAND

Comments: In descriptions of the spores we adopted palynological terminology proposed by Punt *et al.*, (2003), because some terms used in botanical papers concerning *Riccia* morphology might seem misleading for palynologist (e.g. lumina, brochi in reticulate sculpture v. alveolae). In the list below *R. fluitans* has not been included since this species is propagated only vegetatively in Poland (for spores morphology see Jovet-Ast, 1979). Provisional key is based mainly on the features of the proximal side because it appears to be more informative.

Reticulum on proximal side absent

Trilete mark present

Riccia ciliifera Link ex Lindenb.: proximal side with short muri (covered with scabrae), only occasionally forming lumina; wing absent; a distal side with the pattern similar to that on a proximal one (see Jovet-Ast, 1986).

Riccia cavernosa Hoffm.: frayed wing present; inter-radial area with a few shorter or longer muri, partly folded; a characteristic pattern in a centre of a distal side where three irregular muri meet in the central point (Fig. 1).

Riccia beyrichiana Hampe ex Lehm.: proximal side with knobby surface, wing and pores present, on a distal side shallow reticulum covers only about 2/3 of the entire area, the remaining part with small roughly rounded processes (Figs 2, 3) (Damsholt and Hallingbäck, 1986).

Riccia canaliculata Hoffm., *Riccia duplex* Lorb.: broad wing present, a proximal side with rare winding structures; large lumina of the distal side with free-standing elements in the centre (see Koła and Turzańska, 1995; Jovet-Ast, 1986).

Trilete mark absent or indistinct

Riccia sorocarpa Bisch.: sculpture of the proximal side vermiculate with pointy tips, arranged sometimes in in-

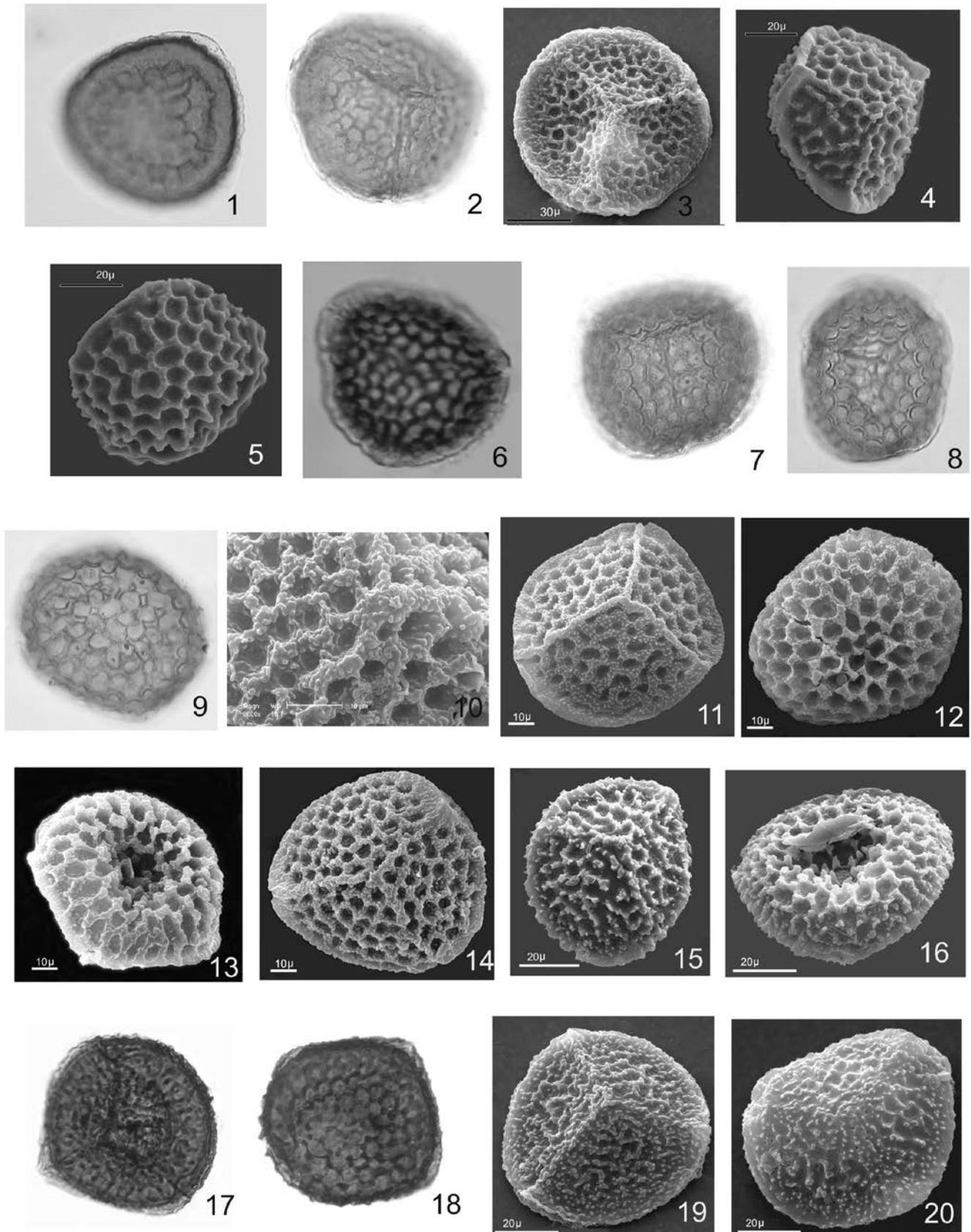


Fig. 2. 1-2 – *Riccia beyrichiana*: 1 – LM distal side, 2 – LM, proximal side; 3 – SEM proximal site, spore with reticulum (Eemian, Dziewule site, eastern Poland); 4-6 – *Riccia warnstorffii*: 4 – SEM proximal side, 5 – distal side, 6 – LM proximal side (recent, Kosmy Pruski); 7-14 – *Riccia crinite*: 7-8 – LM proximal side, 9 – distal side, 10 – SEM, microsculpture of muri x 10 000, 11 – SEM, proximal side, 12 – distal side (Medieval, Borsuki side, eastern Poland), 13 – SEM, distal side, 14 – SEM proximal side (recent, Wojnów, eastern Poland); 15-20 – *Riccia sorocarpa*: 15 – SEM proximal side, 16 – distal side, 17 – LM proximal side, 18 – distal side (recent), 19-20 – SEM proximal side.

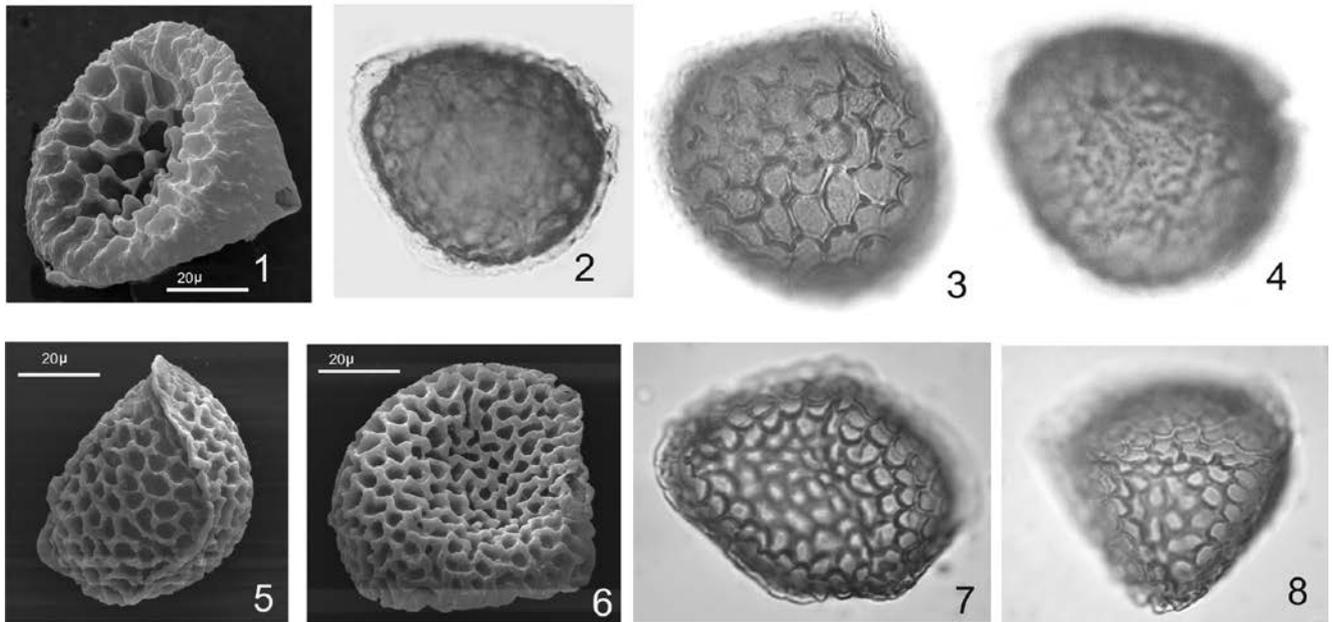


Fig. 3. 1-4 – *Riccia sorocarpa*: 1 – SEM distal side, 2 – LM visible wing of the spore, 3 – distal side, 4 – proximal side (Medieval, Borsuki site, eastern Poland); 5-8 – *Riccia* sp. Spores of modern species of *Riccia*, probably new for sciences – SEM and LM (Dunaj, northern Poland).

complete single lumina; narrow wing present; on a distal side lumen corners of the reticulum highly elevated (Figs 2, 3).

Riccia bifurca Hoffm.: wing present, muri similar to these in *R. cavernosa*, but somewhat longer, with the tendency to form not fully closed lumina (Fig. 1).

Reticulum present

Riccia crinita Taylor: Y-mark less or more visible; very regular lumina of the reticulum, muri of which with numerous, homogeneous scabrae, narrow non-serrated wing (Fig. 2).

Riccia glauca L.: Y-mark absent or indistinct, broad wing present, on a proximal side regular numerous, small funnellum lumina (6–7 brochi along the inter-radial area) (Jovet-Ast, 1986; Andrejeva, 2012; Berg and Pörtl, 2020).

Riccia warnstorffii Limpr. ex Warnst.: trilete mark absent; lumina (sometimes interrupted) equipped with small processes on the surface of three adjacent muri at their junction, pore and wing present (5 brochi along the inter-radial area) (Fig. 2, see also Jovet-Ast, 1986).

Riccia huebeneriana Lindenb.: wing frayed on the edges, Y-mark rather indistinct, on the proximal side about 5–6 brochi across the inter-radial area, lumina sometimes with incomplete muri, on both sides numerous projecting processes in the corners of muri (see Jovet Ast, 1986).

Riccia beyrichiana Hampe ex Lehm.: trilete mark present, proximal side with knobby surface passing into outline(!) of reticulum towards the corners of the inter-radial area; wing and pores present (Figs 1, 2; see also Andrejeva, 2012).

TRANSPORT OF *RICCIA* SPORES TO DEPOSITS

Dispersal of *Riccia* spores and their deposition in lake sediments is based on the structure of its generative organs. Sporangia with spores are immersed in the prostrate, fleshy thallus and after the death of plants and decay of outer body, spores are exposed to external factors. However, flat thallus and large size of spores do not promote their dispersion over long distances. Transport of spores starts when the soil is displaced during ploughing. After desiccation, soil particles with spores are partly carried by wind to the depositional basins. Next year, without heavy tillage work spores are not displaced and they germinate in the sporangia at the same place. Dispersed spores of *Riccia* are also found very rarely during analysis of the modern pollen rain (Glais *et al.*, 2016).

FINDINGS OF *RICCIA* SPORES IN THE DEPOSITS

Fossils of *Riccia* occurring relatively often in the Quaternary deposits are also reported from the Tertiary deposits as macrofossils (Hoffman and Stockey, 1997; Hemanta Singh and Kishor, 2009).

Spores noted in the Quaternary deposits include the following species:

Riccia cavernosa Hoffm.

Riccia cavernosa appears very regularly in numerous sequences of the Holsteinian Interglacial, e.g. Wilczyn (Bińka *et al.*, 1997), Kalińów (Bińka and Nitychoruk, 1996) and Woskrzenice (Bińka and Nitychoruk, 1995). First of

all, its spores are noted in periods with water level fluctuations and exposition of the lake shore deposits, e.g. at the beginning of the interglacial and in the middle of the *Carpinus* phase when the Holsteinian basins were gradually filled with sediments. At Wilczyn, the occurrence of *R. cavernosa* spores is correlated with findings of macrofossils of annual plants of the order of *Bidention tripartitae* and *Nanocyperion flavescens*: *Rumex maritimus*, *Chenopodium* cf. *glaucum*, *Ranunculus sceleratus*, *Cyperus fuscus*, *Rorippa palustris*, *Bidens* t., *Polygonum nodosum*, *Scirpus* cf. *radicans* and *P. persicaria* t. (pollen).

Riccia cavernosa is noted in the final stage of the Eemian sequences, however less frequently than in the Holsteinian, e.g. at Jurowlany, northeastern Poland (Bińka, 1996).

Riccia beyrichiana Hampe ex Lehm.

Spores with characteristics similar to that in *R. beyrichiana* were observed in two Eemian sequences at Jurowlany and Dziewule (Bińka, 1996; Bińka and Nitychoruk, 2003), in peaty sediments (low water level with regular drying events). They represent one of the two types of spore morphology, in which we can see only an outline of the reticulum on the proximal side, decreasing into equatorial area, and the reticulum covering only 2/3 of the surface on the distal side with (Figs 1, 2) (Damsholt and Hallingbäck, 1986). In Poland, this species is recorded very rarely, at 11 historical sites only (Ochyra and Piątek, 2001). The authors found two new ones in northern regions (Niemiry near Wyszaków and Kosmy Pruski near Ciechanów). *R. beyrichiana* is the Atlantic-Mediterranean element in the Polish flora, found on damp soils as well as on drying lake shores (op. cit.).

Riccia sorocarpa Bisch., *Riccia crinita*, *Riccia bifurca*

The species *Riccia sorocarpa* Bisch., *Riccia crinita* Taylor and *Riccia bifurca* Hoffm. were exclusively found in the Holocene spectra since the Early Medieval Ages, when Slavs arrived in this area and agriculture opened suitable habitats for *Riccia*. For this reason, it can be assumed that this species should be treated as the archaeophytes in the modern Polish flora. Spores occur regularly in deposits, however they were more numerous in younger layers which could be referred to intensified farming. The last species is particularly interesting, because in broad. “*R. bifurca* group” the new, unknown modern species can be expected (Christian Berg, oral information). One of them, new for plant world was found by the author at Dunaj near Mława, northern Poland (Fig. 3).

It seems that arable fields close to the lake basin are the main source of spores, because of their dispersion potential. As a result, the spore frequency in deposits depends mainly on the proximity of arable fields, thus on the local conditions at the examined site. The influence of the age-old method of cultivation on the spore/plant frequency remains rather insignificant. Two-field system used in Poland up to 12th century was replaced by three-field one and this should not result sig-

nificantly on distribution of the *Riccia* communities. Both in winter and summer cereals as well as in root crops *Riccia* by adequate soil moisture occurs regularly. Also in fallow, land used as pastures crystalwort grows well, disappearing when the field is not cultivated in the subsequent periods. Among the species listed above, the spores of *R. sorocarpa* and *R. bifurca* appear most often in the Quaternary deposits while *R. crinita* is rare. The authors observed such proportion of particular species also during palynological investigation of soils at many sites in central Poland.

During pollen analysis of fossil sequences, spores of *Riccia* were identified to the genus level. The oldest ones date back to the Ferdynandovian Interglacial at Wólka site near Dąbrowa Białostocka (Bińka, 2007) and Steniatyń site in southeastern Poland (Boratyn, 2014).

FINAL REMARKS

Generally, *Riccia* as well as other hepatics in their life cycle need rather wet environment and for fertilisation, a thin layer (or even drop) of water is necessary. Some of the species identified in the sequences are characterized by narrower spectrum of environmental requirements. *Riccia beyrichiana*, rarely noted in Poland now, is the plant that prefers the oceanic climate of western Europe (Jovet-Ast, 1986). In turn, *Riccia cavernosa*, because of the specific nature of the thallus with conspicuous air chambers, is more resistant to flooding than most other species. Hence, it can also occur in more wet habitats.

In the Quaternary of Poland, a fossil record of the *Riccia* spores is subdivided into two clear parts represented by somewhat different suite of species. The Pleistocene is characterized by their rare presence, because of scarcity of suitable habitats. Both closed forest communities as well as tundra/steppe ones are not optimal for their expansion. Spores of *Riccia* are recorded almost exclusively on temporary exposed surfaces, e.g. lake shores drained in the late summer and the autumn indicating low water level in this period. They suggest the presence of *Elatini–Eleocharition ovatae* association. Human migrations in the Late Holocene resulted in creation of suitable habitats (order *Radiolion linoideis*) that is arable fields, pastures (cattle footprints!), wet areas with exposed soil, lake shores used or penetrated by man or farm animals.

However, in this case rainfalls in the vegetation season support expansion of *Riccia*, especially on arable fields. Climate change in Poland and particularly reduced precipitation restrict a number of appropriate habitats and in the future, spores of *Riccia* rather disappear in lake deposits.

Acknowledgements

We thank Dr. Christian Berg from Karl-Franzens-Universität Graz for comments about the problems of the *Riccia* taxonomy and identification of specimens. We also thank the anonymous reviewers for their careful reading of our manuscript and helpful comments.

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