Lichenopeltella mizerniana sp. nov. from the upper Pliocene of Mizerna (southern Poland)

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Received: 24 January 2020 / Revised: 15 June 2020 / Accepted: 18 June 2020
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Abstract

Fungal sporocarps having ostiole with setae were found in the upper Pliocene deposits from Mizerna (borehole Mizerna-Nowa), southern Poland. These remains morphologically correspond to the fossil-genus *Trichothyrites* Rosend., although the structure of the ostiolar collar with non-septate setae seems unique and is typical for sporocarps (catathecia) of some modern species of the genus *Lichenopeltella* Höhn. Other contemporary fungal genera with setose sporocarps differ considerably from *Lichenopeltella* in respect of their morphology. Taking this into consideration, a new fossil-species *Lichenopeltella mizerniana* G. Worobiec is proposed. Morphologically, *Lichenopeltella mizerniana* is similar both to some modern lichenicolous [*L. peltigericola* (D. Hawksw.) R. Sant., *L. rangiferinae* Brackel, and *L. uncialicola* Brackel] and non-lichenicolous species [*L. ammophilae* (J.P. Ellis) P.M. Kirk & Minter, *L. palustris* (J.P. Ellis) P.M. Kirk & Minter] of this genus. The presence of *Lichenopeltella mizerniana* suggests that the Pliocene climate of the Mizerna locality was probably at least moderately humid.

Keywords *Lichenopeltella* · Trichothyriaceae · Fossil fungi · Palaeoecology · Upper Pliocene · Poland

Introduction

Fungi are an important group of fossils of eukaryotic organisms found as fungal hyphae, sporocarps and spores that apparently appeared in the late Proterozoic (Taylor et al. 2015). Fossil fungi are useful both as a palaeoecological proxy (Dilcher 1965; Lange 1976; Elsik 1978; Bera and Mandal 2014; Worobiec and Worobiec 2017; Worobiec et al. 2018) and for calibration of the phylogenetic trees of fungi obtained using molecular clock methods (Geml et al. 2004; Lopandic et al. 2005; Beimforde et al. 2014; Moreno et al. 2015; Liu et al. 2017; Halbwachs 2019). Chitinous fungal remains, even almost unaltered, are frequently found in palynological samples (Elsik 1996; Worobiec et al. 2009). Microremains of sporocarps are commonly found both as detached sporocarps during palynological investigations and on cuticles of fossilised leaves. These sporocarps, mainly of epiphyllous

fungi, are classified as members of the modern families Microthyriaceae, Micropeltidaceae, Trichothyriaceae (Microthyriales) and Asterinaceae (Asterinales) (Cookson 1947; Dilcher 1965; Elsik 1978; Worobiec and Worobiec 2013). However, as most of these sporocarps are preserved without any spores, and rarely with mycelium attached, they lack many features important in the taxonomy of these fungi, based mainly on the morphological features of asci and ascospores. Thus, determination of the generic position of sporocarps of fossil fungi is rather difficult, and in many cases resulted in serious mistakes. Contrary to the taxonomy of present-day fungi that could be based on molecular data obtained from DNA analysis, in the fossil state DNA is almost never preserved and there is no possibility to use molecular investigation in the case of fossil fungi. Considering these limitations, the taxonomy of sporocarps of fossil (epiphyllous) fungi is usually based on an artificial morphological taxonomic system (Elsik 1978).

One of the most frequently found fossil sporocarps are those classified as an artificial fossil-genus *Trichothyrites* Rosend., related to the modern family Trichothyriaceae. Fossil-species *Trichothyrites hordlensis* P.H. Sm., based on the morphological similarity of their ostiolar collar to the contemporary *Trichothyrina ammophilae* Ellis [= *Lichenopeltella ammophilae* (J.P. Ellis) P.M. Kirk & Minter], suggested by

Section Editor: Gerhard Rambold

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Smith (1980), has been proposed by Samarakoon et al. (2019) as a representative of genus *Lichenopeltella* Höhn. Samarakoon et al. (2019) did not propose the use of the fossil-genus *Trichothyrites* for divergence calibration, avoiding the discussion about the inclusion of *Trichothyrites* in modern genus *Lichenopeltella*. In addition, morphologically identical to *Trichothyrites hordlensis* sporocarps can be found not only in the genus *Lichenopeltella*, but also in other genera of the Trichothyriaceae and in the Microthyriaceae family (see Wu et al. 2011). Thus, the taxonomical relationships of *Trichothyrites hordlensis* and genus *Lichenopeltella* based only on ostiolar collar morphology seem rather weak.

During palynological investigations of pollen samples taken from upper Pliocene deposits from Mizerna, Poland, we found remains of fungal sporocarps corresponding to the fossil-genus *Trichothyrites*, although having an ostiolar collar with preserved setae. The morphology of ostiole with setae of these *trichothyrites*-like fossil sporocarps is rather characteristic and seems unique for sporocarps of some modern species of genus *Lichenopeltella* (Spooner and Kirk 1990). After considering this, we decided to describe a new fossil-species of genus *Lichenopeltella*. We discuss its recent counterparts and the importance of presence of the remains of genus *Lichenopeltella* for the palaeoecology of fossil assemblages.

Material and methods

The Mizerna-Nowa borehole was drilled in 1979 in the eastern part of the Nowy Targ Intramontane Depression, Polish Western Carpathians (49° 28' N, 20° 18' E), southern Poland. The borehole was 39 m deep and the core contained deposits of a shallow late Pliocene palaeolake (Birkenmajer and Worobiec 2013; Worobiec and Birkenmajer 2014). In the fine-grained sediments of the Mizerna palaeolake, well-preserved spores, pollen grains, and non-pollen palynomorphs, including algae and fungal remains, were recorded (Worobiec et al. 2017). The results of the palynological analysis were used to reconstruct vegetation in and around the palaeolake (Birkenmajer and Worobiec 2013). The water body was surrounded by herbaceous vegetation, with sedges and grasses, as well as by mixed and coniferous forests.

The samples from Mizerna-Nowa were processed using successively hydrochloric acid, potassium hydroxide and hydrofluoric acid to remove silicates (Moore et al. 1991). A total of 160 samples have been studied. Remains of the studied fungal sporocarps were recorded in one sample from 26.4-m depth. From this sample, 22 microscope slides were made, using glycerine jelly as a mounting medium. Fossil specimens are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków), under catalogue number Mizerna-Nowa 1979/244.

The terminology for the morphology of fungal remains of *Lichenopeltella* follows Korf (1958), Kirk et al. (2008) and Wu et al. (2011). The method of measuring the size of fungal structures depended on their shape. Diameter measurements were used for regular, round or broadly elliptical structures, and length and width for quadrangular structures. Microphotographs were taken with a Nikon Eclipse E400 microscope fitted with a Canon A640 digital camera.

The classification of fossil and recent fungi follows Kalgutkar and Jansonius (2000), Wu et al. (2011), Hyde et al. (2013) and Wijayawardene et al. (2018).

Results

Taxonomy

Dothideomycetes, families *incertae sedis*

Trichothyriaceae Theiss. (1914)

Lichenopeltella Höhn. (1919)

Lichenopeltella mizerniana G. Worobiec sp. nov. Fig. 1–6
Mycobank: MB835847

Type: Slide Mizerna-Nowa 244(2), slide location 6/24. Stored in W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, collection Mizerna-Nowa 1979/No 244(2). Illustrated on Fig. 1–3

Etymology: The species name refers to the type locality

Type locality: Mizerna-Nowa, southern Poland

Stratigraphic horizon: upper Pliocene

Distribution: Mizerna-Nowa, southern Poland

Other specimens examined: Collection Mizerna-Nowa 1979/No 244(10), W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków; Poland

Repository: W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland, collection Mizerna-Nowa 1979

Diagnosis. Sporocarps orbicular, scutate, ostiolate, margin slightly sinuate. Upper wall of scutellum composed of hardly visible cells, arranged in radiating rows extending outward (*textura prismatica*). Ostiole central, surrounded by a clearly delimited collar composed of dark cells. Setae attached to the ostiole, divergent, smooth, non-septate, thick-walled, with flask-shaped base and acute apex.

Description. Sporocarps (catathecioid ascoma) orbicular, scutate, ostiolate, about 80 µm in diameter, margin slightly sinuate. Upper wall of scutellum composed of hardly visible cells, arranged in radiating rows extending outward (*textura prismatica*), about 5 µm in size. Lower wall (basal plate) not visible. Ostiole central, presumably 10 µm in diameter, surrounded by clearly delimited collar composed of dark, more or less isodiametric cells, 2–4 µm in size. Setae present, attached to ostiole, divergent, smooth, non-septate, with rather thick walls (2.0–2.5 µm), 15–50 µm long and about 5 µm

Fig. 1–6 *Lichenopeltella mizerniana* sp. nov. **1–2** sporocarp. **3** Detail of ostiole and setae. **4–6** Detached collar of ostiole with attached setae, note structure of setae. Bars 1–2, 4–5 = 20 μ m, 3, 6 = 10 μ m

wide. Base of setae flask-shaped, about 7.5 μ m in size, apex acute. Vegetative hyphae and ascospores absent.

Discussion

The above described fungal sporocarps morphologically correspond to the fossil-genus *Trichothyrites*. Sporocarps of this genus are roundish, thyrtothecium-like with a centrally located ostiole usually surrounded by a distinct collar composed of some rows of thick-walled and melanized cells. Fossils of this type were reported starting from the beginning of the twentieth century and were usually classified as representatives of the Microthyriaceae family (e.g. fig. 7, Kräusel 1920). Rosendahl (1943), on the basis of fossil sporocarps from early Pleistocene deposits at Springfield, Minnesota, created a new fossil-genus *Trichothyrites* to accommodate fossil sporocarps with a central ostiole. For the same type of fossils, Cookson (1947) created a new fossil-genus *Notothyrites* Cookson and assigned it to the Microthyriaceae family. Later, Venkatachala and Kar (1969), for trichothyriaceous sporocarps, proposed a

new fossil-genus *Sphaerialites* Venkatach. & R.K. Kar. Considering the priority of the name *Trichothyrites*, both *Notothyrites* and *Sphaerialites* should be considered younger synonyms of the fossil-genus *Trichothyrites* (Kalgutkar and Jansonius 2000). Smith (1980) described a new fossil-species *T. hordlensis*, along with some other morphotypes of sporocarps of trichothyriaceous fungi, and emended diagnosis of fossil-genus *Trichothyrites*. He wrote that the “Uppermost tier (ostiole margin) of cells may have short prolongations (setae) in some cases”. Most of the fossil-species of *Trichothyrites*, however, have no setae around the ostiole (Kalgutkar and Jansonius 2000; Samarakoon et al. 2019). The fossil-species *T. setifer* (Cookson) R.K. Saxena & N.K. Misra has up to eight setae, up to 13 μ m long, non-septate, arising from ostiole cells (Cookson 1947). Another two fossil-taxa, *T. denticulatus* (Ramanujam & K.P. Rao) Kalgutkar & Janson. and *T. echinatus* (K.P. Rao & Ramanujam) Kalgutkar & Janson. have short setae-like processes oriented towards the ostiole cavity (Kalgutkar and Jansonius 2000). All fossil-taxa listed above were described from pre-Quaternary deposits. Thyrtothecioid sporocarps with prominent setae were found

Fig. 7–9 Diverse trichothyriaceous sporocarps from the upper Pliocene of Mizerna-Nowa. Bars = 20 μ m

in Quaternary deposits as well, e.g. in Pleistocene deposits in Great Britain (Godwin and Andrew 1951), Finland (Eriksson 1978) and in the Holocene of the Pyrenees (López-Vila et al. 2014). Fungal sporocarps in form of thyriothecium (or catathecium) with setae around the ostiole have only the modern fungal genera *Chaetothyriothecium* Hongshan & K.D. Hyde and *Lichenopeltella*. Among them, catathecia with setae around the ostiole with its morphology directly corresponding to the setose representatives of fossil-genus *Trichothyrites* have only some species of the modern genus *Lichenopeltella*. *Chaetothyriothecium elegans* Hongshan & K.D. Hyde, a representative of Microthyriales, has thyriothecia similar to *Lichenopeltella*, but differs considerably, having septate and more numerous setae (Hongshan et al. 2014). Many other fungal genera have setae around or close to the ostiole [e.g. *Capronia* Sacc., *Coniochaeta* (Sacc.) Cooke, *Phoma* Sacc., *Pleospora* Rabenh. ex Ces. & De Not., *Podospora* Ces., *Pyrenochaeta* De Not., *Setosphaeria* K.J. Leonard & Suggs, *Trichomerium* Speg., and *Wentomyces* Koord.] but differ essentially in having perithecioid-like ascomycetes. Thus, fossil fungal thyriothecia (or catathecia) with an ostiole possessing non-septate setae could be directly related to the *Lichenopeltella* genus. Taking into account the above deductions we decided to describe a new fossil-species, *Lichenopeltella mizerniana*. Earlier mentioned setae-bearing fossil-species *Trichothyrites setifer*, most probably also related to *Lichenopeltella*, differs in having shorter setae (Cookson 1947). Relationships of fossil *Trichothyrites denticulatus* and *T. echinatus* that have short setae-like outgrowths to the genus *Lichenopeltella* seem unclear. Fossil *Lichenopeltella mizerniana* could be compared with a modern species of *Lichenopeltella*, bearing setae around the ostiole. Aptroot et al. (1997) listed 7 lichenicolous species of *Lichenopeltella* with ostiolar setae known at the time [*L. bunodophoronis* Diederich, *L. lobariae* Etayo & Diederich, *L. pannariacearum* Diederich, *L. peltigericola* (D. Hawksw.) R. Sant., *L. santessonii* (P.M. Kirk & Spooner) R. Sant., *L. swaminathaniana* Hariharan, Mibey & D. Hawksw., and *L. setifera* Matzer]. Among these, only *L. peltigericola*, similarly to *Lichenopeltella mizerniana*, has divergent setae around the ostiole (Aptroot et al. 1997). Later, von Brackel (2010) described two other setae-bearing lichenicolous species, *L. uncialicola* Brackel and *L. rangiferinae* Brackel, both with divergent setae around the ostiole. In terms of the collar structure (see fig. 1, von Brackel 2010, and fig. 2, von Brackel 2011), fossil *L. mizerniana* (Fig. 1–3) seems more similar to *L. uncialicola* than to *L. peltigericola*. Considering the non-lichenicolous taxa of *Lichenopeltella*, there are four modern species which have an ostiolar collar surrounded by setae: *L. alpestris* (Sacc.) P.M. Kirk & Minter, *L. ammophilae* (J.P. Ellis) P.M. Kirk & Minter, *L. palustris* (J.P. Ellis) P.M. Kirk & Minter, and *Micropeltopsis* (= *Lichenopeltella*, Wijayawardene et al. 2017) *cannabis* McPartl. (Ellis 1977;

Kirk and Spooner 1989; McPartland and Cubeta 1997). *Lichenopeltella mizerniana*, having divergent setae (Fig. 1–3), seems closest to *L. ammophilae*, *L. palustris*, and less so to *Micropeltopsis cannabis*, contrary to *L. alpestris* with its convergent setae (Ellis 1977). The overall shape and orientation of the setae of *L. palustris* (see fig. 10 a, b, Ellis 1977) are more similar to *Lichenopeltella mizerniana* (Fig. 1–6) than to *L. ammophilae* (see fig. 2c, Kirk and Spooner 1989). *L. ammophilae* and *L. palustris* are found on the dead stems of mono- and dicotyledons (*Ammophila arenaria*, *Filipendula ulmaria*, *Phalaris arundinacea*, and *Thalictrum flavum*, Ellis 1977) and *L. palustris* on peatmoss *Sphagnum* (Laukka 2005).

Following Smith (1980) and Samarakoon et al. (2019), we can agree that some of the remaining fossil-species of *Trichothyrites* that have an ostiolar collar without setae could probably also represent sporocarps of *Lichenopeltella*. Smith (1980), on the basis of the ostiolar collar structure, compared the fossil *Trichothyrites hordlensis* with the contemporary species *Lichenopeltella ammophilae* (syn. *Trichothyrina ammophilae*) (see Samarakoon et al. 2019). In Mizerna, *L. mizerniana* was found accompanied by other trichothyriaceous sporocarps (Fig. 7–9), resembling modern *Lichenopeltella ammophilae*, *Lichenopeltella nigroannulata* (J. Webster) P.M. Kirk & Minter, and *Lichenopeltella pinophylla* (Höhn.) P.M. Kirk & Minter as well. These sporocarps were found without any traces of setae around the ostiole. Similarly to the case of modern *L. palustris* (Ellis 1977) and *L. ammophilae* (Kirk and Spooner 1989), which have catathecia both with and without setae, it should not be overruled that at least some of these sporocarps could also represent the genus *Lichenopeltella*. On the other hand, the thyriothecia of some other than *Lichenopeltella* modern fungi without collar setae, e.g. from genus *Arnaudiella* Petr., especially species *A. caronae* (Pass.) Petr. (family Microthyriaceae, see Wu et al. 2011) have an ostiolar collar rather similar to those fossil-species of *Trichothyrites*.

Genus *Lichenopeltella* Höhn. [syn. *Didymopyrostroma* Bat. & Cavalc., *Micropeltopsis* Vain., *Microthyris* Clem., *Trichothyrina* (Petr.) Petr., Wu et al. 2011] belongs to the family Trichothyriaceae Theiss. (Wu et al. 2011; Wijayawardene et al. 2017) and comprises 48 modern species. Among them, 39 are parasitic on lichens (Wu et al. 2011; Diederich et al. 2018). The remaining taxa are partly bryophilous and are partly found as saprobes on dying or dead vascular plants (Marsh et al. 2010).

Ascomycetes of *Lichenopeltella* which have both the upper and lower wall (basal plate) are classified as both catathecia (Pérez-Ortega and Spribille 2009) and as thyriothecia (Wu et al. 2011; Hyde et al. 2013). The catathecia of *Lichenopeltella* are circular, in section lenticular, with a mostly entire margin [very rarely fimbriate, as in case of *L. fimbriata* (J.P. Ellis) P.M. Kirk & Minter], superficial, black, and with a central ostiole. The upper wall (scutellum)

of these catathecia is composed of rectangular cells, arranged in parallel lines radiating from the central ostiole (*textura prismatica*). The lower wall (basal plate) cells have a similar arrangement. Asci 8-spored, ascospores 2–3-seriate, hyaline, ellipsoid, and 2-celled (comp. Wu et al. 2011). The presence and orientation of setae is considered an important diagnostic feature in modern *Lichenopeltella* (Ellis 1977; Spooner and Kirk 1990; Aptroot et al. 1997; Earland-Bennett and Hawksworth 1999; von Brackel 2010).

Genus *Lichenopeltella* is worldwide distributed from tropical to polar areas (Aptroot et al. 1997; von Brackel 2010; Wijayawardene et al. 2017), and thus, annual temperatures seem to not limit their range. On the other hand, as there are no records of this genus from arid areas, its distribution probably depends on significant moisture of the environment resulting from an adequate amount of precipitation. When considering this in relation to *Lichenopeltella mizerniana*, we can only infer that the Pliocene climate of the Mizerna locality was probably at least moderately humid. The results of earlier palynological investigations of deposits from Mizerna confirm a humid climate and point to mild, temperate climatic conditions. In the sub-mountainous area, the annual rainfall was probably higher than in the lowlands (Birkenmajer and Worobiec 2013).

A significant problem in the palaeoecology of *Lichenopeltella mizerniana* is the presumed host on which the fossil-taxon existed at that time. As was noted before, most of the modern species of *Lichenopeltella* are parasitic on lichens, but there are some bryophilous taxa and also saprophytic on dying or dead vascular plants. Taking into account that the morphology of *Lichenopeltella mizerniana* is most similar both to some modern lichenicolous (*L. peltigericola*, *L. rangiferinae*, and *L. uncialicola*) and non-lichenicolous species (*L. ammophilae*, *L. palustris*), it is extremely difficult to make a decision about the presumed host of *Lichenopeltella* from Mizerna. No features other than the morphology of sporocarp are preserved in fossil *Lichenopeltella mizerniana* (lack of asci and ascospores), thus precluding any close comparison with the listed modern *Lichenopeltella* species. Nonetheless, we can make some assumptions on the host of *Lichenopeltella mizerniana* after taking into account the results of palynological investigations of the Mizerna deposits. The palynological profile from Mizerna-Nowa (Birkenmajer and Worobiec 2013) shows the considerable presence of pollen from grasses and sedges. Among the above suggested modern counterparts of fossil *Lichenopeltella mizerniana*, only non-lichenicolous *L. ammophilae* and *L. palustris* were found on the body of grasses. Similarly in the case of the closest modern counterparts, it is probable that the presumed host/s of *Lichenopeltella mizerniana* could be some grass/es.

Results of the investigation on fossil *Lichenopeltella* from Mizerna are of great importance for mycologists.

We proved the presence of genus *Lichenopeltella* in the past, dating it back at least to the late Pliocene (earlier than 2.6 Ma BP). This dating is of importance for the calibration of the divergence time estimations in the phylogenetic trees of genus *Lichenopeltella*, as well as the Trichothyriaceae family.

Acknowledgements Dr. hab. Marcin Piątek (Department of Mycology, W. Szafer Institute of Botany, Polish Academy of Sciences) is acknowledged for valuable suggestions to the manuscript. We would like to thank the anonymous reviewer for critically reading the manuscript and for his suggestions.

Funding information This work was supported by the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland through the statutory funds.

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