Terrestrial-aquatic wood-inhabiting ascomycete *Potamomyces* from the Miocene of Poland

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We report fungal ascospores of *Potamomyces* affinities from four Miocene localities in Poland. The spores are similar to the ones known from extinct species of *Potamomyces invaginatus*, *Potamomyces batii*, and *Potamomyces pontidiensis*, as well as to living *Potamomyces armatisporus*. Living representatives of *Potamomyces* are saprophytic, and usually found on decaying wood. They are mainly found in a freshwater or brackish environment, and sometimes also on terrestrial, moist to damp substrates. Therefore, the species of *Potamomyces* can be classified as a facultative-aquatic or terrestrial-aquatic fungus. Both living and extinct species of *Potamomyces* prefer a tropical to subtropical, and usually humid climate as their past and recent distribution is mostly confined to the intertropical zone. Fossil record of the *Potamomyces* ranges from the Lower Miocene to the Holocene, covering all continents with the exception of the Antarctica. Miocene findings of *Potamomyces* from Poland represent the first known fossil record of this genus from Europe and confirm the warm temperate to subtropical and humid climate during Middle to Late Miocene of present Poland previously inferred from palaeobotanical investigations.

Key words: Fungi, palaeoecology, palaeoenvironment, non-pollen palynomorphs, Neogene.

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Introduction

Fungi are one of the kingdoms of eukaryotic organisms that apparently appeared during the late Proterozoic (Krings et al. 2017; Loron et al. 2019; Bonneville et al. 2020) and their living species richness is estimated to be 2.2–3.8 million species (Hawksworth and Lücking 2017). They are usually terrestrial organisms, although some (about 3000–4000 species) have been reported from the aquatic environment (Shearer et al. 2007; Grossart and Rojas-Jimenez 2016). Fungi show many parasitic or symbiotic interactions with living plants (Krings et al. 2012), or they could be saprophytic on dead plant tissues (Dix and Webster 1995). The main ecological role of saprophytic fungi, both in terrestrial and aquatic environments, is the decomposition of organic matter including dead plant material (Dix and Webster 1995; Wong et al. 1998; Gessner et al. 2007; Tsui et al. 2016; Gulis et al. 2019). Especially freshwater ascomycetes prefer to colonize woody substrates (Shearer and Raja 2010). Remains of terrestrial-aquatic fungi that accompanied Miocene wetland plant associations were preserved in the Adamów lignite deposits, central Poland, as chitinous non-pollen palynomorphs (NPP) found during palynological investigations (Widera et al. 2021; Worobiec et al. 2021, 2022b). They are represented by species that were saprophytic on decaying wood and on fallen leaves in a very humid, periodically flooded environment (Worobiec et al. 2022b). Among the

fungal remains a spore was found that is identical to those of living fungus *Potamomyces* Hyde, 1995. Comparable spores were also found in other Miocene localities from Poland (Babczyn, Bełchatów, and Komorniki). Similarly to many fossil fungi that have potential as a non-pollen palynomorph palaeoecological proxy (Lange 1978; Conran et al. 2016; Worobiec and Worobiec 2017; Worobiec et al. 2018), *Potamomyces* is considered useful for the reconstruction of palaeoenvironment and palaeoclimate (Nuñez Otaño et al. 2017). Considering this, the main goal of the present investigations was a detailed taxonomical and palaeoecological study of *Potamomyces* in the Miocene of Poland in terms of its importance as a palaeoecological proxy and the diversity of Miocene fossil ascomycetes.

Institutional abbreviations.—KRAM-P, Palaeobotanical collections of W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland.

Other abbreviations.—NPP, non-pollen palynomorphs.

Material and methods

Ascospores of *Potamomyces* were collected from four Miocene localities from Poland (Fig. 1): the Middle Miocene of the Adamów lignite deposit, Upper Miocene from the Bełchatów Lignite Mine, the Middle Miocene of the Komorniki 97/72 borehole in the Ruja lignite deposit, and the Middle Miocene of the Babczyn 2 borehole. All of the ascospores were found during palynological studies.

The examined section of the lignite seam from the Adamów deposit was located in the north-western part of the Adamów opencast mine, central Poland (52°01'17"N 18°37'45"E). An ascospore belonging to *Potamomyces* genus was found in a palynological sample taken from the 3-m thick 1st mid-Polish lignite seam (Worobiec et al. 2022b). The age of the 1st mid-Polish seam was determined as the middle part of the Middle Miocene (Piwocki and Ziembińska-Tworzydło 1997; Kasiński and Słodkowska 2016; Worobiec et al. 2021, 2022b). Palynological analysis revealed that the Adamów area was overgrown by palustrine wetland communities similar in composition to modern pocosins (Worobiec et al. 2021).

Deposits with plant macroremains from Bełchatów, central Poland (sites KRAM-P 210 and KRAM-P 218) were found in the open pit of the Bełchatów Lignite Mine (51°14'42"N 19°17'14"E) in overburden sediments belonging to the clayey-coal unit (I-W) which are considered to be the latest Middle–Late Miocene age (Worobiec and Lesiak 1998; Worobiec and Worobiec 2016). According to Wilczyński (1992) and Krzyszkowski and Winter (1996) deposits of the lower part of the clayey-sandy unit were formed in a fluvial environment of braided to meandering rivers with dense vegetation along riverbanks.

The Komorniki 97/72 borehole in the Ruja lignite deposit was located in the southernmost part of the Legnica-

Fig. 1. Location of the investigated Miocene localities in Poland (asterisks) where ascospores of *Potamomyces* were found.

Ścinawa lignite resource complex in Lower Silesia, SW Poland (51°11'N 16°23'E). About 100 samples were taken from the borehole core for palynological analysis. An ascospore of *Potamomyces* genus was found in a palynological sample taken from the 2nd Lusatian lignite seam. This seam developed during the Middle Miocene, in the warmest phase of the lignite origin of the Ruja deposit. In this phase, riparian, swamp and peat-bog vegetation dominated (Worobiec et al. 2022a).

The Babczyn 2 borehole (50°14'04.26"N 23°12'44.88"E) was located in the northern part of the Polish Carpathian Foredeep, SE Poland (Peryt et al. 2020). The palynologically studied section of the borehole core is composed of marine marls and clays. They came from the sediments lying on the upper Badenian Babczyn tuff (Peryt et al. 2021) and were radiometrically dated at 13.06±0.11 Ma (Serravalian, Middle Miocene) (Śliwiński et al. 2012; Peryt et al. 2020). The analysed samples yielded well preserved terrestrial (sporomorphs) and marine (dinoflagellate cysts) palynomorphs, along with fungal remains. The preliminary results of the palynological analysis revealed the presence of mesophytic and wetland vegetation along the Paratethys sea shoreline at the time of sedimentation.

The samples from the Adamów and Bełchatów mines outcrops and from the borehole Komorniki 97/72 were processed using successively 10% hydrochloric acid (HCl) to remove carbonates, 10% potassium hydroxide (KOH), 40% hydrofluoric acid (HF) for four days to remove silicates, and subsequently 10% hydrochloric acid (HCl) to remove silicofluorides (Moore et al. 1991). Additionally, the residuum was sieved at 5 μm on a nylon mesh. The samples from the Babczyn 2 borehole core were processed using 38% hydrochloric acid (HCl) followed by 40% hydrofluoric acid (HF),

heavy liquid (ZnCl$_2$ + HCl; density 2.0 g/cm^3) separation, and sieving at 15 μm on a nylon mesh in and ultrasonic bath for 10–15 s (Peryt et al. 2020). Palynological slides from all of the localities were made using glycerine jelly as a mounting medium. They are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków). Microphotographs were taken with a Nikon Eclipse E400 microscope equipped with a Canon A640 digital camera.

The terminology for the morphology of *Potamomyces* ascospores follows Kirk et al. (2008), taxonomy follows Wijayawardene et al. (2017, 2018).

Systematic palaeontology

Kingdom Fungi Moore, 1980

Phyllum Ascomycota Cavalier-Smith, 1998

Family uncertain

Genus *Potamomyces* Hyde, 1995

Type species: *Potamomyces armatisporus* Hyde, 1995; Recent, North Queensland, Australia.

Potamomyces sp. ex gr. *P. armatisporus* Hyde, 1995

Fig. 2.

Material.—Adamów 2017: slide 0.1(1), one specimen; Bełchatów: KRAM-P 210/10(4), one specimen; KRAM-P 218/109B(5), one specimen; KRAM-P 218/85(1), one specimen; Babczyn 2 borehole: slide 2/31, one specimen; Komorniki borehole 97/72: slides from depth 104.7 m; four specimens. Nine specimens in total from Middle to Upper Miocene of Poland. Collections: Adamów 2017, KRAM-P 218, Babczyn 2, and Komorniki 97/72. Stored in the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Description.—Ascospores distinctly biconical (rhomboid) to obovate, thick-walled, medium-brown to dark brown, more or less translucent, smooth, 52–62 μm long and 25–35 μm wide in the equatorial part. One end of the ascospore more or less rounded and one end usually more or less attenuated, while in the case of some ascospores both ends obtuse to nearly rounded. Mostly four, very rarely five, distinct verrucae arranged around the equator. The verrucae rounded, 3–5 μm high and 5–10 μm in diameter. An indistinct germ pore usually visible on one end of ascospore.

Remarks.—A biconical shape along with verrucae arranged around the equator of the above described fungal spores is rather unique among fungal spores. For the first time Muller (1959) reported such spores from the Recent sediments of the Orinoco Delta, Venezuela. Then, for many years, these spores were reported and informally classified as *Mediaverrunites* Jarzen and Elsik, 1986 or *Mediaverrusporonites* Elsik, 1976, without diagnostic features and without specified type specimens (Elsik 1976; Jarzen and Elsik 1986; Banerjee and Nandi 1992; Nandi and Sinha 2007). Only Nandi and Sinha (2007) formally described and validated the *Mediaverrunites*

Jarzen and Elsik 1986 ex Nandi and Sinha, 2007. Schlütz and Shumilovskikh (2013) for the first time linked fossil spores of *Mediaverrunites/Mediaverrusporonites* with ascospores of living *Potamomyces armatisporus* Hyde, 1995, described earlier from submerged wood from Australia, Ecuador, and Malaysia (Hyde 1995). Furthermore, these authors described a new species *Potamomyces nepalensis* Schlütz and Shumilovskikh in Nuñez Otaño et al., 2017, and they compared living representatives of *Potamomyces* Hyde, 1995, with spores of the fossil-genus *Mediaverrunites*. However, according to Nuñez Otaño et al. (2017), the fungal taxonomical novelties of Schlütz and Shumilovskikh (2013) were published without any identifiers from a recognised repository and, thus, these names were invalid. Nuñez Otaño et al. (2017) validated the name *Potamomyces nepalensis* and made new combinations of the extinct species described in *Mediaverrunites* and re-assigned them to *Potamomyces* in accordance with the International Code of Nomenclature for algae, fungi and plants (Turland et al. 2018).

Potamomyces includes two living species (*Potamomyces armatisporus* Hyde, 1995, and *Potamomyces nepalensis* Schlütz and Shumilovskikh in Nuñez Otaño et al., 2017), and eight fossil-species (*Potamomyces batii* Sancay, 2014 ex Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces elsikii* (Nandi and Sinha, 2007) Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces fournieri* (Elsik and Jarzen, 2009) Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces invaginatus* (Elsik and Jarzen, 2009) Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces magnus* (Elsik and Jarzen, 2009) Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces mulleri* (Nandi and Sinha, 2007) Nuñez Otaño, di Pasquo, and Bianchinotti, 2017, *Potamomyces pontidiensis* Sancay, 2014 ex Nuñez Otaño, di Pasquo, and Bianchinotti, 2017 including subfossil *Potamomyces palmarensis* Nuñez Otaño, di Pasquo, and Bianchinotti, 2017) (MycoBank 2021). The fossil and living *Potamomyces* species can be divided into two morphological groups depending on the number of verrucae. The first group are taxa corresponding to the living *P. armatisporus* usually have 4, but sometimes 3–5 equatorial verrucae and besides living *P. armatisporus* this group includes the fossil-species *P. invaginatus*, *P. batii*, and *P. pontidiensis*. A second group are taxa close to living *P. nepalensis* and are represented by fossil-taxa having 6–8 verrucae and include *P. palmarensis*, *P. elsikii*, *P. mulleri*, and *P. magnus*. However, in the case of specimens illustrated by Nandi and Sinha (2007) as *Mediaverrunites elsikii* (= *P. mulleri*), and *Mediaverrunites mulleri* (= *P. mulleri*), it can be seen that contrary to the original description of *Mediaverrunites elsikii* (6–8 verrucae), and *Mediaverrunites mulleri* (4–8 verrucae), they have a maximum of 4–5 verrucae. Therefore, *P. elsikii* and *P. mulleri* should be included in the *Potamomyces armatisporus* group. Considering all fossil and living *Potamomyces* species they can be grouped into taxa close to *P. armatisporus* usually having 4 (3–5) verrucae (*P. armatisporus*, *P. batii*, *P. elsikii*, *P. invagina-*
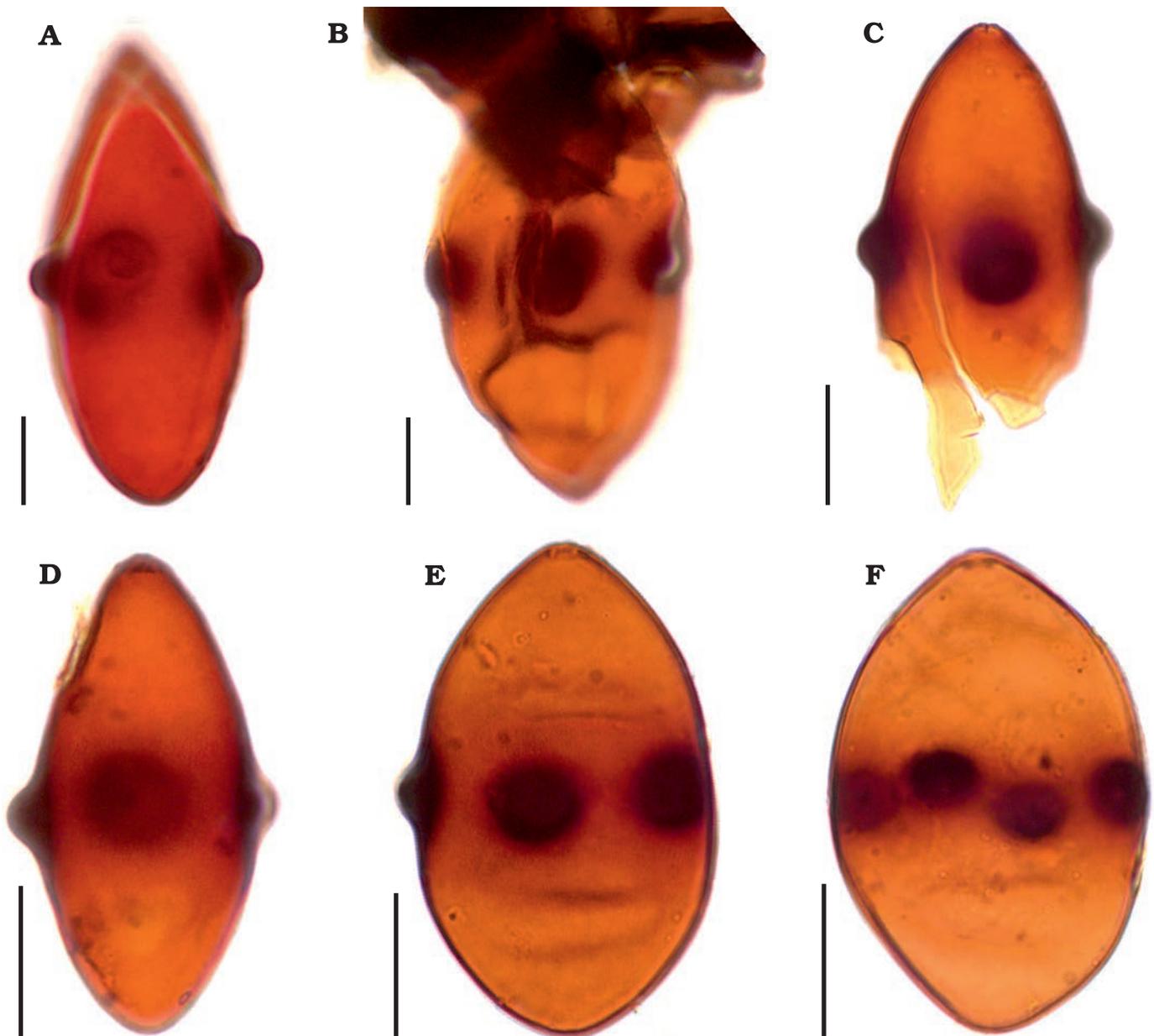
Fig. 2. Fossil ascospores of *Potamomyces* sp. ex gr. *P. armatisporus* Hyde, 1995, from Middle (A, B, D–F) and Middle/Upper (C) Miocene of Poland. **A**. Adamów 2017, slide Adamów 2017/0.1(1) (modified from Worobiec et al. 2022b: fig. 4c). **B**. Babczyn 2, slide Babczyn 2/2(31). **C**. Bełchatów KRAM-P 218, slide KRAM-P 218/85(1). **D–F**. Komorniki 97/72. **D**. Slide Komorniki 97/72/104.7(2). **E**. Slide Komorniki 97/72/104.7(3). **F**. Slide Komorniki 97/72/104.7(4). Scale bars 10 μm.

tus, *P. mulleri*, and *P. pontidiensis)* and taxa corresponding to *P. nepalensis* having 6–8 verrucae (*P. nepalensis*, *P. palmarensis*, and *P. magnus*). The fossil-species of *P. fournierii* seems to be a transitional form between these groups having 5–6 verrucae (Nuñez Otaño et al. 2017). A peculiar feature of some fossil ascospores of *Potamomyces* is the presence of two bands of verrucae (Elsik and Jarzen 2009; Nuñez Otaño et al. 2017), additional verrucae near both poles in the case of *P. nepalensis* (Schlütz and Shumilovskikh 2013) or verrucae covering the whole surface of the ascospore, as in the case of the spore described as cf. *Gliomastix*-type (Jarzen and Elsik 1986: pl. 3: 7) that surely could be assigned to *Potamomyces*. These atypical features, however,

could be teratological abnormalities which occurred during the formation of the ascospores. It seems especially true in the case of the above mentioned spore of Jarzen and Elsik (1986), with verrucae covering the whole surface of the ascospore. Other features of the morphology of *Potamomyces* ascospores (e.g., verrucae dimensions, and the presence or absence of an apical germ pore) are rather variable or sometimes hardly visible (compare Elsik and Jarzen 2009) and, thus, their taxonomical utility in these cases seems limited.

The shape and dimensions of ascospores are also variable, and in a given locality the same type of *Potamomyces* spores could be both biconical and wide elliptic. This concerns the ascospores of *Potamomyces* found in Poland as

well. They correspond to the *Potamomyces armatisporus* group usually having 4 verrucae (the only specimen of *Potamomyces* from Adamów has 5 verrucae, Fig. 2A) and a biconical (Fig. 2A–D) to wide elliptic (Fig. 2E, F) shape. Fossil *Potamomyces* ascospores from Poland correspond to the fossil *P. invaginatus*, *P. batii*, and *P. pontidiensis*, and to living *P. armatisporus*. *Potamomyces invaginatus* differs with its smaller ascospores and larger verrucae (10–12 μm), when compared to the *Potamomyces* from the Miocene localities of Poland (Elsik and Jarzen 2009). *Potamomyces batii* and *P. pontidiensis* within the limits of variability, have a similar size and shape to our specimens of *Potamomyces*. However, they have 3–4 verrucae (Sancay 2014), contrary to *Potamomyces* from the Miocene localities of Poland, which mostly have 4 verrucae. *Potamomyces pontidiensis* is morphologically most similar to some of our specimens. Contemporary *P. armatisporus* differs with its smaller ascospores (Hyde 1995; Nuñez Otaño et al. 2017). As no fossil and living species of *Potamomyces* is identical to fossil ascospores from Poland, we decided to classify them as *Potamomyces* sp. ex gr. *P. armatisporus* Hyde, 1995.

It should be added that besides the *Potamomyces*, the fossil-genus *Parapotamomyces* O'Keefe, 2017, with fossil-species *Parapotamomyces maydiformis* O'Keefe, 2017, which is considered to be a fungal spore, has been described from the Miocene Heath Formation, Tumbes Province, Peru (O'Keefe 2017). However, *Parapotamomyces maydiformis* certainly should not be considered as a fungal spore but possibly represents plant remain resembling an isolated fragment of seed testa.

The ascospores of *Potamomyces* are rather similar to those of the living *Biconiosporella* Schaumann, 1972, represented by marine species *Biconiosporella corniculata* Schaumann, 1972, and are saprophytic on decayed wood (Hyde 1995; Jones et al. 2009). Both taxa posses biconical ascospores with equatorial verrucae (Hyde 1995). However, *Potamomyces* and *Biconiosporella* differ markedly as *Biconiosporella corniculata* has four-celled ascospores with 7–9 equatorial verrucae, while *Potamomyces armatisporus* is one-celled with 4 equatorial verrucae (Kohlmeyer and Kohlmeyer 1979; Hyde 1995). Moreover, *Biconiosporella corniculata* differs from all species of *Potamomyces* through its having two germ pores at each end of the ascospore (Huang et al. 2021). *Amphisphaerella dispersella* (Nylander, 1859) Eriksson, 1966, has ascospores with characteristic meridional germ pores that somewhat resemble verrucae that characterize all taxa of *Potamomyces* (Hyde 1995; Van Geel and Aptroot 2006; Schlütz and Shumilovskikh 2013). *Ascorhombispora aquatica* Cai and Hyde, 2007, found saprophytic on submerged bamboo culms, has a similar, more or less rhombic shape and a dark equatorial belt. It differs from fossil and living species of *Potamomyces* with its absence of verrucae (Cai and Hyde 2007). There is a similarity to ascospores of *Potamomyces* (with a biconical shape) also displayed in the conidia of some members of the family Beltraniaceae Nannizzi, 1934 (e.g., *Beltrania rhombica*

Penzig, 1882, *Pseudobeltrania cedrelae* Hennings, 1902, *Beltraniomyces lignicola* Manoharachary, Agarwal, and Rao, 2003) but there is a clear difference in the absence of equatorial verrucae (Rajeshkumar et al. 2016).

Discussion

Geographical and stratigraphical distribution of *Potamomyces*.—The oldest fossil record of *Potamomyces*-like spores concerns a spore described as *Diporicellaesporites* sp. from the early Eocene (53–52 Ma) Vastan Lignite Mine, Gujarat, western India (Rao et al. 2013). As can be seen (Rao et al. 2013: pl. 3: 33) in the spore illustrated there is similar to species of *Potamomyces* in its having characteristic equatorial verrucae (two are visible) and in the shape. It differs markedly from species of *Potamomyces*, however, with two clearly visible germ pores on both poles. Contrary to spore from the Vastan Lignite Mine, ascospores of *Potamomyces* species have only one, sometimes hardly visible germ pore. This Eocene *Potamomyces*-like fungal spore could belong to an ancestor of *Potamomyces* or, through its having two germ pores, could be another fossil-genus displaying a similarity to ascospores of the living *Biconiosporella* Schaumann, 1972. All of the remaining fossil records of *Potamomyces*-like fungal spores range from the Lower Miocene to the Holocene (SOM: table 1, the Supplementary Online Material available at http://app.pan.pl/SOM/app67-Worobiec_etal_SOM.pdf). Neogene records come from Africa, Asia, and South America (i.e., Brazil, Colombia, India, Mexico, Nigeria, Peru, and Turkey), and Quaternary *Potamomyces* is known from Africa, Asia, North and South America, and Australia (i.e., Argentina, Australia, Brazil, Colombia, Dominican Republic, Fiji Islands, Gulf of Mexico, India, Jamaica, Marianas Islands, South Africa, and Turkey). Recent distribution of *Potamomyces* includes Africa, Asia, North and South America, and Australia (i.e., Australia, Brazil, Brunei, Colombia, Ecuador, Hong Kong, Malaysia, Nepal, USA, Venezuela, Zambia). Ascospores of *Potamomyces*, both fossil and living have not been known in Europe and Antarctica (compare SOM: table 1). Thus, the findings of *Potamomyces* sp. from the Miocene of Poland document the first fossil record of this fungus from Europe and represent the northernmost known occurrence of this genus.

Ecology of fossil and living *Potamomyces*.—*Potamomyces armatisporus* was found for the first time as a living saprophytic fungus isolated from submerged wood from Australia, Ecuador and Malaysia (Hyde 1995). Other records similarly suggest that *Potamomyces* occurs on decaying wood (Ho et al. 2001; Canto et al. 2020) or on driftwood in a brackish environment (Hyde 1988, 1995). Most fossil and modern findings of *Potamomyces* are confined to an aquatic, freshwater (riverine, lacustrine, swampy) or brackish (deltaic, coastal, mangrove) environment (SOM: table 1). Some modern findings, however, are not connected

to an aquatic environment but rather to a terrestrial environment and there *Potamomyces* also prefers moist to damp substrates (Macphail 2006; Elsik and Jarzen 2009; Schlütz and Shumilovskikh 2013). These findings of *Potamomyces* (both aquatic and terrestrial localities) indicate that, ecologically, this fungus, by analogy with modern saprophytic facultative-aquatic hypomycetes (Goh 1997), could be classified as facultative-aquatic or terrestrial-aquatic fungus. Both fossil and living species of *Potamomyces* prefer a tropical to subtropical, and usually humid climate. Occasionally, *Potamomyces* is also found in warm temperate climate localities (SOM: table 1). Considering the data of past and modern distribution of *Potamomyces* (SOM: table 1), it is clear that this fungus is mostly confined to an intertropical zone.

Miocene findings of *Potamomyces* sp. from Poland (Adamów, Babczyn, Bełchatów, and Komorniki) are also associated with an aquatic, swampy, riverine or even marine (originally swampy or brackish) palaeoenvironment, and suggest its lignicolous habitat. Palynological analysis of the Middle Miocene lignite seam from Adamów revealed the presence of sporomorphs of peat-forming vegetation of palustrine wetland communities and mesophytic forests, along with fungal microremains of ascomycetes and hyphomycetes that were saprophytic on decaying wood and on fallen leaves in a very humid, periodically flooded environment and indicate that the climate was warm temperate and humid, with an estimated mean annual temperature at 15.7–18.0°C (Worobiec et al. 2021, 2022b). The floristic composition of Middle Miocene plant assemblages from the Komorniki borehole in the Ruja lignite deposit are characterized by dominance of wetland, swamp and riparian vegetation and suggest warm temperate climate conditions with mild winters (Worobiec et al. 2008), with a mean annual temperature in the range of 15.7–17.8°C (Worobiec et al. 2022a). In the Middle Miocene of Babczyn, the preliminary results of palynological analysis revealed the presence of remains of mesophytic and wetland plants and wood-inhabiting fungi in a warm-temperate to subtropical, mild and rather humid climate. Middle to Late Miocene fossil plant assemblages from Bełchatów were dominated by plant remains of wetland vegetation of swamp and riparian forests, along with taxa of mesophytic upland communities growing in a warm temperate climate with mild winters (Worobiec 2003; Worobiec and Lesiak 1998; Worobiec and Szynkiewicz 2016; Worobiec and Worobiec 2016). A mean annual temperature of 13.5–16.5°C for the KRAM-P 218 assemblage from Bełchatów was estimated (Worobiec and Szynkiewicz 2016). Therefore, the presence of ascospores of *Potamomyces* sp. in the Miocene of Poland fits well with warm temperate to subtropical and humid climate of Middle to Late Miocene of Poland inferred from palaeobotanical investigations and confirms that *Potamomyces* is a useful and credible non-pollen palynomorph proxy for reconstruction of a palaeoenvironment and palaeoclimate.

Conclusions

We found that ascospores of *Potamomyces* sp. from Poland correspond to *Potamomyces armatisporus* group. Ecologically, both fossil and living species of *Potamomyces* are usually found on decaying wood in an aquatic, freshwater, and sometimes brackish environment, but also in terrestrial, moist to damp settings. *Potamomyces* prefers a tropical to subtropical, usually humid climate and only occasionally it is also found in a warm temperate climate. Similar to modern saprophytic facultative-aquatic hypomycetes (Goh 1997), we consider *Potamomyces* to be a facultative-aquatic or terrestrial-aquatic fungus. The results of our investigations confirm that *Potamomyces* is a useful and credible non-pollen palynomorph proxy for reconstruction of a palaeoenvironment and palaeoclimate. Therefore, palynologists during palynological investigation of pre-Quaternary deposits should pay more attention to the various types of fungal non-pollen palynomorphs, including *Potamomyces*, as in many cases they are ignored by researches. More data on the stratigraphical range of *Potamomyces* obtained in this report could shed light on the problem of the time of emergence of *Potamomyces* and allow to determine the full palaeogeographical range of this genus, especially in the case of the Cenozoic of Europe. The results of our study may be informative not only for palaeobotanists and geologists, but also for mycologists regarding the calibration of the divergence time estimations in the phylogenetic trees of fungal lineages.

Acknowledgements

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