

**Taxonomy and palaeoecology of the fossil
anamorphic fungus *Mycoenterolobium eccentricum*
(R.K. Kar) G. Worobiec, n. comb.**

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Taxonomy and palaeoecology of the fossil anamorphic fungus *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb.

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ABSTRACT

Microremains of fungi from Neogene deposits from the Gray Fossil Site (Tennessee, United States) and the Belchatów Lignite Mine (Poland), similar to the enigmatic fossil-species *Kutchiathyrites eccentricus* R.K. Kar, 1979, were reconsidered as representatives of the modern mitosporic genus *Mycoenterolobium* Goos, 1970. A new combination, *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb., is proposed. The geographical and stratigraphical range and ecology of the fossil and modern *Mycoenterolobium* species are discussed. Investigated remains of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. document the first fossil record of this fungus from both Northern America and Europe, while the Belchatów mine represents the northernmost known fossil and modern occurrence of the *Mycoenterolobium* genus. Both modern and fossil species of *Mycoenterolobium* seem to prefer warm (tropical to warm temperate), usually humid climates. They are associated with plant debris (mainly wood) decaying in a damp or aquatic environment. *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. is suggested to be used as a non-pollen palynomorph proxy for palaeoclimatic and palaeoenvironmental reconstructions.

KEY WORDS

Europe,
fossil fungi,
Kutchiathyrites,
Mycoenterolobium,
Neogene,
North America,
palaeoecology,
new combination.

RÉSUMÉ

Taxonomie et paléocologie du champignon anamorphe fossile Mycoenterolobium eccentricum (R.K. Kar) G. Worobiec, n. comb.

Des microrestes de champignons provenant de gisements du Néogène du Gray Fossil Site (Tennessee, États-Unis) et de la mine de lignite de Belchatów (Pologne), similaires à l'énigmatique espèce fossile *Kutchiathyrites eccentricus* R.K. Kar, 1979, ont été réévalués comme des représentants du genre mitosporique moderne *Mycoenterolobium* Goos, 1970. Une combinaison nouvelle, *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb., est proposée. La répartition géographique et strati-

MOTS CLÉS
 Europe,
 champignons fossiles,
Kutchiathyrites,
Mycoenterolobium,
 Néogène,
 Amérique du Nord,
 paléoécologie,
 combinaison nouvelle.

graphique, ainsi que l'écologie des espèces fossiles et modernes de *Mycoenterolobium* sont discutées. Les restes étudiés de *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. constituent le premier enregistrement fossile de ce champignon pour l'Amérique du Nord et l'Europe, tandis que la mine de Bełchatów représente l'occurrence fossile et moderne la plus septentrionale connue du genre *Mycoenterolobium*. Les espèces modernes et fossiles de *Mycoenterolobium* semblent préférer les climats chauds (tropicaux à tempérés chauds), généralement humides. Elles sont associées à des débris végétaux (principalement du bois) en décomposition dans un milieu humide ou aquatique. *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. est proposé comme indicateur palynomorphe non pollinique (NPP) pour les reconstructions paléoclimatiques et paléoenvironnementales.

INTRODUCTION

As one of the kingdoms of eukaryotic organisms, fungi most likely appeared in the late Proterozoic (Loron *et al.* 2019; Berbee *et al.* 2020; Bonneville *et al.* 2020). Their taxonomic diversity is estimated to be between 2 and 4 million species (Hawksworth & Lücking 2017), but the list of fungal taxa, both modern and fossil, is expanding continually. Many fossil fungal taxa have the potential as a non-pollen palynomorph (NPP) palaeoecological proxy (Lange 1976; Conran *et al.* 2016; Worobiec & Worobiec 2017; Worobiec *et al.* 2018, 2020). The particular group of fossil fungi that play an essential role as palaeoenvironmental proxies is wetland fungi saprophytic on decaying plant remains (Widera *et al.* 2021; Worobiec *et al.* 2021, 2022). On wetlands (swamps, bogs, fens, marshes, bottomland hardwoods) can be found various fungal taxa, both terrestrial and aquatic (Stephenson *et al.* 2013). Saprophytic fungi play an important ecological role in wetlands as decomposers of organic matter, mainly dead plant material (Dix & Webster 1995; Gessner *et al.* 2007; Gulis *et al.* 2019). Microremains of fungi, including those of wetland origin, were found during palynological investigations of Neogene deposits from the Gray Fossil Site (United States) and from the Bełchatów Lignite Mine in Poland (plant remains assemblages KRAM-P 218 and KRAM-P 226) as chitinous non-pollen palynomorphs (Zobaa *et al.* 2011; Ochoa *et al.* 2012; Worobiec *et al.* 2013, 2018, 2020; Worobiec & Worobiec 2017). Pollen slides from these localities were reinvestigated then for new fungal forms. Among them, conidia of dictyosporous anamorphic fungus apparently similar to the enigmatic fossil-species *Kutchiathyrites eccentricus* R.K. Kar, 1979 were found. *Kutchiathyrites eccentricus* previously has been considered to be similar to “Microthyriaceous ascostromata” (Kar 1979), *Mycoenterolobium platysporum* Goos, 1970, *Arbuscula eugeniae* Bat. & Peres, 1965, and *Tretopileus sphaerophorus* (Berk. & M.A. Curtis) S. Hughes & Deighton, 1960 (Jain & Kar 1979) or as similar to *Mycoenterolobium platysporum* and classified as Fungi Imperfecti, Dictyosporae (Kalgutkar & Jansonius 2000; Berbee *et al.* 2015). Thus, the relationship of the fossil *Kutchiathyrites eccentricus* with modern fungal genera has been disputable so far. However, establishing the affinities of fossil fungi with their modern counterparts is essential for palaeoenvironmental and palaeoclimatic reconstructions

(Saxena & Wijayawardene 2022). The aim of our study is to describe and re-interpret the *Kutchiathyrites*-like remains from Neogene deposits of the United States, and Poland and to consider their importance as a proxy in term of palaeoecology.

MATERIAL AND METHODS

The investigated fossils were found in palynological samples from two localities. Most fossil specimens came from the Gray Fossil Site, Washington County, Tennessee, United States. Two specimens were found in two sites from the Bełchatów Lignite Mine, Poland.

Lacustrine deposits of the Gray Fossil Site in Washington County, Tennessee, United States (36°23'9.6"N, 82°29'52.8"W) were suggested to be a multiple sinkholes/sub-basins fills that could represent asynchronous events (Zobaa *et al.* 2011; Worobiec *et al.* 2013). Laminated sediments of the Gray Fossil Site, previously dated to the latest Miocene—the earliest Pliocene (Wallace & Wang 2004; Shunk *et al.* 2006) and an updated analysis indicating an Early Pliocene age of latest Hemphillian to early Blancan (4.5–4.9 Ma) (Samuels *et al.* 2018), preserved various animal and plant remains (see Worobiec *et al.* 2018). Fungal remains from the Gray Fossil Site were earlier reported four times. Zobaa *et al.* (2011) found remains of *Callimothallus* sp. (now *Neomycoleptodiscus pertusus* (Dilcher) G. Worobiec, 2020), Ochoa *et al.* (2012) mentioned the presence of fungal remains, Worobiec *et al.* (2013) noted the occurrence of epiphyllous fungi (Microthyriales) and, finally, Worobiec *et al.* (2018) reported remains of *Cephalothecoidomyces neogenicus* G. Worobiec, Neumann & E. Worobiec, 2017, *Cenococcum* cf. *geophilum* Fr., 1829, and *Trichothyrites* cf. *padappakarensis* (Jain & Gupta) Kalgutkar & Jansonius, 2000. In the present investigation, the palynological slides from samples collected earlier from the Gray Fossil Site (Worobiec *et al.* 2013) from the Bear Pit (three slides) and Elephant Pit (five slides) were reinvestigated.

At the Bełchatów Lignite Mine situated in Central Poland (51°14'42"N, 19°17'14"E), south of the town of Bełchatów, fungal remains were found in palynological samples collected from the fossil plant assemblages KRAM-P 218 and KRAM-P 226. Deposits with the plant macro- and micro-remain assemblage KRAM-P 218 were left as abandoned

channel fill in the floor part of clayey-sandy unit (I-P) of the Neogene deposits of the Bełchatów Lignite Mine (Worobiec & Szykiewicz 2016; Worobiec & Worobiec 2016, 2019), considered to be Late Miocene in age (Szykiewicz 2000). Investigated fungal remains were found in one palynological slide from the specimen (rock sample) with plant macroremains numbered KRAM-P 218/85. The assemblage KRAM-P 226 with plant macroremains came from the borehole core No. 1326/B from the mine outcrop. The stratigraphical position of the fossil leaf litter sample found in the core corresponds to the clayey-coal unit (I-W). The complicated tectonics of this part of the mine outcrop makes it difficult to establish the exact geological position and age of the plant macroremain assemblage KRAM-P 226. However, the age of the discussed plant assemblage is probably the Late Miocene (Worobiec 2014). In one palynological slide from this locality, one specimen of the fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. was found. Fungal remains from the fossil assemblage KRAM-P 218 of the Bełchatów Lignite Mine were previously reported by Worobiec & Worobiec (2017) and Worobiec *et al.* (2020). These authors reported remains of *Callimothallus pertusus* Dilcher, 1965 (now *Neomycoleptodiscus pertusus*), *Phragmothyrtes* cf. *lutosus* (Dilcher) R.K. Kar & R.K. Saxena, 1976, *Phragmothyrtes* sp. 1, *Phragmothyrtes* sp. 2, *Trichothyrites* cf. *hordlensis* P.H. Smith, 1980, and *Trichothyrites* sp. From the fossil assemblage KRAM-P 226, Worobiec (2014) described “bodies of epiphyllous, microthyriaceous fungus” on the abaxial epidermis of the fossil leaf of ?*Magnolia* sp. Detailed descriptions of the geology of the localities KRAM-P 218 and KRAM-P 226 were provided by Worobiec & Szykiewicz (2016) and Worobiec (2014), respectively.

Palynological samples from the Gray Fossil Site and the Bełchatów Lignite Mine were processed in the laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków), using hydrochloric acid, potassium hydroxide, and sulfuric acid (Moore *et al.* 1991). Additionally, hydrofluoric acid was used to remove mineral matter, and the residuum was sieved at 5 µm on a nylon mesh. The microscope slides were made using glycerine jelly as a mounting medium (Worobiec *et al.* 2013).

The fossil specimens are housed in the W. Szafer Institute of Botany, Polish Academy of Sciences, under catalogue numbers KRAM-P 218 and KRAM-P 226 as well as GFS/Bear Pit and GFS/Elephant Pit. Microphotographs were taken with a Nikon Eclipse E400 microscope equipped with a Canon A640 digital camera. Terminology for the morphology of fungal remains follows Goos (1970) and Calabon *et al.* (2020).

ABBREVIATIONS

Institutional abbreviations

GFS Gray Fossil Site, Washington County, Tennessee;
KRAM-P Palaeobotanical collections of W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Other abbreviation

NPP non-pollen palynomorphs.

SYSTEMATIC PALAEONTOLOGY

Kingdom FUNGI R.T. Moore, 1980
Phylum ASCOMYCOTA Caval.-Sm., 1998
Order PLEOSPORALES Luttr. ex M.E. Barr, 1987,
incertae sedis
Genus *Mycoenterolobium* Goos, 1970

Mycoenterolobium eccentricum (R.K. Kar) G. Worobiec,
n. comb.
(Fig. 1)

Kutchiathyrites eccentricus R.K. Kar, 1979: 32; pl. 3, figs 49-52.

MYCOBANK. — MB849812.

MATERIAL EXAMINED. — **United States.** Tennessee, Gray Fossil Site, slides: Bear Pit 2(6), 19(2), Elephant Pit 3(1), 10(3), 12(2), 12(6), 12(8).

Poland. Bełchatów Lignite Mine, slides: KRAM-P 218/85(4), KRAM-P 226B. Ten specimens.

REVISED DIAGNOSIS. — Dictyosporous conidia, strongly flattened in one plane, variable in shape, but mature specimens mostly fan-shaped, sometimes lobed. Conidia composed of two layers of smooth-walled muriform cells radiating from a single cell at the point of attachment of conidiophore. Cells of conidium usually isodiametric, sometimes rectangular, with cell walls straight or rounded.

DESCRIPTION

Dictyosporous conidia, strongly flattened in one plane, variable in shape but mature specimens mostly fan-shaped (Fig. 1A-C), sometimes lobed, 62-146 µm long and 52-106 µm wide. Conidia composed of two layers of smooth-walled muriform cells (Fig. 1E), radiating from a single cell at the point of attachment of conidiophore (Fig. 1A-D). Cells of conidium usually isodiametric, sometimes rectangular, 5-10 µm in size. Cell walls straight or rounded.

DISCUSSION

RECONSIDERATION OF FOSSIL *KUTCHIATHYRITES ECCENTRICUS*
Dictyosporous fungal conidia above described have rather unique morphology, and they are the same as fungal remains described first by Kar (1979) from the Oligocene deposits of Kutch, western India, as new fossil-genus *Kutchiathyrites* R.K. Kar, 1979, represented by the fossil-species *Kutchiathyrites eccentricus* R.K. Kar, 1979. These remains were considered by Kar (op. cit.) as “Microthyriaceous ascostromata” and compared with the microthyriaceous fossil fungal genera *Notothyrites* Cookson, 1947 (synonym of *Trichothyrites* Rosend., 1943), *Paramicrothallites* K.P. Jain & R.C. Gupta, 1979, *Parmathyrites* K.P. Jain & R.C. Gupta, 1970, and *Phragmothyrtes* W.N. Edwards, 1922. However, these genera in the opinion of Kar (1979) show significant differences in morphology from *Kutchiathyrites eccentricus*. Then, Jain & Kar (1979) compared fossil *Kutchiathyrites eccentricus* with modern fungal species with “eccentric ascostromata” as *Mycoenterolobium platysporum*, *Arbuscula eugeniae* [now *Neoarbuscula eugeniae* (Bat. & Peres) B. Sutton, 1983],

and *Tretopileus sphaerophorus*. Jain & Kar (1979) noticed that “in *Mycoenterolobium platysporum*, the ascostromata is like a fish scale as in *Kutchiathyrites* and also possesses similar pseudoparenchymatous cells”. Indeed, *Kutchiathyrites eccentricus* seems much the same as modern *Mycoenterolobium platysporum* and thus should not be considered as microthyriaceous sporocarp (Kalgutkar & Jansonius 2000; Berbee *et al.* 2015). No researcher, however, so far decided to revise *Kutchiathyrites eccentricus* as fossil species of the modern genus *Mycoenterolobium*. Considering the close similarity between *Kutchiathyrites eccentricus* and *Mycoenterolobium platysporum*, we compared modern *Mycoenterolobium platysporum* from various localities around the world with known fossil records of *Kutchiathyrites eccentricus*. It is clear that there are no significant morphological differences between *Kutchiathyrites eccentricus* and *Mycoenterolobium platysporum*. The observed variability in specimens shape depends mostly on the stage of conidial development. Cell shape and arrangement of both taxa seem identical; the only found differences are at least somewhat greater dimensions of the fossil *Kutchiathyrites eccentricus* compared to conidium of modern *Mycoenterolobium platysporum*. Thus, we decided to transfer *Kutchiathyrites eccentricus* to the modern genus *Mycoenterolobium*, and to make a new combination *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. We are of the opinion that regardless of the significant similarity of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. and *Mycoenterolobium platysporum* based only on the morphology of conidia, it is not possible to synonymize both taxa. No significant differences between specimens of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. from the Gray Fossil Site and the Bełchatów mine have been observed. These specimens differ mainly in size (Fig. 1A-D), but it cannot be excluded that *Mycoenterolobium* from Bełchatów (Fig. 1D) represents younger stages of conidia development compared to those from the Gray Fossil Site.

Fossil conidia of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb., by analogy with its modern counterpart *Mycoenterolobium platysporum*, are rather similar to the conidia of modern representatives of the anamorphic genus *Cancellidium* Tubaki, 1975 (Calabon *et al.* 2020). Conidia of *Mycoenterolobium* differ from those of *Cancellidium*, having rows of cells radiating in a fan-shaped pattern from a basal cell attached to the conidiophore (Fig. 1A-D). The *Cancellidium* cells are arranged in parallel, adherent rows, and conidia of *Cancellidium* contain chains of monilioid cells developing from the base (Seifert *et al.* 2011; Zhao *et al.* 2013). *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. also shows similarities to conidia of some modern representatives of helicosporeous anamorphic fungi from the genus *Xenosporium* Penz. & Sacc., 1902, and especially to *Xenosporium mirabile* Penz. & Sacc., 1902 (Zhao *et al.* 2007). *Mycoenterolobium* differs, however, from *Xenosporium mirabile* in lacking well-defined conidiophores and secondary conidia (Zhao *et al.* 2007), and also in cell arrangement of conidia. Conidia of other modern dictyosporous genera differ considerably from both the fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. and modern *Mycoenterolobium platysporum*.

OTHER FOSSIL-SPECIES OF *KUTCHIATHYRITES*

AND THEIR RELATIONSHIPS WITH *MYCOENTEROLOBIUM*

Besides *Kutchiathyrites eccentricus*, there were described four fossil-species of *Kutchiathyrites*, namely *K. canadensis* Kalgutkar & Janson., 2000, *K. mehrotrae* R.K. Saxena & S.K.M. Tripathi, 2011, *K. palmatus* (P. Ke & Z.Y. Shi) Kalgutkar & Janson., 2000, and *K. perfectus* (R. Kar, Mandaokar & R.K. Kar) R.K. Saxena & S.K.M. Tripathi, 2011. Two more fossil-species, *K. ramanujamii* (P. Kumar) Kalgutkar & Janson., 2000 and *K. singhii* R.K. Saxena & S.K.M. Tripathi, 2000, were mistakenly included in MycoBank (2022) as members of the fossil-genus *Kutchiathyrites*. *Kutchiathyrites canadensis* previously was reported as *Dictyosporites eccentricus* Kalgutkar, 1993 from the Paleogene deposits (Bonnet Plume Formation) from Peel River, Yukon Territory, Canada (Kalgutkar 1993), and later from the Paleogene of Axel Heiberg Island, Canada (Kalgutkar 1997). Then it was reconsidered as a representative of the fossil-genus *Kutchiathyrites* by Kalgutkar & Jansonius (2000). Kalgutkar & Jansonius (2000), however, did not point to any morphological features of this fossil that could indicate that *Dictyosporites eccentricus* should be included in the fossil-genus *Kutchiathyrites*. The classification of *Dictyosporites eccentricus* as a member of the fossil-genus *Kutchiathyrites* is questionable in our opinion. *Dictyosporites eccentricus* differs having some rows of cells that are longer than other contrary to muriform rows of cells of conidium of *Mycoenterolobium* which are proportionally of more or less equal length. *Dictyosporites eccentricus* can also represent other than *Kutchiathyrites* fungal genera having dictyosporous conidia. Thus, the taxonomic position of *Kutchiathyrites canadensis* seems still enigmatic, and we could not reconsider it as a fossil representative of the modern *Mycoenterolobium* genus.

Kutchiathyrites mehrotrae, originally described as *Kutchiathyrites* sp. (Singh *et al.* 1986), was then considered a new fossil-species of this fossil-genus by Saxena & Tripathi (2011). Original illustrations of *Kutchiathyrites* sp. “ascmata” (Singh *et al.* 1986: pl. 1, figs 11, 12) suggest that the specimen on pl. 1, fig. 11 could be related to the fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. (obovate conidium with similar row of cells) and the specimen on pl. 1, fig. 12, that differs considerably from the specimen on fig. 11, is somewhat similar to above discussed *Kutchiathyrites canadensis* (some rows of muriform cells are longer than those at the sides). Considering this, in our opinion *Kutchiathyrites mehrotrae* seems doubtful as a new fossil-species probably comprising two different species, and only specimen on pl. 1, fig. 11 could represent the *Mycoenterolobium* genus.

Kutchiathyrites palmatus, originally described as *Microthyriacites palmatus* P. Ke & Z.Y. Shi, 1978 from the Paleogene deposits from Shandong Province, China (Ke Shi 1978), was transferred to the fossil-genus *Kutchiathyrites* considering its similarity to *Kutchiathyrites eccentricus* (Kalgutkar & Jansonius 2000; Berbee *et al.* 2015). Indeed, the morphology of this fungal remain is similar to the fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. and modern *Mycoenterolobium platysporum*. However, the present authors did not see the original illustration of *Microthyriacites*

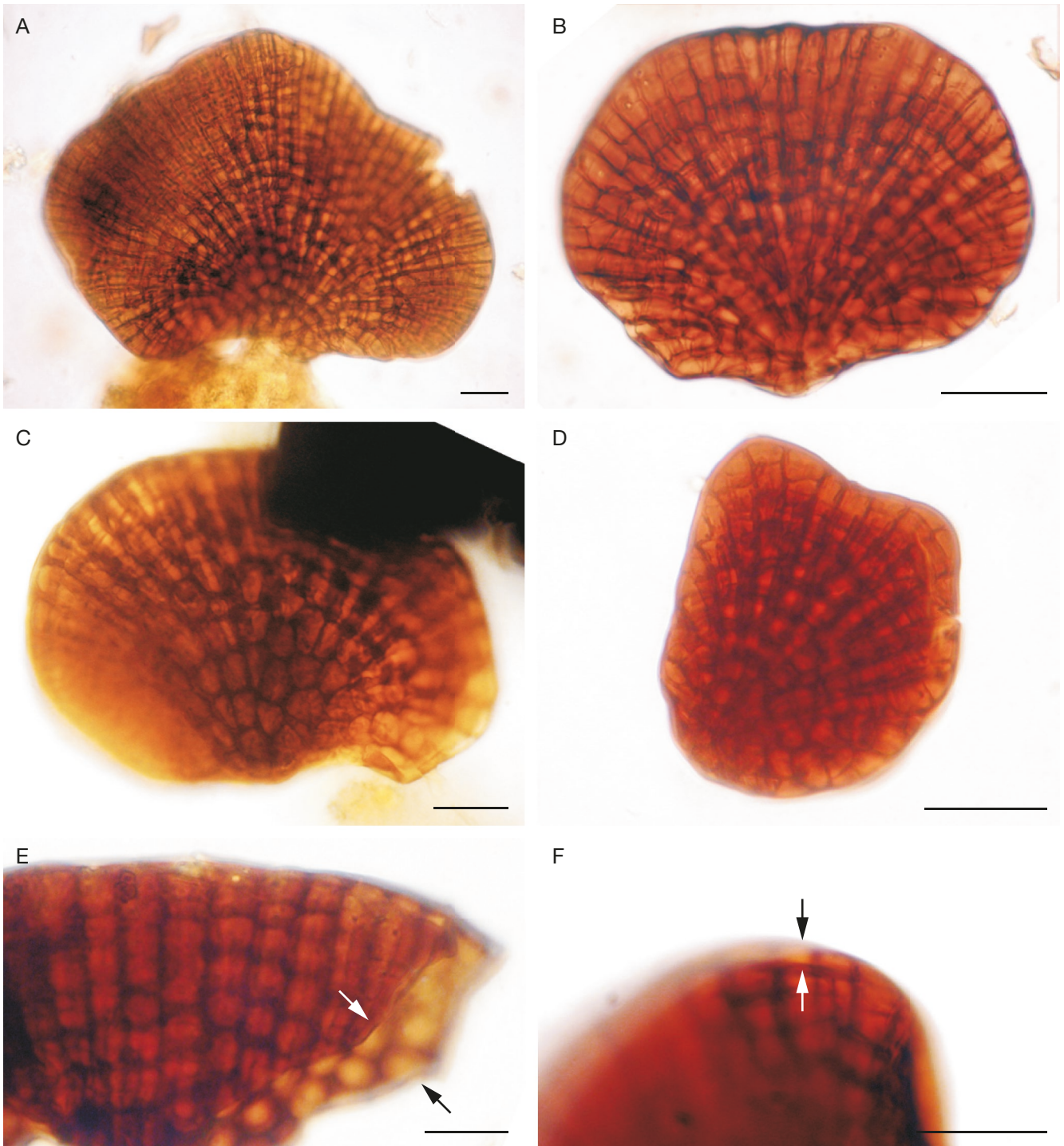


FIG. 1. — **A-F**, Fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb.: **A**, large conidium, slide Elephant Pit 12(2), Gray Fossil Site; **B**, conidium, slide Elephant Pit 12(6), Gray Fossil Site; **C**, conidium, slide Bear Pit 19(2), Gray Fossil Site; **D**, small conidium, slide KRAM-P 218/85(4), Belchatów Lignite Mine; **E**, broken fragment of conidium, **arrows** point at two layers of cells of conidium tightly attached together, slide Bear Pit 19(2), Gray Fossil Site; **F**, upper margin of the conidium, **arrows** point at two layers of cells of conidium forming double margin, slide Elephant Pit 12(6), Gray Fossil Site. Scale bars: 20 μ m.

palmatus. Description of this fossil points that dimensions of “ascmata” of *Microthyriacites palmatus* (50-70 μ m) are smaller than those of conidia of *Kutchiathyrites eccentricus* (64-110 \times 41-73 μ m) (Kalgutkar & Jansonius 2000; Berbee *et al.* 2015). Cells of *Microthyriacites palmatus* “ascmata” are also smaller than those of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. from North America and

Poland. Considering the above facts, *Kutchiathyrites palmatus* could probably belong to the fossil-genus *Kutchiathyrites*. The differences in the size of specimens and their cells shown above between *Kutchiathyrites palmatus* and *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb., in our opinion, allow only a conditional classification of *Kutchiathyrites palmatus* to the modern genus *Mycoenterolobium*.

Kutchiathyrites palmatus indeed differs from *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb., and both fossil-taxa should be treated as separate species. Kar *et al.* (2010) described a fungal remain from the Miocene of Mizoram, India, as the fossil-species *Dictyostromata perfecta* R. Kar, Mandaokar & R.K. Kar, 2010. Later, Saxena & Tripathi (2011) moved it to the fossil-genus *Kutchiathyrites*, as a new combination *Kutchiathyrites perfectus* (R. Kar, Mandaokar & R.K. Kar) R.K. Saxena & S.K.M. Tripathi, 2011. Nevertheless, the original illustration of *Dictyostromata perfecta* (Kar *et al.* 2010: pl. 2, fig. 6), and these authors' comments, raise doubts about the classification of *Dictyostromata perfecta* as a representative of the fossil-genus *Kutchiathyrites*. Kar *et al.* (2010) compared *Dictyostromata perfecta* with the modern hypomycetes genera *Mycoenterolobium*, *Tretopileus* B.O. Dodge, 1946, and *Trichodocheium* von Sydow, 1927 (the last genus name was wrongly cited by Kar *et al.* (2010) as *Trichodocheum*). They recognized that although modern *Mycoenterolobium platysporum* is closely related to *Dictyostromata perfecta*, it differs from *D. perfecta* by divergent lateral sides stromata and their fan-like shape. Indeed, the cell arrangement of the fungal body of *Kutchiathyrites perfectus* seems different from conidia of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. and modern *Mycoenterolobium platysporum*, which is usually similar to water flowing from a fountain. Considering all, the present authors question the classification of *Dictyostromata perfecta* as *Kutchiathyrites perfectus* and thus a representative of the modern *Mycoenterolobium* genus.

COMPARISON OF *MYCOENTEROLOBIUM ECCENTRICUM* (R.K. KAR) G. WOROBIEC, N. COMB. WITH LIVING REPRESENTATIVES OF *MYCOENTEROLOBIUM*

Based on results of phylogenetic analysis, modern *Mycoenterolobium* is referred to as Pleosporales *incertae sedis* (Calabon *et al.* 2020) and is represented by *Mycoenterolobium platysporum* and its varieties (*Mycoenterolobium platysporum* var. *platysporum* Goos, 1970 and *M. platysporum* var. *magnum* Mercado & J. Mena, 1986), *M. borivaliense* Rashmi Dubey, 2020, *M. flabelliforme* K.G. Karandikar, P.N. Singh & S.K. Singh, 2015, and *M. aquadictyosporium* M.S. Calabon, Boonmee, E.B.G. Jones & K.D. Hyde, 2020 (Dubey & Pandey 2020; Calabon *et al.* 2020; MycoBank 2022). *Mycoenterolobium aquadictyosporium* can be distinguished from *M. platysporum* in having shorter but wider conidia (Calabon *et al.* 2020). *Mycoenterolobium borivaliense*, contrary to *M. platysporum* poses a long conidiophore, and their conidia are much smaller than in *M. platysporum* (Dubey & Pandey 2020). Moreover, a close comparison of the morphology of conidia of *Mycoenterolobium borivaliense* (especially their cell morphology) with other modern species of *Mycoenterolobium* raises doubts about whether *M. borivaliense* really belongs to the *Mycoenterolobium* genus. *Mycoenterolobium flabelliforme* differs from *M. platysporum* in considerably smaller, fan-shaped conidia. As stated before, fossil *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. directly corresponds to *M. platysporum* and its varieties.

Relationships of the remaining modern *Mycoenterolobium* species and *Mycoenterolobium* fossils seem not so obvious as in the case of *M. platysporum* and *M. eccentricum* (R.K. Kar) G. Worobiec, n. comb. Some specimens of modern *Mycoenterolobium aquadictyosporium* (immature, elongated specimens, see Calabon *et al.* 2020: fig. 2h) show some similarity to the fossil *Kutchiathyrites canadensis*. For modern *Mycoenterolobium borivaliense* and *M. flabelliforme* no similar fossils could be identified.

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION OF *MYCOENTEROLOBIUM ECCENTRICUM* (R.K. KAR) G. WOROBIEC, N. COMB. AND RELATED MEMBERS OF THE FOSSIL-GENUS *KUTCHIATHYRITES*

Mycoenterolobium eccentricum (R.K. Kar) G. Worobiec, n. comb. (as *Kutchiathyrites eccentricus*) was reported from various localities in India ranging from Eocene to Holocene (Saxena & Tripathi 2011; Padmalal *et al.* 2014). Up till now, however, it has not been reported outside India, but in several publications, we have found pictures of the fossil fungal remains, which we have identified as undoubtedly representing *M. eccentricum* (R.K. Kar) G. Worobiec, n. comb. Besides our record from the Gray Fossil Site and the Bełchatów mine, *M. eccentricum* (R.K. Kar) G. Worobiec, n. comb. was identified in the Miocene deposits of Barreiras Group, Amazon region, North Brazil (as Fungo tipo B, Arai *et al.* 1988: pl. 3, fig. 14), Pliocene of Slovakia (as remains of Musci, Planderová 1972: fig. 1: 8), Holocene of the South Coastal Plain of Santa Catarina, Brazil (as Esporo indeterminado 1, Cancelli *et al.* 2012: fig. 2: 11), and Holocene to recent deposits from Saipan, Northern Mariana Islands (as *Phragmothyrites* sp., Jarzen & Dilcher 2009: fig. 3R). It is very probable that the fungal remains described as *Microthyriacites* sp. from the Eocene deposits of the Petrified Forest Member, King George Island, Antarctica (Song 1997: pl. 6, fig. 18), represents fossil *Mycoenterolobium*. Discussed fungal remains from Antarctica are almost identical to modern *M. flabelliforme*. In deposits of the another Eocene locality, Fossil Hill Formation, King George Island, Antarctica, Song (1998) found fungal remains interpreted as *Microthyriacites* sp. as well. The morphology of these fossils, however, is different from the fossil-genus *Microthyriacites* Cookson, 1947. One specimen (Song 1998: pl. 5, fig. 18) presumably could be assigned to *Mycoenterolobium* and the second specimen (Song 1998: pl. 5, fig. 18) is similar to *Kutchiathyrites canadensis*. Finally, *Kutchiathyrites palmatus*, probably closely related to *M. eccentricum* (R.K. Kar) G. Worobiec, n. comb. was reported from the Middle-Upper Eocene deposits of the Jarillal, Pauji, and Caus formations from the east coast of the Maracaibo Lake, Venezuela (Ramírez 2004). Thus, the present findings of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. from the United States and Poland document the first fossil record of this fungus from Northern America and Europe, and the presence of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. in Poland represents the northernmost known occurrence of both the fossil and modern *Mycoenterolobium* genus.

GEOGRAPHICAL RANGE AND ECOLOGY OF MODERN *MYCOENTEROLOBIUM*

Mycoenterolobium platysporum is a saprophytic fungus occurring on decaying wood or leaves both in the aquatic, mostly freshwater (exceptionally brackish) environment and in terrestrial localities. It prefers tropical to subtropical, usually humid climate, exceptionally it is reported from warm temperate climate localities. Modern distribution of *Mycoenterolobium platysporum* includes Africa (Republic of Côte d'Ivoire), Asia (China, Japan, Thailand), North and Central America (Cuba, Mexico, United States), Polynesia (Hawaii), and South America (Brasil) (Goos 1970; Kilbertus *et al.* 1980; Chamuris *et al.* 1985; Nakagiri 1993; Heredia-Abarca & Mercado-Sierra 1998; Arias Mota *et al.* 2008; Wang *et al.* 2008; Tianyu 2009; Leão-Ferreira *et al.* 2009; Wang 2010; Mena-Portales & Delgado-Rodríguez 2017; Portales *et al.* 2020; Farr & Rossman 2022). Other species of the *Mycoenterolobium* genus have a rather limited range. *Mycoenterolobium aquadictyosporium* was reported from decaying wood found in the tropical aquatic environment in Thailand (Calabon *et al.* 2020). *Mycoenterolobium borivaliense* and *M. flabelliforme* were found only in India on decaying wood in the tropical, terrestrial environment (Karandikar *et al.* 2015; Dubey & Pandey 2020). The only known modern record of *Mycoenterolobium* from Europe concerns five localities from the Mediterranean evergreen forest in Tuscany, Italy (Zucconi *et al.* 1997). Conidia of *Mycoenterolobium* sp. were found abundantly on decaying leaf litter in a warm, Mediterranean climate. From the above facts, it is possible to conclude that modern representatives of *Mycoenterolobium* prefer tropical, subtropical to Mediterranean, usually humid climates, and are associated with decaying plant debris (mainly wood).

Modern *Mycoenterolobium* found both in aquatic and terrestrial localities were classified as aero-aquatic hyphomycetes (Goh & Hyde 1996). These mitosporic fungi are usually found in small and shallow water reservoirs with stagnant slow-running water like ponds or ditches as saprophytes on submerged leaves or woody substrates. They sporulate only when the substrate is exposed to air in a moist interface between air and water. It could happen when previously submerged substrate, like leaves or twigs, become exposed to air at a reservoir margin when the water dries up, for example, during the hot summer months (Dix & Webster 1995; Goh & Hyde 1996; Webster & Weber 2007; Markovskaja 2012). Calabon *et al.* (2022) considered *Mycoenterolobium aquadictyosporium* and *M. platysporum* as freshwater Dothideomycetes.

PALAEOECOLOGY OF *MYCOENTEROLOBIUM ECCENTRICUM* (R.K. KAR) G. WOROBIEC, N. COMB.

Similarly to modern representatives of *Mycoenterolobium*, the fossil findings of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. from the Gray Fossil Site, United States and the Bełchatów Lignite Mine, Poland are associated with freshwater, aquatic or swampy palaeoenvironment and suggest its lignicolous habitat (Ochoa *et al.* 2012; Worobiec *et al.* 2013, 2018; Worobiec & Szyrkiewicz 2016; Worobiec &

Worobiec 2016, 2017, 2019). Palynological analysis at the Gray Fossil Site revealed moderately diversified palynoflora with domination of angiosperm pollen, mainly *Quercus* Linnaeus, 1753 and *Carya* Nuttall, 1818. These trees were the main components of oak-hickory forest with a small admixture of other plants, such as *Ulmus* Linnaeus, 1753, *Juglans* Linnaeus, 1753, *Pinus* Linnaeus, 1753, and *Vitis* Linnaeus, 1753, and with vines and shrubs existing in a warm temperate to subtropical climate (Liu & Jacques 2010; Gong *et al.* 2010; Ochoa *et al.* 2012; Worobiec *et al.* 2013). The presence of epiphyllous fungal sporocarps in palynological samples from all the pits of the Gray Fossil Site (Worobiec *et al.* 2018) and the palaeoclimatic reconstruction of the fossil flora (Liu & Zavada 2009) point to high (over 1000 mm) mean annual precipitation at that time.

Mycoenterolobium eccentricum (R.K. Kar) G. Worobiec, n. comb. from the plant assemblage KRAM-P 218 from the Bełchatów Lignite Mine was accompanied by numerous plant macroremains of riparian vegetation of bottomland hardwood forest. Palynological spectra revealed the dominant role of wetland, mainly riparian vegetation, at the time of sedimentation. The riparian forests were probably composed of *Carya*, *Pterocarya* Kunth, 1824, *Celtis* Linnaeus, 1753, and *Ulmus*, accompanied by *Alnus* Miller, 1754, *Acer* Linnaeus, 1753, *Fraxinus* Linnaeus, 1753, *Juglans*, *Liquidambar* Linnaeus, 1753, *Vitis*, *Zelkova* Spach, 1841, and *Salix* Linnaeus, 1753. *Fagus* Linnaeus, 1753, *Quercus*, *Carpinus* Linnaeus, 1753, *Eucommia* D. Oliver, 1890, *Corylus* Linnaeus, 1753, Tilioideae, and conifers, as well as some thermophilous taxa (*Castanea* Miller, 1754, *Symplocos* Jacquin, 1760, *Reevesia* Lindley, 1827, Mastixiaceae, *Tricolporopollenites pseudocingulum* (Potonié, 1931) Thomson and Pflug, 1953) represent mixed mesophytic forest components. *Taxodium* Richard, 1810, *Nyssa* Linnaeus, 1753, *Glyptostrobus* Endlicher, 1847, and *Alnus* composed swamp communities (swamp forests and bush swamps) along with representatives of Ericaceae, Cyrtellaceae, Clethraceae as well as *Myrica* Linnaeus, 1753, and presumably *Ilex* Linnaeus, 1753. The floristic composition of the palaeovegetation of the plant assemblage KRAM-P 218 points to a warm and moderately wet temperate climate with mild winters, comparable to the Cfa climate type in the Köppen-Geiger climate classification with a presumable mean annual temperature of 13.5–16.5°C (Worobiec & Szyrkiewicz 2016; Worobiec & Worobiec 2016). These climatic inferences are consistent with the results of the analysis of fungal remains that accompanied plant remains in the locality KRAM-P 218 (Worobiec & Worobiec 2017). Plant macroremains of the assemblage KRAM-P 226 from the Bełchatów Lignite Mine suggest the dominance of mesophytic vegetation; only a few taxa are typical for azonal, riparian, and swamp forests. Remains of aquatic vegetation were completely absent there, suggesting that the freshwater sedimentary reservoir formed the plant assemblage KRAM-P 226 was shallow and/or only periodically existed (e.g. after flooding). Plant taxa of this assemblage, along with remains of epiphyllous, microthyriaceous fungi indicate warm palaeoclimate with mild winters (Worobiec 2014).

From the above data, we may conclude that palaeoenvironmental factors inferred from palaeobotanical investigations of both the Gray Fossil Site, United States, and the Bełchatów Lignite Mine, Poland, suggest a warm temperate to subtropical and humid climate associated with *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. in Late Miocene to Early Pliocene of North America and Central Europe. It is in accordance with other fossil records of *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. (see above), where this taxon was associated with subtropical to tropical palaeovegetation. The same concerns the distribution of the modern species of *Mycoenterolobium* which prefers tropical, subtropical to Mediterranean, usually humid climate.

Similarly to the living species of *Mycoenterolobium* classified as aero-aquatic hyphomycetes (Goh & Hyde 1996), *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. found in the Gray Fossil Site and the Bełchatów Lignite Mine suggests the presence of small, shallow water bodies with accumulated plant debris (decaying leaves, wood, and bark) and with fluctuating water level or even presence of periodic reservoirs existing only in the wet season or after floods. It is especially true in the case of the locality KRAM-P 226 from the Bełchatów mine.

CONCLUSION

Considering all the above discussion, we may conclude that modern and fossil species of *Mycoenterolobium* prefer warm (tropical to warm temperate), usually humid climates, and lignicolous habitats associated with freshwater, aquatic or swampy environments. Thus, these investigations may be informative for mycologists, palaeobotanists, and geologists as *Mycoenterolobium eccentricum* (R.K. Kar) G. Worobiec, n. comb. could be considered as a non-pollen palynomorph proxy for the reconstruction of palaeoenvironment, and palaeoclimate, and could be used for the calibration of the divergence time estimations in the phylogenetic trees of fungi.

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