

Accepted Manuscript

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PII: S0034-6667(16)30026-4
DOI: doi: [10.1016/j.revpalbo.2016.09.010](https://doi.org/10.1016/j.revpalbo.2016.09.010)
Reference: PALBO 3797

To appear in: *Review of Palaeobotany and Palynology*

Received date: 1 March 2016
Revised date: 21 September 2016
Accepted date: 23 September 2016



Please cite this article as: Hawksworth, David L., van Geel, Bas, Wiltshire, Patricia E.J., The enigma of the *Diporothea* palynomorph, *Review of Palaeobotany and Palynology* (2016), doi: [10.1016/j.revpalbo.2016.09.010](https://doi.org/10.1016/j.revpalbo.2016.09.010)

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RH: The *Diporothea* palynomorph

The enigma of the *Diporothea* palynomorph

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Abstract: In the Quaternary palynological literature, the name *Diporothea rhizophila* has come to be applied for fungal spores labelled in the Hugo de Vries-Laboratory (HdV) in Amsterdam (The Netherlands) as Type HdV-143. The widespread occurrence of this taxon in palynological preparations was difficult to understand as the species is definitely known only from *Solanum* species in Washington State in the USA.

Comparison of spores found in palaeoecological and forensic samples with those of the original material (holotype) of *D. rhizophila* established that the name had been misapplied. Type HdV-143 is distinguished from the holotype by the shape, size, and ornamentation of the ascospores. The spores in the palaeoecological material are navicular to fusiform, and not oval when mature. They develop robust, dark brown, anastomosed ridges from an early stage, and are much longer, measuring 44–59 μm and not 25–37 μm in length. Similarities in spore structure and development indicate that both can be accommodated in the same genus, but as different species. The specimens from palynological preparations are described here as *D. webbiae* sp. nov. Circumstantial evidence, gained from palaeoecological analysis, suggests that the new species may be associated with the fern genus *Thelypteris*, and today occurs most commonly in wet *Alnus* carr. Similar spores have been reported from the pre-Quaternary fossil record under the generic name *Striadiporites*.

Keywords: *Diporotheca webbiae*, fossil fungi, *Meliolales*, palaeoecology, *Striadiporites*, *Thelypteris*.

1. Introduction

Large, broadly navicular, brown spores with subapical septa, a coarsely ridged ornamentation, and abruptly truncated porate ends, have been referred to as *Diporotheca rhizophila* in recent palynological literature (e.g. Hillbrand et al., 2012; Revelles et al., 2016) following Van Geel and Aptroot (2006). These distinctive spores

have been recognized in palaeoecological studies of soils and sediments in Africa, North America, and Europe. The deposits date from the Eemian (Ipswichian – Marine Isotope Stage 5e) interglacial period of 130,000–115,000 ya through to modern times, and they have also been encountered during archaeological (Van Geel et al., 2003; Revelles et al., 2016) and modern forensic (Wiltshire et al., 2014) investigations. The use of the species name *D. rhizophila* for this spore type, which for many years had been referred to as "Type-143" (Van der Wiel, 1982) or later "Type HdV-143" following the notation adopted in Haas (2010), was surprising as examination of the type material of *D. rhizophila* had not revealed similarly sized and ornamented spores (Mibey and Hawksworth, 1995).

This paper clarifies the identity of "Type HdV-143", a notation retained in the catalogue of Quaternary non-pollen palynomorphs by Miola (2012), and provides a name that can be used with confidence by mycologists, palaeoecologists, and palynologists.

2. Material and Methods

The name-bearing material of *Diporotheca rhizophila* (the holotype) was obtained on loan from the collections of the Department of Plant Pathology, Washington State University, Pullman, WA (WSP). The details on the specimen label were identical to those given for the holotype in the original publication (Gordon and Shaw, 1961: 332).

Three microscopic slide preparations and a suspension in glycerol of "Type HdV-143" were analyzed for the current study. These were all from sub-recent peat deposits from a nature reserve, De Suikerpot, near Hilversum, in The Netherlands, the site from which the material reported on by Van Geel et al. (1986) was obtained. The preparations were made in connection with the study of a masters degree student (Looze, 1989) and comprised three slides numbered: no. 165 = S239 [Suik. 30] "fruitbody with ascospores"; no. 1966 [Suik. 31] "fruitbody fragments with ascospores and *Glomus*, chlamydospores in the same slide"; and no 1967 = S240 [Suik. 31, 36, 37] "fruitbody-fragments with ascospores". These slides have now been deposited in the fungarium of the Royal Botanic Gardens Kew, K (M) as the name-bearing type of the newly described species (see below).

Specimens and microscopic preparations were studied using a Nikon zoom stereomicroscope (to x60), an Olympus BH-2 research microscope fitted with Nomarski differential interference contrast optics and a drawing tube (to x1500), and also with a Leica DM750 microscope with phase contrast optics (to x1000). Squash preparations from the holotype of *D. rhizophila* were mounted in both water and lactofuchsin, and measurements made in those mountants. The mounting medium of the slides of Type HdV-143 was Gummisyrup Apathy. Photomicrographs were digitally captured with Leica Application Suite software and MultiFocus Montage image capture.

3. Results

Diporotheca rhizophila C.C.Gordon et C.G. Shaw

(Figs 1–2)

Original description: Gordon and Shaw (1961: 331).

Type: USA: Washington State: Benton County, Prosser, Irrigation Experiment Station, on roots of *Solanum melongena* [egg plant or aubergine], 15 Sept. 1958, coll. C.C. Gordon (WSP 48900 – holotype).

The microscopic details found in our re-examination of the type material conformed to those provided in the original accounts of the species by Gordon and Shaw (1961, 1964) and Gordon et al. (1961). The spores were oval in shape, with a subapical septum at each end, often with a conspicuous central guttule, enclosed in a perispore which sometimes tended to become separated, and generally smooth, but occasionally the sheath became wrinkled and delicately reticulate (Fig. 2D–E). We found the overall measurements to be: (25-)28-30-35(-37) x (14.5-)17-18-19(-20) μm , and the l/b (length/breadth) ratio 1.34-1.67-2.09 ($n = 30$). The measurements originally given by Gordon and Shaw (1961) were 30–35 x 16–20 μm .

The spores in the material of Type HdV-143 had a similar structure to that seen in the type material of *Diporotheca rhizophila*, being dark brown, with subapical septa, and a sheath, but differed in several respects. The length of the smallest spores found exceeded that of the largest in *D. rhizophila*, the spores were elongate-ellipsoid to broadly navicular to fusiform when mature with abruptly truncated rather than

rounded ends. The difference in shape is reflected in the mean length/breadth ratios of 2.32 vs. 1.67. In addition, the perispore in HdV-143 is also rather smooth at first (Fig. 3A), but soon develops coarse raised anastomosed ridges, but no delicate reticulation such as that observed in young spores of *D. rhizophila* was seen. These observations agree with the description and illustrations provided in Van Geel et al. (1986). Gordon and Shaw also described *D. rhizophila* as having elongated perithecial necks, supported by basal "hyphal struts", but these were not seen in the fragmented perithecia of Type HdV-143.

As spore Type HdV-143 is clearly distinguished from *Diporotheca rhizophila* in the length, shape, and ornamentation of the spores, we recognize this as a separate species of *Diporotheca* here.

Diporotheca webbiae D. Hawksworth., B. van Geel et P. Wiltshire, *sp.nov.*

Registration number: MycoBank MB818181

(Figs 3–4)

Etymology: Named in honour of Judith A. Webb, co-author of the often used guide to pollen identification (Moore et al., 1991) who also first discovered the spores of this fungus in forensic samples.

Diagnosis: Distinguished from *Diporotheca rhizophila* by the ascospores which, at maturity, are navicular to fusiform with truncated ends, have robust dark brown

anastomosed ridges on the perispore from an early stage, and measure (44-)48-53-57(-59) x (17.5-)21-23-27(-29) μm , l/b ratio 1.49-2.32-3.73.

Type: The Netherlands: Hilversum, De Suikerpot, in subrecent peat deposits mainly formed by *Thelypteris palustris*, 1982, coll. G.A.M. Looze [Slides nos 165–167] (K(M) 206632 – holotype).

Description: Ascomata superficial, brown to black, ovoid, perithecioid, ca. 180–300 μm in diameter (*vide* Van Geel et al., 1986); exciple pseudoparenchymatous, brown, cells polyhedral, forming a *textura angularis* but not strongly compressed, exciple surface uneven, some protruding wart-like for 15–20 μm (*vide* Van Geel et al., 1986), individual cells variable in size, 7–25 μm in diameter, cell walls 2.5–3.5 μm thick, walls smooth. *Mycelium* of two types; flexuous pale brown and thin-walled hyphae 2–2.5(-3) μm wide, apparently originating from basal tissues of the ascomata; flexuose but more rigid darker brown hyphae (the colour of the excipular cells), thick-walled, and 6–8 μm wide; appressoria not seen. *Interascal tissues* not seen. *Asci* not seen. *Ascospores* brown, broadly navicular, abruptly truncated at the apices, apices mainly 6–7 μm in diameter, each with a germ pore ca. 3 μm , 2-septate, each septum subapical, the apical cells paler when young, with a well-developed perispore, smooth at first, becoming folded and raised, at maturity appearing as a network of coarse raised anastomosed dark brown ridges, ridges mainly 2–3 μm wide, overall (44-)48-53-57(-59) x (17.5-)21-23-27(-29) μm , l/b ratio 1.49-2.32-3.73 ($n = 30$).

Occurrence: In mosses, soils, sediments and peat deposits; modern and subfossil; sometimes associated with wood remains or with the fern *Thelypteris palustris*.

Frequent in modern surface litter samples of wet *Alnus* carrs in Germany (Prager et al., 2006). Considered as an indicator of meso- to eutrophic conditions (Van Geel et al., 1986), but currently regarded as of limited value for ecological interpretation (Barthelmes et al., 2006).

Distribution: Africa (Kenya, Tanzania, Uganda), Europe (e.g., Austria, France, Germany, Italy, The Netherlands, Spain, Switzerland, and the UK), and North America (Canada and USA, Idaho and eastern US).

Comments: A comprehensive description of the species, and confirmation of the systematic position of both the new species and of *Diporotheca rhizophila*, must await the discovery of fresh material and sequencing. The placement in *Meliolales* has to be regarded as tentative in the absence of the superficial hyphae with enteroblastic conidiogenous cells ("mucronate hyphopodia") expected in the order; their absence and the lack of interascal tissues (lateral paraphyses) were the primary reasons for placement of the genus in a separate family from *Meliolaceae*, *Diporothecaceae* (Mibey and Hawksworth, 1995). We wish to stimulate field mycologists to search for fresh material of *D. rhizophila* and *D. webbiae* in order to clarify the positions of these two fungi. *D. webbiae* should be sought particularly in *Alnus* carr, and in association with the rhizoids of *Thelypteris palustris*.

The sizes of spores are not given in all published reports, and in some cases these are at or below the lower limit of the range of sizes measured in the holotype (Table 1). It is unclear whether these specimens are part of the natural range of the species, represent changes over time in the fossil record, due to different preparatory procedures, or if one or more additional species await formal recognition. This issue can only be clarified through the examination of additional material as it becomes available.

The three slides curated as a single collection in the fungarium at the Royal Botanic Gardens Kew (K (M)) are acceptable as an holotype as they come from the same sample; a type can consist of "multiple small organisms" (Art. 8.2) and also "more than one preparation, so long as the parts are clearly labelled as being part of the same specimen" (Art. 8.3; McNeill et al., 2012). A proposal to clarify this matter in the *Code*, making clear that different numbers, such as field numbers, constitute parts of a single gathering provided they were obtained on the same date from the same place has now been made (Sennikov, 2015).

4. Discussion

The generic name *Diporotheca* was introduced by Gordon and Shaw (1960) for a meliolaceous fungus, named *D. rhizophila*, found on the roots of *Solanum melongena*, *S. nigrum*, and *S. tuberosum* in the Irrigation Experimental Station in Prosser, Benton County, in Washington State. The infection process was

subsequently described in detail, and the pathogenicity tested against 56 *Solanum* species, of which 54 were susceptible (Gordon et al., 1961); no other genera were infected. These authors went on to document the ontogeny of the ascomata in considerable detail (Gordon and Shaw, 1964). The fungus remains only listed from Washington State in Farr *et al.* (1989). The genus was moved from the family *Meliolaceae* to the new family *Diporotheceae* by Mibey and Hawksworth (1995) on the basis of the persistent perispore, lack of mucronate hyphopodia, and absence of interascal tissues. The systematic position has, however, yet to be confirmed by molecular phylogenetic methods.

The generic name entered the palynological literature when it was used by Van Geel et al. (1986) for spores found in Upper Eemian lake deposits in The Netherlands. These spores conform to those named *Diporotheca webbiae* here, and measured 47–57 x 17–25 µm. They had previously been referred to as "Type 143" by Van der Wiel (1982), and were also found in the Somerset Levels in the U.K. (Van Geel et al., 1986). Ascomata with ascospores found in *Thelypteris*-peat deposits in "De Suikerpot", The Netherlands, were examined by mycologists J.A. von Arx and H.A. van der Aa, who suggested the genus *Diporotheca*, but were definite "that they do not belong to the common root-parasitizing species *D. rhizophila* which has smaller spores" (Van Geel et al., 1986). Despite this difference, the name *D. rhizophila* was, however, adopted by Van Geel and Aptroot (2006) for "Type 143", and that species name has come to be used by other researchers (e.g. Hillbrand et al., 2012; Revelles et al., 2016) for *D. webbiae*.

The only other fungus ever to be named in *Diporotheca* is *D. litseae* M.S. Patil 1989 (Hosagoudar et al., 1989), is a meliolaceous fungus described from the underside of leaves of *Litsea* sp. in India, with a superficial mycelium with mucronate hyphopodia, spores that are at first simple, later developing a septum near each apex, but can also have 1–2 additional septa, and are smooth-walled, with just a thin "gelatinous sheath", no conspicuous perispore, and measure 40–50 x 15.5–18.5 μm ; the name is now treated as a synonym of *Basavamyces patilii* Hosagoudar 2008 (Hosagoudar, 2008).

Some pre-Quaternary spores, which are somewhat similar from the Oligocene/Miocene boundary (ca. 23 Ma) in India, were described as a new genus and species, *Striadiporites reticulatus* C.P. Varma et Rawat 1963 (Varma and Rawat, 1963). While the spores were similarly reticulate, however, they were oval and not navicular, 46 x 29 μm , and no subapical septa could be seen in the published photographs. Two additional spore types from the Paleocene/Eocene (ca. 56 Ma) of northern Canada with shapes more similar to those of *Diporotheca webbiae* were referred to *Striadiporites* by Norris (1997): *S. bistratus* (P. Ke et Z.Y. Shi ex S.Z. Sung et al.) G. Norris 1986 (spores 40–49 x 21–24 μm) and *S. anceps* G. Norris 1997 (spores 37–46 x 20–26 μm) differing from each other in the shapes of the apices. In neither of those species, however, were subapical septa evident in the published photographs; it is possible that subapical septa were originally present but had not survived decomposition processes and (or) specimen preparation. Taylor et al. (2015) comment that somewhat similar ornamentation is known from some species of the

extant, primarily tropical, discomycete genus *Cookeina*. Ascospores in *Cookeina*, however, are almost colourless, lack any rigid sheath, lack septa, and when ornamented have much more delicate reticulate nets, as shown in scanning electron micrographs (Weinstein et al., 2002).

Fifteen fossil fungal species are listed in *Striadiporites* (Index Fungorum 2016).

Kalgutkar and Jansonius (2000) illustrated examples of 13 species of that fungal genus. None of the spore drawings shows any subapical septa, or the elongate anastomosing, robust ridges of *Diporotheca webbiae*. Subapical septa are, however, illustrated in *Striadiporites sanctaebartolomaeae*, and Sherwood-Pike (1988) referred to an undescribed species in that genus found in early Miocene sediments (ca. 15–20 Ma) in northern Idaho. The illustrations of *S. sanctaebartolomaeae* evidently represented the *Diporotheca* described here, while the undescribed one had much less ridged ascospores, although smooth and ridged spores can occur in the same ascoma of *D. webbiae* (Van Geel et al., 1986). Spore measurements were not provided in the text, but the scales on Sherwood-Pike's illustrations indicated that they were about 38 μm long in the spore named as *S. sanctaebartolomaeae* Elsik et Jansonius 1974, and 33–33.5 μm long in the unnamed species. It seems possible, however, that the name *S. sanctaebartolomaeae* was misapplied by Sherwood-Pike (1988) as the spore illustrated in Kalgutkar and Jansonius (2000) is oval, lacks subapical septa, and has a more regular net-like ornamentation. These reports suggest that *D. webbiae*-like fungi have an ancient origin and that some *Striadiporites* species could be congeneric with

Diporothea. If the two genera were united, *Diporothea* would be the name to be used as it was published two years earlier than *Striadiporites*;

we do not make any name changes for those here as we have not examined the pertinent type materials.

Hillbrand et al. (2012) discuss the palynological evidence for the ecology of the new species, under the name *Diporothea rhizophila*. They did not find a correlation with *Solanum* pollen, but noted that several seeds of *S. dulcamara* and *S. nigrum* had been found in other Neolithic deposits in the region, and concluded that the spores may have value as a palaeoecological indicator of major soil disturbance and erosion. A correlation between *Alnus* macrofossils (seeds and catkin scales), but not pollen was found, but they also noted that the fern *Thelypteris palustris* was present and supported the view that wetland plants such as that could be hosts for the fungus. This fern was first suggested as a candidate host plant by Van Geel et al. (1986), and it is characteristic of wet *Alnus* carr where *Diporothea* spores occur in modern litter samples (Barthelmes et al., 2006). The pollen diagram published by De Klerk (2016) from North-East Germany had some of the highest levels of *Diporothea* spores reported with over 300 at some levels in the profile; the maxima occurred, however, when *Alnus* pollen values were low, there was no consistent correlation with *Thelypteris* spore numbers, and no *Solanum* pollen was reported. The discovery of ascomata attached to the parts of freshly collected plants is needed to clarify the ecology of *D. webbiae*. This case recalls that of another large-spored ascomycete,

Caryospora callicarpa, whose spores have been found in palynological preparations from archaeological and forensic samples, but which has not been collected in the field since 1865 (Hawksworth *et al.*, 2010).

Acknowledgements

We are indebted to Jack D. Rogers (Washington State University) for the loan of the type material of *Diporotheca rhizophila*. In addition, Paul F. Cannon, Ove E. Eriksson, Kevin D. Hyde, Keith A. Seifert, and James A. Trappe are all thanked for commenting on photographs of the enigmatic spore. We also appreciated the helpful remarks of Editor Hans Kerp and Jean N. Haas which greatly improved the manuscript.

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[Legends to Figures and Table]

Fig. 1. *Diporotheca rhizophila* (WSP 48900 – holotype). A. Infected roots of *Solanum melongena*. B. Perithecia on root surface, note the ostioles (appearing as white dots on the black perithecia). Scale bar A : 1 cm, B: 0.2 mm.

Fig. 2. *Diporotheca rhizophila* (WSP 48900 – holotype). A–C. Mature smooth-walled ascospores; note the subapical septa and perispore sheath. D–E. Developing spores with a reticulately wrinkled perispore sheath. Scale bar: 10 μ m.

Fig. 3. *Diporotheca webbiae* (K(M) 206632 – holotype). A. Developing ascospore with smooth sheath. B. Developing ascospore with ridges developing on the perispore. C. Perispore sheath detached from an ascospore. D. Ascospores with a basal germ tube. Scale bars: 10 μ m.

Fig. 4. *Diporotheca webbiae* (K(M) 206632 – holotype). A–D. Mature ascospores; note the subapical septa and coarsely reticulately ridged perispore sheath. Scale bar: 10 μ m.

Table 1. Reported sizes of reticulately ornamented *Diporotheca* and *Striadisporites* palynomorphs.

* = subapical septa not seen.

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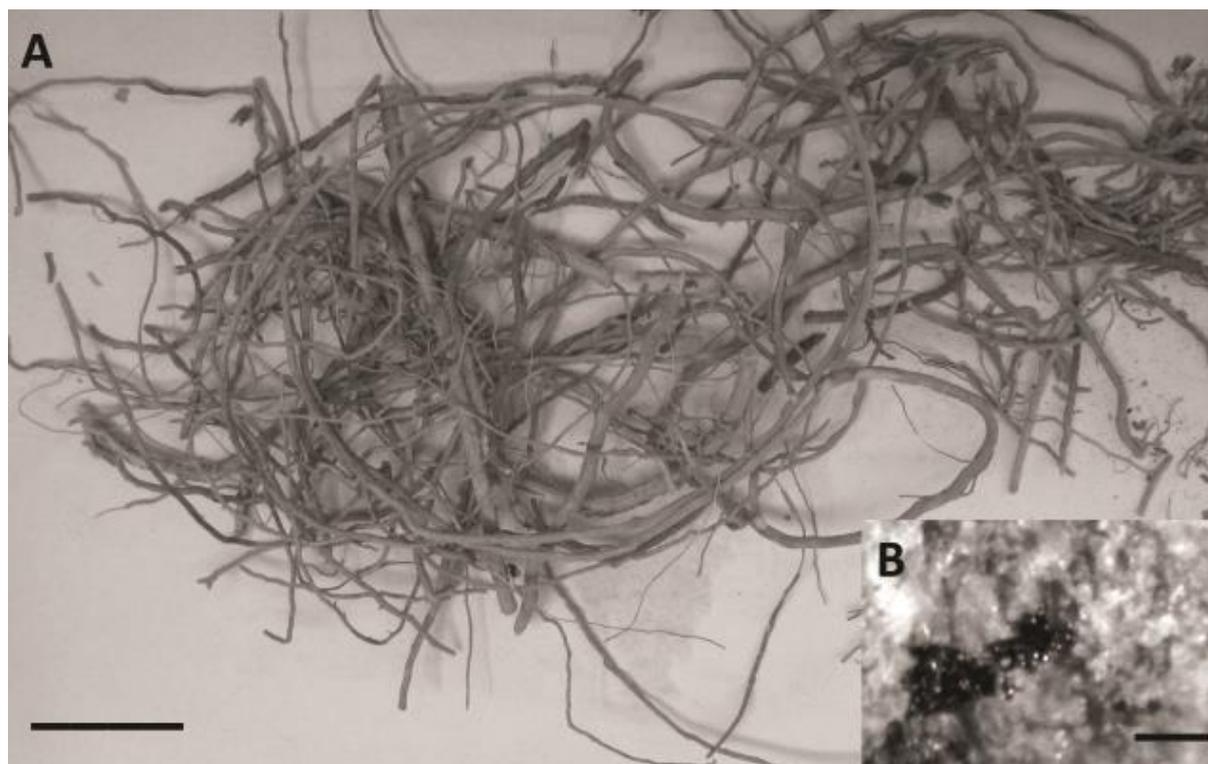


Fig. 1

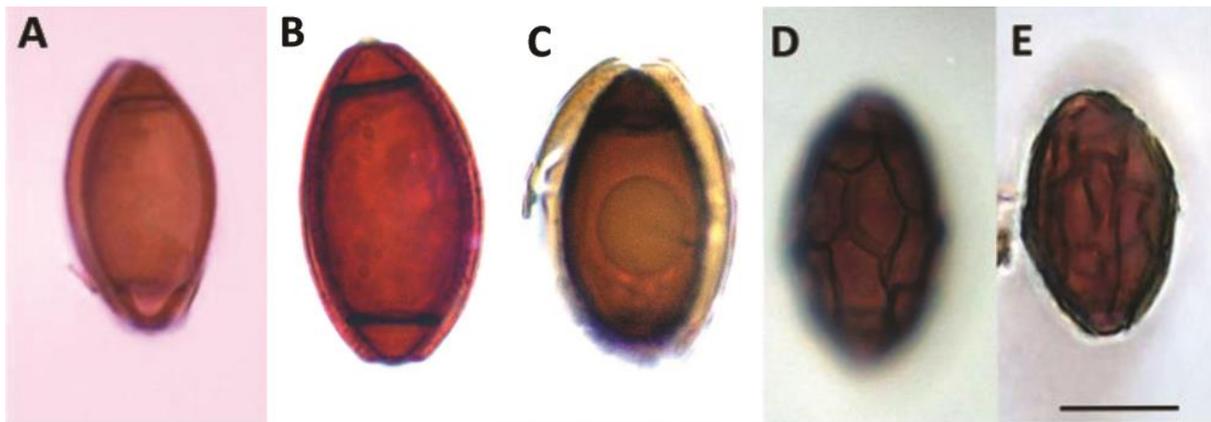


Fig. 2



Fig. 3



Fig. 4

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Table 1

Name used	Length	Breadth	Deposits	Country	Reference
<i>D. sp.</i>	47-57	17-25	Upper Eemian	The Netherlands	Van Geel et al. (1986)
<i>D. rhizophila</i>	47-52	17-25	Roman period	The Netherlands	Van Geel et al. (2003)
<i>D. sp.</i>	34-45 *	24-30	Modern	Uganda	Gelorini et al. (2011)
<i>D. sp.</i>	43	18	Modern	Uganda	Gelorini et al. (2011)
<i>D. sp.</i>	39-48	24-25	Modern	UK	Hawksworth (2009)
<i>S. anceps</i>	37-46	20-26	Paleocene/Eocene	Canada	Norris (1997)
<i>S. bistratus</i>	40-49	21-24	Paleocene/Eocene	Canada	Norris (1997)
<i>S. reticulatus</i>	46	29	Oligocene/Miocene	India	Varma & Rawat (1963)
<i>S. sanctaebarae</i>	ca. 38	?	Miocene	USA	Sherwood-Pike (1988)
<i>S. sp.</i>	ca. 33-33.5	?	Miocene	USA	Sherwood-Pike (1988)
<i>D. webbiae</i>	44-59	17.5-29	Upper Eemian	The Netherlands	Present work (holotype)



D. rhizophila



D. webbiae

Graphical abstract

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Highlights

- The identity of spore type Type HdV-143 is examined.
- Placement in the fungal genus *Diporotheca* is confirmed.
- Identification as *D. rhizophila*, associated with *Solanum*, is shown to be incorrect.
- The palynomorph is named as *D. webbiae* sp. nov. and may be associated with *Thelypteris*.
- Some of the fossil spores referred to *Striadiporites* may be congeneric.