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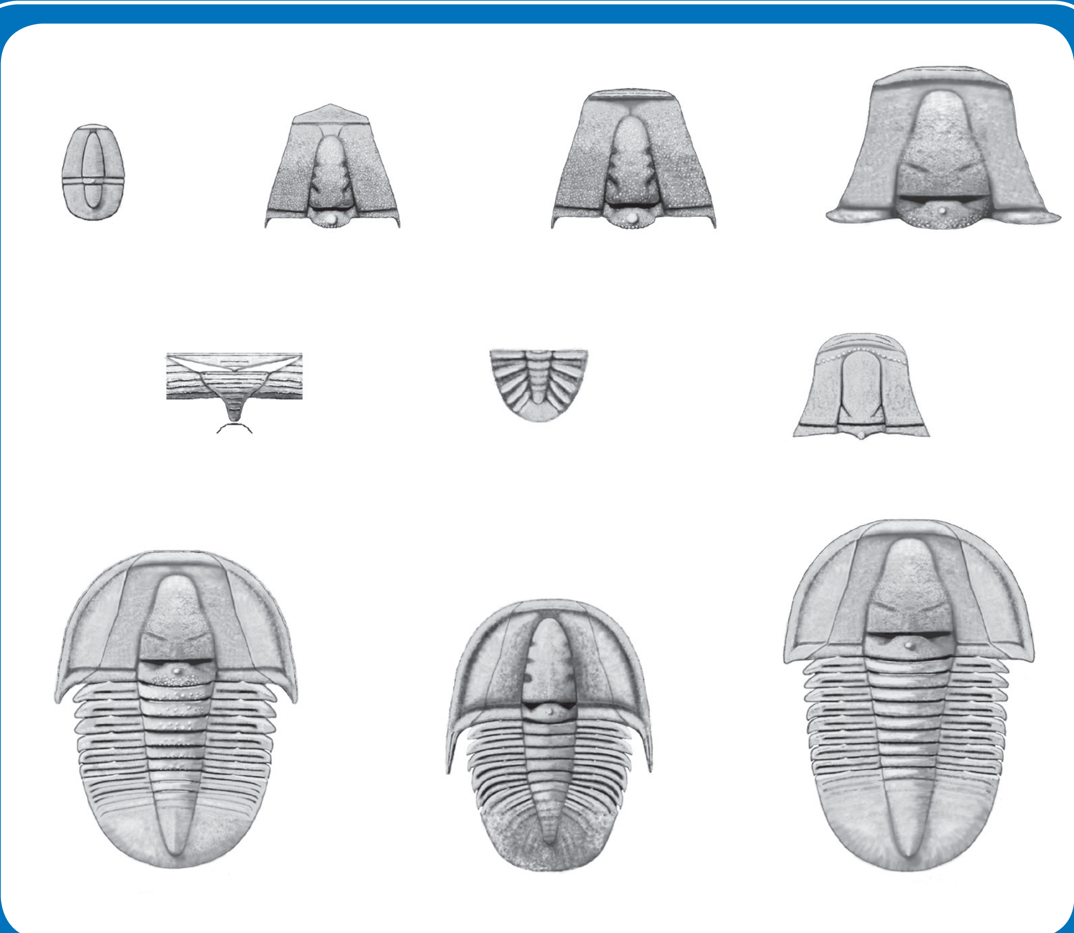

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Cover illustration: Tentative reconstructions of different taxa and ontogenetic stages in the trilobite genus *Drevermannia*, as well as of *Silesiops*? sp. For details, see Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, pp. 9–58 in this issue.
Back cover: Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbild: Rekonstruktionsversuche für verschiedene Taxa und ontogenetische Stadien der Trilobitengattung *Drevermannia* sowie für *Silesiops*? sp. Für weitere Informationen siehe Basse, M.: Revision und Ontogenie des Trilobiten *Drevermannia schmidti* Richter 1913 aus dem Oberdevon des Bergischen Landes, S. 9–58 in diesem Heft.
Rückseite: Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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Microfossils with possible affinities to the zygomycetous fungi in a Carboniferous cordaitalean ovule

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Abstract

A structurally preserved cordaitalean ovule from the Lower Pennsylvanian of Great Britain contains several specimens of a conspicuous spherical microfossil, which is characterized by a small, dome-shaped associated structure. Fused to the tip of this structure is a smaller, spherical to dome-shaped element. We interpret the microfossils as zygosporangium-gametangia complexes of a zygomycetous fungus based on morphological correspondences to the reproductive structures of certain extant Endogonaceae.
Key words: *Endogone* Link: Fr., fossil fungi, gametangium, Lower Coal Measures, zygosporangium

Kurzfassung

In einer strukturbietend erhaltenen Cordaiten-Samenanlage aus dem Unter-Pennsylvanium von Großbritannien wurden mehrere Exemplare eines auffälligen kugeligen Mikrofossils gefunden, dem eine kleine, kuppelförmige Struktur ansitzt, welche ihrerseits mit einer noch kleineren, kugel- oder kuppelförmigen Struktur verbunden ist. Auf Grund morphologischer Übereinstimmungen mit den Reproduktionsstrukturen einiger moderner Endogonaceae interpretieren wir diese Fossilien als Zygosporangium-Gametangien-Komplexe eines fossilen Zygomyzeten.
Schlüsselwörter: *Endogone* Link: Fr., fossile Pilze, Gametangium, Lower Coal Measures, Zygosporangium

1. Introduction

The coal balls from the Lower Coal Measures of Great Britain contain a diverse, structurally preserved Early Pennsylvanian (Carboniferous) flora that has been studied intensively for more than 100 years (for details, see Galtier 1997). In addition to plants, the coal balls also contain an abundance of microbial remains, principally Fungi and fungus-like life forms (e.g., Cash & Hick 1879; Williamson 1880, 1881, 1883; Ellis 1918), which contribute to our knowledge of the organisms that co-occur, and possibly interact, with the land plants in Early Pennsylvanian ecosystems. While a few of these fungal fossils exhibit distinctive morphological features that allow for assignment to one of the major lineages of fungi (Krings et al. 2010a, 2011; Strullu-Derrien et al. 2011), the systematic affinities of most remain elusive, due primarily to the lack of diagnostic characters. Microorganisms, including fungi, today are usually classified based on complements of structural and life history features, together with molecular and genetic data, that are difficult or even impossible to resolve with fossils. As a result, direct comparisons between fossil microorganisms and modern representatives are seldom feasible (Krings et al. 2010b). On the other hand, certain microfossils from the coal balls exhibit distinctive structural features, but still remain difficult to identify because they occur isolated, with no information available on the system in/on which they were produced.

This paper describes a conspicuous type of spherical microfossil characterized by paired associated structures that occurs within a structurally preserved *Mitrospermum*-type cordaitalean ovule. Based on structural correspondences to the zygosporangium-apposed gametangia complexes seen in certain modern Endogonaceae (zygomycetous fungi), we interpret these fossils as sexual reproductive structures of a Carboniferous zygomycete. The discovery provides new information on the diversity of microorganisms in the Carboniferous, and may contribute in refining ideas about the levels of biological complexity in ancient ecosystems.

2. Material and methods

The thin section containing the microfossils was prepared from a coal ball collected in the Lower Coal Measures of Great Britain. The coal ball comes from the Union Seam at Dulesgate (Lancashire), which is Westphalian A or Langsettian (Bashkirian/Lower Pennsylvanian) in age (Galtier 1997).

The thin section was prepared according to standard procedures in which a piece of the coal ball was cemented to a glass slide and subsequently ground with an appropriate abrasive until it was thin enough to be examined in transmitted light. The slide is deposited in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG) in Munich, Germany (acquisition number BSPG 1964 XX 145). The fossils were analyzed using transmitted light microscopy equipment; digital images were captured with a Leica DFC-480 camera.

3. Description

The platyspermic ovule containing the microfossils is approximately 6.5 mm long and 1.1 mm wide proximally; the chalazal region and integument are well preserved, while the interior is devoid of tissue. The ovule is identified as cordaitalean based on size, shape, and organization of the integument; it most probably belongs to the genus *Mitrospermum* Arber (see Arber 1910; Taylor & Stewart 1964; Baxter 1974).

Ten specimens of the microfossil occur in the space that the nucellus and megaspore would occupy if preserved (Fig. 1a, b [arrows]). Specimens occur singly (Fig. 1b) or in groups of two to five (Fig. 1a); most are located close to the inner surface of the integument, but two occur in the centre of the ovule. Vegetative mycelia and other microbial remains are not present. This type of microfossil has not been detected in any other plant tissue preserved in the chert, nor has it been found in the chert matrix surrounding the ovule. The microfossils consist of a relatively thin- and smooth-walled near perfect sphere ~55 µm in diameter to which is attached a hollow, dome-shaped structure that is up to 16 µm wide and open at its wide end (Fig. 1c–e). The wall of the dome-shaped structure becomes thinner towards the wide end. Attached to the tip of the dome-shaped structure is a smaller element, which may be more or less spherical, drop- or dome-shaped (Fig. 1d, e). This element, which is between 5 and 8 µm in diameter, also appears to be open at one end (Fig. 1e [arrow], g). While in most specimens the small element is directly fused with the dome-shaped structure, there is one specimen in which the two structures are interconnected via a cylindrical segment ~2.9 µm long (Fig. 1f). The lumina of the large sphere and dome-shaped structure (Fig. 1f [arrow]), as well as the lumina of the dome-shaped and small element (Fig. 1g [arrow]) are interconnected.

4. Discussion

All specimens of this interesting microfossil demonstrate the same configuration, i.e. a sphere to which is attached a small, dome-shaped structure that, in turn, is fused to an even smaller spherical, drop- or dome-shaped element. The consistency in configuration, together with the fact that only one pair of associated structures accompanies each sphere, indicates that the sphere and associated structures have a common origin, or that the sphere was produced from the associated structures (or vice versa), rather than representing some type of spherical propagule infected by a parasitic organism that forms reproductive structures on the outer surface of its host.

We offer two hypotheses to explain the biological nature and affinities of the microfossils. One views the large sphere as some type of plant spore to which is attached a pair of aborted spores. Abortion is frequently observed in extant spores of ferns and fern allies (Hemsley 1997), and several examples are known from the fossil record of fully developed (mega-)spores to which are attached much smaller, abortive spores (e.g., Williamson & Scott 1895; Chaloner 1958; Hemsley 1997). Arguing against this hypothesis, however, is the fact that the development of spores involves the formation of a tetrad. If spore abortion took place there should be evidence of three aborted and one normally developed (or two normally developed and two aborted) spores. Moreover, the large spheres lack features indicative of spores (e.g., suture, surface ornamentation). In addition, the spheres are ~55 µm in diameter, which can be in the size range of megaspores. However, multiple megaspores within an ovule is not logical, and it is very unlikely that ten specimens of the same megaspore type accidentally became washed into the ovule, especially since similar spheres have not been found in the matrix surrounding the ovule.

An alternative, more plausible hypothesis views the microfossils as zygosporangium-apposed gametangia complexes of a zygomycetous fungus. In this scenario, the sphere represents the zygosporangium. The dome-shaped associated structure accordingly represents a large gametangium (i.e. macrogametangium), while the small element that is fused to the dome-shaped structure would represent a small gametangium (i.e. microgametangium). This condition closely corresponds to that seen in certain modern zygomycetes in the genus *Endogone* Link: Fr. (Endogonaceae), in which the zygosporangium does not develop in the fusion area between the

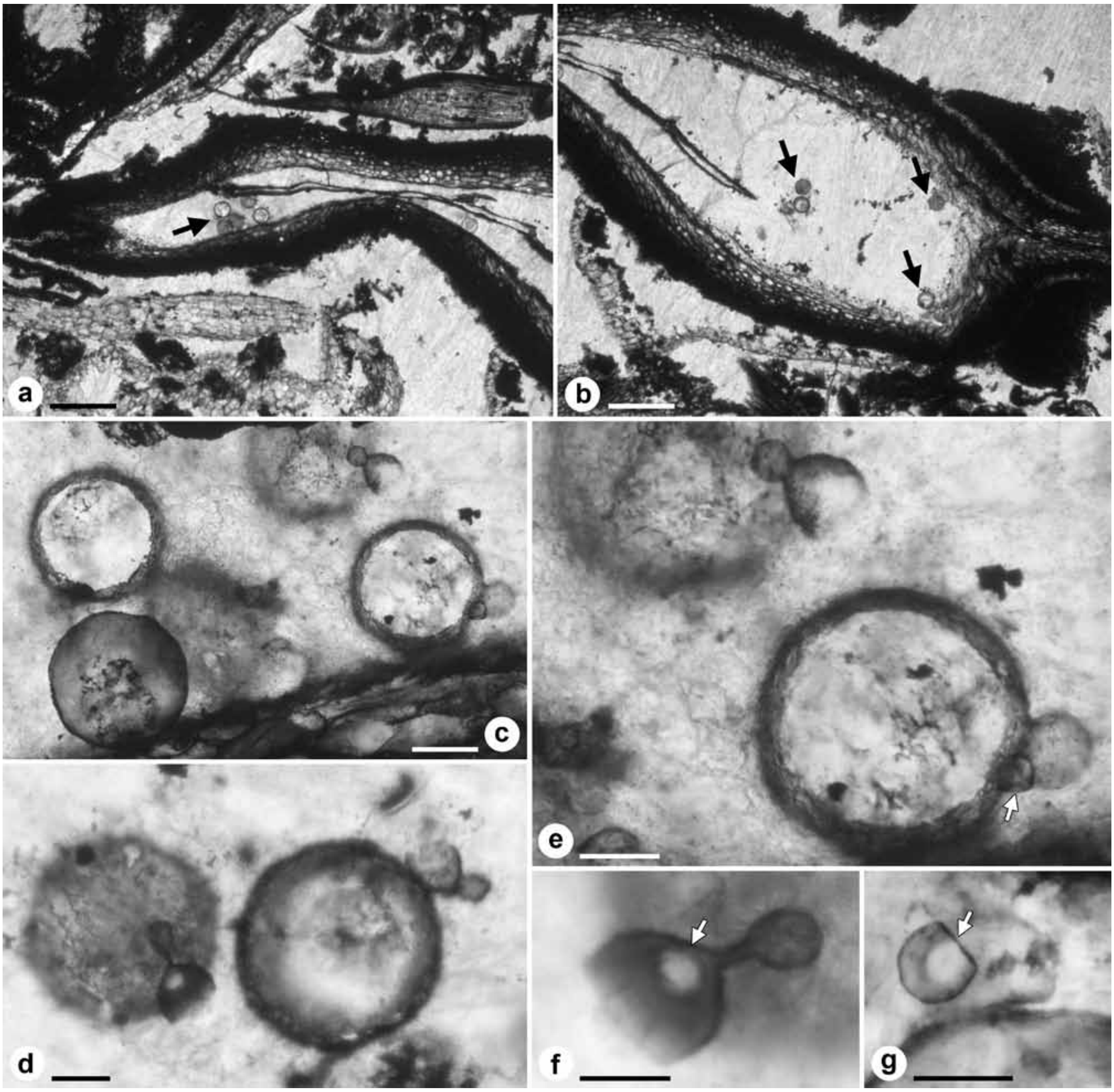

Figure 1: Microfossils in a *Mitrospermum*-type cordaitalean ovule from the Lower Coal Measures (Lower Pennsylvanian) of Great Britain (all images from slide BSPG 1964 XX 145). **(a, b)** Portions of the ovule (a: micropylar region; b: chalazal region) containing microfossils (arrows); bars = 250 µm. **(c)** Cluster of microfossils, showing near perfect spheres and associated structures in some of the specimens; bar = 25 µm. **(d)** Specimens showing paired associated structures; bar = 15 µm. **(e)** Paired associated structures; note that large and small (arrow) associated structure are open at one end; bar = 15 µm. **(f, g)** Paired associated structures; arrow in (f) indicates connection between the sphere and large associated structure, while arrow in (g) shows small associated structure that is open at one end; note interconnection of associated structures via a short cylindrical bridge in (f); bars = 10 µm

two gametangia, but rather buds out from the larger gametangium (Bucholtz 1912; Thaxter 1922; Yao et al. 1996). Moreover, it has been observed that in certain Endogonaceae the gametangium walls increase in thickness after gametangial fusion (Fig. 2), and thus may remain intact even until zygosporangium/zygospore maturation. With regard to *Endogone lactiflua* Berk., Bucholtz (1912: 162) writes: "Die Membran der Gamete, besonders der weiblichen, verdickt sich während und nach der Befruchtung nach oben hin." (The membrane of the gamete, especially the female one, increases in thickness from the bottom up during and after fertilization). This observation may explain why both the large and small associated structure in the fossil are open at one end (Fig. 1d–f). Accordingly, the open ends would represent the attachment sites of the gametangia to the subtending suspensors, which do not have secondarily thickened walls, and thus rapidly disintegrate following maturation of the zygosporangium and zygospore. Adding support to this interpretation is the fact that the configuration exhibited by the fossils is virtually identical to that seen in several of the zygosporangia with attached paired gametangia of extant Endogone species figured in the literature (e.g., Yao et al. 1996: pl. 4, fig. 30; Błaszkowski et al. 1998: fig. 5, 2004: fig. 8).

It is possible to envision a mycelium of a zygomycete growing within the ovule, and, at some point,

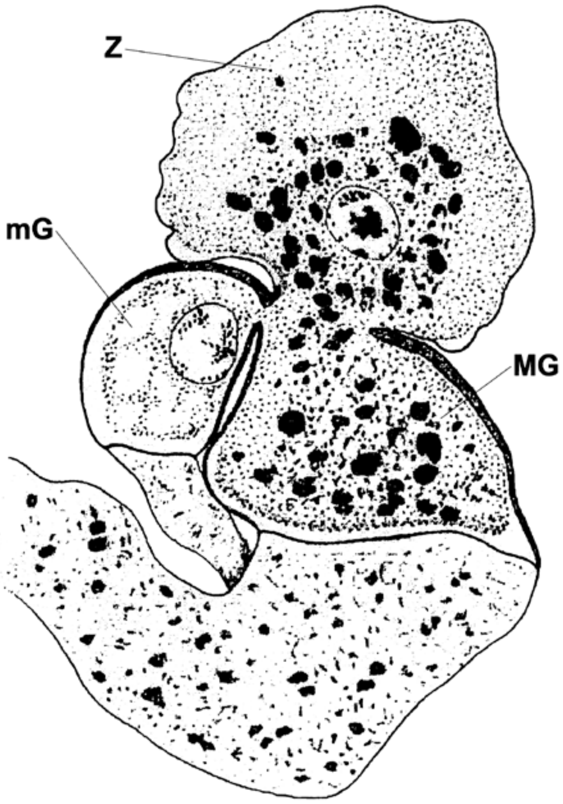

Figure 2: Developing zygosporangium (Z) of *Endogone lactiflua* Berk., showing budding from tip of large gametangium (MG) that is laterally fused with a small gametangium (mG); note relatively thick walls of the gametangia (modified from Bucholtz 1912: pl. V, fig. 37).

forming gametangia. After gametangial fusion, the zygosporangia develop as outgrowths of the macrogametangium. The delicate vegetative hyphae, as well as the thin-walled suspensors, disintegrate upon maturation of the zygospores, but the thick-walled zygosporangia with their persistent, thick-walled gametangia remain intact and, in this way, preserved. The presence of this putative fossil zygomycete within the confines of an ovule concurs with observations on the only previously described Carboniferous zygomycete, *Protoascon missouriensis* L.R. Batra, Segal et R.W. Baxter from the Upper Pennsylvanian of North America, which occurs within a specimen of a putative seed (Taylor et al. 2005).

One hundred years ago, the British paleontologist R.C. McLean (1912: 509) stated that "there can be no doubt that such structures [he refers to sexual reproductive structures of zygomycetes] do occur in the coal-beds, and that in no small number." Nevertheless, documented evidence of fossil zygomycetes remains exceedingly rare to date (Taylor et al. 2009). This lack of evidence remains unexplained, especially in light of the fact that (micro-)habitats conducive to the growth of zygomycetes, together with depositional environments conducive to the preservation of these fungi in recognizable form, were available at least by the Paleozoic (see Krings et al. 2012). Moreover, molecular clock estimates suggest that the first zygomycetous fungi occurred on Earth during the Precambrian, sometime between 0.8 and 1.4 Ga ago (Berbee & Taylor 2001; Heckman et al. 2001; Blair 2009). If our interpretation of the microfossils described in this paper as zygosporangium-apposed gametangia complexes is correct, then this discovery is important since it provides a rare insight into the morphology of a late Paleozoic zygomycetous fungus. We anticipate that additional and more complete specimens of this intriguing microfossil will be discovered as work on the microbial life preserved in the coal balls from the Lower Coal Measures of Great Britain continues. This will hopefully lead to a more accurate understanding of the organism on which the fossils described in this paper were produced, and help to more completely gather the full extent of the biodiversity that existed in Early Pennsylvanian coal swamp ecosystems. Moreover, it will expand our understanding of the evolutionary history of zygomycetous fungi, which to date have been greatly underrepresented in fossils. To a large degree we believe that this is the result of our inability to recognize the more ephemeral phases and delicate features of some of these organisms.

Acknowledgments

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