

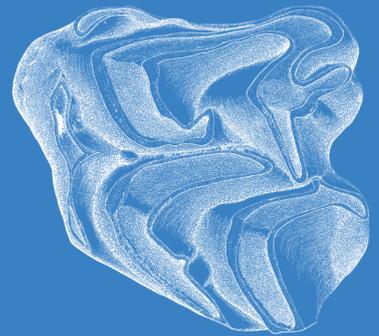
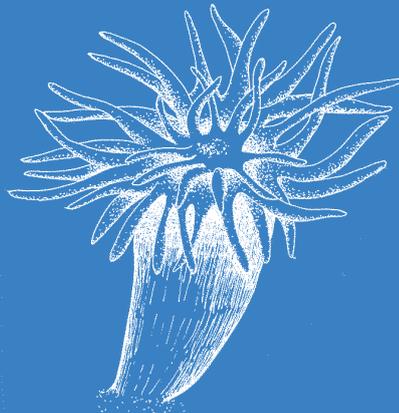
Zitteliana

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Mitteilungen der Bayerischen Staatssammlung
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50

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Cover illustrations: (from left to right) Shell of the gastropod *Loxonema regium* DE KONINCK from the Carboniferous of Belgium (redrawn from DE KONINCK 1881); Solitary coral *Caninia* sp. from the Carboniferous of England (redrawn from RAMSBOTTOM in MCKERROW 1978); Tooth of the rare ruminant *Orygotherium escheri* VON MEYER from the Miocene of Germany (after RÖSSNER & MÖRS 2001). **Back cover:** Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbilder: (von links nach rechts) Gehäuse der Schnecke *Loxonema regium* DE KONINCK aus dem Karbon von Belgien (neu gezeichnet nach DE KONINCK 1881); Solitärkoralle *Caninia* sp. aus dem Karbon von England (neu gezeichnet nach RAMSBOTTOM in MCKERROW 1978); Zahn des seltenen Wiederkäuers *Orygotherium escheri* VON MEYER aus dem Miozän von Deutschland (nach RÖSSNER & MÖRS 2001). **Rückseite:** Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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Microfungi from the upper Visean (Mississippian) of central France: Structure and development of the sporocarp *Mycocarpon* *cinctum* nov. sp.

By

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Abstract

Small spherical fungal sporocarps are widespread elements in Carboniferous permineralized peat. While the morphology and diversity of these structures are well documented, their development and systematic position remain largely unknown. A new sporocarp, *Mycocarpon cinctum* nov. sp., characterized by a complex, two-part wall occurs in a Middle Mississippian chert from France. The outer wall consists of interlaced, thin-walled, septate hyphae extending around the circumference of the structure; the inner wall is constructed of densely spaced and interwoven, thick-walled hyphal branches produced by the hyphae of the outer wall. Intermixed with the thick-walled elements are thinner-walled hyphal branches suggesting that the inner wall expanded by additional branches intruding between the pre-existing ones. Moreover, hyphal lysis along the interior wall surface appears to have been an integral process in sporocarp development. *Mycocarpon cinctum* provides important new information that expands our knowledge about the structural diversity and developmental biology of fossil sporocarps.

Key words: Carboniferous, chert, fossil fungi, ontogeny, reproduction, Zygomycota

Zusammenfassung

Verkieselter Torf aus dem Karbon enthält nicht selten kleine, runde Sporokarpe von Pilzen. Während die Morphologie und Diversität dieser Strukturen heute gut dokumentiert sind, ist über ihre Entwicklung und systematische Zugehörigkeit kaum etwas bekannt. Ein neues Sporokarp, *Mycocarpon cinctum* nov.

sp., mit einer komplexen zweiteiligen Wand ist in einem Chert aus dem mittleren Mississippium von Frankreich entdeckt worden. Die äußere Wand besteht aus locker verflochtenen, dünnwandigen und septierten Hyphen, die entlang der Kreislinie verlaufen; die innere Wand stellt ein kompaktes System dickwandiger Hyphenäste dar, welche von den Hyphen der äußeren Wand gebildet werden. Zwischen den dickwandigen Ästen finden sich auch dünnerwandige, was darauf hindeutet, dass die innere Wand durch Einfügen zusätzlicher Äste in das bestehende System gewachsen ist. Auflösungsprozesse entlang der inneren Wandoberfläche scheinen ebenfalls ein integraler Bestandteil der Sporokarpentwicklung gewesen zu sein. *Mycocarpon cinctum* liefert wichtige Erkenntnisse über die morphologische Vielfalt und Entwicklungsbiologie fossiler Pilz-Sporokarpe.

Schlüsselwörter: Chert, fossile Pilze, Karbon, Ontogenese, Reproduktion, Zygomycota

1. Introduction

Within Carboniferous permineralized peat from Europe and North America are a variety of small (usually <1 mm in diameter) spherical structures, including some that are ornamented, which have collectively been termed sporocarps (e.g., HUTCHINSON 1955; BAXTER 1960; DAVIS & LEISMAN 1962; STUBBLEFIELD et al. 1983). All are composed of a central cavity surrounded by a wall of loosely arranged interlacing and/or tightly compacted hyphae, which may be aseptate or septate. Some sporocarps contain one to several spherical structures in the cavity, which has led to their interpretation as ascomycete cleistothecia (e.g., STUBBLEFIELD & TAYLOR 1983). In

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this hypothesis, the larger internal spherical structures would represent asci, and smaller ones ascospores. An alternative interpretation, however, views the sporocarps as belonging to the Zygomycota (TAYLOR & WHITE 1989; WHITE & TAYLOR 1989b). The large, inner spore-like body is suggested as representing the zygospore, while the surrounding structure would be equivalent to the hyphal envelope or mantle seen in certain modern Endogonales (e.g., see TRAPPE & GERDEMANN 1972; BENJAMIN 1979; YAO et al. 1995; BŁASZKOWSKI et al. 1998). The smaller internal spheres reported in some specimens are regarded as mycoparasites.

Based primarily on wall composition and surface ornamentation, several morphogenera have been introduced for fossil sporocarps. For example, *Mycocarpon* S.A. HUTCH., a common form in Pennsylvanian deposits, is characterized by a wall of interlaced hyphae up to four layers thick (HUTCHINSON 1955). An amorphous, cuticle-like membrane extends along the inner surface of the wall. Specimens of *Sporocarpon* WILL. possess a pseudoparenchymatous wall that extends outward into narrow, conical processes (STUBBLEFIELD et al. 1983). A third morphogenus, *Dubiocarpon* S.A. HUTCH., is distinguished by a wall constructed of radially elongated segments and spines extending out from the sporocarp (STUBBLEFIELD et al. 1983; GERRIENNE et al. 1999). The most prominently ornamented taxon is *Traquairia* CARRUTH., a sporocarp type initially described from the Lower Coal Measures of Great Britain as a radiolarian rhizopod (CARRUTHERS 1872). Since that time, numerous specimens have been reported from many Pennsylvanian localities (STUBBLEFIELD & TAYLOR 1983). The wall of *Traquairia* is complex, with the outer layer constructed of branching hyphae, some of which are organized into hollow spines.

While sporocarps are relatively common in Pennsylvanian deposits, they have rarely been reported from geologically older and younger strata. Several forms are known from the Mississippian. One of these, *Roannaisia bivittilis* T.N. TAYLOR, GALTIER et AXSMITH, occurs in a late Visean chert from the Roanne area in France (TAYLOR et al. 1994), while a second comes from Esnost (REX 1986), another French locality yielding late Visean cherts (see GALTIER 1971). However, the sporocarp from Esnost has not yet been studied in detail and formally described. Two Mississippian representatives of *Traquairia* have been reported from the vicinity of Burntisland, Scotland (SCOTT 1911). An interesting sporocarp similar to forms known from the Carboniferous is described as *Mycocarpon asterinum* T.N. TAYLOR et J.F. WHITE from the Triassic of Antarctica (TAYLOR & WHITE 1989). This fossil is characterized by a two-parted wall constructed of an outer mycelial and inner noncellular component.

Although the morphology and internal organization of

many sporocarp types are well understood today, the development (ontogeny) of these structures, especially of the complex walls, remains largely unknown. In this paper we present a description and photographic documentation of *Mycocarpon cinctum* nov. sp., the heretofore undescribed Visean sporocarp type mentioned in REX (1986), based on a newly discovered exquisitely preserved specimen from Esnost. This fossil shows the organization of the two-parted wall, together with specific developmental details, and thus represents a significant segment of new information that expands our knowledge about fossil sporocarps.

2. Material and methods

The chert block containing the sporocarp comes from the upper Visean (Mississippian [= Lower Carboniferous]) of the Autun Basin at the locality of Esnost, which is located about 10 km north of the city of Autun in the northern part of the Massif Central, central France. Details regarding the geological setting can be found in SCOTT et al. (1984); for information on the preservation of fossils and a paleoecological reconstruction of the Visean ecosystem see REX (1986). The Visean landscape at this site is interpreted as a series of pools and small lakes within an open swamp forest ecosystem; the environment was dominated by active volcanism. The cherts, which originally formed in the pools and lakes (REX 1986), occur as loose blocks within rhyolitic tuffs, and can be collected in cultivated fields.

Based on the structure of the chert matrix and composition of the flora, several distinct lithologies have been recognized (REX 1986). The sporocarp occurs in what has been termed "Facies 2: *Botryopteris* chert I". This lithology is characterized by abundant foliar branching systems, rootlets, and sporangia of *Botryopteris antiqua* KIDSTON, as well as *Sublagenicula*-type lycophte megaspores, some with well-preserved gametophyte tissue.

The specimen was identified in a thin section prepared by cementing a piece of chert to a glass slide and then grinding the wafer until it is thin enough to be examined in transmitted light. The section is housed in the paleobotanical collections of the Université Montpellier II, France, under accession number ES-A7945. The fossil was analyzed using normal transmitted light microscopy equipment (Leica); digital images were taken with a Leica DFC-480 camera.

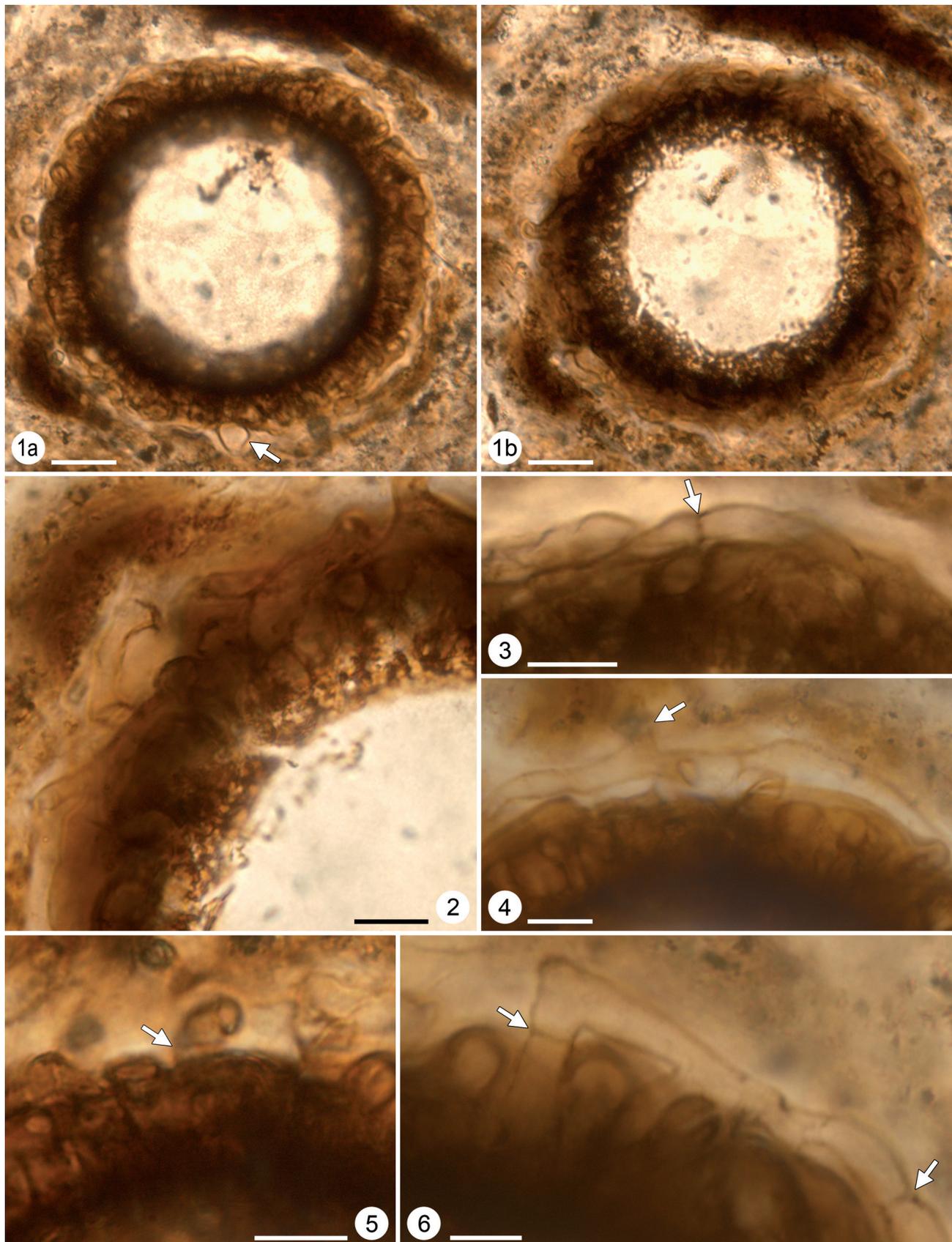
3. Systematic paleontology

Fungi incertae sedis

Morphogenus *Mycocarpon* S.A. HUTCH.

Plate 1:

Mycocarpon cinctum nov. sp. from the Middle Mississippian of France; general morphology and outer wall layer. (1) Holotype specimen in two different focal planes, 1a: plane close to centre, focusing on inner wall layer, 1b: plane off centre, focusing on outer wall layer; arrow in Fig. 1a indicates bulbous structure extending from outer surface of sporocarp; bar = 20 µm. (2) Outer wall layer constructed of interlacing hyphae extending around circumference of sporocarp; bar = 10 µm. (3 & 4) Septate hyphae of outer wall layer; arrow in Fig. 3 indicates septum, arrow in Fig. 4 shows hyphal branch directed outwardly; bars = 10 µm. (5) Transition from outer to inner wall layer; note hyphal branch bending inwardly to form inner wall layer (arrow indicates septum); bar = 10 µm. (6) Hypha from outer wall layer contributing to formation of inner wall layer by producing inwardly directed branches; arrows indicate septa; bar = 5 µm.



Type species: *Mycocarpon pachyderma* (WILL.) S.A. HUTCH.

Mycocarpon cinctum nov. sp.
Pls 1 and 2

Holotype: Specimen illustrated in Pl. 1, Fig. 1 (and all other figures): Slide ES-A7945, paleobotanical collections Université Montpellier II, France.

Other specimens included: The sporocarp illustrated by REX (1986: pl. 2, fig. 6) and denoted as “Fungi (?)” in the figure caption is slightly larger (i.e. ~200 µm in diameter), but exhibits the same organization as the holotype specimen, and therefore is referred to *Mycocarpon cinctum* as well.

Diagnosis: Spherical sporocarp, ≤200 µm in diameter, with two-parted wall enclosing a central cavity; outer wall layer up to 10 µm thick, constructed of interlaced, thin-walled, translucent septate hyphae, 3–6 µm in diameter, extending around circumference of structure; inner wall layer up to 15 µm thick, constructed of hyphae of outer layer through the formation of inwardly directed hyphal branches; hyphal branches irregular in size and shape but mostly pillar-like, up to 6 µm in diameter, densely spaced and intertwined, often proximally thin-walled but then abruptly becoming distinctly thicker-walled and more opaque; inmost portion of inner wall layer showing varying degrees of disintegration.

Etymology: The epithet *cinctum* [*cinctus*, -a, -um (Lat.) = girdled] refers to the hyphae of the outer wall layer that appear to gird the structure.

Locality: Esnost, located ~10 km north of Autun (Autun Basin) in the northern part of the Massif Central, central France (for details, see REX, 1986: fig. 1)

Age: Late Visean (Middle Mississippian; c. 330 Ma old) (e.g., GALTIER, 1971)

Description: *Mycocarpon cinctum* occurs in the chert matrix within a dense accumulation of largely homogenized plant fragments and other fungal debris; a few well preserved rachides and rootlets of the fern *Botryopteris antiqua*, spores and pollen grains, including large lycophyte megaspores of the *Sublagenicula nuda*-type, as well as clusters of small coprolites occur in proximity to the sporocarp.

The sporocarp is spherical in shape, ~125 µm in diameter, and composed of a central cavity enveloped by a prominent

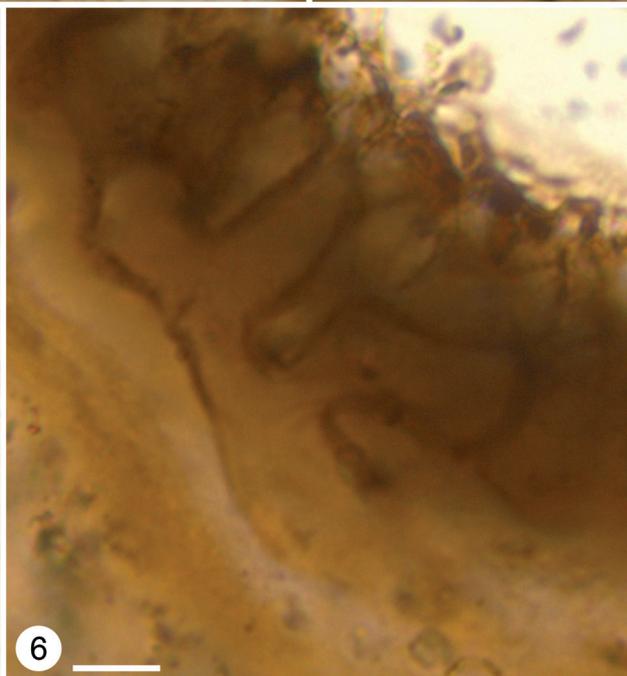
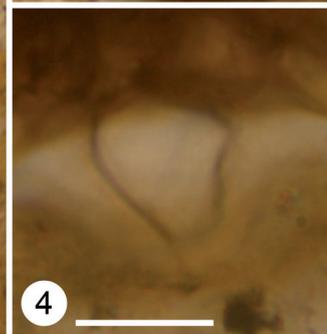
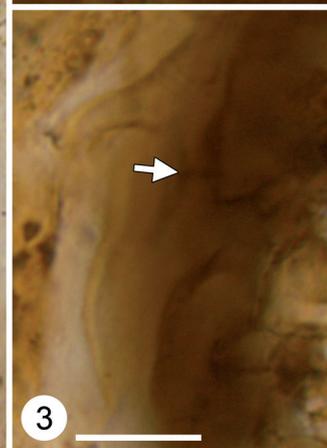
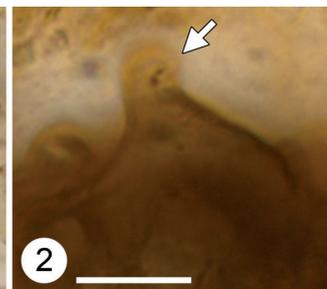
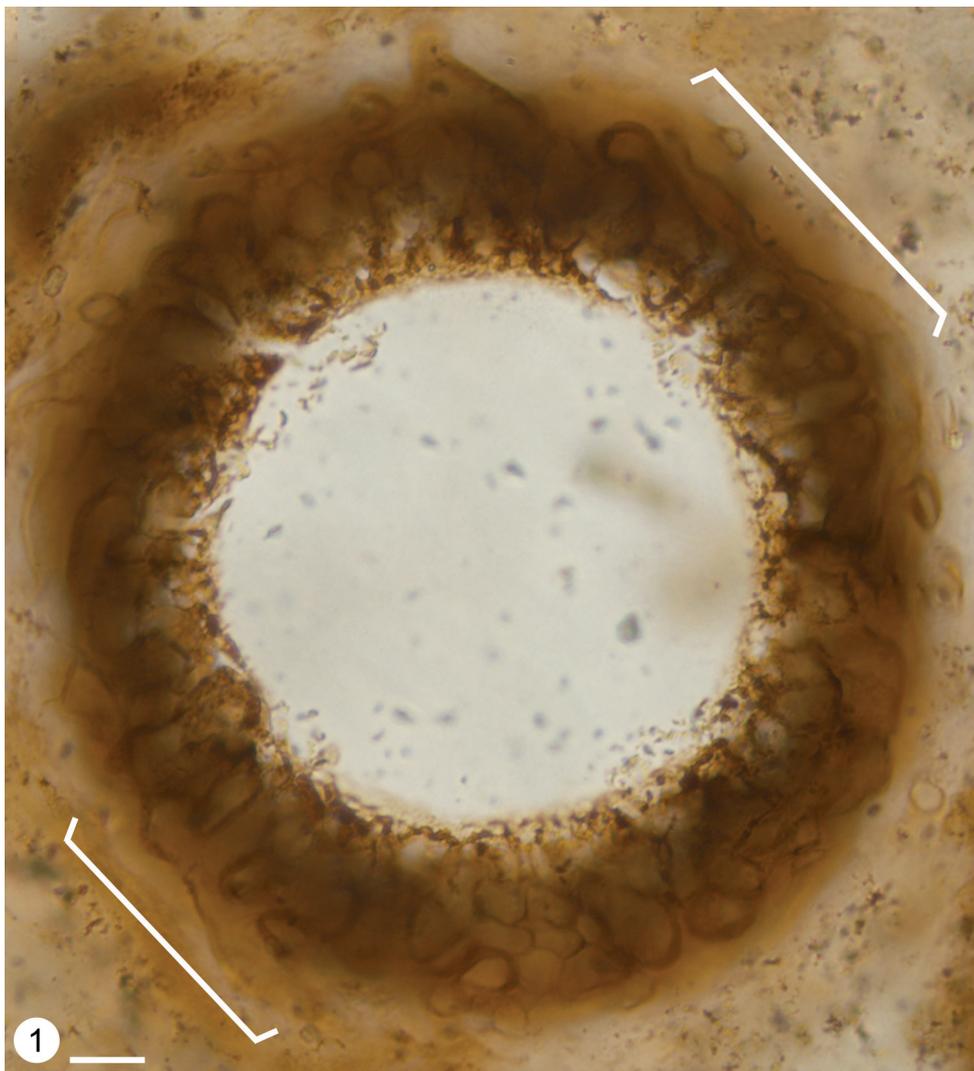
wall up to 25 µm thick (Pl.1, Fig. 1a,b). Surface ornamentations in the form of processes or hollow spines, as have been described in other fossil sporocarps, are not present, but a single bulbose structure, up to 12 µm high and 9 µm wide, extending from the outer surface is visible in (near-)centre-plane section (arrow in Pl. 1, Fig. 1a; Pl. 2, Fig. 4).

The sporocarp wall is relatively complex and two-parted, with the outer wall layer up to 10 µm and the inner layer approximately 15 µm thick; the central cavity has a diameter of ~90 µm. The outer wall layer (Pl. 1, Figs 2–4, and 6) consists of a loose system of interlaced tubular hyphae, each between 3 and 6 µm in diameter, which are thin-walled, translucent, septate (arrows in Pl. 1, Figs 3, 4, and 6), and extend around the circumference of the structure. Septa appear to be complete and simple. Hyphae of the outer wall layer produce branches in three directions. Branch hyphae may extend around the circumference of the structure, and thus add to the outer wall layer, or extend out into the surrounding matrix (arrow in Pl. 1, Fig. 4). A third type of hyphal branch appears to be responsible for the formation of the inner wall layer. These branches, which are produced in large numbers, are up to 6 µm in diameter, consistently directed inwardly, and may be either septate (arrow in Pl. 2, Fig. 3) or aseptate (Pl. 2, Fig. 6). They are mostly pillar-like and oriented radially or near-radially (Pl. 1, Fig. 6), but some may also extend along the outer surface of the inner wall layer for a short distance and branch irregularly, with the second-order branches oriented (near-)radially (Pl. 2, Fig. 6). Dense spacing and interweaving of the hyphal branches results in a compact structure, which, in tangential sections (e.g., in Pl. 2, Figs 1, 5, and 6), gives the impression of a tissue system of cells. Hyphal branch segments within the inner wall layer usually are distinctly thicker-walled, with the walls more opaque than those of the hyphae in the outer wall layer. It is interesting to note that the inwardly directed hyphal branches typically are still thin-walled proximally (i.e. close to their origin), but then abruptly become thicker-walled and opaque as they enter the inner wall layer (e.g., Pl. 1, Fig. 5; arrow in Pl. 2, Fig. 2). This change in wall thickness and opacity usually occurs close to the site of a septum. A few radially oriented hyphal branches lack thickened and darkened walls (Pl. 1, Fig. 6).

The inmost portion of the inner wall layer exhibits disintegration at varying degrees, ranging from mild ablation/thinning of the hyphal walls to complete disruption (Pl. 1, Fig. 2; Pl. 2, Figs 1, 5, and 6). The central cavity of the sporocarp is empty; neither a cuticle-like membrane along the interior surface of the cavity nor a central, spore-like body or small spheres, as reported in other sporocarps, has been observed in *Mycocarpon cinctum*.

Plate 2:

Mycocarpon cinctum nov. sp. from the Middle Mississippian of France; inner wall layer. (1) Inner wall layer constructed of thick-walled hyphal branches (focal plane off centre); bracketed area in upper right magnified in Fig. 5, bracketed area in lower left magnified in Fig. 6; note varying degrees of hyphal disruption (lysis) along inner surface of sporocarp wall; bar = 10 µm. (2 & 3) Transition from outer to inner wall layer; note proximal, thin-walled (arrow in Fig. 2) and distal, thicker-walled hyphal portions, arrow in Fig. 3 indicates septum; bars = 10 µm. (4) Bulbous structure extending from outer sporocarp wall; bar = 10 µm. (5) Transition from outer to inner wall layer, showing differences in hyphal wall thickness and coloration, as well as hyphal disruption (lysis) along inner surface; bar = 10 µm. (6) Thick-walled hyphal branch from inner wall layer; bar = 5 µm.



4. Discussion

The late Paleozoic and Mesozoic microfossils that are today collectively termed sporocarps were initially brought to the attention of the scientific community more than 120 years ago, and since that time have remained a matter of debate. Early workers have variously interpreted these structures as radiolarians (CARRUTHERS 1872; MCLEAN 1912, 1922), some cryptogamic form of reproductive structure (WILLIAMSON 1880), and *Azolla* L. *massulæ* (in SCOTT 1911). More recently, however, detailed (re-)investigations of their structure and organization, together with the discovery of additional forms, have been used to suggest that the vast majority of sporocarps are fungal in nature (DAVIS & LEISMAN 1962; STUBBLEFIELD et al. 1983; STUBBLEFIELD & TAYLOR 1983; TAYLOR & WHITE 1989; WHITE & TAYLOR 1991). Nevertheless, the precise systematic affinities and biological function of the sporocarps continue to remain uncertain, due in part to the fact that these structures have never been observed in organic attachment to the biological system that produced them. Moreover, a puzzling inconsistency exists with regard to the content of the central cavity. Specimens may be empty or contain a single, large spore-like structure, or they may contain one to several small spheres, the latter sometimes even occur within the confines of a spore-like structure (e.g., DAVIS & LEISMAN 1962; STUBBLEFIELD et al. 1983).

4.1 Affinities

The sporocarp type from the upper Viséan of France described in this paper conforms most closely to the genus *Mycocarpon*, which has been established by HUTCHINSON (1955) for forms constructed of a spherical cavity surrounded by one or more layers of septate hyphae (pg. 426). Although STUBBLEFIELD et al. (1983) have questioned the presence of septa in *Mycocarpon* (pg. 1486), this hyphal trait has later been documented convincingly in the Triassic *M. asterineum* (TAYLOR & WHITE 1989), and is also unquestionably present in *M. cinctum* (e.g., arrows in Pl. 1, Figs 3 and 6). Because septa are unknown in any other fossil sporocarp genus (STUBBLEFIELD et al. 1983), their presence in *M. cinctum* is regarded as an important diagnostic feature at genus level.

Mycocarpon cinctum differs from previously described forms of *Mycocarpon* by its comparatively small size (i.e. ≤ 200 μm in diameter). Diameters of the other forms of *Mycocarpon* range between 300 and 600 μm in the Carboniferous specimens (MCLEAN 1922; HUTCHINSON 1955; DAVIS & LEISMAN 1962; STUBBLEFIELD et al. 1983), and from 200 to 400 μm in *M. asterineum* (TAYLOR & WHITE 1989). The most distinctive feature of *M. asterineum* is the presence of a massive, non-cellular inner wall component (TAYLOR & WHITE 1989: figs 1 and 4), which has not been observed in *M. cinctum*. A thin, apparently noncellular inner wall has also been recorded for the Carboniferous species of *Mycocarpon*, and included in the emendation of HUTCHINSON's original diagnosis of that genus by STUBBLEFIELD et al. (1983: 1488). However, TAYLOR & WHITE (1989) demonstrate that, in *M. asterineum*, the noncellular inner wall component develops and increases in thickness as the sporocarp ages, and thus may not be present in all speci-

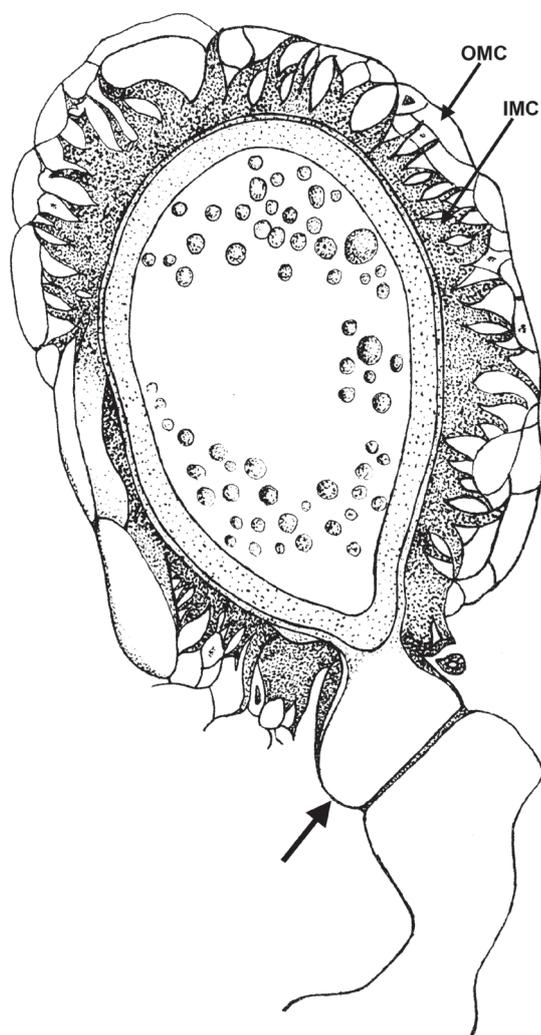
mens. As will be discussed later in this paper (section 4.2), *M. cinctum* shows hyphal disintegration along the inner surface of the wall (e.g., Pl. 1, Fig. 2; Pl. 2, Figs 1, 5, and 6). It may be that accumulation and successive compaction of the residual material from this developmental process ultimately formed a coherent noncellular inner wall or wall component.

Mycocarpon cinctum also differs from *Roannaisia bivittilis*, the second sporocarp type in the late Viséan cherts from France (TAYLOR et al. 1994). *Roannaisia bivittilis* may be up to 600 μm in diameter, and is characterized by a delicate, epidermis-like covering, which has not been observed in *M. cinctum*. Moreover, the two-parted wall of *R. bivittilis* is constructed in a distinctly different pattern than that in *M. cinctum*. The outer wall layer of the *R. bivittilis* sporocarp consists of wide, sometimes bulbous hyphae, while the inner layer is characterized by interlaced narrow hyphae (TAYLOR et al. 1994: pl. II, figs 1 and 2). Finally, a large and relatively thick-walled spore-like body occurs in the central cavity of *R. bivittilis*, while the cavities of both specimens of *M. cinctum* are empty (see Pl. 1, Fig. 1; Pl. 2, Fig. 1, and REX 1986: pl. 2, fig. 6).

Two hypotheses on the systematic affinities of the fossil fungal sporocarps have been advanced to date. One suggests that these structures were produced by Ascomycota (e.g., STUBBLEFIELD et al. 1983), whereas the other views them as belonging to the endogonaceous Zygomycota (e.g., TAYLOR & WHITE 1989; WHITE & TAYLOR 1991). Both Ascomycota and Zygomycota are believed to have diverged well before the Carboniferous based on fossil evidence (e.g., TAYLOR et al. 2005a, 2005b) and molecular data (BLAIR 2009), and thus could have produced the sporocarps. *Mycocarpon cinctum* does not resolve this dilemma. However, certain characteristics in basic structure present in *M. cinctum* and the mantled zygosporangia of certain extant Endogonales are similar. Especially interesting is a camera lucida drawing in BUCHOLTZ (1912: pl. VII, fig. 52) of a structure attributed to *Endogone lactiflua* BERK. (later reassigned to *Endogone flammicorona* TRAPPE et GERD.; see TRAPPE & GERDEMANN 1972). This drawing (reproduced here as Textfig. 1) depicts a mature zygosporangium enveloped in a two-parted hyphal mantle. The outer mantle component (OMC in Textfig. 1) is constructed of thin-walled hyphae, while the inner component (IMC in Textfig. 1) consists of interwoven hyphal segments with unevenly thickened walls. According to ZYCHA et al. (1969: 253), the entire structure may be up to 150 μm long and 100 μm wide, with the hyphal mantle up to 26 μm thick. A similar configuration in *E. flammicorona* has later also been reported by BONFANTE-FASOLO & SCANNERINI (1976: pl. III, figs 10 and 11). Moreover, these authors state that the thin-walled hyphae in the periphery of the structure (OMC in Textfig. 1) technically belong to the confluent hyphal network of the carpophore that, upon lysis, releases the zygosporangia into the soil. It is interesting to note that the presence of a confluent hyphal envelopment has also been reported in a cluster of *M. pachyderma* sporocarps from the Carboniferous of Great Britain (MCLEAN 1922: 83, pl. IX, fig. 1).

At the base of the mantled zygosporangium depicted in BUCHOLTZ (1912) is a distinct swelling (i.e. the persistent female gametangium; large arrow in Textfig. 1), which is reminiscent of the bulbous appendage extending from the surface of the holotype specimen of *M. cinctum* (arrow in Pl. 1, Fig. 1a; Pl. 2, Fig. 4) where it appears to interface the sporocarp with its source

organism. It is also possible, however, that the appendage in *M. cinctum* is part of a surface ornamentation that otherwise is not preserved.



Textfigure 1: Mantled zygosporangium of *Endogone flammicorona* TRAPPE et GERD.; OMC = outer mantle component, IMC = inner mantle component; large arrow indicates persistent female gametangium; width of structure ~100 μm (modified from BUCHOLTZ 1912: pl. VII, fig. 52).

4.2 Sporocarp development

One aspect that rarely has been addressed in descriptions of fossil sporocarps is their ontogenetic development; this represents an important factor hampering determination of the precise systematic affinities of these structures. We are aware of only two studies elaborating on developmental processes in fossil sporocarps. TAYLOR & WHITE (1989) suggest that the inner, noncellular wall component of the Triassic *Mycocarpon asterineum* was produced by a layer of special hyphae along the inner surface of the outer wall layer through continuous secretion of wall material. As the sporocarp expands, the outer

wall layer becomes successively compacted. It is interesting that a similar developmental sequence has also been reported in the zoospore mantle of the extant zygomycete *Endogone flammicorona* (BONFANTE-FASOLO & SCANNERINI 1976). In *Endochaetophora antarctica* J.F. WHITE et T.N. TAYLOR, another sporocarp-like fungal structure from the Triassic, the middle layer of the three-part wall is believed to have formed secondarily between the two pre-existing wall layers (WHITE & TAYLOR 1988, 1989a).

Based on the structural features of *Mycocarpon cinctum*, we offer hypotheses on some of the processes that may have been involved in the development of this sporocarp. The outer wall layer consists of hyphae extending along the circumference of the structure (Pl. 1, Figs 2–4). These hyphae are loosely interlaced and produce branches in various directions. Some of the branches assume the same orientation as their parental hyphae, and in this manner appear to have maintained the configuration of the outer wall layer during expansion. Other hyphal branches are relatively short and directed inwardly. These branches, which have also been noted in other species of *Mycocarpon* (e.g., McLEAN 1922: pl. X, fig. 19), may directly extend between the pre-existing hyphal segments constituting the inner wall layer (Pl. 1, Fig. 6), or extend along the outer surface of the inner layer and produce secondary branches, which advance into the inner wall (Pl. 2, Figs 5 and 6). This scenario suggests that, by addition of new hyphal branches, the circumference of the compact inner wall layer gradually increases. Some of the hyphal branches within the inner layer are distinctly thinner-walled than the surrounding ones. We suggest that newly added hyphal branches secondarily became thick-walled, after they had reached their ultimate position within this system. It is also possible that a few hyphal segments within the inner wall remained thin-walled as development proceeded.

The inner portion of the interior wall layer is disintegrated to varying degrees (Pl. 1, Fig. 2; Pl. 2, Figs 1, 5, and 6). This pattern may represent an early stage of the natural *post mortem* decay process or a preservational artifact. Arguing against natural *post mortem* and preservational decay is the absence of similar disintegration on the opposite, outer surface of the sporocarp. These decay processes would likely have started at the periphery of the sporocarp where hyphae were thin-walled, loosely arranged, and directly exposed to the substrate, rather than along the protected inner wall surface where hyphae were densely packed and thick-walled. As a result, we hypothesize that hyphal lysis along the interior wall surface was an integral morphogenetic process in the growth and maturation of the sporocarp.

Both specimens of *Mycocarpon cinctum* are empty. It is possible that the contents were simply not preserved. Alternatively, the sporocarps may have been relatively young and the (wall of the) internal element(s) not yet fully developed. The cavity may have contained cytoplasm with nuclei and lipid droplets, but a solid spore wall was perhaps not deposited until the sporocarp had reached final size. Adding some support to this hypothesis is the fact that *M. cinctum* is smaller than virtually all other fungal sporocarps. On the other hand, a loose accumulation of debris from hyphal lysis occurs along the inner wall surface in *M. cinctum*. This debris perhaps accumulated over time and became compacted, and in this way may have

become transformed into a coherent inner spherical structure resembling the spore-like spheres reported in other sporocarps. Another, albeit highly speculative scenario explains the absence of content in some sporocarps as a result of abortion of the internal elements at some point during development, upon which the sporocarp continued to develop and matured, but remained empty.

5. Conclusions

Fungal sporocarps like *Mycocarpon cinctum* represent interesting components of late Paleozoic and early Mesozoic continental ecosystems that continue to result in speculation as to their systematic affinities and biological significance. The presence of various patterns of internal organization in what have been interpreted as mature structures may now be seen to more accurately reflect at least some difference in development. Nevertheless, within these structures there also are some basic similarities in size and organization that suggest at least some may belong to the same higher taxonomic category – perhaps a lineage of Zygomycota. It is interesting to note that the Zygomycota represents one of only two major groups of fungi that have not been conclusively demonstrated in rocks older than the Carboniferous (TAYLOR et al. 2005b). Not even the Lower Devonian Rhynie chert, which has yielded evidence of the Chytridiomycota, Blastocladiomycota, Glomeromycota, Ascomycota, as well as specimens of the Straminipila in the form of Peronosporomycota (TAYLOR et al. 2004, 2006), has produced compelling fossils of zygomycetes. This lack of evidence may be related to the type of ecosystem represented by the Rhynie chert since molecular clock estimates place the divergence of the group far earlier than the ~400 Ma date of the Rhynie chert site (e.g., HECKMAN et al. 2001). Their apparent absence may also be related in some way to the type of plants that were present. Similarly, we are uncertain whether there may be some relationship between the Carboniferous swamp forest plants and fungal sporocarps such as *Mycocarpon* that directly links to their biological interactions, for example dispersal or resting propagules. Yet, like so many aspects of studying fossil fungi, one specimen, or direct association with another organism, often is the single necessary segment of information that helps to elucidate the affinities or degree of biological interaction that has remained elusive. We anticipate that this will be the same trajectory regarding fossil fungal sporocarps as they are continuously reported and studied.

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6. References

BAXTER, R. W. (1960): *Sporocarpon* and allied genera from the American

- Pennsylvanian. – *Phytomorphology*, **10**: 19–25.
- BENJAMIN, R. K. (1979): Zygomycetes and their spores. – In: B. KENDRICK (Ed.), *The Whole Fungus: The Sexual-Asexual Synthesis*. Vol. 2; Ottawa (National Museum of Natural Sciences, National Museums of Canada, and the Kananaskis Foundation), 573–616.
- BLAIR, J. E. (2009): Fungi. – In: S. B. HEDGES & S. KUMAR (Eds), *The Timetree of Life*; New York, NY (Oxford University Press), 215–219.
- BEŁAZKOWSKI, J., TADYCH, M. & MADEJ, T. (1998): *Endogone maritima*, a new species in the Endogonales from Poland. – *Mycological Research*, **102**: 1096–1100.
- BONFANTE-FASOLO, P. & SCANNERINI, S. (1976): The ultrastructure of the zygospore in *Endogone flammicorona* Trappe & Gerdemann. – *Mycopathologia*, **59**: 117–123.
- BUCHOLTZ, F. (1912): Beiträge zur Kenntnis der Gattung *Endogone* Link. – Beihefte zum Botanischen Centralblatt, II, **39**: 147–224.
- CARRUTHERS, W. (1872): On *Traquairia*, a radiolarian rhizopod from the Coal Measures. – Report of the 42nd Meeting of the British Association for the Advancement of Science, p. 126.
- DAVIS, B. & LEISMAN, G. A. (1962): Further observations on *Sporocarpon* and allied genera. – *Bulletin of the Torrey Botanical Club*, **89**: 97–109.
- GALTIER, J. (1971): Sur les flores du Carbonifère inférieur d'Esnot et du Roannais. – *Bulletin trimestriel de la Société d'histoire naturelle et des amis du Museum d'Autun*, **57**: 24–28.
- GERRIENNE, P., FAIRON-DEMARET, M. & GALTIER, J. (1999): A Namurian A (Silesian) permineralized flora from the Carrière du Lion at Engihoul (Belgium). – *Review of Palaeobotany and Palynology*, **107**: 1–15.
- HECKMAN, D. S., GEISER, D. M., EIDELL, B. R., STAUFFER, R. L., KARDOS, N. L. & HEDGES, S. B. (2001): Molecular evidence for the early colonization of land by fungi and plants. – *Science*, **293**: 1129–1133.
- HUTCHINSON, S. A. (1955): A review of the genus *Sporocarpon* Williamson. – *Annals of Botany*, **19**: 425–435.
- MCLEAN, R. C. (1912): A group of rhizopods from the Carboniferous period. – *Proceedings of the Cambridge Philosophical Society*, **16**: 493–513.
- MCLEAN, R. C. (1922): On the fossil genus *Sporocarpon*. – *Annals of Botany*, **36**: 71–90.
- REX, G. M. (1986): The preservation and palaeoecology of the Lower Carboniferous silicified plant deposits at Esnot, near Autun, France. – *Geobios*, **19**: 773–800.
- SCOTT, A. C., GALTIER, J. & CLAYTON, G. (1984): Distribution of anatomically preserved floras in the Lower Carboniferous in Western Europe. – *Transactions of the Royal Society Edinburgh, Earth Sciences*, **75**: 311–340.
- SCOTT, R. (1911): On *Traquairia*. – *Annals of Botany*, **25**: 459–467.
- STUBBLEFIELD, S. P. & TAYLOR, T. N. (1983): Studies of Paleozoic fungi. I. The structure and organization of *Traquairia* (Ascomycota). – *American Journal of Botany*, **70**: 387–399.
- STUBBLEFIELD, S. P., TAYLOR, T. N., MILLER, C. E. & COLE, G. T. (1983): Studies in Carboniferous fungi. II. The structure and organization of *Mycocarpon*, *Sporocarpon*, *Dubiocarpon*, and *Coleocarpon* (Ascomycotina). – *American Journal of Botany*, **70**: 1482–1498.
- TAYLOR, T. N., GALTIER, J. & AXSMITH, B. J. (1994): Fungi from the Lower Carboniferous of central France. – *Review of Palaeobotany and Palynology*, **83**: 253–260.
- TAYLOR, T. N., HASS, H., KERP, H., KRINGS, M. & HANLIN, R. (2005a): Perithecial ascomycetes from the 400-million-year-old Rhynie chert: an example of ancestral polymorphism. – *Mycologia*, **97**: 269–285.
- TAYLOR, T. N., KLAVINS, S. D., KRINGS, M., TAYLOR, E. L., KERP, H. & HASS, H. (2004): Fungi from the Rhynie chert: a view from the dark side. – *Transactions of the Royal Society Edinburgh, Earth Sciences*, **94**: 457–473.
- TAYLOR, T. N., KRINGS, M. & KERP, H. (2006): *Hassiella monospora* nov. gen. et sp., a microfungus from the 400 million year old Rhynie chert. – *Mycological Research*, **110**: 628–632.
- TAYLOR, T. N., KRINGS, M., KLAVINS, S. D. & TAYLOR, E. L. (2005b): *Protoascon missouriensis*, a complex fossil microfungus revisited. – *Mycologia*, **97**: 725–729.
- TAYLOR, T. N. & WHITE, J. F. Jr. (1989): Fossil fungi (Endogonaceae) from the Triassic of Antarctica. – *American Journal of Botany*,

- 76: 389–396.
- TRAPPE, J. M. & GERDEMANN, J. W. (1972): *Endogone flammicorona* sp. nov., a distinctive segregate from *Endogone lactiflua*. – Transactions of the British Mycological Society, **59**: 403–407.
- WHITE, J. F. JR. & TAYLOR, T. N. (1988): Triassic fungus from Antarctica with possible ascomycetous affinities. – American Journal of Botany, **75**: 1495–1500.
- WHITE, J. F. JR. & TAYLOR, T. N. (1989a): An evaluation of sporocarp structure in the Triassic fungus *Endochaetophora*. – Review of Palaeobotany and Palynology, **61**: 341–345.
- WHITE, J. F. JR. & TAYLOR, T. N. (1989b): Triassic fungi with suggested affinities to the Endogonales (Zygomycotina). – Review of Palaeobotany and Palynology, **61**: 53–61.
- WHITE, J. F. JR. & TAYLOR, T. N. (1991): Fungal sporocarps from Triassic peat deposits in Antarctica. – Review of Palaeobotany and Palynology, **67**: 229–236.
- WILLIAMSON, W. C. (1880): On the organization of the fossil plants of the Coal-measures. Part 10 – including an examination of the supposed radiolarians of the Carboniferous rocks. – Philosophical Transactions of the Royal Society, London, **B171**: 493–539.
- YAO, Y.-J., PEGLER, D. N. & YOUNG, T. W. K. (1995): *Yungiomyces*, a new genus in Endogonales (Zygomycotina). – Kew Bulletin, **50**: 349–357.
- ZYCHA, H., SIEPMANN, R. & LINNEMANN, G. (1969): Mucorales. Eine Beschreibung aller Gattungen und Arten dieser Pilzgruppe; Lehre (Verlag von J. Cramer), viii + 355 p.
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