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A microfungal assemblage in *Lepidodendron* from the Upper Visean (Carboniferous) of central France

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Abstract

A diverse assemblage of microfungi and fungi-like microorganisms, composed of several types of hyphae, putative reproductive structures (sporangia), and a variety of spores, occurs in permineralized *Lepidodendron* xylem and periderm from the Upper Visean of central France. Some of the remains can be attributed to the Chytridiomycota and Peronosporomycetes (Oomycota) with some degree of confidence. We suggest that this assemblage represents a community of saprotrophic organisms that colonized the tissues post mortem and participated in the decay process. The permineralized *Lepidodendron* tissues from France offer a rare direct insight into the diversity of microfungi and fungi-like organisms in a Carboniferous terrestrial paleoecosystem. ***To cite this article: M. Krings et al., C. R. Palevol 6 (2007).***

Résumé

Une association de champignons microscopiques dans des *Lepidodendron* du Viséen supérieur (Carbonifère) du Massif central français. Une association variée de champignons microscopiques et de microorganismes de type champignon, composée de plusieurs types d'hyphes, de structures reproductrices (sporanges) et de diverses spores, est présente dans le xylème et le périderme de tiges de *Lepidodendron* perminéralisés du Viséen supérieur du Massif central français. Certains restes peuvent être attribués aux Chytridiomycota et aux Peronosporomycetes (Oomycota), avec un degré certain de confiance. Nous suggérons que cette association représente une communauté d'organismes saprotrophiques qui colonisaient les tissus post mortem et contribuaient au processus de décomposition. Les tissus de ces *Lepidodendron* perminéralisés de France offrent l'exemple rare d'un aperçu direct de la biodiversité des champignons microscopiques et des organismes de type champignon dans un paléoécosystème terrestre du Carbonifère. ***Pour citer cet article : M. Krings et al., C. R. Palevol 6 (2007).***

Keywords: Chert; Chytridiomycota; Combres; Hyphae; *Lepidodendron rhodumnense*; Peronosporomycetes; Saprotrophism; Spore; Sporangium; France

Mots clés : *Chert* ; Chytridiomycota ; Combres ; Hyphes ; *Lepidodendron rhodumnense* ; Peronosporomycetes ; Saprotrophisme ; Spore ; Sporange ; France

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1. Introduction

Microorganisms were critical components of ancient ecosystems, and entered into a wide variety of associations and interactions with other organisms. However, only recently have they received increased scholarly attention based on the fossil record [23]. This is because most information on ancient microorganisms comes from indirect evidence and dispersed specimens, rather than from those preserved in the precise environment in which they lived (in situ). Adding to the paucity of documented fossil microorganisms in situ has been the historical belief that these life forms are too delicate to be adequately preserved, and, if they are preserved, cannot be analyzed properly with the techniques available.

One of the first scholars to systematically document Late Paleozoic microorganisms preserved in situ was the French paleobotanist Bernard Renault [9–19]. Renault's success in detailing fossil microbial life was directly attributed to the exceptional preservation of the fossils in a siliceous chert matrix, his ability to produce high quality thin sections of the cherts, and his obvious understanding and appreciation of details of the microbial world. Although Renault discovered microorganisms in a variety of cherts and other rocks of Carboniferous and Permian age, the majority of these organisms were reported from Late Visean (∼330 Ma) cherts of Combres/Lay and Esnost in central France. Particularly interesting are several forms (bacteria, fungi or fungi-like organisms, and microalgae) that occur in association with land plants. Unfortunately, Renault's extraordinary work and insights into the microbial realm in ancient ecosystems was not followed after his death; only three papers detailing various levels of biological interaction have been published since (i.e. [5,7,24]).

Renault was meticulous in documenting the morphology of the individual microorganisms and, in some instances, their distribution within host plant tissues. Moreover, he was concerned with the natural affinities of these organisms, and in fact was correct in many of his taxonomic identifications. He was less interested, however, in elaborating on the complexity attained by some of the land plant/microbial associations preserved in the cherts. This was certainly due to a large degree by the fact that such topics were not of particular scientific interest at that time. Today, however, the levels of complexity attained by land plant/microbial associations represent key areas in ecological and ecophysiological research. This modern focus has initiated questions at several levels regarding the origin of land plant/microbial associations, and hypotheses that explore how they may have evolved (e.g., [4]). Answers have primarily come from molecular analyses of modern systems, whereas the fossil record has been used only in a limited sense. However, where preservation of microorganisms permits detailed macro- and microscopical documentation, the fossil record is becoming increasingly important as the only method of documenting complex land plant/microbial associations within an evolutionary context [8].

Here, we report on a diverse fossil assemblage of microfungi and/or fungi-like microorganisms consisting of hyphae, reproductive structures, and spores that occurs within the xylem and endophelloderm (i.e. the inner portion of the periderm) of *Lepidodendron rhodumnense* Renault from the Upper Visean of central France.

2. Material and methods

The cherts containing the infected *Lepidodendron rhodumnense* xylem and periderm come from the Upper Visean (Mississippian [= Lower Carboniferous]) of Combres (approximately 12 km south of Roanne), Massif Central, central France. They occur as loose blocks within rhyolitic tuffs, and were collected in cultivated fields or in stream sections. The geological setting and paleoenvironment of the Late Visean in the Roanne area have been interpreted as analogous to that in the Autun basin at the locality of Esnost, about 10 km north of Autun, Massif Central, central France [3]. Information on the geological setting of the Esnost locality can be found in [21]; for details on the preservation of fossils and a paleoecological reconstruction of the Visean wetland ecosystem at Esnost see [20].

The microfungi were identified in two thin sections (i.e. 1. xylem and endophelloderm, radial section, slide No. B49/1118; 2. endophelloderm, tangential section, slide No. B50/1137) prepared by cementing a wafer of chert to a glass slide and then grinding the wafer to a thickness sufficiently thin to be examined in transmitted light. The thin sections were prepared by B. Renault and co-workers during the late 19th and early 20th centuries, and are today housed in the 'Muséum national d'histoire naturelle' ('Laboratoire de paléontologie') in Paris (France).

3. Description of microfungi and fungi-like microorganisms

The permineralized *Lepidodendron* tissues from the Upper Visean of Combres contain abundant remains of intracellular microfungi and fungi-like microorganisms in the form of three distinct types of hyphae, several putative reproductive structures (sporangia), and a variety of

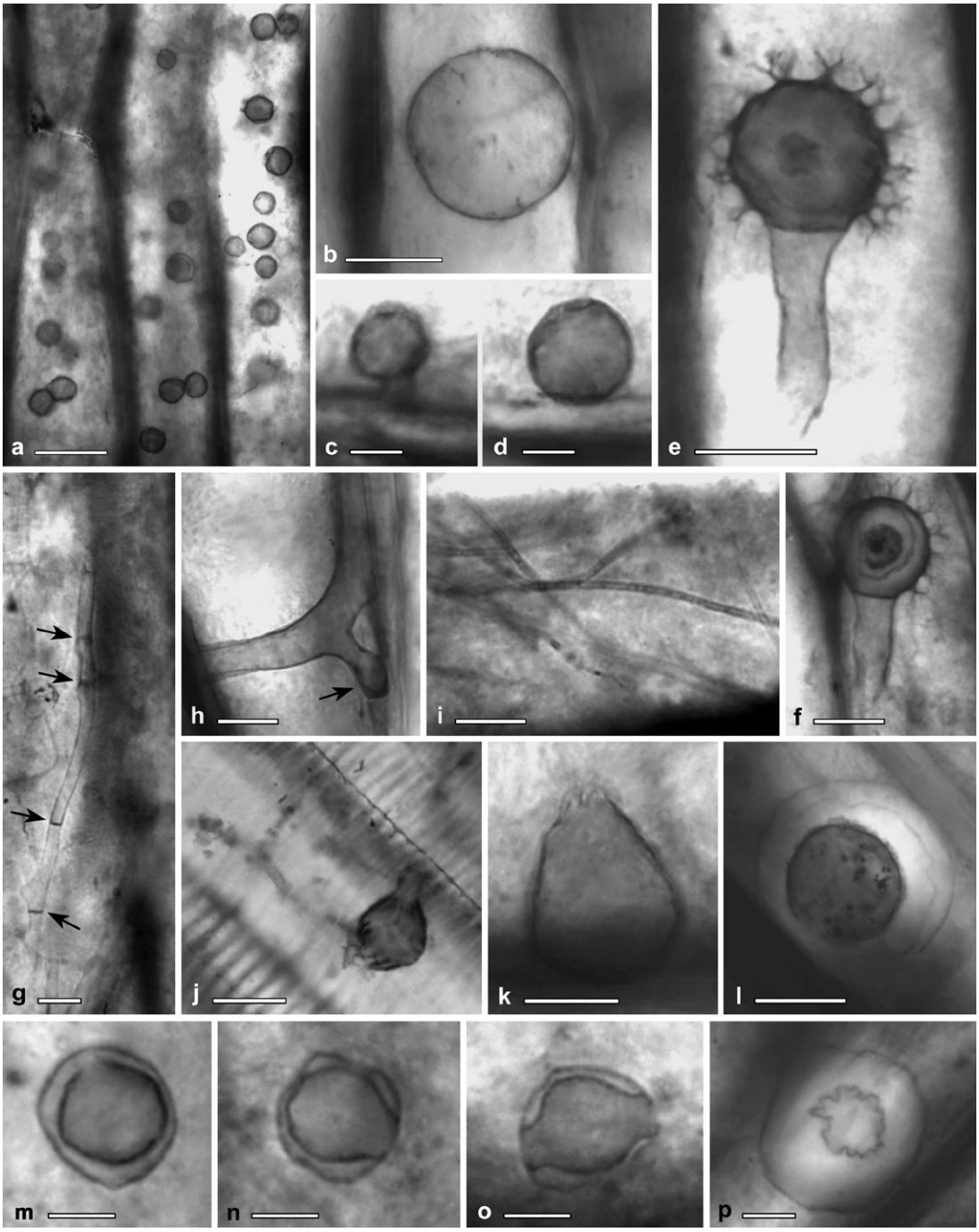

Fig. 1. Intracellular microfungi and fungi-like microorganisms in *Lepidodendron* from the Upper Visean of central France. (**a**) Clusters of small spherical spores in the endophelloderm. Slide B49/1118; bar = 20 μm. (**b–d**) Various types of intracellular spherical spores or sporangia: (**b**) unattached, large, and without orifice; (**c**) attached, small, stalked, and with distal orifice; (**d**) attached, small, unstalked, and with distal orifice. Slide B50/1137; bars = 20 μm (**b**) and 5 μm (**c,d**). (**e,f**) Oosporangia with repeatedly forking surface extensions and wide, aseptate subtending hyphae. Slide B50/1137; bars = 20 μm. (**g**) Medium-sized, irregularly septate hypha; arrows indicate simple septa. Slide B50/1137; bar = 10 μm. (**h**) Wide aseptate hypha with short, terminally swollen lateral branch (arrow). Slide B50/1137; bar = 10 μm. (**i**) Narrow aseptate hyphae. Slide B50/1137; bar = 10 μm. (**j**) Pear-shaped ?zoosporangium with narrow, aseptate subtending hypha growing along the inner surface of a tracheid. Slide B49/1118; bar = 40 μm. (**k**) Pear-shaped ?zoosporangium with apical cleft, attached to a cell wall. Slide B50/1137; bar = 10 μm. (**l**) Large,

spores. Some of the organisms are attached to cell walls, while others appear in the cell lumen. Although the thin sections come from two different chert blocks, the microfungal assemblages found within the tissues are largely composed of the same forms of organisms.

The most abundant fungal remains in the endophelloderm are three distinct types of hyphae, including (1) loose meshworks of narrow, septate, and rarely branching hyphae (Fig. 1i), between 0.9 and 1.1 μm wide, that occur in ∼55% of the cells; (2) medium-sized, septate, and usually unbranched hyphae, between 2.5 and 3.5 μm wide (Fig. 1g) that have been observed in <5% of the cells; and (3) large, aseptate or occasionally septate hyphae, between 4.5 and 12 μm wide, that occur in >75% of the cells and give off medium-sized, typically aseptate hyphae. Most of the large hyphae extend parallel to the long axis of the elongate cells; rarely do they extend perpendicular to the orientation of the cells. Wide hyphae sometimes produce short lateral branches that are terminally swollen (Fig. 1h [arrow]). All hyphal types appear to extend from one cell to another through the pits in the cell walls; host responses to fungal penetration have not been observed. Hyphae also occur in the xylem, but are less well preserved.

Also present in the tissues are numerous forms of spores. In many cells, they occur in large number (e.g., Fig. 1a) and are associated with narrow hyphae. Most spores are spherical, between 5.0 and 15 μm in diameter, and possess thin and translucent or relatively thick and opaque walls. One spore type (Fig. 1m–o) is characterized by a thick but translucent wall and two, usually oppositely positioned, circular openings (Fig. 1o). Other spherical structures in the tissues cannot be identified as to whether they are fungal spores or sporangia. These include (1) large, thin-walled spherical bodies (Fig. 1b), between 30 and 35 μm in diameter, that are borne on narrow hyphae and do not display any surface ornamentation or what can be termed preformed openings; (2) tiny spherules, up to 8.0 μm in diameter, that are attached to the cell walls by a short stalk, up to 3.0 μm long, and characterized by a distal circular orifice, 2.0 μm in diameter (Fig. 1c); (3) medium-sized spherical bodies, up to 15 μm in diameter, that are similar in shape to the previously described structures but lacking stalks (Fig. 1d); (4) large, double-walled structures, 25–30 μm in diameter, containing a single, usually dark-walled sphere that may be ornamented (Fig. 1l); and (5) large, relatively thin-walled spheres, up to 35 μm in diameter, in which the contents have a wrinkled surface and are variously shaped (Fig. 1p).

We interpret two types of structures as probably representing some form of fungal sporangium. One of these is borne terminally on aseptate hyphae that grow along the inner surfaces of cell walls (Fig. 1j). This structure is pear-shaped, up to 60 μm high, and composed of a relatively thick-walled basal sphere (30–40 μm in diameter) to which is distally attached a thin-walled tube. The second form is also pear-shaped, between 45 and 55 μm high, but to date not found in organic connection to a subtending hypha. Rather, this structure is attached directly to the host cell wall; most of the specimens possess an apical cleft embracing a small opening (Fig. 1k).

The most conspicuous structures occur exclusively in cells of the endophelloderm. These are thick-walled spheres, between 25 and 35 μm in diameter, characterized by repeatedly forking, antler-like surface extensions, each up to 6.0 μm high. These spheres are always borne on prominent, aseptate subtending hyphae (Fig. 1e and f), up to 15 μm wide. Most specimens contain a single opaque globe, 10–25 μm in diameter, surrounded by a relatively thin, wrinkled wall (Fig. 1f).

4. Discussion

Bernard Renault's systematic analysis of Visean microorganisms preserved in cherts from central France represents a benchmark contribution to our understan-

double-walled sporangium containing a single dark-walled, ornamented spore. Slide B49/1118; bar = 20 μm. (**m–o**) Small thick-walled spores with two oppositely positioned openings (best seen in Fig. 1o). Slide B50/1137; bars = 5 μm. (**p**) Large ?resting spore. Slide B49/1118; bar = 10 μm.

Fig. 1. Champignons microscopiques et microorganismes de type champignon intracellulaires dans un *Lepidodendron* du Viséen supérieur de France. (**a**) Groupes de petites spores sphériques dans l'endophelloderme. Lame B49/1118; échelle = 20 μm. (**b–d**) Types variés de spores ou sporanges sphériques intracellulaires : (**b**) non attaché, grand et sans orifice ; (**c**) attaché, petit, pédicellé et avec orifice distal ; (**d**) attaché, petit, sessile et avec orifice distal. Lame B50/1137 ; échelles = 20 μm (**b**) et 5 μm (**c,d**). (**e,f**) Oogones/Oosporanges avec des expansions superficielles plusieurs fois ramifiées, terminant une large hyphe non septée. Lame B50/1137 ; échelles = 20 μm. (**g**) Hyphe de taille moyenne, irrégulièrement septée ; les flèches désignent des cloisons simples. Lame B50/1137 ; échelle = 10 μm. (**h**) Large hyphe sans cloison, avec une courte ramification à terminaison renflée (flèche). Lame B50/1137 ; échelle = 10 μm. (**i**) Hyphes étroites non septées. Lame B50/1137 ; échelle = 10 μm. (**j**) ?Zoosporange pyriforme à l'extrémité d' une hyphe étroite, non septée, qui s'étend le long de la face interne d'une trachéide. Lame B49/1118 ; échelle = 40 μm. (**k**) ? Zoosporange pyriforme avec une ouverture apicale, attaché à une paroi cellulaire. Lame B50/1137 ; échelle = 10 μm. (**l**) Grand sporange, à double paroi, contenant une seule spore à paroi sombre et ornementée. Lame B49/1118 ; échelle = 20 μm. (**m–o**) Petites spores à paroi épaisse avec deux ouvertures diamétralement opposées (bien visible en Fig. 1o). Lame B50/1137 ; échelles = 5 μm. (**p**) Large spore ? non fonctionnelle. Lame B49/1118 ; échelle = 10 μm.

ding of the diversity of microbial life in Late Paleozoic non-marine ecosystems. The significance of Renault's work parallels that of Kidston and Lang's study of microscopic life in the Early Devonian Rhynie chert [6]. Unlike the Rhynie chert microorganisms, however, the existence of exquisitely preserved minute life forms in Visean cherts from France has largely been forgotten since Renault's death. Nevertheless, his meticulous work and detailed studies represent another chapter in the investigation of microorganisms in ancient ecosystems, and constitute a largely untapped source of information about microbial life some 330 Ma ago.

The microfungal remains discovered in the *Lepidodendron* tissues indicate that these life forms were abundant and diverse, and therefore played an important role in the ecology of the Visean ecosystem at this site. It is difficult at present to accurately determine the systematic affinities of most of the microfungal remains because they consist of isolated parts and propagule, or stages of the life cycle in which critical features required in microfungal systematics are lacking. Only a few of the specimens documented here can be referred to a particular group of microfungi or fungi-like microorganisms with some degree of confidence based on comparisons to extant and other fossil forms. For example, the specimen illustrated in Fig. 1k probably represents an empty chytrid zoosporangium. There is some morphological resemblance to *Lyonomyces pyriformis* T.N. Taylor, Hass et W. Remy described as a parasite of the green alga *Palaeonitella cranii* (Kidston et W.H. Lang) J. Pia from the Rhynie chert [25]. An organism described from Carboniferous lycophyte tissues by Renault [14] as *Oochytrium lepidodendroni* consists of narrow hyphae and spherical or spindle-shaped sporangia. The narrow hyphae depicted in Fig. 1i and the spore-like structures illustrated in Fig. 1m–o might belong to this organism, which we interpret as a peronosporomycete (oomycete). Other structures described by Renault [14] from lycophyte tissues closely resemble the fossils illustrated in Fig. 1c and d, and probably also represent peronosporomycetous oospores/oosporangia. Similar structures have been found in the Carboniferous seed-like structure *Nucellangium glabrum* (Darrah) H.N. Andrews from North America, and interpreted as oogonia/oosporangia of an *Albugo*-like microorganism [22].

The most conspicuous microfossils occurring in the *Lepidodendron* endophelloderm are the specimens illustrated in Fig. 1e and f. This fossil is abundant in both samples (more than 60 individuals), and thus makes it possible to provide a detailed description and assessment of the organism that produced these structures. The structures most closely resemble the oosporangia produced by extant peronosporomycetes. This hypothesis is based principally on the presence of several specimens displaying a laterally adpressed antheridial hypha with terminal antheridium that resembles antheridia seen in modern members of the Peronosporomycetes. While the oosporangia in most extant peronosporomycetes are thin-walled and non-ornamented, some forms are characterized by a relatively thick wall, which may be variously ornamented [1]. However, we are not aware of any extant peronosporomycete that produces antler-like surface ornamentation. Within the extant peronosporomycetes, the number of oospores contained in an oosporangium is variable, ranging from one to several. The fossils consistently contain a single oospore. Extant pernonosporomycetes producing oosporangia with a single oospore are found in the Peronosporaceae, Pythiogetonaceae, Verrucalvaceae, and in some members of the Leptomitales and Rhipidiales [2]. It is possible that the fossil oogonia/oosporangia were borne on the wide hyphal type (Fig. 1h) based on the corresponding diameters of these hyphae and the subtending oogonial hyphae. The possibility exists that the short, terminally swollen lateral branches produced by the wide hyphae (Fig. 1h [arrow]) represent the initial stage in oogonium formation. If this hypothesis is accurate, then the process of oogonium formation in this Carboniferous organism resembles that of the Early Devonian peronosporomycete *Hassiella monospora* T.N. Taylor, M. Krings and Kerp, which includes short, terminally swollen hyphal branches that also represent the initial stage in oogonium formation [26].

It is equally difficult to determine the nature of the associations between the individual microorganisms and the *Lepidodendron rhodumnense* plant based on the fossils. The microorganisms may represent space endophytes or true parasites that entered the host plant while it was alive and subsequently colonized the interior tissues. On the other hand, host reactions have not been observed, which may indicate that the fungi were saprotrophs that entered the tissues post mortem and participated in the decay process. This interpretation, however, is somewhat problematic since some of the infected cells are tracheids, which are non-living at maturity, and thus not capable of producing any structural alteration in response to an invading parasite. Adding support to the hypothesis that the microorganisms represent saprotrophs colonizing the tissues after death of the plant is perhaps their abundance and ubiquitous occurrence in the samples. In addition, some of the structures discovered inside the tissues have also been observed in other thin sections where they occur in the chert matrix, associated with an accumulation of small degrading

plant fragments. Moreover, the cauline system of *L. rhodumnense* is to date known only from narrow twigs, up to 2.0 cm in diameter, which probably were positioned high up in the plant, and thus in vivo not easily accessible for soil-borne microbial endophytes. Additional material will be required to more accurately define the systematic affinities of the specimens, and to more fully understand the diversity and nature of this complex community of microfungi and fungi-like microorganisms that lived inside the tissues of *L. rhodumnense*.

The initial work by Renault in describing some of these microorganisms has opened a new window into the microbial world that existed during the Late Paleozoic. Documenting these minute life forms and the organisms in which they occur makes it possible to infer the existence of various levels of biological interaction. Renault's work clearly indicates that he understood the significance of the biological interactions represented in the fossils he prepared and examined. It is our intent to completely analyze the slides from the 'collection Renault' and other collections in order to fully document the microbial diversity and associations and interactions with other organisms in the Visean ecosystems from central France. We believe that continuing the work that Renault initiated more than 100 years ago will help to underscore the incredible genius of this paleobotanist.

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References

[1] M.W. Dick, Morphology and taxonomy of the Oomycetes, with special reference to Saprolegniaceae, Leptomitaceae and Pithyaceae. I. Sexual reproduction, New Phytol. 68 (1969) 751–775.
[2] M.W. Dick, P.T.W. Wong, G. Clark, The identity of the oomycete causing 'Kikuyu Yellows', with a reclassification of the downy mildews, Bot. J. Linn. Soc. 89 (1984) 171–197.
[3] J. Galtier, Sur les flores du Carbonifère inférieur d'Esnost et du Roannais, Bull. Soc. Hist. Nat. Autun 57 (1971) 24–28.
[4] R.M. Goodman, J.B. Weisz, Plant-microbe symbioses: an evolutionary survey, in: J.T. Staley, A.L. Reysenbach (Eds.), Biodiversity of Microbial Life. Foundation of Earth's Biosphere, John Wiley & Sons Inc, New York, Chichester, Weinheim, Germany, 2002, pp. 237–287.
[5] A. Grewing, M. Krings, J. Galtier, H. Kerp, S.D. Klavins, T.N. Taylor, The oldest fossil endophytic alga and its unusual habitat, Symbiosis 34 (2003) 215–230.
[6] R. Kidston, W.H. Lang, On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The Thallophyta occurring in the peat-bed; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit, Trans. R. Soc. Edinb. 52 (1921) 855–902.
[7] M. Krings, A. Grewing, T.N. Taylor, H. Kerp, J. Galtier, *Lageniastrum macrosporae* (fossil Volvocales, Lageniastraceae nov. fam.), an endophyte in megaspores from the Carboniferous of the French Massif Central, Geobios 38 (2005) 451–465.
[8] M. Krings, T.N. Taylor, H. Hass, H. Kerp, N. Dotzler, E.J. Hermsen, Fungal endophytes in a 400-million-yr-old land plant: infection pathways, spatial distribution, and host responses, New Phytol. 174 (2007) 648–657.
[9] B. Renault, Bactéries des temps primaries, Bull. Soc. Hist. Nat. Autun 7 (1894) 433–468.
[10] B. Renault, Sur quelques nouveaux parasites des Lépidodendrons, Soc. Hist. Nat. Autun, Procès-Verbal des Séances 1893 (1894) 168–178.
[11] B. Renault, Chytridinées fossiles du Dinantien (Culm), Rev. Mycol. 17 (1895) 158–161.
[12] B. Renault, Parasites des écorces de Lépidodendrons, Le Naturaliste 9 (1895) 77–78.
[13] B. Renault, Sur quelques *Micrococcus* du Stéphanien, terrain houiller supérieur, C. R. Acad. Sci. Paris 120 (1895) 217–220.
[14] B. Renault, Bassin houiller et Permien d'Autun et d'Épinac. Fascicule IV : Flore fossile, deuxième partie, Études des Gîtes Minéraux de la France, Imprimerie Nationale, Paris, 1896.
[15] B. Renault, Notice sur les travaux scientifiques de M. Bernard Renault, Imprimerie Dejussieu Père et fils, Autun, France, 1896.
[16] B. Renault, Recherches sur les Bactériacées fossiles, Ann. Sci. Nat., Ser. 8 Bot. 2 (1896) 275–349.
[17] B. Renault, Sur quelques microorganismes des combustibles fossiles, Société de l'imprimerie Théolier, J. Thomas et Cie, Saint-Étienne, France, 1900.
[18] B. Renault, Sur quelques nouveaux champignons et algues fossiles, de l'époque houillère, C. R. Acad. Sci. Paris 136 (1903) 904–907.
[19] B. Renault, C.E. Bertrand, *Grilletia Spherospermii*, Chytridiacée fossile du terrain houiller supérieur, C. R. Acad. Sci. Paris 100 (1885) 1306–1308.
[20] G.M. Rex, The preservation and palaeoecology of the Lower Carboniferous silicified plant deposits at Esnost, near Autun, France, Geobios 19 (1986) 773–800.
[21] A.C. Scott, J. Galtier, G. Clayton, Distribution of anatomically preserved floras in the Lower Carboniferous in western Europe, Trans. R. Soc. Edinb., Earth Sci. 75 (1984) 311–340.
[22] B.M. Stidd, K. Cosentino, *Albugo*-like oogonia from the American Carboniferous, Science 190 (1975) 1092–1093.
[23] T.N. Taylor, M. Krings, Fossil microorganisms and land plants: associations and interactions, Symbiosis 40 (2005) 119–135.
[24] T.N. Taylor, J. Galtier, B.J. Axsmith, Fungi from the Lower Carboniferous of central France, Rev. Palaeobot. Palynol. 83 (1994) 253–260.
[25] T.N. Taylor, H. Hass, W. Remy, Devonian fungi: interactions with the green alga *Palaeonitella*, Mycologia 84 (1992) 901–910.
[26] T.N. Taylor, M. Krings, H. Kerp, *Hassiella monospora* nov. gen. et sp., a microfungus from the 400 million year old Rhynie chert, Mycol. Res. 110 (2006) 628–632.