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Galtierella biscalithecae nov. gen. et sp., un oomycète endophyte (Peronosporomycetes) du Pennsylvanien supérieur de France

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ABSTRACT

A new fossil water mold (Peronosporomycetes), *Galtierella biscalithecae* nov. gen. et sp., consisting of coenocytic hyphae occurs as an intracellular endophyte in a partially degraded specimen of the reproductive organ *Biscalitheca* cf. *musata* (Zygopteridales) from the Upper Pennsylvanian Grand-Croix cherts (Saint-Étienne Basin, France). Some hyphal tips produce small spheres that subsequently develop into ornamented, opaque-walled oogonia; amphigynous antheridia encircle the necks of several immature oogonia. Also present are ovoid structures, which may represent differently shaped oogonia, hyphal swellings, or zoosporangia. Small dome-shaped structures, probably zoospore cysts, are attached to numerous host cell walls. This discovery sheds new light on the morphology and biology of water molds in a Carboniferous ecosystem.

RÉSUMÉ

Un nouvel oomycète (Peronosporomycetes), *Galtierella biscalithecae* gen. et sp. nov., constitué d'hyphes coenocytiques est présent sous forme d'endophyte intracellulaire dans un spécimen partiellement dégradé de l'organe reproducteur *Biscalitheca* cf. *musata* (Zygopteridales) des cherts du Pennsylvanien supérieur de Grand-Croix (bassin de Saint-Étienne, France). Certaines hyphes produisent à leur extrémité de petites sphères qui se développent par la suite en oogones à paroi ornementée et opaque ; des anthéridies amphigynes entourent le col de plusieurs oogones immatures. Des structures ovoïdes qui représentent peut-être des oogones de formes différentes, des renflements des hyphes ou des zoosporanges sont aussi présentes. De petites structures en forme de dôme, probablement des cystes de zoospores, sont attachées à de nombreuses parois cellulaires de l'hôte. Cette découverte apporte un nouvel éclairage sur la morphologie et la biologie des oomycètes dans un écosystème du Carbonifère.

Mots clés :
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1. Introduction

Water molds (Peronosporomycetes; Oomycota in older treatments) are heterotrophic fungal-like microorganisms, which are known as saprotrophs and parasites of plants, animals, and other fungi (Dick, 2001a, b). Although it has been suggested that peronosporomycetes occurred on Earth as early as the Precambrian (Pirozynski, 1976), fossil evidence has remained meagre and largely equivocal (Johnson et al., 2002), mainly because these organisms are defined by characters that are difficult or sometimes even impossible to resolve with fossils (Dick, 2001a). The characteristic oogonium-antheridium complexes that occur during the sexual reproduction process represent the only structural feature that can be used to positively identify fossil peronosporomycetes. However, a key requisite for being able to accurately document fossil oogonium-antheridium complexes is the three-dimensional preservation (e.g., in a chert or amber matrix) in which the physical configuration of these structures can be examined in detail.

Two fossil peronosporomycetes displaying oogonium-antheridium complexes have been described to date. The first, *Hassiella monospora* Taylor et al. from the Lower Devonian Rhynie chert (Taylor et al., 2006), is composed of coenocytic hyphae that produce ornamented (verrucate) oogonia containing single oospores. What is interpreted as an amphigynous antheridium is present as a funnel-shaped appendage in some of the oogonia. The second, *Combresomyces cornifer* Dotzler et al. from the Visean (Upper Mississippian) cherts of central France (Dotzler et al., 2008) and Middle Triassic cherts of Antarctica (Schwendemann et al., 2009), produces monosporous oogonia with a prominent surface ornament of antler-like extensions on hollow papillations of the oogonial wall. Paragynous antheridia are adpressed in several of the Visean specimens.

The Late Pennsylvanian Grand-Croix cherts from central France are widely known for their structurally preserved terrestrial plants (e.g., Doubinger et al., 1995; Galtier, 2008). Co-occurring with these plants is a plethora of microorganisms, including various fungi (e.g., Renault et al., 1896; Renault, 1900; Krings et al., 2009a, b). This paper presents the first record of a peronosporomycete from Grand-Croix. *Galtierella biscalithecae* nov. gen. et sp. is an intracellular endophyte that occurs in the zygopterid reproductive organ *Biscalitheca* cf. *musata*. This discovery provides important details about the morphology and biology of water molds in a terrestrial ecosystem ~300 Ma years ago.

2. Material and methods

The Grand-Croix cherts come from the eastern part of the Saint-Étienne Basin in central France where they occur within the "Poudingue mosaïque" at several localities in the vicinity of the city of La Grand-Croix (Galtier, 2008). The exact stratigraphic provenance and age of the cherts remain controversial. They have been interpreted as belonging either to the terminal portion of the Rive de Gier Formation, which has been dated as Stephanian A (Vetter, 1971), or to the overlying deposits, which are earliest Stephanian B in age (Pruvost, 1947). Nevertheless, the plants contained in the Grand-Croix cherts are probably reworked, and hence slightly older, i.e. Late Stephanian A (equivalent to the late Barruelian) in age (Doubinger et al., 1995). The flora from Grand-Croix represents one of only a few European equivalents to the Late Pennsylvanian coal balls floras from North America (Galtier and Phillips, 1985; Galtier, 2008).

Biscalitheca cf. *musata* Mamay is a reproductive organ of a zygopterid fern that consists of clusters of elongate, slightly curved sporangia (Fig. 1a) positioned on soral stalks that are attached to minute rachides. It has been suggested that *B.* cf. *musata* belongs to the plant that produced *Etapteris* cf. *lacattei* Renault petioles (Galtier, 1978; Galtier and Grambast, 1972; Galtier, 2008). The sporangium walls, in which most specimens of *G. biscalithecae* were discovered, are complex and composed of at least four different types of cells (Galtier and Grambast, 1972), including elongate annulus cells that have massive walls up to 15 μm thick (Fig. 1f).

The infected specimen of *Biscalitheca* cf. *musata* was identified in a thin section prepared by cementing a piece of chert to a glass slide and then grinding the rock wafer until it is thin enough to be examined in transmitted light. The thin section, which was prepared during the late 19th century, is today housed in the *Muséum national d'histoire naturelle* (*Laboratoire de paléontologie, 'collection Renault'*) in Paris (France).

3. Systematic paleontology

Peronosporomycetes M.W. Dick, 2001b, *incertae sedis*.
Morphogenus *Galtierella* nov. gen.

3.1. Type species

G. biscalithecae nov. sp.

3.2. Diagnosis

Hyphae coenocytic, thin-walled, aseptate, usually Ω-shaped in cross-section; oogonia terminal, more or less spherical, up to 20 μm in diameter, opaque-walled at maturity, ornamented, subtended by wide or narrow hypha (oogonial stalk); oogonial wall ornament of short bristles or hairs; simple septum between oogonium and oogonial stalk; stalk often slightly narrower immediately below oogonium; antheridium amphigynous; ovoid structures occasionally present in cells containing oogonia, terminal on hyphae, typically larger than oogonia, separated from partental hypha by constriction; putative zoospore cysts dome-shaped, usually < 10 μm in diameter, thick-walled, faintly ornamented; endophytic in *Biscalitheca* cf. *musata*, intracellular, vegetative hyphae extending along inner surfaces of host cells, oogonial stalks and ovoid structures extending into cell lumen, putative zoospore cysts sessile.

3.3. Description

G. biscalithecae is common in the thick-walled annulus cells of the *Biscalitheca* cf. *musata* sporangia (Fig. 1a), but has also been found in other cells of the complex sporangium wall, as well as in other tissues of the reproductive structure. The organism has not been detected in any other plant tissue preserved in the chert, nor has it been found in the chert matrix.

The vegetative system consists of coenocytic hyphae, (3–)8–11(–14,5) μm wide and (2–)5–12(–16) μm high, which are more or less Ω-shaped in cross-section (Fig. 1j), relatively thin-walled (Fig. 1f), and aseptate. They typically extend along the inner surfaces of the host cell walls.

Thin-walled spherical structures (marked with an O in Fig. 1b, c, l), 8–13 μm in diameter (17.5 μm in the specimen illustrated in Fig. 1c), occur in a terminal position on some hyphae; a simple septum is present between the spherical structure and subtending hypha (Fig. 1b). The distal portion of the subtending hypha may be as wide as the normal, vegetative hyphae (Fig. 1b, l) or considerably narrower (Fig. 1c); wide subtending hyphae are usually slightly narrower immediately below the septum (Fig. 1k, l). The distal portion of the parental hypha extends into the host cell lumen. The wall of the spherical structures is < 0.5 μm thick (slightly thicker and more opaque in the specimen illustrated in Fig. 1c); a surface ornament of delicate short bristles is faintly recognizable in some specimens (Fig. 1b, c). Encircling the necks of some spheres are collar-like structures up to 6 μm wide (indicated by arrows in Fig. 1c, l).

Other spherical structures are larger [(12–)15–18(–19.5) μm in diameter], and have a thicker (∼0.8–1 μm) and distinctly more opaque wall (Fig. 1d–g) that forms a more or less complete circle in longitudinal section (e.g., Fig. 1d, g). Spheres are usually positioned on hyphal tips (Fig. 1e), but some may also occur isolated (Fig. 1g). If they are attached to a hypha, the distal portion of the hypha typically extends into the cell lumen (Fig. 1e), but in a few instances it appears to be adpressed to the host cell wall (Fig. 1f). The spheres have a surface ornamentation composed of mostly delicate bristles or hairs. A few of the bristles, however, are distinctly longer, more massive, and opaque (Fig. 1e[arrows]); some even appear to be forked (Fig. 1g[arrow]).

Some hyphae also produce ovoid structures (Fig. 1b, c) that we interpret as terminal, which may occur singly (Fig. 1b[S]) or in chains of two or three (Fig. 1k[S] in upper right of image]). These structures are up to 31 μm long and 25 μm wide, possess slightly thinner (∼0.6 μm) and more translucent walls than the large spherical structures; a surface ornament like that in the large spherical structures may be present but is less conspicuous. Septa do not apparently occur between the ovoid structures and the parental hypha; however, in one specimen there is a constriction at the base of the ovoid structure and what appears to be an imperfect septum with a central pore (Fig. 1b[arrow]). The ovoid structures extend into the cell lumen (Fig. 1b). It is interesting that spherical and ovoid structures typically co-occur in the same host cells (Fig. 1b, c, k), whereas cells containing exclusively vegetative hyphae rarely show the formation of ovoid structures.

Many infected host cells contain small structures [(3.5–)5–9(–11) μm in diameter] that are more or less dome-shaped, relatively thick-walled, and attached to the host cell walls (Fig. 1h, i). These structures occur isolated (i.e. not positioned on a hyphal tip), and usually are arranged in small clusters (Fig. 1i). Some are distally open (Fig. 1h). The portion of the wall that is in contact with the host cell wall appears thinner than the wall that extends into the host cell lumen; as a result, spheres in longitudinal section often appear like an inverted letter U; see Fig. 1h[arrow], i). The spheres appear to possess a delicate surface ornament of short bristles or hairs, but this is difficult to document. Longitudinal sections through the spheres may appear similar to cross-sections of vegetative hyphae. However, the latter are usually Ω-shaped and the wall is thinner (e.g., compare Fig. 1j with Fig. 1h, i). They differ from longitudinal sections through the large spherical structures in that the opaque wall forms a more or less complete circle in the latter (compare Fig. 1d, f, g with Fig. 1h, i).

3.4. Material

Slide REN-2219, *Muséum national d'histoire naturelle* (*Laboratoire de paléontologie, 'collection Renault'*) in Paris (France); Fig. 1c in this paper (holotype).

3.5. Type locality

Vicinity of the city of La Grand-Croix, eastern part of the Saint-Étienne Basin, central France.

3.6. Age

Late Stephanian A according to (Galtier, 2008).

3.7. Etymology

The generic name is proposed in honor of Pr Jean Galtier for his extraordinary contributions to our understanding of the biodiversity of Carboniferous terrestrial ecosystems, including Grand-Croix; the epithet acknowledges the occurrence of this organism in *Biscalitheca* cf. *musata*.

3.8. Remark

What appears to be a slightly smaller, thin-walled spherical structure is visible in the interior of most spherical and ovoid structures (Fig. 1b–g). This interior sphere represents an optical artifact resulting from the natural curvature of the walls of these structures within the thin section, and thus is not included in the description.

4. Discussion

G. biscalithecae includes both vegetative and sexual reproductive features that correspond to those seen in modern peronosporomycetes. These include the coenocytic hyphae in which septa are only produced to delimit reproductive structures. Moreover, collar-like structures encircle the necks of several small spheres positioned on hyphal tips (Fig. 1l). This configuration corresponds to the oogonium-amphigynous antheridium complexes seen in some modern peronosporomycetes, e.g., *Phytophthora* de Bary (Shaw, 1988, and references therein). We therefore interpret the small spheres as immature terminal oogonia and the collar-like structures as amphigynous

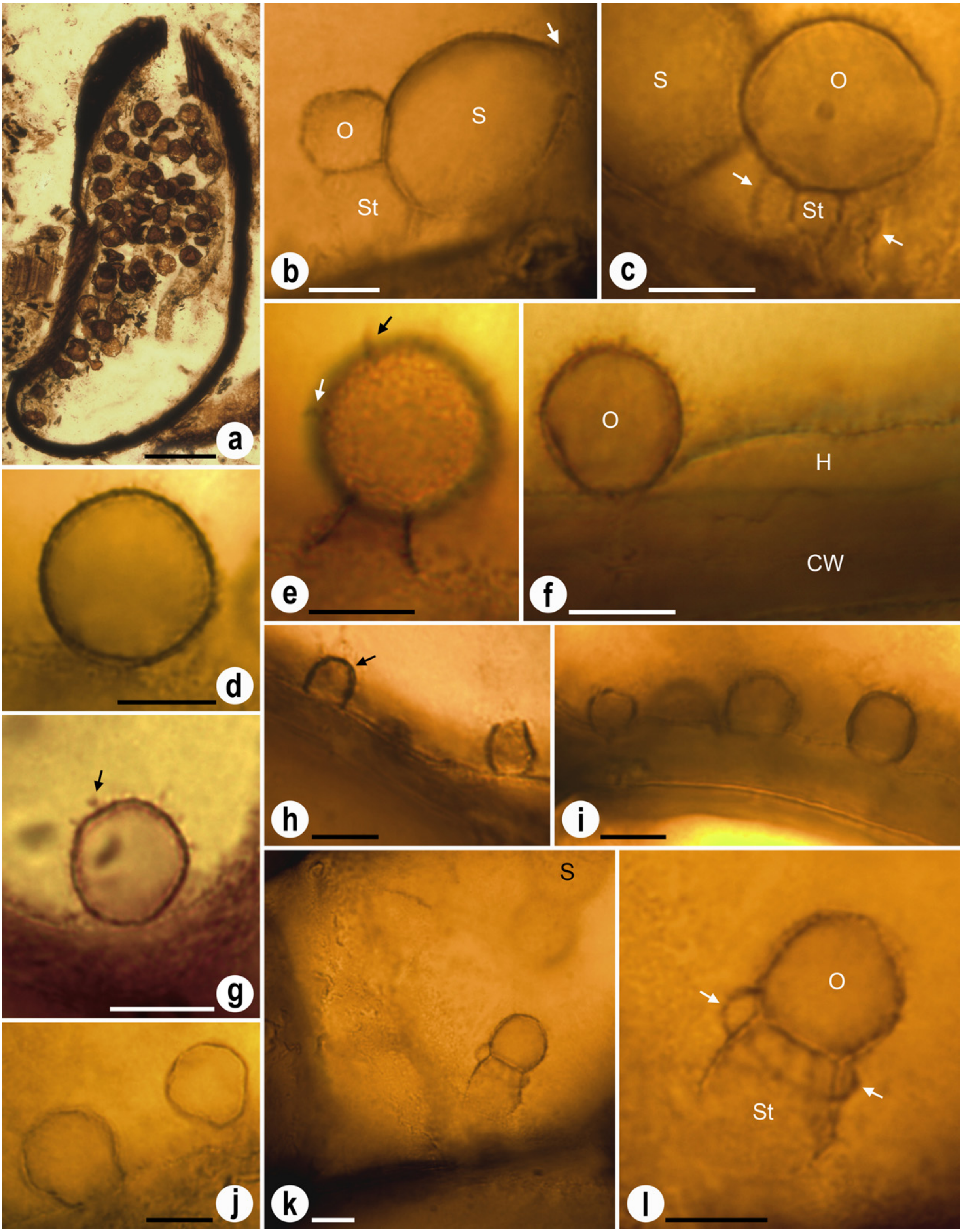

Fig. 1. *Galtierella biscalithecae* nov. gen. et sp., a Late Pennsylvanian peronosporomycete from Grand-Croix; all specimens in slide REN-2219 (collection Renault, Paris); CW: host cell wall; H: hypha, O: oogonium, S: ovoid structure, St: subtending hypha (oogonial stalk); scale bars = 10 μm unless otherwise indicated. (**a**) Sporangium of *Biscalitheca* cf. *musata* containing spores in situ; note relatively thick-walled cells of the sporangium wall; bar = 0.25 mm. (**b**) Immature oogonium positioned terminally on a wide subtending hypha; note large ovoid structure to the right; arrow indicates what appears to be an imperfect septum with a central pore. (**c**) Oogonium-amphigynous antheridium complex and ovoid structure; arrows indicate antheridium. (**d**) Large

antheridia. As a result, we assign *G. biscalithecae* to the Peronosporomycetes.

The specimen illustrated in Fig. 1c has the same basic configuration as the specimen illustrated in Fig. 1l. However, the oogonium (marked O) is distinctly larger and possesses a wall that is slightly thicker and more opaque than that of the specimens interpreted as immature oogonia. Based on this we conclude that the oogonium in Fig. 1c represents a near-mature stage, which has already reached its final size but wall formation has not yet been completed. The large spherical structures (Fig. 1d–g) we believe represent mature oogonia since they differ from the oognium in Fig. 1c only in their thicker and more opaque walls, as well as the more prominent surface ornamentation. Mature oogonia that occur isolated (i.e. not attached to hyphal tips) perhaps became dislodged from the parental hyphae during fossilization, or the oogonia and oospores represent functional (dispersal) units, in which the oogonium remains intact upon maturity of the oospore(s) and decay of the parental hypha. Similar dispersal units have been demonstrated in certain modern peronosporomycetes (e.g., Voglmayr et al., 1999), and this strategy has also been suggested in the fossil *C. cornifer* (Dotzler et al., 2008).

Mature oognia are characterized by a surface ornamentation of bristles or hairs, most of which are delicate and translucent, but some appear to be more massive and opaque. While the oogonia of most extant peronosporomycetes lack ornamentation, some forms may be variously ornamented, ranging from small verrucae and papillae to prominent spines (Dick, 1969, 2001b). It has been suggested that surface ornamentation is a useful character for the identification of extant peronosporomycetes (e.g., Spring and Thines, 2004), and hence may also be utilized in the systematics of fossil forms. However, the ornamentation of *G. biscalithecae* cannot be resolved with sufficient clarity to provide a useful diagnostic character that can allow comparison with extant forms. Recent research also suggests that fossil peronosporomycetes may have had ornamentation patterns that do not directly compare with any pattern seen in extant forms (Dotzler et al., 2008).

The ovoid structures produced by some hyphae (Fig. 1b[S], c[S], k[S]), as well as the small dome-shaped structures (Fig. 1h, i), remain difficult to interpret. The ovoid structures may represent mature oogonia that remained thinner-walled than the spherical oogonia, or immature oogonia that have not yet attained their ultimate wall thickness. However, none of the ovoid structures has been found physically associated with an antheridium. Moreover, a septum appears to be lacking between the ovoid structures and their parental hyphae. Alternatively, these structures may represent undifferentiated hyphal swellings, such as those that are known to occur in many extant *Pythium* Pringsheim species where they may form in a terminal or intercalary position, and may occur singly or in chains (van der Plaats-Niterink, 1981). A third interpretation would be that the ovoid structures are morphologically differentiated zoosporangia. Perhaps arguing against a zoosporangium affinity is the fact that discharge structures in the form of pores, papillae, or tubes have not been observed in any of the specimens.

The dome-shaped structures attached to host cell walls are characterized by a wall that is uneven in thickness (Fig. 1h, i), i.e., the wall portion in contact with the host cell wall is thinner than the portions extending into the host cell lumen. This suggests that the wall formed after the structure had docked at the host wall. The most plausible interpretation of the dome-shaped structures then would be that they represent encysted zoospores. Support for this view comes from the fact that most extant members in the two principal subclasses of the Peronosporomycetes (i.e., Peronosporomycetidae and Saprolegniomycetidae) have zoospore cyst diameters of 8–12 μm (Dick, 2001b), which is consistent with the size range of the fossil structures [i.e. (3.5–)5–9(–11) μm in diameter]. Moreover, encystment of zoospores directly on a host has repeatedly been described for modern phytopathogenic peronosporomycetes (Jones et al., 1991; Deacon, 1996; and references therein). Zoospores are released in an aqueous environment (Walker and van West, 2007), move to a host, form a short-lived thin-walled cyst on the host surface, and subsequently germinate, or they undergo a sequence of two or more zoosporic phases interspersed by encysted phases (Dick, 2001a). However, the putative zoospore cysts of *G. biscalithecae* occur within the host cells and their walls are relatively thick. These cysts may occur within the host cells simply because the host tissue was not surrounded by water at the time of zoospore liberation. An alternative, although somewhat speculative premise, is that the zoospores of *G. biscalithecae* remained

(probably mature) oogonium. (**e**) Same as in (d), different focal plane, showing the oogonial stalk; arrows indicate longer, more massive, and opaque bristles/hairs. (**f**) Oogonium, and hypha (possibly the parental hypha) extending along the inner surface of the host cell wall. (**g**) Oogonial surface ornamentation; arrow indicates possible forking of surface extension. (**h, i**) Putative zoospore cysts; arrow in (h) indicates the typical, inverted U-shape of cysts in longitudinal section. (**j**) Large hyphae in cross-section. (**k**) Oogonium-amphigynous antheridium complex in host cell; note pair of ovoid structures [S] in other focal plane [upper right of image]. (**l**) Same as in (k), focusing on the oogonium-antheridium complex; arrows indicate position of antheridium.

Fig. 1. *Galtierella biscalithecae* nov. gen. et sp., un peronosporomycète du Pennsylvanien supérieur de Grand-Croix ; tous les spécimens sont sur la lame REN-2219 (collection Renault, Paris) ; CW : paroi cellulaire de l'hôte ; H : hyphe, O : oogone, S : structure ovoïde, St : hyphe portant l'oogone (pédicelle de l'oogone) ; échelle = 10 μm sauf indication contraire. (**a**) Sporange de *Biscalitheca* cf. *musata* contenant des spores in situ ; noter les cellules à paroi relativement épaisse de la paroi du sporange ; échelle = 0,25 mm. (**b**) Oogone immature situé en position terminale sur une large hyphe ; noter la large structure ovoïde sur la droite ; la flèche indique ce qui semble être une cloison imparfaite avec un pore central. (**c**) Complexe oogone-anthéridie amphigyne et structure ovoïde ; les flèches indiquent l'anthéridie. (**d**) Gros oogone (probablement mature). (**e**) Comme (d), dans un plan focal différent, montrant le pédicelle de l'oogone ; les flèches indiquent les poils plus long, plus massifs et opaques. (**f**) Oogone et hyphe (peut-être l'hyphe porteuse) qui s'étend sur la face intérieure de la paroi cellulaire de l'hôte. (**g**) Ornementation de la surface de l'oogone ; la flèche indique une possible ramification d'une expansion superficielle. (**h, i**) Possible cystes de zoospores ; la flèche sur (h) indique la forme en U inversé, typique des cystes en coupe longitudinale. (**j**) Large hyphe en coupe transversale. (**k**) Complexe oogone-anthéridie amphigyne dans une cellule de l'hôte ; noter la paire de structure ovoïdes [S], dans un autre plan focal (en haut à droite de l'image). (**l**) Comme (k), focalisé sur le complexe oogone-anthéridie ; les flèches indiquent la position de l'anthéridie.

encysted for an extended period of time, perhaps due to some life history strategy of *G. biscalithecae* or ecological circumstance. The thickness of the walls suggests that the dome-shaped structures were long-lived, and perhaps did not normally develop further until the host tissue fully disintegrated.

In spite of the similarities between *G. biscalithecae* and extant peronosporomycetes, we are unable to determine the precise systematic position of the fossil because several features (e.g., the large ovoid and small dome-shaped structures) cannot be unambiguously correlated with phases of the life cycle in modern peronosporomycetes. Moreover, all oogonia of *G. biscalithecae*, as well as the ovoid structures and putative zoospore cysts, appear to be empty; perhaps the mode and timing of the silicification process did not favor preservation of the contents. As a result, nothing is known about the number of oospores produced by each oogonium, and whether the oospores were plerotic or aplerotic. Based on these inherent uncertainties with regard to the morphology and biology of *G. biscalithecae*, we refrain from formally referring the fossil to any extant taxon, but rather introduce a new morphogenus to accommodate this interesting organism. In a similar context we are unable to offer an analysis about the interrelationship between *G. biscalithecae* and the plant that produced the *Biscalitheca* cf. *musata* reproductive organ.

5. Conclusions

Although fossil microorganisms preserved in cherts have been studied for more than 100 years, there are only three persuasive examples for fossil peronosporomycetes (i.e., *H. monospora*, *C. cornifer*, and *G. biscalithecae*) to date. These fossils demonstrate that the Peronosporomycetes as a group was quite diverse already in the late Paleozoic. It is anticipated that additional forms will be discovered as work on the various fossiliferous chert deposits from throughout the world continues. This will lead to a more accurate depiction of the evolutionary history of the Peronosporomycetes, and contributes to a more sharply focused concept of the complexity of microbial life in ancient ecosystems. Moreover, recent studies indicate that it is possible to offer various hypotheses that can be used in association with studies based on modern communities to depict the role of peronosporomycetes and other microorganisms in the ecology and evolution of ancient ecosystems.

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