Zitteliana

An International Journal
of Palaeontology and Geobiology

Series A/Reihe A
Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

51

München 2011

Zitteliana

An International Journal of Palaeontology and Geobiology

Series A/Reihe A

Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie

51

CONTENTS/INHALT

Nora Dotzler, Thomas N. Taylor, Jean Galtier & Michael Krings
Sphenophyllum (Sphenophyllales) leaves colonized by fungi from the Upper Pennsylvanian Grand-Croix cherts of central France 3

Evelyn Kustatscher, Christian Pott & Johanna H.A. van Konijnenburg-van Cittert
Scytophyllum waehneri (Stur) nov. comb., the correct name for *Scytophyllum persicum* (Schenk) Kilpper, 1975 9

Alfred Selmeier & Dietger Grosser
Lower Cretaceous conifer drift wood from Sverdrup Basin, Canadian Arctic Archipelago 19

Wolf Ohmert
Radiolarien-Faunen und Stratigraphie der Pattenau-Formation (Campanium bis Maastrichtium) im Helvetikum von Bad Tölz (Oberbayern) 37

Joachim Gründel, Martin Ebert & Roger Furze
Die Gastropoden aus dem oberen Aalenium von Geisingen (Süddeutschland) 99

Wagih Ayoub-Hannaa & Franz Theodor Fürsich
Revision of Cenomanian-Turonian (Upper Cretaceous) gastropods from Egypt 115

Thérèse Pfister, Urs Wegmüller & Beat Keller
Die Molluskenfauna der St. Galler Formation (Belpberg-Schichten, Obere Meeresmolasse) bei Bern (Schweiz): Taphonomie und Paläoökologie 153

Volker Dietze, Günter Schweigert, Uwe Fidder & Norbert Wannenmacher
The Giganteuston Member of Öschingen (Humphriesianum Zone, Lower Bajocian, Swabian Alb), with comments on the genera *Dorsetensia* Buckman, 1892 and *Nannina* Buckman, 1927 209

Wolfgang Witt
Mixed ostracod faunas, co-occurrence of marine Oligocene and non-marine Miocene taxa at Pınarhisar, Thrace, Turkey 237

Peter Schäfer
Beiträge zur Ostracoden- und Foraminiferen-Fauna der Unteren Süßwassermolasse in der Schweiz und in Savoyen (Frankreich). 3. Das Findreuse-Profil (Département Haute-Savoie, Frankreich) 255

Christian Foth, Johannes Kalbe & René Kautz
First evidence of Elasmosauridae (Reptilia: Sauropterygia) in an erratic boulder of Campanian age originating from southern Sweden or the adjacent Baltic Sea area 285

Jérôme Prieto
The Miocene small mammals from Münchsmünster (North Alpine Foreland Basin, Bavaria) 291

Jérôme Prieto
The Miocene insectivores and marsupial from Affalterbach (North Alpine Foreland Basin, Germany) 297

Instructions for authors 303

Zitteliana	A 51	308 Seiten	München, 31.12.2011	ISSN 1612-412X

Editors-in-Chief/Herausgeber: Gert Wörheide, Michael Krings
Production and Layout/Bildbearbeitung und Layout: Martine Focke
Bayerische Staatssammlung für Paläontologie und Geologie

Editorial Board

A. Altenbach, München
B.J. Axsmith, Mobile, AL
F.T. Fürsich, Erlangen
K. Heißig, München
H. Kerp, Münster
J. Kriwet, Stuttgart
J.H. Lipps, Berkeley, CA
T. Litt, Bonn
A. Nützel, München
O.W.M. Rauhut, München
B. Reichenbacher, München
J.W. Schopf, Los Angeles, CA
G. Schweigert, Stuttgart
F. Steininger, Eggenburg

Bayerische Staatssammlung für Paläontologie und Geologie
Richard-Wagner-Str. 10, D-80333 München, Deutschland
http://www.palmuc.de
email: zitteliana@lrz.uni-muenchen.de

Für den Inhalt der Arbeiten sind die Autoren allein verantwortlich.
Authors are solely responsible for the contents of their articles.

Copyright © 2011 Bayerische Staassammlung für Paläontologie und Geologie, München

Die in der Zitteliana veröffentlichten Arbeiten sind urheberrechtlich geschützt.
Nachdruck, Vervielfältigungen auf photomechanischem, elektronischem oder anderem Wege
sowie die Anfertigung von Übersetzungen oder die Nutzung in Vorträgen, für Funk und Fernsehen
oder im Internet bleiben – auch auszugsweise – vorbehalten und bedürfen der schriftlichen Genehmigung
durch die Bayerische Staatssammlung für Paläontologie und Geologie, München.

ISSN 1612-412X
Druck: Gebr. Geiselberger GmbH, Altötting

Cover illustration: The ammonite *Dorsetensia liostraca* Buckman from the Lower Bajocian (Middle Jurassic) Giganteuston Member of Öschingen, Middle Swabian Alb, Germany. For details, see Dietze, V. et al.: The Giganteuston Member of Öschingen (Humphriesianum Zone, Lower Bajocian, Swabian Alb), with comments on the genera *Dorsetensia* Buckman, 1892 and *Nannina* Buckman, 1927, pp. 209–236 in this issue.
Back cover: Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbild: *Dorsetensia liostraca* Buckman, ein Ammonit aus dem Giganteuston des Unter-Bajociums (Mittlerer Jura) von Öschingen, Mittlere Schwäbische Alb, Deutschland. Für weitere Informationen siehe Dietze, V. et al.: The Giganteuston Member of Öschingen (Humphriesianum Zone, Lower Bajocian, Swabian Alb), with comments on the genera *Dorsetensia* Buckman, 1892 and *Nannina* Buckman, 1927, S. 209–236 in diesem Heft.
Rückseite: Lichthof des paläontologischen Museums München, Blick vom Haupteingang.

Bayerische Staatssammlung für Paläontologie und Geologie

- Zitteliana A 51, 3 – 8
- München, 18.04.2011
- Manuscript received 12.12.2010; revision accepted 01.06.2011
- ISSN 1612 - 412X

Sphenophyllum (Sphenophyllales) leaves colonized by fungi from the Upper Pennsylvanian Grand-Croix cherts of central France

Nora Dotzler[1]*, Thomas N. Taylor[2], Jean Galtier[3] & Michael Krings[1, 2]

[1]*Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany*
[2]*Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence KS 66045-7534, U.S.A.*
[3]*AMAP, UMR 5120 CNRS, CIRAD TA A-51/PS2, Boulevard de la Lironde, 34398 Montpellier, France*

**Author for correspondence and reprint requests; E-mail:* n.dotzler@lrz.uni-muenchen.de

Abstract

Structurally preserved (permineralized) *Sphenophyllum* leaves from the Upper Pennsylvanian (Carboniferous) Grand-Croix cherts (Saint-Etienne Basin, France) host a diverse assemblage of fungal remains, including several types of spherical structures that differ from one another in size, wall thickness, and ornamentation, as well as mycelia constructed of narrow hyphae/filaments and intercalary swellings. The affinities of the fungi, as well as their nutritional mode(s), are difficult to determine. Some of the remains resemble resting spores and zoosporangia seen in extant chytrids. This discovery provides the first evidence of fossil sphenophyte leaves colonized by fungi, and provides new insights into the diversity of leaf-inhabiting microorganisms in Carboniferous forest ecosystems.

Key words: Carboniferous, Chytridiomycota, fossil fungi, permineralization, sphenophytes

Zusammenfassung

In strukturbietend erhaltenen (permineralisierten) *Sphenophyllum*-Blättern aus den ober-pennsylvanischen (Karbon) Grand-Croix Cherts (Saint-Etienne Becken, Frankreich) wurden diverse Reste von Pilzen gefunden, unter Anderem mehrere Arten kugeliger Strukturen, die sich voneinander in Größe, Wanddicke und Ornamentierung unterscheiden, sowie Myzelien bestehend aus dünnen Hyphen/Filamenten und interkalaren Schwellungen. Die systematische Zugehörigkeit der Pilzreste sowie ihre Beziehung zur Wirtspflanze sind schwer zu bestimmen. Einige der Strukturen erinnern an Dauersporen und Zoosporangien heutiger Chytridien. Der hier beschriebene Fund stellt den ersten Nachweis für die Besiedlung fossiler Sphenophytenblätter durch Pilze dar, und liefert neue Informationen zur Diversität blattbewohnender Mikroorganismen in karbonischen Wald-Ökosystemen.

Schlüsselwörter: Chytridiomycota, fossile Pilze, Karbon, Permineralisation, Sphenophyta

1. Introduction

The leaves of land plants today function as habitats for a wide variety of fungi. Moreover, fungi play an important role in the decomposition of leaf litter (Osono 2002). Although the available estimates of the diversity of fungi associated with leaves are still preliminary, there is strong evidence to suggest that leaf-colonizing fungi represent a significant proportion of today's total fungal diversity (e.g., Petrini 1991; Arnold 2007; Rodriguez et al. 2009).

Leaves (microphyllous and megaphyllous types) evolved early in the history of plant life on land, and leafy plants were predominant elements of the terrestrial vegetation at least from the Middle Devonian onward (Gensel 2008). Although it is likely that fungi utilized leaves as habitats as soon as these plant organs became available, the fossil record of leaf-colonizing fungi remains poor. The oldest fossil evidence of fungi colonizing leaves comes from the Carboniferous, and includes ferns (Krings et al. 2009a, 2010b), seed ferns (Oliver 1903; Krings 2001), and cordaites (Krings et al. 2011) as hosts. On the other hand, fungi associated with the leaves of Carboniferous lycophytes and sphenophytes have not been described to date. The lack of documented evidence of fungi on/in lycophyte leaves is puzzling since diverse assemblages of fungi have been described in other aerial parts of these plants (Krings et al. 2007, 2010a). We are not aware of any study reporting on fungi associated with the above-ground parts of fossil sphenophytes, with one possible exception (see Ryberg et al. 2008); however, fungal endophytes have been recognized in Carboniferous calamite

roots (Agashe & Tilak 1970; Krings et al. in press).

The Upper Pennsylvanian Grand-Croix cherts of central France have been known for more than 100 years for their exquisite structurally preserved vascular plants (surveyed in Doubinger et al. 1995; Galtier 2008). More recently, they have also become increasingly important as a source of new information about fungal life in the Pennsylvanian (Krings et al. 2009a,b, 2010b; Strullu-Derrien et al. 2009). The Grand-Croix flora is dominated by seed plants (55% of specimens) and ferns (25%), whereas lycophytes (3%) and sphenophytes (i.e. calamites and sphenophylls) (17%) represent subordinate elements (Galtier 2008).

In this paper we report on the occurrence of fungal remains (hyphae, spores, sporangia, and other propagules) in structurally preserved *Sphenophyllum* Brongniart leaves from Grand-Croix. *Sphenophyllum* has been reconstructed as relatively small plant that formed a portion of the understorey in Carboniferous forests. The plants are characterized by relatively narrow shoot axes and wedge-shaped leaves borne in whorls (Taylor et al. 2009). The discovery of fungal remains in *Sphenophyllum* leaves from Grand-Croix provides the first evidence of fossil sphenophyte leaves colonized by fungi.

2. Material and methods

The Upper Pennsylvanian 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 around the city of La Grand-Croix (Galtier 2008). The precise stratigraphic provenance and age of the cherts remain controversial. Some have interpreted these rocks 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 general consensus is that the cherts are reworked, and hence may be slightly older, i.e., late Stephanian A (equivalent to the late Barruelian) in age (Galtier & Scott 1981; Doubinger et al. 1995).

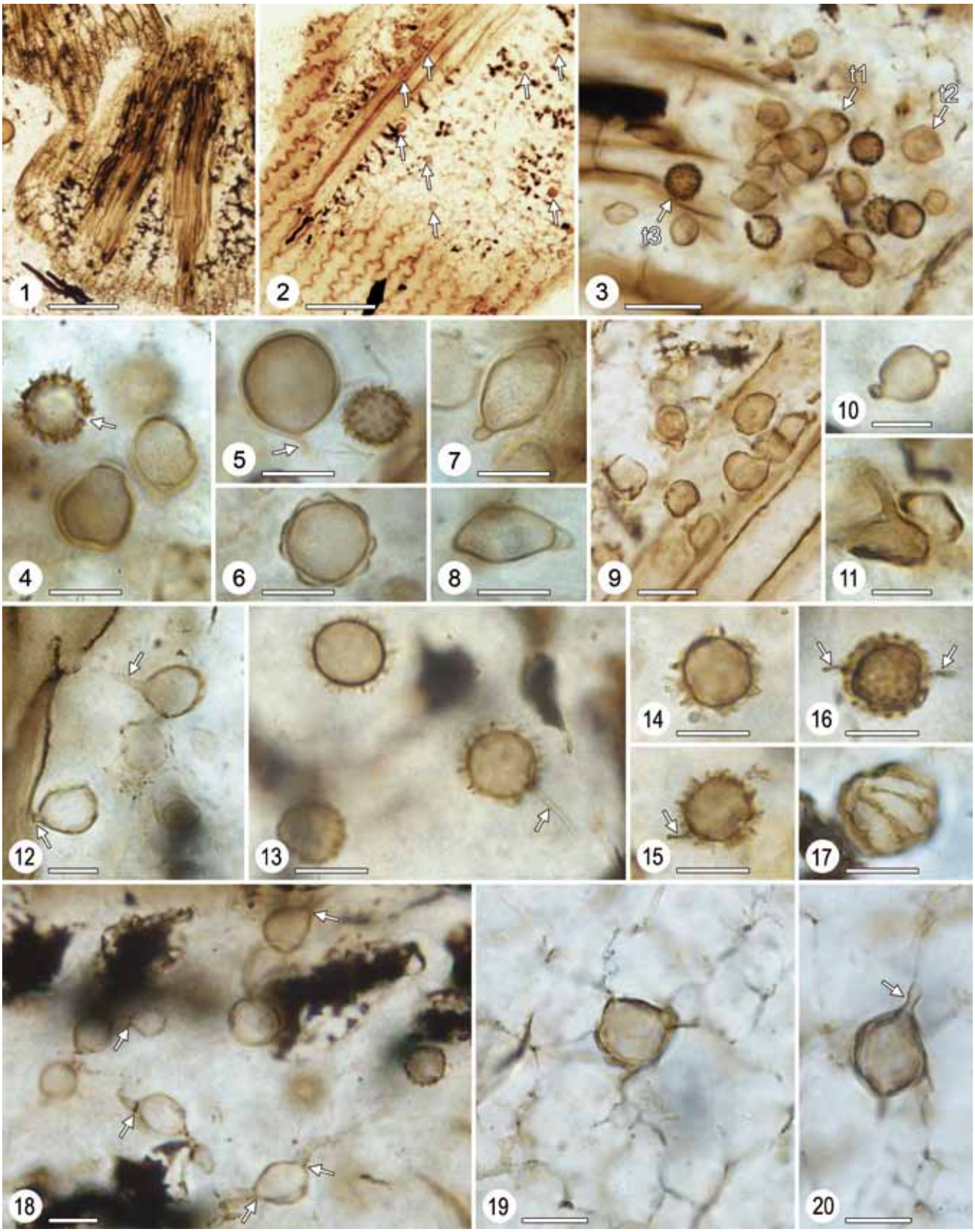
The infected *Sphenophyllum* leaves were identified in thin sections prepared by cementing a wafer of chert to a glass slide, and then grinding the wafer to a thickness sufficiently thin for examination in transmitted light. The thin sections are part of the historical slide collection prepared by Carl Rudolf Florin and co-workers in the 1930's that is today housed in the Naturhistoriska riksmuseet in Stockholm (Sweden). The slides containing the infected *Sphenophyllum* leaf fragments have the accession numbers S038071-12, S038070, and S003404-02.

3. Results

Fungal remains occur within the mesophyll (or what remains of the tissue) of 19 *Sphenophyllum* leaf fragments from Grand-Croix contained in three thin-section preparations from the Florin slide collection. The fragments are between 0.2 and 1 mm long and up to 3 mm wide, and most appear in the thin sections in an oblique paradermal (sagittal) plane (e.g., Pl. 1, Figs 1, 2). The leaf fragments are identified as belonging to *Sphenophyllum* based on the epidermis that consists of elongate cells with strongly undulating anticlinal walls (e.g., see Barthel 1997). While the epidermis and vascular tissues of the leaves appear largely intact, the mesophyll is consistently in an advanced state of disintegration, and individual cell outlines are no longer visible. In places, however, irregularly shaped structures containing opaque material occur that might represent the remains of parenchymatous mesophyll cells (e.g., Pl. 1, Figs 1, 2, 18).

Six morphotypes of fungal remains have been discovered in the *Sphenophyllum* leaf fragments from Grand-Croix. Since the remains represent isolated stages of possibly complex fungal life cycles, there is no way to determine the precise systematic affinities or to distinguish between species. As a result, we refer to the remains simply as *type 1* through *6*. All types of fungal remains occur in *Sphenophyllum* leaves, but are present in different numbers of leaf fragments. *Types 4*, *5*, and *6* are the least encountered forms, each with only a single documented occurrence; the remaining types are common

Plate 1: Fungal remains in Late Pennsylvanian *Sphenophyllum* leaves from Grand-Croix. **(1)** Paradermal (sagittal) section of leaf fragment, showing vascular bundles and mesophyll; slide S038071-12; bar = 200 µm. **(2)** Oblique paradermal section, showing epidermal cells with undulating anticlinal walls and fungal remains (arrows); slide S038071-12; bar = 100 µm. **(3)** Cluster of fungal remains (t1 = *type 1*; t2 = *type 2*; t3 = *type 3*); slide S003404-02; bar = 20 µm. **(4)** *Type-1* (lower spheres) and *type-3* (upper sphere) structures; note pore in wall of *type-3* structure (arrow); slide S038071-12; bar = 10 µm. **(5)** *Type-1* (left sphere) structure with attached filament (arrow) and *type-3* structure (right sphere); slide S038071-12; bar = 10 µm. **(6)** *Type-1* structure with irregular outer wall; slide S038071-12; bar = 10 µm. **(7, 8)** *Type-1* structures showing papilla-like protrusions or germination site; slide S038071-12; bars = 10 µm. **(9)** Cluster of *type-2* structures; slide S003404-02; bar = 20 µm. **(10)** *Type-2* structure with knob-like protrusions; slide S038071-12; bar = 10 µm. **(11)** *Type-2* structure with tube-like extension; slide S003404-02; bar = 10 µm. **(12)** Stalked *type-2* structures attached to host cell wall; slide S038071-12; bar = 10µm. **(13)** *Type-3* structures; note subtending hypha/filament in one specimen (arrow); slide S038070; bar = 10 µm. **(14–16)** *Type-3* structures; arrows indicate delicate parental hyphae/filaments; slide S038070; bars = 10µm. **(17)** *Type-4* structure; slide S003404-02; bar = 10µm. **(18)** *Type-5* assemblage; note swellings separated by septations (arrows); slide S038071-12; bar = 10µm. **(19)** *Type-6* structure located in an intercalary position within network of tenuous filaments; slide S003404-02; bar = 10 µm. **(20)** *Type-6* structure, showing what appears to be a discharge tube (arrow); slide S003404-02; bar = 10µm.


1
2
3
t1
t2
t3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

and usually also co-occur in dense spacing in the leaf fragments (Pl. 1, Fig. 3).

Type 1 (Pl. 1, Figs 4 [lower two spheres], 5 [left sphere], 7, 8) is the most frequent fungal remain in the *Spenophyllum* leaves, and often occurs in loose clusters. This form consists of spherical to ellipsoid or pyriform, sometimes slightly irregular structures, between 5 and 17 µm in diameter, that are characterized by a double wall which may be smooth (Pl. 1, Fig. 5) or wrinkled (Pl. 1, Fig. 6). Some of the structures appear to be at some stage of germination or possess papilla-like protrusions (Pl. 1, Figs 7, 8). In a few specimens, a tenuous subtending hypha/filament is recognizable (Pl. 1, Fig. 5 [arrow]). *Type 2* (Pl. 1, Figs 9–12) is similar to *type 1* in size and shape and is also common, but differs from *type 1* in having a thinner and consistently single-layered wall. Some of the *type-2* specimens possess one or two bud-like protrusions (Pl. 1, Fig. 10). In others, a single tube-like structure up to 9 µm long extends out from the surface (Pl. 1, Fig. 11), while in still others a narrow subtending hypha or filament is attached to host cell walls (Pl. 1, Fig. 12 [arrows]).

Type 3 (Pl. 1, Figs 4 [upper left], 5 [lower right], 13–16) is consistently spherical, 8–10 µm in diameter, and distinct from all other fungal remains occurring in the *Sphenophyllum* leaves. This type is characterized by a prominent surface ornament composed of densely spaced bristles or hairs. Several specimens show what appear to be pores in the wall (Pl. 1, Fig. 4 [arrow]), while others possess one or two delicate, thread-like appendices (Pl. 1, Figs 13, 15, 16 [arrows]), which probably represent the remains of the parental hypha.

Type 4 (Pl. 1, Fig. 17) is reported from a single leaf fragment. This form is spherical, up to 14 µm in diameter, and characterized by a prominent surface ornament composed of irregular ridges. *Type 5* (Pl. 1, Fig. 18) and *type 6* (Pl. 1, Figs 19, 20) also have been discovered in only one of the leaf fragments. *Type 5* consists of series of spherical to pyriform, smooth- and single-walled swellings up to 14 µm long and 11 µm wide that occur in the intercalary region on narrow hyphae or filaments. The swellings are sometimes separated from the parental hypha by septa (Pl. 1, Fig. 18 [arrows]). *Type 6* is represented by a dense network of tenuous, multi-branched hyphae or filaments. Unornamented, thin-walled, more or less spherical to pear-shaped structures, each up to 13 µm in diameter, occur in an intercalary position within the network of tenuous hyphae/filaments. Extending from one of these structures is what appears to be a discharge tube (Pl. 1, Fig. 20 [arrow]).

4. Discussion

The fungal remains described in this paper present the first evidence of fungi colonizing the aerial parts of a fossil sphenophyte. Previous records of fungi associated with fossil sphenophytes include unidentified hyphal fragments and spores in the cortical tissues of Pennsylvanian calamite roots from North America (Agashe & Tilak 1970), as well as a complex fungal interaction with calamite rootlets from Grand-Croix (Krings et al. in press; Taylor et al., in prep.) In addition, Ryberg et al. (2008) speculate that tiny spherical bodies occurring in large numbers in upright axes of the sphenophyte *Spaciinodum collinsonii* Osborn et Taylor from the Triassic of Antarctica may represent fungal spores. However, the fungal nature of the spherical bodies remains questionable. The scarcity of documented evidence of fungi associated with fossil sphenophytes is somewhat surprising since modern representatives of this group of plants (i.e. members of the genus *Equisetum* L.) are hosts to several epiphytic and endophytic fungi (e.g., Seaver 1932; Ellis & Ellis 1997; Künkele et al. 2005; Hodson et al. 2009), some of which may even become major pathogens (e.g., Schaffner 1931). As to whether the scarcity of documented fossil evidence of fungi on/in sphenophytes indicates that these plants were rarely colonized by fungi, or simply reflects study bias, cannot be determined at present.

Although the fungal remains in the *Sphenophyllum* leaves are generally well preserved, they are difficult to interpret for several reasons. All of the remains represent isolated stages of fungal life cycles, and thus cannot be assigned to a particular group of fungi with any degree of confidence. Moreover, it is highly probable that two or more of the types reported here based on morphology may in fact represent different life history stages of the same organism, or different varieties of the same life history stage of a single organism. It is also possible that the individual types each represent several morphologically similar species. What can be suggested from the material described here is that the *type-2* and *type-6* structures may represent chytrid zoosporangia based on their overall morphology (see Karling 1977), whereas the *type-3* and *type-4* forms resemble chytrid resting spores. It is interesting to note that the modern chytrid *Nowakowskiella sculptura* Karling produces resting spores that vary considerably in the type and degree of sculpturing; some spores are smooth, whereas others have fusiform ridges, or are warty or tuberculate in appearance (Karling 1961). As a result, if the *type-3* and *type-4* fungal remains are in fact chytrid resting spores, they may have been produced by the same organism. However, the affinities of all fungal remains described in this paper with other groups of Fungi or fungus-like microorganisms, including Hyphochytridiomycota and Peronosporomycetes, cannot be ruled out.

The *type-1* and *type-2* fungal remains in *Sphenophyllum* leaves are quite similar to fungal fossils described previously in cordaite leaves from Grand-Croix (Krings et al. 2011: fig. 2C, F–Q), and the *type-6* structure is comparable to chytrid-like organisms documented in the rachidal cortex of a specimen of the fern reproductive structure *Biscalitheca* cf. *musata* Mamay from Grand-Croix (Krings et al. 2009b: pl. II, figs 1–6d). Moreover, *type 4* is somewhat similar to another type of fungus reported in cordaite leaves from Grand Croix (compare Pl. 1, Fig. 17 with Krings et al. 2011: fig. 1H). Also present in the cordaite leaves from Grand-Croix is a structure that resembles the *type-5* form (compare Pl. 1, Fig. 18 with Krings et al. 2011: fig. 1B–E). Only the spiny *type-3* form (Pl. 1, Figs 4, 5, 13–16) has not been recorded previously from Grand-Croix. This provokes the question as to whether the organism that produced the *type-3* structures might have been a specialist that only was associated with sphenophytes, while the producers of the other structures rather were generalists. Although this question is difficult to address, especially when there are only a few assemblages of fungal remains recorded from Grand-Croix, we still find the restricted occurrence of this characteristic structure interesting.

The time of fungal colonization of the *Sphenophyllum* leaves is uncertain, and thus not much can be said about the ecological role(s) that the fungi played in the Grand-Croix paleoecosystem. It is possible that the leaves were infected by parasitic fungi while they were alive and still attached to the plant, or that the fungi were saprotrophs that invaded senescing or dead and partially decomposed plant parts on the forest floor or in water. The host leaves are highly fragmented, which indicates that they were exposed to mechanical forces and/or biological degradation for a considerable period of time prior to fossilization. On the other hand, most of the fungal remains in the *Sphenophyllum* leaves appear in a life history stage in which the mycelia have completely disintegrated, which suggests that the time of infection predates the condition of the leaves at the time of preservation by some time. Krings et al. (2009b) have argued, however, that the three-dimensional configuration of delicate (and mostly ephemeral) vegetative systems of fungi such as the *type-6* form (Pl. 1, Figs 19, 20) would probably not survive and become preserved intact if these systems were already established during the lifetime of the leaf. As a result, neither the condition of the leaves nor that of the fungal remains provides incontrovertible evidence allowing for the determination of the time of colonization of the leaves.

While leaf-inhabiting fungi from Grand-Croix have been described to date based on single occurrences (e.g., Krings et al. 2009a,b, 2010b) or at best based on two infected leaf fragments (Krings et al. 2011), the fungal remains in *Sphenophyllum* provide the first account on fungi occurring in a larger number of leaf fragments contained in different thin sections. This may suggest that *Sphenophyllum* leaves, either moribund or alive, were more susceptible to colonization by fungi than the leaves of other plants in the Grand-Croix paleoecosystem. Since the leaf fragments occur in clusters in all three thin sections, it is also possible that several or all leaves came from the same plant that was heavily infected by parasitic fungi, or that all leaves rested in the same area on the forest floor or the bottom of a body of water and were simultaneously invaded by the same fungal saprotrophs.

Despite the fact that neither the systematic affinities nor the ecological role(s) of the fungi in the *Sphenophyllum* leaves from Grand-Croix can be resolved, it is important to document these fossils. The few fungal assemblages in leaves that have been reported to date from Grand-Croix suggest that certain fungi occurred more widely distributed, while others appear to have had a rather limited host range. This inevitably raises the question as to whether this observation reflects generalists and specialists among the fungi or is due merely to the current lack of resolution. The application of the inappropriate technique to the study of fossil fungi (Taylor et al. 2011), together with a lack of knowledge about their preservation potential, has resulted in a failure to fully appreciate the diversity of these organisms in paleoecosystems. However, the discovery and description of additional fossil fungi and fungus-like organisms in recent years now makes it possible to ask a second-level set of questions pertaining to the role of these organisms in interactions and associations with their hosts. Information gathered to date clearly indicates that many of the fungal interactions present today also existed in ancient ecosystems. We believe that describing various types of fungi in time and space will ultimately make it possible to address such questions as to whether certain fungi were generalists, or were in fact host specific, and what types of adaptations evolved in certain plants to counteract the arms race with their fungal contemporaries. We also believe that it will be possible to more fully discuss hypotheses about the transitional stages leading from parasitism and/or saprophytism to various degrees of mutualism. The plants that existed during the late Paleozoic have few modern relatives, and in those instances in which they occur, the plant body, tissue system development, and general morphology and organ adaptation are quite different. This means that for those plants there were additional host niches available to be colonized by the fungi that were present. On the other hand, the fossil record is replete with examples of plant groups that have become extinct although they were once major elements of the paleoecosystems in which they lived. Both of these scenarios provide the opportunity to view the interactions between fungi and their hosts in time and space, and in some instances to track the fungal interactions within different types of ecosystems based on plant community and physical parameters.

Acknowledgments

Financial was support was received from the National Science Foundation (EAR-0949947 to TNT and MK). ND acknowledges support for her project SE-TAF-508 performed at the Swedish Museum of Natural History within SYNTHESYS. SYNTHESYS receives funding from the European Community – Research Infrastructure Action under the FP7 "Capacities" Specific Programme. We thank EM Friis and C Pott (Stockholm, Sweden) for making the Florin slide collection available for study, and JF White (New Brunswick, NJ, U.S.A.) for his constructive review of the manuscript.

5. References

Agashe SN, Tilak ST. 1970. Occurrence of fungal elements in the bark of arborescent calamite roots from the American Carboniferous. Bulletin of the Torrey Botanical Club 97, 216–218.

Arnold AE. 2007. Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. Fungal Biology Reviews 21, 51–66.

Barthel M. 1997. Epidermal structures of sphenophylls. Review of Palaeobotany and Palynology 95, 115–127.

Doubinger J, Vetter P, Langiaux J, Galtier J, Broutin J. 1995. La flore fossile du bassin houiller de Saint-Etienne. Mémoires du Muséum national d'Histoire naturelle, Paris 164, 1–357.

Ellis MB, Ellis JP. 1997. Microfungi on Land Plants. An Identification Handbook. Slough, The Richmond Publishing Co. Ltd., vi + 868 p.

Galtier J. 2008. A new look at the permineralized flora of Grand-Croix (Late Pennsylvanian, Saint-Etienne basin, France). Review of Palaeobotany and Palynology 152, 129–140.

Galtier J, Scott, AC. 1981. Sur la présence de végétaux à structure conservée du Viséen dans le Poudingue mosaïque du Stéphanien du bassin de Saint-Etienne (France). Geobios 14, 529–531.

Gensel PG. 2008. The earliest land plants. Annual Review of Ecology, Evolution and Systematics 39, 459–477.

Hodson E, Shahid F, Basinger J, Kaminskyj S. 2009. Fungal endorhizal associates of *Equisetum* species from Western and Arctic Canada. Mycological Progress 8, 19–27.

Karling JS. 1961. *Nowakowskiella sculptura* sp.nov. Transactions of the British Mycological Society 44, 453–547.

Karling, J.S. 1977. Chytridiomycetarum Iconographia. An Illustrated and Brief Descriptive Guide to the Chytridiomycetous Genera with a Supplement of the Hyphochytridiomycetes. Vaduz, J. Cramer, viii + 414 p.

Krings M. 2001. Pilzreste auf und in den Fiedern zweier Pteridospermen aus dem Stefan von Blanzy-Montceau (Zentralmassiv, Frankreich). Geologica Saxonica – Abhandlungen des Museums für Mineralogie und Geologie Dresden 46/47, 189–196.

Krings M, Dotzler N, Taylor TN, Galtier J. 2007. A microfungal assemblage in *Lepidodendron* from the Upper Visean (Carboniferous) of central France. Comptes Rendus Palevol 6, 431–436.

Krings M, Dotzler N, Taylor TN, Galtier J. 2009a. A Late Pennsylvanian fungal leaf endophyte from Grand-Croix, France. Review of Palaeobotany and Palynology 156, 449–453.

Krings M, Galtier J, Taylor TN, Dotzler N. 2009b. Chytrid-like microfungi in *Biscalitheca* cf. *musata* (Zygopteridales) from the Upper Pennsylvanian Grand-Croix cherts (Saint-Etienne Basin, France). Review of Palaeobotany and Palynology 157, 309–316.

Krings M, Dotzler N, Taylor TN, Galtier J. 2010a. A fungal community in plant tissue from the Lower Coal Measures (Langsettian, Lower Pennsylvanian) of Great Britain. Bulletin of Geosciences 85, 679–690.

Krings M, Taylor TN, Galtier J, Dotzler N. 2010b. Microproblematic endophytes and epiphytes of fern pinnules from the Upper Pennsylvanian of France. Geobios 43, 503–510.

Krings M, Taylor TN, Dotzler N, Galtier J. 2011. Fungal remains in cordaite (Cordaitales) leaves from the Upper Pennsylvanian of central France. Bulletin of Geosciences 86, 777-784.

Krings M, Taylor TN, Dotzler N. In press. Fungal endophytes as a driving force in land plant evolution: evidence from the fossil record. In: D Southworth (Ed.), Biocomplexity of Plant-Fungal Interactions. Ames IA, ISUP/John Wiley & Sons, Inc.

Künkele U, Lohmeyer TR, Baral HO. 2005. *Stamnaria americana*, ein in Auwäldern vermutlich häufiger, aber aus Deutschland bisher nicht berichteter Parasit an *Equisetum hyemale*. Mycologia Bavarica 7, 3–20.

Oliver FO.1903. Notes on fossil fungi. New Phytologist 2, 49–53.

Osono T. 2002. Ecology of ligninolytic fungi associated with leaf litter decomposition. Ecological Research 22, 955–974.

Petrini O. 1991. Fungal endophytes of tree leaves. In: JH Andrews, SS Hirano (Eds), Microbial Ecology of Leaves. New York, Springer-Verlag, 179–197.

Pruvost P. 1947. Le Stéphanien du bassin houiller de la Loire. Annales de la Société Géologique du Nord 67, 279–295.

Rodriguez RJ, White JF Jr., Arnold EE, Redman RS. 2009. Fungal endophytes: diversity and functional roles. New Phytologist 182, 314–330.

Ryberg PE, Hermsen EJ, Taylor EL, Taylor TN, Osborn JM. 2008. Development and ecological implications of dormant buds in the high-Paleolaltitude Triassic sphenophyte *Spaciinodum* (Equisetaceae). American Journal of Botany 95, 1443–1453.

Schaffner JH. 1931. Injurious fungus parasite of *Equisetum*. American Fern Journal 21, 75.

Seaver FJ. 1932. Photographs and descriptions of cup-fungi – XVI. *Stamnaria*. Mycologia 24, 1–3.

Strullu-Derrien C, Rioult JP, Strullu DG. 2009. Mycorrhizas in Upper Carboniferous *Radiculites*-type cordaitalean rootlets. New Phytologist 182: 561–564.

Taylor TN, Taylor EL, Krings M. 2009. Paleobotany. The Biology and Evolution of Fossil Plants. Burlington MA, London, San Diego CA, New York NY, Elsevier/Academic Press Inc., xxi + 1230 p.

Taylor TN, Krings M, Dotzler N, Galtier J. 2011. The advantage of thin section preparations over acetate peels in the study of Late Paleozoic fungi and other microorganisms. Palaios 26: 239–244.

Vetter P. 1971. Le Carbonifère supérieur et le Permien du Massif Central. In: J Jung (Ed.), Symposium. Clermont-Ferrand, Plein-Air Service, 169–213.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Zitteliana Serie A

Jahr/Year: 2011

Band/Volume: 51

Autor(en)/Author(s): Dotzler Nora, Taylor Thomas N., Galtier Jean, Krings Michael

Artikel/Article: Sphenophyllum (Sphenophyllales) leaves colonized by fungi from the Upper Pennsylvanian Grand-Croix cherts of central France 3-8