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FIRST REPORT OF FUNGI AND FUNGUS-LIKE ORGANISMS FROM MESOZOIC HOT SPRINGS

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ABSTRACT

Herein we provide the first report of the diversity of fungi and fungus-like organisms within a Mesozoic hot spring ecosystem. The Jurassic San Agustín hot spring deposit (Patagonia, Argentina), represents only the second known Phanerozoic hot spring ecosystem with an associated microflora and contains diverse, exceptionally preserved microorganisms. Preserved propagules include flask-shaped pycnidia produced by extant coelomycetes, shield-like and nearly round thyrtothecia of extant Microthyriales in the ascomycetes, variously shaped spore-like bodies representing chytrid and chytrid-like zoosporangia and other life cycle forms, and additional fungal and fungus-like remains (spores, hyphal fragments, reproductive structures) of uncertain affinity. Many of these microorganisms are associated with variously decayed organic remains, most commonly of horsetails. This expands the fungal fossil record and provides a unique opportunity to learn about the biology of Mesozoic microorganisms.

INTRODUCTION

Microorganisms, especially fungi, are important in modern ecosystems as primary decomposers and symbionts (Blackwell and Powell, 2000; Blackwell, 2011). The fungi have an extensive fossil record, possibly extending back 1500 million years to the Precambrian (Heckman et al., 2001; Taylor et al., 2009). However, despite their near-ubiquity and importance in modern ecosystems and their hypothesized Precambrian origin, the fossil record of fungi and fungus-like organisms is sparse, with large intervals of geological time and vast geographic areas lacking even basic information on their diversity (Kalgutkar and Jansonius, 2000; Heckman et al., 2001; Taylor et al., 2009).

Most information on the evolution and roles of fungi and other microorganisms in ancient terrestrial ecosystems comes from a limited number of fossil deposits, most notably cherts that originated from either geothermal activity (Taylor et al., 2004, 2009), or chemical dissolution of volcanic ash or diatomite and subsequent re-precipitation of silica within peat deposits (e.g., Le Page et al., 1994; García Massini, 2007a, 2007b; Krings et al., 2009a, 2009b, 2009c). Plant and fungal preservation is favored in both settings because silica-saturated water infiltrates cells and tissues of organisms early postmortem or even in life. Deposition of opal-A results in encrustation and permineralization of organic structure. This conserves fungal anatomical features and their host substrates, allowing the study of interactions and associations between fungi and other organisms at multiple cellular levels (García Massini, 2007a, 2007b).

Herein, we report for the first time the presence of fungi and fungus-like microorganisms from the first well-characterized Mesozoic (Middle to Upper Jurassic) hot spring ecosystem. This is the only hot spring

deposit known to contain a microorganism assemblage from the Mesozoic, and only one other such deposit, the Rhynie cherts from the Devonian of Scotland, is known from the entire Phanerozoic. A sample of preserved fungal and fungus-like remains from the Deseado Massif, southern Patagonia, Argentina, showing affinities to the ascomycetes, chytridiomycetes, glomeromycetes, deuteromycetes, and oömycetes is described and illustrated.

Included are pycnidia fruiting bodies that have been grouped (along with fungi that have acervular states) in the artificial taxon coelomycetes (Sutton, 1980; Kirk et al., 2001). Also present are dispersed thyrtothecia that can be related to extant Microthyriaceae in the ascomycetes, which are characterized by being epiphyllous and by the production of variously shaped fruiting bodies consisting of radially arranged or anastomosed hyphae (Schoch et al., 2009). We also report the presence of a number of structures that are morphologically similar to chytrid and chytrid-like organisms. Extant chytrids are separated mainly based on molecular and ultrastructural data, whereas morphologically they are represented by simple, although diverse, thalli that also look similar to structures produced by other fungal-like taxa (Porter, 1990; Webster and Weber, 2007). Among available characters that have been used to describe fossil chytrids are the presence or absence of an operculum for the liberation of zoospores, characteristics of their development (holocarpic or eucarpic and monocentric or polycentric), and type of habit (endobiotic or epibiotic) (Millay and Taylor, 1978; Taylor et al., 1992a, 1992b; Krings et al., 2007). A variety of dispersed spores, hyphae, and possible fruiting structures complete the cohort of fungi and fungus-like microorganisms.

GEOLOGICAL CONTEXT

The Deseado Massif geological province, part of the Chon Aike Large Igneous Province, formed during bimodal volcanic activity that characterized the Santa Cruz area of South America during the Jurassic, or in ages from 177.8 to 150.6 Ma (Pankhurst et al., 2000; Riley et al., 2001). This activity has been related to the breakup of Gondwana during separation of South America from Africa (Ramos, 2002). The volcanic and volcanoclastic rock succession (Bahía Laura Group) of the Deseado Massif comprises calc-alkaline rhyolite, minor andesite and rare dacite, extensive ignimbrites intervals and tuff layers, plus intercalated alluvial, fluvial and lacustrine sediments dominated by reworked volcanic materials. Calcareous travertine and siliceous sinter hot spring deposits occur across the region but dominantly in the west of the Massif (Guido and Schalamuk, 2003; Guido and Campbell, 2011). They represent the surface expression of widespread geothermal systems that produced epithermal mineralization in the province (Guido and Schalamuk, 2003). The hot spring deposits of the Deseado Massif (Fig. 1) are the first well-documented examples from the Mesozoic and fill a major gap in the Phanerozoic record for this type of deposit (Guido et al., 2010).

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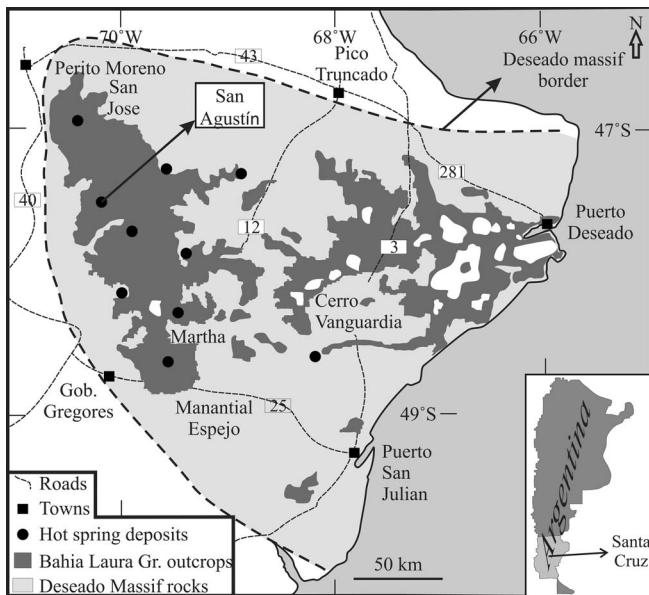


FIGURE 1—Map of the San Agustín hot spring deposits area within the Deseado Massif (Patagonia, Argentina).

MATERIALS AND METHODS

This paper focuses on chert of the San Agustín deposit (Fig. 1; W $70^{\circ} 22.296'$, S $47^{\circ} 39.013'$), which represents the only well-studied hot spring ecosystem of the Mesozoic (Guido et al., 2010). The deposit includes a nearly intact paleosurface comprising hot spring environments associated with a ~ 150 Ma geothermal system. The distribution of chert textures indicates four dominant sub-environments: (1) proximal areas of sinter aprons where water temperature likely exceeded 70°C ; (2) more distal apron areas (water temperature $70\text{--}30^{\circ}\text{C}$); (3) apron margins and geothermally influenced wetlands (water temperature 30°C to ambient); and (4) peripheral sedimentary areas (dryland environments and lake shorelines) subject to flooding with thermal runoff and post-depositional sediment silicification (Guido et al., 2010). Richly fossiliferous chert accumulated primarily on geothermally influenced wetland (supra-apron pools and peripheral marsh) where water temperatures were sufficiently low to allow colonization of the hot spring runoff by plants and animals. Information from active thermal areas such as Yellowstone, Wyoming, United States (Channing and Edwards, 2009a, 2009b; Guido et al., 2010) indicates that the San Agustín waters were brackish (1.3–1.4 ppt salinity) with high pH (typically pH 8–9) and high concentrations of potentially phytotoxic metals and metalloids. Silicification in such a setting would occur immediately after the death of the preserved biota.

Fossils were studied from acetate peels and standard thin sections mounted on microscope slides and examined with transmitted light microscopy (Galtier and Phillips, 1999; Hass and Rowe, 1999). Fossil identification and description were based on comparison with similar taxa from modern and ancient ecosystems (e.g., Nag Raj, 1993; Domsch et al., 2007; Taylor et al., 2009). Illustrated samples form part of accession MPM-PB 2029, Museo Padre Jesús Molina, Río Gallegos City, Santa Cruz Province.

RESULTS

The San Agustín chert samples contained abundant fungal and fungal-like remains. These include (1) flask-shaped structures representing fruiting bodies (pycnidia) like those produced by extant coelomycetes; (2) shield-like and nearly round structures indistinguishable from thyrithocia produced by extant Microthyriales in the ascomycetes; (3) circular to pyriform and cylindrical to rectangular

bodies similar to chytridiomycetes and chytridiomycetes-like zoosporangia; (4) uni- to multicellular spores; (5) fragments of hyphae of different morphologies; and (6) possible fruiting structures related to the oömycetes. Most fungi occurred embedded in organic remains (plant parts, spores, coprolites) with variable levels of preservation. The identifiable host plant remains were primarily from the horsetail *Equisetum thermale* (Channing et al., 2011), the dominant vascular plant in geothermally influenced environments of the deposit, where it occurs in dense, monotypic stands (Guido et al., 2010).

The fossil pycnidia from Patagonia occur embedded in partially decayed organic remains that probably represent plant parts and consist of several flask-shaped (mature) to depressed (immature) structures (empty or with partially preserved contents) with an ostiole-like aperture in more mature specimens (Figs. 2A–B). The wall of the pycnidia is apparently formed of at least two (or four based on pigmentation differences) layers of hyphae, respectively, interwoven (inner) and arranged in parallel (outer), which decrease in thickness toward the ostiole, where they are absent (Fig. 2C). The contents appear to be unicellular conidia with a single slit-like, pole-to-pole aperture (Fig. 2D), but incomplete preservation precludes confidence in their identification as conidia.

Sporocarpic structures (e.g., pycnidia) are often recorded in Paleozoic to Cenozoic sediments, but only the most recent and better-preserved examples have been confidently compared to modern taxa (Kalgutkar and Jansonius, 2000; Taylor et al., 2009). A number of characters used to classify extant taxa (e.g., type of conidiomata, location within the substrate, mode of dehiscence, conidiophores, conidia, wall structure) sometimes allow identification of fossil specimens (Nag Raj, 1993; Kalgutkar and Jansonius, 2000). With respect to such characters, the overall morphology and preserved contents of pycnidia from the Deseado Massif resemble most closely those produced by extant coelomycetes (Nag Raj, 1993). Coelomycetes include morphologically asexually reproducing fungi, which represent in most cases anamorphs of ascomycetes and, less commonly, basidiomycetes (Nag Raj, 1993). Some of the features observed in the fossil pycnidia (slit-like apertures in spores) are seen in extant taxa (e.g., *Coniochaeta cephalothecoides*; Kamiya et al., 1995), but these characters alone are usually of only relative taxonomic use.

A number of fossil fungal fructifications from the Deseado Massif that occur dispersed in the chert matrix most closely resemble ancient representatives of the Microthyriales (ascomycetes) (Kalgutkar and Jansonius, 2000). The Microthyriales are characterized by an epiphyllous habit and variously shaped, typically dimidiate-scutate or hysterothecoid, ascostromata with radiating or meandering cells or pseudoparenchymatic tissue (Barr and Huhndorf, 2001). The fossils from Patagonia include shield-like thyrithocia made up of radially arranged pseudoparenchymatic tissue (Fig. 2E) as in *Phragmothyrites* (Edwards, 1922). Also present are nearly round thyrithocia, commonly ostiolate, made up of plectenchymous tissue that consists of irregularly arranged sinuous cells (Fig. 2F) as in *Stomiopeltites* (Alvin and Muir, 1970).

The chytrid and chytrid-like fossils occur associated with degraded organic material, including the epidermis and cortex tissues of stems and roots of *Equisetum thermale*, plant tissue of unknown affinity, and thick-walled fungal and fungal-like spores and spore-like structures (Figs. 3A–E). They consist of morphologically variable, spherical to pyriform and rectangular structures similar to reproductive structures produced by extant taxa such as *Chytridium*, *Nowakowskiella*, *Olpidium*, *Rhizophydium*, and *Synchytrium* (Karling, 1964, 1977). Some of these fossils have thin rhizoids, a short apophysis (or stalk) or are sessile, and are commonly attached to plant tissue (Figs. 4A–C). A number of them have a circular opening on their surface, which possibly represents the space for an operculum (Fig. 4D). The lumen in some specimens is filled with presumptive zoospores or some sort of cyst or endospore consisting of spherical to slightly elongated, thin-

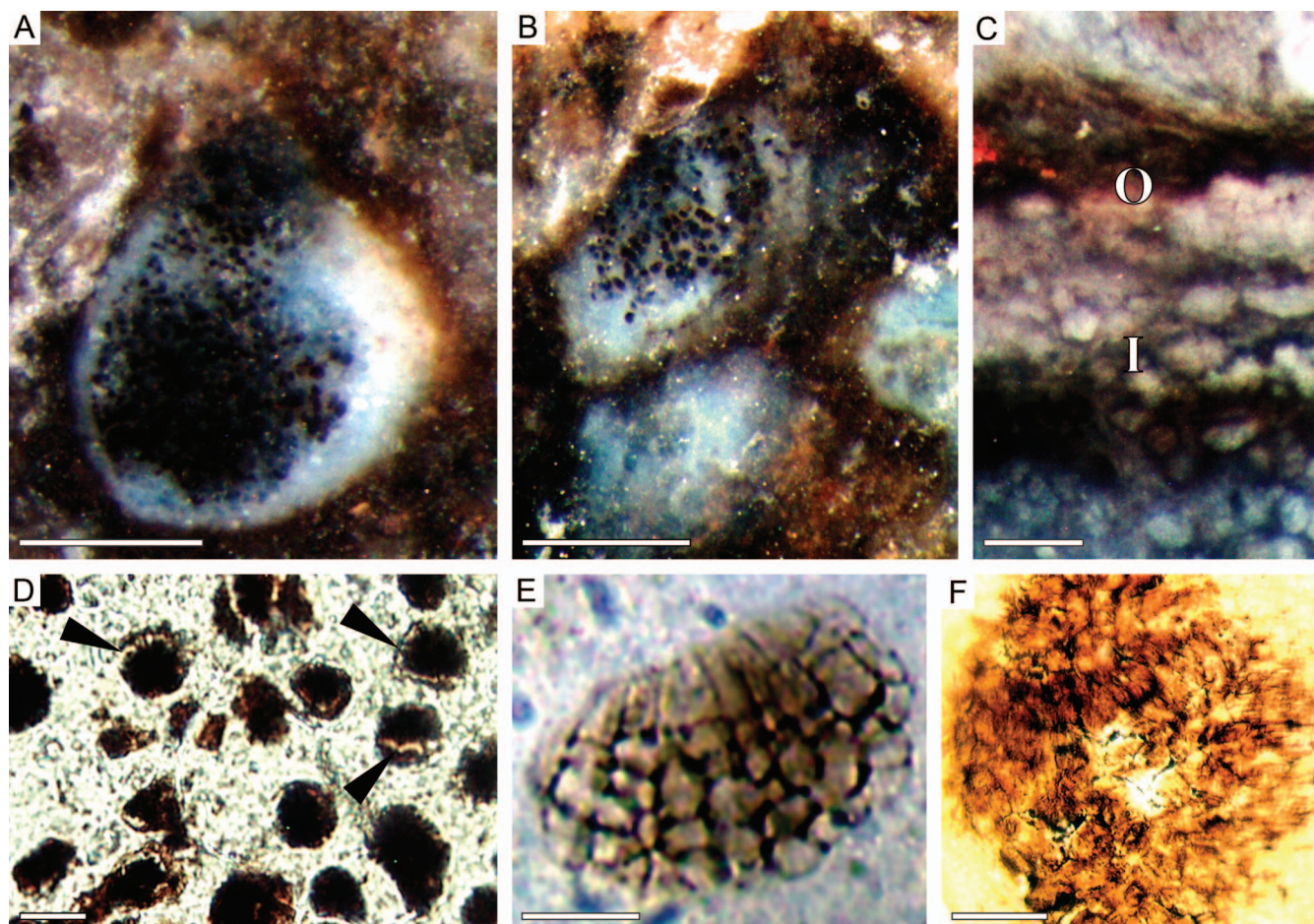


FIGURE 2—Fungal and fungal-like remains from the Jurassic of Patagonia (Argentina). Scale bars = 500 μm (A, B), 100 μm (C, E, F), 15 μm (D). A) Pycnidium immersed in decayed plant remains of unknown affinity. B) Immature pycnidia. C) Detail of wall of mature pycnidia. (I) layer of interwoven hyphae and outer (O) layer of hyphae arranged in parallel. D) Detail of contents of pycnidia: unicellular conidia with slit-like apertures (arrowheads). E) *Phragmothyrtes*-like microthyriaceous thyrithoeceia. F) *Stomiopeltites*-like microthyriaceous thyrithoeceia.

walled bodies with a uniform diameter of $\sim 7 \mu\text{m}$ (Fig. 4E). Those individuals inside hosts (plant cells and thick-walled spores) can be classified as endobiotic, whereas some of the rhizoidal-bearing or \sim pyriform fossils on thick-walled spores and plant tissue might have lived epibiotically, with rhizoids inside and sporangia external to the host (Webster and Weber, 2007).

The fossil zoosporangia appear to represent both holocarpic and eucarpic forms, where a primary distinction is based on production of dispersing units (zoospores, gametes) from, respectively, the whole vegetative thallus (except wall) or, if rhizoids are present, only part of the vegetative thallus (Alexopoulos et al., 1996). Fossil holocarpic zoosporangia are monocentric, with the vegetative thallus producing a single reproductive unit, whereas eucarpic forms might have had mono- or polycentric origins (Webster and Weber, 2007). However, the rhizoids apparently project from a single point in the rhizoid-bearing fossils (Fig. 4A), a feature that, in extant forms, is characteristic of monocentric taxa (Webster and Weber, 2007). However, systematic assessment of any fossil chytrids is difficult because, even with exceptional preservation, characters used to classify extant taxa (molecular, zoospore ultrastructure, life cycle) are not available (Taylor et al., 2009). For the Deseado Massif specimens, preserved thallus parts are similar to extant chytrids as well as to non-fungal groups, such as the thraustochytrids (Karling, 1964, 1977; Sparrow, 1960; Porter, 1990). More specific identification depends upon recognition of unique morphologies, life cycles, and association with particular hosts and reaction patterns (Remy et al., 1994; García Massini, 2007b).

Numerous remains in the chert matrix including coenocytic or septate hyphae of different lengths and thicknesses, uni- to multicellular spores that are commonly darkly pigmented, and possible fruiting structures represent fungi of uncertain identification and some may represent organisms other than fungi (Figs. 5A–E).

Hyphal filaments in the chert matrix are associated with plant and animal remains. They can form dense masses, commonly in association with well-preserved sections of roots and stems or with decayed plant remains, especially *Equisetum* (Fig. 5A). Hyphae were also found profusely colonizing animal remains, including coprolites of unknown microorganisms (Fig. 5B).

Most unicellular spores have the simple morphologies associated with a number of fungal taxa. Some, however, represent pyriform chlamydo-spores bearing fragments of subtending hyphae reminiscent of the genus *Glomus* of the glomeromycetes (Fig. 5C) (Morton and Benny, 1990). The unidentifiable multicellular spores are elongate, sometimes with appendages radiating from a common center (Fig. 5D). In extant hyphomycetes, such morphologies are associated with dispersal and anchorage to substrates in aquatic settings (Webster and Descals, 1981). Some of the fossil spores are most similar to extant dematiaceous hyphomycetes (Imperfect Fungi) like the facultative parasite *Alternaria* (Domsch et al., 2007).

Some of the San Agustín fossils resemble oogonia and oospores of extant members of the Peronosporomycetes (oömycetes; Kingdom Straminipila) as described by Sparrow (1960) and Dick (2001). These are smooth-walled, multilayered (2, 3, and possibly more layers),

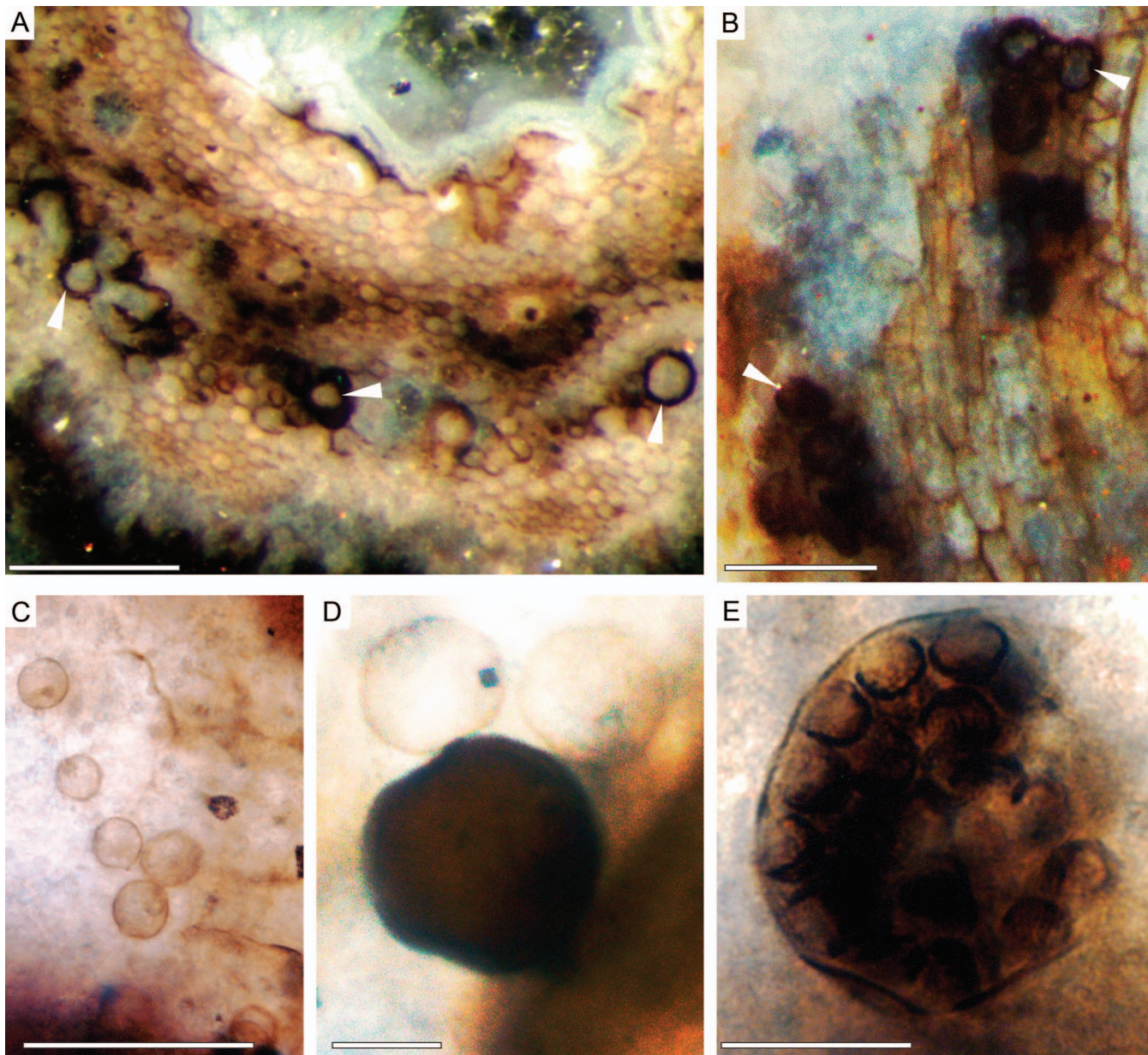


FIGURE 3—Fungal and fungal-like remains from the Jurassic of Patagonia (Argentina). Scale bars = 750 μm (A), 500 μm (B), 25 μm (C, D, E). A) Cross section of *Equisetum thermale* stem with chytrid-like zoosporangia (arrowheads). B) Chytrid or chytrid-like zoosporangium on *Equisetum thermale* roots (arrowheads). C) Chytrid-like zoosporangia in tissue of unknown affinity. D) Chytrid-like zoosporangia epibiotic on a darkly pigmented propagule of unknown affinity. E) Chytrid-like zoosporangia lined along the inner perimeter of a propagule of unknown affinity.

spherical (or nearly so) structures that are sometimes terminal on subtending coenocytic hyphae that appear septate at the base of the main structure (Fig. 5E). Apparent oospores or their remains occur singly inside oogonia, filling the lumen completely (plerotic) or only partly (aplerotic; more mature?). These features (a single oospore/oogonia, sometimes subtended by a hyphal stalk, a relatively thin wall), resemble those of a number of extant oömycetes taxa, such as *Araiospora*, *Pythium* and *Phytophthora* (Sparrow, 1960; Dick, 2001).

A few of the putative oogonia lack subtending hyphae and have a flat side with remains of a septum that probably represents the former attachment site for hyphae. These have an indented irregular wall (~papillate) and are filled with a small, opaque, apparently centrally located oospore (Fig. 5F). They could represent another oogonial developmental stage of the same taxa as the hyphae-bearing oogonia, or they might represent taxa such as *Achlya*, *Aphanomyces*, *Brevilegnia*,

and *Leptolegnia* (Dick, 1969; Steciow, 2003; Gomes and Pires-Zottarelli, 2008).

DISCUSSION

Fossil and molecular data suggest that the fungi in modern geothermal ecosystems belong to the same principal taxonomic groups as those present in the Paleozoic (Hibbett et al., 2007; Taylor et al., 2009). However, prior to this study, nothing was known of the mycoflora in geothermal deposits from the Mesozoic. This first report illustrates a diversity of forms that appear related to ascomycetes, chytridiomycetes, glomeromycetes, and deuteromycetes present in a variety of modern ecosystems including those with similar physico-chemical features (Redman et al., 1999; Steiman et al., 2004; Gleason et al., 2010).

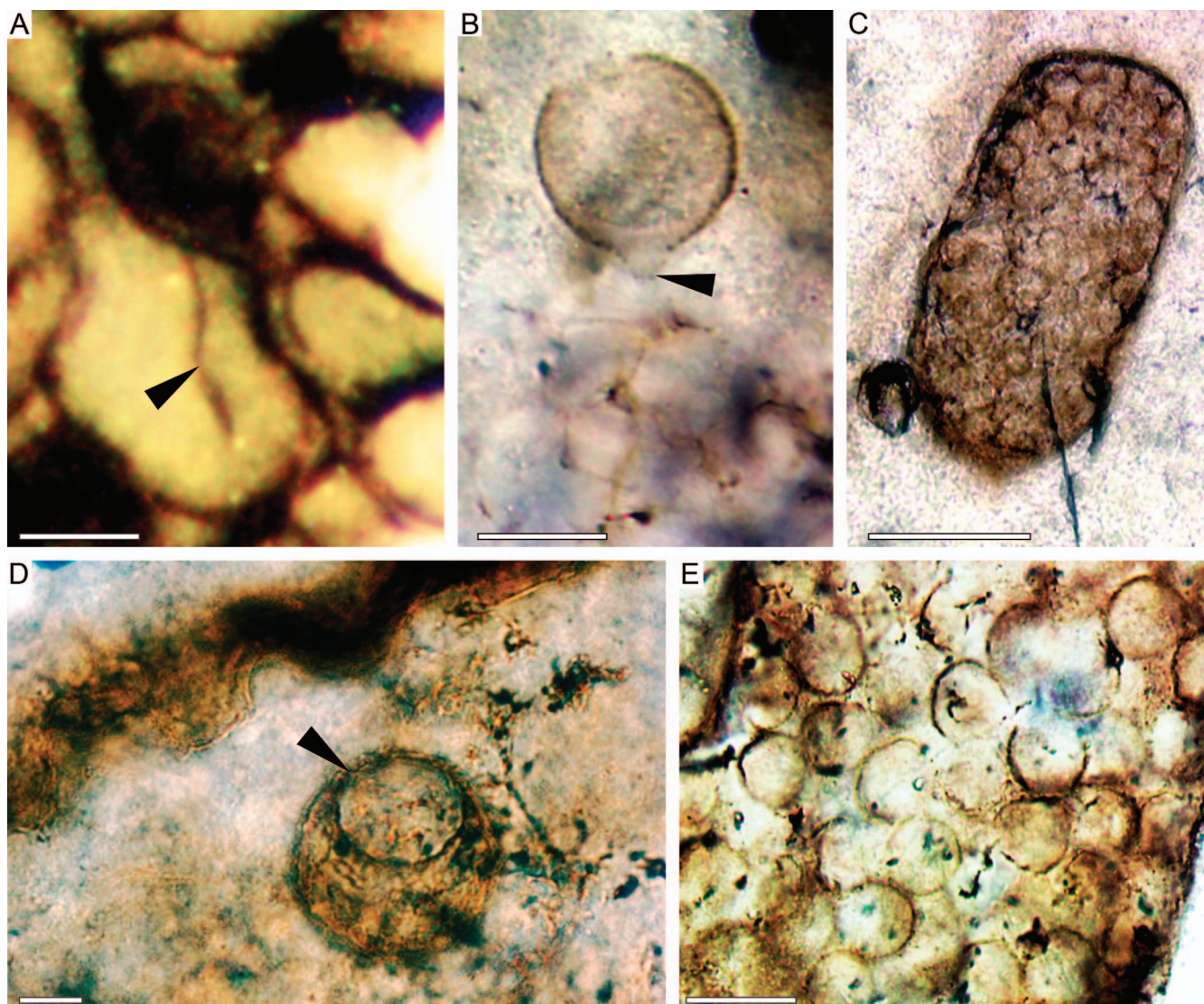


FIGURE 4—Fungal and fungal-like remains from the Jurassic of Patagonia (Argentina). Scale bars = 50 μm (A), 25 μm (B), 150 μm (C), 10 μm (D, E). A) Rhizoid-bearing chytrid-like zoosporangium (arrowhead). B) Chytrid-like zoosporangium with basal apophysis (arrow). C) Rectangular chytrid-like zoosporangium attached to highly degraded plant tissue. D) Dehiscent chytrid-like zoosporangium with a single circular opening on its surface (arrowhead). E) Detail of contents of rectangular chytrid-like zoosporangium.

Direct comparison of the San Agustín fungal assemblage with those in similar modern environments is difficult because there has been no systematic mycological survey of geothermally influenced wetlands around modern springs. However, broad comparisons can be made by reference to other modern environments with similar physical and chemical stresses, such as geothermal dryland soils and saline wetlands. Biotic communities of modern geothermal environments are distributed in a discrete fashion depending on, in decreasing order of importance, temperature, pH, and H_2S and O_2 concentrations (Walter and Des Marais, 1993; Burns, 1997; Subrahmanyam, 2010). These factors, and others, including nutrient levels, salinity, moisture, and presence of non-fungal competitors and predators, make fungal communities in geothermal and related settings a physiologically heterogeneous group of organisms (Magan, 1997; Gessner et al., 2007). In addition, distribution of hosts for symbiosis-forming taxa also influences occurrence and location of fungi within geothermal and related environments (Burns, 1997; Redman et al., 1999, 2002). The symbiotic associates can colonize harsh habitats where high temperatures and oligotrophy limit the occurrence of competitors (Glime and Iwatsuki, 1994; Redman et al., 2002; Bunn and Zabinsky, 2003). Consequently,

fungi in geothermal soils and saline wetlands are represented by ubiquitous taxa and taxa specifically adapted to, and tolerant of, such harsh conditions (Redman et al., 2002; Kogej et al., 2007; Appoloni et al., 2008; Subrahmanyam, 2010).

This is the first report of coelomycetes (ascomycetes or, less likely, basidiomycetes) in ancient hot spring environments. Previous coelomycete records indicate a Cretaceous radiation associated with the evolution of angiosperms (Watanabe et al., 1999). However, the Jurassic age of the San Agustín fossils, together with their hot spring environment, suggests an ecological role independent of co-evolution with angiosperms. The San Agustín fossils might represent extinct ascomycete and/or basidiomycete ancestors, much like similar sporocarps in Triassic cherts from Antarctica (Taylor and White, 1989). The presence of coelomycetes in the Jurassic hot springs of Patagonia is consistent with the presence of ascomycetes (including pycnidia-forming taxa) in modern ecosystems with similar physico-chemical conditions (Steiman et al., 2004). Moreover, the presence of ascomycetes associated with decaying plants in shallow, ambient temperature, alkaline and saline, wetland pools on sinter-apron surfaces of Yellowstone hot springs supports that members of this

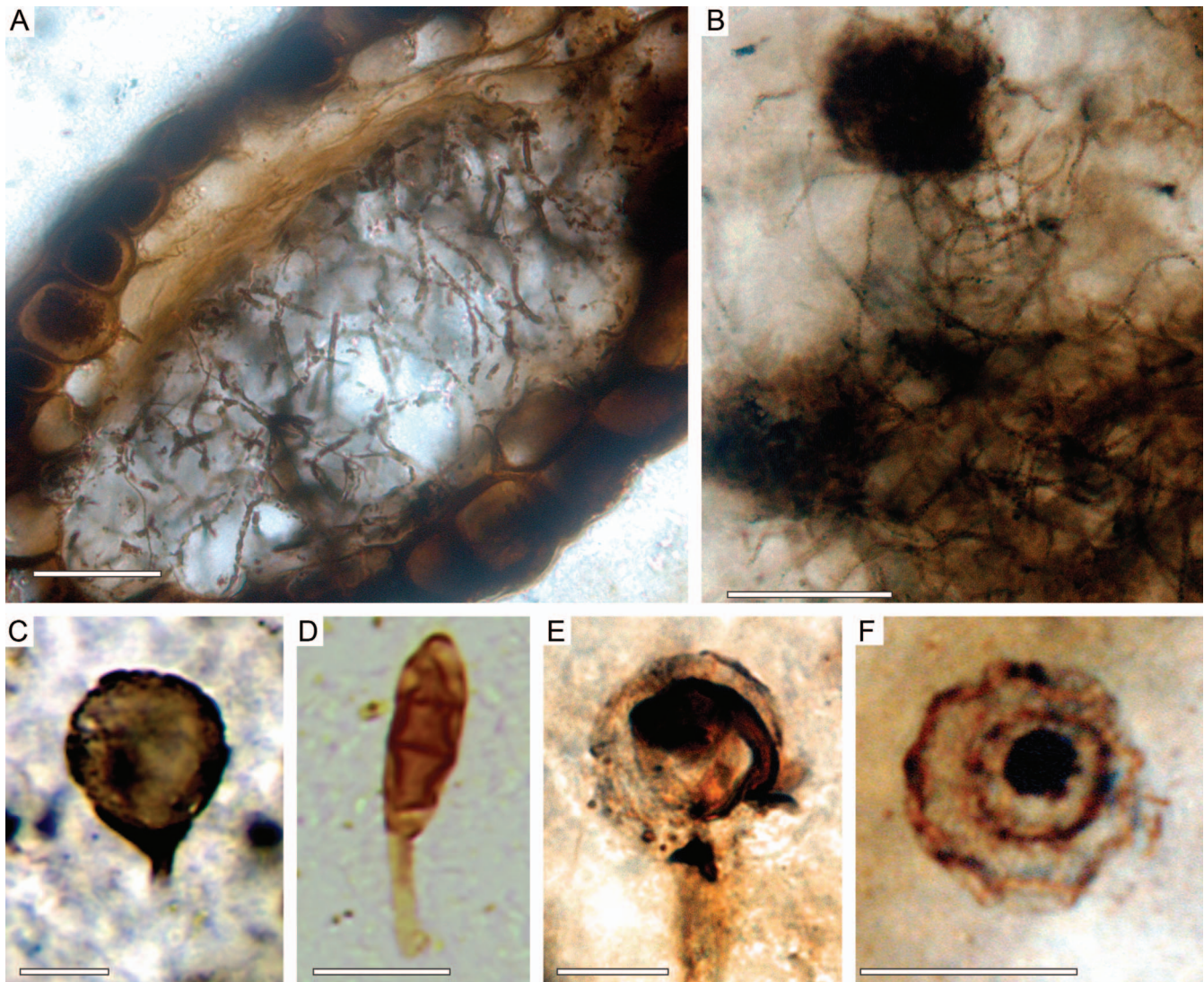


FIGURE 5—Fungal and fungal-like remains from the Jurassic of Patagonia (Argentina). Scale bars = 50 μm (A, B), 25 μm (C), 20 μm (C, E, F). A) Cross section of *Equisetum thermale* stem filled with septate hyphae. B) Hyphal filaments in a microcoprolite of an unknown microorganism. C) *Glomus*-like chlamydospore. D) *Alternaria*-like spore. E) Oogonium-like multilayered structure. F) Partially preserved oogonium-like multilayered structure.

group are common inhabitants of hot spring and related environments (Channing, 2001).

The presence of Microthyriales (ascomycetes) in the San Agustín cherts is the first record of this group in hot spring paleoenvironments and sheds light on the evolutionary history of the group. Microthyriales has an extensive fossil record extending back to the Early Cretaceous (Kalgutkar and Jansonius, 2000). This led to the suggestion that the group's origin paralleled that of angiosperms (Dilcher, 1965). However, their wide geographic distribution early after their first appearance in the Cretaceous, and a Devonian record from Siberia of thyrtothecia similar to more recent fossil Microthyriales, suggests that the epiphyllous habit developed earlier, perhaps in response to a new habitat, the phylloplane (Krassilov, 1981; Taylor, 1994; Kalgutkar and Jansonius, 2000). The San Agustín fossils represent the second pre-Cretaceous record of the Microthyriales, and the absence of angiosperms in the deposit shows that these fungi lived epiphytically on another form of host.

Modern representatives of the Microthyriales occur in moist tropical to temperate regions and as fossils they have been used to indicate similar paleoconditions (e.g., García Massini et al., 2004). Microthyriales would have been well suited to the moist conditions of the Deseado Massif hot spring areas and probably were associated with

conifers at the periphery of the geothermally influenced landscape. Dryland conifer forest fringes were commonly flooded by encroachment of geothermal wetland and sinter-apron environments (Channing et al., 2007; Guido et al., 2010). Such areas in active hot spring settings are characterized by drowned and decaying tree trunks and branches (Channing and Edwards, 2009b)

The Jurassic San Agustín mycoflora holds an interesting diversity of chytrid and chytrid-like fossils. Diverse chytrid assemblages are also characteristic in modern habitats physico-chemically similar to the postulated San Agustín paleoenvironment (Gleason et al., 2010; Guido et al., 2010). Chytrid and chytrid-like diversity in the San Agustín deposit might reflect their association with the dense monotypic stands of *Equisetum* in geothermal ponds (Guido et al., 2010; Channing et al., 2011) and the long-term viability of chytrid propagules in soil (Johnson and Speare, 2005).

Chytrids are scarce in the fossil record, and information on their paleobiology is mainly from the Paleozoic, especially the Devonian Rhynie Chert (Taylor et al., 2009). The Rhynie hot spring ecosystem apparently supported a high diversity of saprotrophic and parasitic chytrids on plants and fungi, including epibiotic and endobiotic, holo- and eucarpic forms that differ little from extant taxa in morphology and host reactions (Taylor et al., 1992a, 1992b; Krings et al., 2007). The

San Agustín and Rhynie chert chytrids are strikingly similar in habitat and style of preservation. In both deposits the chytrids occur in plant-rich cherts along with aquatic arthropods, microcoprolites and chlorophyte algae. Provisionally, there are similarities in morphological and ecological diversity, suggesting that further study of the Deseado Massif will provide an equally deep understanding of the paleobiology of chytrids in Mesozoic ecosystems. Such studies might reveal host taxa adapted to the specific conditions characterizing the Jurassic of Patagonia. So far, chytrids from the Deseado Massif appear similar to a number of extant taxa from a broad range of habitats (Sparrow, 1960; Karling, 1964, 1977).

The San Agustín deposit contains dispersed spores attributable to extant glomeromycetes (*Glomus*) that might have had a significant role in the San Agustín ecosystem. Extant glomeromycetes are associated with vegetation in modern saline marshes and geothermal soils (Redman et al., 1999; Wilde et al., 2009). Other fossils resemble extant hyphomycetes (*Alternaria*) that occur in modern brackish to saline environments (Abdel-Fattah et al., 1977; Steiman et al., 2004; Wilde et al., 2009). These observations are consistent with the brackish and moist depositional setting inferred for the study site (Guido et al., 2010). Moreover, like fungi in modern geothermal and saline settings (Redman et al., 2002; Kogej et al., 2007), melanization of cellular walls is common among San Agustín fungal propagules.

The San Agustín fungi and fungus-like organisms illustrated, like those of the Rhynie chert, represent a diversity of finely preserved forms associated with plant and animal remains, which most likely reflects the predominance of geothermal wetlands as an environment conducive to fossilization. This ecosystem-level preservation is rare in the fossil record but it appears common in hot spring settings, such as is illustrated here. The initial diversity observed and the fine preservation evident within the San Agustín hot spring deposit presents a unique opportunity to fill significant gaps in our understanding of the diversity, evolution and diversification of fungi during the Mesozoic and from a kind of setting previously known only from the Paleozoic.

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REFERENCES

- ABDEL-FATTAH, H.M., MOUBASHER, A.H., and ABDEL-HAFEZ, S.I., 1977, Studies on microflora of salt marshes in Egypt. 1. Sugar Fungi: *Mycopathologia*, v. 61, p. 19–26.
- ALEXOPOULOS, C.J., MIMS, C.W., and BLACKWELL, M., 1996, *Introductory Mycology*: John Wiley and Sons, New York, 868 p.
- ALVIN, K.L., and MUIR, M.D., 1970, An epiphyllous fungus from the Lower Cretaceous: *Biological Journal of the Linnean Society*, v. 2, p. 55–59.
- APPOLONI, S., LEKBERG, Y., TERCEK, M., ZABINSKI, C., and REDECKER, D., 2008, Molecular community analysis of arbuscular mycorrhizal fungi in roots from geothermal soils in Yellowstone National Park (USA): *Microbial Ecology*, v. 56, p. 649–659.
- BARR, M.E., and HUHNDRORF, S.M., 2001, Loculoascomycetes, in McLaughlin, D.J., McLaughlin, E.G., and Lemke, P.A., eds., *Systematics and Evolution*, vol. 7, part A, *The Mycota*: Springer-Verlag, Berlin, p. 283–305.
- BLACKWELL, M., 2011, The Fungi: 1, 2, 3 ... 5.1 million species? *American Journal of Botany*, v. 98, p. 426–438.
- BLACKWELL, W.H., and POWELL, M.J., 2000, A review of group filiation of stramenopiles, additional approaches to the question: *Evolutionary Theory*, v. 12, p. 49–88.
- BUNN, R.A., and ZABINSKI, C.A., 2003, Arbuscular mycorrhizae in thermal-influenced soils in Yellowstone National Park: *Western North American Naturalist*, v. 63, p. 409–415.
- BURNS, B., 1997, Vegetation change along a geothermal stress gradient at the Te Kopia steamfield: *Journal of the Royal Society of New Zealand*, v. 27, p. 279–294.
- CHANNING, A., 2001, *Processes and Environments of Vascular Plant Silicification*: Unpublished Ph.D. thesis, Cardiff University, Cardiff, Wales, 291 p.
- CHANNING, A., and EDWARDS, D., 2009a, Silicification of higher plants in geothermally influenced wetlands: Yellowstone as a Lower Devonian Rhynie analog: *PALAIOS*, v. 24, p. 505–521.
- CHANNING, A., and EDWARDS, D., 2009b, Yellowstone hot spring environments and the palaeoecophysiology of Rhynie chert plants: towards a synthesis: *Plant Ecology and Diversity*, v. 2, p. 111–143.
- CHANNING, A., ZAMUNER, A.B., and ZUÑIGA, A., 2007, A new Middle–Late Jurassic flora and hot spring chert deposit from the Deseado Massif, Santa Cruz province, Argentina: *Geological Magazine*, v. 144, p. 401–411.
- CHANNING, A., ZAMUNER, A.B., EDWARDS, D., and GUIDO, D.M., 2011, *Equisetum thermale* sp. nov. (Equisetales) from the San Agustín hot spring deposit, Patagonia: Anatomy, paleoecology and inferred palaeoecophysiology: *American Journal of Botany*, v. 98, p. 680–697.
- DICK, M.W., 1969, Morphology and taxonomy of the oömycetes, with special reference to Saprolegniaceae, Leptomitaceae and Pythiaceae. I. Sexual reproduction: *New Phytologist*, v. 68, p. 751–775.
- DICK, M.W., 2001, Straminipilous Fungi: Systematics of the peronosporomycetes including accounts of the marine straminipilous protists, the plasmodiophorids and similar organisms: Kluwer Academic Publishers, London, 364 p.
- DILCHER, D.L., 1965, Epiphyllous fungi from Eocene deposits in western Tennessee, USA: *Palaentographica Abt. B*, v. 116, p. 1–54.
- DOMSCH, K.H., GAMS, W., and ANDERSON, T.-H., 2007, *Compendium of Soil Fungi*: IHW-Verlag, Eching, Germany, 672 p.
- EDWARDS, W.N., 1922, An Eocene microthyriaceous fungus from Mull, Scotland: *Transactions of the British Mycological Society*, v. 8, p. 66–72.
- GALTIER, J., and PHILLIPS, T.L., 1999, The acetate peel technique, in Jones, T.P., and Rowe, N.P., eds., *Fossil Plants and Spores: Modern Techniques: The Geological Society, London*, p. 67–70.
- GARCÍA MASSINI, J.L., ZAMALOA, M.C., and ROMERO, E.J., 2004, Fungal fruiting bodies in the Cullen Formation (Miocene) in Tierra del Fuego, Argentina: *Ameghiniana*, v. 41, p. 1–9.
- GARCÍA MASSINI, J.L., 2007a, A Glomalean fungus from the Permian of Antarctica: *International Journal of Plant Sciences*, v. 168, p. 673–678.
- GARCÍA MASSINI, J.L., 2007b, A possible endoparasitic chytridiomycete fungus from the Permian of Antarctica: *Palaentologia Electronica*, vol. 10, no. 3; 24.93 MB, http://palaeco-electronica.org/2007_3/121/index.html. Checked August 2011.
- GESSNER, M.O., GULIS, V., KUEHN, K.A., CHAUVET, E., and SUBERKROPP, K., 2007, Fungal decomposers of plant litter in aquatic ecosystems, in Kubicek, C.P., and Druzhinina, I.S., eds., *Environmental and Microbial Relationships*, vol. 4, 2nd ed., *The Mycota: A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research*: Springer Verlag, Berlin, p. 301–324.
- GLEASON, F.H., SCHIMDT, S.K., and MARANO, A.V., 2010, Can zoospore true fungi grow or survive in extreme or stressful environments? *Extremophiles*, v. 14, p. 417–425.
- GLIME, J.M., and IWATSUKI, Z., 1994, Geothermal communities of Ponponyama, Hokkaido, Japan: *Journal of the Hattori Botanical Laboratory*, v. 75, p. 133–147.
- GOMES, A.L., and PIRES-ZOTTARELLI, C.L.A., 2008, Oomycota (Straminipila) da Reserva Biológica de Paranapiacaba, Santo André, SP, Brasil: *Acta Botanica Brasileira*, v. 22, p. 373–392.
- GUIDO, D.M., and CAMPBELL, K.A., 2011, Jurassic hot spring deposits of the Deseado Massif (Patagonia, Argentina): Characteristics and controls on regional distribution: *Journal of Volcanology and Geothermal Research*, v. 203, p. 35–47.
- GUIDO, D., and SCHALAMUK, I.B., 2003, Genesis and exploration potential for low sulfidation epithermal deposits in the Deseado Massif, Argentinean Patagonia, in Eliopoulos, D. et al. eds., *Mineral Exploration and Sustainable Development*, vol. 1: Balkema-Rotterdam, Rotterdam, p. 493–496.
- GUIDO, D.M., CHANNING, A., CAMPBELL, K., and ZAMUNER, A., 2010, Jurassic geothermal landscapes and ecosystems at San Agustín, Patagonia, Argentina: *Journal of the Geological Society of London*, v. 167, p. 11–20.
- HASS, H., and ROWE, N.P., 1999, Thin sections and wafering, in Jones, T.P., and Rowe, N.P., eds., *Fossil Plants and Spores: Modern Techniques: Geological Society of London*, London, p. 76–81.
- HECKMAN, D.S., GEISER, D.M., EIDELL, B.R., STAUFFER, R.L., KARDOS, N.L., and HEDGES, S.B., 2001, Molecular evidence for the early colonization of land by fungi and plants: *Science*, v. 293, p. 1129–1133.
- HIBBETT, D.S., BINDER, M., BISCHOFF, J.F., BLACKWELL, M., CANNON, P.F., ERIKSSON, O.E., HUHNDRORF, S., JAMES, T., KIRK, P.M., LÜCKING, R., THORSTEN LUMBSCH, H., LUTZONI, F., MATHENY, P.B., McLAUGHLIN, D.J., POWELL, M.J., REDHEAD, S., SCHOCH, C.L., SPATAFORA, J.W., STALPERS, J.A., VILGALYS, R., AIME, M.C., APROOT, A., BAUER, R., BEGEROW, D., BENNY, G.L., CASTLEBURY, L.A., CROUS, P.W., DAI, Y.-C., GAMS, W., GEISER, D.M., GRIFFITH, G.W., GUEIDAN, C., HAWKSWORTH, D.L., HESTMARK, G., HOSAKA, K., HUMBER, R.A., HYDE, K.D., IRONSIDE, J.E., KÖLJALG, U., KURTZMAN, C.P., LARSSON, K.-H., LICHTWARDT, R., LONGCORE, J., DLIKOWSKA, M.J., MILLER, A., MONCALVO, J.-M., MOZLEY-

- STANDRIDGE, S., OBERWINKLER, F., PARMASO, E., REEB, V., ROGERS, J.D., ROUX, C., RYVARDEN, L., SAMPAIO, J.P., SCHÜBLER, A., SUGIYAMA, J., THORN, G., TIBELL, L., UNTEREINER, W.A., WALKER, C., WANG, Z., WEIR, A., WEISS, A., WEISS, M., WHITE, M.M., WINKA, K., YAO, Y.-J., and ZHANG, N., 2007, A higher-level phylogenetic classification of the Fungi: *Mycological Research*, v. 111, p. 509–547.
- JOHNSON, M., and SPEARE, R., 2005, Possible modes of dissemination of the amphibian chytrid *Batrachochytrium dendrobatidis* in the environment: *Diseases of Aquatic Organisms*, v. 65, p. 181–186.
- KALGUTKAR, R.M., and JANSONIUS, J., 2000, Synopsis of Fossil Fungal Spores, Mycelia and Fructifications: American Association of Stratigraphic Palynologists, Contribution Series, No. 39, Dallas, 429 p.
- KAMIYA, S., UCHIYAMA, S., and UDAGAWA, S.-I., 1995, Two new species of *Coniochaeta* with cephalothecoid peridium wall: *Mycoscience*, v. 36, p. 377–383.
- KARLING, J.S., 1964, *Synchytrium*: Academic Press, New York, 457 p.
- KARLING, J.S., 1977, *Chytridiomycetorum Iconographia. An Illustrated and Brief Descriptive Guide to the Chytridiomycetous Genera with a Supplement of the Hyphochytriomycetes*: J. Cramer, Vaduz, Liechtenstein, 414 p.
- KIRK, P.M., CANNON, P.F., DAVID, J.C., and STALPERS, J.A., eds., 2001, *Ainsworth & Bisby's Dictionary of the Fungi*, 9th ed.: CABI Publishing, 650 p.
- KOGEJ, T., STEIN, M., VOLKMAN, M., GORBUSHINA, A.A., GALINSKY, E.A., and GUNDE-CIMERMAN, N., 2007, Osmotic adaptation of the halophilic fungus *Hortaea werneckii*: Role of osmolytes and melanization: *Microbiology*, v. 153, p. 4261–4273.
- KRASSILOV, V.A., 1981, Changes of Mesozoic vegetation and the extinction of dinosaurs: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 34, p. 207–224.
- KRINGS, M., DOTZLER, N., TAYLOR, T.N., and GALTIER, J., 2007, A microfungal assemblage in *Lepidodendron* from the upper Viséan (Carboniferous) of central France: *Comptes Rendus Palevol*, v. 6, p. 431–436.
- KRINGS, M., DOTZLER, N., GALTIER, J., and TAYLOR, T.N., 2009a, Microfungi from the upper Viséan (Mississippian) of central France: Chytridiomycota and chytrid-like remains of uncertain affinity: *Review of Palaeobotany and Palynology*, v. 156, p. 319–328.
- KRINGS, M., DOTZLER, N., TAYLOR, T.N., and GALTIER, J., 2009b, A Late Pennsylvanian fungal leaf endophyte from Grand-Croix, France: *Review of Palaeobotany and Palynology*, v. 156, p. 440–444.
- KRINGS, M., GALTIER, J., TAYLOR, T.N., and DOTZLER, N., 2009c, Chytrid-like microfungi in *Biscalitheca* cf. *musata* (Zygopteridales) from the Upper Pennsylvanian Grand-Croix cherts (Saint-Etienne Basin, France): *Review of Palaeobotany and Palynology*, v. 157, p. 309–316.
- LEPAGE, B.A., CURRAH, R.S., and STOCKEY, R.A., 1994, The fossil fungi of the middle Eocene Princeton Chert, British Columbia, Canada: *International Journal of Plant Sciences*, v. 155, p. 829–836.
- MAGAN, N., 1997, Fungi in extreme environments, in Wicklow, D.T., and Soderstrom, B., eds., *Environmental and Microbial Relationships*, vol. 4, The Mycota: Springer-Verlag, Berlin, p. 85–103.
- MILLAY, M.A., and TAYLOR, T.N., 1978, Chytrid-like fossils of Pennsylvanian age: *Science*, v. 200, p. 1147–1149.
- MORTON, L.B., and BENNY, G.L., 1990, Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): A new order, Glomales, two new suborders, Glomineae and Gigasporineae, and two new families, Acaulosporaceae and Gigasporaceae, with an emendation of Glomaceae: *Mycotaxon*, v. 37, p. 471–491.
- NAG RAJ, T.R., 1993, *Coelomycetous Anamorphs with Appendage-Bearing Conidia*: Mycologue Publications, Waterloo, Ontario, 1101 p.
- PANKHURST, R.J., RILEY, T.R., FANNING, C.M., and KELLEY, S.R., 2000, Episodic silicic volcanism in Patagonia and the Antarctic Peninsula: Chronology of magmatism associated with the break-up of Gondwana: *Journal of Petrology*, v. 41, p. 605–625.
- PORTER, D., 1990, Phylum Labyrinthulomycota, in Margulis, L., Corliss, J.O., Melkonian, M., and Chapman, J., eds., *Handbook of Protozoists*: Jones and Barlett Publishers, Boston, p. 338–398.
- RAMOS, V., 2002, Evolución tectónica, in Haller, M.J., ed., *Recursos Naturales de Santa Cruz, Relatorio del XV Congreso Geológico Argentino, El Calafate: Asociación Geológica Argentina*, p. 365–387.
- REDMAN, R.S., LITVINTSEVA, A., SHEENAN, K.B., HENSON, J.M., and RODRIGUEZ, R.J., 1999, Fungi from geothermal soils in Yellowstone National Park: *Applied Environmental Microbiology*, v. 65, p. 5193–5197.
- REDMAN, R.S., SHEEHAN, K.B., STOUT, R.G., RODRIGUEZ, R.J., and HENSON, J.M., 2002, Thermotolerance generated by plant/fungal symbiosis: *Science*, v. 298, p. 1581.
- REMY, W., TAYLOR, T.N., HASS, H., and KERP, H., 1994, Four hundred million-year-old vesicular arbuscular mycorrhizae: *Proceedings of the National Academy of Sciences of the United States of America*, v. 91, p. 11841–11843.
- RILEY, T.R., LEAT, P.T., PANKHURST, R.J., and HARRIS, C., 2001, Origins of large volume silicic volcanism in the Antarctic Peninsula and Patagonia by crustal melting: *Journal of Petrology*, v. 42, p. 1043–1065.
- SCHOCH, C.L., CROUS, P.W., GROENEWALD, J.Z., BOEHM, E.W.A., BURGESS, T.I., DE GRUYTER, J., DE HOOG, G.S., DIXON, L.J., GRUBE, M., GUEIDAN, C., HARADA, S., HATAKEYAMA, Y., HIRAYAMA, K., HOSOYA, T., HUHDORF, S.M., HYDE, K.D., JONES, E.B.G., KOHLMAYER, J., KRUYIS, Á., LI, Y.M., LUCKING, R., LUMBSCH, H.T., MARVANOVÁ, L., MBATCHOU, J.S., MCVAY, A.H., MILLER, A.N., MUGAMBI, G.K., MUGGIA, L., NELSEN, M.P., NELSON, P., OWENSBY, C.A., PHILLIPS, A.J.L., PHONGPAICIT, S., POINTING, S.B., PUJADE-RENAUD, V., RAJA, H.A., RIVAS PLATA, E., ROBERTSE, B., RUIBAL, C., SAKAYAROI, J., SANO, T., SELBMANN, L., SHEARER, C.A., SHIROUZU, T., SLIPPERS, B., SUETRONG, S., TANAKA, K., VOLKMAN-KOHLMEYER, B., WINGFIELD, M.J., WOOD, A.R., WOUDEBERG, J.H.C., YONEZAWA, H., ZHANG, Y., and SPATAFORA, J.W., 2009, A class-wide phylogenetic assessment of Dothideomycetes: *Studies in Mycology*, v. 64, p. 1–15.
- SPARROW, F.K., 1960, *Aquatic Phycmycetes*: The University of Michigan Press, Ann Arbor, Michigan, 1187 p.
- STECIOW, M.M., 2003, A new species of *Brevilegnia* (Saprolegniales, Straminipila) from Buenos Aires Province, Argentina: *Mycologia*, v. 95, p. 934–942.
- STEIMAN, R., FORD, L., DUCROS, V., LAFOND, J.-L., and GUIRAUD, P., 2004, First survey of fungi in hypersaline soil and water of Mono Lake area (California): *Antonie van Leeuwenhoek*, v. 85, p. 69–83.
- SUBRAHMANYAM, A., 2010, *Ecology and Distribution*, in Johri, B.N., Satyanarayana, T., and Olsen, J., eds., *Thermophilic Moulds in Biotechnology*: Kluwer Academic Publishers, Dordrecht, p. 13–42.
- SUTTON, B.C., 1980, *The Coelomycetes* (CAB, IMI): Kew, Surrey, United Kingdom, p. 696.
- TAYLOR, T.N., 1994, The fossil history of ascomycetes, in Hawksworth, D.L., ed., *Ascomycete Systematics: Problems and Perspectives in the Nineties*: Plenum Press, New York, p. 167–174.
- TAYLOR, T.N., and WHITE, J.F., 1989, Fossil fungi (Endogonaceae) from the Triassic of Antarctica: *American Journal of Botany*, v. 76, p. 389–396.
- TAYLOR, T.N., HASS, H., and REMY, W., 1992a, Devonian fungi: interactions with the green alga *Palaeoniella*: *Mycologia*, v. 84, p. 901–910.
- TAYLOR, T.N., REMY, W., and HASS, H., 1992b, Fungi from the Lower Devonian Rhynie chert: Chytridiomycetes: *American Journal of Botany*, v. 79, p. 1233–1241.
- TAYLOR, T.N., HASS, H., KRINGS, M., KLAVINS, S.D., and KERP, H., 2004, Fungi in the Rhynie chert: A view from the dark side: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 94, p. 457–473.
- TAYLOR, T.N., TAYLOR, E.L., and KRINGS, M., 2009, *Paleobotany: The Biology and Evolution of Fossil Plants*: Elsevier Academic Press, Burlington, Massachusetts, 1230 p.
- WALTER, M.R., and DES MARAIS, D.J., 1993, Preservation of biological information in thermal spring deposits: Developing a strategy for the search for fossil life on Mars: *Icarus*, v. 101, p. 129–143.
- WATANABE, K., NISHIDA, H., and KOBAYASHI, T., 1999, Cretaceous deuteromycetes on a cycadeoidalean bisexual cone: *International Journal of Plant Sciences*, v. 160, p. 435–443.
- WEBSTER, J., and DESCALS, E., 1981, Morphology, distribution, and ecology of conidial fungi in freshwater habitats, in Cole, G.T., and Kendrick, B., eds., *Biology of Conidial Fungi*, vol. 1: Academic Press, Inc., New York, p. 295–355.
- WEBSTER, J., and WEBER, R., 2007, *Introduction to Fungi*: Cambridge University Press, Cambridge, UK, 841 p.
- WILDE, P., MANAL, A., STODDEN, M., SIEVERDING, E., HILDEBRANDT, U., and BOTHEL, H., 2009, Biodiversity of arbuscular mycorrhizal fungi in roots and soils of two salt marshes: *Environmental Microbiology*, v. 11, p. 1548–1561.