A PERITHECIAL SORDARIOMYCETE (ASCOMYCOTA, DIAPORTHALES) FROM THE LOWER CRETACEOUS OF VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

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A perithecial ascomycete, *Spataporthe taylori* gen. et sp. nov., represented by >70 sporocarps is preserved by cellular permineralization in marine carbonate concretions dated at the Valanginian-Hauterivian boundary (Early Cretaceous) from Vancouver Island, British Columbia, Canada. The spheroid perithecia with lumina 330–470 μm wide and 220–320 μm high are densely distributed and entirely immersed in the tissues of a coniferous leaf. The perithecial wall consists of an outer layer of large pseudoparenchyma and an inner layer of thin filamentous nature. Perithecial necks are incompletely preserved due to taphonomic abrasion; they have a bell-shaped chamber at the base and a narrow channel, with longitudinally aligned hyphae above. The basal chamber of the neck is filled with a plug of pseudoparenchyma, which subsequently disintegrates to form a peripheral collar; periphyses are present on the basal chamber walls. A pseudoparenchymatous hymenium lines the bottom of perithecia. Asci are clavate, with thinly tapered bases, and small (30–47 μm long and 12–20 μm wide at tip), ornamented with minute papillae. They become detached from the hymenium to float freely in the perithecium. No unequivocal ascospores were found, although smaller units are present in some of the asci. The combination of immersed perithecia with complex wall structure and a well-defined hymenium, absence of paraphyses, and persistent, detachable inoperculate asci is consistent with order Diaporthales of class Sordariomycetes. The small clavate asci are comparable to those found in family Gnomoniaceae. Perithecioid ascomata are rare in the fossil record, and bona fide perithecia are known with certainty only from the Early Devonian Rhynie Chert and Cenozoic amber. *Spataporthe taylori* contributes a well-characterized Early Cretaceous occurrence, which is also the oldest to date, to the scarce fossil record of the Sordariomycetes and a second taxon to the fungal flora of the locality, which also includes a basidiomycete. As the oldest representative of the Diaporthales, *Spataporthe* provides a minimum age (136 Ma) for the order and a direct calibration point for studies of divergence times in the ascomycetes.

Keywords: Ascomycota, Cretaceous, Diaporthales, Gnomoniaceae, Sordariomycetes, *Spataporthe*.

Introduction

Several large-scale phylogenies address relationships within the Fungi (Zhang et al. 2006; Hibbett et al. 2007; McLaughlin et al. 2009; Schoch et al. 2009a, 2009b). The hypotheses of relationships proposed in these studies based on sampling of extant taxa can rarely be tested independently on account of the relative scarcity of data extracted thus far from the fossil record. While the fossil record of fungi is certainly far from poor (Tiffney and Barghoorn 1974; Kalgutkar and Jansonius 2000), compared to plants, fungi have a much lower fossil : extant taxon ratio. That is why new fungal fossils, particularly if well preserved, can allow for calibration and testing of both evolutionary relationships and divergence times, as well as paleoecological hypotheses.

A survey of the fungal fossil record reveals that a large proportion of fossil fungi are known from Cretaceous and younger deposits, and many of these fungi are assigned to the ascomy-cetes (Tiffney and Barghoorn 1974; Stewart and Rothwell 1993; Kalgutkar and Jansonius 2000). The Early Cretaceous (Albian) mycoparasite *Mycetophagites* Poinar and Buckley (2007), preserved as networks of hyphae (some conidiogenous), has been compared to hypocrealean sordariomycetes. Another Cretaceous fungal fossil, *Paleoophiocordyceps* Sung et al. (2008), provides indirect evidence (as an anamorph) of order Hypocreales, a perithecial sordariomycete lineage. An interesting occurrence is *Pleosporites* Suzuki, an anatomically preserved perithecioid ascomycete described from the leaves of *Cryptomeriopsis* Stopes et Fujii in the Upper Cretaceous of Japan and compared to loculoascomycetes (Suzuki 1910). The Upper Cretaceous of Belgium has produced epiphyllous pleosporalean hypostromata—*Pteropus* van der Ham and Dortangs (Venturiaceae)—as well as thyriothecia and stromata of unresolved taxonomic placement described from the Maastrichtian type area (van der Ham and Dortangs 2005). Epiphyllous microthyriacean fungi are fairly abundant in Cretaceous deposits (Elsik 1978), and fossil fruiting structures include the ostiolate ascomata of the Early Cretaceous *Stomiopeltites cretacea* Alvin and Muir (1970) and the Late Cretaceous fruiting structure *Trichopeltinites* Cookson (Sweet and Kalgutkar 1989).

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Evidence that epiphyllous fungal diversity was associated with the diversification of angiosperms in tropical and subtropical environments comes from Eocene localities in Tennessee and Texas (Dilcher 1965; Sheffy and Dilcher 1971; Daghlian 1978). Eocene permineralized ascomycetes include the cleistothecial *Cryptocolax* Scott (1956) from dicotyledonous wood in the Clarno Chert, the corticolous pseudothecial pleosporalean *Margaretbarromyces* Mindell et al. (2007) from Vancouver Island carbonate nodules, and the example of hyperparasitism described from the Princeton Chert, including *Cryptodidymosphaerites* Currah et al. (1998) (Melanommatales), a perithecioid intralocular parasite of *Paleoserenomyces* Currah et al. (Phyllachorales), itself a parasite of palm leaves. Another important source of fossil fungal diversity is represented by paleogene amber deposits, from which five of the 11 classes and eight of the 56 orders of the Ascomycota, including perithecial forms, have been documented, according to Rossi et al. (2005).

Here we describe *Spataporthe taylori* gen. et sp. nov., a perithecial ascomycete assigned to order Diaporthales (Sordariomycetes), from Early Cretaceous deposits at the Apple Bay locality on Vancouver Island, British Columbia. This is the first ascomycete and the second fungal taxon described at the locality. *Spataporthe* is one of the rare perithecial ascomycetes in the fossil record and the oldest well-characterized sordariomycete, providing a minimum age (136 Ma) for order Diaporthales.

Material and Methods

Fungal sporocarps and the plant host tissue are preserved by cellular permineralization in an iron-rich carbonate concretion. The nodule was collected from sandstone (graywacke) exposed on the western shore of Apple Bay, Quatsino Sound, Vancouver Island, British Colombia, Canada (lat. 50°36′21″N, long. 127°39′25″W; UTM 9U WG 951068). The nodule-containing layers are regarded as Longarm Formation equivalents and have been dated by oxygen isotope analysis to the Valanginian-Hauterivian boundary (~136 Ma; Stockey et al. 2006).

Concretions were sliced into slabs and then peeled using the cellulose acetate peel technique (Joy et al. 1956). Slides were prepared using Eukitt xylene-soluble mounting medium (Kindler, Freiberg, Germany). Micrographs were taken using a Nikon Coolpix E8800 digital camera on a Nikon Eclipse E400 compound microscope. For scanning electron microscopy, parts of acetate peels containing sections of the specimen were mounted on aluminum stubs, shiny side up. All acetate was solubilized (by immersing the SEM stub in acetone for 5–10 min) and then gently rinsed with acetone for ~5 min, thus leaving the organic material glued to the stub in anatomical connection. The stubs were coated with 100 Å Au on a Desk II sputter-coater (Denton Vacuum, Moorestown, NJ) and examined using an ABT-32 (Topcon, Paramus, NJ) scanning electron microscope at 25 kV. Images were processed using Photoshop 7.0 (Adobe, San Jose, CA). Three-dimensional reconstructions were rendered using AMIRA 5.2.2 visualization software (TGS Software, San Diego, CA). All specimens (P 13172 B(1) bottom) are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

Systematics

Phylum—Ascomycota

Class—Sordariomycetes

Subclass—Sordariomycetidae

Order—Diaporthales

Genus—Spataporthe *Bronson, Klymiuk, Stockey et Tomescu, gen. nov.*

MycoBank Number—800815

Generic diagnosis. Perithecia immersed in host tissue, spherical up to 500 μm in diameter, with two-layered wall. Outer perithecium wall layer pseudoparenchymatous, inner layer filamentous. Perithecium neck forms widened basal chamber at contact with centrum. Basal neck chamber occupied by transient pseudoparenchyma plug and, later, periphyses. Hymenium basal in perithecium. Asci clavate, inoperculate, without conspicuous apical ring, detach from hymenium at maturity. Hamathecium absent at maturity.

Etymology. *Spataporthe* is named for mycologist Joseph W. Spatafora, Oregon State University, who pointed our searches for taxonomic affinities in the direction of the Diaporthales, in recognition of his contributions to fungal systematics.

Type Species—Spataporthe taylori *Bronson, Klymiuk, Stockey et Tomescu, sp. nov.*

MycoBank Number—800816

Specific diagnosis. Perithecia densely distributed, immersed at >150 μm in host tissue, spherical (320–470 μm in diameter), with two-layered wall. Outer perithecium wall layer pseudoparenchymatous, two to four cells thick, intergrading with plant host tissue. Inner wall layer light colored, fine filamentous, up to 25 μm thick. Perithecium neck with hemispherical to bell-shaped chamber at base. Basal neck chamber 115–140 μm in diameter at base (contact with centrum), 75–105 μm tall. Perithecium neck above basal chamber lined with longitudinal hyphae and 30–35 μm wide. Basal neck chamber filled with pseudoparenchyma (8–18 μm diameter) that disintegrate, leaving collar that forms constriction at contact with centrum; short periphyses present in basal neck chamber. Hymenium consisting of pseudoparenchyma (12–33 μm diameter) overlying inner wall layer, basal in perithecium. Asci clavate, inoperculate, without conspicuous apical ring, thinly tapered at base, 30–47 μm long and 12–20 μm wide at tip, with fine papillae on surface, detach from hymenium at maturity to become free-floating. Hamathecium absent at maturity.

Holotype hic designatus. Fragment of coniferous leaf with >70 perithecia; specimen P13172 B(1) bottom, slides 1–5, 7–21, 23–45, and one SEM stub containing specimens from peels 6 and 22 (figs. 1–6, 7A); UAPC-ALTA.

Type locality. Apple Bay locality, Quatsino Sound, northern Vancouver Island, British Columbia (lat. 50°36′21″N, long. 127°39′25″W; UTM 9U WG 951068).

Stratigraphic occurrence. Longarm Formation equivalent.

Age. Valanginian-Hauterivian boundary, Early Cretaceous.

Etymology. The species is named in honor of Thomas N. Taylor, University of Kansas, in recognition of the significant
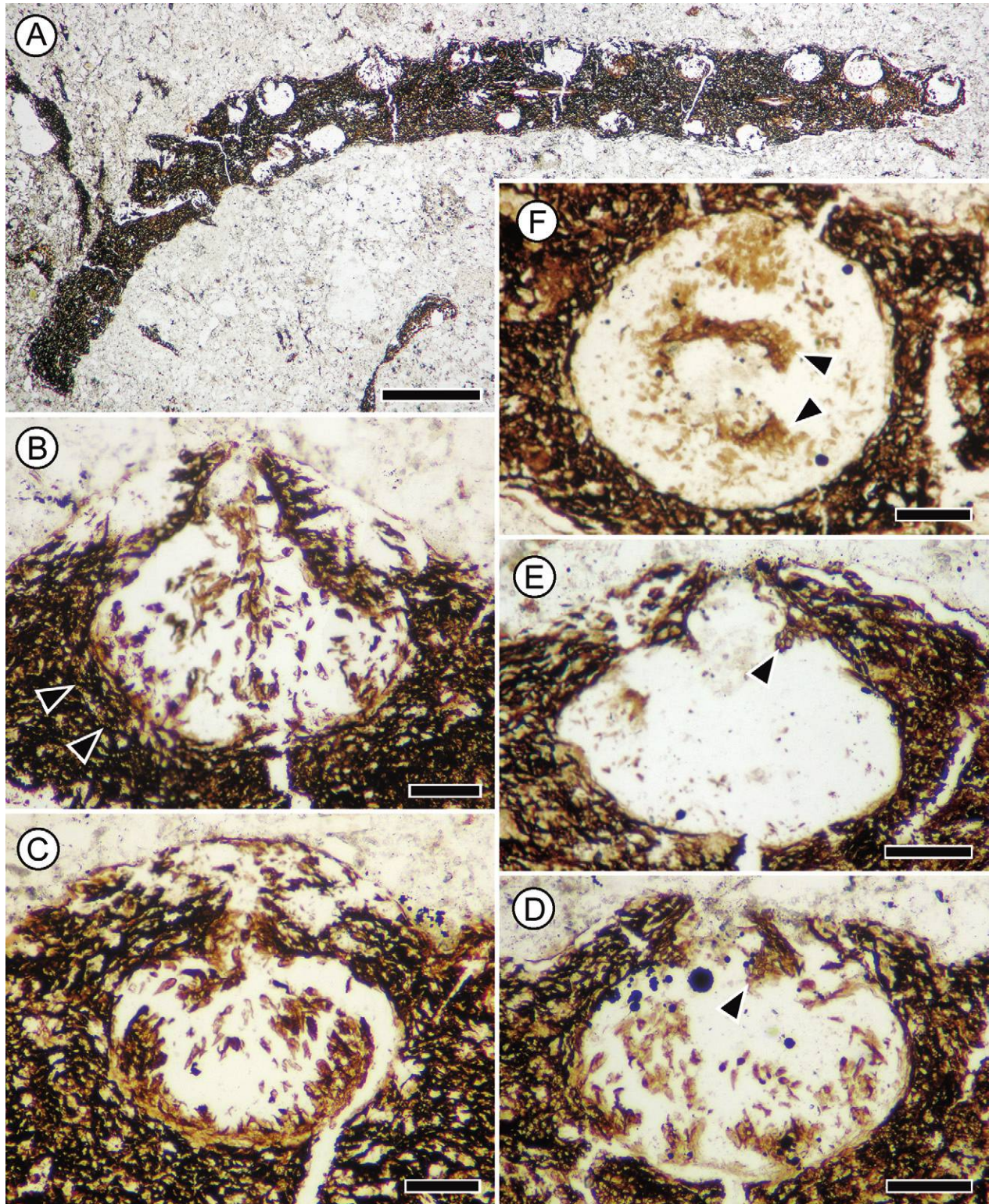
Fig. 1 *Spataporthe taylori* gen. et sp. nov. Perithecia. Holotype UAPC-ALTA P13172 B(1) bottom. *A,* Oblique longitudinal section of coniferous leaf; perithecia embedded on adaxial and abaxial side. Slide 5; scale bar = 10 mm. *B–E,* Longitudinal sections of perithecia; note circular shape, bell-shaped chamber at base of neck, pseudoparenchyma collar (arrowheads in *D, E*), inner perithecium layer lining base of perithecium (*C*), and asci, detached (*B, C*) and attached to hymenium at bottom of perithecium (*C*). Arrowheads in *B* indicate putative perithecium boundary marked by patterning of tissues. Note distinctly different texture of host plant tissue to left and right of perithecium, reflecting variable preservation in *E*. Slides 5 (*B, C*) and 23 (*D, E*); scale bars = 100 μm. *F,* Cross section of perithecium (note circular shape) with partial pseudoparenchyma ring of basal neck chamber (arrowheads). Slide 29; scale bar = 100 μm.

contributions his research has made to our understanding of the fossil record of fungi.

Description

Spataporthe taylori is represented by more than 70 perithecial ascocarps preserved immersed in the tissues of a coniferous leaf (figs. 1*A*, 2), in slab P 13172 B(1) (UAPC-ALTA). The quality of preservation, although somewhat variable between perithecia (a few appear taphonomically distorted), is very good overall. About half of the leaf was lost in the kerf of the lapidary saw used to slice the nodule. Based on the remaining tissues, we estimate that the leaf was needle shaped, ~1 mm thick, 3–4 mm wide, and at least 12–15 mm long. Two vascular bundles represented by xylem strands can be traced along the leaf (figs. 2*D*, 7*B*). The shape of the leaf and the presence of structures reminiscent of resin ducts (fig. 7*C*) suggest a coniferous leaf.

The perithecia are more or less spherical, ~330–470 μm wide and 220–320 μm high, and located ~165 μm beneath the surface of plant tissues. The vertical diameter (height) is smaller than the width due to limited but conspicuous vertical compression produced by taphonomic factors (as indicated by cracks in perithecium wall and plant host tissue). Perithecia are preserved in proximate developmental stages, near or at maturity, as evidenced by their well-defined, open neck canals and narrow size range (fig. 1*B*–1*F*). Three-dimensional reconstructions based on serial sections (fig. 2) show the perithecia densely distributed, sometimes with their walls adjacent to each other. They are embedded in the plant tissues, making the leaf surface bulge out, on all sides of the leaf, with their necks perpendicular to the adaxial and abaxial faces. Perithecia, which probably pointed sideways, perpendicular to the leaf margin, are preserved only in their lower parts because they have been opened by abrasion during transport and deposition of the leaf.

The perithecial wall consists of two layers: an outer layer of relatively large pseudoparenchyma (paraplectenchyma) and an inner layer of fine filamentous structure. The outer perithecial wall layer is at least two cells thick, possibly forming a textura epidermoidea (fig. 3*C*), but the limit between this layer and the host plant tissue is difficult to trace due to preservation that makes the two tissues very similar: cell walls are dark and irregularly thickened, the outlines of many cells are indistinguishable or distorted, and organic material fills some of the cells (figs. 1*B*, 1*E*, 3*C*). The inner wall layer appears as a light brown–yellow layer in light microscopy and is ~17–26 μm thick (fig. 3). When seen in cross sections, this layer often seems to lack consistent structures, although it can be traced as a continuous lining in many perithecia (fig. 3*A*, 3*B*, 3*D*, 3*F*, 3*G*). Its fine filamentous structure becomes apparent in grazing sections of the perithecium wall (fig. 3*H*, 3*I*), suggesting that it formed a textura intricata of periclinal prosoplectenchyma. We hypothesize that the difficulty in characterizing the structure of this layer unequivocally is due to the fact that it was formed of very fine, thin-walled hyphae that became fused diagenetically into a quasi-amorphous material.

The necks of all perithecia are preserved only for the length embedded in the plant tissue. The fact that they do not pro-trude above the surface of the plant fragment is due to significant abrasion during transport, which also removed part of the plant fragment, cutting some perithecia open through the middle of their lumina (fig. 2*B*–2*D*). In the plant tissues, perithecial necks form canals ~30–35 μm in diameter lined with longitudinal hyphae oriented perpendicular to the plant epidermis (figs. 4*D*, 4*H*, 4*I*, 5*D*).

The contact between the neck and the centrum is marked by a widening of the neck, forming a bell-shaped to hemispherical chamber ~115–140 μm in diameter at the base (contact with the centrum) and 75–105 μm tall (figs. 4*A*–4*H*, 5*D*–5*F*). The basal neck chamber is filled with pseudoparenchyma (cells 8–18 μm in diameter). Study of serial sections through the basal neck chamber in many perithecia shows that the pseudoparenchyma plug disintegrates progressively, leaving a collar that forms a constriction at the base of the neck chamber (figs. 4*A*–4*C*, 5*E*). Disintegration of the pseudoparenchyma starts at the center so that in intermediate stages the basal neck chamber is separated from the centrum by a diaphragm consisting of pseudoparenchyma (fig. 4*D*, 4*E*, 4*H*), which finally recedes centrifugally (fig. 5*D*) to form the basal collar. When perithecia
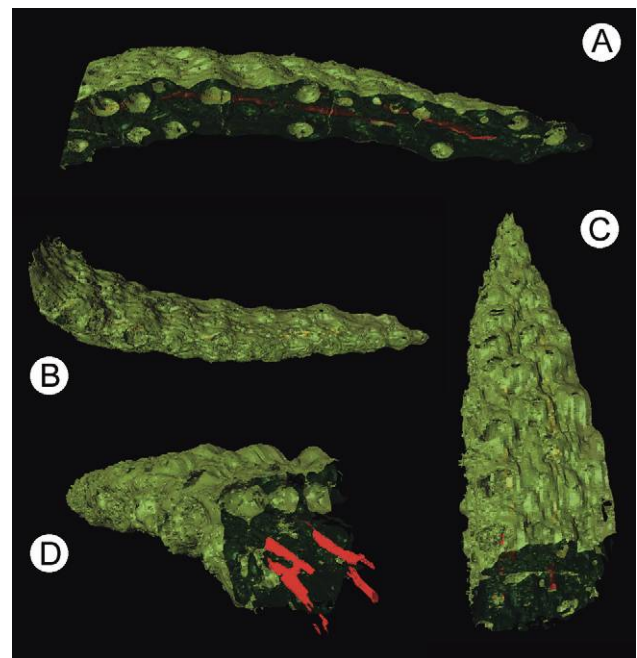

Fig. 2 *Spataporthe taylori* gen. et sp. nov. Holotype UAPC-ALTA P13172 B(1) bottom. Three-dimensional reconstructions of leaf fragment with embedded perithecia, based on serial sections; green = plant tissue (dark green = sections; light green = specimen surface); red = xylem strands; suboptimal preservation precludes recognition of abaxial and adaxial surfaces; upper and lower surfaces are arbitrarily designated. *A*, Longitudinal section with perithecium lumina and xylem strands. *B*, Lower surface with bulges marking the position of perithecia; note bases of perithecia exposed by abrasion on leaf side (left). *C*, Upper surface with ostiolate bulges marking the position of perithecia; note dense distribution of perithecia and bases of perithecia exposed by abrasion (lower left). *D*, Cross section of leaf showing adjacent perithecia beneath the upper surface and xylem strands; note bases of perithecia exposed by abrasion along leaf side.
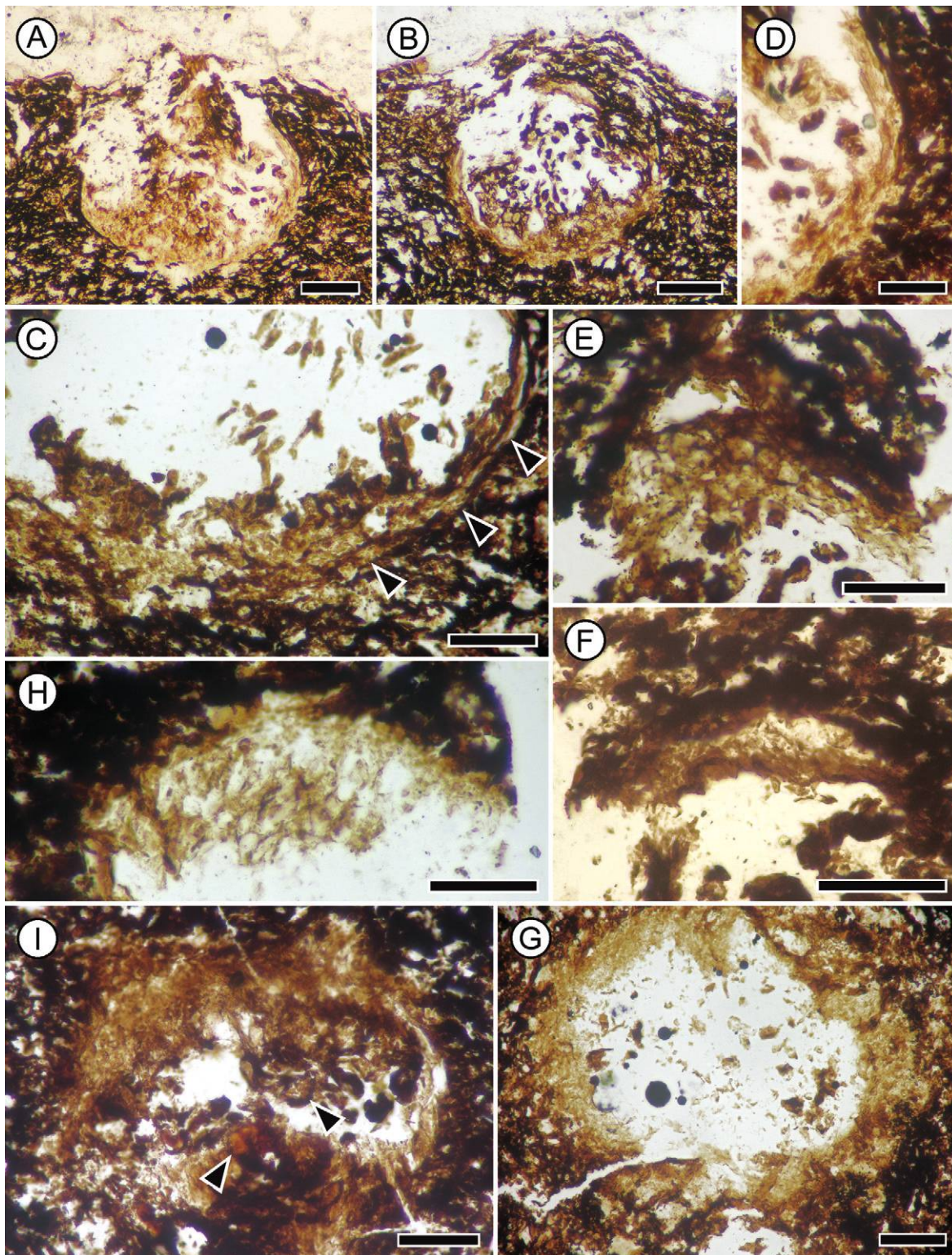
Fig. 3 *Spataporthe taylori* gen. et sp. nov. Perithecium walls. Holotype UAPC-ALTA P13172 B(1) bottom. *A*, *B*, Perithecia with well-preserved inner wall layer represented by light brown tissue lining bottom and sides (partially); note hymenium overlying inner wall at base of perithecium (*B*). Slides 15 (*A*) and 16 (*B*); scale bars = 100 μm. *C*, Perithecium bottom with flattened, large pseudoparenchyma of outer wall (arrowheads); incompletely preserved inner perithecial wall (light brown) and hymenium are present. Slide 20; scale bar = 50 μm. *D*, Inner wall (light brown) along perithecium side; detail of *A*. Slide 15; scale bar = 50 μm. *E*, Tangential section of basal neck chamber with pseudoparenchyma cells and inner perithecial wall. Slide 16; scale bar = 50 μm. *F*, Inner wall lining the top of a perithecium; detail of *B*. Slide 16; scale bar = 50 μm. *G*, Cross

are sectioned transversally at the base of the neck chamber, the pseudoparenchymatous collar is seen as a ring (figs. 1F, 5A–5C). A few perithecia with well-preserved neck structures in final stages of development exhibit short periphyses replacing the pseudoparenchymatous lining of the basal neck chamber (fig. 5E, 5F).

At the base of perithecia, the inner sporocarp wall layer is lined with a hymenium (figs. 1C, 3B, 3C, 3I, 6A–6D) consisting of a one- to three-cell-thick layer of pseudoparenchyma (cells 12–33 μm in diameter) to which the asci are attached (fig. 6A–6D). Paraphyses are absent. Asci are relatively small but well preserved. They are clavate to teardrop shaped, 30–47 μm long and 12–20 μm wide at tip, with thinly tapered bases (figs. 6B, 6D, 6E, 7A). Numerous asci are found detached from the hymenium, floating in the centrum of many perithecia in various positions and orientations (figs. 1B, 1C, 3B, 6A, 6B, 6D). The walls of well-preserved asci exhibit small papillae (0.4–0.8 in diameter) spaced 0.5–1.8 μm apart (figs. 6E, 7A). No operculum or apical ring was observed in the ascus wall. Although objects recognizable unequivocally as ascospores could not be ascertained, small subunits are recognized within some of the asci in the position of ascospores. One ascus contains ovoid units ~4.7 × 3.2 μm in size (fig. 6G); another one is torn open exposing a structure that is 10 μm long and 6 μm wide and could have consisted of two subunits (fig. 6F).

Discussion

Taxonomic Placement of Spataporthe

Perithecioid (i.e., partially enclosed) ostiolate sporocarps have evolved independently in the Sordariomycetes and Dothideomycetes (Schoch et al. 2009b). The distinction between the bona fide perithecia of the Sordariomycetes and the ascolocular pseudothecia of the Dothideomycetes is not always straightforward. Furthermore, ascomycete anamorphs produce pycnidia (asexual locules bearing conidiophores that produce conidia also known as pycnidiospores), which can exhibit morphologies similar to those of perithecia (Webster and Weber 2007). In Spataporthe, a combination of several characters indicates that the fruiting bodies are bona fide perithecia and not pseudothecia or pycnidia: (1) presence of a well-defined neck with complex morphology (pseudoparenchymatous plug, periphyses); (2) presence of longitudinally aligned hyphae in the neck, consistent with schizogenous (as opposed to lysigenous) ostiole development (Webster and Weber 2007); and (3) well-defined hymenium (4) producing asci with features comparable to those of diaporthalean Sordariomycetes (as discussed below). While none of these characters can be used individually to separate sordariomycete perithecia from other similar structures, the combination points to the Sordariomycetes as a logical taxonomic placement of Spataporthe. In accordance with this placement, Spataporthe exhibits perithecial ascomata producing inoperculate asci from a basal hymenium, all of which are characteristic of class Sordariomycetes (Zhang et al. 2006).

In addition to the independent origin in the Sordariomycetes and Dothideomycetes, perithecioid sporocarps also evolved independently in lineages of the Pezizomycetes, Eurotiomycetes, Lecanoromycetes, and Laboulbeniomycetes (Schoch et al. 2009b). However, these lineages are lichenized (Lecanoromycetes) or specialized insect symbionts (Laboulbeniomycetes) or have sporocarps dissimilar to those of Spataporthe (McCormack 1936; Weir and Blackwell 2001; Hansen et al. 2005; Lorenzo and Messuti 2005; Schmitt et al. 2005; Geiser et al. 2006; Hibbett et al. 2007).

Recent phylogenetic studies of the Ascomycota based on gene sequence data (Schoch et al. 2009b) have shown homoplasy of several morphological characters at different taxonomic levels. This could be perceived as a deterrent of discussions in pursuit of morphology-based decisions on taxonomic placement at suprageneric levels. In extant species, it has led to the use of gene sequences in parallel with morphological characters to support taxonomic decisions. As gene sequences are unobtainable for fossils, attempts at reaching taxonomic decisions for fossils may appear futile to the neontologist, especially in cases where the potential for homoplasy of morphological characters is significant. However, in paleobiology it is common practice to strive for the most detailed taxonomic placement of fossils as achievable using morphology. This approach is habitual even for fossils representing groups with simple morphology (and thus a short list of diagnostic characters) and that are relatively old geologically. Such is the Early Devonian thalloid liverwort *Riccardiothallus* Guo et al. (2012), which has been placed in the modern family Aneuraceae. Furthermore, the fossil record of taxa can be traced back in time to considerable ages, even at the genus level—e.g., fossils of the modern genus *Equisetum* described from the Early Cretaceous at the same locality as *Spataporthe*, Apple Bay (Stanich et al. 2009). Seen in this context, *Spataporthe* is comparatively young, both geologically (Early Cretaceous, 136 Ma) and as an ascomycete (the oldest ascomycete fossils are at least 420 million years old; Sherwood-Pike and Gray 1985). Consideration of the placement of *Spataporthe* within modern ascomycete orders therefore in no way falls outside the usual paleobiological approach to systematics. Most important, a survey of the distribution of traditional morphological characters among the different lineages of sordariomycetes as circumscribed by the most recent taxonomic treatments (table 1) reveals that they allow for assignment *Spataporthe* to a modern order.

The characters of *Spataporthe* that allow for ordinal-level taxonomic placement are (1) absence of paraphyses, reflecting either that they were evanescent or that they were not part of perithecim development in *Spataporthe*; (2) presence of periphyses; and (3) ascus features. Ascus features include (1) clavate shape, (2) detachment from the hymenium as part of the developmental sequence, and (3) persistence. Examination of more than 70 perithecia in serial sections shows that the only asci found attached to the perithecium wall are those attached at the base, hence the interpretation of a basal hymenium. All other asci are found detached, in various positions and with various orientations inside the perithecia. More important, when well preserved the unattached asci have teardrop-shaped, thinly tapered bases, which are consistent with the morphology of asci that become detached from the hymenium developmen-

section of perithecium base with complete lining of inner wall. Slide 25; scale bar = 50 μm. H, I, Grazing sections of perithecium; note filamentous nature of inner wall and large pseudoparenchyma of hymenium (arrowheads in I). Slides 10 (H) and 15 (I); scale bars = 50 μm.
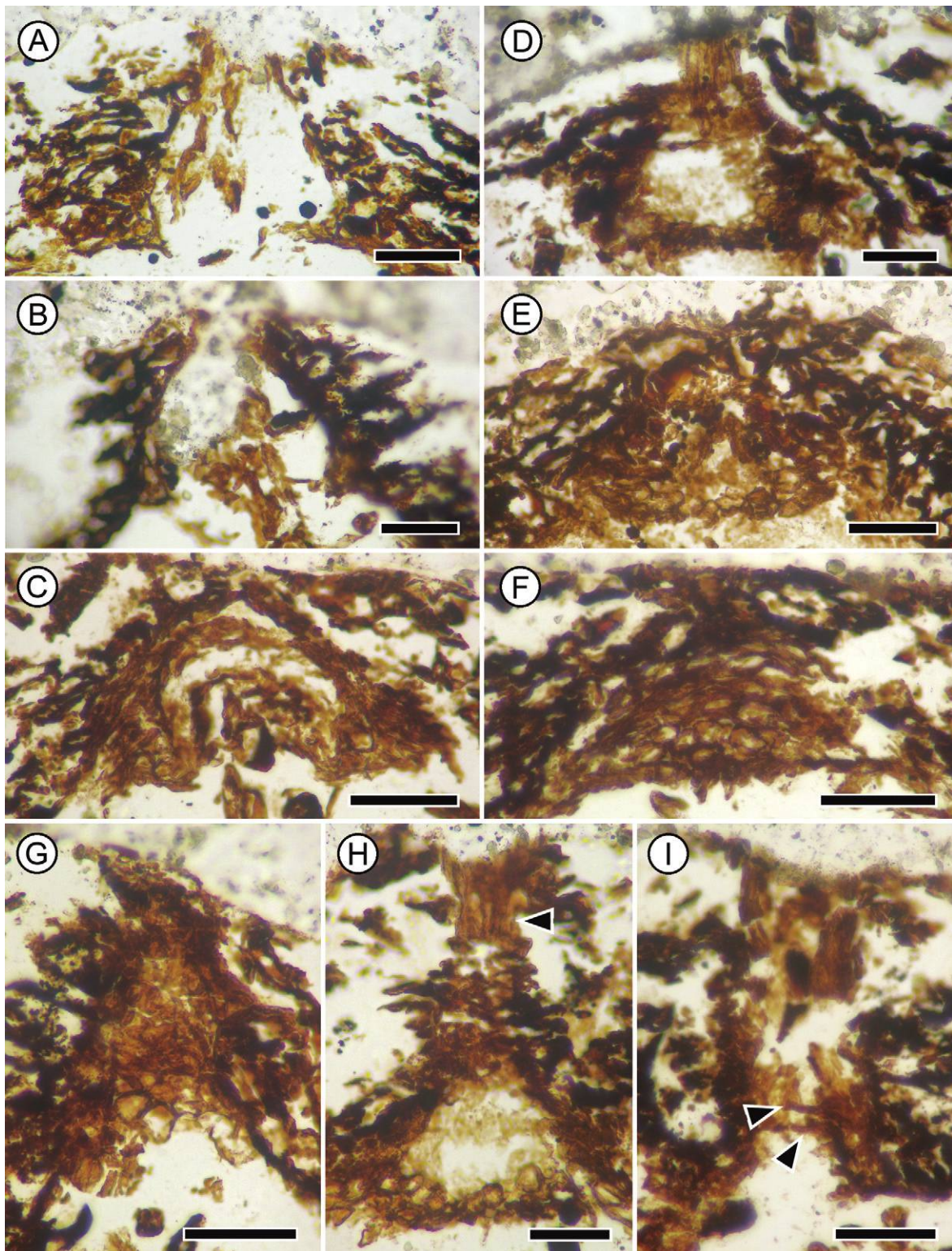
Fig. 4 *Spataporthe taylori* gen. et sp. nov. Basal neck chamber pseudoparenchyma and hyphae. Holotype UAPC-ALTA P13172 B(1) bottom. *A, B,* Basal neck chamber, late developmental stage; note bell shape, remnants of pseudoparenchyma collar forming constriction at base, and poorly preserved asci. Slides 21 (*A*) and 5 (*B*). *C–F,* Developmental sequence (*F–C*) of basal neck chamber pseudoparenchyma: *F,* pseudoparenchyma filling the chamber; *E, D,* pseudoparenchyma disintegrate at center but line sides of the chamber and form a floor; note longitudinal neck hyphae at top of chamber in *D; C,* pseudoparenchyma floor disintegrated leaving a thick collar; note tips of asci at bottom. Slides 21 (*C*), 3 (*D*), and 20 (*E, F*). *G, H,* Tangential section through basal neck chamber with pseudoparenchyma and base of narrow neck section
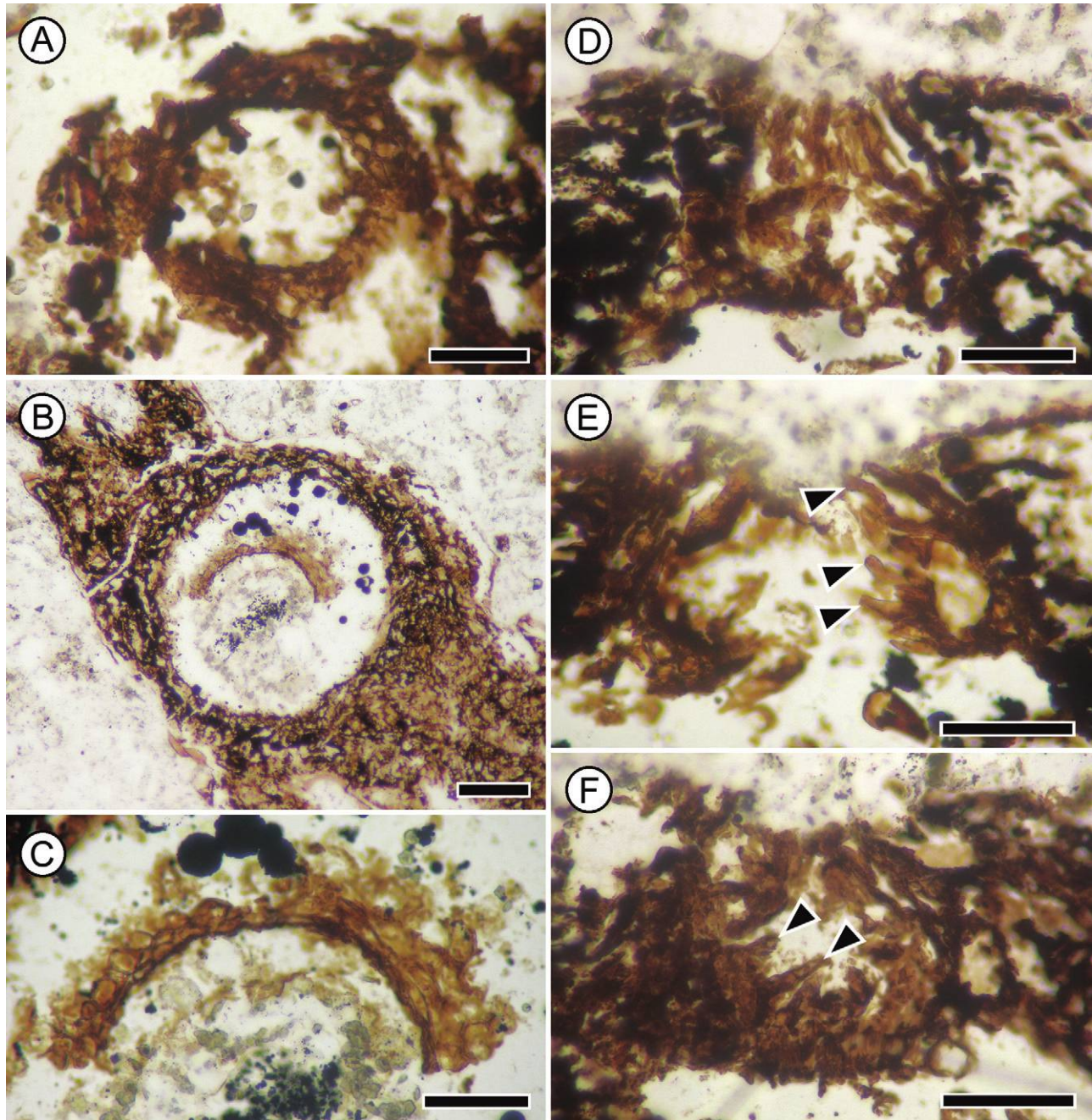
Fig. 5 *Spataporthe taylori* gen. et sp. nov. Perithecial neck pseudoparenchyma and periphyses. Holotype UAPC-ALTA P13172 B(1) bottom. *A–C*, Pseudoparenchyma collar forming a ring in perithecium cross sections cut close to base of neck; ring incomplete in *B* and *C*; *C* is a detail of *B*. Slides 12 (*A*) and 37 (*B*, *C*). *D*, Basal neck chamber with incomplete pseudoparenchyma floor and longitudinal hyphae (at top). Slide 11. *E*, *F*, Basal neck chamber with periphyses (arrowheads); note ascus at bottom in *E*. Slides 12 (*E*) and 24 (*F*). Scale bars = 50 μm, except for *B*, where scale bar = 100 μm.

tally (Sogonov et al. 2008), as opposed to cylindrical bases representing the tips of broken-off ascigerous hyphae, which characterize attached asci that become separated from the hymenium accidentally. Additionally, the asci of *Spataporthe* are well preserved despite their small size. This is due to thick

walls, indicating that the asci are persistent. The transient walls of deliquescent asci (e.g., *Melanospora zamiae* Corda; Goh and Hanlin 1994) are thin and would not have preserved well.

Class Sordariomycetes includes 13 orders grouped into three subclasses: Xylariomycetidae (one order), Hypocreomycetidae

at top; note pseudoparenchyma floor and longitudinal neck hyphae (arrowhead) in *H*. Slides 25 (*G*) and 24 (*H*). *I*, Narrow part of perithecial neck with longitudinal hyphae (at top) and periphyses (arrowheads). Slide 4. Scale bars = 50 μm.
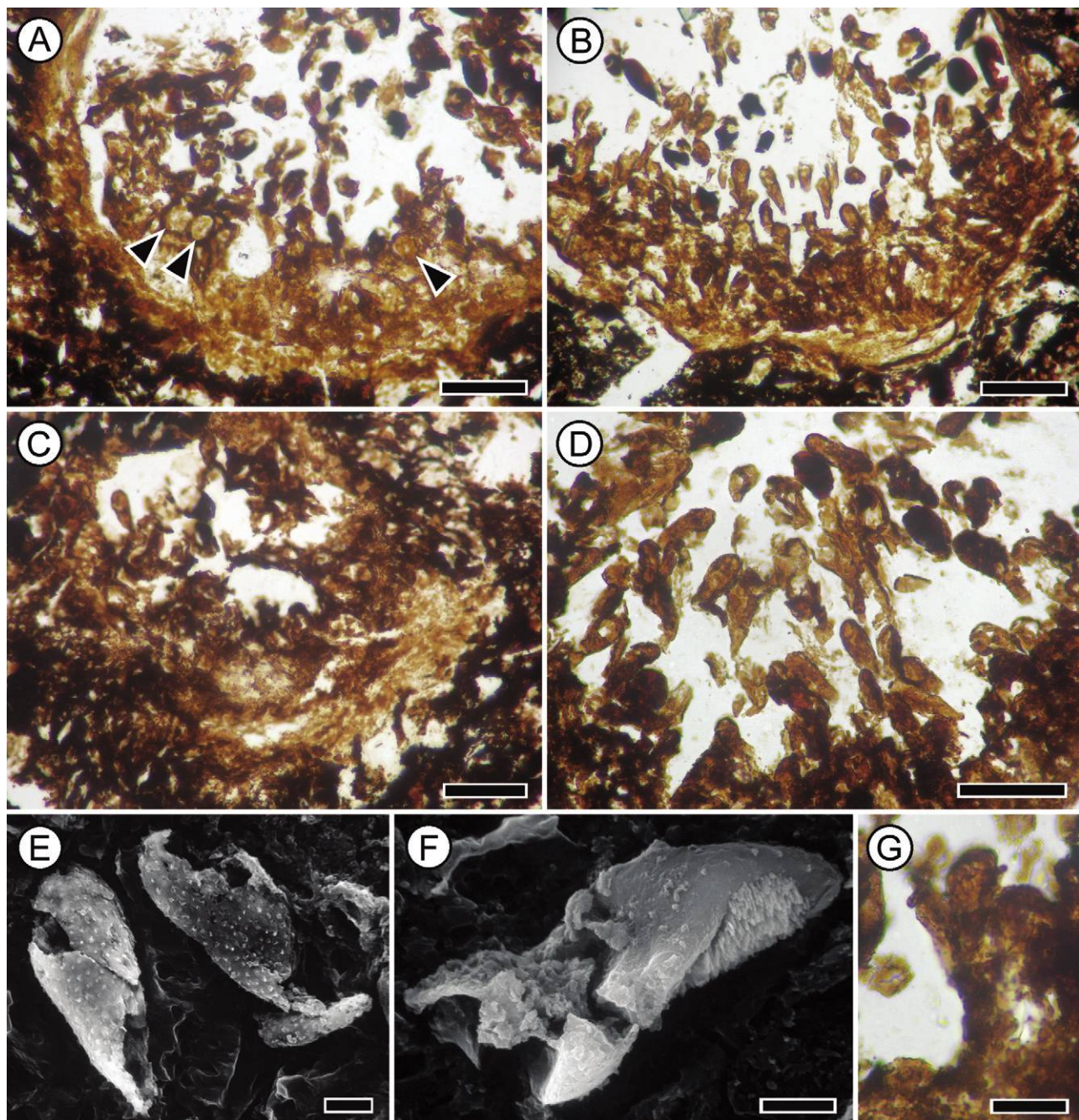
Fig. 6 *Spataporthe taylori* gen. et sp. nov. Hymenium and asci. Holotype UAPC-ALTA P13172 B(1) bottom. *A, B,* Bottom of perithecia with inner perithecial wall (light brown) overlain by hymenium with attached asci; note numerous detached asci and large pseudoparenchyma of the hymenium (arrowheads in *A*). *A* is detail of fig. 3*B*. Slides 16 (*A*) and 20 (*B*); scale bars = 50 μm. *C,* Tangential section through bottom of perithecium showing inner perithecial wall (light brown), parts of hymenium with large pseudoparenchyma (center right), and a few asci (top left). Slide 17; scale bar = 50 μm. *D,* Detached asci in perithecium centrum. Slide 4; scale bar = 50 μm. *E,* Two asci exhibiting wall surface with evenly distributed minute punctae. *F,* Broken ascus exposing oblong object at left (putative ascospore?). Scale bar = 5 μm. *G,* Ascus attached to hymenium and containing ovoid units (putative ascospores?). Slide 10; scale bar = 20 μm.

(five orders), and Sordariomycetidae (six orders), plus order Lulworthiales (subclass incertae sedis; Zhang et al. 2006). Subclasses Hypocreomycetidae and Sordariomycetidae also include one and three families with order incertae sedis, respectively (table 1). All these groups of sordariomycetes are compared to

Spataporthe for ordinal-level taxonomic placement. Orders Halosphaeriales, Microascales, Coronophorales, Melanosporales, Ophiostomatales, and Lulworthiales are characterized by impersistent asci that deliquesce during development of the perithecium (table 1), unlike *Spataporthe*. The Coronophor-
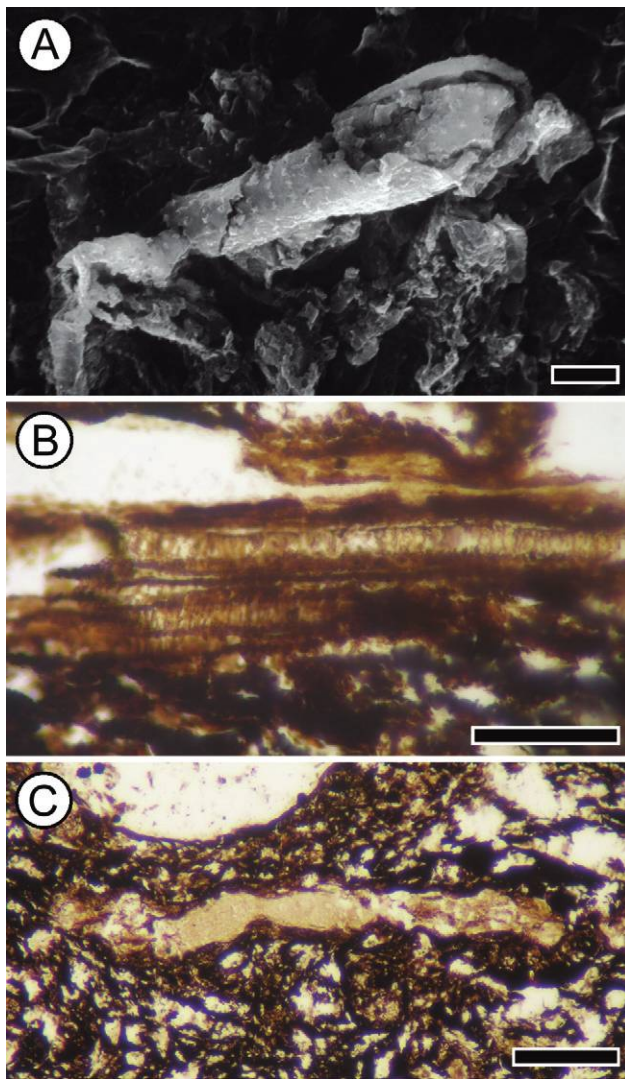
Fig. 7 *Spataporthe taylori* gen. et sp. nov. Perithecia. Holotype UAPC-ALTA P13172 B(1) bottom. *A*, Ascus; note evenly distributed minute punctae on surface. Scale bar = 5 μm. *B*, Tracheids of leaf hosting the perithecia; detail of fig. 1*A*. Slide 5; scale bar = 50 μm. *C*, Resin duct of leaf hosting the perithecia. Slide 19; scale bar = 100 μm.

ales, Coniochaetales, and Sordariales have superficial, semi-immersed, or erumpent perithecia, different from those of *Spataporthe*, which are immersed. Furthermore, in contrast to *Spataporthe*, the Boliniales and Chaetosphaeriales, as well as the four families incertae sedis (Glomerellaceae, Magnaporthaceae, Annulatascaceae, and Papulosaceae), have a hamathecium of persistent paraphyses, while the Halosphaeriales are characterized by a persistent hamathecium that consists of catenophyses derived from early-developmental pseudoparenchyma. Other characters of contrast with *Spataporthe* are globose asci in orders Microascales and Ophiostomatales, cylindrical asci in order Chaetosphaeriales and families Annulatascaceae and Papulosaceae, filiform or filamentous ascospores (and therefore elongated ascus shapes) in family Magnaporthaceae and order Lulworthiales, and absence of periphyses in order Ophiostomatales.

Of these, sordariomycetes in order Melanosporales, with their clavate asci and lacking a hamathecium, can appear similar to *Spataporthe*. However, the fact that asci are typically deliquescent, with thin walls, in Melanosporales excludes the order from consideration as a possible taxonomic placement. The Xylariales and Hypocreales are also unlikely placements for *Spataporthe*, for various reasons. Perithecia are superficial in the nonstromatic, nonsubiculate representatives of the Hypocreales. A survey of a broad spectrum of Hypocreales (Samuels et al. 2012) reveals that although the order, as a whole, may be perceived as potentially allowing for the combination of characters documented in *Spataporthe*, most major perithecial, ascal, and spore characters are broadly variable within the order and no extant genus is closely comparable to *Spataporthe*. The Xylariales are typically stromatic, and most have a persistent hamathecium. Furthermore, neither the Hypocreales nor the Xylariales typically have asci that detach from the hymenium at maturity like those of *Spataporthe*.

Spataporthe is closely comparable to sordariomycetes in order Diaporthales, which includes representatives with immersed perithecia producing evanescent paraphyses (so a hamathecium is absent in mature sporocarps) and persistent asci that become detached from the hymenium developmentally and free-floating inside the perithecium (Zhang et al. 2006; Rossman et al. 2007*b*). The ascus dehiscence and spore release mechanisms of *Spataporthe* are unresolved. Wall thickness, especially in the detached (and therefore more mature) asci, excludes the possibility that they were deliquescent. None of the asci observed in the fossil material shows structures reminiscent of an operculum. Diaporthalean asci often have conspicuous apical rings as a spore release mechanism (Zhang et al. 2006), and these correlate with a characteristic slight narrowing of the overall round ascus tip. An apical ring is a feature difficult to ascertain in fossils, due to its position inside the ascus, especially in small asci with relatively thick walls, such as those of *Spataporthe*. Asci with inconspicuous apical rings and bluntly round ascus tips are not uncommon in the Diaporthales. *Spataporthe*, with its bluntly round ascus tips closely comparable to those of gnomoniacean asci documented by Sogonov et al. (2008, figs. 6*H*, 13*F*, 14*T*, 19*A*, 22*E*), likely represents such a case. Taken together all these characters indicate that *Spataporthe* is a fossil member of order Diaporthales.

Order Diaporthales includes the following nine families: the Diaporthaceae, Gnomoniaceae, Sydowiellaceae, Melanconidaceae, Schizoparmeaceae, Cryphonectriaceae, Valsaceae, Pseudovalsaceae, and Togniniaceae (Rossman et al. 2007*b*). Of these, the Melanconidaceae and Togniniaceae are unlikely placements for *Spataporthe*. Melanconidaceae is a monotypic family that currently includes only three species restricted to trees in the Betulaceae, whereas the Togniniaceae is composed of species that exhibit features absent in the other Diaporthales, such as undetachable asci produced in fascicles and persistent paraphyses (Rossman et al. 2007*b*). The Schizoparmeaceae, Cryphonectriaceae, and Pseudovalsaceae produce erumpent ascomata, unlike *Spataporthe*. Furthermore, also unlike *Spataporthe*, the ascomata of Cryphonectriaceae are stromatic, semi-immersed, or superficial, and their asci are fusoid (Gryzenhout et al. 2006); the ascomata of Schizoparmeaceae become superficial at maturity and have walls with characteristic platelike ornamentation. The monotypic Pseudo-

Table 1

Comparison of Sordariomycete Orders and Families incertae sedis (Classification from Zhang et al. 2006)

	Stroma/subiculum	Perithecium morphology and position	Asci	Ascospores	Paraphyses and periphyses	Substrate/environment	References
Subclass Xylariomycetidae: Order Xylariales	Stromatic; rarely nonstromatic or subiculate	Embedded in stroma; some immersed in substrate, erumpent, or superficial	Persistent; often amyloid apical rings	Unicellular or two celled with striations, allantoid; one or several germ slits/pores, some lack defined germination sites	Paraphyses present, sometimes evanescent	Saprobes or plant parasites, often on wood and bark; some in freshwater or marine	Moore-Landecker 1996; Zhang et al. 2006; Webster and Weber 2007
Subclass Hypocreomycetidae: Order Hypocreales	Nonstromatic or stromatic; some subiculate	Superficial when nonstromatic or nonsubiculate; soft textured; rarely cleistothecia	Persistent; ±apical apparatus	Nonseptate globose to one/ multiseptate ellipsoidal to filiform; colorless	Apical (and sometimes centripetal) paraphyses (pseudoparaphyses), often evanescent; periphyses present	Plant and insect pathogens, mycoparasitic, endophytic, saprobic	Moore-Landecker 1996; Zhang et al. 2006; Webster and Weber 2007; Samuels et al. 2012
Order Halosphaeriales	Nonstromatic	Usually immersed	Deliquescent	Distinctive ascospore appendages	Thin-walled pseudoparenchyma that breaks down forming catenophyses	Mostly marine, some freshwater	Zhang et al. 2006
Order Microascales	Nonstromatic	Long neck; rarely cleistothecia	Globose, deliquescent, develop singly or in chains, scattered throughout perithecial cavity	Nonseptate, often with ridges or wings; colorless	Paraphyses absent	Primarily saprobic in soil, rotting vegetation, dung	Zhang et al. 2006; Webster and Weber 2007
Order Coronophorales	Some have subiculum or basal stroma	Erumpent to superficial, often collapse on drying; pseudoparenchymatous wall	Thin-walled, clavate, stipitate, deliquescent; lack apical ring	Small, hyaline, allantoid	Paraphyses absent, with few exceptions	Primarily on wood; often mycoparasitic	Zhang et al. 2006
Order Melanosporales	Nonstromatic	Translucent, pseudoparenchymatous wall; sometimes cleistothecia	Clavate, deliquescent	Dark colored	Paraphyses absent	Often mycoparasitic	Zhang et al. 2006
Family Glomerellaceae (order incertae sedis)	Nonstromatic	Long neck	Persistent, clavate; apical ring	Unicellular, hyaline, smooth, often curved; passively released	Paraphyses abundant, thin walled; well-developed periphyses	Plant pathogens	Zhang et al. 2006; Webster and Weber 2007
Subclass Sordariomycetidae: Order Boliniales	Stroma carbonaceous or soft textured		Persistent, small	Ellipsoidal; frequently flattened and with polar germ pores	Paraphyses present	Primarily on wood	Zhang et al. 2006; Huhndorf and Miller 2008

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Order Chaetosphaeriales	Nonstromatic	Small, often setose	Persistent, cylindrical; usually pronounced apical ring	Fusiform 1–3 septate most typical; can be ellipsoidal, nonseptate to elongate-filiform, septate; ±hyaline	Paraphyses present, filiform	Often on wood, saprobic	Zhang et al. 2006
Order Sordariales	Nonstromatic	Large, erumpent, or superficial; wall large-celled membraneous or coriaceous; sometimes cleistothecia	Nonamyloid, cylindrical to clavate; deliquescent in some taxa	Cylindrical, hyaline, ellipsoid, brown-black, mostly unicellular with 1 germ pore, often with mucilaginous appendages or sheaths	Paraphyses present in some taxa, filiform; sometimes deliquescent; periphyses sometimes present	Mostly on wood, dung, or soil; some in freshwater	Moore-Landecker 1996; Zhang et al. 2006; Webster and Weber 2007
Order Coniochaetales	Nonstromatic	Superficial or semi-immersed, some setose; sometimes cleistothecia	±Clavate; nonamyloid apical ring or lacking apical ring; evanescent in some taxa	Ellipsoidal, fusoid or discoid; one germ slit	Paraphyses generally present; sometimes evanescent	On wood, dung, or soil	Garcia et al. 2006; Webster and Weber 2007
Order Diaporthales	Nonstromatic or stromatic	±Immersed	Persistent, free-floating at maturity; often conspicuous amyloid apical rings	Allantoid, colorless or ellipsoidal, one-septate or elongate or large, multiseptate, black; sometimes free-floating inside perithecium, along with detached asci	Paraphyses evanescent; periphyses sometimes present	Primarily plant associated; some in freshwater	Zhang et al. 2006; Rossman et al. 2007b; Webster and Weber 2007
Order Ophiostomatales	Nonstromatic	Often long neck	Globose, deliquesce early in development	Often have ornamenting sheaths, ridges, wings	Paraphyses and periphyses absent	On wood and bark; mostly saprobes	Zhang et al. 2006; Webster and Weber 2007
Family Magnaporthaceae (order incertae sedis)	Nonstromatic	Usually long neck	Persistent	Filiform	Paraphyses present, tapering	Plant pathogens; some in freshwater	Zhang et al. 2006; Webster and Weber 2007
Family Annulatascaceae (order incertae sedis)	Nonstromatic	Sometimes long neck	Persistent, cylindrical; large nonamyloid apical rings	Often have polar appendages or gelatinous sheath	Paraphyses present	In rotting wood in freshwater (tropical)	Zhang et al. 2006
Family Papulosaceae (order incertae sedis)	Nonstromatic	Long neck	Persistent, cylindrical; amyloid apical ring	Ellipsoidal, aseptate, verruculose, with gelatinous sheath	Paraphyses present, lateral; periphyses present	Marine, obligate on *Juncus* leaves	Zhang et al. 2006
Order Lulworthiales (subclass incertae sedis)	±Subiculum		Thin walled, deliquesce early in development	Filamentous, with mucus-containing apical chambers or appendages	Paraphyses absent; centrum filled initially with pseudoparenchyma	Marine and estuarine saprobes, on wood and marsh plants	Zhang et al. 2006

valsaceae are known to occur only on plants in order Fagales (Rossman et al. 2007*b*). The Valsaceae and Diaporthaceae are also unlikely placements for *Spataporthe*. The erumpent perithecia of the former occur aggregated in a prosenchymatous stroma, whereas the latter, currently including two genera (*Mazzantia* Montagne and the highly speciose *Diaporthe* Nitschke), produce aggregated, stromatic ascocarps (Castlebury et al. 2002; Rossman et al. 2007*b*). The Sydowiellaceae, as recently circumscribed based on gene sequences (Kruys and Castlebury 2012), form an assemblage of morphologically diverse genera that seem to lack shared defining morphological characters.

Family Gnomoniaceae is the diaporthalean family that combines the set of characters most comparable to *Spataporthe*. The Gnomoniaceae produce immersed, solitary, nonstromatic ascocarps; species with erumpent or superficial ascocarps and species with ascocarps aggregated in a rudimentary stroma are rare in the family (Rossman et al. 2007*b*; Sogonov et al. 2008). The asci, which may or may not have distinct apical rings, are generally small and fusoid-clavate, producing small spores (Sogonov et al. 2008); particularly, several species of *Gnomonia* Cesati and De Notaris, *Ambarignomonia* Sogonov, *Apiognomonia* Höhnel, and *Gnomoniopsis* Berlese produce asci very similar in size and shape to those of *Spataporthe*. Although gnomoniacean ascocarps are known mostly from stems and leaves of herbaceous dicotyledonous angiosperms, as well as from bark or wood, anamorphs have been described from conifers (Rossman et al. 2007*a*; Sogonov et al. 2008). Gnomoniacean affinities could also explain our inability to document ascospores in *Spataporthe*. The ascospores of many Gnomoniaceae are small and delicate, especially in those species with smaller asci that fall in the same size range as *Spataporthe* asci. The lack of ascospores in *Spataporthe* could be, therefore, a preservational issue.

Spataporthe *in the Context of the Apple Bay Flora and the Ascomycete Fossil Record*

The Apple Bay flora is currently the most diverse and best-characterized permineralized flora for the Early Cretaceous. The vascular plants are represented by lycopodialean and selaginellalean lycopsids, equisetopsids, at least 10 families of filicalean ferns, and diverse gymnosperms, both extant (Pinaceae, Cupressaceae) and extinct (a voltzialean-like conifer, cycadophytes, cycadeoids, and a putative corystospermalean; Stockey and Rothwell 2009). A rich bryophyte flora including several taxa is currently being characterized. On the fungal side, the Apple Bay locality has yielded the poroid hymenophore of *Quatsinoporites cranhamii* Smith, Currah and Stockey (2004), the oldest homobasidiomycete sporocarp. Now, *Spataporthe taylori* contributes an ascomycete component to the fungal flora of the locality, which also contains a lichen (Matsunaga et al. 2013), as well as at least one other type of fruiting body and evidence for wood-rotting fungi.

The pre-Silurian fossil record of Ascomycota is sparse at best. A Precambrian ascus-like microfossil reported by Schopf and Barghoorn (1969) from the Skillogalee Dolomite of South Australia, which would have been the oldest ascomycete fossil, was reinterpreted as an oomycete sporangium by Sherwood-Pike and Gray (1985). By the Early Silurian, diverse fungi with septate hyphae were present, such as those described by Pratt et al. (1978) in the Early Silurian (Llandoverian) Masanutten Sandstone of Virginia. These consist of branching filaments with flask-shaped bases, tentatively classified as dematiaceous hyphomycetes in the Deuteromycota. Ascomycete fossils of Ludlovian (Late Silurian) age were found in the Burgsvik Sandstone of Gotland, Sweden (Sherwood-Pike and Gray 1985). They consist of hyphae and multiseptate spores. The hyphae have perforate septa and verticillate branching, with some branches resembling conidiogenous phialides. Older multiseptate spores assignable to ascomycetes are reported by Tomescu (2004) from rocks dated at the Ordovician-Silurian boundary (Sub-Lockport) in Ohio.

Ascomycetes become more frequent in the fossil record beginning in the Devonian. The Early Devonian hosts diverse forms. Putative microthyrialean hyphae and asci have been reported on the cuticle of *Orestovia devonica* Ergolskaya from Siberia (Krassilov 1981; Taylor 1994). The ascocarp-like fruiting bodies of *Mycokidstonia* Pons and Locquin (1981) from the Rhynie Chert of Scotland have also been discussed as chytrid zoosporangia (Taylor et al. 2009). The thalloid forms assigned to *Spongiophyton* Kräusel, whose stratigraphic range extends into the Middle Devonian and which have been interpreted as lichens (Stein et al. 1993; Taylor et al. 2004), bear with cuplike structures similar to ascomycete apothecia.

The oldest occurrence of perithecial ascomycetes is also Early Devonian. It consists of spherical ascocarps with short necks designated as *Paleopyrenomycites devonicus* Taylor et al., preserved in the cortical tissues of *Asteroxylon mackiei* Kidston and Lang (Taylor et al. 1999, 2005*a*) in the Rhynie Chert. *Paleopyrenomycites* is also known from conidiophores, making it one of the best-characterized fossil fungi, and is comparable to the xylarialean sordariomycetes (Taylor et al. 2004).

In the Pennsylvanian, *Palaeosclerotium pusillum* Rothwell, described from Illinois coal balls, consists of ovoid cleistothecia with asci preserved inside (Rothwell 1972; Dennis 1976). Because these structures also include hyphae with dolipore septa and clamp connections (Dennis 1976), they can and have been interpreted either as an instance of basidiomycete parasitism on ascomycetes or as representatives of a fungal group combining ascomycete and basidiomycete characteristics (Dennis 1976; McLaughlin 1976; Singer 1977). Pennsylvanian coal balls from North American and British localities have yielded numerous other fruiting bodies reminiscent of ascomycete cleistothecia, including *Sporocarpon* Williamson, *Coleocarpon* Stubblefield et al., *Mycocarpon* Hutchinson, *Dubiocarpon* Hutchinson, and *Traquairia* Carruthers (Hutchinson 1955; Davis and Leisman 1962; Batra et al. 1964; Stubblefield et al. 1983; Taylor et al. 2005*a*), but these genera were later reinterpreted as zygomycete sporocarps (Taylor et al. 2009). Pennsylvanian coal balls also yielded *Protoascon missouriensis* Batra et al. (1964), initially interpreted as a perithecioid ascocarp and subsequently reinterpreted as a saprolegnialean oomycete (Baxter 1975; Kalgutkar and Jansonius 2000) or a zygomycete sporangium (Pirozynski 1976; Taylor et al. 2005*b*). The Triassic *Endochaetophora* White and Taylor (1988), described from Antarctica, is a permineralized ostiolate reproductive structure containing spores. Compared to an ascomycete perithecium or pycnidium (White and Taylor 1988) and considered a putative zygomycete by Kalgutkar and Jansonius (2000), its taxonomic affinities remain unresolved due to the absence of diagnostic characters.

Despite a fossil record that stretches back in time at least as far as the Silurian and increased rates of post-Jurassic ascomycete diversification, perithecioid ascomata are rare in the fossil record. Bona fide perithecia are known with certainty only from the Early Devonian Rhynie Chert (Taylor et al. 1999, 2005a) and Cenozoic amber (Poinar and Poinar 1999; Rossi et al. 2005). *Spataporthe* contributes a well-characterized Cretaceous occurrence and the only one known from the Mesozoic to the sparse fossil record of perithecia. Although represented only by the anamorph stage, the Late Albian (105–100 Ma) *Paleoophiocordyceps* is included in order Hypocreales (Sung et al. 2008) and, as such, a perithecial sordariomycete. At least 30 Ma older than *Paleoophiocordyceps*, *Spataporthe* is now the oldest sordariomycete, as well as the oldest perithecial ascomycete assigned to an extant order, and provides a minimum age (136 Ma) for that order—Diaporthales. This age falls well within the 193-Ma age of the hypocrealean node (based on *Paleoophiocordyceps* calibration; Sung et al. 2008), which also provides a minimum age predicted for the sordariomycetes, and the ~220-Ma age of the split between the Hypocreomycetidae and the Sordariomycetidae (including order Diaporthales), calculated based on calibration points outside the Fungi (Berbee and Taylor 2010). In this context, Spataporthe will provide a valuable internal calibration point for estimating divergence times within the Ascomycota and Fungi.

The diverse fungal content recently gleaned in the Apple Bay flora indicates that *Quatsinoporites* and *Spataporthe* are not isolated cases and that this flora includes a significant fungal component that could be similarly important for the fossil history and phylogeny of fungi. In-depth studies of the type pioneered by Thomas N. Taylor, aimed at exhaustive discovery and characterization of the fungal component of the Apple Bay flora and other anatomically preserved floras, are bound to lead to better understanding of the inconspicuous and yet undoubtedly diverse Cretaceous fungi and plant-fungal interactions.

Acknowledgments

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