Mycologia, 96(1), 2004, pp. 180–186.

Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia

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Abstract: Two fossil poroid hymenophore fragments, one from the Cretaceous Period and the other from the Eocene Epoch, are described. The permineralized specimens were obtained from marine calcareous concretions on Vancouver Island, British Columbia, Canada, and were studied using the cellulose acetate peel technique. Size and distribution of pores in the hymenophores, as well as the hyphal anatomy of the dissepiments and some hymenial elements, were examined. In the Cretaceous specimen, *Quatsinoporites cranhamii* sp. nov., pores are round to elliptical, three per mm, and 130–540 μm diam. Dissepiments consist of narrow, simple septate, hyphae. Neither basidia nor basidiospores are present, but acuminate hymenial cystidia, up to 54 μm in length, are common. The Eocene specimen, *Appianoporites vancouverensis* sp. nov., has a pore density of six per mm and pores are 130–163 μm in diam. Dissepiments consist of narrow, simple septate, thin-walled hyphae. Neither basidia nor basidiospores are present, but acuminate, thick-walled hymenial cystidia, up to 32 μm in length, are common. The poroid hymenophore is a characteristic of a number of extant basidiomycete taxa, including the Boletales, Polyporales and Hymenochaetales. It is unlikely that the fleshy, ephemeral, terrestrial basidiomata of the Boletales would be preserved in a marine environment, and thus the specimens are interpreted as belonging to basidiomycete lineages, with persistent, leathery or corky basidiomata. The simple septate hyphae, the minute pores and presence of cystidia most closely resemble taxa of the Hymenochaetales. These fossils unequivocally push back the minimum age of homobasidiomycetes and extend their paleogeographical range.

Key words: Cretaceous, Eocene, fossil fungi, homobasidiomycete, Hymenochaetales, paleomycology, poroid hymenophore

INTRODUCTION

The fungi fossil record extends back to the Ordovician Period (460 million years ago), based on glomalean fungi preserved in dolomite (Redecker et al 2000). The next oldest fungi are those of the Rhynie chert. Fossils from this locality include zygomycetes, chytridiomycetes and ascomycetes (Taylor et al 1992, 1995, 1999, Remy et al 1994. However, the first evidence of basidiomycetes in the fossil record is from the middle Pennsylvanian Period and is based on observations of hyphae with clamp connections found in the coenopterid fern *Zygopteris illinoiensis* (Dennis 1970). However, hyphae with clamp connections cannot be used to distinguish between two major groups of basidiomycetes—the homobasidiomycetes and heterobasidiomycetes. More taxonomically definitive fossils of homobasidiomycetes, i.e., preserved basidiocarps, rarely are found (Poinar and Singer 1990, Hibbett et al 1995, 1997b). Not convincing are some bracket fungi reports, such as that of *Eopolyporoides kukelii* of the middle Triassic Period of Australia (Playford et al 1982); it lacks both details of the presence of pores and detailed anatomy, and Hibbett et al (1997b) suggest it should be re-examined. Others, such as the Cretaceous *Polyporites stevensoni* (Brown 1936) and *P. browni* (Wieland 1934), were discovered later to be nonfungal (Brown 1938). *Phellinites digiustoi*, from the Jurassic Period petrified forests of Patagonia, was described as a fossil bracket fungus (Singer and Archangelsky 1958) but later was re-identified as the outer bark of a conifer (Hibbett et al 1997b). The earliest unequivocal basidiocarps in the fossil record are different agaricoid basidiomata in amber of the mid-Cretaceous (Turonian) and Eocene; *Coprinites dominicana* (Poinar and Singer 1990), *Archaeomarasmius leggetti* and *Protomycena electra* (Hibbett et al 1997a) and a recent fourth specimen, *Aureofungus yaniguaensis* (Hibbett et al 2003).

In this paper we describe two poroid hymenophore fragments, one of the early Cretaceous and the other of late Eocene, from British Columbia. These specimens are so well preserved at the cellular level that the detection of several microscopic characters used in polypore taxonomy was possible. These characters indicate that the two fragments represent different taxa, although both are similar to some extant genera in the Hymenochaetales. The Cretaceous basidiocarp

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Accepted for publication February 23, 2003.

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fragment provides an unequivocal earlier minimum age estimate for the Basidiomycota based on fruiting bodies, and both fossils extend the known paleogeographical distribution of the phylum.

MATERIAL AND METHODS

The first specimen was collected from the western shore of Apple Bay, Quatsino Sound, northern Vancouver Island, British Columbia, Canada (50° 36′ 21″ N 127° 39′ 25″ W; UTM 9U WG 951068). Permineralized plant remains are found in small, round calcareous concretions embedded in a sandstone (greywacke) matrix. Rocks at this locality are Longarm Formation equivalents, from the lower Cretaceous (Barremian) (118–113 MaBP) (Jeletzky 1976, Haggart and Tipper 1994) and correspond to Jeletzky's (1976) Barremian variegated clastic unit.

The second specimen was collected from the Appian Way on the eastern side of Vancouver Island, south of Campbell River (49° 56′ 00″ N 125° 11′ 15″ W; UTM 10U CA 433331). Abundant plant remains are preserved in large calcareous concretions embedded in a shale-mudstone matrix. Marine sediments at this locality are from the Eocene (Haggart et al 1997), and the stratigraphy currently is being examined (Jim Haggart pers comm Oct 2001).

Concretions were cut into slabs and peeled using the cellulose acetate peel technique (Joy et al 1956). Slides were prepared using xylene-soluble Eukitt (O. Kindler GmbH, Freiberg, Germany) mounting medium.

Images were captured with a PowerPhase digital scanning camera (Phase One, Denmark) and a MicroLumina digital scanning camera (Leaf Systems, Bedford, Massachusetts). They were stored as TIFF files and processed with Adobe Photoshop 6.0.

RESULTS

Apple Bay specimen.—Phylum: Basidiomycota.
Order: Hymenochaetales.
Family: Hymenochaetaceae.
Genus: **Quatsinoporites** Smith, Currah et Stockey gen. nov.
Species: **Quatsinoporites cranhamii** Smith, Currah et Stockey sp. nov.

Generic diagnosis. Poroid hymenophore, measuring at least 3 mm deep × 5 mm × 2 mm. Pores round to elliptical, 3 per mm, 130–540 μm diam. Dissepiments of loosely arranged hyphae. Hyphal system monomitic, generative hyphae 1.5–2.5 μm diam, simple septate, thin-walled. Hymenial setae up to 54 μm long, 5–8 μm wide at base; ampulliform, blunt at apex; walls pitted. Basidia and basidiospores unknown.

Specific diagnosis. As described in the generic diagnosis.

Holotype. P13021 E top, University of Alberta Paleobotanical Collection (UAPC-ALTA) (FIGS. 1–7).

Locality. Apple Bay, Vancouver Island, British Columbia, Canada.

Age. Early Cretaceous (Barremian).

Etymology. The generic name *Quatsinoporites* is proposed because the fossil fungus was found near Quatsino Sound; the specific epithet *cranhamii* is proposed in recognition of Gerald Cranham, Parksville, British Columbia, who generously has provided numerous plant specimens for study at the University of Alberta.

Description. The specimen represents an abraded fragment of the tube layer of a polypore, at least 3 mm deep × 5 mm × 2 mm (FIG. 1). Tubes are three per mm and in cross section show pores that are 130–540 μm in diam and round to elliptical and irregular. Pores rarely anastomose (FIGS. 1, 2) and many are filled with hyphae. Hyphae of the dissepiments are loosely arranged, although in some places they are more densely packed (FIG. 3). Dissepiment tissues are monomitic with generative hyphae that are 1.5–2.5 μm diam, thin-walled and have infrequent simple septa (FIGS. 3, 4). Broad hyphae, up to 5 μm in diam with rugose walls (FIGS. 3, 4), are intermixed with the generative hyphae. Hymenial setae arise terminally from dissepiment hyphae (FIGS. 5, 6) and are up to 54 μm long and 5–8 μm wide at the base. Up to 11 setae per pore were observed in sections approximately 25 μm thick. Hymenial setae have pitted walls and are ampulliform (FIGS. 5, 6, 7). Basidia and basidiospores unknown.

Appian Way specimen.—Phylum: Basidiomycota.
Order: Hymenochaetales.
Family: Hymenochaetaceae.
Genus: **Appianoporites** Smith, Currah et Stockey gen. nov.
Species: **Appianoporites vancouverensis** Smith, Currah et Stockey sp. nov.

Generic diagnosis. Poroid hymenophore, at least 3.3 mm deep × 7.0 mm × 2.5 mm. Tubes circular, 6 per mm, 130–163 μm diam. Hyphal system monomitic, generative hyphae 1.5–3.0 μm diam, simple septate, thin-walled. Hymenial cystidia up to 32.5 μm long and 6.5 μm wide at base; acuminate; thick-walled. Basidia and basidiospores unknown.

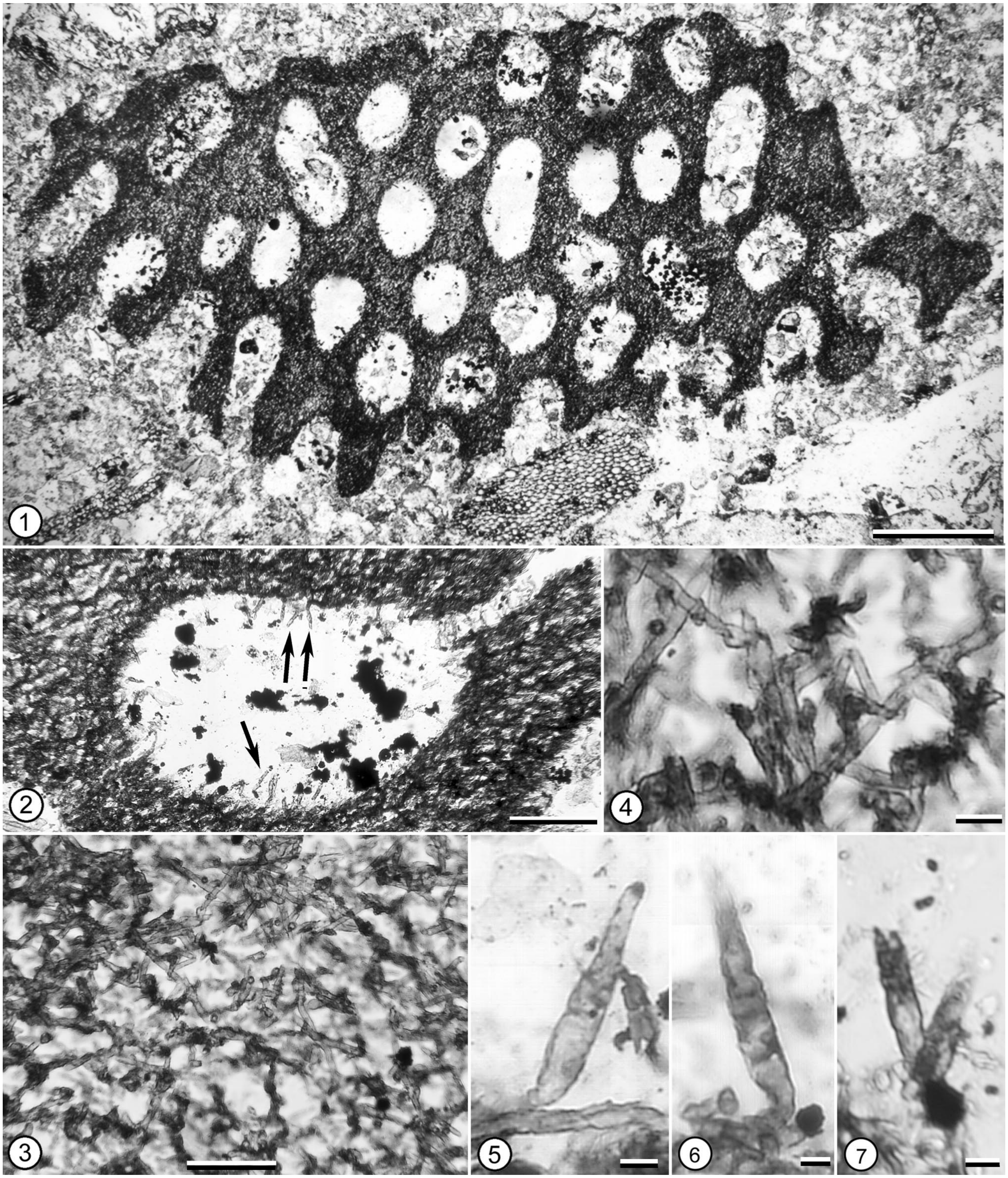
Specific diagnosis. As described in the generic diagnosis.

Holotype. AW 104 D top, Royal British Columbia Museum, Victoria, British Columbia (FIGS. 8–13).

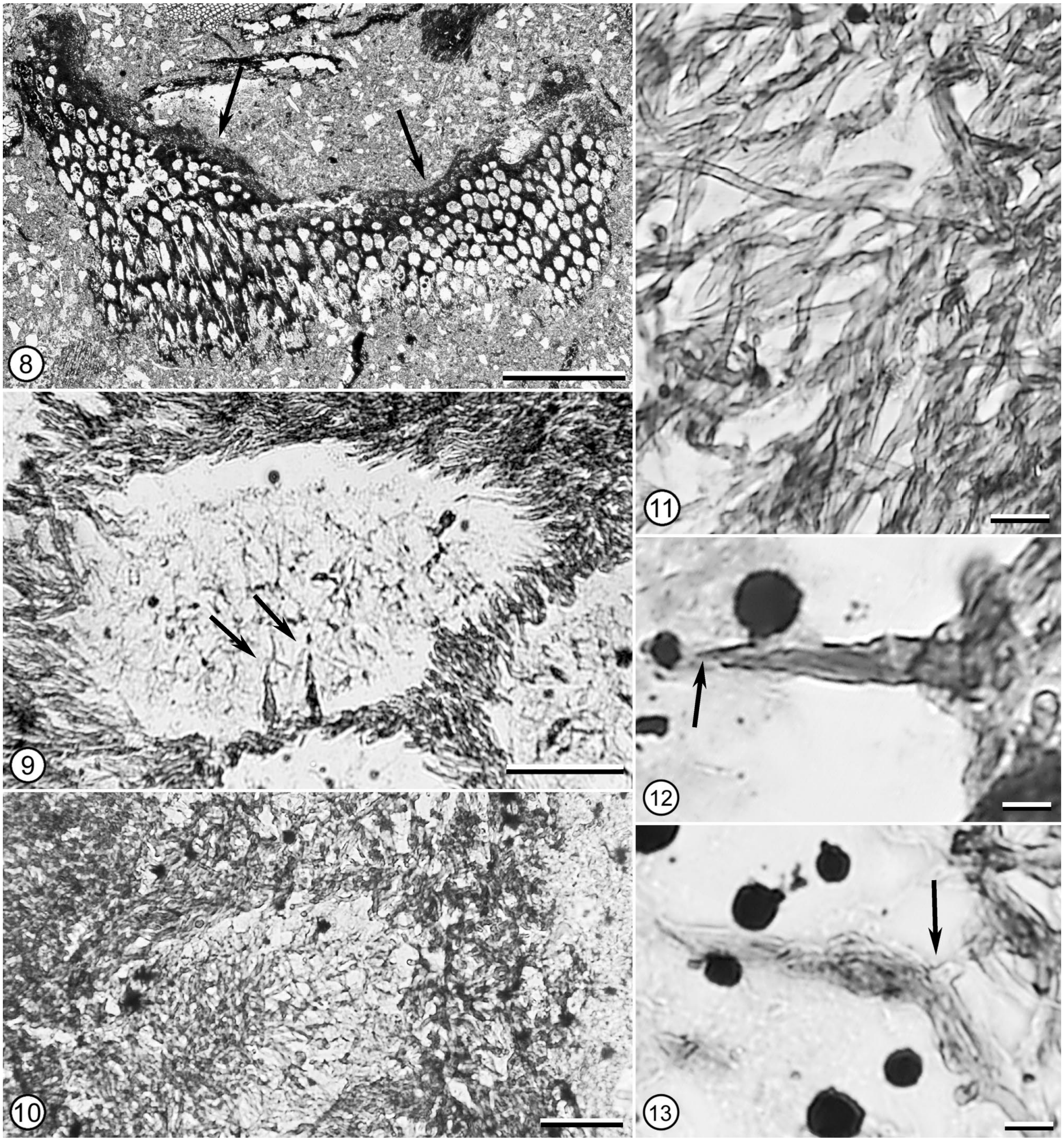
Locality. Appian Way, Vancouver Island, British Columbia, Canada.

Age. Tertiary (Eocene).

Etymology. The proposed generic name recognizes that this is a fossil polypore from the Appian Way.



FIGS. 1–7. *Quatsinoporites cranhamii* gen. et sp. nov., Holotype P13021 E top a 1. Cross section through poroid hymenophore. #9a, bar = 0.5 cm. 2. Cross section through a pore showing cystidia protruding into pore space (arrows). #27a, bar = 0.1 cm. 3. Loose arrangement of hyphae in dissepiments. #5a, bar = 30 μm. 4. Close up of hyphae, showing smooth and encrusted hyphae. #5a, bar = 6 μm. 5. Ampulliform cystidium with blunt apex and pitted walls. #30a, bar = 6 μm. 6. Ampulliform cystidium with irregular walls. #5a, bar = 6 μm. 7. Two broken cystidia. #57a, bar = 6 μm.



FIGS. 8–13. *Appianoporites vancouverensis* gen. et sp. nov., Holotype AW 104 D top 8. Section through poroid hymenophore. Note pores in both cross and oblique section. Irregular margin with stuffed pores indicated by arrows. #48b, bar = 1.5 mm. 9. Cross section through pore showing ''stuffing'' inside and cystidia (arrows) protruding into pore space. #5b, bar = 50 μm. 10. Edge of specimen showing dense hyphae and pore almost completely stuffed. #15b, bar = 50 μm. 11. Loose arrangement of hyphae in dissepiments. #4b, bar = 12 μm. 12. Close up of acuminate cystidium, showing straight shape, irregular outline and blunt apex (arrow); black circles are debris in specimen. #42b, bar = 5 μm. 13. Close up of cystidium, showing lateral origin (arrow); black circles are debris in specimen. #21b, bar = 5 μm.

The epithet *vancouverensis* is proposed because the specimen is from Vancouver Island.

Description. The specimen represents an abraded fragment of a poroid hymenophore, 3.3 mm deep × 7.0 mm × 2.5 mm (FIG. 8). The tubes are isodiametric in cross section, 130–163 μm in diam and six per mm (FIG. 8). In many sections the tubes are filled with loosely arranged hyphae (FIGS. 9, 10). One edge of the specimen has a subtly different hyphal arrangement, and the pores in this area frequently are stuffed with hyphae. Reconstruction from serial sections shows this margin to be irregular and sloped. Hyphae of the dissepiments often are packed densely, although areas of loosely arranged hyphae also occur (FIGS. 10, 11). The hyphal system is monomitic with sparingly septate generative hyphae that measure 1.5–3.0 μm in diam (FIG. 11). Hymenial setae are present, measuring up to 32.5 μm long and 6.5 μm wide at the base, with thick walls (FIG. 12). They arise laterally from dissipiment hyphae and are acuminate, tapering to a sharp point (FIGS. 12, 13). Often these setae have a rough surface texture. They can number up to seven per pore in sections approximately 25 μm thick. Basidia and basidiospores have not been observed.

DISCUSSION

The taphonomic processes preceding the deposition of these specimens probably involved their movement, possibly along with some woody substrate, along a watercourse to the ocean where subsequent abrasion by wave action might have caused further weathering. Thus, it would seem likely that the fossil hymenophores were abraded from basidiocarps that were leathery or corky rather than fleshy in texture (e.g., Boletales). Tough basidiocarps with a poroid hymenophore are found in a number of different polypore lineages, so these characters alone are not definitive for taxonomic purposes (Hibbett and Thorn 2001). Critical diagnostic features, such as basidiocarp shape, reaction to KOH, host identity and type of rot, are unavailable in the fossil material. Nevertheless, the poroid hymenophore, in combination with a monomitic hyphal system of simple septate hyphae, and the distinctive hymenial setae, make both the Cretaceous and Eocene specimens comparable to a few representatives in the Polyporales and Hymenochaetales. (Classification follows Kirk et al 2001).

Among the Polyporales, *Phaeolus* (Pat.) Pat., represented by *P. schweinitzii* (Fr.) Pat., is a brown-rot fungus that is similar in many respects, especially in having gloeopleurous hyphae, if indeed that is what the broader hyphae we see in the Apple Bay specimen represent. However, *P. schweinitzii* differs in that it has hyphae up to 17 μm in diam, much larger than the fossils with hyphae 1.5–3.0 μm diam. There are a smaller number of pores per mm in *P. schweinitzii* (1–2) compared to three in the Apple Bay fungus and six in the Appian Way specimen. Also, the shape and size of cystidia in *P. schweinitzii* are cylindrical and up to 90 um in length, compared to the acuminate cystidia that are up to 54 μm in *Quatsinoporites cranhamii* or 32.5 μm long in *Appianoporites vancouverensis.* The monomitic species of *Rigidoporus* Murr. lack cystidia, and *R. lineatus* (Pers.) Ryv. is pseudodimitic and may have clublike cystidia (Gilbertson and Ryvarden 1986), unlike the fossils that have a monomitic hyphal system and acuminate cystidia.

Among the Hymenochaetales, species of *Cyclomyces* Fr. are good candidates for comparison because extant taxa are monomitic, bear cystidia and are inhabitants of warmer, pantropical environments. However, species of *Cyclomyces* have elongated,concentric, pores, an arrangement that clearly differs from both of the fossils. Most species of *Inonotus* Karst. differ in having thick-walled setae that are shorter and/or curved and thick-walled hyphae (Gilbertson and Ryvarden 1986). Species of *Oxyporus* Donk might be comparable to the Apple Bay specimen, because they are monomitic, have cystidia and some have the same number of pores per mm. However, cystidia can be of two types in some *Oxyporus* species, while the fossils have one. *Oxyporus* cystidia often are club-shaped, as opposed to the acuminate cystidia in the fossil, and some *Oxyporus* species have a shorter tube layer than in the fossil (Gilbertson and Ryvarden 1986). Thus, based on the available characters, it is not possible to place with any confidence the fossil specimens in, or close to, an extant genus of North American polypores. We have chosen to place both fossils in the Hymenochaetales, due to the poroid hymenophore, presence of setae and monomitic hyphal system lacking clamp connections.

Quatsinoporites cranhamii and *Appianoporites vancouverensis* differ from each other in pore shape and density and in the size of the cystidia that are longer and sometimes wider in the Cretaceous Apple Bay specimen than in the Eocene Appian Way specimen. In addition, the Apple Bay specimen has narrower generative hyphae than the Appian Way specimen. The broad hyphae in *Q. cranhamii* might represent gloeopleurous hyphae and have encrustations on the outer wall that distinguish them from the generative hyphae. Gloeopleurous hyphae are absent in *A. vancouverensis.* Therefore, we consider these fossils to represent two new taxa.

Both specimens described here are preserved in marine calcareous nodules filled with abraded and broken plant material and some marine invertebrate fossils. The lack of basidiospores and basidia could be due to the age of the basidiocarps before deposition, to the effects of being waterlogged and abraded, or to both. Basidiospores could have been detached and washed out of the tubes, and the thin-walled basidia might have collapsed or broken free of the inner tube layer during transport.

The basidiocarps of extant polypores can develop on the ground, but the majority of species form these structures on standing or fallen timber and associated woody debris. It is not possible to reconstruct the growth habit of either of the fossil basidiocarps, although the Eocene specimen has an undulating margin of roughly parallel hyphae that could indicate the position of the hymenophore in the fissures of a woody stem. The Cretaceous Apple Bay locality is dominated by fern and conifer remains, and it is probable that this specimen would have been associated with a living or dead coniferous host. Concretions from the Eocene Appian Way locality are filled with angiosperm, conifer and fern material, so a wide range of woody hosts are possible. These sites had warmer climates than they do now, based on preliminary investigations of the preserved plant remains at both localities.

These Vancouver Island specimens extend the paleogeographical range of basidiomycetes farther west and north than before and provide earlier records of polypore taxa. The Eocene Appian Way specimen, *Appianoporites vancouverensis*, represents another Eocene basidiocarp record to accompany the mushrooms *Coprinites dominicana* (Poinar and Singer 1990), *Archaeomarasmius leggeti* (Hibbett et al 1997a), *Protomycena electra* (Hibbett et al 1997a) and *Aureofungus yaniguaensis* (Hibbett et al 2003) from Dominican and New Jersey amber. Other accepted records of polypore fossils are known from the Cretaceous Period and the Miocene, Pliocene and Pleistocene epochs, and some are placed in extant genera, such as *Fomes* and *Ganoderma* (Tiffney and Barghoorn 1974). Several other younger, nonpolypore fossil basidiocarps, such as *Geastrum tepexensis* Magallon-Puebla and Cevallos-Ferriz (1993), an earthstar of Miocene to lowermost Pliocene origin, also are recognized.

The Cretaceous Apple Bay specimen, *Quatsinoporites cranhamii*, represents the oldest known polypore and extends the fossil record of basidiomycete sporocarps from the Turonian (Hibbett et al 1995, 1997a) to the Barremian, i.e., by 6–28 million years. Relative to the putative age of the phylum, these specimens are quite recent because hyphae bearing clamp connections are known from the middle Pennyslvanian, 290 MaBP (Dennis 1970), and molecular clock analyses (Berbee and Taylor 2001, Heckman et al 2001) place the origin of basidiomycetes at 200–700 million years earlier than that. Nonetheless, *Q. cranhamii* is a significant discovery because it shows beyond a doubt that the poroid hymenophore and its associated hyphal anatomy had evolved to its current level of organization among polyporoid taxa more than 100 million years ago.

ACKNOWLEDGMENTS

Thanks to Gerald Cranham of Vancouver Island for donating the Apple Bay specimen; Graham Beard, Vancouver Island Paleontology Museum, Qualicum Beach, for loan of Appian Way material; Jim Haggart, Geological Survey of Canada, for help with geological information; Stefan Little for technical help and useful comments on the manuscript. This work was supported in part by Natural Sciences and Engineering Research Council of Canada Grant A-6908 to R.A. Stockey.

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