

Wood-Destroying Soft Rot Fungi in the Historic Expedition Huts of Antarctica

Robert A. Blanchette,^{1*} Benjamin W. Held,¹ Joel A. Jurgens,¹ Douglas L. McNew,²
Thomas C. Harrington,² Shona M. Duncan,³ and Roberta L. Farrell³

Department of Plant Pathology, University of Minnesota, St. Paul, Minnesota 55108¹; Department of Plant Pathology, Iowa State University, Ames, Iowa 55001²; and Department of Biological Sciences, University of Waikato, Hamilton, New Zealand³

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Three expedition huts in the Ross Sea region of Antarctica, built between 1901 and 1911 by Robert F. Scott and Ernest Shackleton, sheltered and stored the supplies for up to 48 men for 3 years during their explorations and scientific investigation in the South Pole region. The huts, built with wood taken to Antarctica by the early explorers, have deteriorated over the past decades. Although Antarctica has one of the coldest and driest environments on earth, microbes have colonized the wood and limited decay has occurred. Some wood in contact with the ground contained distinct microscopic cavities within secondary cell walls caused by soft rot fungi. *Cadophora* spp. could be cultured from decayed wood and other woods sampled from the huts and artifacts and were commonly associated with the soft rot attack. By using internal transcribed spacer sequences of ribosomal DNA and morphological characteristics, several species of *Cadophora* were identified, including *C. malorum*, *C. luteo-olivacea*, and *C. fastigiata*. Several previously undescribed *Cadophora* spp. also were found. At the Cape Evans and Cape Royds huts, *Cadophora* spp. commonly were isolated from wood in contact with the ground but were not always associated with soft rot decay. Pure cultures of *Cadophora* used in laboratory decay studies caused dark staining of all woods tested and extensive soft rot in *Betula* and *Populus* wood. The presence of *Cadophora* species, but only limited decay, suggests there is no immediate threat to the structural integrity of the huts. These fungi, however, are widely found in wood from the historic huts and have the capacity to cause extensive soft rot if conditions that are more conducive to decay become common.

Three huts, *Discovery* hut built by Robert F. Scott and his crew in 1901, Cape Royds hut erected by Ernest Shackleton's *Nimrod* expedition in 1908, and Cape Evans hut built by Scott's *Terra Nova* expedition in 1911, were used for sheltering men and equipment for several years during scientific investigations and exploration of the South Pole region. The Cape Evans hut also was used by the Ross Sea party in 1914 to 1917, which was part of Shackleton's Imperial Trans-Antarctic expedition. These huts are now international heritage sites that are protected for their historic significance and cultural materials from the "Heroic Era" of exploration. Serious wood deterioration has become evident in the huts and artifacts during the past few decades, causing concern for the long-term preservation of these historic sites (2, 16, 17). It is a great misconception that the cold, dry polar climate protects organic material from decomposition (8, 19), and significant deterioration has occurred in the 90 to 100 years since the huts were built. Nonbiological deterioration of wood from the huts and artifacts caused by salt corrosion has resulted in significant damage (8). Microbial degradation of wood at these historic sites also may occur (6, 18), but nothing is known about the organisms responsible for the degradation, the frequency of occurrence, their distribution, or the extent of degradation that has occurred.

Wood deterioration in temperate and tropical forest ecosystems and in wood products has been widely studied, and many

studies on microbial decay and the mechanisms of wood degradation have been published (11, 12, 27). Decay caused by many common white and brown rot fungi has been well characterized, but other types of decay, such as soft rot by fungi or bacterial degradation of wood, are not well understood (8). Soft rot is caused by fungi taxonomically classified in the phylum *Ascomycota*, including related asexual taxa, and the resulting decay usually is characterized by chains of cavities that form within the cell walls of wood. These biconical and cylindrical cavities form along the microfibrillar structure of the secondary wall and have a spiral orientation. The attack is localized to the secondary walls, and no degradation of the middle lamella occurs. Decay with microscopic evidence of such cavities is classified as type 1 soft rot (4). Another form of soft rot, type 2, also can occur. This type of attack does not form cavities within the cell wall but causes a progressive degradation of the secondary wall from the cell lumen to the middle lamella. In advanced stages of decay, the entire secondary wall may be completely degraded but the middle lamella between cells is not affected. The term soft rot is used because it was first identified from soft, decayed wood surfaces in contact with excessive moisture (14). Soft rot can occur not only when wood is wet but also in dry environments (5, 7, 13). Conditions that are exceedingly wet or dry apparently inhibit the growth of common and usually more aggressive wood-decaying basidiomycetes, but these adverse conditions do not limit colonization and decay by soft rot fungi. The extreme environmental conditions found in Antarctica have a strong impact on microbial growth and biodegradation. Cold temperatures, short austral summers, elevated salt concentrations,

* Corresponding author. Mailing address: Department of Plant Pathology, 1991 Upper Buford Circle, 495 Borlaug Hall, University of Minnesota, St. Paul, MN 55108-6030. Phone: (612) 625-0202. Fax: (612) 625-9728. E-mail: robertb@umn.edu.

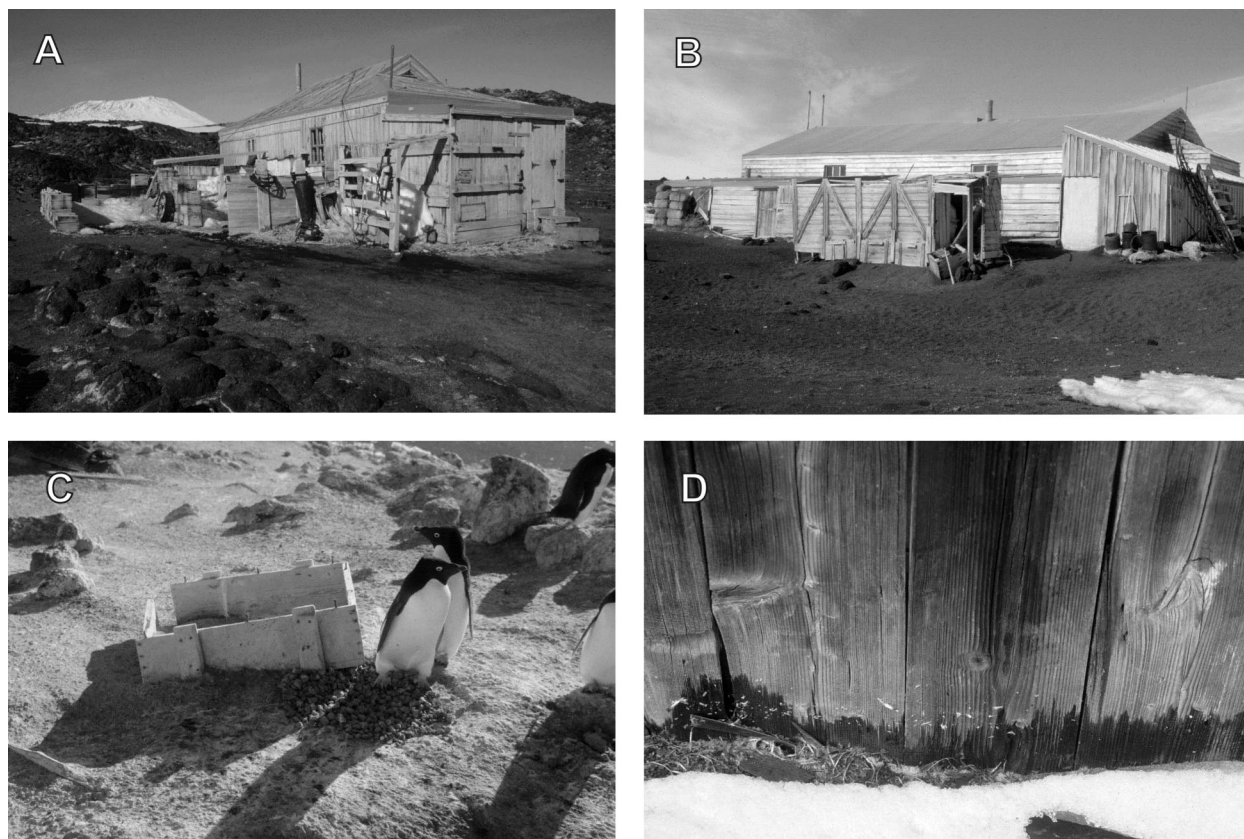


FIG. 1. Historic huts and artifacts left in Antarctica after expeditions by Robert F. Scott and Ernest Shackleton. (A) Cape Royds hut built in 1908, showing the hut structure and area used for the stables and storage adjacent to the hut. (B) Cape Evans hut built in 1911. The hut structure contains an annex and stable area enclosed within the walls of the hut. A row of historic latrines is in front of the hut. (C) Wooden storage box and Adele penguins nesting at Cape Royds. Many wooden storage boxes and other artifacts are located in the area around the huts. (D) Exterior wall boards from Cape Evans hut. Melt water from the ground is absorbed by the lower boards during the austral summer.

and high UV exposure as well as many other factors strongly influence the type of microorganisms that can survive at the site. The large quantities of wood from Europe used to build the expedition huts provide an unusual opportunity to study microbial decay processes occurring in this unique environment where wood did not previously exist. The origin of the decay microbes also is of interest, since no native higher plants with lignocellulose occur in the Ross Sea region. If wood-destroying fungi were brought into Antarctica with the wood used for the prefabricated huts, or subsequently by visitors, then these fungi would be similar to organisms found where the wood originated or would be common to other regions of the world.

This investigation was done to (i) evaluate wood decay present at the three historic huts in the Ross Sea region, (ii) identify fungi isolated from the decayed wood by using internal transcribed spacer (ITS) sequences of ribosomal DNA (rDNA), (iii) determine where these fungi are located in the historic huts, and (iv) evaluate their decay potential in laboratory studies. Little is known about deterioration of wood in polar regions, and our results provide new information on decay fungi that are present in the woods taken to Antarctica by the early explorers and elucidate the type and extent of degradation that has occurred over the past decades. In addition

to advances in polar biology, these results should provide information crucial to conservators for preservation of these important historic sites.

MATERIALS AND METHODS

Collection of samples. Samples of wood were obtained from the huts and wooden artifacts within the historic boundaries of the *Discovery*, Cape Royds (Fig. 1A), and Cape Evans (Fig. 1B) huts on Ross Island, Antarctica. A wide range of woods, including pine, spruce, and birch, were used in the construction of the huts and for storage boxes and other items (18). Samples were obtained under Antarctic Conservation Act permit numbers 2001-015 and 2002-001. This work was done in cooperation with the Antarctic Heritage Trust, Antarctic New Zealand program K021, and the National Science Foundation (Washington, D.C.). Minute segments of wood exhibiting decay in contact with the ground and wood from various locations in the hut structures and from wooden objects outside of the huts were taken. Samples were placed in sterile plastic bags and brought to the laboratory for analysis. A portion of each sample was used for culturing microorganisms, and another was used for scanning electron microscopy. No excavations were made to obtain samples from the hut foundations below ground, and samples were taken only from accessible locations that did not disturb the historic site. When a sample was taken, only a small sliver of wood was removed from an inconspicuous location.

To compare fungi obtained from the historic huts with other fungi that may have colonized wood at another location in Antarctica, samples were obtained from a wooden structure taken to New Harbor, Antarctica, by New Zealand researcher John McCraw in November 1959. This wooden hut was used for shelter and storage and is located across the Ross Sea, approximately 64 km from

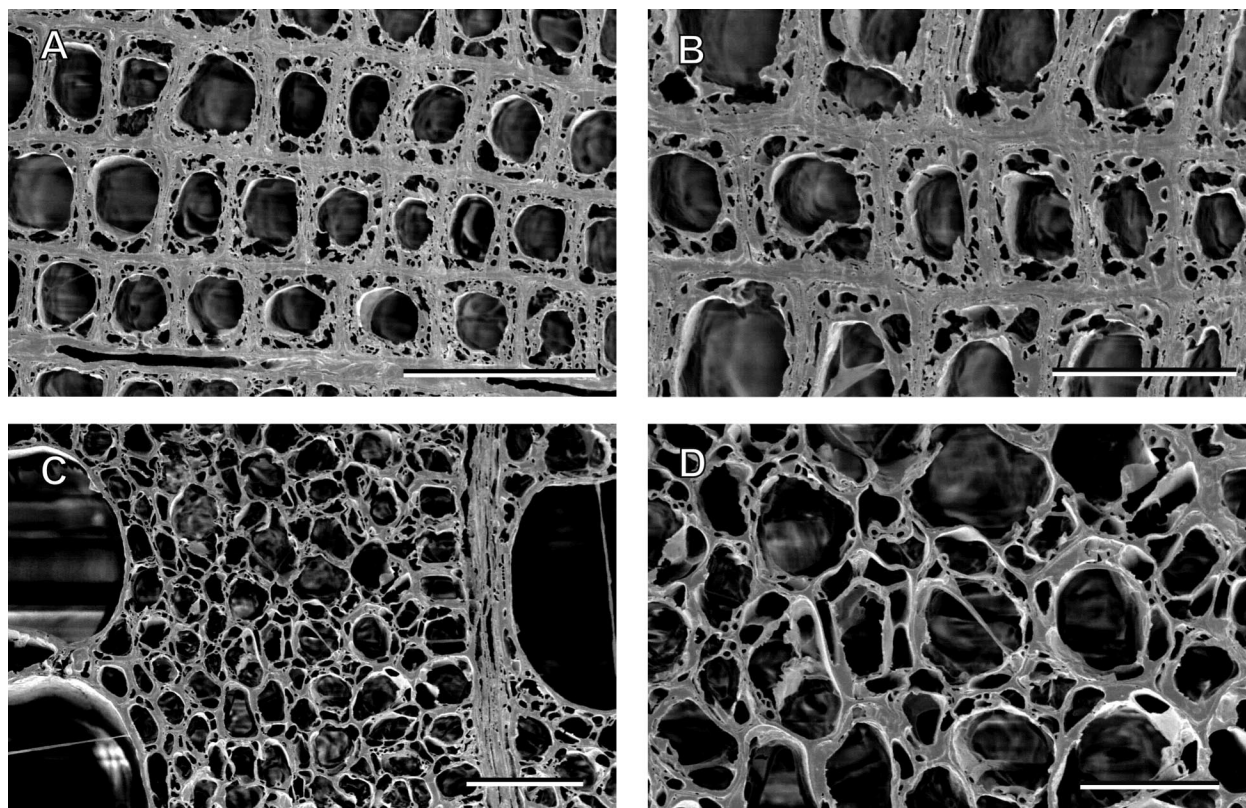


FIG. 2. Scanning electron micrographs of transverse sections of historic wood decayed by soft rot fungi. (A and B) Soft rot cavities in pine wood that was in contact with the ground from the exterior of Cape Evans hut. The secondary walls of tracheids contain numerous cavities of varying size. (C and D) Soft rot cavities in birch wood from a wooden storage box outside of the Cape Evans hut that was in contact with the ground. Advanced decay is present and large holes, formed by many secondary wall cavities that have coalesced together, are seen in fiber cell walls. Bar, 50 μm (A and C) or 25 μm (B and D).

the historic expedition huts. Samples were obtained by methods similar to those used for sample collection at the historic huts.

Sample analyses. Small wood segments were cut aseptically and placed on culture media to isolate the microorganisms present. Media used for isolations included 1.5% Difco malt extract agar (MEA), a basidiomycete-selective agar medium (24), and acidified MEA containing 2 ml of lactic acid added after autoclaving. Wood samples were prepared for scanning electron microscopy as previously described (9). Samples were frozen and cut in a cryostat freezing microtome, mounted on aluminum stubs, coated with gold, and examined with a Hitachi S3500N variable-pressure scanning electron microscope. Thin sections of wood also were cut and examined using light microscopy to detect soft rot cavities.

Identification of fungi based on rDNA sequences. Fungal cultures obtained from isolations were transferred and maintained on MEA. The two ITS regions ITS1 and ITS2 and the highly conserved 5.8S gene of the ribosomal repeat region were amplified and sequenced. The protocols for growing cultures, extracting DNA, PCR and automated sequencing, sequencing primers, and the cycling conditions were described previously (20). We sequenced both strands of all fragments to assure fidelity. BLAST searches were done with sequences from each of the fungi obtained from the wood samples, and similar sequences identified by the BLAST searches were used in phylogenetic analyses as previously described (15). The phylogenetic studies also utilized ITS sequences of related taxa from an earlier study (15), many of which were from cultures obtained from the Centraalbureau voor Schimmelcultures (CBS), including Antarctic strains of *Cadophora malorum* (CBS 257.89 [ITS sequence AY249058], CBS100584 [AY249062], CBS 100591 [AY249063], and CBS 377.77 [AY249064]); *C. luteo-olivacea* (CBS 141.41 [AY249066]); and *C. melinii* (CBS 268.33 [AY249072]). The nucleotide sequences were manually aligned, and the aligned DNA sequences were analyzed using PAUP version 4.0b10a (D. L. Swofford, Sinauer Associates, Sunderland, Mass.). After alignment, no gaps were greater than 3 bases, and gaps were treated as a "Newstate." Of 580 aligned characters, includ-

ing gaps, 125 were eliminated because of ambiguous alignment, 287 were constant, and 47 were parsimony uninformative. *Tapesia cinerella* was the outgroup taxon in the ITS analysis, and 1,000 bootstrap replications were run to determine confidence levels at branching points.

Laboratory decay studies. Wafers 10 by 10 by 2 mm were cut from sound wood of *Betula*, *Populus*, *Picea*, and *Pinus* samples, soaked in distilled water for 1 h, and autoclaved. Three sterile wood wafers were placed onto the surface of each actively growing fungal culture 8 to 10 days after inoculation on MEA. Duplicate plates of *C. malorum*, *C. luteo-olivacea*, and an undescribed *Cadophora* species designated as *Cadophora* sp. strain E were used for each wood type. Petri dishes were sealed with parafilm and incubated at 24°C. Thin sections were aseptically removed from the wafers and observed after 3- and 6-month incubations. Sections were examined using light microscopy for evidence of soft rot cavities within the secondary wall layers. Samples showing soft rot were prepared for scanning electron microscopy and photographed.

RESULTS

Many samples of wood in contact with the ground from the Cape Royds hut (Fig. 1B) had evidence of soft rot. These samples included wood from the stables area on the north side of the hut and wood from storage boxes and other wooden artifacts on the ground around the hut (Fig. 1C). Soft rot decay also was found at the Cape Evans hut in various wooden artifacts and miscellaneous pieces of historic wood located outside the hut (Fig. 1D). No soft rot was found in wood from the *Discovery* hut. Soft rot observed in the historic woods contained secondary cell wall cavities that were typical of a

TABLE 1. Isolate numbers, collection information, and DNA sequence accession numbers for representative isolates of *Cadophora* species from Antarctica

Species	Isolate number ^a and collection data	ITS rDNA ^b
<i>C. malorum</i>	2R20; Cape Royds hut, exterior wall board from northeast corner of hut just below ground	AY371503
	3R47; Cape Royds hut, miscellaneous piece of historic wood beneath ground	AY371505
	3E41-1; Cape Evans hut, exterior wall board from stable at ground line	AY371504
<i>C. luteo-olivacea</i>	E114; Cape Evans hut, exterior board from stable door at ground line	AY371507
	2E37; Cape Evans hut, wood from storage crate below ground	AY371508
	3E84; Cape Evans hut, board from latrine below ground	AY371509
	3E41-2; Cape Evans hut, exterior wall board from stable at ground line	AY371510
<i>C. fastigiata</i>	NH5-1; McCraw hut at New Harbor, exterior wood from east wall below ground	AY371511
<i>Cadophora</i> sp. strain E	4E71-1; Cape Evans hut, wood from bottom of fuel box located near hut	AY371506
<i>Cadophora</i> sp. strain H	H37; <i>Discovery</i> hut, interior wood from below floor in meat room	AY371512
<i>Cadophora</i> sp. strain NH	NH1-2; McCraw hut at New Harbor, exterior wood from southwest corner below ground	AY371513

^a Isolate numbers are from collection of R. A. Blanchette, University of Minnesota.

^b GenBank accession number.

type 1 form of soft rot. In transverse sections, the decay appeared as numerous holes of varying diameter within the secondary walls (Fig. 2). Some samples had only incipient stages of decay, with small cavities present in the cell walls of some cells, but others contained extensive soft rot and cell wall degradation. Soft rot was found in conifer woods (Fig. 2A and B) and in hardwoods (Fig. 2C and D). In decayed Venesta storage boxes made of birch plywood, very advanced stages of decay were found and cells were severely decayed. In woods with advanced soft rot, most of the secondary wall was removed and only remnants of the outer secondary wall and the middle lamella between cells remained (Fig. 2C and D). No evidence of brown or white rot by fungi or bacterial degradation of the wood was found in any of the woods examined. Salt defibrillation, a form of nonbiological deterioration with surface wood cells detaching due to a chemical attack on the middle lamella region, was common on exterior woods of the huts (8).

Phialophora-like fungi were the dominant microorganisms in isolations from wood with soft rot and other woods in contact with the ground. Based on the recent taxonomic revision of some of the *Phialophora*-like fungi (15), the isolated fungi belong to the genus *Cadophora*. Morphological characteristics of the fungi in culture and ITS sequences of rDNA identified the isolates as *C. malorum*, *C. luteo-olivacea*, *C. fastigiata*, and three undescribed *Cadophora* species designated strain E, H, and NH (Table 1; Fig. 3). Isolations made from other wood samples from the hut also yielded *Cadophora* spp. Eleven isolates of *C. malorum* and 6 of *C. luteo-olivacea* were obtained from Cape Royds hut, and 18 *C. malorum* isolates, 8 *C. luteo-olivacea* isolates, and 1 *Cadophora* sp. strain E isolate (isolate 4E71-1) were obtained from the Cape Evans hut. These species were not found in wood from the *Discovery* hut, but a different *Cadophora*, designated *Cadophora* sp. strain H (isolate H37), was obtained. Isolates of other fungi, such as species of *Geomyces*, *Penicillium*, and *Rhinochadiella*, also were recovered (<20% of the total isolates recovered) from wood in ground contact taken from the huts, but *Cadophora* species were the dominant fungi found. In the Cape Evans hut, the *Cadophora* spp. were widely distributed throughout the hut (Fig. 4). The wood from which *Cadophora* was isolated was often soft and sometimes discolored, but the wood did not

always have distinct soft rot cavities when sections were examined with light or scanning electron microscopy.

Samples of wood from a structure erected at New Harbor, Antarctica, in 1959 also were obtained to compare the types of decay and fungi isolated from another location in Antarctica with that found at the historic huts on Ross Island. Wood from the hut at New Harbor in contact with the ground had extensive soft rot. Advanced stages of decay were observed using light and electron microscopy within the wood cell walls of many samples (micrographs not shown). Isolations from this wood yielded three different species of *Cadophora*: *C. malorum*, *C. fastigiata*, and *Cadophora* sp. strain NH (isolate NH1-2) (Table 1; Fig. 3).

Wood wafers of *Betula* and *Populus* inoculated in the laboratory with *C. malorum*, *C. luteo-olivacea* or *Cadophora* sp. strain E had a type 1 soft rot after 12 months of incubation (Fig. 5). Numerous soft rot cavities were present within secondary walls of wood fiber cells. These cavities often coalesced, resulting in large voids within the cell walls (Fig. 5C and D). In some cells, the entire S₂ layer of the secondary wall was degraded, leaving only the S₃ and middle lamella regions. Wafers of *Picea* and *Pinus* inoculated in the laboratory and examined after 12 months were stained with dark fungal growth, but no soft rot was found.

DISCUSSION

The only form of wood decay found at the historic huts on Ross Island in Antarctica was caused by soft rot fungi. Soft rot commonly occurs in wood exposed to extreme and adverse environmental conditions that inhibit other types of fungi from becoming established and causing wood decay. These conditions include waterlogged woods, wood treated with preservatives, and wood from relatively dry sites, such as buried ancient tombs (5, 10, 13, 23). This report is the first of wood decay from Antarctica, and its discovery suggests that the harsh and extreme environmental conditions found in Antarctica are favorable only for decay caused by soft rot fungi. Degradation apparently occurs when the ground surface thaws and melted water provides moisture for fungal growth. These fungi are active for a very short time each year during the austral sum-

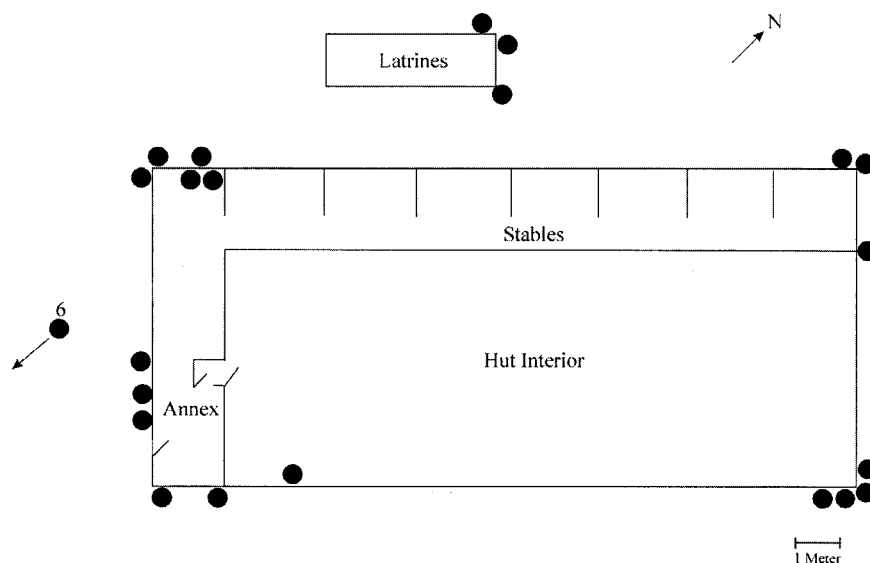


FIG. 4. Schematic drawing of Cape Evans hut showing locations (●) where *Cadophora* species were isolated. Six isolates were obtained from wooden artifacts around the hut, and the direction where these woods were located is indicated by an arrow. Although cultures of *Cadophora* were obtained from all of these locations, not all of the samples had soft rot.

Discovery hut, and there is no evidence of latrines next to the hut. The lack of penguins visiting this hut area, minimal levels of historic sources of nutrient deposits at this site, and reduced amounts of melt water adjacent to the hut due to its unique hut construction and good drainage at the site likely contributed to the near absence of soft rot fungi at *Discovery* hut.

In the wood wafer decay studies, no additional nutrients were added to the wood, yet the three species of *Cadophora* tested caused decay in *Betula* or *Populus* wood blocks. The extensive decay that occurred in the inoculated wood (Fig. 5) demonstrates the potential of *Cadophora* species to cause very serious degradation if conditions are favorable for decay. Soft rot was not found in the *Picea* or *Pinus* wood wafers. The presence of soft rot in conifer wood in contact with the ground at the Cape Evans and Cape Royds huts indicates that these fungi are able to attack these types of wood in the Antarctic environment. Laboratory conditions used for our analyses may not have been suitable for decay to occur in the conifer woods, since colonization occurred but no soft rot was evident. Increased incubation time and addition of nutrients also could have stimulated soft rot attack in the laboratory studies (25, 26). Additional studies are warranted to determine the optimal conditions for soft rot development in conifer wood and to determine the effect of other factors, such as exogenous nutrients, moisture, salts, and temperature, on fungal growth and degradation.

Recent phylogenetic analyses (15) showed that members of the genus *Cadophora* are anamorphs of *Helotiales* (discomycetes) and are distinct from the morphologically similar anamorph genus *Phialophora* in the *Chaetothyriales*. Morphologically, species of *Cadophora* are not easily differentiated from other species of *Cadophora* or from *Phialophora* species, but rDNA sequence analyses clearly separate these fungi. Since these fungi differ little in morphology, some misidentifications of *Phialophora*-like isolates from Antarctica probably have

been made in the past. For example, two isolates (CBS 100584 [AY249062] and CBS 377.77 [AY249064]) from soil in Antarctica are listed as *C. fastigiata* but have the same ITS sequence as isolates of *C. malorum*. In addition, we found at least three unknown *Cadophora* species among our isolates, including the only isolate obtained from the *Discovery* hut, *Cadophora* sp. strain H. A second unknown species (NH 1-2) was obtained from McCraw's hut at New Harbor, and a third, *Cadophora* sp. strain E, was obtained from the Cape Evans hut. Additional sampling at the *Discovery* hut and at other locations in Antarctica is needed to obtain accurate information on the distribution of these species and their role as soft rot fungi or as decomposers of other organic materials in the Antarctic environment.

Cadophora species have been reported previously in Antarctica on mosses (3, 22) and in soils (21), including oil-contaminated soils (1). The occurrence of *Cadophora* spp. from Victoria Land to the Antarctic Shetland Islands demonstrates their wide distribution on the Antarctic continent. Results presented in this paper indicate these fungi are very common in the Ross Sea region in wood from the historic expedition huts. Their prevalence at the Cape Evans hut, the Cape Royds hut, and in the hut used by McCraw in 1959 suggests that *Cadophora* species are well adapted to the Antarctic environment and effectively colonize resources, such as wood. Extensive soft rot decay in wood at the McCraw hut after 44 years of exposure to the Antarctic environment indicates that some sites may be more conducive to soft rot decay than others. The hut at New Harbor is located near a stream channel that fills with melt water, and the gravel near the hut is wet for many weeks each summer. Although the expedition huts are 90 to 100 years old, soft rot is less extensive there than at the McCraw hut, indicating the conditions for decay at these locations on Ross Island may not be as conducive for decay. Nonetheless, *Cadophora* species have extensively colonized the historic

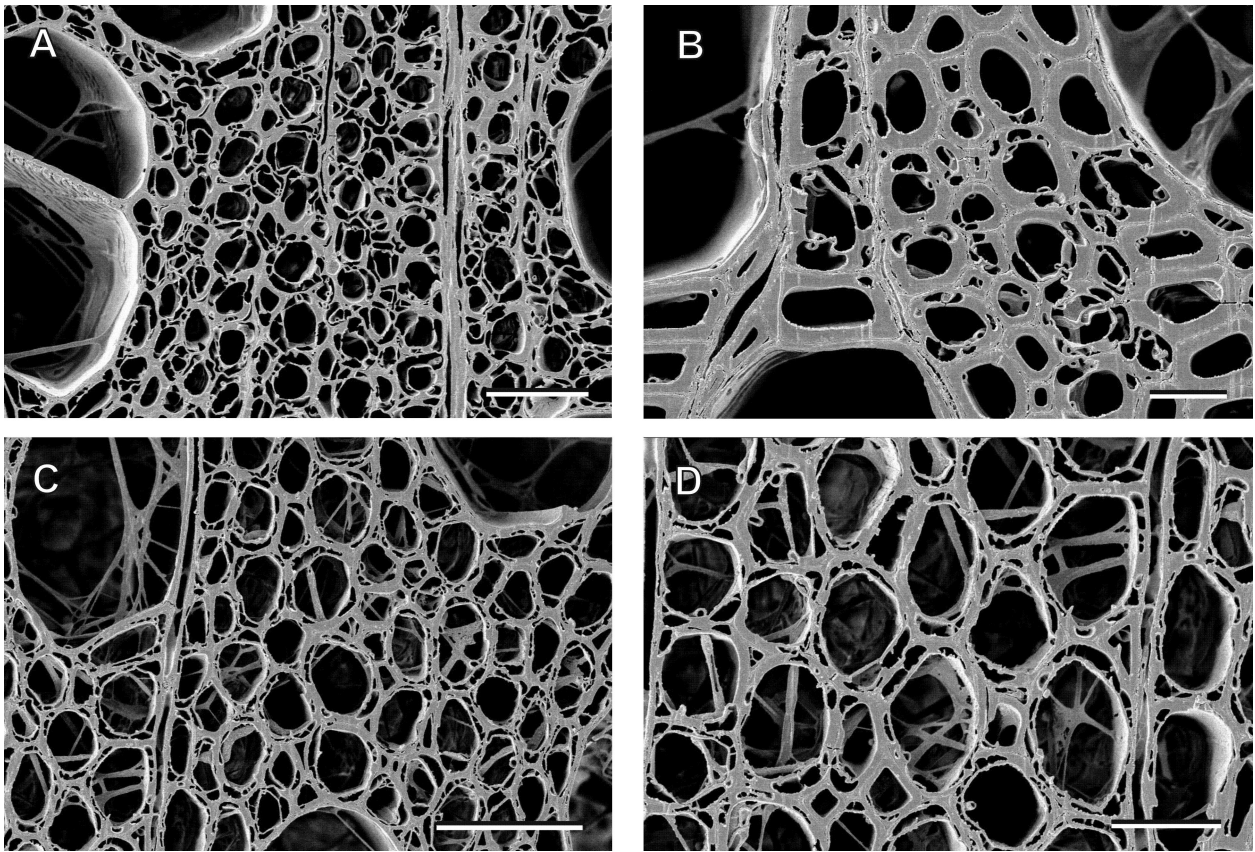


FIG. 5. Scanning electron micrographs of transverse sections from wood decayed in the laboratory with isolates of *Cadophora* from Antarctica. (A) Soft rot cavities in wood from *Betula* inoculated with *Cadophora* sp. strain E. Fibers between vessel elements are riddled with holes caused by the soft rot fungus. (B) Soft rot in birch wood inoculated with *C. malorum*. Cavities within the secondary walls of fibers are evident, with hyphae present in cell lumina and within the cavities created by the soft rot fungus. (C and D) Extensive soft rot in *Populus* wood inoculated with *C. luteo-olivacea*. Large cavities have formed in the fiber cell walls, and large numbers of hyphae are present. In many cells, the entire S₂ region of the secondary wall has been degraded. A residual S₃ layer adjacent to cell lumina and the middle lamella between cells are left. Wood cells with advanced soft rot have lost most of their original cell wall strength. Bar, 50 μ m (A and C) or 25 μ m (B and D).

woods at Cape Evans and Cape Royds, and since they are well established they could pose serious threats to the huts if conditions for decay were to become more favorable.

The soft rot fungi found in the historic huts probably were not brought to Antarctica by the early explorers. *Cadophora* species occur in temperate regions of the world, but they are not common wood decay fungi and are not frequently found in wood used for buildings. The great diversity of *Cadophora* species found in the historic woods, including several undescribed species, and their presence in soils and on dead moss thalli strongly suggest that these fungi are endemic to Antarctica. Additional investigations are needed to provide a more complete understanding of the biology of these microbes in Antarctica and to elucidate their role in the polar ecosystem. Studies of *Cadophora* and their ability to degrade wood also are needed as part of long-term conservation plans to preserve the huts and minimize conditions under which soft rot occurs.

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